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Life History and Demographic Modelling of Shark Species Caught in Indo-Pacific Fisheries

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Abstract

Understanding a species' life history and its demographics is paramount to effective population and fisheries management. Many aspects of a species life history are reflected in how it grows – making accurate estimates of age and growth some of the most important information on a species' biology. However, the approach to modelling growth for elasmobranchs (sharks and rays) has changed considerably over time and a variety of approaches are now used in the literature. Therefore, a review of these approaches was justified along with recommendations for a best practice framework to maximise the accuracy of resulting growth estimates. This dissertation defined such a framework and applied it to species of fisheries and conservation interest in the western and central Indo-Pacific regions of Indonesia and Papua New Guinea. These life history estimates were used to perform demographic analyses designed to determine these species susceptibility to overfishing.

Elasmobranch growth modelling approaches were founded on the techniques used for teleosts (bony fishes). These approaches typically use one growth model *a priori* – the von Bertalanffy growth function (VBGF), which was originally based on the growth of humans but is now commonly used to estimate growth for a variety of taxa. The use of the VBGF was justified as it is based on biological processes and provides reasonable fits for a variety of aquatic taxa such as teleosts, molluscs and crustaceans. However, contemporary approaches to growth modelling include multi-model approaches – where multiple models are fit to the data and selected based on comparative fits. Previous studies on elasmobranch growth have hypothesised that different candidate growth models produce better fits for different elasmobranch taxa. Sigmoid functions (e.g. Gompertz and logistic) are a popular alternative to the commonly used VBGF as they are hypothesised to better suit certain taxa based on body shape (such as batoids) or reproductive mode (such as egg-layers). However, this hypothesis has never been tested.

This dissertation examined 74 elasmobranch multi-model growth studies by comparing the growth curves of their respective candidate models. Hypotheses regarding model performances were rejected as the VBGF was equally likely to fit best for all taxa and reproductive modes. Subsequently no

individual model was suited to be used *a priori*. Differences between candidate model fits were greatest at age-zero with Gompertz and logistic functions providing estimates that were 15% and 23% larger on average than the VBGF, respectively. However, length-at-age estimates of the different models became negligible at older ages. Differences between candidate models were mostly small (≤ 5%) and the multi-model framework only marginally affected length-at-age estimates. However, there were cases where some candidate models provided inappropriate fits that contrasted considerably to the best fitting model. In some of these instances a single model framework could have yielded biologically unrealistic growth estimates. Therefore, no study should pre-empt whether or not it required a multi-model framework.

Based on this evaluation of elasmobranch growth modelling this dissertation determined that a basic growth modelling framework should at least include the VBGF, Gompertz function and logistic function as well as any additional functions that could reasonably fit the data. Model selection should be based on *AIC* results with a weighted model produced by multi-model inference if there is no outright best model (w = > 90%). An averaged L_∞ and L_0 should be calculated from the multi-model inference estimates and a tabulated set of length-at-age estimates presented to allow reproducibility. If data are limited from the smaller length classes, then techniques such as back-calculation should be used to prevent model constraint.

Life history information such age and growth is rarely available for tropical shark species which often confounds their management and fisheries status in developing nations. This dissertation addressed this issue for three species of whaler sharks (family Carcharhinidae) that occur in the western and central Indo-Pacific around Indonesia and Papua New Guinea (PNG). These species were the common blacktip shark (*Carcharhinus limbatus*), the grey reef shark (*C. amblyrhynchos*) and the silvertip shark (*C. albimarginatus*). Estimates of age and growth were produced for all three species using the framework outlined by this dissertation. Maturity estimates were also produced for *C. amblyrhynchos* and *C. albimarginatus.*

Age and growth estimates were produced for the common blacktip shark *Carcharhinus limbatus* sampled from Indonesia. Back-calculation techniques were used due to a low sample size (n = 30) which was dominated by large mature sharks. The VBGF provided the best fit for the separate sexes using the back-calculation data. The VBGF estimates for males were L_0 = 69 cm TL, k = 0.14 yr^{-1} and L_∞ = 230 cm TL. The VBGF estimates for females were L_0 = 62 cm TL, k = 0.11 yr^{-1} and L_∞ = 264 cm TL. These age and growth estimates were then compared to other populations of *C. limbatus* from the USA and South Africa using a combination of VBGF parameters and growth rates at birth (dL/dt_0) and maturity (dL/dt_{mat}). In comparison to populations from the USA, *C. limbatus* from Indonesia grow substantially larger and are more similar to South African populations. These results indicated that life history information from other regions would introduce error if used in population assessments for *C. limbatus* from the Indo-Pacific.

Life history estimates were produced for *C. amblyrhynchos* and *C. albimarginatus* using samples collected by fisheries observers from the National Fisheries Authority (NFA) of PNG. However, observer error may misidentify shark species in areas such as PNG where many whaler shark species have similar morphologies. Therefore, this dissertation quantified this observer error by validating species identifications using diagnostic photographs taken on board supplemented with DNA barcoding. In addition to ensuring that the life history estimates produced in this dissertation were not affected by observer error, this also provided insights into potential error rates from samples that have not had species identifications verified. This was achieved by producing life history estimates with and without the misidentified individuals for *C. amblyrhynchos*.

Vertebrae were retained from a total of 155 sharks identified by observers as *C. amblyrhynchos*. However, 22 (14%) of these were sharks were misidentified by the observers and were subsequently re-identified based on photographs and/or DNA barcoding. Of the 22 individuals misidentified as *C. amblyrhynchos*, 16 (73%) were detected using photographs and a further 6 via genetic validation. If misidentified individuals had been included, substantial error would have been introduced to both the length-at-age and the maturity estimates. Thus validating the species identification, increased the accuracy of estimated life history parameters for *C. amblyrhynchos*. From the corrected sample a multi-model inference approach was used to estimate growth for *C. amblyrhynchos* using three candidate models. The model averaged length-at-age parameters for *C. amblyrhynchos* with the sexes combined were $\bar{L}_{\infty}$ = 159 cm TL and $\bar{L}_0$ = 72 cm TL. Females mature at a greater length (l_{50} = 136 cm TL) and older age (A_{50} = 9.1 years) than males (l_{50}= 123 cm TL; A_{50} = 5.9 years).

A total of 48 *C. albimarginatus*: 28 males (95 – 219 cm TL) and 20 females (116 – 250 cm TL) were collected by NFA fisheries observers without any species misidentifications occurring. Back-calculation techniques were used to account for missing juvenile length classes and supplemented the sample size. The VBGF provided the best fitting growth estimates. Parameter estimates were L_0 = 72.1 cm TL, k = 0.04 yr^{-1} and L_{∞}= 311.3 cm TL for males; and L_0 = 70.8 cm TL, k =0.02 yr^{-1} and L_{∞}= 497.9 cm TL for females. The biologically implausible L_{∞} occurred for females as their growth did not asymptote; a typical trait of large shark species where older age classes were unavailable. The maximum age estimated from vertebral analysis was 18 years for both sexes while the calculated longevity from the VBGF parameters were 27.4 years for males and 32.2 years for females. Males matured at 174.7 cm TL and 10.5 years old, while females matured at 208.9 cm TL and 14.8 years old.

Demographic analyses were performed using the life history estimates produced for *C. albimarginatus* and *C. limbatus*. These analyses were age-structured Leslie Matrix models which incorporated stochasticity by varying vital rates though Monte Carlo simulations. Varying levels of fishing mortality (F) were introduced to the analyses to determine how both species respond to fishing pressure. Management scenarios were further developed to determine strategies that could facilitate sustainable harvesting. The demographic estimates demonstrated that without fishing both species would have increasing populations (λ = 1.07yr^{-1} for both species) until density dependent effects occur. However, both populations would decline when low levels of F (> 0.1 yr^{-1}) were applied to all age-classes. The matrix elasticities revealed that changes to fertility elements had little effect on λ, while changes in juvenile survival produced the largest changes. However, age-at-first-capture analysis suggests protecting the juvenile life stage of both species would be an ineffective management strategy as both species mature at old ages. An age-at-last-capture analysis suggests

these species could be harvested while maintaining increasing populations through a gauntlet fishery. This required *F* to be restrained to individuals < 100cm TL while protecting the older age-classes to preserve the breeding stock. This strategy would allow up to 16% and 22% of this size class to be harvested for *C. limbatus* and *C. albimarginatus,* respectively, until density dependent effects begin to manifest. However, this strategy is dependent on the ability to successfully protect all other age-classes from fishing – a strategy which may not be pragmatic in developing nations where little regulation occurs.

Through the use of robust life history and demographic analyses, this dissertation has produced important information for the fisheries and conservation management of several species from the Indo-Pacific. The approaches outlined in this thesis now also provides opportunities for other species from the region to be assessed.

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Chapter 1

General Introduction

Shark fishing has a long history with some fisheries dating back to before the 1800's (Stevens et al. 2000). However, the success of many shark fisheries has been limited with many of the early fisheries (*c.* 1930- 1950) going through a "boom and bust" cycle (Holden 1974). This in part is due to the low productivity of many of the species that were targeted and subsequently species such as the basking shark *Cetorhinus maximus* (Compagno 1984a, Kunzlic 1988) , school shark *Galeorhinus* galeus (Punt and Walker 1998) and porbeagle *Lamna nasus* (Bonfil 1994) underwent severe population declines and in some instances stock collapses. These particular species were targeted originally targeted for their livers as a source of vitamin A. However, more recent fisheries have targeted elasmobranchs (sharks and rays) for a variety of products that include meat, livers, fins, and gill plates (Stevens et al. 2000). Fishing pressure on elasmobranchs is increasing as teleosts (bony fishes) become less accessible due to overfishing, management restrictions or an inability to meet increasing demand (Dulvy et al. 2014a). Subsequently, elasmobranch landings have increased considerably throughout the 1980's and 1990's until they peaked in 2003 (Davidson et al. 2016). At this peak, elasmobranch landings were worth US $1 billion with much of this value tied to the lucrative Asian shark fin trade which was worth US$400 – 550 million per year (Clarke et al. 2007, Musick and Musick 2011). Since 2003, elasmobranch catches have dropped 20% which was believed to be caused by overexploitation rather than positive results of management (Dulvy et al. 2014a, Davidson et al. 2016). Therefore, elasmobranchs have been highlighted as one of the taxa with the greatest extinction risk and need for conservation (Dulvy et al. 2014a).

The vulnerability of many elasmobranchs to population declines lies with their low productivities (Musick 1999, Musick et al. 2000). Elasmobranchs are some of the latest maturing and slowest reproducing vertebrates, resulting in very low population growth rates and increased sensitivity to elevated fishing mortality (Cortés 2000, 2002). Many species of teleost and invertebrates have recruitment that can vary considerably each year due to environmental factors affecting survival of their eggs and larvae (Lasker 1978). They therefore have a high fecundity – high mortality trade-off that allows them to recover from population declines through compensation effects (Stevens et al. 2000). However, elasmobranchs lack the same capacity as teleosts for density-dependent changes to their productivity (Forrest and Walters 2009). This means that many species of elasmobranchs take several decades to recover once overfished (Smith et al. 1998, Simpfendorfer and Kyne 2009) and therefore many fisheries have a poor record of sustainability (Stevens et al. 2000). As well as being the target species, elasmobranchs are also taken incidentally in many fisheries worldwide which have been historically underreported (Stevens et al. 2000). This is concerning as this lack of data means that the actual catch of elasmobranchs could be as much as three to four times the reported landings (Clarke et al. 2006). Many nations have attempted to address this by implementing National Plans of Action (NPOA) under the FAO's International Plan of Action (IPOA) for sharks (Fischer et al. 2012). The greatest concern for elasmobranchs lies in much of Asia, including the Coral Triangle which has the world's highest elasmobranch diversity as well as the world's highest elasmobranch catches (Dulvy et al. 2014a).

Indonesia and Papua New Guinea (PNG) are two adjacent nations located within the Coral Triangle – a region that contains the world's highest marine endemism (Briggs 2003). They have a shared land mass – the island of New Guinea – which is almost equally divided between the two nations. This island is noted as a biodiversity hotspot containing recently described shark species such as the Cenderwasih epaulette shark (*Hemiscyllium galei)* (Allen and Erdmann 2008) as well as rare species of river sharks (*Glyphis* spp.) (White et al. 2015) and sawfish (family: Pristidae) (White and Kyne 2010). The region including Indonesia and PNG has one of the world's largest elasmobranch (shark and ray) diversities with approximately 150 species found in their waters (White and Kyne 2010). However, heavy fishing in the region means that large numbers of sharks and rays are taken amongst commercial, artisanal and subsistence fisheries. It is estimated that 60-70% of Indonesia's protein intake comes from marine resources (White and Kyne 2010) and it is likely that PNG has a similar reliance. This level of dependence on marine fisheries means that effective management is needed to balance both conservation and food security.

Indonesia has the world’s largest shark fishery which caught an estimated 100,000 t per year between 2000 and 2007 (Lack and Sant 2009). This high harvest level is further exacerbated by illegal fishing from Thai trawlers which is unquantified but believed to have large catches (Lack and Sant 2012). Indonesia’s elasmobranch fisheries have two sectors: a large-scale commercial sector and a small-scale artisanal sector (Vieira and Tull 2005). Within the commercial sector, sharks are taken using gill nets, longlines, trawls and seine nets (Lack and Sant 2012). Catches from the artisanal and subsistence fisheries have been difficult to quantify as no fishing permits are required (Varkey et al. 2010) and are therefore largely unregulated and under-reported (White and Kyne 2010). The rapid growth of commercial elasmobranch fisheries in Indonesia has thus far outstripped effective management (Lack and Sant 2012). Additional difficulties also exist for the artisanal sector as the reliance of communities on shark fishing means that serious impacts could arise in impoverished communities if catch limits were imposed (Vieira and Tull 2005). Therefore, the lack of effective fisheries management means that there is considerable conservation concern for shark populations in Indonesian waters (White and Kyne 2010).

Papua New Guinea’s shark fisheries closely resemble those of Indonesia (White and Kyne 2010), although they occur on a much smaller scale (Lack and Sant 2012). Many of PNG’s fisheries are artisanal in nature whereby fishers target finfish, invertebrates and sharks for both export and local markets (Teh et al. 2014). Subsistence fisheries are also widespread and are important for the food security of island and coastal communities. However, as these fishers only catch as much as they intend to consume, the catches of individual fishers are believed to be quite limited (Teh et al. 2014). In addition to artisanal and subsistence fisheries, a large scale commercial fishery for sharks also operated until recently. This dedicated shark fishery developed in the 1990’s from the tuna longline fleet as a market became available for shark meat and fins (Kumoru 2003b). In 2001 this fishery was officially regulated by the National Fisheries Authority (NFA) when they introduced a shark longline management plan (Kumoru 2003a). This fishery operated until 2014 when a moratorium was placed on silky sharks (*Carcharhinus falciformis*) which constituted the majority of the catch (Lack and Sant 2012, WCPFC 2013). The fisheries highest catch occurred in 2006 when more than 68,000 sharks were caught (Usu 2011). While in operation, this fishery was largely managed through a combination of input and output controls that limited the number of vessels, hooks set per day and set a total allowable catch (TAC) of 2000 t dressed weight (Kumoru 2003a).

There is considerable conservation concern for elasmobranchs in Indonesia and PNG (White and Kyne 2010). The large shark catches of the region coupled with high levels of endemism means that several species may face extinction if the regions fisheries are not well managed (Dulvy et al. 2014a). However, appropriate management is currently lacking for most of the region due to a lack of assessments on the various shark fisheries. Currently, only limited assessments are available for Indonesian fisheries which have been hindered due to a lack of data collection and reporting (Blaber et al. 2009). Papua New Guinea has had greater success in collecting these data due to the successful implementation of fisheries observer programs in both its shark and tuna fisheries (Usu 2011). Despite this, stock assessments for PNG have been limited to only forming portions of stock assessments for the western and central Pacific region (Rice and Harley 2012, 2013). Therefore, there is still a need to produce thorough assessments on the regions shark stocks that can be used to inform local fisheries management.

Robust stock assessment models can be difficult to implement for fisheries in developing nations due to the paucity of data available. Dynamic fisheries models such as delay difference, surplus production and virtual population analysis require accurate estimates of catch, effort and abundance over a reasonable time period (Cortés et al. 2012). However, given that many fisheries from Indonesia and PNG are largely unregulated or underreported (typically the artisanal and subsistence sectors), these data are rarely available (Dillingham et al. 2016). While data collection efforts have improved in the region, historical data cannot be retrospectively accounted for to an accurate level. Therefore, stock assessments require techniques that can make use of what data is available and provide reasonable measures of uncertainty. In such circumstances the answer may not lie with fisheries models but rather conservation approaches that can provide estimates of population status and trajectories.

Demographic models are frequently used for a variety of taxa that include plants, mammals, birds and fish (Morris and Doak 2002). They are flexible models that can be fit to available data to provide basic outputs such as the finite rate of population increase (λ) (Simpfendorfer 2004a). These models determine λ by mapping the reproductive and mortality schedules of a species. Therefore, the only information needed to produce demographic models are life history estimates (Simpfendorfer 2004a). This makes them very useful for species that interact frequently with fisheries such as turtles (Crouse et al. 1987) or that are often taken in data poor fisheries such as sharks (Coelho et al. 2015) as fisheries data aren't required by the models. However, as they rely solely on life history data, it is imperative that accurate life history estimates are used. This can be challenging as determining life history parameters with a high degree of certainty can be especially difficult for marine species that are difficult to sample (Smart et al. 2013, Cortés 2016).

Life history estimates have been successfully produced for many elasmobranch species – particularly those caught in well monitored fisheries in countries such as the U.S and Australia (e.g. Carlson et al. 2003, Braccini et al. 2007, Harry et al. 2013). However, many species of shark can be difficult to sample and therefore life history estimates may be difficult to produce for them (Smart et al. 2013). This is often the case for species that are not caught regularly in fisheries, or that only limited portions of the population are caught by fisheries. Gear selectivity is often an issue when sampling sharks as fishing methods such as gill nets and longlines do not have an equal probability of catching all size classes (Kirkwood and Walker 1986). As many species of shark are long lived, this selective sampling often leaves large portions of the population underrepresented in life history studies. Accurate estimates of length-at-age are the most important life history parameter as these are needed to provide the age-structure to any population model. Fisheries scientists often have a good understanding of a species maximum size, size-at-maturity and size-at-first-reproduction. However, without length-at-age data, the scheduling of these events can be difficult to interpret (see Dulvy et al. 2014b). Therefore, in order to successfully apply age-structured demographic models to various species of shark, accurate estimates of length-at-age are imperative.

Given current knowledge gaps and research needs, the primary aims of this dissertation were to: 1) determine a best practice approach to modelling the length-at-age of elasmobranchs, 2) use this approach to produce life history estimates for species of fisheries and conservation interest from the western Indo-Pacific region, and 3) produce demographic models for these species using these newly determined life history estimates. To accomplish these aims a thorough review and meta-analysis was conducted which examined the history of elasmobranch growth modelling approaches and the benefits of using a multi-model approach for growth estimation (Chapter 2). A best practice framework was determined from this research and used to produce length-at-age data as well as maturity estimates for three species of whaler shark: *Carcharhinus limbatus, C. amblyrhynchos* and *C. albimarginatus* (Chapters 4 – 6). Age-structured Leslie matrix models were then produced for two of these species (*C. albimarginatus* and *C. limbatus*) and used to determine their population trajectories, susceptibility to fishing and the relative success of potential management strategies (Chapter 7). Currently, standard mortality estimators cannot be appropriately applied for *C. amblyrhynchos* which precluded demographic analyses for this species. This will be addressed through future work by developing new techniques that address this issue. This dissertation provides new and important information on the application of life history and demographic modelling for sharks caught in Indo-Pacific fisheries and will contribute important findings towards conservation and fisheries management.

Chapter 2

Multimodel approaches in shark and ray growth studies: strengths, weaknesses and the future

2.1 Introduction

Growth is a fundamental component of life history and the ability to model it has a wide range of applications in population dynamics. For example, growth models are a vital component of many stock assessments as they reflect aspects of a species life history (Haddon 2001, Cailliet and Goldman 2004, Juan-Jordá et al. 2015). Estimating growth in aquatic species such as sharks and rays is most commonly achieved using size-at-age data whereby the age of known-size individuals is determined using vertebrae, fin spines or other hard parts (Cailliet et al. 2006). These data are used to produce length-at-age curves (typically fit using non-linear models) that represent the average size-at-age for populations at a set location or time. Using models to represent somatic growth allows for the comparison between species or populations and provides parameters for use in population dynamic models (Thorson and Simpfendorfer 2009). Conventionally, a single model was applied based on the presumed growth profile and biological assumptions for the population. The resulting growth estimates were based on that single fitted model and presumed to be precise (Katsanevakis, 2006). However, using a single growth model risks several problems that include: predictive uncertainty being underestimated, an inappropriate model potentially biasing growth estimates (Katsanevakis 2006), and growth estimates that may not converge on the true value even if sample sizes are increased. In light of these issues, contemporary growth literature has started to move away from the *a priori* use of a single growth model (Cailliet et al. 2006).

The von Bertalanffy growth function (VBGF) (von Bertalanffy 1938) is the most common model used in teleost (bony fishes) and elasmobranch (sharks and rays) growth literature. Growth curves fitted with the VBGF have an inverse exponential shape, producing growth rates declining linearly with age (Fig. 2.1a) (Katsanevakis 2006). This shape is the net product of anabolism (weight gain) and catabolism (weight loss) (Mangel 2006). However, an assumption of the VGBF is that anabolism and catabolism are constant processes when in fact they vary spatially, temporally and amongst individuals (Snover et al. 2005, Vincenzi et al. 2014, Thorson and Minte-Vera In press). Therefore, the linear decrease in somatic growth described by the VBGF is not always appropriate as it cannot detect nuanced changes in growth over time (Soriano et al. 1992).

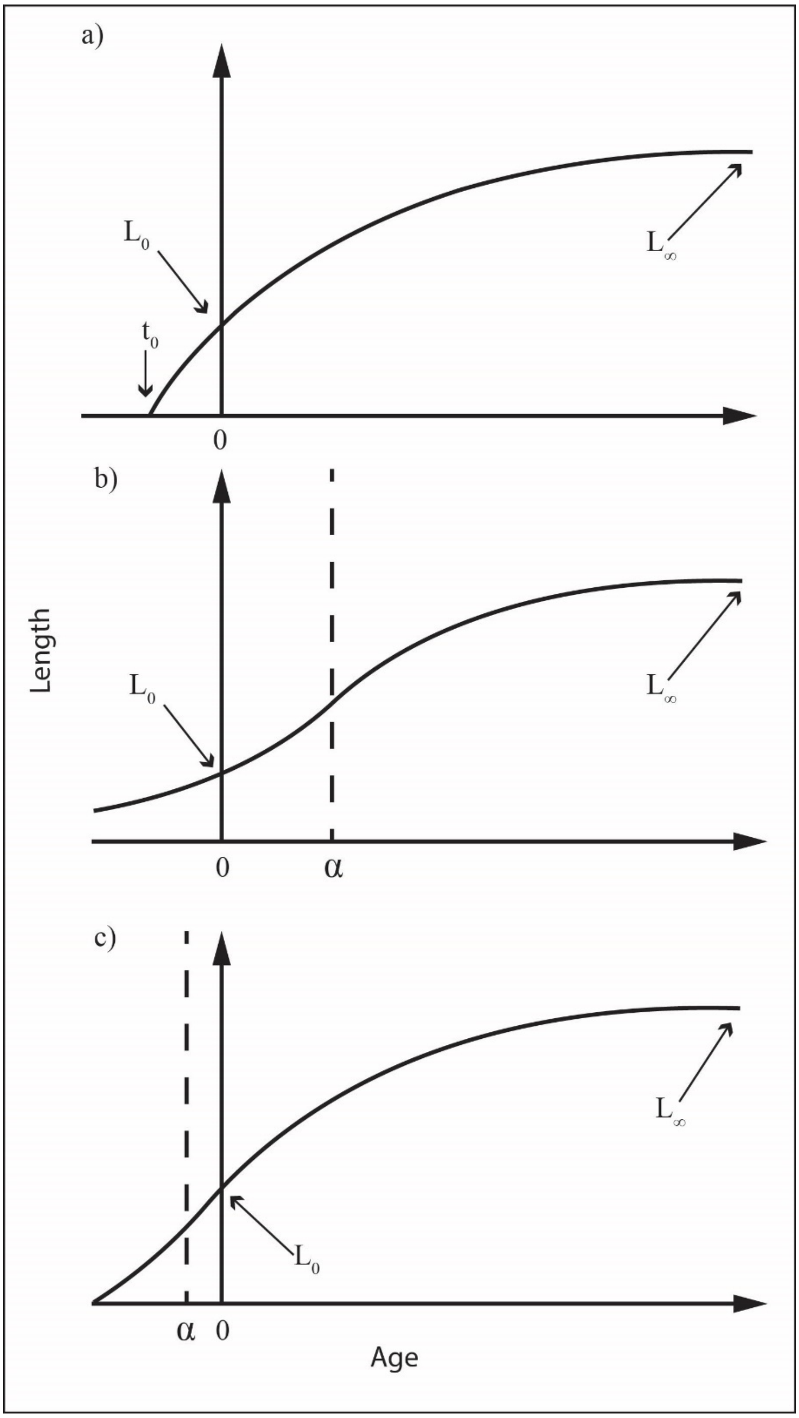

Figure 2.1: A comparison of the shape of commonly used growth models in elasmobranch literature, demonstrating a) the shape and parameters of the von Bertalanffy growth function (VBGF), b) the shape of a sigmoid function when the inflection point α occurs at an age older than zero, and c) the shape of a sigmoid function when the inflection point α is not included in the model as it occurs at an age younger than zero.

Sigmoid curves (e.g. logistic and Gompertz functions), characterised by two asymptotes rather than one (Ricker 1979), offer an alternate model shape to the VBGF. Their shape differs to the VBGF as their sigmoid structure does not guarantee continuously declining growth with age. Unlike the VBGF, sigmoid functions include an inflection point (α) which can be biologically interpreted as a shift where growth stops increasing and begins to decrease (Fig. 2.1b) (Thorson and Simpfendorfer 2009). However, α does not always feature as part of the length-at-age-curve as it’s x-axis position (age) can be less than zero (Fig. 2.1c). In fact, Ricker (1975) cautioned that as α typically lies at ages less than zero, the lower asymptote of sigmoid functions is biologically meaningless in regards to growth. Despite this, some taxa that have growth rates that continue increasing post-partum and are best described by sigmoid curves where α occurs at ages older than zero (Moreau 1987).

Changes in growth rate could result from species-specific growth patterns or by ontogenetic changes in a species environment or resources. Ontogenetic shifts in growth often occur as juveniles emigrate from nursery grounds (King 2007). For example, juvenile Scalloped Hammerheads (*Sphyrna lewinii,* Sphyrnidae) in Kāneʻohe Bay, Hawaii remain in resource depleted nursery grounds to avoid predation to the detriment of their own body condition (Bush and Holland 2002). Subsequent emigration from these areas will lead to higher anabolism and increased growth. Similarly, Arctic Char (*Savelinus alpinus*, Salmonidae), grow slowly in freshwater before migration into salt water speeds growth markedly (Moore and Moore 1974, Moreau 1987). This initial delay in post-partum growth during the juvenile life stage is demonstrative of how sigmoid curves may be a better biological descriptor of growth in these situations. Early elasmobranch multi-model growth studies selected sigmoid functions instead of the VBGF for: 1) batoids (rays, skates and sawfishes) which grow larger in mass rather than length in comparison to sharks and, 2) egg-laying species that undergo transitions in their early nutrient sources that aren't experienced by live-bearing species (Zeiner and Wolf 1993, Mollet et al. 2002). Subsequently, it was hypothesised that sigmoid functions were the most appropriate model shape for these taxa (Cailliet and Goldman 2004). However, these hypotheses remain untested.

More contemporary approaches to modelling growth are multi-model frameworks (Mollet et al. 2002, Carlson and Baremore 2005) and multi-model inference (Burnham and Anderson 2002, Katsanevakis and Maravelias 2008). These methods fit multiple candidate models (e.g. VBGF, logistic and Gompertz functions) to size-at-age data, using Akaike's Information Criteron (*AIC*) (Akaike 1973) to either select the best fitting model (multi-model frameworks) or produce a weighted model average (multi-model inference). As the shapes of candidate models can differ, *AIC* identifies the most appropriate models for the data; avoiding the use of a singular model that might be inappropriate. It has also been suggested that multi-model inference should be used to estimate growth for aquatic taxa (Katsanevakis and Maravelias 2008). As it is possible for data sets to support multiple models using multi-model inference to produce an averaged model frees the researcher from having to select a best fitting model, therefore reducing model selection uncertainty (Katsanevakis 2006).

Multi-model frameworks may provide different benefits to aquatic taxa with disparate life histories. This approach has previously been evaluated using multiple datasets that were composed of mostly teleosts with some elasmobranchs (Katsanevakis and Maravelias 2008). As their data was mostly comprised of teleosts, Katsanevakis and Maravelias (2008) used candidate models that did not include a size-at-birth parameter (L_0) which is more commonly used for elasmobranchs (Cailliet et al. 2006). Therefore, they mainly focused their analyses on the L_∞ parameter; recommending the use of a model averaged value ($\bar{L}_\infty$) as it was the only comparable parameter between candidate models. Little attention was paid to L_0 - which is also comparable between candidate models. As L_∞ differs greatly between candidate models (Katsanevakis and Maravelias 2008), it is possible that L_0 could be equally contrasting for elasmobranchs as they have large and diverse sizes at birth (Cailliet et al. 2006). Therefore, multi-model frameworks and multi-model inference may have greater potential than previously realised to improve growth model fits.

As multi-model frameworks provide multiple growth curve possibilities, they have the ability to overcome some sampling limitations. Scientists studying elasmobranchs often encounter issues such as small sample sizes or limited size ranges (usually due to gear selectivity) as many species are naturally rare or life stages are spread across multiple locations that are not equally sampled (Smart et al. 2013). Additionally, unrepresentative sampling of fished populations can occur due to Rosa Lee's phenomenon (Walker et al. 1998) where size selective fishing mortality is more likely to catch faster growing individuals from the population. Consequently, slow growing individuals have a higher probability of reaching maximum size and are not representative of the unfished population (Taylor and Methot 2013). These issues can limit the number of juveniles or maximum size of individuals in a sample, causing substantial error in growth estimates as a model's trajectory is strongly determined by these length classes (Haddon 2001). However, as multi-model frameworks provide a range of curve options that vary the most at the curves extremes (Katsanevakis and Maravelias 2008), they may have the ability to produce more biologically reasonable growth estimates in data limited situations (Thorson and Simpfendorfer 2009). As a range of model trajectories are available, multi-model frameworks can provide curve options that provide better fits over a single model framework when sampling limitations occur.

Many elasmobranch researchers continue to model growth using a single model framework despite evidence suggesting that this may affect the precision and accuracy of their estimates (Katsanevakis 2006, Katsanevakis and Maravelias 2008, Thorson and Simpfendorfer 2009). This reluctance to use multi-model frameworks could be caused by a lack of conceptual understanding or by a lack of evidence of that these approaches offer improved model fits. Currently, recommendations regarding multi-model frameworks are mostly theoretical, focusing on model selection (Katsanevakis and Maravelias 2008, Thorson and Simpfendorfer 2009). However, there is a lack of evidence that the use of multi-model frameworks will provide improved model fits. To demonstrate their full potential and make the case for consistent use of multi-model frameworks, this study reproduced and evaluated the results of 74 elasmobranch multi-model studies. It investigated the following questions: 1) to what degree do candidate model estimates differ and how do they affect resulting growth estimates? 2) Which variables (e.g. sample size, taxa, body size, sex separation, etc.) influence these differences in candidate model fits? And, 3) do sigmoid functions provide improved model fits for batoids rather than sharks and egg-laying rather than live-bearing species? Based on these findings, a framework was outlined that maximises the accuracy of growth model fits.

2.2 Methods

2.2.1 Evaluation of elasmobranch growth literature

Existing literature was reviewed to access available elasmobranch size-at-age studies. Studies using tag recapture or length frequency data were omitted as they use different data to fit growth models (Francis 1988). Studies were divided into two classes based on their modelling framework: 1) single model frameworks, and 2) multi-model frameworks. Here, a multi-model framework was defined as any study that used two or more growth models. This included studies that used multiple parameterisations of the same model; for example, a standard VBGF as well as a VBGF with a fixed L_0 (or t_0) (VBGF-2) (Carlson et al. 2003, Neer et al. 2005). Both classes were examined to determine the trends in model framework choice over time. However, only multi-model studies were used in analyses regarding model performance.

To explore trends in growth model selection and fit, a data set was created using the results of individual studies. For each study, the number of data sets that growth model parameters were estimated for were determined and termed as "groups". These groups were either different species or populations that were included in the same study or sexes that were separated due to sexual dimorphism. For each group, information was recorded that included the sample size, the maximum body length, the model candidates included (e.g. VBGF, Gompertz, etc.), which was the best fitting model and the model selection technique.

In order to examine the differences between candidate model predictions, the size-at-age estimates at each whole age of each model were reproduced for each group. A large diversity of candidate models (n = 15) exist and many (n = 11) of these were used too infrequently (< 15 studies) to permit their inclusion in the analyses (Table 2.1). Therefore, length-at-age estimates were reproduced for the four most commonly used models (Table 2.1): the VBGF , the VBGF-2 (Fabens 1965), the Gompertz function (Ricker 1975) and the logistic function (Ricker 1979). Length-at-age estimates for these four model candidates were reproduced using the model equations and model parameters from their respective studies. The error distribution was assumed to be identical for all model candidates within each group unless specified.

Table 2.1 The frequency of candidate models used in multi-model frameworks for elasmobranch length-at-age studies

Function	***n* of studies**	***n* of groups**
von Bertalanffy growth function	74	147
Gompertz function	53	107
von Bertalanffy growth function with a fixed (L_0)	48	95
Logistic function	28	63
Schnute function	12	22
Gompertz with a fixed L_0	12	21
von Bertalanffy - two phase growth function	4	9
Francis function	3	5
Richards function	3	3
polynomial function	2	2
von Bertalanffy growth function with fixed L_0 and L_∞	2	2
Gompertz function with fixed L_0 and L_∞	2	2
power function	1	2
stochastic von Bertalanffy growth function	1	2
sigmoid function	1	2

It is important to note that many candidate models can be mathematically expressed by different equations with different parameters (Ricker 1979). For example, the model equations for the VBGF can be expressed using a t_0 parameter (x-axis intercept) or a L_0 parameter (y-axis intercept) (Table 2.2) (Cailliet et al. 2006). Alternate equations for the logistic and Gompertz functions also exist that exclude the α parameter (occasionally referred to as t_0 in the literature **(Ricker 1979, Dale and Holland 2012)**) and include an L_0 parameter instead (Table 2.2) (Ricker 1979). However, regardless of the parameterisation used, the resulting model fits were identical and therefore groups that used different equations of the same function (VBGF, logistic function and Gompertz function) were comparable.

Table 2.2 Mathematical expressions of the VBGF, Gompertz and logistic functions. Each model has multiple equations that usually include a version incorporating a length-at-birth parameter (L_0) and an alternate version that does not. Regardless of which equation is used for each candidate model, the fitted growth curve will be equivalent provided the error structure remains unchanged.

Model	**Growth equation incorporating L_0**	**Alternate growth equation**
von Bertalanffy Growth Function (VBGF)	$L_t = L_0 + (L_\infty - L_0)(1 - exp(-kt))$	$L_t = L_\infty(1 - exp^{(-k(t-t_0))})$
Gompertz function	$L_t = L_0\left(exp^{G(1-exp(-gt))}\right)$	$L_t = L_\infty(exp^{(-exp^{(-g(t-\alpha))})})$
logistic function	$L_t = \frac{L_\infty L_0(exp(gt)}{L_\infty + L_0(exp(gt) - 1)}$	$L_t = \frac{L_\infty}{1 + exp^{-g(t-\alpha)}}$

where L_t is length-at-age t, L_0 is length-at-age 0, L_∞ is asymptotic length, α is the inflection point of the Gompertz and logistic functions, t_0 is time-at-length 0 and k, g and G are the different growth coefficients of the respective models.

2.2.2 Sigmoid models and their inflection point

It was previously thought that α had no biological meaning when sigmoid models were fitted to length-at-age data (Ricker 1975). However, if α occurs at a point on the age axis older than zero, it does have a biological meaning as it represents the age at which there is a change in growth rate (Thorson and Simpfendorfer 2009). To determine whether α is biologically relevant to elasmobranchs, the age it occurred at in Gompertz and logistic functions was calculated. For some studies no calculation was needed as parameterisations were used that included α as a fitting parameter. However, when an alternative parameterisation of the Gompertz function was used, α was calculated as:

$$\boldsymbol{\alpha = t - \left(\frac{\ln\left(1 \big/ \ln\frac{L_\infty}{L_t} \right)}{g} \right)} \tag{2.1}$$

where L_∞ was the asymptotic length, g is the Gompertz growth completion parameter and L_t is the estimated length produced by the model at time t.

For studies that used an alternative parameterisation of the logistic function, α was calculated as:

$$\boldsymbol{\alpha = \frac{gt + ln\left(\frac{L_\infty}{L_t} - 1\right)}{g}} \tag{2.2}$$

where L_∞ was the asymptotic length, g the logistic growth completion parameter and L_t the estimated length produced by the model at time t.

While they are both sigmoid functions, the shape of Gompertz and logistic functions is different (Ricker 1979). Therefore, a paired t-test was used to determine if the position of α differed between both models when they were both included as candidate models. A generalised linear model (GLM) was used to determine if differences existed between the ages that α occurred at for taxa (shark or batoid) and reproductive mode (placental live-bearing, yolk only live-bearing and egg-laying). A

GLM was performed separately for the logistic and Gompertz functions. The models were computed in the R statistical environment (R Core Team, 2013) and compared using *AICc*. Both additive and multiplicative models were included to determine if interaction effects occurred between taxa and reproductive mode. Models with the lowest *AICc* values were considered to best describe the ages that α occurred for that respective model. Models were tested for significance against the null model using likelihood ratio tests.

2.2.3 Species biology influences on model selection

To test the hypothesis that sigmoid functions are better suited to certain taxa and reproductive modes, a chi square (χ^2) goodness of fit analysis was performed to determine if these models were selected more often for these groups. As this analysis tested the selection of sigmoid functions against the VBGF, only groups that contained both types of functions in their candidate models were included. A Yates correction for continuity was used to reduce bias in the taxa analysis as this produced a 2 x 2 contingency table.

2.2.4 Multi-model effects on growth estimates

Multi-model frameworks can only improve growth model fits if alternative candidate models provide contrasting fits to the model that would have been used *a priori.* As this *a priori* model is typically the VBGF, the length-at-age estimates of the alternative candidate models (VBGF-2, logistic and Gompertz) were compared to those of VBGF for each group as a percentage difference at each age class.

This was calculated for each age class as:

$$\boldsymbol{\Delta Lt = \frac{Lt_{alt} - Lt_{comp}}{Lt_{comp}} \times 100} \tag{2.3}$$

where ΔLt was the percent difference in length between models at age t, Lt_{comp} was the length at age t of the comparison model (in this instance the VBGF) and Lt_{alt} was the length-at-age t for the alternative model (either the VBGF-2, logistic or Gompertz) being compared. These differences in model results were calculated for each age class up until the maximum age of the group. If the ΔLt was a negative value, then this indicated that the Lt_{alt} was smaller in length than the Lt_{comp}.

To examine whether model differences changed between the VBGF and the alternate candidate models as t increased, a mean ΔLt for each age class was calculated for the VBGF-2, logistic and Gompertz models. These were calculated up to a maximum age of 26 years as few groups surpassed this age.

2.2.5 Drivers of diversity in candidate model fits

A range of factors could cause contrasting candidate model fits. Therefore, a GLM was used to determine if differences in candidate model fits were affected by: taxonomic group, reproductive mode, sample size, combining or separating sexes and the maximum size of the species. Preliminary analysis indicated that the differences between models were largest when $t = 0$. Therefore, the ΔLt at age zero (ΔL_0) of each alternative model to the best fitting model were used as the response variable in the GLM. Any ΔL_0 estimates that were negative were transformed into positive values as the direction of the difference was not being examined. The models were computed in the R statistical environment (R Core Team, 2013) and compared using $AICc$. Models with the lowest $AICc$ values were considered to include the factors that were significant drivers of contrasting candidate model fits. Models that had a $\Delta AICc < 2$ were tested for significance against the null model using likelihood ratio tests.

2.3 Results

2.3.1 Development of length-at-age modelling frameworks over time

Between 1963 and 2014 a total of 210 length-at-age studies were published on elasmobranchs. Of these, 35% ($n = 74$) used multiple models and included the VBGF as a candidate model. All of the studies that used a single model framework ($n = 136$) used a version of the VBGF. Multi-model frameworks were first used by Cailliet et al. (1983) although their use did not become common until 2004 (Fig. 2.2). Multi-model inference was only used in three studies (Harry et al. 2010, Barreto et al. 2011, Smart et al. 2013).

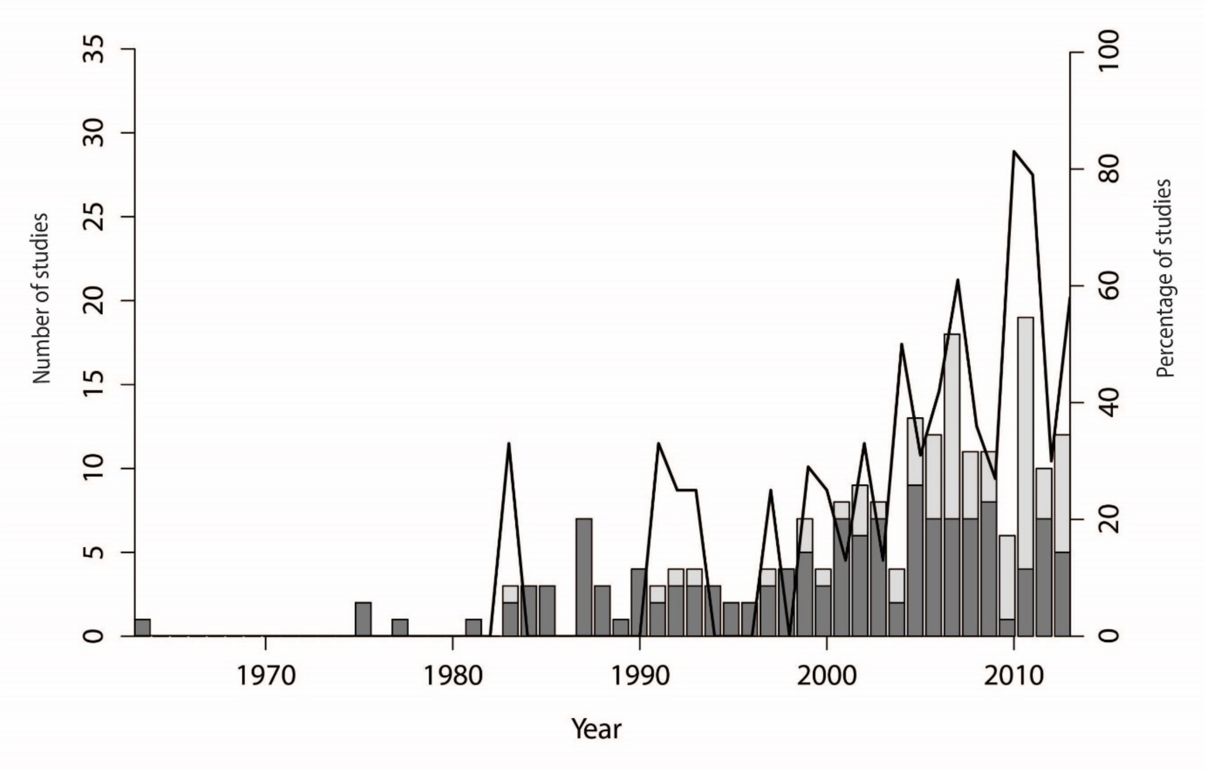

Figure 2.2: Trends in use of single (dark grey bars) and multi-model (light grey bars) frameworks between 1963 and 2013. The percentage of studies that used multi-model frameworks (black line) has generally increased over time.

Akaike's information criterion was the most common model selection technique used in the elasmobranch growth literature. Since first being employed by Manning and Francis (2005), it has been used to determine model choice in 39 additional elasmobranch multi-model studies. Studies that did not incorporate *AIC* either used an alternative statistical approach (n = 13) such as R^2 (e.g. Davis et al. 2007, Matta and Gunderson 2007) or subjectively selected the best model (n = 21) based on visual assessment of fit or the similarity of the model parameters to known biological data (e.g. size at birth).

2.3.2 Biological influence on model selection

A total of 105 groups met the criteria to be included in the analysis (Table 2.3). Overall, the majority of groups (57%) selected the VBGF over a sigmoid function. Both shark and batoid groups were equally likely to select the VBGF (Table 2.3) ($df = 1$, $\chi^2_{yates} = 1.14$, $p = 0.29$). Similarly, the VBGF was also equally likely to be chosen by all reproductive modes (Table 2.3) ($df = 2$, $\chi^2 = 1.65$, $p = > 0.44$).

Table 2.3 The number of groups for 1) shark and batoid taxa and 2) reproductive Modes

	Group	n of groups	% of groups that selected VBGF
Taxa			
	Shark	58	62%
	Batoid	47	51%
Reproductive Mode			
	Egg-laying	31	51%
	Placental live-bearing	32	59%
	Yolk only live-bearing	42	60%

2.3.3 Sigmoid models and inflection points

The α of logistic and Gompertz functions occurred at an age older than zero for 79% and 38% of groups, respectively. When both functions were included as candidate models the position of α in the logistic model occurred at older ages than the Gompertz ($df = 31$, $t = 2.93$, $p = 0.003$) The ages that α occurred for the logistic function were influenced by an interaction between taxa and reproductive mode with older ages for batoid taxa that were also egg-layers and sharks that were yolk only live-bearers (Table 2.4; Fig. 2.3a, b). The ages that α occurred for the Gompertz function were influenced most by reproductive mode (Table 2.4), where the position of α occurred at older ages for egg-laying species regardless of whether they were sharks or batoids (Fig. 2.3c, d).

Table 2.4 The effect of reproductive mode (placental live-bearing, yolk only live-bearing and egg-laying), and taxonomic group (shark or batoid) on the ages that α occurred for the logistic and Gompertz functions.

	df	***P***	***AICc***	***ΔAICc***	***Weight***
Logistic function					
Model					
α ~Reproductive Mode*Taxa	4	< 0.001	190.0	0	0.96
α ~ Reproductive Mode	2	< 0.001	197.0	6.99	0.03
α ~ Reproductive Mode+Taxa	3	< 0.001	198.9	8.86	0.01
α ~ Taxa	1	< 0.001	202.2	12.14	0
α ~1	-	-	207.8	17.8	0
Gompertz Function					
Model					
α ~Reproductive Mode	2	< 0.001	300.6	0	0.60
α ~ Reproductive Mode+Taxa	3	< 0.001	302.0	1.40	0.30
α ~ Reproductive Mode*Taxa	5	< 0.001	304.0	3.43	0.11
α ~ Taxa	1	0.145	322.6	22.02	0
α ~1	-	-	322.6	22.04	0

degrees of freedom (*df*), χ^2 significance probability (*P*), Akaike's information criterion correction with sample size bias correction (*AICc*), difference in *AICc* (*ΔAICc*), and Akaike weight (weight).

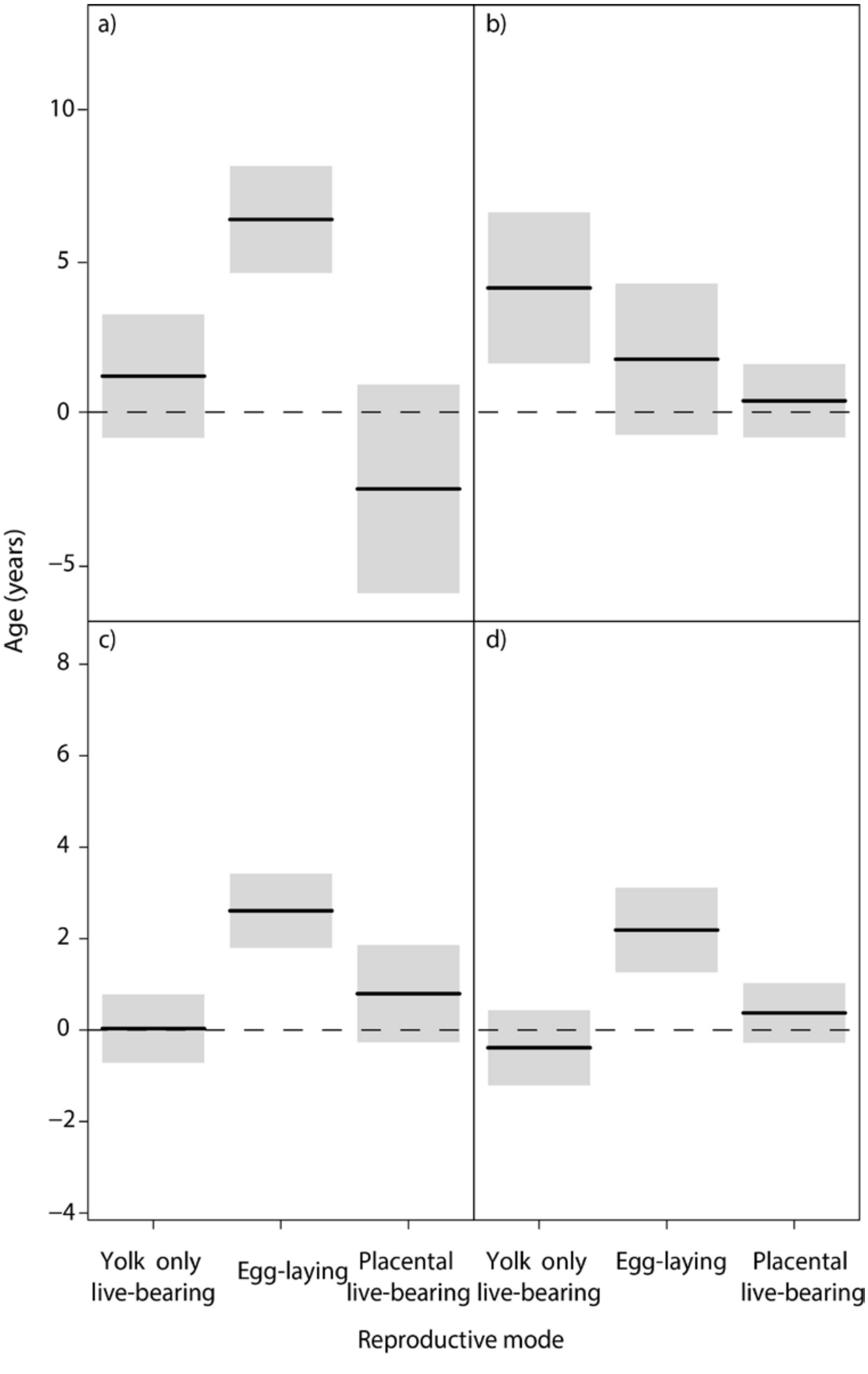

Figure 2.3: Effect of reproductive mode (yolk only live-bearing, placental live-bearing and egg-laying) and taxa (shark or batoid) on the age that α occurred for the logistic (a - b) and Gompertz (c - d) functions. Reproductive modes are grouped for batoids (a, c) and sharks (b, d) to show interaction effects. Black bars are the mean predicted value and the grey bands are the 95% confidence intervals. A dashed line represents an age of zero.

The occurrence of α at an age older than zero showed that changes in growth trajectory were supported by sigmoid functions. However, whether or not a change in growth rate was supported for the population was determined by whether or not sigmoid models were selected over the VBGF in these instances. When $\alpha > 0$ this model performed better than the VBGF in 46% of cases according to *AIC* results. However, as α increased the rate of selection of sigmoid models over the VBGF also increased. When α => 1 yr a sigmoid model was selected in 67% of cases while α = > 2 yr and α = > 3 yr increased selection to 79% and 85%, respectively. When a sigmoid model was selected as the best fitting model by the *AIC* any additional sigmoid candidate models also outranked the VBGF.

2.3.4 Multi-model effects on growth estimates

The shapes of different candidate models strongly influenced differences in their fits. Growth curves differed the most between models at age zero (Fig. 2.4). The largest estimates of L_0 were produced by the logistic and Gompertz functions which were 23% and 15% larger on average than the VBGF, respectively. Meanwhile the L_0 estimates of the VBGF-2 and VBGF were on average similar (Fig. 2.4). Despite this similarity in L_0 estimates between the VBGF-2 and the VBGF, a large error estimate indicated there were groups where L_0 differed considerably between the two models. The ΔL_0 of the Gompertz and logistic models were larger than the VBGF in 91% and 90% of cases, respectively, while the ΔL_0 VBGF-2 was smaller than the VBGF in 79% of cases. However, after the 2nd age-class the average ΔLt was (< 3%) for all models (Fig.2.4). Despite distinct trends in ΔL_0 between candidate models, these differences were small for most groups. However, for some groups the ΔLt differed markedly, especially at age zero (Fig. 2.5). All three alternative models had occurrences where their estimates were more than 200% larger than the VBGF at age zero (Fig. 2.5). In each of these instances, an alternative model to the VBGF was selected by the *AIC* (Serra-Pereira et al. 2008, Liu et al. 2011). These indicate instances where the poor fit of the VBGF would have jeopardised growth estimate accuracy if a multi-model framework had not been implemented.

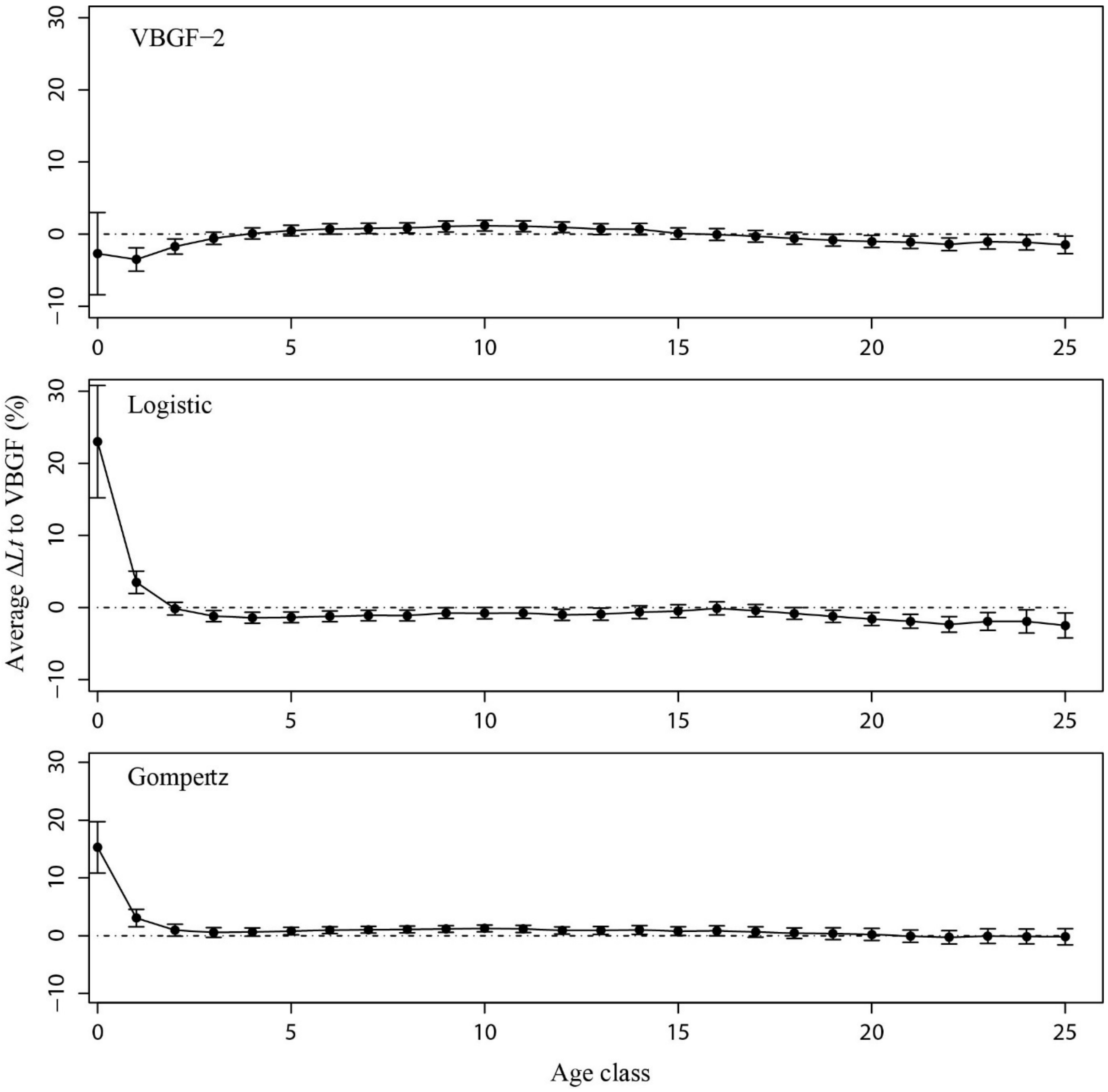

Figure 2.4: The percentage difference (Δ*Lt*) of three alternative candidate models (VBGF-2, logistic function and Gompertz function) to the VBGF (dashed zero difference line) averaged between groups at each age class (years).

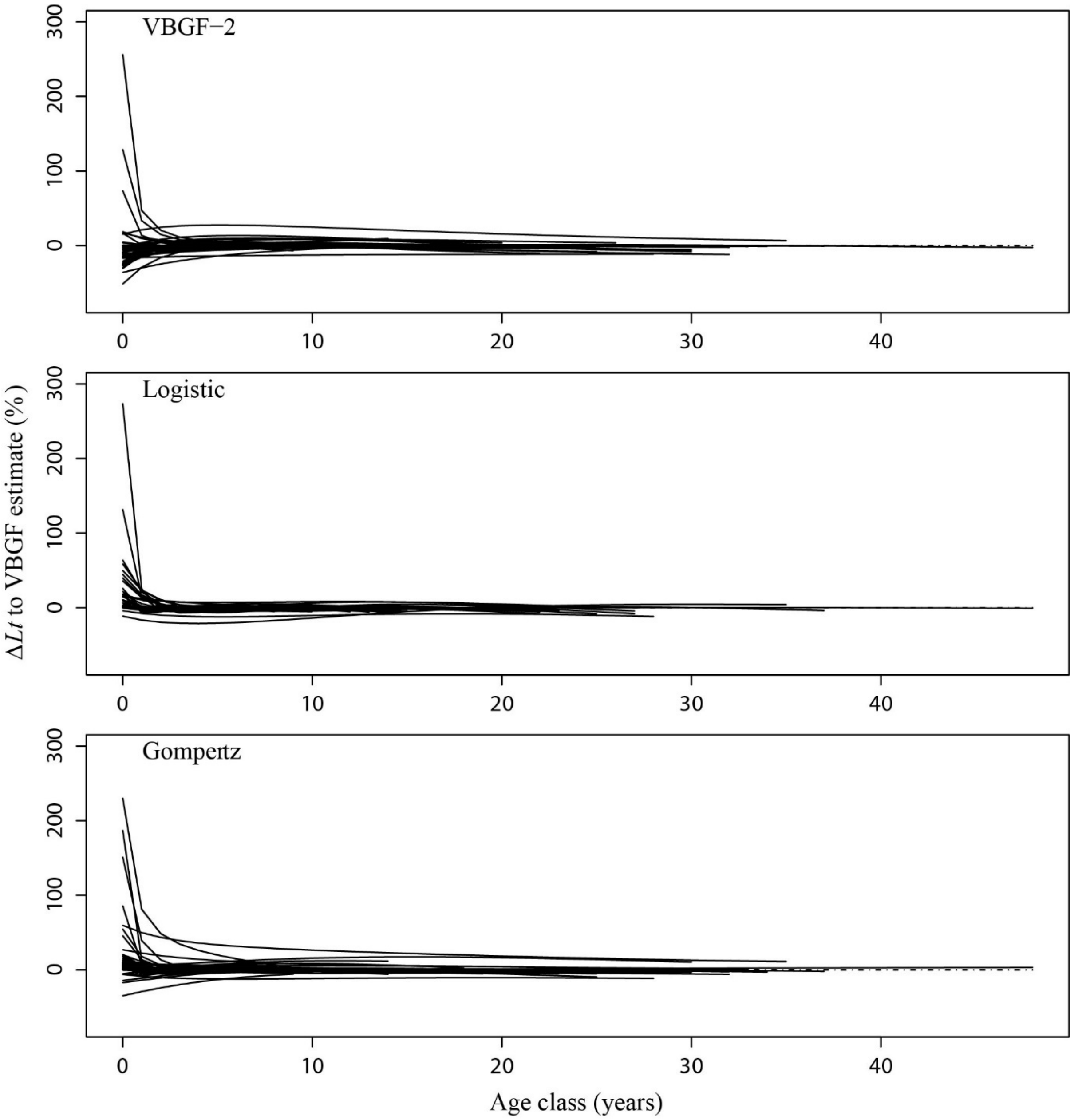

Figure 2.5: The percentage difference (Δ*Lt*) across age classes (years) of the three alternative candidate models (VBGF-2, logistic function and Gompertz function) to the VBGF (dashed zero equivalence line) for individual groups.

2.3.5 Variables that influenced differences in candidate model fits

Differences in candidate model fits were most strongly influenced by reproductive mode and sample size (Table 2.5). The GLM revealed that models where $\Delta AICc$ = < 2 were significantly different to the null model and incorporated a variety of response variables (Table 2.5). Of these, reproductive mode was the most influential variable with egg-laying taxa causing the largest ΔL_0 values (Fig. 2.6a). The other highly influential variable was sample size which showed greater ΔL_0 as sample sizes increased regardless of the spread of the data (Fig. 2.6b).

Table 2.5 The effect of reproductive mode (placental live-bearing, yolk only live-bearing and egg-laying), sample size, body size, separation or combination of sexes, and taxonomic group (shark or batoid) on the difference in fit at age-zero between alternative candidate models and the best fitting model (ΔL_0).

Model	***df***	***P***	***r^2***	***AICc***	***ΔAICc***	**Weight**
ΔL_0 ~Reproductive Mode	2	<0.001	0.12	1427.6	0	0.17
ΔL_0 ~Reproductive Mode+Sample Size	3	<0.001	0.13	1427.6	0.03	0.17
ΔL_0 ~Reproductive Mode+Body Size	3	<0.001	0.13	1428.9	1.28	0.09
ΔL_0 ~Reproductive Mode+Body Size+Sample Size	4	<0.001	0.14	1428.9	1.29	0.09
ΔL_0 ~Reproductive Mode+Sexes combined/separated	3	<0.001	0.12	1429.1	1.56	0.08
ΔL_0 ~Reproductive Mode+Sample Size+ Sexes combined/separated	4	<0.001	0.13	1429.2	1.65	0.07
ΔL_0 ~Reproductive Mode+Taxa	3	<0.001	0.12	1429.4	1.84	0.07
ΔL_0 ~1	-	-	-	1443.8	16.22	0

degrees of freedom (df), χ^2 significance probability (P), coefficient of determination (r^2), Akaike's information criterion correction with sample size bias correction (*AICc*), difference in *AICc* (*ΔAICc*), and Akaike weight (weight). Only models with a *ΔAICc* < 2 are presented.

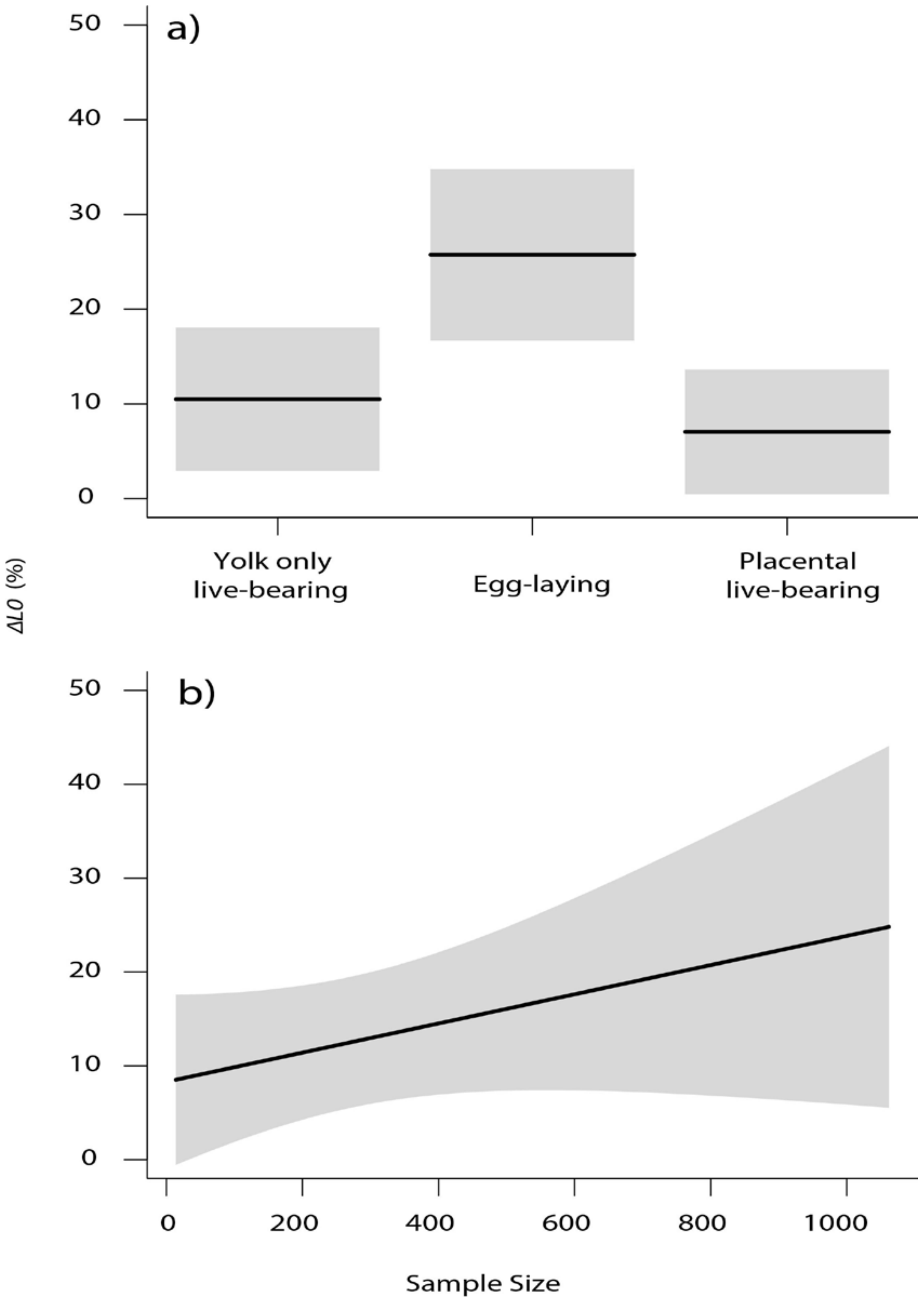

Figure 2.6: Effect of a) reproductive mode and b) sample size on the difference in fit at age-zero between alternative candidate models and the best fitting model (ΔL_0). Black bars are the mean predicted value and the grey bands are the 95% confidence intervals.

2.4 Discussion

The use of a VBGF in a single model framework remains a popular method of estimating elasmobranch growth. However, this study has showed that the VBGF provided a worse fit for 40% of groups and in some instances provided growth estimates that would likely have been considerably inaccurate. Continued *a priori* use therefore risked biasing and increasing the residual error of their growth estimates. Different candidate models offer contrasting fits and subsequently inappropriate model choice can affect growth estimates. Growth parameters such as L_∞ are greatly model dependent with the VBGF estimates typically larger than those of sigmoid functions (Katsanevakis and Maravelias 2008). Here, it was demonstrated that the greatest model differences occur at the youngest age classes of the growth curve close to L_0. Multi-model frameworks therefore provide a good way of ensuring that early growth is best captured and predicted accurately. Sigmoid functions have been hypothesised to provide improved growth model fits for batoids as they grow larger in mass rather than length (i.e. disc width) in comparison to sharks due to their dorso-ventrally flattened body shape (Cailliet and Goldman 2004). Similarly, egg-laying species were also hypothesised to benefit from sigmoid functions more than live-bearing species as they undergo a transition in post-partum nutrient sources. However, this study demonstrated that model choice was neither dependent on taxa nor reproductive mode. Consequently, inferring model choice by species alone may exclude an appropriate model from the set of candidates. Multi-model frameworks thus offer an improved approach over single model frameworks as the selection of an appropriate model can increase growth estimate accuracy by reducing residual error and bias (Katsanevakis 2006).

Despite hypotheses to the contrary, the selection of specific growth models was not influenced by taxa nor reproductive mode. Half of the batoid groups selected the VBGF as the best fitting model despite this model supposedly being less suited to their morphology (e.g. Davis et al. 2007, Natanson et al. 2007, Smith et al. 2007). Similarly, egg-laying groups only selected sigmoid models as the best fitting model 60% of the time - a result similar to placental and yolk only live-bearers. This occurred either because sigmoid models were inappropriate, or that the omission of juveniles precluded detecting delayed juvenile growth (Katsanevakis and Maravelias 2008). A number of instances also occurred where a sigmoid model was selected for sharks and live-bearing taxa (e.g. Barreto et al. 2011, Tillett et al. 2011, Chin et al. 2013). Additionally, there were groups where a sigmoid model was still selected even if delayed juvenile growth was not present ($\alpha \leq 0$) (Henningsen and Leaf 2010, Jacobsen and Bennett 2010, Barreto et al. 2011). Thus, the VBGF can still provide a suboptimal fit even if it is supposedly well suited to a species' growth pattern. This reaffirms that while certain growth patterns may typify certain taxa, variable growth trajectories still exist within them. It is therefore recommended that both sigmoid functions and the VBGF are included in multi-model frameworks.

For many of the elasmobranchs included in this analysis, α occurred at ages older than zero and was biologically informative. This elucidates previous findings where sigmoid models were shown to provide the most contrast to the VBGF which does not possess an inflection point (Katsanevakis and Maravelias 2008). Sigmoid functions were selected over the VBGF more frequently when α occurred at older ages; reaffirming that VBGF is unable to describe delayed juvenile growth. For both the logistic and Gompertz functions α occurred at the oldest ages for egg-laying taxa. Subsequently, the fit of candidate models differed the most for egg-laying taxa, especially at age zero. The ages that α occurred at were always largest for the logistic function. Consequently, differences in α only occurred at older ages for between shark and batoid taxa with the logistic function and not the Gompertz function. This discrepancy occurred as the logistic function is anti-symmetrical (the inflection point on the y axis = $L_\infty / 2$) whereas the Gompertz is not (the inflection point on the y axis = L_∞ / e) (Ricker 1979). Therefore, the position of α is disparate between these candidate models and produces contrasting shapes. In this study the logistic function always estimated a larger L_0 while the Gompertz function provided larger estimates of L_∞ (Katsanevakis and Maravelias 2008). Likewise, L_0 was also model dependent with the reverse trend (i.e. logistic yielded the largest values and VBGF the smallest). Larger L_0 parameters occur with older inflection points in sigmoid functions as these parameters co-vary. The logistic and Gompertz functions will probably provide more accurate growth estimates in instances where delayed growth is present. However, even if delayed growth is detected by one or both of these models, it does not guarantee that it will be selected as the most appropriate candidate as demonstrated with egg-laying taxa.

The results of this study showed that sigmoid functions differed most to the VBGF at age zero. This is an artefact of the inclusion of α which altered their trajectories so that L_0 estimates were larger than the VBGF. Alternatively, similar fits were provided on average by the VBGF-2 to the VBGF across all age classes. However, some groups had VBGF-2 growth estimates that were considerably different to the VBGF; typically when the fixed value of L_0 differed considerably to that of the 3 parameter VBGF (Pardo et al. 2013). When candidate model fits differ considerably, the full benefits of a multi-model framework are gained. For example, it has been demonstrated that the VBGF was inappropriate for the blacktip sawtail catshark (*Galeus sauteri*, Scyliorhinidae) as it provided an estimate of L_0 that was only 30% of the known size at birth (Liu et al. 2011). In a single model framework, these estimates would not have accurately represented the growth trajectory. This was avoided as alternate models with contrasting shapes were included as candidates (Gompertz function, logistic function and VBGF-2) and provided appropriate estimates of L_0. As empirical growth rates are rarely available, the true accuracy of length-at-age estimates can be difficult to determine. However, as multi-model frameworks determine and provide growth models that best fit the data, they reduce the risk that a poor fitting model will produce biologically unrealistic growth estimates.

The divergence of candidate model fits increased with sample size. This occurred as models only converged on their true shape when sufficient data were available. Therefore, at small sample sizes candidate models were forced through the same trajectory and unable to achieve their divergent shapes - producing similar fits. Growth models are most sensitive to data in the smallest and largest size classes of the growth curve (Haddon 2001). Therefore, model fits are most constrained when these data are omitted. Missing larger size classes are difficult to account for and currently no technique exists that can substitute these data. A fixed L_∞ has been attempted in previous studies, although it provided a poor fit for all candidate models (Farrell et al. 2010). Smaller size classes can be accounted for by including known age-zero individuals (Bishop et al. 2006) or back-calculation techniques (Smart et al. 2013). However, one popular technique for correcting growth estimates for juvenile size classes is to fix the L_0 parameter to the empirical length-at-birth to adjust the model trajectory (Cailliet et al. 2006, Coelho et al. 2011). However, Pardo et al. (2013) has demonstrated that the L_0 value of the VBGF-2 function is not equivalent to empirical length-at-births as it lies outside the range of the data. Therefore, fixing L_0 biases the remaining parameters due to their strong correlation (Pardo et al. 2013**)**. As the growth completion parameter covaries negatively with L_∞ (Pilling et al. 2002), an erroneous L_0 will introduce error into every parameter (Pardo et al. 2013). A better alternative are back-calculation techniques which estimate lengths-at-previous-ages for each individual included in length-at-age analysis (Francis 1990, Cailliet and Goldman 2004). These techniques can compensate for missing juvenile length classes through the addition of interpolated data (Smart et al. 2013). Rather than constraining the model by fixing L_0, they increase the sample size of the younger age classes; correcting the model trajectory without biasing parameter estimates. Back-calculation offers an improvement over using a VBGF-2 since candidate models can provide biologically reasonable L_0 estimates without introducing error into the remaining growth parameters (Pardo et al. 2013).

Multi-model inference is an additional step that can further realise the potential of multi-model frameworks. However, this approach has rarely been included elasmobranch growth studies (e.g. Harry et al. 2010, Barreto et al. 2011). If there is a clear best fitting model in the set of candidates (*AIC* weight [*w*] = > 90%) then multi-model inference is not required as the result would be unchanged (Katsanevakis and Maravelias 2008). However, it's underutilisation in elasmobranch literature is a missed opportunity as few studies have met the criterion of having an outright best fitting model (e.g. Jacobsen and Bennett 2010, Harry et al. 2013). It is possible that multi-model inference is currently underutilised as the growth estimates are more difficult to reproduce. Two important outputs are required from any age and growth study: 1) length-at-age values that can be used to estimate the age at different life history events (e.g. maturity), and 2) growth completion parameters that can be used in analyses such as mortality estimation (Pauly 1980), inferring consumption rates (Essington et al. 2001) and yield per recruit models (Beverton and Holt 1957). Reproducing length-at-age estimates from any particular candidate model is achieved by simply inserting the parameters into the respective model equation. However, as multi-model inference produces an averaged model from a set of candidates, reproducing these estimates is more complicated. It is therefore recommended that tabulated length-at-age estimates are given to facilitate their reproducibility. Calculating an averaged L_∞ is common practice in multi-model inference as this parameter is equivalent amongst all asymptotic candidate models (Katsanevakis and Maravelias 2008). As L_0 is also equivalent amongst the same candidate models, producing an averaged L_0 using the same methodology is also recommended. Unfortunately, a model averaged growth completion parameter cannot be calculated as these are incomparable between candidate models (Thorson and Simpfendorfer 2009). However, a suite of analyses exist that specifically require the *k* parameter from the VBGF. Therefore, the VBGF should be included as a candidate model if estimates of *k* are required for other purposes. This poses no issue when the VBGF is the most appropriate model., although defaulting back to it when it is inappropriate is an issue. Therefore, the ability to fully incorporate multi-model inference results in future population analyses needs to be further considered.

Future work should also focus on the application of semi-parametric modelling in growth analysis. The use of non-parametric and semi-parametric growth models are becoming increasingly common in ecology and fisheries (Munch et al. 2005, Sugeno and Munch 2012). Multi-model frameworks are limited where growth is biphasic as growth estimate error would not be eliminated. Semi-parametric models avoid this misspecification as they incorporate a family of functions *a priori* as parametric priors, while allowing the model to estimate any possible shape (Thorson and Taylor 2014). In situations that are data poor, semi-parametric models can revert back to this family of functions (Thorson et al. 2014). Currently, these techniques have not been used to estimate fish growth although their potential has been highlighted (Maunder et al. 2015). The results of this study would fit well with these techniques as the recommendations made here on *a priori* candidate model choice would be transferrable as potential priors.

This study demonstrated that multi-model frameworks provided improved model fits at L_0; a growth phase which has received less attention than L_∞. Therefore, the benefits of multi-model frameworks are most applicable for taxa with large sizes-at-birth such as elasmobranchs. Additionally, many elasmobranch species are targeted in gauntlet fisheries where fishing pressure is limited to the younger age classes, preserving the breeding stock (Prince 2005). Gauntlet fisheries have a greater propensity as sustainable fishing approaches for slow growing and late maturing species such as sharks (Simpfendorfer 1999b). As gauntlet fisheries rely on limited mortality for age classes outside of the fishery (Prince 2005), accurately understanding the age that individuals leave the fishery is imperative. Therefore, multi-model frameworks are especially effective for elasmobranchs and taxa where understanding the growth rates of younger age classes is valuable.

2.5 Conclusion

Overall, the fits of candidate growth models for most shark and ray studies were very similar and in most cases the use of a multi-model framework may have only incrementally affected length-at-age estimates. However, pre-emptively predicting how much variation will occur between candidate model fits was not possible. It was also not possible to assign particular growth models to broad taxonomic groups. Therefore, multi-model frameworks should be used to provide the best model fit possible and avoid using an inappropriate model *a priori*. Multi-model frameworks are most robust when including a range of growth functions that produce models with contrasting shapes (e.g. inverse exponential, sigmoid, etc.). If only models with similar shapes are included as candidates (e.g. VBGF and VBGF-2) then *AIC* cannot account for the omission of models that would improve the growth model fit. A set of model candidates should, therefore, be focused on including appropriate models so that a good candidate is not omitted (Burnham and Anderson 2002). The VBGF and sigmoid functions should be included as candidate models as their fits are the most contrasting (Katsanevakis and Maravelias 2008). Further, as model candidates differ the most when $t = 0$ it is recommended that parameterisations that incorporate L_0 are used for all model candidates (see Table 2.2). However, fixing the L_0 parameter should be avoided as this can constrain model fit, add substantial bias to the resulting growth estimates and potentially bias *AIC* results (Pardo et al. 2013).

Based on this evaluation of elasmobranch growth modelling, a basic framework should at least include the VBGF, Gompertz function and logistic function. Additional models can also be included that could not be evaluated in this study due to their infrequent use. Model selection should be based on *AIC* results with a weighted model produced by multi-model inference if there is no outright best model (*w* = > 90%). An averaged L_∞ and L_0 should be calculated from the multi-model inference estimates and a tabulated set of length-at-age estimates presented to allow reproducibility. If data are limited from the smaller length classes, then techniques such as back-calculation should be used to prevent model constraint.

Chapter 3

General Methods

3.1 Sample Collection

3.1.1 Papua New Guinea

Samples were collected in May and June 2014 by observers from the PNG National Fisheries Authority (NFA) on board longline vessels operating in the Bismarck and Solomon Seas. The vessels targeted shark species by setting their gear close to the surface while using a maximum of 1200 hooks per set for an average soak time of 8–10 hours (Kumoru 2003b). Biological information was recorded for each landed individual including the total length (TL), sex and maturity stage. The TL of each individual was measured to the nearest 1 mm by straightening the caudal fin and measuring in a straight line from the snout, following Francis (2006). A section of vertebrae consisting of about 4–6 centra were removed from the vertebral column below the first dorsal fin and stored frozen. Frozen vertebral sections were sorted at the NFA provincial office in Rabaul, East New Britain, and then sent to the laboratories at James Cook University (JCU) in Townsville.

While on board the vessels, the NFA observers photographed each individual before processing. These images usually consisted of a roughly lateral view of the shark (Fig. 3.1a), but sometimes also included secondary images of other key diagnostic features (e.g. ventral view of the head, upper dentition, close-ups of fins [Fig. 3.1b]). These images were later examined by William White (CSIRO, Hobart) to verify on-board species identifications. In some instances, the image did not include the key diagnostic feature, i.e. the caudal fin, and thus accurate confirmation could not be made from the image. *Carcharhinus amblyrhynchos* identifications were verified by the presence of a black margin along the caudal fin and *C. albimarginatus* identifications were verified by white tips on the first dorsal, pectoral and caudal fins. Individuals that only had white markings on their first dorsal fin were identified as *C. amblyrhynchos* as this can occur for some individuals.

Figure 3.1: Diagnostic photographs taken by the NFA observers on board longline vessels. These photographs include a) a ventral view of the whole specimen and b) a view of the caudal fin.

3.1.2 Indonesia

Samples were collected between April 2001 and August 2005 from the Tanjung Luar fish landing site in eastern Lombok, Indonesia by William White. Full details of sample collection can be found in White (2007). The total length (TL) of each individual was measured to the nearest 1 mm by straightening the caudal fin and measuring in a straight line from the snout, as per Francis (2006). A section of vertebrae was removed from below the first dorsal fin. Each section of vertebrae was stripped of tissue using a scalpel and stored frozen for transportation.

3.2 Growth Analysis

3.2.1 Vertebrae processing

Vertebrae were processed following protocols described by Cailliet and Goldman (2004). Once transported to the laboratory the vertebrae were defrosted and remaining muscle tissue was removed using a scalpel. Individual vertebral centra were then separated and soaked in a 4% sodium hypochlorite solution for 30 mins to remove any remaining tissue. Centra were then dried in an oven at 60°C for 24 hours. A low speed circular saw with two diamond-tipped blades (Beuhler, Illinois, USA) was used to section individual centra. These longitudinal sections were made through the centrum focus at a thickness of 400 µm. Sections were mounted onto microscope slides using Crystal Bond adhesive (SPI supplies, Pennsylvania, USA).

3.2.2 Age determination

Individual ages were estimated by counting translucent and opaque centrum band pairs in the *corpus calcareum* under a microscope using transmitted light (Cailliet and Goldman 2004). The transition from pre-to post-natal growth was identified from a change in the angle of the *corpus calcareum* and marked an age of zero. Each subsequent growth band pair was assumed to be one year of growth.

Annual growth deposition could not be validated for *C. amblyrhynchos*, *C. albimarginatus* or *C. limbatus* as the short sample collection periods precluded validation techniques such as marginal increment analysis. However, age validation was previously attempted for *C. amblyrhynchos* from northern Australia using oxytetracycline mark recapture methods (Robbins 2006). While these attempts were unsuccessful, individuals that were at liberty for 10 months displayed growth consistent with annual growth band deposition (Robbins 2006). Annual growth band pair deposition has previously been confirmed for *C. limbatus* through the use of marginal increment analysis (Killam and Parsons 1989) and was therefore assumed here as well. No age validation has ever been conducted on *C. albimarginatus*. However, annual growth band deposition was also assumed for this species due to the strong body of literature which has validated the ages of several carcharhinid species (Killam and Parsons 1989, Chin et al. 2013, Harry et al. 2013).

Growth bands of individual centra were counted independently by two readers to reduce age estimate bias (Cailliet and Goldman 2004). Neither reader had any prior knowledge of the TL or sex of the individuals. When counts differed between readers, those centra were re-examined by both readers until a consensus age was reached. If no consensus age was reached, then those individuals were omitted from further analyses.

Inter-reader precision analyses were conducted on the original counts of both readers. Percent agreement (*PA*) and percent agreement ± 1 year (*PA* ± 1 year) was calculated with individuals grouped by 10 cm TL classes. For long-lived species, greater variation in growth band reading occurs as age increases (Goldman et al. 2006). By grouping individuals by length class, the variability in calculating *PA* and *PA* ± 1 year as age increases was accounted for. Grouping individuals by length rather than age avoids introducing bias to this approach as length is an empirical measurement whereas age is estimated (Cailliet and Goldman 2004, Goldman et al. 2006). Average percent error (*APE*) and Chang's coefficient of variation (*CV*) (Chang 1982) were used to test precision of inter-reader growth band reads (Campana 2001). These statistics were calculated using the FSA package (Ogle 2016) in the 'R' program environment (R Core Team 2013).

3.2.3 Back-calculation

Back-calculation techniques were applied when a limited number of juveniles occurred in the samples (Cailliet and Goldman 2004). Individual centra sections were photographed using a compound video microscope and the distances between growth band pairs were measured using image analysis software (Image Pro Plus version 6.2 for Windows, Media Cybernetics, 2002). The centrum radius (CR) was measured as straight line from the focus to the centrum edge. The birth mark and each growth band pair were measured along this line as the distance from the focus to the nearest 1µm. A Dahl Lea direct proportions back calculation technique was applied (Carlander 1969):

$$L_i = (\frac{L_c}{CR_c}) \times CR_i \qquad (3.1)$$

where L_i = length at growth band pair 'i', L_c = length at capture, CR_c =centrum radius at capture and CR_i = centrum radius at growth band pair 'i'. A size-at-birth modified Fraser-Lee method was also applied. However, visual inspection determined that the spread of data for the younger age classes was very narrow for both *C. limbatus* and *C. albimarginatus*. Therefore, the Dahl-Lea direct proportions method was used in both chapters.

3.2.4 Growth modelling

Growth was estimated using the multi-model framework outline in Chapter 2 that included three candidate growth functions *a priori* (Table 3.1). Model selection was determined using Akaike's information criterion (Akaike 1973) with a small sample size adjusted bias correction (*AICc*) as recommended for sample sizes less than 200 (Zhu et al. 2009). A multi-model approach was used as *a priori* selection as use of only one model such as the von Bertalanffy growth function (VBGF) can generate biased growth estimates if it is inappropriate for species' growth patterns (Katsanevakis 2006). Using a multi-model framework which incorporates *AICc* circumvents the risk of using an inappropriate model and produces the most robust growth estimates possible (Chapter 2). A parameterisation that included length-at-birth (L_0) and asymptotic length parameters (L_∞) was used for all three candidate models (Table 3.1).

Table 3.1: Model equations of the three *a priori* growth functions used to estimate length-at-age.

Growth function	**Equation**	**Reference**
von Bertalanffy growth function (VBGF)	$L_t = L_0 + (L_\infty - L_0)\,(1 - \exp(-kt))$	(von Bertalanffy 1938)
Gompertz function	$L_t = L_0 \exp(\ln\left(\frac{L_\infty}{L_0}\right)\left(1 - \exp\left(-g_{gom}t\right)\right))$	(Ricker 1975)
logistic function	$L_t = \frac{L_\infty\, L_0(\exp\left(g_{log}t\right))}{L_\infty + L_0(\exp\left(g_{log}t\right) - 1)}$	(Ricker 1979)

where L_t is length-at-age t, L_0 is length-at-age 0, L_∞ is asymptotic length, k, g_{log} and g_{Gom} are the different growth coefficients of the respective models (which are incomparable).

Best fit parameter estimates were determined for all three candidate models using the ‘nls’ function in the ‘R’ program environment (R Core Team 2013). *AICc* was also calculated in the ‘R’ program environment as

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1} \tag{3.2}$$

where $AIC = nlog(\sigma^2) + 2k$, k is the total number of parameters +1 for variance (σ^2) and n is the sample size. The model with the lowest *AICc* value (AIC_{min}) had the best fit to the data and was thus identified as the most appropriate of the candidate models. The remaining models were ranked using the *AIC* difference (Δ) which was calculated for each model (i = 1 - 3) as:

$$\Delta = AIC_c - AIC_{min} \tag{3.3}$$

Models with Δ of 0-2 had the highest support while models with Δ of 2-10 had considerably less support and models with Δ of >10 had little or no support (Burnham and Anderson 2001). *AIC* weights (w) represent the probability of choosing the correct model from the set of candidate models and were calculated for each model (i = 1 - 3) as:

$$w_i = \frac{\exp(-\frac{\Delta_i}{2})}{\sum_{j=1}^{3} \exp(-\frac{\Delta_j}{2})} \tag{3.4}$$

Multi-model inference (MMI) is recommended when no model candidate is the outright best model for the data ($w > 0.9$) (Katsanevakis and Maravelias 2008). Therefore, in instances where candidate models performed similar according to *AICc*, model averaged length-at-age estimates, parameters and standard errors were calculated. Only L_∞ and L_0 were comparable between the three model candidates as the three growth completion parameters (k, g_{log} and g_{Gom}) are incomparable between them. Therefore, a model averaged value was calculated as:

$$\bar{L}_\infty = \sum_{i=1}^{3} w_i * L_{\infty,i} \tag{3.5}$$

where $\bar{L}_\infty$ was the model averaged asymptotic length (Burnham and Anderson 2002, Katsanevakis 2006). The unconditional standard error of $\bar{L}_\infty$ was estimated as:

$$SE(\bar{L}_{\infty}) = \sum_{i=1}^{3} w_i * (var(L_{\infty,i} | g_i) + (L_{\infty,i} - \bar{L}_{\infty})^2)^{1/2} \quad (3.6)$$

where $var(L_{\infty,i}|g_i)$ is the variance of parameter L_{∞} of model g_i (Katsanevakis and Maravelias 2008). A model averaged estimate and standard error of L_0 were calculated using the same equations.

A likelihood ratio test was performed to determine if sexes should be combined or separated (Kimura 1980). This was performed for each candidate model of both the observed and back calculated data using the method outlined by Haddon (2001) modified for the 'R' program environment (R Core Team 2013). When missing age classes occurred for one sex, the age range of the other sex was truncated to be equivalent for this analysis (Haddon 2001). Growth curves were produced for separate sexes if the likelihood ratio test of the best fitting model (or any individual candidate model where MMI was required) determined a significant difference existed for either data set.

Where the VBGF was the best fitting growth model, estimates of longevity were calculated as:

$$t_{max} = 7 * \ln(\frac{2}{k}) \quad (3.7)$$

Where t_{max} is longevity in years and k is the growth coefficient of the VBGF (Mollet et al. 2002).

3.3 Maturity Analysis

Maturity stages were recorded for each individual during the PNG sample collection. This was determined on board vessels by the NFA fisheries observers using an index modified from Walker (2005) (Table 3.2). These maturity stages were verified post-cruise by William White using photographs of the gonads taken by the observers. Male maturity stages were based on clasper condition (C = 1 - 3) and female maturity stages were based on uteri condition (U = 1 – 5) (Table 3.2). Maturity stage data was converted to a binary maturity category (immature = 0 and mature = 1) for statistical analysis.

Table 3.2: Indices for staging maturity condition. Adapted from Walker (2005)

Organ	Index	Description	Binary maturity category
Female Uteri	U = 1	Uniformly thin tubular structure. Ovaries small and without yolked ova	Immature
	U = 2	Thin, tubular structure which is partly enlarged posteriorly. Small yolked ova developing	Immature
	U = 3	Uniformly enlarged tubular structure. Yolked ova developed	Mature
	U = 4	*In utero* eggs or embryos macroscopically visible	Mature
	U = 5	Post-partum - enlarged tubular structure distended	Mature
Male Clasper	C = 1	Pliable with no calcification	Immature
	C = 2	Partly calcified	Immature
	C = 3	Rigid and fully calcified	Mature

Estimates of length-at-maturity were produced for males and females using a logistic regression model (Walker 2005):

$$P(l) = P_{max}\left(1 + e^{-\ln(19)(\frac{l - l_{50}}{l_{95} - l_{50}}}\right)^{-1} \tag{3.8}$$

where $P(l)$ is the proportion of the population mature at TL, l and P_{max} is the maximum proportion of mature individuals. The lengths that 50% and 95% of the population were mature (l_{50} and l_{95}) were estimated using a generalised linear model (GLM) with a binomial error structure and a logit-link function in the 'R' program environment (R Core Team 2013). Population estimates of age-at-maturity (a_{50} and a_{95}) were estimated using the same methods. l_{50} and a_{50} were used as metrics to describe the approximate length-and-age-at-maturity for the population.

Maturity analyses that determined l_{50} were previously carried out on the *C. limbatus* samples collected from Indonesia by White (2007). A population estimate of a_{50} was produced by extrapolating the age that l_{50} occurred at using the best fitting growth function.

Chapter 4

Age and growth of the common blacktip shark *Carcharhinus limbatus* from Indonesia, incorporating an improved approach to comparing regional population growth rates

4.1 Introduction

Many species of elasmobranchs (sharks and rays) have circumglobal distributions and can be composed of different regional or subregional populations (e.g. Duncan et al. 2006, Ovenden et al. 2009). Life history theory hypothesises that a population's life history traits (e.g. growth, size at maturity and fecundity) will adapt to maximise individual fitness and offspring survival due to natural selection pressures (Stearns 1992). Therefore, while different populations may belong to the same species, different regional selection pressures may alter their life histories. Subsequently, the life history information of a species in one location cannot be assumed to be representative of other populations from different regions (White and Sommerville 2010). Life history information is an integral component of demographic models and age-structured stock assessment models. Therefore, the use of inaccurate age and growth information in these assessments will lead to errors in their outputs. This can potentially bias management (Cailliet and Goldman 2004) and cause population declines when the surplus production estimates of the models are erroneous (Beamish and McFarlane 1995, Musick 1999). Therefore, there is a risk of unintentional overexploitation if life history data for a population from another region is used in lieu of data from the local population.

The common blacktip shark *Carcharhinus limbatus* (Müller & Henle, 1839) is a large bodied carcharhinid with a circumglobal distribution in tropical and subtropical seas (Last and Stevens 2009). *Carcharhinus limbatus* is an important component of many regional shark fisheries and is targeted in many countries, including Australia (Macbeth et al. 2009, Harry et al. 2011) and the United States of America (US) (Branstetter and Burgess 1996). It is also a common species in South Africa and although it does not form a large component of any commercial fishery, *C. limbatus* are caught in a bather protection program at a rate of approximately 130 sharks per year^{-1} (Dudley and Cliff 1993). Growth estimates for *C. limbatus* are available from several locations and show regional variation in growth rates and maximum lengths (Branstetter 1987, Killam and Parsons 1989, Wintner and Cliff 1996, Carlson et al. 2006). In the USA, *C. limbatus* in the Gulf of Mexico attain a smaller theoretical maximum length and grow faster than conspecifics in the South Atlantic Bight (Carlson et al. 2006), while substantially larger individuals are caught in South Africa in comparison (Wintner and Cliff 1996). These regional variations in life history traits suggests that *C. limbatus* requires regional population management.

Indonesia has one of the largest shark fisheries in the world (Blaber et al. 2009) and *C. limbatus* was found to be the seventh most frequently caught species in the pelagic longline fishery operating out of Tanjung Luar in Lombok (White 2007). While it is not a targeted species, catches of *C. limbatus* are substantial given Indonesia's high elasmobranch catch, estimated to be more than 100,000 tonnes per annum (Blaber et al. 2009). Indonesia has a high reliance on its marine resources with 60–70% of the country's protein coming from their fisheries (White and Kyne 2010). Given that Indonesia's population is in excess of 237 million people, this puts substantial pressure on these fisheries and increases the importance of effective management. However, these fisheries remain data limited with few data on catch, abundances and life history. Without time series catch or abundance data, dynamic population models or production models cannot be undertaken for *C. limbatus*. However, the availability of life history data will facilitate the production of static age-structured models that can be used to inform local fisheries management. Although reproductive data are now available for *C. limbatus* from Indonesia (White 2007), these age-structured models cannot be constructed until age and growth estimates from the local population of *C. limbatus* are determined.

The aim of this study was to determine length-at-age and growth parameters for *C. limbatus* being exploited in Indonesia to inform future fisheries management. Growth parameters were combined with the reproductive data (White 2007) to produce estimates of length-and age-at-maturity. This information was also compared with the available life history information from other *C. limbatus* populations to examine inter-regional differences in life history traits.

4.2 Data Analysis

4.2.1 Assignment of partial ages

As growth is more accurately modelled using partial ages, and samples were collected from different months, partial ages were assigned based on month of capture. *Carcharhinus limbatus* reproduce seasonally in Indonesian waters with partuition occurring between October and December (White 2007). Thus, December was nominated as the birth month and the partial age was calculated based the month the sample was collected. For example, an individual with 9 growth bands that was caught in August was assigned a partial age of 9.75 years (Harry et al. 2013, Smart et al. 2013). The methods outlined in Chapter 3 were then applied to determine back-calculated ages, estimate growth parameters and calculate length-at-age estimates using a multi-model approach.

4.2.2 Regional growth rate comparison

In order to compare the instantaneous growth rates of *C. limbatus* between regions, the VBGF fits for other populations were reproduced using the parameter estimates from previously published length-at-age studies from populations in the Gulf of Mexico (Branstetter 1987, Carlson et al. 2006), Florida/South Atlantic Bight (Killam and Parsons 1989, Carlson et al. 2006) and South Africa (Wintner and Cliff 1996). In instances where TL was not the length measurement used in the model, length conversions from published studies were used to calculate TL model length-at-age and parameter estimates (Wintner and Cliff 1996, Carlson et al. 2006). Instantaneous rates of growth at birth and maturity were then calculated as:

$$\frac{dL}{dt} = \frac{L(t+\Delta t)-L(t)}{\Delta t} \tag{4.1}$$

where dL/dt is the instantaneous rate of growth at time t, $L(t)$ is length at time t from the respective model estimates and Δt is a period of time over which the growth rate is to be calculated where $\Delta t = 1$ is equal to 1 year (Sparre and Venema 1998). In this instance it was set to $\Delta t = 0.00001$ to provide an instantaneous rate of growth. The growth rate at birth (dL/dt_0) was calculated using $t = 0$ and the growth rate at maturity (dL/dt_{mat}) was calculated by setting t as the age-at-maturity estimates sourced from each respective study. Where an age-at-maturity range was given (e.g. 4–5 years) rather than a discrete age-at-maturity in any respective study, the mid-point of this range was used in all calculations.

4.2.3 Influence of juvenile exclusion on growth estimation

Since only a small number of juveniles were included in the sample ($n = 5$), additional analysis was undertaken to determine the influence that these individuals had in determining the shape of the model. This was performed using the best fitting model for the sexes combined from the observed length-at-age data only. Five hypothetical sampling scenarios were created with different numbers of juveniles omitted from the model estimation process. The number of juveniles included in these five hypothetical scenarios started at zero (mature individuals only) and increased one juvenile at a time until they had all been re-introduced. Each juvenile was re-introduced in order of youngest to oldest and a new model fit was estimated for each scenario. The fits of each scenario (*n of* juveniles = 0–4) were then compared back to the complete model (*n of* juveniles = 5) by calculating the proportional difference between the length-at-age estimates of each scenarios model to that of the complete model.

4.3 Results

4.3.1 Growth estimation

A sample of 30 *C. limbatus* with an even sex ratio was collected from Indonesian waters. Only five juveniles were included in the sample (74.1–87.3 cm TL), all of which were female (Fig. 4.1c). The remaining 25 individuals were large and mature individuals of both sexes (175.6–245.8 cm TL) (Fig. 4.1e). The length ranges for males and females were 180.1–226.9 cm TL and 74.1–245.8 cm TL, respectively. The use of back-calculation techniques accounted for the missing size classes (Fig. 4.1b; d; f) and also increased the number of age at length data points from 30 to 294 through the inclusion of interpolated data (Table 4.1). The age ranges for males and females were 5.8–16.8 yr and 0.3–17 yr, respectively.

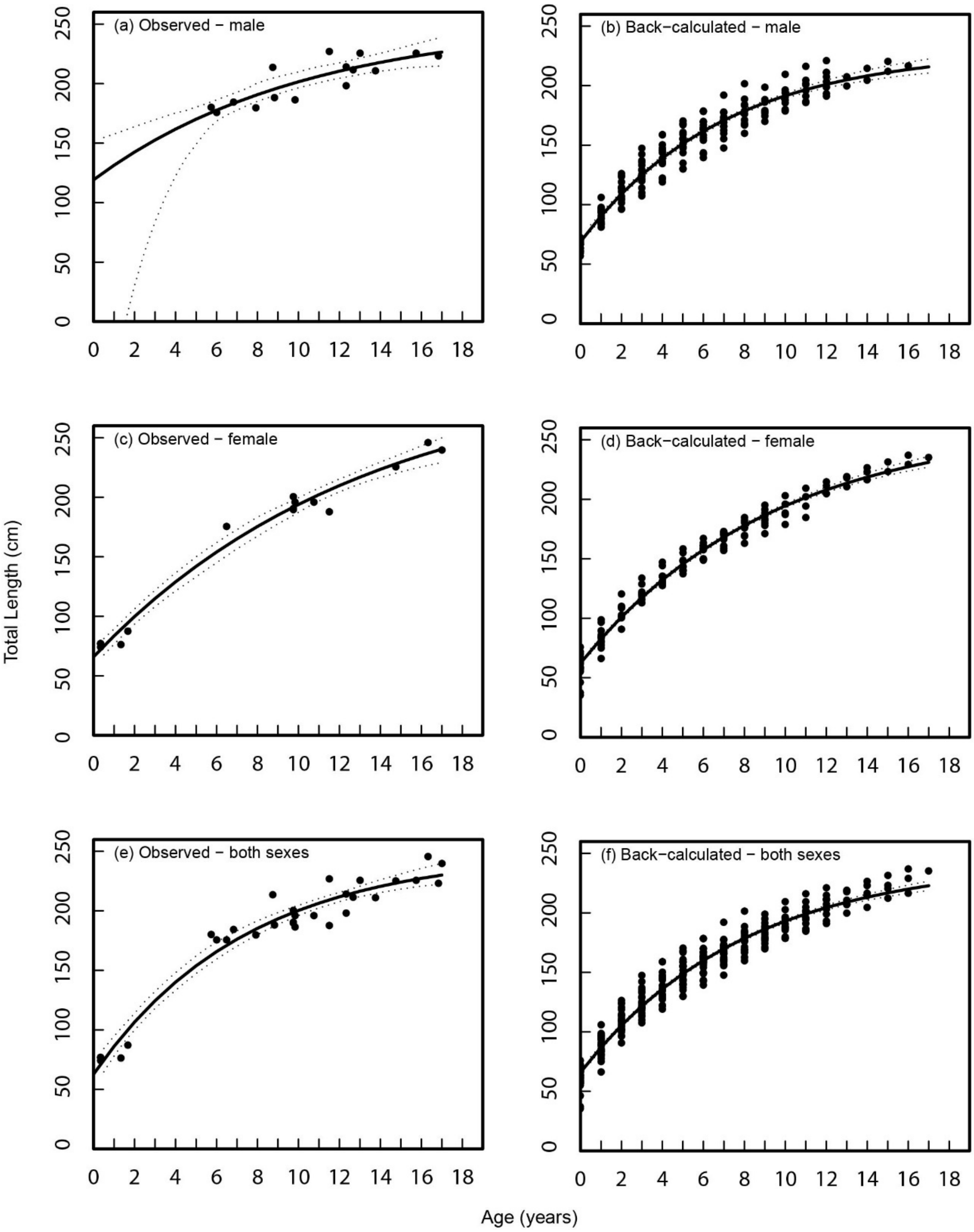

Figure 4. 1: Length-at-age of *Carcharhinus limbatus* using observed data (a, c and e) and back-calculated data (b, d and f) with VBGF model estimates and 95% confidence intervals.

Table 4.1: Summary of model parameters and AIC_c results for the observed length-at-age and back-calculated data for *Carcharhinus limbatus*

Sex	**Model**	***n***	**AIC$_C$**	Δ	***w* (%)**	L_∞	L_0	k	g_{Gom}	g_{log}
Observed										
Sexes combined	VBGF	30	375.96	0.00	57	249.2	62.9	0.13	-	-
	Logistic	30	379.46	3.50	10	228.5	70.1	-	-	0.29
	Gompertz	30	377.01	1.05	33	234.4	66.9	-	0.21	-
Male	VBGF	15	190.45	0.05	33	252.6	119.2	0.10	-	-
	Logistic	15	190.40	0.00	34	243.1	129.2	-	-	0.15
	Gompertz	15	190.43	0.03	33	247.1	125.2	-	0.12	-
Female	VBGF	15	185.67	0.00	46	307.1	65.9	0.08	-	-
	Logistic	15	187.71	2.04	17	252.4	70.8	-	-	0.22
	Gompertz	15	186.13	0.45	37	269.2	68.6	-	0.15	-
Back-Calculation										
Sexes combined	VBGF	294	3535.04	0.00	99	244	66	0.13	-	-
	Logistic	294	3605.34	70.30	<1	216	73	-	-	0.29
	Gompertz	294	3569.49	34.45	<1	238	70	-	0.21	-
Male	VBGF	167	2023.77	0	99	230	69	0.14	-	-
	Logistic	167	2050.03	26.27	<1	209	75	-	-	0.31
	Gompertz	167	2035.95	12.18	<1	225	72	-	0.23	-
Female	VBGF	127	1478.84	0	99	264	62	0.11	-	-
	Logistic	127	1530.54	51.70	<1	227	70	-	-	0.27
	Gompertz	127	1505.05	26.21	<1	245	66	-	0.19	-

n is the sample size, AIC_C is the small-sample bias adjusted form of Akaike's Information Criteria, Δ is the difference in AIC_C values between models, *w* (%) are the AIC_C weights, L_∞ is asymptotic length parameter in mm, L_0 is the length-at-birth parameter in mm, k is the growth rate parameter in yr-1 for the VBGF, g_{Gom} and g_{log} are the growth coefficients of the Gompertz and logistic models. Only L_0 and L_∞ are comparable between the three models.

The *PA* ± 1 year across 10 cm TL classes was 40.67% with no systematic bias detected by Bowker's test of symmetry (df = 18, $\chi^2 = 17$, p =0.52). A low *PA* ± 1 year occurred due to the sample containing mostly older age classes. As older age classes have more growth bands that require identification, it is these age classes where most inter-reader discrepancy typically occurs during growth band reading, therefore decreasing the *PA* ± 1 year value (Beamish and McFarlane 1995). In this study, for all individuals that were less than 100 cm TL, an *PA* ± 1 year of 100% was achieved (Fig. 4.2). Therefore, the low *PA* ± 1 year was not a result of poor reader agreement but a reflection on the lack of younger age classes that are easier to read and would normally increase the *PA* ± 1 year. A consensus age was produced for each age disagreement and therefore no vertebrae were omitted from further analysis.

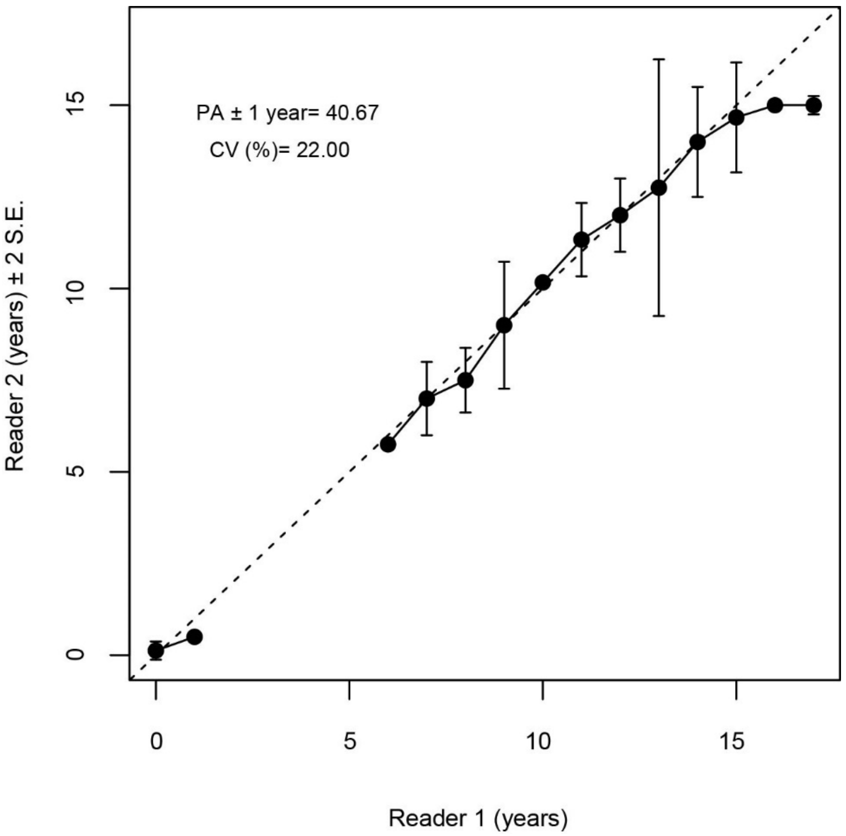

Figure 4.2: Age-bias plot for *Carcharhinus limbatus* incorporating the age-specific agreements between Readers 1 and 2 used for Bowker's test of symmetry. Mean age-specific agreements ± 2 standard errors are plotted along a 1-1 equivalence line for comparison.

The results of the multi-model AIC_c analysis showed that the VBGF produced the best model fit for the combined sexes for both the observed length-at-age data (w = 57%) and the back-calculated length-at-age data (w = 99%) (Table 4.1). The logistic and Gompertz models provided some support for the combined sexes for the observed data (w = 10% and w = 33%, respectively) but offered little support in comparison to the VBGF for the back calculated data (Table 4.1). The VBGF also provided the best model fits for the separate sexes from the back-calculation data (w = 99% for both sexes) with the Gompertz and logistic models providing little support (Table 4.1). For the female observed length-at-age data, the VBGF also produced the best fit (w = 46%) with some support provided by the Gompertz and logistic models (w = 37% and w = 17%) (Table 4.1). However, for the male observed length-at-age data, equal fits were provided by the three models (Table 4.1). This was caused by an unrealistically high L_0 estimate (119.2 cm TL for the VBGF) which resulted from a lack of male juveniles in the sample (Table 4.1; Fig. 4.1a).

While the VBGF parameter estimates provided an unrealistic L_0 estimate for the male observed length-at-age data, the estimates for the females were far more reasonable; L_0 = 65.9 cm TL, k = 0.08 yr^{-1} and L_∞ = 307.1 cm TL (Table 4.1; Fig. 4.1c). However, the VBGF parameter estimates which were most biologically realistic for the observed length-at-age data were produced for the sexes combined; L_0 = 62.9 cm TL, k = 0.13 yr^{-1} and L_∞ = 249.2 cm TL (Table 4.1). These estimates match the known maximum length of 250 cm TL and the size of birth of 62.8 cm TL for the region (White et al. 2006, White 2007). The VBGF parameter estimates produced for the back-calculation data for the combined sexes and the separate sexes were similar to one another and also matched the biological parameters (Table 4.1; Fig. 4.1b; d; f). The L_0 estimates for the back calculated data suggested that males had a slightly larger length-at-birth than females (L_0 = 68.8 and 62.3 cm TL, respectively) and females had a larger L_∞ than males (L_∞ = 264 and 229.7 cm TL, respectively). The values of k were similar for the back-calculation data between the combined and separate sex models (Table 4.1).

No significant difference between sexes was found for the truncated observed length-at-age data by the likelihood ratio tests (df = 3, χ^2 = 6.33, p = 0.09). However, the likelihood ratio tests produced a significant difference between sexes for the back-calculation data (df = 3, χ^2 = 32.31, p = <0.001).

Given that these results were contradicting, the most conservative conclusion was to accept the result for the back-calculation data as there have been previous suggestions that likelihood ratio tests can be biased at low sample sizes (Cerrato 1990). This avoids the larger risk of a type II error. Additionally, the combined sexes VBGF for the back-calculation data was an intermediate of the two separate sexes which was not the case for the observed data – bringing the observed VBGF estimates into question. Therefore, the VBGF model fits for the separate sexes from the back-calculation data were considered the most appropriate for the Indonesian *C. limbatus* population.

4.3.3 Influence of juvenile exclusion on growth estimation

The sequential removal of juveniles from the VBGF estimation process demonstrated that small numbers of neonates can have significant effects on the estimation of L_0. In the scenario where only mature individuals were included the results resembled those of the male observed length-at-age data where the curve was flat and the L_0 was unrealistically high (Table 4.2; Fig. 4.3). The L_0 estimate that this scenario produced was 75% larger than that of the complete model (*n* of juveniles = 5) (Table 4.2). The VBGF length-at-age estimates for this scenario did improve as age increased but did not converge with the complete model at a difference of <5% until reaching age 6 when empirical data were available (Table 4.2), after which the estimates became comparable (Fig. 4.3). Re-introducing one neonate back into the VBGF estimation process produced an L_0 estimate of 75 cm TL (Table 4.2). This estimate fell within the range of worldwide length-at-birth estimates for *C. limbatus* (Carlson et al. 2006), indicating some biological realism. The inclusion of one juvenile in the VBGF estimation process reduced the L_0 estimate to a difference of 19% to the complete model which was an improvement of 56% over the scenario which only included mature individuals (Table 4.2). As more juveniles were iteratively re-introduced to the data during the VBGF estimation process, the length-at-age estimates continued to improve and once four individuals were included the model did not differ from the complete model by more than 4% at any age (Table 4.2; Fig 4.3).

Table 4.2: Comparison of VBGF length estimates (cm TL) for sexes combined under hypothetical sampling conditions with varying numbers of juveniles ranging from 0 - 5. Proportional differences to the complete model (5 juveniles) at each age class are in parentheses.

Age	**Complete Age Range**	**Mature Individuals only**		**1 Juvenile**		**2 Juveniles**		**3 Juveniles**		**4 Juveniles**	
0	62.9	109.9	(0.75)	75.0	(0.19)	72.1	(0.15)	70.1	(0.11)	65.2	(0.04)
1	86.2	122.5	(0.42)	95.9	(0.11)	93.8	(0.09)	92.3	(0.07)	88.3	(0.02)
2	106.6	134.1	(0.26)	114.3	(0.07)	112.8	(0.06)	111.8	(0.05)	108.5	(0.02)
3	124.5	144.8	(0.16)	130.5	(0.05)	129.5	(0.04)	128.8	(0.03)	126.1	(0.01)
4	140.1	154.6	(0.10)	144.7	(0.03)	144.1	(0.03)	143.7	(0.03)	141.5	(0.01)
5	153.8	163.7	(0.06)	157.3	(0.02)	156.9	(0.02)	156.7	(0.02)	154.9	(0.01)
6	165.8	172.1	(0.04)	168.3	(0.02)	168.1	(0.01)	168.0	(0.01)	166.7	(0.01)
7	176.2	179.9	(0.02)	178.0	(0.01)	178.0	(0.01)	178.0	(0.01)	177.0	(0.00)
8	185.4	187.0	(0.01)	186.6	(0.01)	186.6	(0.01)	186.7	(0.01)	185.9	(0.00)
9	193.4	193.6	(0.00)	194.1	(0.00)	194.2	(0.00)	194.3	(0.00)	193.8	(0.00)
10	200.4	199.7	(0.00)	200.7	(0.00)	200.8	(0.00)	200.9	(0.00)	200.6	(0.00)
11	206.4	205.3	(-0.01)	206.5	(0.00)	206.6	(0.00)	206.7	(0.00)	206.6	(0.00)
12	211.8	210.4	(-0.01)	211.6	(0.00)	211.7	(0.00)	211.8	(0.00)	211.8	(0.00)
13	216.5	215.2	(-0.01)	216.1	(0.00)	216.2	(0.00)	246.2	(0.00)	216.4	(0.00)
14	220.6	219.6	(0.00)	220.1	(0.00)	220.1	(0.00)	220.1	(0.00)	220.4	(0.00)
15	224.2	223.7	(0.00)	223.6	(0.00)	223.5	(0.00)	223.5	(0.00)	223.9	(0.00)
16	227.3	227.4	(0.00)	226.7	(0.00)	226.5	(0.00)	226.4	(0.00)	226.9	(0.00)
17	230.1	230.9	(0.00)	229.4	(0.00)	229.2	(0.00)	229.0	(0.00)	229.6	(0.00)

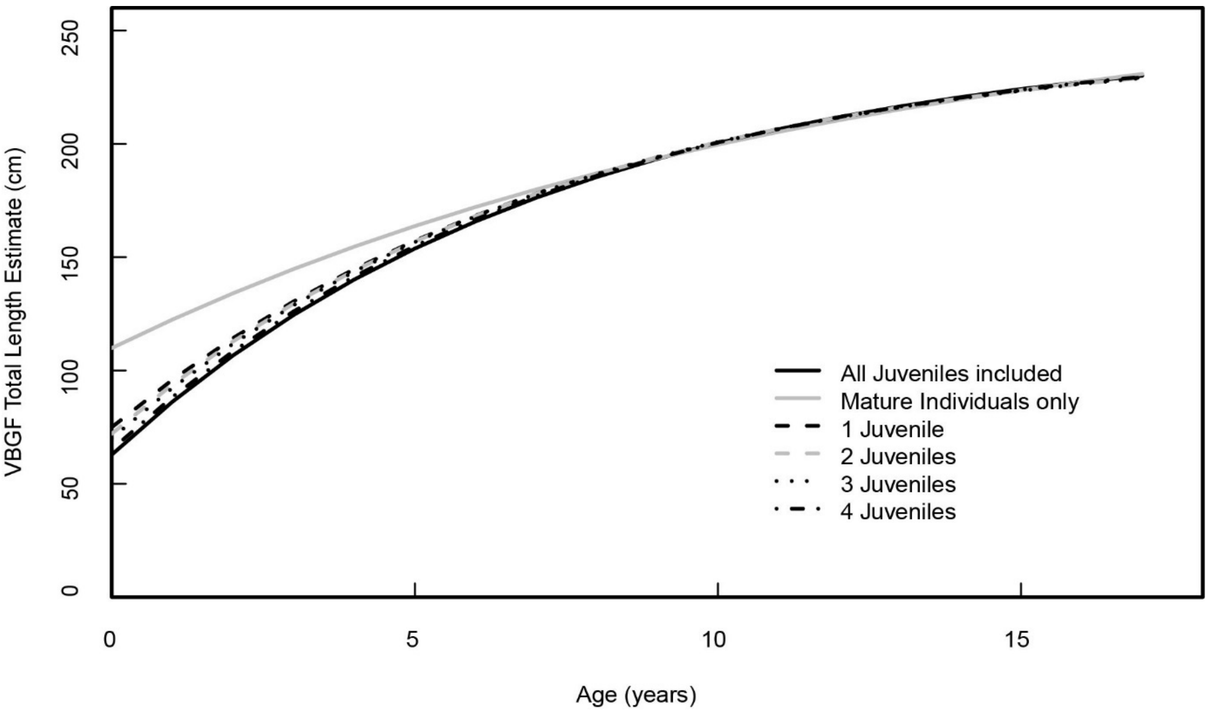

Figure 4.3: A comparison of VBGF length-at-age estimates under hypothetical conditions with varying numbers of juveniles included (*n* of juveniles = 0 - 5).

4.3.4 Regional variation in life history estimates

There was a substantial difference between the growth of *C. limbatus* from Indonesia to that of other regional populations (Table 4.3; Fig. 4.4). The Indonesian population has the highest maximum age with males and females being 16.8–17 years old, respectively (Table 4.3; Fig. 4.4). Maximum age estimates for US populations ranged from 9.5 to 11.5 years in the Gulf of Mexico (Branstetter 1987, Carlson et al. 2006) and 9 to 15.5 in Florida/South Atlantic Bight (Killam and Parsons 1989, Carlson et al. 2006). Maximum age estimates for *C. limbatus* from South Africa were also younger than those from this study at 10 and 11 years old for males and females respectively, despite attaining substantially larger maximum lengths than their conspecifics from the US (Wintner and Cliff 1996). The L_∞ of *C. limbatus* in South Africa were 261.5 and 258.4 cm TL for males and females, respectively, whereas neither population form the US attained a L_∞ larger than 195 cm TL (Branstetter 1987, Killam and Parsons 1989, Wintner and Cliff 1996, Carlson et al. 2006). The L_∞ of 264 cm TL estimated in this study for females was the largest L_∞ estimated for any population of *C. limbatus* (Table 4.3). The L_0 for *C. limbatus* varied between regions with Carlson et al. (2006) producing the largest estimates for the South Atlantic Bight (75 cm TL for females) while the smallest L_0 estimate was from South Africa (51.6 cm TL for males) (Wintner and Cliff, 1996). All of the other L_0 estimates occurred within this range (Table 4.3). The instantaneous growth rate at birth (dL/dt_0) also differed between regions and ranged from 16.4 cm^{yr-1} in the South Atlantic Bight to far more than twice that in South Africa at 42 cm $^{yr-1}$ (Table 4.3).

Table 4.3: A summary of VGBF parameters, maximum age, age at maturity (t_{mat}), growth rate at birth (dL/dt_0) and growth rate at maturity (dL/dL_{mat}) for *Carcharhinus limbatus* from different regions.

			VBGF parameters								
Study	**Location**	**Sex**	**L_∞ (cm)**	**k**	**L_0 (cm)**	**t_0 (years)**	**Maximum Age (years)**	**t_{max} (years)**	**Age-at-Maturity (t_{mat})**	**Growth Rate at Birth dL/dt_0 (cm)**	**Growth Rate at Maturity dL/dt_{mat} (cm)**
Branstetter (1987)	Northern Gulf of Mexico	Both	171	0.28	59	-1.50	9.5	13.8	4-5 (males)	31.7	8.8
									7-8 (Females)	31.7	3.8
Killam and Parsons (1989)	Florida	Male	166.5	0.28	53	-0.88	9.0	13.8	4-5	31.4	9
		Female	195	0.20	54	-1.15	10.0	16.1	6-7	27.8	7.7
Wintner and Cliff (1996)	South Africa	Male	261.5	0.20	52	-1.10	10.0	16.1	6.0	42	12.6
		Female	258.4	0.21	62	-1.30	11.0	15.8	7.0	41.3	9.5
Carlson et al. (2006)	Gulf of Mexico	Male	141.2	0.27	64	-2.21	9.5	14.0	4.5	21	6.2
		Female	158.7	0.24	65	-2.18	11.5	14.8	5.7	22.6	5.7
	South Atlantic Bight	Male	165.2	0.21	69	-2.58	13.5	15.8	6.7	20.2	4.9
		Female	177.6	0.16	75	-3.43	15.5	17.7	5	16.4	7.4
This study	Indonesia	Male	230	0.14	69	-	16.8	18.6	8.8	22.5	6.6
		Female	264	0.11	62	-	17	20.3	7.6	22.2	9.6

L_∞ and L_0 are given in measurements of TL. Total lengths for *C. limbatus* from Wintner and Cliff (1996) and Carlson et al. (2006) were converted from pre-caudal length (PCL) and fork length (FL) respectively using the length relationships given in these studies. Age at maturity was estimated in this study using length at 50% mature (l_{50}) estimates from White (2007).

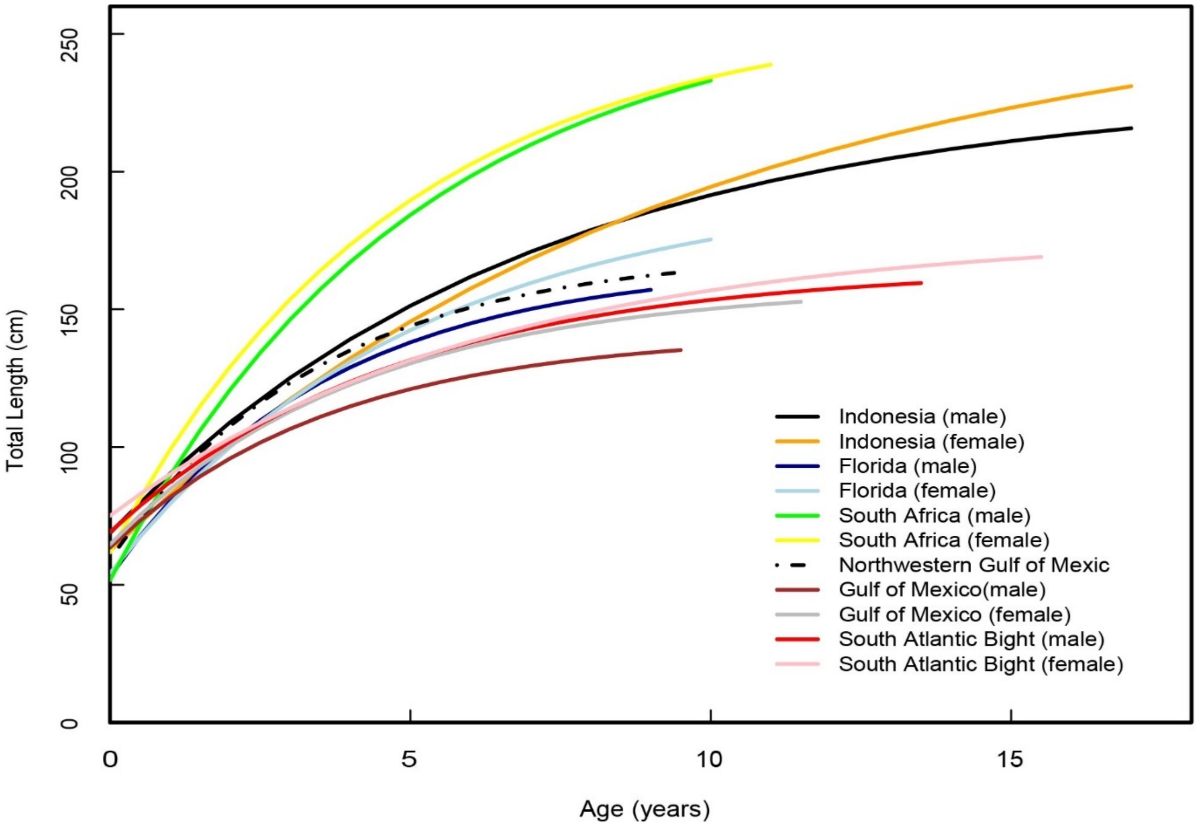

Figure 4.4: A comparison between the growth rates of *Carcharhinus limbatus* from Indonesia to previously published growth rates from other regions (Branstetter 1987, Killam and Parsons 1989, Wintner and Cliff 1996, Carlson et al. 2006). Growth rates for both sexes are included for the studies that separated them.

The age-at-maturity for *C. limbatus* in Indonesia was 8.8 years for males and 7.6 years for females (Table 4.3) based on the lengths at which 50% of individuals are mature (l_{50}), i.e. 189.4 cm TL for males and 179.6 cm TL for females (White 2007). These are the oldest age at maturities estimated for any population of *C. limbatus* with other populations maturing between 4 and 8 years of age (Branstetter 1987, Killam and Parsons 1989, Wintner and Cliff 1996, Carlson et al. 2006). The instantaneous growth rate at maturity (dL/dt_{mat}) varied between regions and ranged from 4.9 cm^{yr-1} for males in the South Atlantic Bight (t_{mat} = 6.7 years) to 12.6 cm^{yr-1} for males in South Africa (t_{mat} = 6 years).

4.4 Discussion

Regional variation in life history traits exists for several species of wide-ranging elasmobranchs (Driggers et al. 2004, Neer and Thompson 2005). The results of this study demonstrate that *C. limbatus* is one such species as its growth characteristics differ substantially on a circumglobal scale. In comparison with length-at-age studies from other regions, *C. limbatus* from Indonesia mature later and attained older ages than their conspecifics. There was also an obvious difference in the maximum lengths of the different populations, with *C. limbatus* from Indonesia growing larger than populations from the USA (Branstetter 1987, Killam and Parsons 1989, Carlson et al. 2006) but were more comparable with those from South Africa (Wintner and Cliff 1996). The L_∞ estimates of *C. limbatus* from Indonesia and South Africa were similar although the maximum ages differed substantially (Wintner and Cliff 1996). Consequently, large differences were found between two populations for the dL/dt_0 and the VBGF growth completion parameter (k) as *C. limbatus* from South Africa reach their L_∞ faster than those from Indonesia. As the age and growth estimates of *C. limbatus* in this study were substantially different to the populations from the USA and South Africa it was determined that using these existing estimates as surrogate data would significantly compromise demographic analyses or stock assessments on the Indonesian population. Therefore, producing age and growth data using individuals from the local Indonesian population was needed to support fisheries management and conservation of this population.

The model estimates produced by the VBGF provided the best fit for both the observed and back-calculation data for *C. limbatus*. Back-calculation techniques were included in the study as longline fisheries can result in length selectivity which is biased towards catching larger individuals (White et al. 2008). Indeed, this may have occurred in this study as individuals between 900 and 1750 mm TL were missing. The VBGF (as well as other growth models) is particularly sensitive to missing data points at either end of the length range as two of its parameters (L_∞ and L_0) are strongly influenced by these data (Haddon 2001). Therefore, a typical consequence when juveniles are missing from length-at-age data is an inflated L_0 estimate, which occurred in this study for male *C. limbatus* when only using the observed length-at-age data. This in turn biases the remaining VBGF parameters (k and L_∞) as a strong correlation exists between the three parameters during the non-linear estimation process (Pilling et al. 2002). Therefore, when the L_0 estimate is inflated in this manner estimates of k will be underestimated (Pardo et al. 2013). However, the inclusion of a small number of juveniles corrected the VBGF model for the females, producing an L_0 estimate which was biologically realistic (White 2007). The same results occurred through the experimental removal of juveniles as the inclusion of a small number of 0+ age class individuals corrected the VBGF model so that it more closely matched the fit of the complete model. This emphasises the sensitivity of the VBGF to the omission of juveniles and highlights that their inclusion will improve the accuracy of the growth models, producing more biologically reasonable results in the same manner as back-calculation. While back-calculation helped overcome the missing male size classes in this study, this exercise serves as useful example that the inclusion of just one to three neonates can significantly improve the accuracy of growth estimates even when sample size is limited. Therefore, in sampling situations where juveniles are not captured due to gear selectivity or other factors, targeted sampling of these individuals outside of the regular sampling methodology, such as in nursery areas, could be highly beneficial.

As the VBGF parameters for the observed length-at-age data for the males were biologically unrealistic, the VBGF for the back-calculation data were considered the most accurate as their L_0 and L_∞ estimates were within range of the known length-at-birth and maximum size of *C. limbatus* from the region (White et al. 2006, White 2007). While these back-calculated growth estimates appear biologically realistic, care must still be taken when including these results in further analyses due to the small sample size of this study. While back-calculation increased the sample size by adding interpolated data – these are not independent and a biased growth curve could still have resulted if the observed data were not representative of the population. However, for the back-calculated data of this study, the L_0 matched empirical length-at-birth measurements and the L_∞ matched the known maximum length for this population – adding credibility to these results despite the limited number of samples.

The VBGF growth estimates for the separate sexes were significantly different for Indonesian *C. limbatus* with females growing larger than males. However, it cannot be determined if this sexual dimorphism is an accurate representation of differences in the population, or if it is an artefact of the small sample size attained in this study. Since there were no male juveniles in the sample this could have led to them producing a larger L_0 than females, while the largest individuals being female could also have resulted in a larger L_∞ than the males. While the presence of sexual dimorphism is not definitive in this study, it was in previous studies where it was confirmed in regions such as South Africa (Wintner and Cliff 1996) and the USA (Killam and Parsons 1989, Carlson et al. 2006) with females also typically growing larger. Sexual dimorphism was also apparent for the age-at-maturity in every region. There was also disparity as to which sex matured earliest between regions as males matured younger in some populations (Branstetter 1987, Killam and Parsons 1989, Wintner and Cliff 1996, Carlson et al. 2006) while females matured younger in others (Carlson et al., 2006; this study).

As many species of elasmobranchs have circumglobal distributions, it is common to compare growth estimates among different regions (Driggers et al. 2004, Neer and Thompson 2005). Consequently, several studies have based their model choice (use of the VBGF, Gompertz, logistic or other model types) on that of previous studies to compare the resulting growth parameters to these populations (Neer and Cailliet 2001, Carlson et al. 2007, Piercy et al. 2007). There have also been instances where studies have performed multi-model approaches only to disregard their *AIC* results and choose a model used in previous studies to facilitate these comparisons (Henningsen and Leaf 2010). The primary argument for doing so is that the growth completion parameters (k, g_{Gom} and $g_{\log}$) of the different models are incomparable. Therefore, if a previous study has used a VBGF model to estimate growth, future authors are reluctant to use Gompertz or logistic models as their growth completion parameters (g_{Gom} and $g_{\log}$) cannot be compared to k for the VBGF. However, this is a poor reason for limiting model choice as none of these parameters represent an empirical growth rate. They can more precisely be defined as curvature parameters for their respective model types. For example, k in the VBGF is a non-biological curvature parameter that represents the rate at which the asymptotic length (L_∞) is reached (Haddon 2001). Therefore, two populations with different maximum sizes can have the same value of k despite having contrasting rates of empirical growth. This occurs as the population with the larger maximum size will grow faster than the population with the smaller maximum size to reach their L_∞ at the same rate. Previous studies on different *C. limbatus* populations demonstrate this as the highest value of k produced for the species was 0.28 yr^{-1} in Florida and in the Gulf of Mexico (Branstetter 1987, Killam and Parsons 1989). However, when the growth curves for *C. limbatus* from different regions are compared to one another it is evident that populations from Florida and in the Gulf of Mexico are not the populations with the fastest growth rate, demonstrating that a higher value of k does not equate to a faster rate of empirical growth.

Instantaneous rates of growth at birth (dL/dt_{L0}) and maturity (dL/dt_{mat}) have previously been used in addition to growth models as they provide an empirical measurement of growth (Thorson and Simpfendorfer 2009, Harry et al. 2010) In this study, these measurements of dL/dt_{L0} and dL/dt_{mat} were calculated for each *C. limbatus* population and used to compare the empirical growth rates to one another. These values for *C. limbatus* corroborate that the populations in Florida and the Gulf of Mexico are not the fastest growing for this species despite having the highest values of k. As these values are calculated from the model length-at-age estimates and not the resulting growth parameters, values of dL/dt_{L0} and dL/dt_{mat} can be calculated from any growth model and can subsequently be compared to other model types. This means that future studies can implement a multi-model approach without concern that the resulting model choice may restrict the comparability to previous studies. Furthermore, as dL/dt_{L0} and dL/dt_{mat} are calculated in mm yr-1, they are biologically relevant values.

Therefore, their use is recommended over the sole use of growth completion parameters to compare the growth of different populations.

As *C. limbatus* from Indonesia live longer and mature later than other regional populations, their life histories are increasingly K-selected in comparison. Subsequently, the proportion of the stock that can be harvested sustainably is likely to be lower than populations that are less K-selected and are also likely to recover more slowly from overfishing (Musick 1999). While management strategies exist that facilitate the sustainable harvest of slow growing species such as *C. limbatus*, these involve limiting the fishing pressure on the older age classes and focusing effort on juvenile or young of the year classes (Simpfendorfer 1999b, Prince 2005). However, the Indonesian fishery predominantly uses longlines which are biased towards catching larger individuals due to hook size selectivity (White et al. 2008). This observation is supported by the samples collected from Indonesia, of which 66% of the individuals caught were mature. In the event that fishing effort cannot be redirected to target more suitable and resilient size and age classes, other management measures will need to be developed to identify and achieve sustainable fishing practices. In order to facilitate these efforts, demographic analyses and stock assessments of the Indonesian *C. limbatus* stock are needed. This study has taken an important step towards facilitating such future assessments by producing accurate growth estimates from the local population.

Chapter 5

Effects of including misidentified sharks in life history analyses: a case study on the Grey Reef Shark *Carcharhinus amblyrhynchos* from Papua New Guinea

5.1 Introduction

Life history information such as growth and maturity are fundamental prerequisites for many demographic and population dynamics models (Cortés et al. 2012). Without life history estimates, demographic assessments can be produced using life history theory, although the estimates will contain higher levels of uncertainty (Dulvy et al. 2014b). Producing accurate life history information is therefore crucial to inform fisheries management and conservation. However, in instances where available life history information has been inaccurate, population declines have occurred through incidental overfishing (Beamish and McFarlane 1995). The production of accurate life history estimates or a quantifiable uncertainty around them is therefore imperative for sustainable fishing and effective population management.

The Grey Reef Shark *Carcharhinus amblyrhynchos* is a medium bodied whaler shark (Family Carcharhinidae) which is reef associated and has a Indo–West and Central Pacific distribution (Last and Stevens 2009). *Carcharhinus amblyrhynchos* are caught in tropical fisheries throughout their range (White 2007, Aneesh Kumar et al. 2015) and are often landed as incidental catch in some commercial fisheries (Liu et al. 2015, Spaet and Berumen 2015). In PNG a dedicated shark long-line fishery existed until July 2014 which developed from the tuna fishery in the 1990s (Kumoru 2003b). *Carcharhinus amblyrhynchos* was a common species caught in this fishery, where they comprised ~11 % of the total catch (Kumoru 2003b). Despite being susceptible to fisheries across much of its range, complete information on life history for *C. amblyrhynchos* is only available from Australia (Stevens and Mcloughlin 1991, Robbins 2006), with some limited data available from Hawaii (Decrosta et al. 1981, Wetherbee et al. 1997) and Indonesia (White 2007). However, as *C. amblyrhynchos* is caught in larger numbers in PNG (Kumoru 2003b), life history information is needed from the local population to form the basis of effective fisheries management and conservation.

Many elasmobranch life history studies have used observer programs as an effective source for collecting life history samples (e.g. Davenport and Stevens 1988, Bishop et al. 2006, Fernandez-Carvalho et al. 2011). However, many tropical fisheries do not have operational observer programs and as a result many reef associated shark species are still data deficient with regards to life history information. Recent studies have started to fill these gaps by providing life history information for reef elasmobranchs through fishery independent sampling – where researchers conducted field work to collect the samples (Robbins 2006, Chin et al. 2013, O'Shea et al. 2013). While these studies are valuable for species that cannot be sampled by other means, they add mortality to the population and are logistically disadvantaged as they cannot match the level of fishing effort that observer programs can sample. Observer programs therefore have several benefits for collecting life history samples including larger sample sizes, shorter sampling time frames, greater spread of samples across size ranges, and greater geographic coverage. The opportunistic use of observer programs to source life history samples can therefore have considerable benefits for species that have previously been difficult to sample.

While observer programs provide several benefits in collecting biological data, an important factor to consider is the accuracy of species identification. When collecting life history samples for sharks, many observer programs require observers to record basic biological information (species, length and sex), record the maturity status of an individual when possible, and remove a section of vertebrae for ageing. While this allows a great amount of information to be collected quickly without the need for storing large volumes of biological samples, only the observer witnesses the whole specimen. Therefore, an important assumption of observer data is that species identification is accurate.

However, realistically some level of error is inherent in observer species identifications and only recently has this been quantified (Tillett et al. 2012). Genetic validation has shown that observer error can be substantial for carcharhinid sharks caught in multi-species fisheries in northern Australia (Tillett et al. 2012). In the northern Australian study, species misidentification occurred at different rates depending on a combination of factors such as species, sex and size (Tillett et al. 2012). The highest misidentification rates (~20%) occurred for *C. limbatus* and *C. tilstoni;* two species that are morphologically similar and known to hybridise (Morgan et al. 2012, Tillett et al. 2012). When using observer sourced samples, these findings raise questions about how often misidentified sharks are unintentionally included in life history analyses and the level of error this introduces into estimates.

Species validation is becoming increasingly feasible due to recent technological advances. Identifying species in the field can be complicated as closely examining features such as dentition or fin morphology can be difficult in field conditions, especially for cryptic or “look-alike” species. However, preserving entire specimens is often not possible for fisheries observers as sharks are typically processed at sea. Recent advances in digital camera technology are beginning to overcome this issue as many “all weather” rugged camera models are now available that survive exposure at sea and can store large numbers of images. This technology facilitates the post-cruise validation of species identifications using photographs taken by fisheries observers at sea. While digital cameras have great potential for species validation *in situ*, genetic analyses in the laboratory are increasingly being used for species identifications. DNA barcoding of the cytochrome c oxidase I (COI) mitochondrial (mtDNA) gene has become an important tool that can rapidly and accurately assist in species identification and can overcome issues such as unknown or poorly defined morphological characteristics that complicate accurate identification of individuals at sea (Ovenden et al. 2015). Due to these advantages, the use of DNA barcoding is becoming increasingly common in fisheries science (Ovenden et al. 2015) and has already been used to validate species identifications for fisheries observer programs (Tillett et al. 2012). Both DNA barcoding and the post-fishing trip inspection of specimen photos provide an opportunity to determine what effects species misidentification might have on life history estimates and ultimately minimise them.

In order to determine the effects of species misidentification in life history analyses, a case study is presented using *C. amblyrhynchos* sampled from the PNG longline fishery. Two types of species validation techniques were used to identify the misidentification rate: 1) diagnostic photographs of the specimens taken on-board by the fisheries observers; and 2) DNA barcoding using the COI gene. This integrated approach of combining genetic and life history analyses allowed the effects of including misidentified individuals in life history studies to be explored.

5.2 Data Analysis

5.2.1 DNA barcoding of tissue samples

Tissue samples for DNA barcoding were excised from the vertebrae for any samples that were identified by NFA observers as *C. amblyrhynchos*. These tissue samples (approximately 150 mg) were excised from the remaining muscle around the vertebrae or from the vertebral chord (nerve tissue) and preserved in 100% analytical-grade ethanol. These samples were sent to CSIRO Oceans & Atmosphere in Hobart where Sharon Appleyard and Madeleine Green conducted DNA barcoding of the tissue samples.

DNA from vertebral chord or muscle samples was extracted using the Wizard® SV Genomic DNA Purification system (Promega, Australia) with starting material of approximately 0.25 g. Tissue extractions were undertaken using SV minicolumns following manufacturer’s instructions (including an overnight digestion at 55°C on an Eppendorf Thermomixer Comfort (Eppendorf, Australia) and the modifications of 400 μg Proteinase K and DNA precipitated in 160 μl nuclease free water. Each DNA sample was quantified on a Nanodrop 8000 UV-Vis Spectrophotometer (Thermo Scientific, USA).

Genetic species identification through barcoding of the COI mtDNA gene was undertaken using the universal Fish-BCL (5’-TCAACYAATCAYAAAGATATYGGCAC-3’) and Fish-BCH (5’-ACTTCYGGGTGRCCRAARAATCA-3’) primers (Baldwin et al. 2008). PCRs were undertaken in 25 μl using GoTaq® Green Master Mix (Promega, USA), Bovine Serum Albumin (Promega, USA), 10 μM primers and DNA quantities of between 8 and 20 ng. PCRs were performed in an Applied

Biosystems GeneAmp® PCR System 9700 (Life Technologies, Thermo Fisher Scientific, USA) with cycling conditions of 94°C × 3 min; 35 cycles of 94°C × 1 min, 50°C × 1 min 30sec, 72°C × 1 min; and a final extension of 72°C × 10 min. PCR products were visualised on 2.5% TAE agarose gels and fragments cleaned using an Agencourt AMPure XP PCR purification kit (Beckman Coulter, Australia) according to the manufacturer's instructions.

PCR products were sequenced bi-directionally using the same primers as in the original PCR, BigDye® Terminator v3.1 Cycle sequencing kit (Life Technologies) and an annealing stage of 50°C × 5 sec across 25 cycles. Cycle sequenced products were cleaned using the CleanSEQ kit (Beckman Coulter) according to the manufacturer's instructions and run on an ABI 3130XL AutoDNA sequencer (Life Technologies).

Forward and reverse sequences (per gene fragment) were assembled into consensus sequences in Geneious® R8.1.4 (Biomatters Ltd Auckland, New Zealand; http://www.geneious.com) using the de novo assembly tool. Consensus sequences were aligned within Geneious using the MUSCLE algorithm and sequence identity was confirmed by using the BLAST module in Geneious (http://blast.ncbi.nlm.nih.gov/Blast.cgi;Megablast) against GenBank (http://www.ncbi.nlm.nih.gov/genbank/). COI sequences were additionally compared to sequences publicly available in the Barcode of Life database (BOLD, http://www.boldsystems.org/index.php/IDS_OpenIdEngine).

5.2.2 Growth modelling

In order to simulate the scenario where misidentified individuals were incidentally included in growth analysis, vertebrae from individuals that were mistakenly identified as *C. amblyrhynchos* were aged concurrently with the verified *C. amblyrhynchos* vertebrae. Neither reader had any knowledge of which individuals had been misidentified nor how many were included.

Growth estimation was carried out on two data sets: 1) with all the individuals identified as *C. amblyrhynchos* in the field and 2) with individuals misidentified as *C. amblyrhynchos* removed. A likelihood ratio test (Kimura 1980) was used to statistically test for coincident curves between the two data sets. The methods outlined in Chapter 3 were then applied to estimate growth parameters and length-at-age estimates using a multi-model approach.

5.2.3 Maturity estimation

Maturity was estimated by fitting logistic ogives to length and age data, as outlined in Chapter 3. These were estimated twice: 1) with all the individuals identified as *C. amblyrhynchos* in the field and 2) with individuals misidentified as *C. amblyrhynchos* removed. A statistical difference between two sets of population maturity estimates was tested for using a likelihood ratio test with a χ^2 distribution using the 'drop1' function in the 'R' program environment (R Core Team 2013).

5.3 Results

5.3.1 Effects of species misidentification on life history estimates

A total of 155 sharks were originally identified as *C. amblyrhynchos* by the on-board fisheries observers. However, 22 of these individuals (14.2 %) were subsequently found to be misidentified and were not *C. amblyrhynchos.* Sixteen of these identification errors (72.2 %) were originally detected by examining the photographs taken by the observers. DNA barcoding corroborated these corrections and also detected an additional six misidentified individuals (Table 5.1). Three of the misidentified individuals were larger than the typical length range for *C. amblyrhynchos* (*c.*190cm TL) (Stevens and Mcloughlin 1991); these larger individuals were detected from the observer photographs (Table 5.1). The species that had been incorrectly identified as *C. amblyrhynchos* were the bull shark (*C. leucas*), common blacktip shark (*C. limbatus*) and silky shark (*C. falciformis*).

Table 5.1: Individuals misidentified as *Carcharhinus amblyrhynchos* by on-board observers

Corrected species ID	**Total Length (cm)**	**Age (Vertebral growth band count)**	**Detected via photograph**	**Detected via DNA barcoding**
Carcharhinus leucas	284	21	Yes	Yes
Carcharhinus limbatus	145	7	Yes	Yes
Carcharhinus falciformis	90	1	No	Yes
Carcharhinus falciformis	92	1	Yes	Yes
Carcharhinus falciformis	95	1	Yes	Yes
Carcharhinus falciformis	95	2	No	Yes
Carcharhinus falciformis	108	5	Yes	Yes
Carcharhinus falciformis	112	5	No	Yes
Carcharhinus falciformis	112	4	Yes	Yes
Carcharhinus falciformis	121	6	Yes	Yes
Carcharhinus falciformis	123	4	No	Yes
Carcharhinus falciformis	124	6	Yes	Yes
Carcharhinus falciformis	127	7	Yes	Yes
Carcharhinus falciformis	127	8	Yes	Yes
Carcharhinus falciformis	137	9	Yes	Yes
Carcharhinus falciformis	146	9	Yes	Yes
Carcharhinus falciformis	149	7	Yes	Yes
Carcharhinus falciformis	150	11	Yes	Yes
Carcharhinus falciformis	170	8	No	Yes
Carcharhinus falciformis	174	5	No	Yes
Carcharhinus falciformis	192	13	Yes	Yes
Carcharhinus falciformis	230	13	Yes	Yes

Likelihood ratio tests determined that the misidentified individuals produced a significantly different growth curve to *C. amblyrhynchos* when they were not removed (VBGF [$df = 3$, $\chi^2 = 20.19$, $p = < 0.0001$]; logistic function [$df = 3$, $\chi^2 = 28.92$, $p = < 0.0001$]; Gompertz function [$df = 3$, $\chi^2 = 27.80$, $p = < 0.0001$]). The L_0 and L_∞ parameter estimates did not resemble empirical length-at-birth or maximum length values and were extremely inflated (Fig. 5.1b). The inclusion of misidentified individuals produced an $\overline{L}_0$ estimate of 105 cm TL which is well outside of the length-at-birth range of *C. amblyrhynchos* (63–72 cm TL) (Stevens and Mcloughlin 1991). However, the greatest amount of error was introduced to the older age ranges of the growth curve (Fig. 5.1b; d). The $\overline{L}_\infty$ estimate with the misidentified individuals included was 5640000 cm TL; a nonsensical value which demonstrated the inability of the model to include anomalous data produced by misidentification. This value was produced as the data was best fit by models that indicated growth increased continuously and therefore did not asymptote (Fig. 5.1b; d). Subsequently all of the growth completion parameters (k, g_{log} and g_{Gom}) were extremely low (Table 5.2). This growth trajectory occurred due to the inclusion of two individuals (230 and 284 cm TL) that were far larger than any of the verified *C. amblyrhynchos* individuals included in this study (Table 5.1).

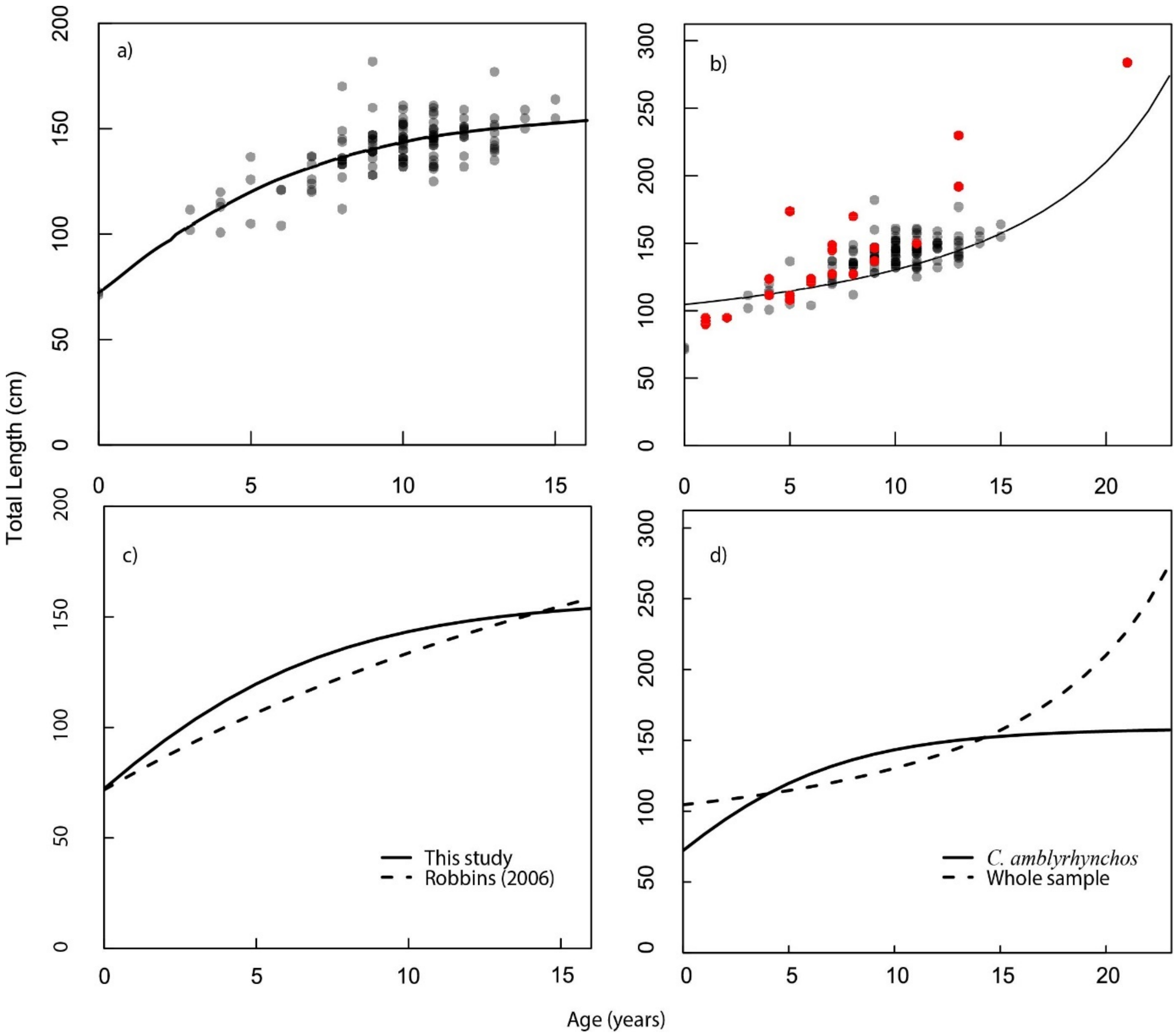

Figure 5.1: Length-at-age curves for: a) *Carcharhinus amblyrhynchos*, b) *Carcharhinus amblyrhynchos* (grey points) with misidentified individuals (red points) included, c) a comparison between *Carcharhinus amblyrhynchos* from PNG (solid line) and northern Australia (Robbins 2006) (dashed line), and d) comparison of curves for *Carcharhinus amblyrhynchos* (solid line) and *Carcharhinus amblyrhynchos* with misidentified individuals included (dashed line). The species of the misidentifications are given in Table 5.1. All curves were fitted using the model averages of the MMI results except for the results from (Robbins 2006) which are the respective VBGF length-at-age estimates. Increasing darkness of grey length-at-age data points represent a higher density of data.

Table 5.2: Summary of model parameters and AIC$_c$ results for the observed length-at-age for *Carcharhinus amblyrhynchos* and *Carcharhinus amblyrhynchos* with misidentified individuals still included

Model	***n***	**AIC$_C$**	**Δ**	***w* (%)**	**L_∞ (± *SE*)**	**L_0 (± *SE*)**	***k* (± *SE*)**	**g_{Gom} (± *SE*)**	**g_{log} (± *SE*)**	***RSE***
*Carcharhinus amblyrhynch*os and misidentified individuals										
VBGF	155	1288.55	5.02	0.07	1.04e+4 (± 4.87e+5)	104 (± 5.69)	5.32e+4 (± 4.87e+5)	-	-	15.2
Logistic	155	1283.53	0.00	0.93	6.10e+6 (± 1.29e+11)	105 (± 4.37)	-	-	0.04 (± 0.02)	14.95
Gompertz	155	1545.85	262.33	0.00	1.27e+5 (± 9.41e+6)	105 (± 10.97)	-	5.93e+3 (± 0.06)	-	34.85
Model average	155	-	-	-	5.64e+6 (± 1.2e+11)	105 (± 4.45)	-	-	-	-
Carcharhinus amblyrhynchos										
VBGF	133	1000.52	0.32	0.30	163 (± 6.27)	71 (± 6.46)	0.15 (± 0.03)	-	-	9.92
Logistic	133	1000.20	0.00	0.35	156 (± 3.77)	73 (± 5.81)	-	-	0.26 (± 0.04)	9.91
Gompertz	133	1000.22	0.02	0.35	158 (± 4.65)	72 (± 6.14)	-	0.21 (± 0.03)	-	9.91
Model average	133	-	-	-	159 (± 5.62)	72 (± 6.20)	-	-	-	-

n is the sample size, *AIC$_C$* is the small-sample bias adjusted form of Akaike's Information Criteria, Δ is the difference in *AIC$_C$* values between models, *w* (%) are the *AIC$_C$* weights, L_∞ is asymptotic length parameter in cm , L_0 is the length-at-birth parameter in cm, *k* is the growth completion parameter in yr-1 for the VBGF, g is the growth parameter for Logistic and Gompertz functions (but is incomparable between the two), *SE* is the standard error of the adjacent parameter and *RSE* is the residual standard error of the model.

The maturity estimates were less affected than the growth estimates when misidentified individuals were included (Fig. 5.2). Likelihood ratio tests determined that failing to remove misidentified individuals altered the maturity ogives for males (Length [$df = 1$, $\chi^2 = 7.66$, $p = 0.005$] and age [$df = 1$, $\chi^2 = 4.03$, $p = 0.045$]) but not for females (Length [$df = 1$, $\chi^2 = 0.26$, $p = 0.61$]; age [$df = 1$, $\chi^2 = 0.03$, $p = 0.85$]). However, the l_{50} and a_{50} estimates for males with misidentified individuals included were 123.3cm TL ($SE = 3.12$) and 5.5 years ($SE = 0.85$) respectively which were only marginally different to confirmed *C. amblyrhynchos*. The l_{50} and a_{50} estimates for females when misidentified individuals were included were 138.6 cm TL ($SE = 2.96$) and 9.5 years ($SE = 0.52$) respectively. Despite there being no significant difference between maturity ogives for females when misidentified individuals were included, the l_{50} and a_{50} estimates were more disparate than the males.

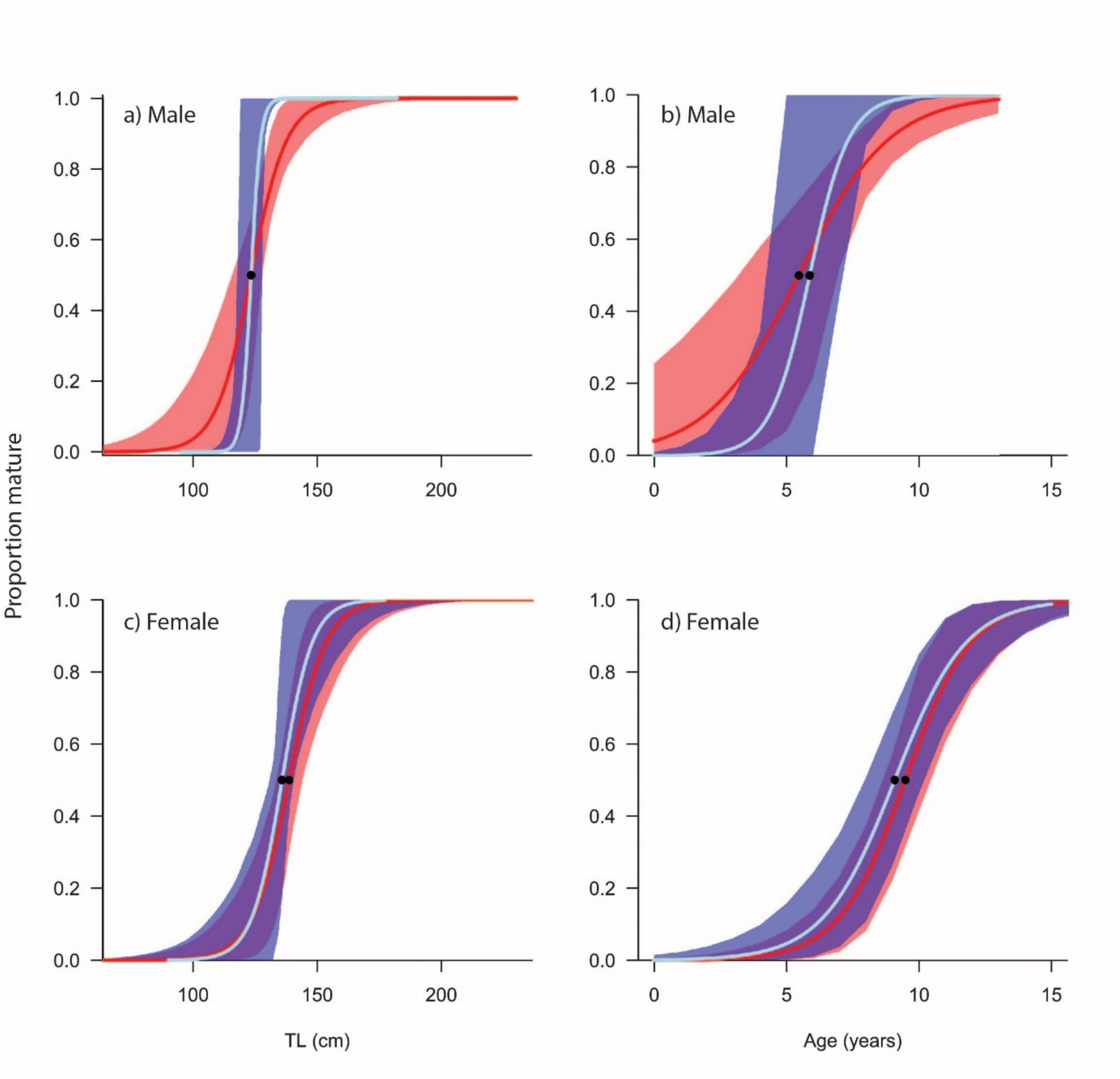

Figure 5.2: Length- and age-at maturity ogives for: (a, b) male and (c, d) female *Carcharhinus amblyrhynchos* (light blue line) with 95% confidence intervals (blue area). The maturity ogives for *Carcharhinus amblyrhynchos* when misidentified individuals were included with 95% confidence intervals are shown by the red line and red area respectively for comparison.

5.3.2 Life history of *C. amblyrhynchos*

The confirmed number of *C. amblyrhynchos* used in the analyses was 133. This sample consisted of 90 males (71–182 cm TL) and 43 females (102–177 cm TL). The age ranges for males and females were 0–13 and 3–15 years, respectively. The *PA* ± 1 year was 46% with no systematic bias detected by Bowker's test of symmetry ($df = 39$, $\chi^2 = 43.15$, $p = 0.30$). Precision was greatest at younger age classes (< 5 years) (Fig. 5.3). The *APE* and *CV* were 9.46% and 13.38% respectively which are typical for long lived species that have a greater number of growth bands to read (Campana 2001).

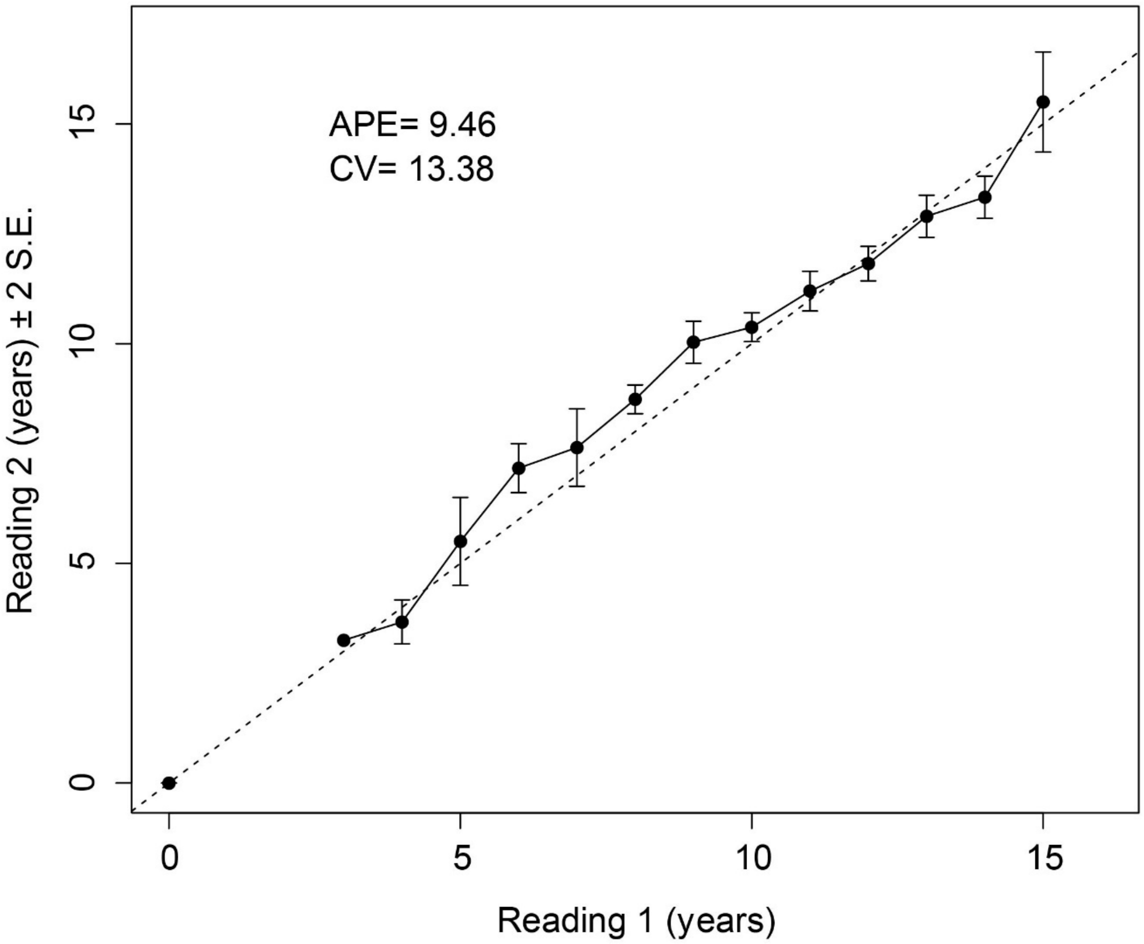

Figure 5.3: Age-bias plot for *Carcharhinus amblyrhynchos* incorporating the age-specific agreements between Readers 1 and 2. Mean age-specific agreements ± 2 standard errors are plotted along a 1:1 equivalence line.

Likelihood ratio tests determined that there was no significant difference between male and female growth curves for any candidate model (VBGF [$df = 3$, $\chi^2 = 1.92$, $p = 0.58$]; logistic function [$df = 3$, $\chi^2 = 2.10$, $p = 0.55$]; Gompertz function [$df = 3$, $\chi^2 = 2.05$, $p = 0.56$]). Therefore, length-at-age estimates were produced with the sexes combined (Fig. 5.1a). All three candidate models produced similar length-at-age estimates that were biologically reasonable; with estimate ranges being $L_0 = 71$-73 cm TL and $L_\infty = 156 – 163$ cm TL (Table 5.2). Subsequently, the residual standard error (*RSE*) was similar between all three candidate models and *AICc* determined that they provided equal support for the data (Table 5.2). Therefore, MMI was used to produce model averaged length-at-age estimates (Table 5.3). The model averaged $\bar{L}_0$ and $\bar{L}_\infty$ were 72 cm TL and 159 cm TL respectively (Table 5.2). Length-at-age estimates for *C. amblyrhynchos* from this study (PNG) were similar to estimates from northern Australia (Robbins 2006) (Fig. 5.1c).

Table 5.3: Model averaged total length-at-age estimates for *Carcharhinus amblyrhynchos* over the age range included in this study

Age	**Model averaged TL estimate (cm)**
0	72
1	84
2	94
3	104
4	112
5	120
6	126
7	132
8	136
9	140
10	143
11	146
12	148
13	150
14	152
15	153
16	154

Male and female *C. amblyrhynchos* mature at different lengths and ages. The maximum likelihood estimates of l_{50} and a_{50} predicted for males were 123 cm TL (*SE* = 2.9) and 5.9 years (*SE* = 2.03) respectively (Fig. 5.2a; b). Female estimates of l_{50} and a_{50} were predicted as 136 cm TL (*SE* = 0.64) and 9.1 years (*SE* = 0.65), respectively, demonstrating that females mature at greater lengths and older ages than males (Fig.5.2c; d).

5.4 Discussion

The misidentification of sharks by observers can have significant effects on the results of life history studies. The inclusion of individuals of species other than *C. amblyrhynchos* added substantial error to the life history analyses from growth models. The greatest error was introduced to the growth analysis which produced inaccurate length-at-age and parameter estimates. In contrast, the amount of error introduced to the maturity ogive analysis was marginal relative to the growth analysis, demonstrating that error can be variable between life history parameters. The maturity estimates (l_{50} and a$_{50}$) produced for both sexes when misidentified individuals were not removed were similar to those of *C. amblyrhynchos*. However, despite producing biologically realistic l_{50} and a_{50} estimates, including misidentified individuals produced male maturity ogives that were significantly different from those of *C. amblyrhynchos*. These maturity ogives along with the length-at-age estimates would have introduced substantial error to future demographic analyses had species identifications not been verified. Consequently, failing to use accurately identified individuals would have precluded this life history information from being usable due to the obvious magnitude of its error.

Regional variability in growth can occur for carcharhinid species (Chapter 4). *Carcharhinus amblyrhynchos* from PNG grows slightly faster than the northern Australian population, although the length-at-birth and the lengths at older ages are similar between the two populations (Robbins 2006). However, no sexual dimorphism in growth curves occurred for *C. amblyrhynchos* in this study nor from northern Australia (Robbins 2006). Additionally, females matured at greater lengths and older ages than males for both populations, a trait typical of many carcharhinid species (e.g. Hall et al. 2012, Chin et al. 2013). In this study females matured three years older than males which is a relatively large difference. However, this was caused as maturity occurred for both sexes at a length where growth began to asymptote. Therefore, while the age difference was three years apart, the length difference was only 13cm TL. Validation techniques such as marginal increment analysis and mark and recapture were precluded for this study. However, annual growth band deposition is likely based on partial results from validation attempts in northern Australia (Robbins 2006). In the PNG population, *C. amblyrhynchos* were aged to a maximum of 15 years which was younger than in northern Australia (19 years) (Robbins 2006). This is likely an artefact of the length-dependent mortality of the PNG population by the dome-shaped selectivity of longline fishing. As increased adult mortality prevents individuals from reaching maximum age, these individuals are often rarer in fished populations and are under-represented in stock assessments (Taylor and Methot 2013).

This study has shown that substantial error may be introduced when misidentified individuals are unknowingly included in life history analyses. The misidentification rate detected in this study for *C. amblyrhynchos* is similar to the largest misidentification rate quantified in the northern Australia observer program (Tillett et al. 2012). Therefore, this study likely demonstrates the full impact of species misidentification on subsequent life history analyses. The severity of this impact was magnified by the inclusion of misidentified individuals that were far larger and older than verified *C. amblyrhynchos* individuals. As growth curves are fitted by minimising the sum of squared residuals, they are strongly influenced by the oldest and youngest data points in the sample (Haddon 2001). Therefore, the inclusion of two misidentified individuals that had disparate length-at-ages to *C. amblyrhynchos* inflated the L_∞ estimate of the candidate growth models. As growth parameters co-vary with one another (Pilling et al. 2002) an inflated L_∞ estimate also caused an overestimated L_0 parameter. The maturity analyses were not influenced as strongly by these misidentifications as sex-specific ogives meant fewer misidentifications were included in each sample. Further as the two largest misidentified individuals were both males, the female maturity ogive was therefore unaffected. Despite minimal error added to the maturity parameters for males, the shape of the ogive was still inaccurate with these misidentifications included. Therefore, the greatest amount of error will be added to life history estimates when misidentified individuals that have length-at-ages which are substantially larger than the true population are incidentally included.

When life history data include outliers, an argument could be made for removing potentially spurious data points. However, removing these individuals from the data without verifying their identity is poor practice. In this study, a *C. leucas* individual was identified as *C. amblyrhynchos* with a length of 284 cm TL; a value far larger than any other individual in the sample. However, there are confirmed records of *C. amblyrhynchos* that were larger than 250 cm TL (Compagno 1984b) despite individuals rarely exceeding 190 cm TL (Last and Stevens 2009). Therefore, removing this large *C. leucas* individual from the sample could have potentially removed an individual from an under-represented demographic of the population. In reality *C. amblyrhynchos* individuals that reach this maximum size would likely be older than a comparably sized *C. leucas* individual. Therefore, a growth curve produced with *c.*250 cm TL *C. amblyrhynchos* individuals would not resemble the inaccurate growth curve produced with misidentified individuals in this study. This situation demonstrates that removing supposedly spurious data points should not be a valid option without a reasonable justification.

The recent advancements in genetic techniques means that they are now an important tool in fisheries science (Ovenden et al. 2015). DNA barcoding detected all of the species misidentifications in this study; avoiding the estimation of inaccurate life history parameters. However, the diagnostic images taken by the observers were also an important resource. While they did not detect all of the species misidentifications, the post cruise inspection of images detected the majority of them; including the two outliers that introduced the majority of the error to the growth curve. In a number of instances, some observers took multiple diagnostic images for individuals whose identities were uncertain in order to maximise their identification accuracy. Therefore, providing the observers with cameras not only allowed misidentifications to be detected (in a cost efficient way) but also meant that observers were more vigilant for potential misidentifications. The presence of misidentifications in observer datasets also highlights the need for improved regional species identification guides in many instances, particularly in developing nations.

Genetic analyses are the only option for determining species identifications when poorly resolved images or only parts of an animal (e.g. fin clips or fillets) are available. However, the cost of such an approach means that the incorporation of DNA barcoding into any life history analyses which emanate from observer programs can be cost prohibitive and not always a realistic tool. In contrast, images are a cost effective means for species identifications (particularly from field observations) as long as the image resolution is suitable and the correct lateral view of the animal (with diagnostic features) are taken. Providing observers with cameras so that they can take diagnostic photographs of each specimen (or at least those to be used in subsequent life history analyses) should be considered a feasible addition to observer program sampling methodologies. Such an approach would be especially beneficial for studies that focus on species that are morphologically similar to others and which are likely to be misidentified; genetic validation however still provides the greatest species resolution (Tillett et al. 2012). By verifying species identifications, accurate data is available to form the basis of life history information and demographic estimates on which informed fishery and population management can be based.

Chapter 6

Life history of the silvertip shark *Carcharhinus albimarginatus* from Papua New Guinea

6.1 Introduction

The silvertip shark, *Carcharhinus albimarginatus* is one of the largest reef associated shark species in the Indo-Pacific (Last and Stevens 2009). It is highly mobile in comparison to other reef associated shark species (Espinoza et al. 2015b) and is known to spend time in deeper pelagic waters near drop offs (Forster et al. 1970, Bond et al. 2015). Despite its wide distribution, *C. albimarginatus* has been poorly studied and we know little of its life history and population status (Espinoza et al. 2015a, Osgood and Baum 2015). Records suggest that *C. albimarginatus* has a wide-ranging, but fragmented distribution across the tropical Indo–Pacific (Bass et al. 1973, Ebert et al. 2013). However, little to no information is available regarding abundances and/or fisheries interactions from any part of its range. Recent studies have examined the habitat use and movement of *C. albimarginatus*, providing useful information about how marine parks may contribute to the species' management and conservation (Bond et al. 2015, Espinoza et al. 2015a, b). However, very little life history information is available for *C. albimarginatus* (White 2007), precluding accurate population assessments from being undertaken.

Carcharhinus albimarginatus are born at 70 – 80 cm and can reach a maximum total length (TL) of 275 cm (Last and Stevens 2009). No length-at-age estimates are available, although a tagging study in the western Pacific Ocean determined growth to be fairly slow (Stevens 1984). According to the limited information available, this species has a gestation period of *c.* 12 months and has litter sizes of 1 – 11 pups with a mean of 6 (Wheeler 1962, Bass et al. 1973). The length-at-maturity of *C. albimarginatus* is poorly understood as mature females have rarely been sampled (Stevens 1984, White 2007). Based on the limited information available, males and females are estimated to mature between 160 – 180 cm TL and 160 – 199 cm TL, respectively (Ebert et al. 2013).

Carcharhinus albimarginatus are caught in longline, subsistence and artisanal fisheries in PNG. Until July 2014, a dedicated shark longline fishery operated in the Bismarck and Solomon Seas of PNG (Kumoru 2003b). As some of the longline vessels operated in pelagic waters adjacent to coral reefs, *C. albimarginatus* were caught regularly (Kumoru 2003b). While they were not one of the main species caught by the shark longline fishery, *C. albimarginatus* composed ~6% of the annual catch prior to 2002 (Kumoru 2003b, a). However, after the enactment of a Shark Longline Management Plan in 2003, their catch had dropped markedly to <1% by 2007 (Rose 2008). Due to the paucity of data from the PNG region, the cause of this catch decline is unknown. Catches of *C. albimarginatus* were region specific with the majority of the catch coming from the Bismarck Sea in northern PNG (Kumoru 2003b). It's therefore, unclear as to whether catch rates declined post 2003 as a result of unsustainable fishing, or a redistribution of effort away from the areas where *C. albimarginatus* were caught. If population declines have occurred, the recent closure of the shark longline fishery now provides opportunity for *C. albimarginatus* to recover.

The National Fisheries Authority (NFA) of PNG has identified a need to develop better fisheries management practices, underpinned by increased knowledge of the key species being exploited. In order to develop these practices, basic life history information such as age, growth and maturity are required to form the basis of population assessments. *Carcharhinus albimarginatus* is caught by several fisheries in PNG waters, including coastal artisanal fisheries. The main aim of this study was to determine the life history characteristics of *C. albimarginatus* in PNG and provide this information towards future demographic assessments.

6.2 Data Analysis

6.2.1 Growth estimation

Growth was estimated using vertebral analysis, back-calculation and a multi-model approach, as outlined in Chapter 3.

6.2.2 Rosa Lee’s phenomenon

An assumption of the Dahl Lea direct proportions method is that there is a linear relationship between L_c and CR_c. This was tested by performing a linear regression between these two measurements.

Rosa Lee’s phenomenon can occur when using back-calculation techniques as some fisheries will selectively harvest the fastest growing individuals. Therefore, the individuals that survive to maximum size will provide slower back-calculated length-at-age estimates than those of the true population (Lee 1912, Ricker 1969). To determine whether Rosa Lee’s phenomenon occurred in the present study, the average radius of each growth band was calculated for each age class to determine if differences in band deposition (and therefore growth) occurred for older individuals (Walker et al. 1998). A repeated-measures ANOVA was applied to determine if a significant difference occurred across ages-at-capture.

6.2.3 Maturity estimation

Maturity was estimated for length and age using logistic ogives, as outlined in Chapter 3.

6.3 Results

6.3.1 Growth estimation

The sample consisted of 48 *C. albimarginatus*, which included 28 males (95 – 219 cm TL) and 20 females (116 – 250 cm TL). Male ages ranged between 0 – 18 years and females between 3 – 18 years. The *APE* and *CV* of the age estimates were 17.2 and 24.4% respectively. The *PA* ± 1 year was 24.5% with age disagreements in age estimates occurring increasingly with age (Table 6.1). These differences occurred as the growth band pairs were poorly defined throughout the centrum regardless of centrum radius. Therefore, ageing differences occurred with Reader 2 consistently estimating ages that were lower than Reader 1 (Fig. 6.1). Additionally, growth band pairs were compressed at the edges of larger individuals suggesting a cessation in formation. This growth band compression meant that the largest ageing discrepancies occurred for the largest individuals in the sample (Table 6.1; Fig. 6.1). However, this discrepancy was overcome during the consensus reads with no individuals requiring omission from the growth analyses. Visual inspection of the growth curve indicates that the consensus reads show little variation either side of the growth curve (Fig. 6.2a).

Table 6.1: Percent agreement (*PA*) and percent agreement ± 1 year (*PA*± 1) between growth band readers for *Carcharhinus albimarginatus* divided into 10 cm TL classes

TL class (cm)	**no. read**	**no. agreed**	**no. agreed ± 1 year**	***PA***	***PA* ± 1**
90-100	1	1	1	100	100
110-120	1	0	0	0	0
120-130	4	1	2	25	50
130-140	2	1	1	50	50
140-150	3	0	1	0	33.34
150-160	7	0	1	0	14.29
160-170	2	0	0	0	0
170-180	6	0	1	0	16.67
180-190	6	1	2	16.67	33.34
190-200	5	1	1	20	20
200-210	5	0	1	0	20
210-220	4	0	0	0	0
220-230	1	0	0	0	0
230-240	1	0	1	0	100
240-250	1	0	0	0	0
n	49	5	12	-	-
Percent agreement	-	-	-	10.20	24.49

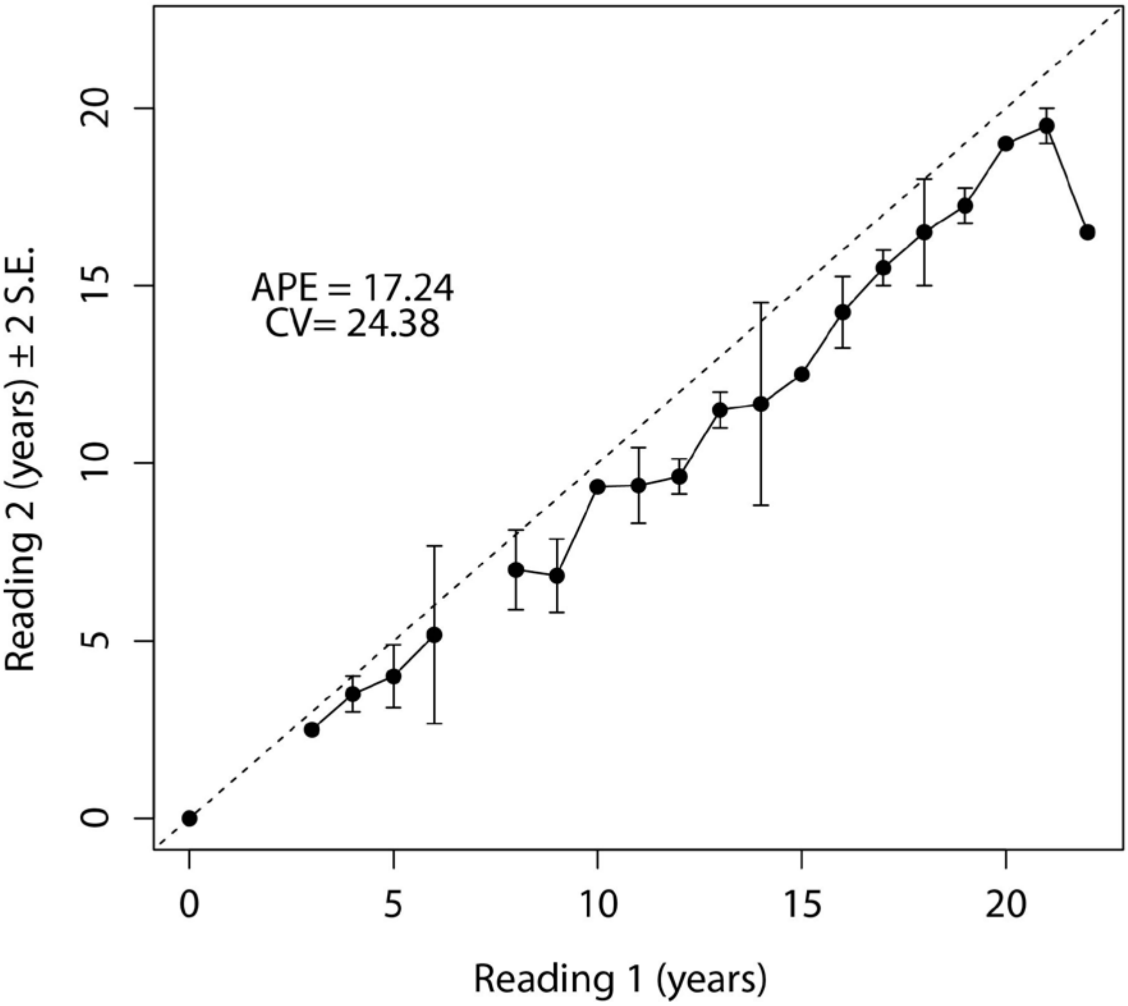

Figure 6.1: Age-bias plot for *Carcharhinus albimarginatus* incorporating the age-specific agreements between Readers 1 and 2. Mean age-specific agreements ± 2 standard errors are plotted along a 1:1 equivalence line.

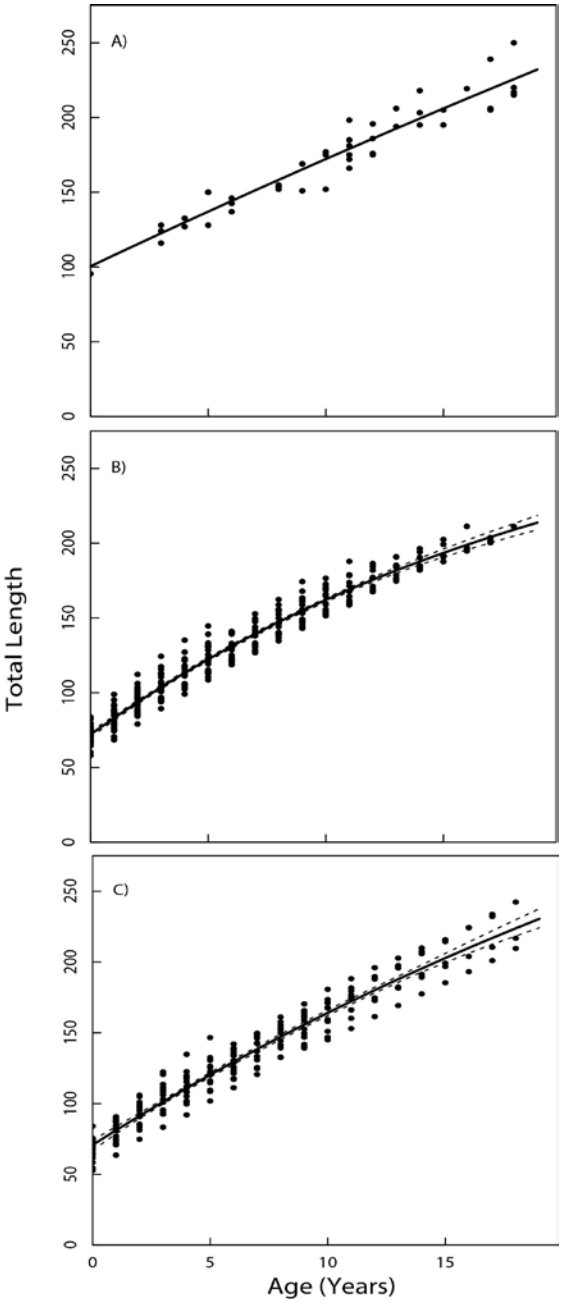

Figure 6.2: Length-at-age curves for *Carcharhinus albimarginatus.* A) the observed data for sexes combined, B) the back-calculated data for males and C) the back-calculated data for females. Likelihood ratio tests identified sexual dimorphism in growth for the back-calculated data but not the observed data. Growth curve A) was predicted using MMI results as all three model candidates performed similarly for the observed data with sexes combined. Growth curves B) and C) were both predicted from the VBGF parameters as this model had w > 0.9 for both males and females for the back-calculated data. The dashed line represents bootstrapped 95% confidence intervals for the VBGF estimates. 95% confidence intervals are not applicable for MMI results.

No significant difference between the sexes was detected (likelihood ratio test using the observed data; VBGF [$df = 3$, $\chi^2 = 6.55$, $p = 0.08$]; Logistic [$df = 3$, $\chi^2 = 7.6$, $p = 0.055$]; Gompertz [$df = 3$, $\chi^2 = 7.79$, $p = 0.051$]). Therefore, a growth curve was produced with the sexes combined (Fig. 6.2a). All three candidate models provided equivalent w for the observed data (Table 6.2). Therefore, MMI was used to provide model averaged length-at-age, $\bar{L}_\infty$ and $\bar{L}_0$ estimates. These estimates were $\bar{L}_0$= 101.9 cm TL and $\bar{L}_\infty$= 598.7 cm TL. A large $\bar{L}_\infty$ was not unexpected as the growth curve lacked a clear asymptote. Therefore $\bar{L}_\infty$ was in this instance not equivalent to maximum size as it is often considered. However, a $\bar{L}_0$ value of 101.9 cm TL was considerably larger than empirical length-at-birth estimates of 70 – 80 cm TL (Last and Stevens 2009). Therefore, the growth curve of the observed data lacked clear biological realism and required back-calculation techniques to supplement the observed data and correct for the low number of juveniles in the sample that caused an overestimated $\bar{L}_0$ value.

Table 6.2: Summary of model parameters and AIC_c results for the observed length-at-age and back-calculated data for *Carcharhinus albimarginatus*. Model parameters were produced for separate sexes for the back-calculated data as sexual dimorphism in growth was determined by likelihood ratio tests. MMI was used to produce model averaged L_∞ and L_0 estimates for the observed data due to similar w. This was not required for the back-calculated data as the VBGF had $w > 0.9$.

Sex	**Model**	***n***	**AIC$_C$**	**Δ**	***w* (%)**	**L_∞ (± *SE*)**	**L_0 (± *SE*)**	***k* (± *SE*)**	**g_{Gom} (± *SE*)**	**g_{log} (± *SE*)**	***RSE***
						Observed data					
Combined	VBGF	48	365.75	0.00	0.35	1044.5 (± 2015.9)	100.5 (± 6.35)	0.01 (± 0.02)	-	-	10.32
	Logistic	48	365.94	0.19	0.32	319.58 (± 57.16)	103.25 (± 5.2)	-	-	0.09 (± 0.02)	10.34
	Gompertz	48	365.85	0.10	0.33	397.1 (± 127.9)	103.3 (± 5.2)	-	0.05 (± 0.02)	-	10.33
	Model average	-	-	-	-	598.7 (±891.5)	101.9 (± 5.9)	-	-	-	-
						Back-calculated					
Males	VBGF	300	2081.69	0.00	0.92	311.3 (± 20.7)	72.1 (± 1.0)	0.04 (± 0.00)	-	-	7.79
	Logistic	300	2095.55	13.85	0.00	220.6 (± 4.5)	75.0 (± 0.9)	-	-	0.17 (± 0.00)	7.97
	Gompertz	300	2086.45	4.75	0.08	242.8 (± 7.3)	73.6 (± 1.0)	-	0.11 (± 0.00)	-	7.85
Females	VBGF	209	1571.59	0.00	0.93	497.9 (± 101.2)	70.8 (± 1.6)	0.02 (± 0.00)	-	-	10.26
	Logistic	209	1582.64	11.05	0.00	256.7 (± 9.8)	74.3 (± 1.4)	-	-	0.14 (± 0.00)	10.54
	Gompertz	209	1576.49	4.90	0.07	297.8 (± 18.1)	72.6 (± 1.5)	-	0.08 (± 0.00)	-	10.39

n is the sample size, AIC_C is the small-sample bias adjusted form of Akaike's Information Criteria, Δ is the difference in AIC_C values between models, w (%) are the AIC_C weights, L_∞ is asymptotic length parameter in cm , L_0 is the length-at-birth parameter in cm, k is the growth completion parameter in yr-1 for the VBGF, g is the growth parameter for Logistic and Gompertz functions (but is incomparable between the two), *SE* is the standard error of the adjacent parameter and *RSE* is the residual standard error of the model.

A linear relationship was determined between L_c and CR_c (Fig. 6.3). Therefore, the Dahl Lea direct proportions technique was appropriate for this species. Using the back calculated data, the likelihood ratio test revealed a significant difference between the growth of males and females (VBGF [$df = 3$, $\chi^2 = 22.86$, $p = < 0.001$]; Logistic [$df = 3$, $\chi^2 = 26.35$, $p = < 0.001$]; Gompertz [$df = 3$, $\chi^2 = 24.64$, $p = < 0.001$]). Therefore, separate growth curves were produced for males and females (Fig. 6.2 b, c). The VBGF provided the best fit and had a $w > 0.9$ for both sexes (Table 6.2). Therefore, MMI was not necessary and estimates of longevity were calculated as 27.4 years for males and 32.2 years for females. The VBGF L_0 and k estimates were both similar for males and females (Table 6.2). However, females had a much larger L_∞ (497.9 cm TL) in comparison to the males (311.3 cm TL). The high VBGF L_∞ value produced for females is far larger than their reported maximum size of 275 cm TL (Last and Stevens 2009). The narrow confidence intervals indicate that the model has high precision (Fig. 6.2c), as does the low standard error (*S.E*) of the L_0 and k parameters. The *S.E* was inflated for the L_∞ parameter as the theoretical age that the species would reach to achieve it lies too far outside of the data. Therefore, it does not represent low precision for the growth curve but instead identifies the lack of asymptotic growth due to an absence of maximum age individuals.

There was no significant difference in the distance between growth band pairs for different ages-at-capture ($df = 1$, $F = 2.543$, $p = 0.112$). While some variation occurred at certain ages, this was negligible and likely caused by a low number of individuals in those age classes (Fig. 6.4). These results demonstrate that Rosa Lee's phenomenon did not occur in this study.

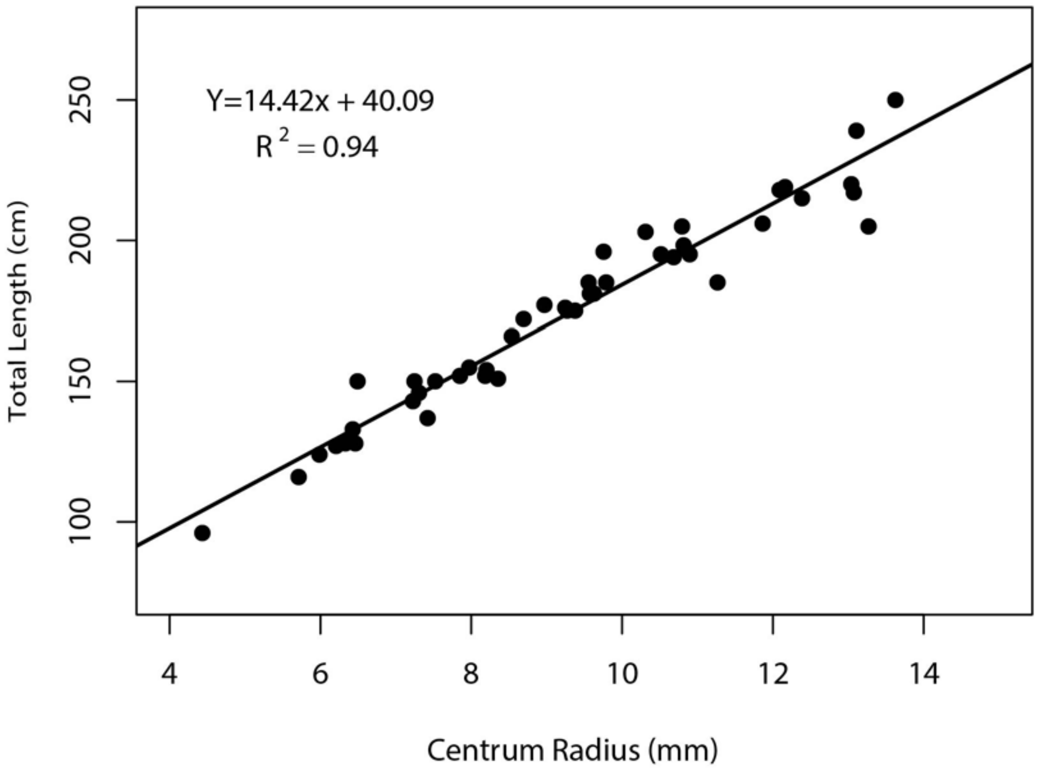

Figure 6.3: Relationship between centrum radius (CR_c) and total length (TL) for *Carcharhinus albimarginatus* (TL = 14.42 CR_c + 40.09, R^2 = 0.94.4, df = 43, $p < 0.001$).

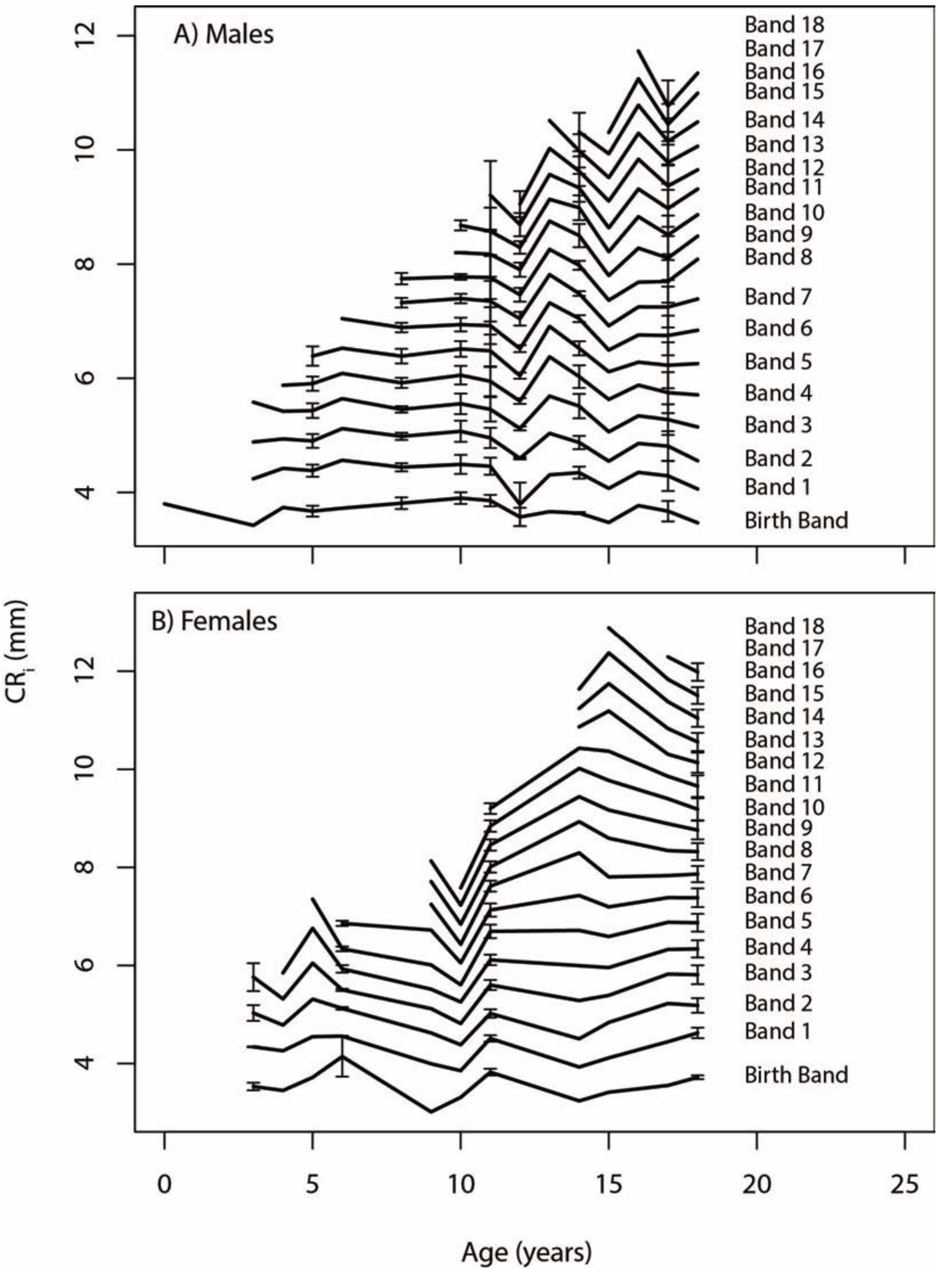

Figure 6.4: Mean growth band radius with S.E (CR_i) for each age-at-capture of A) male and B) Female *Carcharhinus albimarginatus*.

6.3.2 Maturity estimation

Male and female *C. albimarginatus* mature at different ages and lengths. The maximum likelihood estimates of l_{50} and A_{50} for males were 174.7 cm TL (*S.E* ± 1.8 cm TL) and 10.5 years old (*S.E* ± 0.8 years) (Fig. 6.5a; c). Female estimates of l_{50} and A_{50} were 208.9 cm TL (*SE* ± 6.9 cm TL) and 14.8 years (*SE* ± 1.3 years) respectively, identifying that females mature at greater lengths and older ages than males (Fig. 6. 5b; d). Both l_{50} values resemble previously estimated values of 170 cm TL for males and 195 cm TL for females (Last and Stevens 2009).

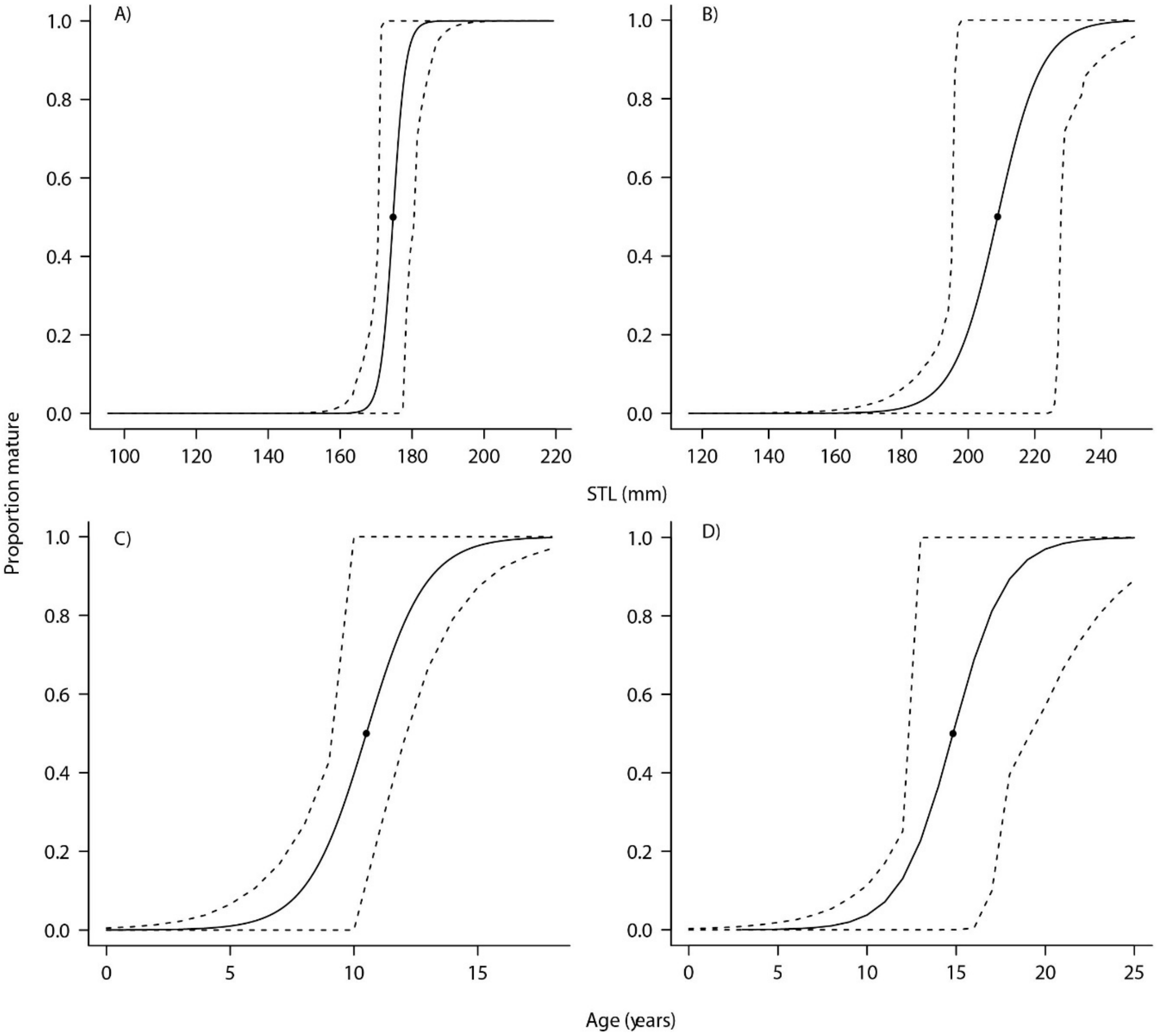

Figure 6.5: Length- and age-at maturity ogives for male (A, C) and female (B, D) *Carcharhinus albimarginatus*. Black point indicates l50 and A50 respectively and the dashed lines represent bootstrapped 95% confidence intervals.

6.4 Discussion

Carcharhinus albimarginatus had been poorly studied in comparison to many other species of reef associated sharks (Osgood and Baum 2015) and consequently little was known about many aspects of its biology (White 2007). The life history estimates presented in this study provide important foundations for future population assessments and the development of management and conservation strategies. These estimates indicate that *C. albimarginatus* grows slowly and matures late in comparison to other carcharhinid species as had previously been suspected (Stevens 1984). Asymptotic growth was not observed, suggesting that either maximum age has been underestimated or that maximum age individuals were not included in the sample – a scenario often encountered with large shark species (Cailliet et al. 1985, Natanson et al. 1995, Simpfendorfer et al. 2002). This study provides the most robust maturity estimates produced for the species so far – especially for females. However, the late age-at-maturity for females also suggests the maximum age has been underestimated. This was caused by age underestimation or a lack of maximum age individuals in the sample.

The application of back-calculation techniques produced length-at-age estimates that better modelled the early growth of *C. albimarginatus*. The observed data lacked young of the year (YOY) individuals which meant that L_0 was overestimated by all three candidate models and subsequently the MMI. This occurs as growth models are most sensitive to the smallest and largest individuals in the sample (Haddon 2001). Therefore, when YOY are missing, the growth curve will overestimate L_0 and hence under-estimate the growth completion parameters (k, g_{log} and g_{Gom}). Recent research has shown that as few as five YOY individuals are sufficient to overcome this issue (Chapter 4). These individuals do not necessarily need to be aged using vertebral analysis, so long as they can be confirmed as YOY by unhealed umbilical scars (Bishop et al. 2006). However, the length selective nature of many fisheries means that YOY individuals can be difficult to sample either because of gear selectivity or that they do not occur in the areas being fished (Gwinn et al. 2010). In this study, young juveniles (ages 0 – 3) were not caught by the fishery and therefore, the application of back-calculation techniques was necessary to account for these missing YOY individuals for both sexes.

Back-calculation techniques must be used with caution when applied to exploited populations due to the potential effects of Rosa Lee's Phenomenon (Lee 1912; Ricker 1969; Walker et al. 1998). This phenomenon can introduce error to back-calculation estimates as some fisheries selectively remove the fastest growing individuals from the population (Walker et al. 1998). When this occurs, slow growing individuals have a greater chance of reaching larger sizes and can bias results when included in back-calculation (Lee 1912). Furthermore, back-calculation can introduce error into length-at-age estimates as it adds interpolated data rather than increasing the sample size. As this interpolated data is not independent, small ageing errors can potentially be magnified through back-calculation. In this study, the back-calculated data provided similar length estimates to the corresponding age-classes in the observed data. This demonstrates that there were no gross errors in the back-calculation estimates, although it should be noted that small amounts of bias cannot be detected in this approach (Francis 1990). In addition, the L_0 estimate produced by the back-calculation matched empirical length-at-birth estimates for the species (Last and Stevens 2009) – demonstrating realistic values. The presence of Rosa Lee's phenomenon was tested in this study using the method of Walker et al. (1998) which compared the distance between growth bands of sharks caught at different ages. A lack of differentiation in the growth of older and younger sharks demonstrated that Rosa Lee's phenomenon was not present in this study. Therefore, the use of back-calculation was appropriate as neither biased estimates nor Rosa Lee's Phenomenon occurred.

The VBGF best fitted the back-calculated data. Multi-model inference is an approach that can improve final growth estimates by avoiding the use of an inappropriate model *a priori* (Katsanevakis 2006, Katsanevakis and Maravelias 2008). However, MMI is not necessary when an individual growth function receives an *AIC w* of > 0.9 (Katsanevakis and Maravelias 2008). This occurred for both the male and female growth curves for the back-calculated data with the VBGF selected for both sexes. However, for the observed data, the three candidate models produced equal *w* and therefore MMI was used. It is not unusual for MMI to be necessary for observed data but not required when the same sample is back-calculated. This occurs as back-calculation is required most often when sample sizes are small (Smart et al. 2013). However, when the sample is small, all candidate models will often provide similar fits as there are insufficient data for them to attain their divergent shapes (Chapter 2). Once interpolated data are added through back-calculation, the sample size is increased and individual candidate models can assume their individual shapes. In this instance the VBGF provided a better fit than the logistic and Gompertz functions. Therefore, even though a multi-model approach was not required in this case; greater confidence can be placed on the estimates of the VBGF as alternate growth functions have been applied and rejected.

The VBGF model estimated that males live until *c.* 27 years old, and females until *c*. 32 years old. While *C. albimarginatus* were aged to a maximum of 18 years by directly counting vertebral rings, these results were likely underestimates. Larger individuals showed signs of growth band compression – where the most recent growth bands in older individuals were laid close together, poorly defined and difficult to distinguish. *Carcharhinus albimarginatus* may cease to lay annual growth bands past a certain age due to insufficient growth to produce discernible growth bands. This has been documented in numerous shark species suggesting that growth band deposition can in many instances be ontogenetic (Cailliet 2015). For example, *Lamna nasus* have been shown to live almost twice as long as was estimated from vertebral analysis (Francis et al. 2007). In the present study, longevity estimates were calculated for *C. albimarginatus* using parameters from the VBGF. These estimates (27.4 and 32.2 years for males and females, respectively) appear far more reasonable than those derived from direct vertebral counts as they are consistent with the longevity of similar sized species (Francis et al. 2007). This uncertainty in longevity should be accounted for when conducting demographic analyses by running multiple scenarios where longevity is varied. The length-at-age estimates presented here remain valid, although they only range from 0-18 and represent a probably incomplete growth curve due to the absence or under-aging of maximum age individuals.

The results of the VBGF show that *C. albimarginatus* is a slow growing species with k values that were similar to other large whaler sharks such as the *C. plumbeus* ($k = 0.046$) (Casey and Natanson 1992) and *C. obscurus* ($k = 0.038$) (Natanson et al. 1995). The values of k for both males and females were low, which indicates that the species takes a long time to reach maximum size. In this instance, it should be noted the L_∞ of *C. albimarginatus* is not equivalent to maximum size as it is often considered. This is because the possible under-aging or absence of maximum age individuals (due to sampling limitations or their absence from the population from the effects of fishing) precluded asymptotic growth from being observed. Therefore, the L_∞ parameter was inflated and outside of the size range of the species. This is often the case with large shark species (Cailliet et al. 1985, Natanson et al. 1995, Simpfendorfer et al. 2002) and does not invalidate the L_∞ parameter or the growth curve. Instead, the L_∞ parameter is the value which is needed to calculate length-at-age estimates over the age range included in the sample (0 – 18 years in this study). The L_0 of the back-calculated data was within range of empirical values recorded for *C. albimarginatus* (Last and Stevens 2009) indicating that missing YOY have been adequately accounted for. Therefore, the results of this study represent biologically realistic length-at-age estimates for *C. albimarginatus* until an age of 18 years.

Limited maturity information is available for *C. albimarginatus* with some disparity between studies. Male *C. albimarginatus* from Indonesia were estimated to mature at *c.* 193 – 199 cm TL (White 2007) while maturity in the Western Indian Ocean was estimated to be 170 – 180 cm TL (Stevens 1984). This study found that male l_{50} (174.7 cm TL) was similar to the western Indian Ocean population (Stevens 1984). However, low numbers of mature females impeded the ability to estimate an accurate length-at-maturity in both Indonesia and the western Indian Ocean (Stevens 1984, White 2007). Two mature females were dissected by Stevens (1984); one 188.1 cm TL individual which was virgin and a 204.7 cm TL individual that was not virgin. In Indonesia two pregnant females were encountered which were both larger than 230 cm TL, providing a preliminary length-at-first-reproduction (White 2007). In the present study, five mature females were examined (205 -250 cm TL) along with a further eight which were maturing (stage 2), providing the most complete dataset to date from which to estimate female maturity. The resulting l_{50} estimate for females was 208.9 cm TL with the largest immature (stage 2) female at 196 cm TL. Given this l_{50} is larger than confirmed pregnant or post-partum females it is likely that *C. albimarginatus* females mature ranging from 190 – 210 cm TL. The A_{50} estimated for females in this study was 14.8 years and the approximate age of the smallest mature female from Stevens (1984) (extrapolated from length-at-age estimates from the present study) was 13 years old. This indicates that *C. albimarginatus* mature at 40 - 46% of their maximum age according to the calculated longevity. According to maximum vertebral age this value would be 80% which suggests that *C. albimarginatus* live longer than 18 years. In comparison, *C. limbatus* and *C. amblyrhynchos* mature at 45- 52% and 46 – 60% of their maximum age, respectively (Chapters 4 and 5). This further indicates that *C. albimarginatus* lives beyond 18 years.

Conducting life history studies on heavily exploited populations has been shown to yield estimates that are different from an unfished (or lightly fished) population (Walker et al. 1998). This occurs for three reasons: 1) length-selective fishing mortality results in a biased sample (Walker et al. 1998), 2) high levels of exploitation have caused changes to the populations life histories, possibly through compensation (Sminkey and Musick 1995), or 3) heavy exploitation has caused a truncated age distribution (Hsieh et al. 2010, Rouyer et al. 2011, Stewart 2011). The absence of Rosa Lee's phenomenon indicates that this sample was likely representative of the current population structure as individuals of different ages displayed similar growth rates. However, the dome-shaped selectivity of fisheries may reduce the likelihood of *C. albimarginatus* from reaching maximum age (Taylor and Methot 2013). As this study aged *C. albimarginatus* to 18 years and determined that females mature at 14.8 years, it is likely that some level of age-truncation may have occurred for this stock. This is difficult to determine as no historical data on age distributions are available for *C. albimarginatus*. However, future work should aim to validate the ages of larger individuals. This will determine whether these individuals have been under-aged and possibly indicate whether the maximum age of this population has been decreased due to exploitation. Given the uncertainty around the maximum age of *C. albimarginatus* – future studies should focus on producing life history information from a larger sample size that includes the largest size classes. However, until such a study can be conducted, the present study provides realistic life history estimates for an exploited population.

The population status of *C. albimarginatus* in PNG waters is not currently understood. The recent closure of the shark longline fishery has likely reduced the number of *C. albimarginatus* harvested in PNG. However, they continue to be taken as bycatch in PNG tuna fisheries (Nicol et al. 2009) as well as in coastal artisanal and subsistence fisheries. The full extent of their catch is unknown as PNG artisanal fisheries are particularly data poor (Teh et al. 2014). Future studies should focus on producing demography estimates for the PNG *C. albimarginatus* population using these life history data and accounting for their uncertainty (particularly longevity and age at female maturity). Given the lack of life history data from other parts of its range the life history information for *C. albimarginatus* from PNG can be used for populations from other regions until further studies are conducted. However, it should be used with caution as regional variation in life history estimates have been documented in other shark species (Chapter 4, Driggers et al. 2004, Carlson et al. 2006). The fragmented distribution and limited dispersal of *C. albimarginatus* (Ebert et al. 2013) makes this species potentially susceptible to this regional variation if selection pressures differ between locations and there is little mixing between populations.

Chapter 7

Stochastic demographic analyses of the silvertip shark (*Carcharhinus albimarginatus*) and the common blacktip shark (*Carcharhinus limbatus*) from the Indo-Pacific

7.1 Introduction

The world's highest shark catches occur in the western central Pacific, in particular Indonesia. Indonesia has the world's largest shark fishery with reported catches of an average 110,000 t per year – more than any other nation (Lack and Sant 2008). Both Indonesia and PNG lie within the Coral Triangle, a region of specific conservation concern due to high biological diversity including some of the world's richest chondrichthyan faunas (White and Kyne 2010, Last and White 2011). However, both nation's shark fisheries remain poorly understood as they are largely unregulated and catches are mostly unreported (White and Kyne 2010). As of yet, no stock assessments have been conducted on Papua New Guinean shark fisheries (White and Kyne 2010), although some data from PNG have been included in assessments for the greater Western Central Pacific (Rice and Harley 2012, 2013). Stock assessments have been attempted in Indonesia although the lack of long term species-specific catch and effort data has so far precluded dynamic stock analyses from being undertaken (Blaber et al. 2009). However, static demographic models do not require such data and may be used to assess populations using only life history parameters (Cortés 1998, Simpfendorfer 2004a). Information on species-specific biology are available from Indonesia (White 2007, White et al. 2008, Hall et al. 2012, Drew et al. 2015) and Papua New Guinea (Chapter 5, Chapter 6). Therefore, the trend in fisheries and ecological literature is moving towards matrix model approaches because of the ability of these methods to assess the potential effects of management and conservation strategies (Simpfendorfer 2004a).

Static demographic models became popular for shark stocks in the 1990’s (Cailliet et al. 1992, Au and Smith 1997, Cortés 1999, Simpfendorfer 1999a, Simpfendorfer 1999b) and now include a range of analyses that can incorporate stochasticity (Cortés 2002, McAuley et al. 2007, Cortés et al. 2012). Demographic estimates provide a variety of statistics that summarise a population’s growth rate, generation length, reproductive outputs and stable-age distribution. Each of these demographic outputs can be produced from either life tables or matrix models (Caswell et al. 1998). While similar estimates are produced by both methods (Mollet and Cailliet 2002), matrix models can be structured to examine either stage or age-classes – allowing them to be tailored to the information available (Simpfendorfer 2004a). Additionally, the elasticities of individual matrix elements can provide useful information on the ages or life stages that will respond best to management (Heppell et al. 1999, Heppell et al. 2000). Therefore, the trend in fisheries and ecological literature is moving towards matrix model approaches as their ability to easily assess the potential effects of management and conservation strategies provides incentives towards selecting this approach (Simpfendorfer 2004a).

The silvertip shark, *Carcharhinus albimarginatus* and the common blacktip shark *Carcharhinus limbatus* are both species that require demographic assessment in the Indo-Pacific region due to human pressures and conservation concern. *Carcharhinus albimarginatus* is a reef associated species with a patchy distribution in the Indo-Pacific (Ebert et al. 2013). It’s reef association means that it is encountered infrequently by commercial tuna fisheries (Chapter 6, Kumoru 2003b), although there is evidence that they are caught in subsistence and artisanal fisheries (White 2007). Information on its life history, space use and habitat preferences are now available (Chapter 6, Bond et al. 2015, Espinoza et al. 2015a). However, as its catches are largely unreported, no population assessments have ever been conducted on this species due to a paucity of data. Therefore, its ability to withstand the effects of fishing is unknown and little information on its population status is available to inform conservation or management.

Carcharhinus limbatus has a circumglobal distribution and is fished throughout much of its range (Ebert et al. 2013). Stock assessments and demographic analyses conducted on US populations have demonstrated that this species can be fished sustainably (Cortés 1998, Cortés et al. 2002, SEDAR 2012). Unfortunately, these assessments cannot be used to manage the Indo-Pacific population as demographic models are strongly dependent on the vital rates used to construct them. As the Indo-Pacific *C. limbatus* population grows larger and matures later than US conspecifics, these demographic estimates would be unsuitable (Chapter 4, Wintner and Cliff 1996). Therefore, demographic analyses that are based on local life history parameters are required to effectively inform conservation and fisheries management in the region.

The data-poor nature of Indonesian and Papua New Guinean shark fisheries has been an impediment to conducting full stock assessments. However, static demographic models can accommodate data paucity and thus, act as an important management tool until sufficient fisheries data becomes available for data-rich conventional stock assessments, or until results of other data-poor approaches become available (Simpfendorfer 2004a). Therefore, the aim of this study was to use static demographic models to produce demographic information on *C. albimarginatus* and *C. limbatus* populations from the Indo-Pacific region. This was achieved by applying age-structured Leslie matrix models for both populations using locally obtained life history parameters. These parameters were sourced from the region of the Indo-Pacific that surrounds PNG and Indonesia. Specifically, the life history parameters for *C. albimarginatus* were sourced from studies published from PNG fisheries (Chapter 6), while the parameters for *C. limbatus* were sourced from studies published from Indonesian fisheries (Chapter 4, White 2007). Inferences about population growth rates, susceptibility to fishing pressure and potential management scenarios were determined from these demographic estimates.

7.2 Methods

7.2.1 Life history parameters

Life history parameters were taken from the chapters 4 and 6 for *C. albimarginatus* and *C. limbatus* to form the foundation of vital rates to use in demographic analyses (Table 7.1). In this study, vital rates are defined as lower level components of the demographic estimates that underlie the Leslie Matrix elements (Brault and Caswell 1993). Reproductive vital rates were used to estimate the age-specific fecundity (number of female pups per year, m_t). As both species have 1:1 embryo sex ratios and biennial reproductive cycles (White et al. 2006, White 2007), this was performed by multiplying the respective litter sizes of each species by 0.5 then dividing this value by 2. Age-at-maturity (α) was determined using the age where 50% of individuals were mature from logistic maturity ogives (Chapter 6, White 2007). Age-at-first-reproduction (t_{repro}) was calculated as α + the gestation period (Mollet and Cailliet 2002).

Table 7.1: Published life history parameters for *Carcharhinus albimarginatus* and *Carcharhinus limbatus* (Indonesian population), the statistical distributions and lower/upper bounds used in Monte Carlo simulations. All parameters are specific to females only. The lower and upper bound of maximum age are the vertebral growth band count and maximum estimated longevity respectively.

Type	**Parameter**	**Estimate**	**Statistical Distribution**	**Lower and Upper Bounds**	**References**
		Carcharhinus albimarginatus			
Growth	L_∞ (cm)	497.9	-	-	Chapter 6
	k (year^{-1})	0.02	-	-	Chapter 6
	t_0 (years)	-7.67	-	-	Chapter 6
	Max. Age, t_{max} (years)	18	Uniform	18, 32	Chapter 6
Fecundity	Age-at-maturity, α (years)	15	Uniform	12, 17	Chapter 6; Stevens (1984)
	Litter size	6	Triangular	1,11	Bass et al. (1973); Wheeler (1962)
	Gestation Period (months)	12	-	-	Bass et al. (1973); Wheeler (1962)
	Reproductive cycle (years)	2	-	-	White et al. (2006)
		Carcharhinus limbatus			
Growth	L_∞ (cm)	264	-	-	Chapter 4
	k (year^{-1})	0.11	-	-	Chapter 4
	t_0 (years)	-2.44	-	-	Chapter 4
	Max. Age, t_{max} (years)	17	Uniform	17, 20	Chapter 4
Fecundity	Age-at-maturity, α (years)	8	Uniform	4, 10	Chapter 4
	Litter size	6	Triangular	1, 10	White (2007)
	Gestation Period (months)	12	-	-	White (2007)
	Reproductive cycle (years)	2	-	-	White (2007)

7.2.2 Natural mortality estimation

Natural mortality (*M*) was estimated for both species using indirect methods. These included the age-independent equations proposed by Pauly (1980), Chen and Yuan (2006), Jensen's (1996) k invariant method and Jensen's (1996) maturity method as modified for use with sharks by Hisano et al. (2011). Two age-dependent methods were also applied following Chen and Watanabe (1989) and Peterson and Wroblewski (1984).

Pauly's (1980) method used the equation:

$$\ln(M) = -0.0066 - 0.279 * \ln(L_\infty) + 0.6743 * \ln(k) + 0.4634 * \ln(T) \qquad (7.1)$$

where L_∞ and k are parameters from the VBGF and T is temperature in °C

Chen and Yuan's (2006) method was calculated as:

$$\ln(M) = 1.46 - 1.01 * \ln(t_{max}) \qquad (7.2)$$

where t_{max} was the longevity. Chen and Yuan (2006) originally calculated t_{max} from VBGF parameters as:

$$t_{max} = \left(t_0 - \frac{\ln(0.05)}{k}\right) \qquad (7.3)$$

Where t_0 and k are parameters from the VBGF. However, this equation overestimated longevity for both species with a particularly implausible estimate of 142 years for *C. albimarginatus*. Therefore, values of t_{max} from the chapters 4 and 6 were used instead.

Jensen's (1996) method was calculated as:

$$M = 1.6 * k \qquad (7.4)$$

Jensen's maturity method (1996) as modified for use with sharks by Hisano et al. (2011) was calculated as:

$$M = \frac{1.65}{\alpha - t_0} \qquad (7.5)$$

Two methods were applied to produce age-dependent mortality estimates (M_t). Chen and Watanabe (1989) hypothesised that M should by highest at the youngest and oldest age-classes producing a "bathtub" shape. They therefore, derived two equations: one which described falling mortality during the early years of life and a second that described increasing mortality towards the end of life (Simpfendorfer 2004b). These equations are also derived using parameters from the VBGF:

$$M_t = \begin{cases} \frac{k}{1-e^{-k(t-t_0)}}, t < t_m \\ \frac{k}{a_0+a_1(t-t_m)+a_2(t-t_m)^2}, t \geq t_m \end{cases} \quad (7.6)$$

where

$$\begin{cases} a_0 = 1 - e^{-k(t_m-t_0)} \\ a_1 = ke^{-k(t_m-t_0)} \\ a_2 = -\frac{1}{2}k^2e^{-k(t_m-t_0)} \end{cases} \quad (7.7)$$

and

$$t_m = -\frac{1}{k}\ln\left(1 - e^{kt_0}\right) + t_0 \quad (7.8)$$

where M_t is the natural mortality at age t, k and t_0 are parameters from the VBGF.

Peterson and Wroblewski's (1984) method estimates M by using dry weight as scaling factor:

$$M_{wt} = 1.92wt^{-0.25} \quad (7.9)$$

Where wt is the weight-at-age t. This is then converted to M_t using a length-weight relationship and length-at-age data (Simpfendorfer 2004b). Such an approach yields wet weight and thus a conversion factor of one fifth is used for sharks to give dry weight (Cortés 2002). Length-at-weight was calculated for *C. limbatus* using the relationship given by (Dudley and Cliff 1993) for the South African population which has a similar growth profile to the Indonesian population (Chapter 4). However, this method could not be used to estimate M_t for *C. albimarginatus*, as no length-weight relationship is for this species available from any region.

Estimates of M were transformed into annual probabilities of age-specific survival (S_t) (to form Leslie Matrix elements) as:

$$S_t = e^{-M} \quad (7.10)$$

The proportion of the population surviving to the beginning of each class (l_t) was also calculated from M as:

$$l_t = l_{t-1}e^{-M} \quad (7.11)$$

7.2.3 Demographic model

Demographic analyses were conducted using a static age-structured Leslie Matrix model with a post-breeding census (Caswell 1989, Mollet and Cailliet 2002, Aires-da-Silva and Gallucci 2007). These demographic analyses were single sex models carried out exclusively for females – as is typical for demographic analyses on elasmobranchs (Simpfendorfer 2004a). Leslie matrices use matrix algebra to estimate the finite rate of population growth (λ) as the dominant eigenvalue from fertility (f) and survival (S) data (Caswell 1989). The finite rate of population growth can be related to the intrinsic rate of population growth (r) produced by life tables via the relationship (Simpfendorfer 2004a):

$$\lambda = e^r \tag{7.12}$$

Population growth is stable when $\lambda = 1$, decreasing when $\lambda = < 1$ and increasing when $\lambda = > 1$. Additionally, the stable age distribution (w) and reproductive values (v) were estimated as the right and left eigenvectors, respectively.

To construct the Leslie Matrices, m_t was estimated using knife-edge maturity – where age-classes older than t_{repro} produced an equal number of female pups per year, while all age-classes younger than the t_{repro} produced none. Following Caswell (1989), fecundity is defined here as the maximum reproductive output (vital rates) while fertility is defined as the actual reproductive performance (matrix elements). Age-specific fertility (f_t) was calculated as:

$$f_t = \begin{cases} 0, t < t_{repro} \\ S_{t-1} * m_t, t \geq t_{repro} \end{cases} \tag{7.13}$$

The basis for the Leslie Matrices was:

$$N_{t+1} = AN_t \tag{7.14}$$

where N is a vector describing the populations age composition at time t and A is the transition matrix (Caswell 1989):

$$A = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_t \\ S_0 & 0 & 0 & \ldots & 0 \\ 0 & S_1 & 0 & \ldots & 0 \\ \vdots & \ddots & \ddots & \ldots & \vdots \\ 0 & 0 & 0 & S_t & 0 \end{bmatrix} \tag{7.15}$$

Mean generation time (G) and net reproductive rate (R_0) were calculated using the results of the Leslie Matrices (Simpfendorfer 2004a). G is the mean period between birth of a parent and the birth of their offspring:

$$G = \sum_{t=t_{repro}}^{t_{max}} t\mathrm{e}^{-\ln(\lambda)t}\, l_t m_t \tag{7.16}$$

R_0 is the total number of female offspring produced per individual in their lifetime according to rates of m_t and l_t:

$$R_0 = \sum_{t=t_{repro}}^{t_{max}} l_t m_t \tag{7.17}$$

7.2.4 Monte Carlo simulations

Estimates of vital rates for marine species can often be difficult to obtain and result in high uncertainty (Caswell et al. 1998). Therefore, it was important to consider the effect of that uncertainty by incorporating stochasticity into demographic analyses (Cortés 2002). In order to incorporate uncertainty into matrix projections and demographic parameters, Monte Carlo simulations were used to stochastically vary specific vital rates This involved randomly selecting vital rates from assumed statistical distributions, performing demographic analyses for 10,000 simulations and summarising the results with mean and quantile values. The statistical distributions of λ, G and R_0 were analysed to ensure that each distribution was well captured during the simulations. The vital rates varied in the Monte Carlo simulations were t_{max}, α, litter size and M_t.

Longevity (t_{max}) was included as a varied vital rate in the simulations as it can be difficult to estimate for large bodied sharks (Francis et al. 2007). Therefore, random estimates of t_{max} for each species were drawn from a uniform distribution. This was created using the maximum age from vertebral analyses as the lower bound and theoretical longevity calculated from VBGF parameters as the upper bound (Table 7.1):

$$t_{max} = 7 * \ln(\frac{2}{k}) \qquad (7.18)$$

Estimates of t_{max} generated during the Monte Carlo simulations were used to estimate M in Chen and Yuan's (2006) method.

Age-at-maturity (α) and litter size were included as varied vital rates to account for variation within the population. Random estimates of α were drawn from a uniform distribution which was created using minimum and maximum reported age-at-maturities from the literature (Table 7.1). Estimates of α generated during the Monte Carlo simulations were used to estimate M in Jensens's (1996) maturity method. A triangular distribution was used to draw random estimates of litter size using the reported mean as the peak value and the minimum and maximum litter sizes as the lower and upper bounds (Table 7.1). Age-specific mortality (M_t) was included as a varied vital rate to account for the uncertainty around this parameter. A triangular distribution was used to draw random estimates of M for each age-class. Where a particular natural mortality estimate was age-independent (Pauly and Jensen) the same estimate of M was applied to all ages. The triangular distribution was produced using the mean M_t as the peak value and the highest and lowest M_t values as the upper and lower bounds (Table 7.2). A condition was placed on the Monte Carlo sampling where M_{t+1} could not be larger than M_t as mortality is typically highest for younger age-classes and should decline with age (Peterson and Wroblewski 1984, Chen and Watanabe 1989). Therefore, if an estimate of M_t was larger than the M of the previous age-class, the triangular distribution was resampled until this condition was met.

Summaries of the stable-age distributions and the reproductive values (w and v) were produced for unfished populations from the Monte Carlo simulations. However, these summaries required a constant t_{max} and therefore this vital rate was not varied. In this study, an unfished population was not considered a virgin stock as all of the vital rates used in the demographic analyses were estimated from fished populations. Therefore, the term “unfished population” was defined here as a scenario where the instantaneous fishing mortality (F) was reduced to zero.

7.2.5 Matrix elasticities

Elasticity analysis measures the proportional changes of individual matrix elements on λ while holding other elements constant (de Kroon et al. 1986). As elasticities identify the ages where changes to S or f will most affect λ, they provide valuable information for conservation and management (Simpfendorfer 2004a). Elasticities of matrix elements (e_{ij}) were calculated as (Caswell 1989):

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{\lambda \langle w, v \rangle \prime} \tag{7.19}$$

where a_{ij} is the matrix element corresponding to row i and column j, v_i is the value of row i in the reproductive value vector v, w_j is the value of column j in the stable age distribution vector w and $\langle w, v \rangle$ is the scalar product of vectors w and v. The sum of all matrix element elasticities equals 1.

As elasticity values are highly dependent on the vital rates used, deterministic methods cannot be calculated from a mean matrix produced from Monte Carlo Simulations (Wisdom et al. 2000). Therefore, to provide a sensitivity analysis following the implementation of Monte Carlo simulations, elasticity values were summed over the age-classes of three life history phases: fertility, juvenile survival and adult survival (Heppell et al. 2000). This was performed after each simulation so that variations to t_{max} and t_{repro} were accounted for. To identify the effects of management on compensation between survival and fertility; elasticity ratios were calculated between fertility and both juvenile and adult survival phases following Cortés (2002). A compensation ratio of 4.0 indicates that a 10% decrease in the respective survival phase would require a 40% increase in fertility to maintain the original λ (Heppell et al. 1999, Cortés 2002).

7.2.6 Management scenarios

The length-selective nature of shark fisheries means that F is rarely constant across age-classes. Therefore, the effects of varying F across age-classes (F_t) was examined and compared to scenarios where F was age-independent. Two age-selective harvest strategies were applied for both species: age-at-first-capture (AAFC) (Cortés 1998, Simpfendorfer 1999a) and age-at-last-capture (AALC). AAFC represents management strategies where juveniles are excluded from the fishery (such as protecting nursery areas). Conversely, AALC represents management strategies that implement gauntlet fisheries – where the juveniles are harvested while the breeding stock is protected (Prince 2005). Each of these scenarios represent commonly implemented management measures designed to protect different population demographics.

To conduct these scenarios, F_t was incorporated into the survivorship elements of the Leslie Matrices such that the total mortality was the sum of F_t and M_t:

$$S_t = e^{-M+F} \tag{7.20}$$

Scenarios that examined the effects of an age-independent F were determined by calculating the limiting level of F that is produces a stable population ($F_{CRITICAL}$). This was estimated by systematically increasing F equally across all age-classes until $\lambda = 1$ (Simpfendorfer 1999a, Brewster-Geisz and Miller 2000). The harvest rate that produces a stable population ($U_{CRITICAL}$) was estimated by transforming $F_{CRITICAL}$ from an instantaneous to an annual mortality rate as:

$$U_{CRITICAL} = 1 - e^{-F_{CRITICAL}} \tag{7.21}$$

$U_{CRITICAL}$ is the maximum proportion of the population that could be harvested each year before population declines occur.

AAFC analyses were performed by applying an equal level of F across all the age-classes caught by the fishery while assuming that $F = 0$ yr^{-1} for age-classes that have not yet entered the fishery. λ was estimated as the AAFC and F are systematically increased (Simpfendorfer 1999a). AALC analysis was conducted by applying F equally across all the age-classes caught by the fishery while assuming that $F = 0$ yr^{-1} for ages that have left the fishery. λ was also estimated as the AALC and F were systematically increased. These analyses also incorporated Monte Carlo simulations to incorporate stochasticity into estimates of λ. Estimates of $F_{CRITICAL}$ and $U_{CRITICAL}$ were calculated for the age-classes exposed to the fishery.

Potentially sustainable harvest strategies that were identified by the AAFC and AALC analyses were explored further. Where analyses identified that a minimum or maximum size limit could be used as sustainable harvest strategies, a selectivity-at-age model was estimated using knife edge selectivity for a given size limit. These selectivity-at-age models were computed using the variation around length-at-age estimates from Chapter 4 and Chapter 6 using a generalised linear model with a binomial error structure and a logit-link function in the ‘R’ programme environment (R Core Team 2013).

All of the matrix models, elasticity analyses and population projections were conducted in the ‘R’ programing environment (R Core Team 2013) using the ‘popbio’ package (Stubben and Milligan 2007).

7.3 Results

7.3.1 Natural mortality estimates

The age-dependent estimates produced by Chen and Watanabe’s (1989) approach produced the highest mortality estimates for both species (Table 7.2). However, the full “U shape” of these curves did not occur as there was no increase in M_t for the final age-classes (Table 7.2). It is likely that the increase in M_t occurs at ages older than t_{max} due to the low k parameters of both species (Table 7.1). The M_t for the first age-class was 0.14 yr^{-1} and 0.47 yr^{-1} which decreased to 0.04 yr^{-1} and 0.12 yr^{-1} for *C. albimarginatus* and *C. limbatus*, respectively. Variation between estimates was low for *C. albimarginatus* and ranged 0.03 yr^{-1} for the Jensen (1996) k invariant method to 0.23 yr^{-1} as upper estimate of Chen and Yuan’s (2006) method (Table 7.2). However, Jensen’s (1996) k invariant method provided a very low estimate of M due to a low k value. This estimate was deemed to be unrealistically low for an age-independent value and was judiciously removed from the analysis.

M estimates were also similar for *C. limbatus* with age-independent estimates ranging from 0.16 to 0.26 yr^{-1}, with both of these estimates based on the lower and upper estimates of the Jensen (1996) maturity method (Table 7.2). Both age-dependent methods provided more variation although by age 3 both methods estimate M_t within the same range as the age-independent methods (Table 7.2).

The distribution of M_t estimates produced during Monte Carlo simulations showed a declining variation as age increases (Fig. 7.1). This occurred as the condition that $M_{t+1} \leq M_t$ provided greater restrictions on the *M* estimates at these ages. However, this restricted variability did not bias *M* estimates at older ages as less variation occurred across all *M* estimates for both species anyway. A narrowing in the 95% quantiles occurred at an age of 15 years for *C. albimarginatus* and 7 years for *C. limbatus.* This occurred as age-dependent methods reached values that were within range of those estimated by age-independent methods at these respective ages, after which they estimated levels of M_t that were lower than the age-independent methods.

Table 7.2: Age-specific natural mortality (M_t) estimates for *Carcharhinus albimarginatus* and *Carcharhinus limbatus*

Age (years)	Pauly	Jensen^1	Jensen^{2*}	Chen and Yuan*	Chen and Watanabe	Pauly	Jensen^1	Jensen^{2*}	Chen and Yuan*	Chen and Watanabe	Peterson and Wroblewski
			Carcharhinus albimarginatus					*Carcharhinus limbatus*			
0	0.06	0.03	0.07 – 0.08	0.13 – 0.23	0.14	0.21	0.17	0.16 – 0.26	0.21 – 0.23	0.47	0.28
1					0.13					0.35	0.29
2					0.33					0.28	0.25
3			Same value for all ages		0.27			Same value for all ages		0.24	0.22
4					0.23					0.22	0.20
5					0.09					0.20	0.18
6					0.08					0.18	0.17
7					0.08					0.17	0.16
8					0.07					0.16	0.16
9					0.07					0.15	0.15
10					0.07					0.15	0.15
11					0.06					0.14	0.14
12					0.06					0.14	0.14
13					0.06					0.13	0.14
14					0.06					0.13	0.13
15					0.05					0.13	0.13
16					0.05					0.13	0.13
17					0.05					0.13	0.13
18					0.05					0.13	0.13
19					0.05					0.12	0.13
20					0.05					0.12	0.12
21					0.05					-	-
22					0.04					-	-
23					0.04					-	-
24					0.04					-	-
25					0.04					-	-
26					0.04					-	-
27					0.04					-	-
28					0.04					-	-
29					0.04					-	-
30					0.04					-	-
31					0.04					-	-
32					0.04					-	-

Jensen^1: k invariant method

Jensen^2: age-at-maturity method

* α and t_{max} varied during Monte Carlo simulations

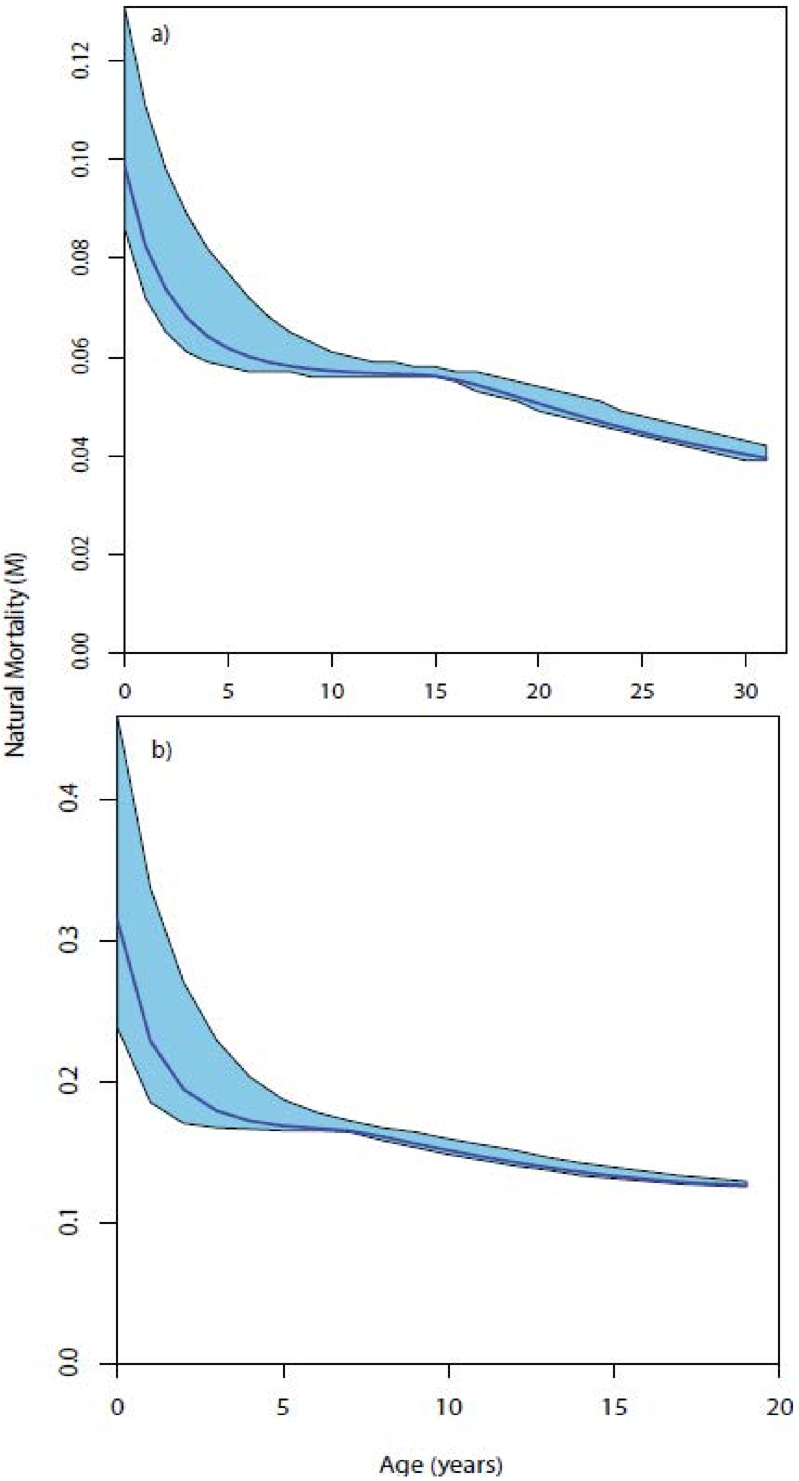

Figure 7.1: The mortality-at-age (M_t) distributions determined through Monte Carlo simulations for unfished populations of *Carcharhinus albimarginatus* (a) and *Carcharhinus limbatus* (b). The blue shaded areas represent the 95% quantiles of the Monte Carlo simulations. These distributions were determined using Monte Carlo simulations with t_{max} set at 32 years for *Carcharhinus albimarginatus* and 18 years for *Carcharhinus limbatus*.

7.3.2 Matrix elasticities

Matrix elasticities did not differ between the unfished population nor varying levels of *F* (Table 7.3). Juvenile survival was the highest elasticity phase for both species, followed by adult survival and then fertility. Juvenile survival elasticities were higher for *C. albimarginatus* than for *C. limbatus* at 0.77 and 0.58, respectively (Table 7.3). This identifies that the population growth of *C. albimarginatus* is more sensitive to changes in juvenile survival than *C. limbatus*. The fertility elasticities were very low for both species (Table 7.3). Accordingly, the elasticity ratios showed that increases in fertility cannot compensate for adult nor juvenile survival for either species without being biologically implausible. For example, for *C. albimarginatus* in order to compensate for an *F* of 0.1 on juveniles, the average number of pups (of both sexes) per year would need to increase to an average of 14.7, which is beyond the capacity of the species

Table 7.3: Demography estimates for *Carcharhinus albimarginatus* and *Carcharhinus limbatus* under different age-independent fishing mortalities. Values in parentheses are 95% confidence intervals

				Elasticities			Elasticity ratios	
F	λ	*G*	R_0	Fertility	Juvenile survival	Adult survival	Juvenile survival	Adult survival
Carcharhinus albimarginatus								
0	1.07 (0.99 - 1.13)	22.24 (14.14 – 30.08)	5.28 (0.82 – 11.91)	0.05 (0.04 - 0.06)	0.77 (0.67 - 0.90)	0.18 (0.05 - 0.27)	14.57	3.41
0.1	0.97 (0.90 – 1.02)	22.20 (14.05 – 30.15)	0.75 (0.14 –1.68)	0.05 (0.04 - 0.06)	0.77 (0.67 - 0.92)	0.18 (0.03 - 0.27)	14.51	3.43
0.2	0.88 (0.81 - 0.92)	22.24 (14.26 – 30.17)	0.12 (0.02 – 0.29)	0.05 (0.04 - 0.06)	0.77 (0.67 - 0.89)	0.18 (0.05 - 0.28)	14.51	3.48
0.3	0.79 (0.73 - 0.83)	22.21 (13.84 – 29.95)	0.02 (0.00 – 0.06)	0.05 (0.04 - 0.06)	0.77 (0.67 - 0.90)	0.18 (0.05 - 0.27)	14.49	3.39
Carcharhinus limbatus								
0	1.07 (0.96 - 1.18)	15.77 (9.30 – 24.27)	3.13 (1.02 – 5.75)	0.10 (0.08 - 0.13)	0.58 (0.47 - 0.66)	0.32 (0.25 - 0.42)	5.96	3.27
0.1	0.97 (0.87 – 1.07)	15.81 (9.28 – 24.53)	1.11 (0.34 – 2.29)	0.10 (0.08 - 0.13)	0.58 (0.47 - 0.67)	0.32 (0.25 - 0.42)	5.98	3.26
0.2	0.88 (0.79 - 0.97)	15.79 (9.35 – 24.40)	0.43 (0.12 – 1.00)	0.10 (0.08 - 0.13)	0.58 (0.48 - 0.66)	0.32 (0.25 - 0.41)	6.01	3.24
0.3	0.79 (0.72 - 0.88)	15.84 (9.32 – 24.25)	0.18 (0.04 – 0.50)	0.10 (0.08 - 0.13)	0.58 (0.47 - 0.67)	0.32 (0.25 - 0.42)	6.02	3.27

7.3.3 Stable-age distribution *(w)* and reproductive values *(v)*

The unfished stable–age distributions of both species showed that the proportion of the population in each age-class declined exponentially with age (Fig. 7.2a, b). *Carcharhinus limbatus* had higher proportions of individuals in its early age-classes in comparison to *C. albimarginatus*. However, this is likely to be an artefact of the older t_{max} of *C. albimarginatus* which means that individuals were spread across more age-classes. The 95% quantiles of the Monte Carlo simulations showed a narrowing at age 5 for *C. limbatus* and age 7 for *C. albimarginatus*. This occurred as low values of w for younger ages classes produce higher values of w in older age-classes and vice versa. Therefore, there is a point on the curve where the same approximation of w occurs regards of the shape of the distribution.

The reproductive values of both species peaked where t_{repro} occurred (Fig. 7.2c, d). For *C. limbatus*, the reproductive values were similar between ages 7 – 12 before decreasing to age 20 (t_{max}) (Fig. 7.2d). The peak in reproductive values was more pronounced for *C. albimarginatus* and occurred between ages 14 – 20 (Fig. 7.2c).

Greater variation occurred during the Monte Carlo simulations for reproductive values than the stable-age distributions for both species (Fig. 7.2c, d). This occurred as reproductive values were dependent on simulated values of α, M_t and litter size whereas the stable-age distributions were only dependent on simulated values of M_t. At their peak, v values had a coefficient of variation of 26.3 for *C. albimarginatus* and 23.7 for *C. limbatus*

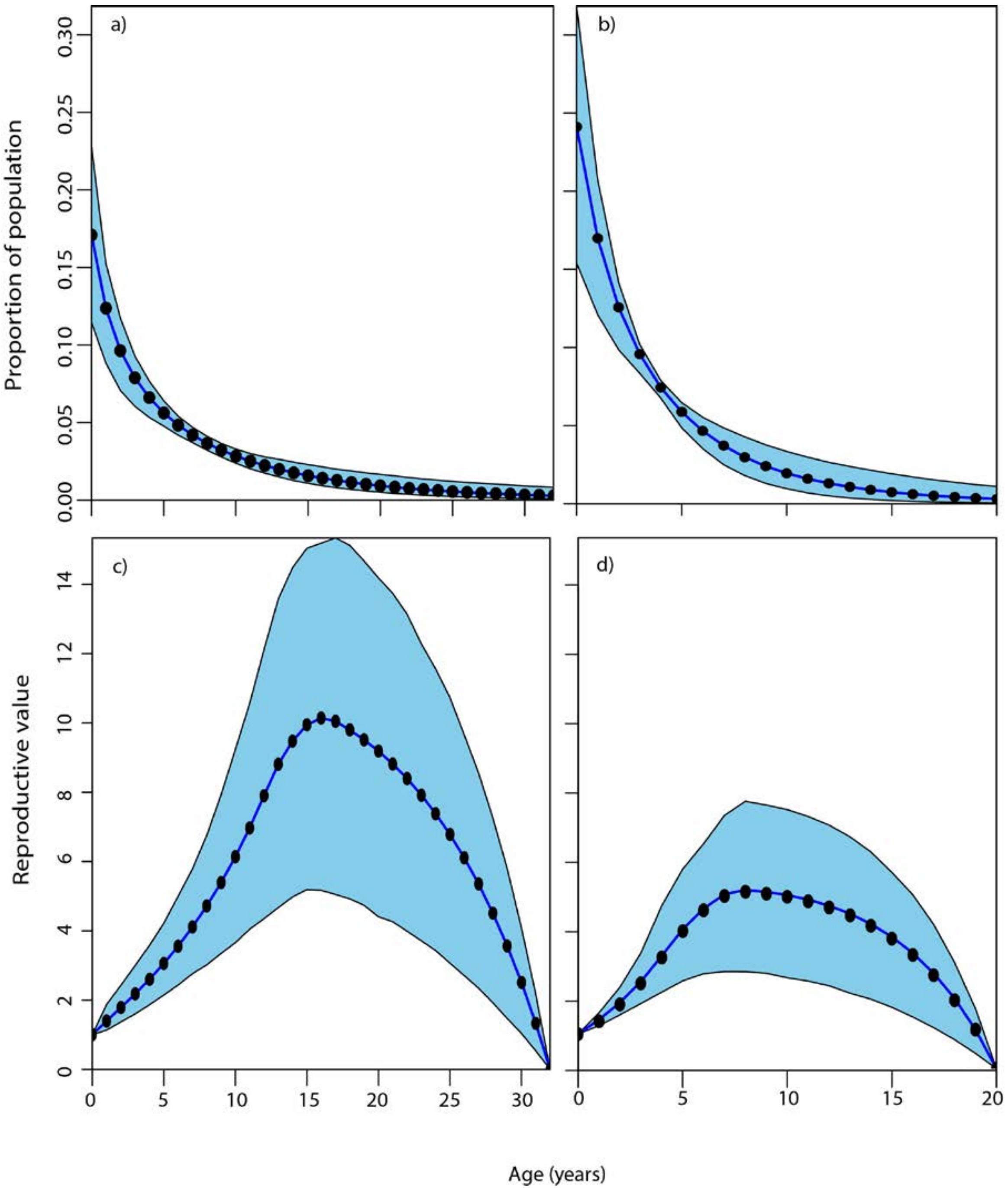

Figure 7.2: The stable age distributions (a-b) and reproductive values (c-d) for unfished populations of *Carcharhinus albimarginatus* (a, c) and *Carcharhinus limbatus* (b, d). The blue shaded areas represent the 95% quantiles of the Monte Carlo simulations. These distributions were determined using Monte Carlo simulations with t_{max} set at 32 years for *Carcharhinus albimarginatus* and 18 years for *Carcharhinus limbatus*.

7.3.4 Population growth under different management scenarios

Increasing population growth occurred for both *C. albimarginatus* and *C. limbatus* in the absence of fishing mortality (Table 7.3). *Carcharhinus albimarginatus* and *C. limbatus* had the same λ (1.07 yr^{-1}) despite *C. limbatus* having more variation around this parameter during the Monte Carlo simulations (Fig. 7.3a, b). However, *C. albimarginatus* had a larger G and R_0 (Table 7.3, Fig. 7.3). Similar decreases in λ occurred for both species as F increased (Fig. 7.4), although R_0 decreased more rapidly for *C. albimarginatus* than for *C. limbatus* (Table 7.3). G did not change for either species as F increased (Table 7.3). The distributions of key demographic parameters (λ, G and R_0) from the Monte Carlo simulations demonstrate that the full variability of each parameter was captured during the 10,000 simulations (Fig. 7.3).

Populations of both species declined when low levels of F were applied across all age-classes (Table 7.3). When F was age-independent, the $F_{CRITICAL}$ was 0.07 yr^{-1} and 0.06 yr^{-1} for *C. albimarginatus* and *C. limbatus*, respectively (Fig. 7.4). The same average λ occurred for both species as F was increased and declined linearly leading to population declines of 3% per year when $F = 0.1$ yr^{-1} (Table 7.3). When F was increased to 0.3 yr^{-1}, *C. albimarginatus* and *C. limbatus* populations declined 21% per year (Table 7.3; Fig. 7.4). These results indicate that neither species can tolerate moderate levels of fishing pressure when all age-classes are exposed to fishing.

The AAFC analysis for both species revealed that all juvenile age-classes (age-classes younger than the age-at-maturity) would need to be excluded from the fishery before F could increase beyond its initial $F_{CRITICAL}$ level (Fig. 7.5). For *C. albimarginatus*, this scenario meant that ages 0-15 all required exclusion from fishing (Fig. 7.5). For *C. limbatus*, F could not be increased beyond the $F_{CRITICAL}$ level unless ages 0 – 6 were excluded from fishing (Fig. 7.5). Each of these values is approximately equivalent to α which identifies that to sustainably harvest the adult age-classes, all of the juvenile age-classes must be protected.

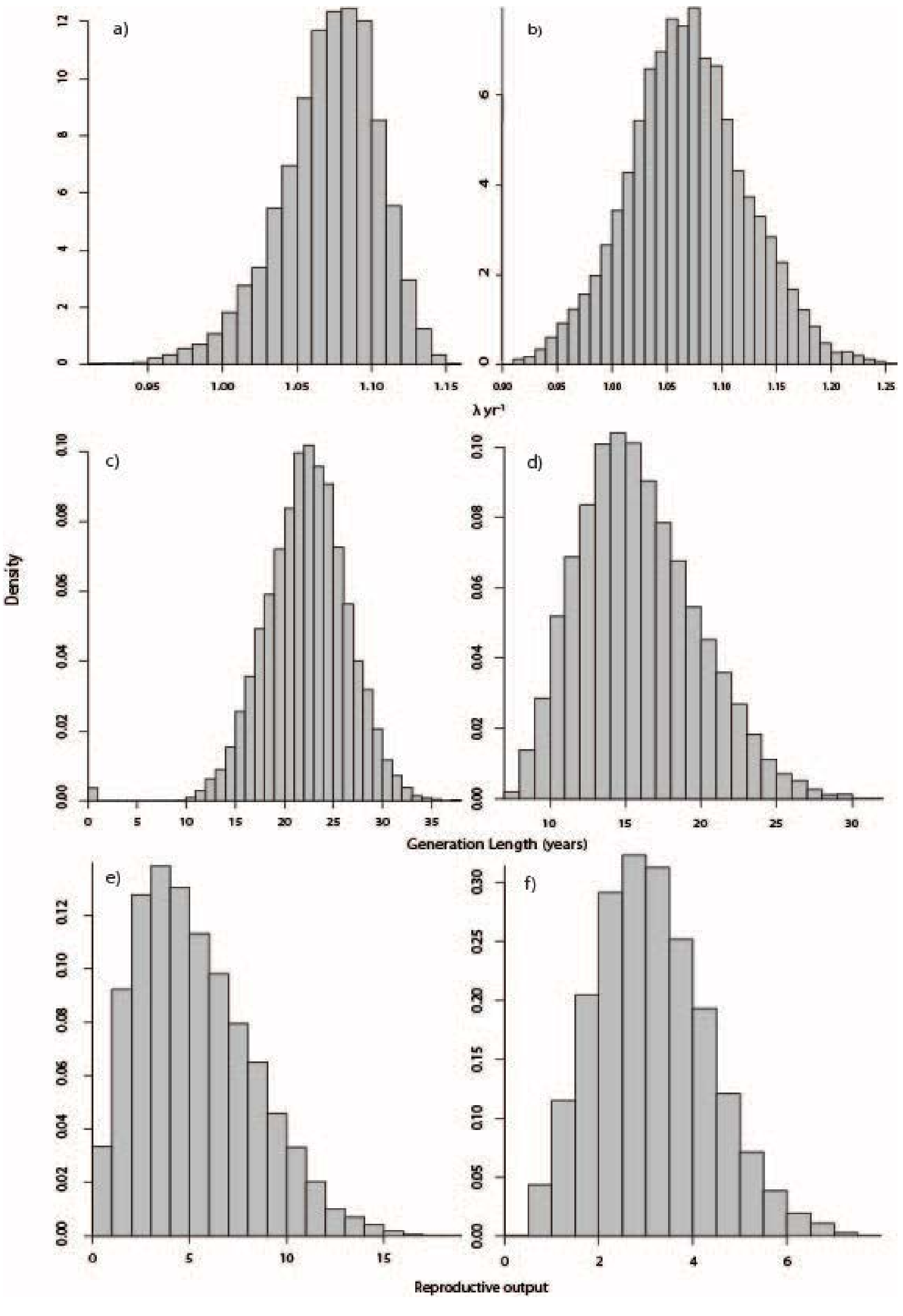

Figure 7.3: The variability of λ (a, b), G (c, d) and R_0 (e, f) from 10,000 Monte Carlo simulations for unfished populations of *Carcharhinus albimarginatus* (a, c and e) and *Carcharhinus limbatus* (b, d and f).

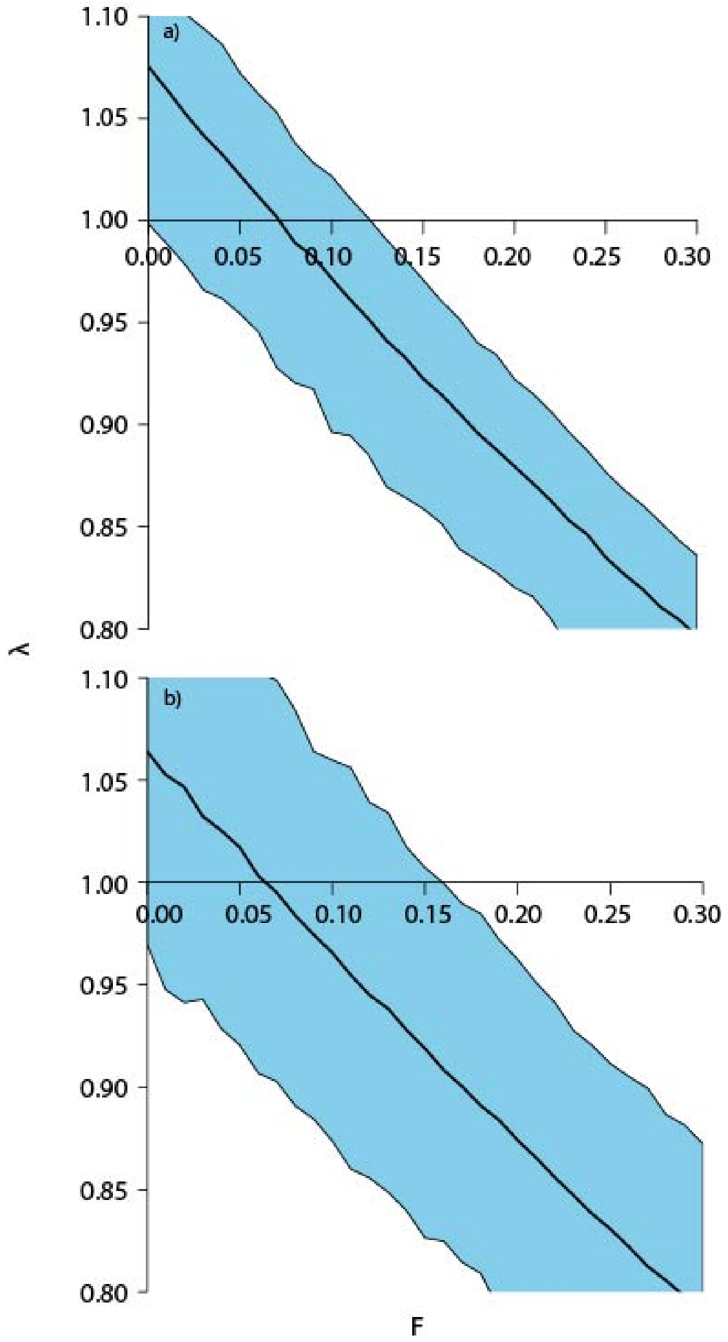

Figure 7.4: The relationship between the finite rate of population increase (λ) and instantaneous fishing mortality (F) for (a) *Carcharhinus albimarginatus* and (b) *Carcharhinus limbatus*. $F_{CRITICAL}$ occurs when $\lambda = 1$. The blue shaded areas represent 95% quantiles of the Monte Carlo simulations

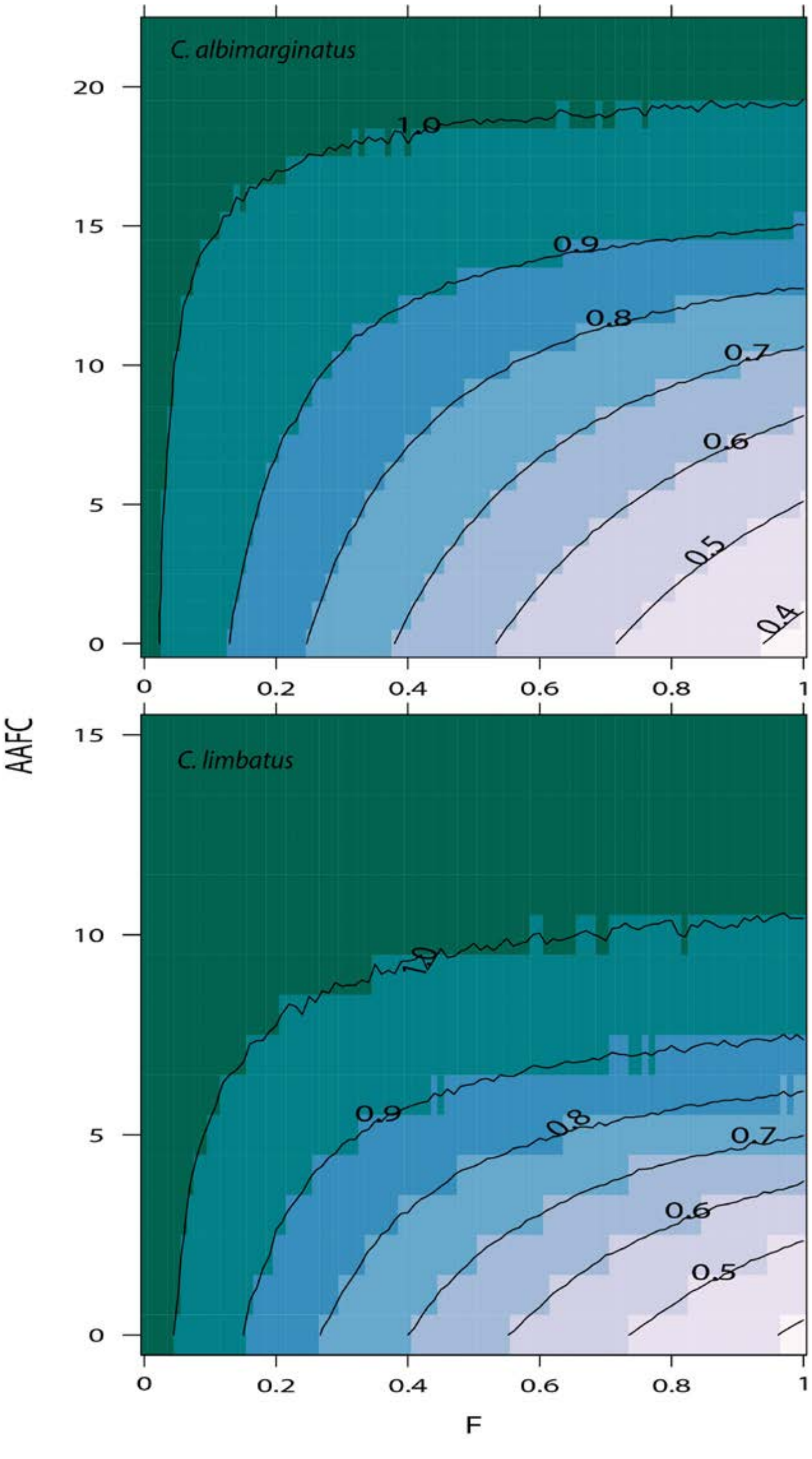

Figure 7.5: Contour plot of finite rate of population increase (λ) as a function of fishing mortality (F) and age-at-first-capture (AAFC) for *Carcharhinus albimarginatus* and *Carcharhinus limbatus*. Estimates of λ were estimated using Monte Carlo simulations to incorporate stochasticity. An increasing population occurs when $\lambda > 1$ (Dark green area).

The gauntlet fishery scenario revealed that exclusively harvesting the young-of-the-year (YOY) of both species could maintain increasing population growth while supporting reasonable harvest levels (Table 7.4; Fig. 7.6). Up to 69% (F = 1.18 yr^{-1}) of YOY *C. albimarginatus* could be harvested each year while maintaining a stable population. This corresponds to a maximum size limit of ~80 cm TL (Table 7.4). If several early age-classes (ages 0 – 5 years) were exposed to the fishery, 22% of those age-classes could be fished (F = 0.25 yr^{-1}). This corresponds to a maximum size limit of ~100 cm TL (Table 7.4).

The gauntlet fishery scenario showed that this strategy would also work for *C. limbatus,* although it could not sustain the same levels of fishing pressure as *C. albimarginatus* (Table 7.4; Fig. 7.6). Up to 38% (F = 0.48 yr^{-1}) of the first age-class and up to 21 % (F = 0.24 yr^{-1}) of the first two age-classes could be harvested while maintaining a stable population. This also corresponds to maximum size limits of ~ 80 cm TL and ~100 cm TL, respectively (Table 7.4).

A selectivity-at-age model identified that a 100 cm TL size limit could be applied for both species (Fig.7.7). An assumption of this model was that knife-edge selectivity occurs where individuals larger than 100cm TL are excluded from fishing. This selectivity captured age-classes up to an age of 5 for *C. albimarginatus* and up to an age of 3 for *C. limbatus* (Fig. 7.7). Therefore, the $F_{CRITICAL}$ for this size limit was 0.25 yr^{-1} for *C. albimarginatus* and 0.17 yr^{-1} for *C. limbatus* (Table 7.4). This selectivity-at-age was possible as less variation in length-at-age occurred at younger ages for both species (Chapter 4 and Chapter 6). However, due to the substantial variation in length-at-age for older ages, no minimum size limit was able to restrict F to specific older ages classes based on the AAFC analysis.

Table 7.4: The effect of age-at-last-capture (AALC) on $F_{CRITICAL}$ and $U_{CRITICAL}$ for *Carcharhinus albimarginatus* and *Carcharhinus limbatus*. The length-at-age estimates are sourced from Chapter 4 and 6 and include standard error (S.E) calculated from the variation in the growth curves.

AALC (years)	$F_{critical}$	U_{critical}	Length-at-age ± S.E (cm)
		Carcharhinus albimarginatus	
1	1.18	0.69	79.3 (± 3.6)
2	0.61	0.46	87.6 (± 5.5)
3	0.40	0.33	95.7 (± 7.4)
4	0.30	0.26	103.6 (± 9.3)
5	0.25	0.22	111.4 (± 11.1)
6	0.21	0.19	119.1 (± 12.9)
7	0.18	0.16	126.6 (± 14.6)
8	0.15	0.14	134.0 (± 16.3)
9	0.13	0.12	141.2 (± 18.0)
10	0.12	0.11	148.2 (± 19.7)
		Carcharhinus limbatus	
1	0.48	0.38	83.2 (± 16.6)
2	0.24	0.21	102.0 (± 22.8)
3	0.17	0.16	118.9 (± 28.4)
4	0.12	0.11	134.0 (± 33.4)
5	0.10	0.10	147.6 (± 37.9)

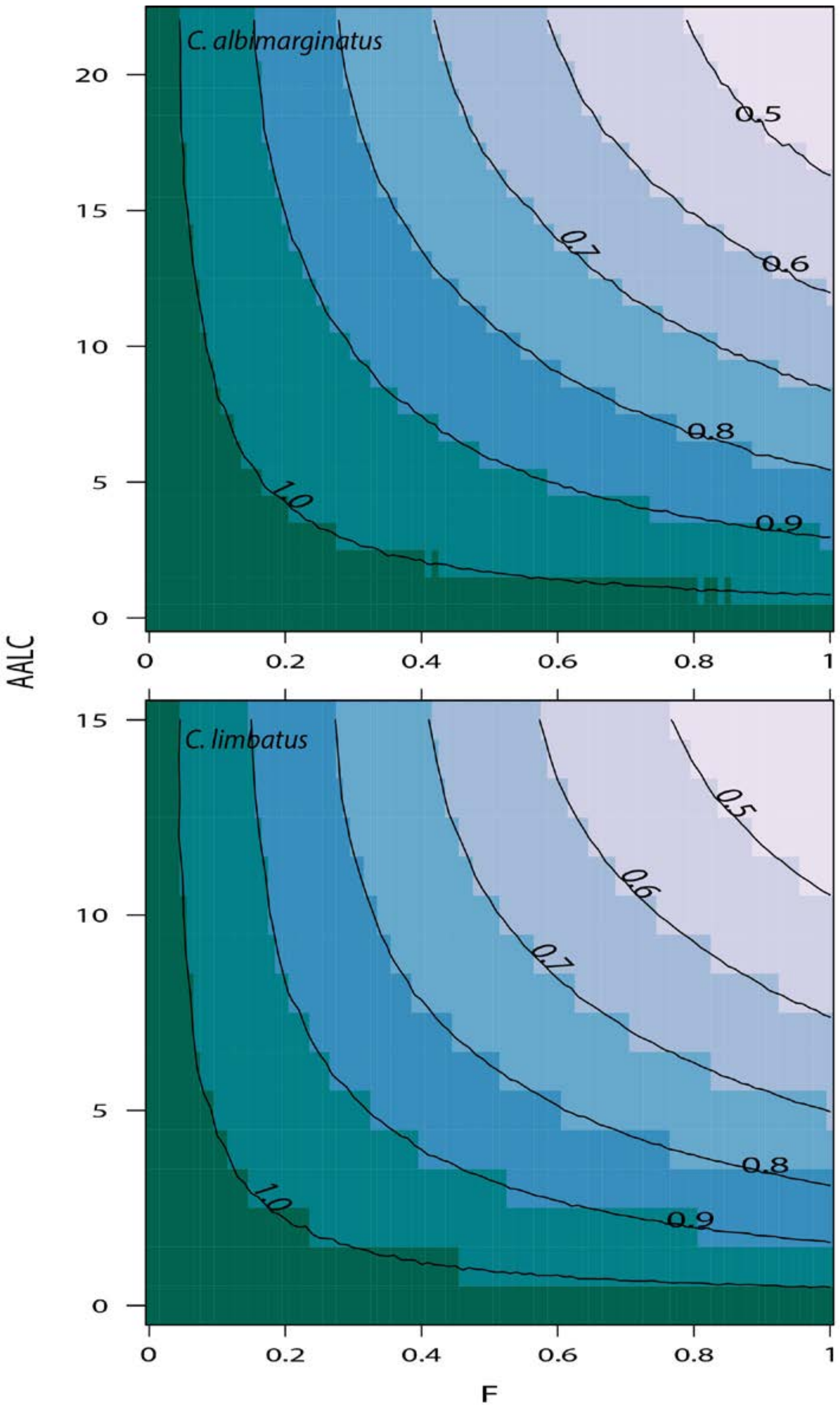

Figure 7.6: Contour plot of finite rate of population increase (λ) as a function of fishing mortality (F) and age-at-last-capture (AALC) for *Carcharhinus albimarginatus* and *Carcharhinus limbatus*. Estimates of λ were estimated using Monte Carlo Simulations to incorporate stochasticity. An increasing population occurs when $\lambda > 1$ (Dark green area).

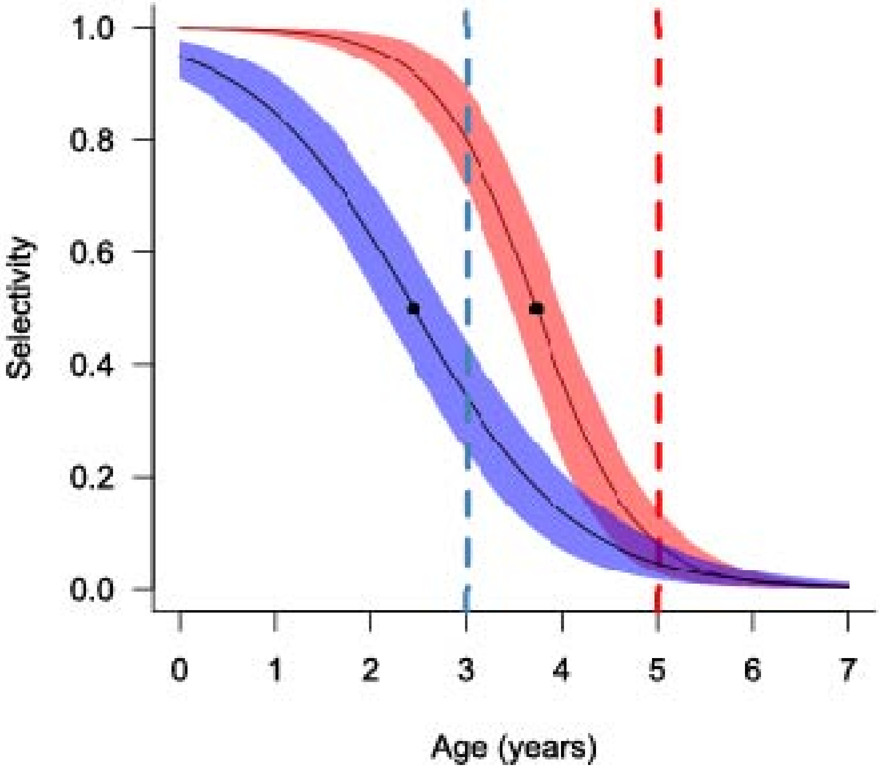

Figure 7.7: Selectivity-at-age for both species at a maximum size limit of 100 cm TL. *Carcharhinus limbatus* is represented by the blue curve with bootstrapped 95% confidence intervals represented by the shaded area. The dashed blue line represents the age-class where an *F* of 0.17 yr^{-1} was sustainable according the AALC analysis. *Carcharhinus albimarginatus* is represented by the red curve with bootstrapped 95% confidence intervals represented by the shaded area. The dashed red line represents the age-class where an *F* of 0.25 yr^{-1} was sustainable according the AALC analysis.

7.4 Discussion

The present study provides an improved understanding of the population biology and demography of harvested sharks in the Indo-Pacific and importantly, predicts how their populations may respond to different management approaches. The demographic estimates show that both *C. albimarginatus* and *C. limbatus* lack the propensity to be harvested sustainably unless fishing is limited to specific age-classes. If the entire age ranges of either species are exposed to fisheries, then overfishing (population declines that do not equilibrate) will occur at very low levels of F (> 0.1 yr^{-1}). Of the different management scenarios examined, the exclusive harvest of YOY individuals was the most sustainable fishing strategy for both species. *Carcharhinus albimarginatus* is one of the least studied reef associated shark species and prior to this study little was known about its demography or the impacts of fishing on its population. While demographic analyses have been conducted on *C. limbatus* populations (Cortés 1998, 2002, Chen and Yuan 2006, Liu et al. 2015), these analyses were lacking for the Indo-Pacific population which grows larger and matures later than its Atlantic Ocean conspecifics (Chapter 4).

Estimates of λ are highly variable for elasmobranchs and can be as high as 1.6 yr^{-1} and 1.4 yr^{-1} for species such as the scalloped hammerhead (*Sphyrna lewinii*) and blue shark (*Prionace glauca*), respectively (Cortés 2002). However, many slow growing and long lived shark species have much lower λ as they are less productive (Cortés 2002, Liu et al. 2015). *Carcharhinus albimarginatus* and *C. limbatus* are two such species as they had slow population growth rates (λ = 1.07 yr^{-1} for both species) when their populations were unfished. The population growth rates of both species declined markedly as low levels of F were introduced to the demographic analyses. When F = 0.1 yr^{-1}, both populations declined by 3% per year and when F was increased to 0.3 yr^{-1} they declined by more than 20% per year. The susceptibility of both species to overfishing is due to their slow life histories with *C. albimarginatus* particularly susceptible due to its long generation length (G). These demographic results coupled with late maturity meant that neither species were able to tolerate moderate levels of harvest when their entire age ranges were exposed to fishing.

Failure to account for any uncertainty or variation in vital rates could potentially jeopardise the accuracy of λ – the most important demographic parameter (Caswell et al. 1998). This study accounted for this uncertainty and variation by using Monte Carlo simulations to provide summary statistics around demographic parameters (Cortés 2002, Beerkircher et al. 2003, Coelho et al. 2015). While the means of λ, G, and R_0 fell within expected ranges, the Monte Carlo simulations showed broad variation around each parameter. The elasticity analyses identified that the majority of this variation resulted from changes to survivorship elements (particularly for juveniles) during the Monte Carlo simulations. Elasticity analyses identify which matrix elements have the greatest proportional effect on λ (de Kroon et al. 1986). For both species, matrix elasticities were low for fertility and highest for juvenile and adult survivorship. By producing matrix elasticities in the Monte Carlo simulations, variation and uncertainty were also factored into these analyses (Cortés 2002). These simulations demonstrated that some variation occurred around juvenile and adult survivorship elasticities but very little around fertility. This indicates that varying vital rates that affected fertility produced few changes to λ while altering M and F had the greatest influence.

As vital rates are used to construct matrix elements they must be carefully scrutinised so that overconfidence in the resulting demographic estimates do not mislead management. The life history parameters of both species were drawn from multiple life history studies (Chapter 4, Chapter 6, Bass et al. 1973, Wheeler 1962, White 2007) and many of these parameters (e.g. 12-month gestation period and biennial reproductive cycle) are typical of the genus *Carcharhinus* (Last and Stevens 2009). While the litter sizes were variable for both species, these were empirical values recorded in the field (Wheeler 1962, Bass et al. 1973, White 2007) and thus confidence can be placed around their means and ranges. The greatest uncertainty in these life history parameters is around t_{max} and α as these parameters were drawn from life history studies with limited samples (Chapter 4 and Chapter 6). However, the elasticities for both species determined that fertility elements had little influence on λ in comparison to survivorship. Therefore, small deviations from true population values of reproductive and longevity parameters would have little effect in comparison to inaccurate *M* estimates. This is problematic as *M* is one of the most difficult parameters to estimate for marine taxa (Kenchington 2014). The estimates of *M* produced for both species varied between approaches and therefore this vital rate had the most uncertainty. While this study has accounted for this uncertainty by incorporating Monte Carlo simulations, its results should still be interpreted with caution until more definitive estimates of *M* are available for both species.

The demographic estimates produced for both species are within expected ranges as they are comparable to those of similar whaler shark species (family: Carcharhinidae). When Leslie Matrices with Monte Carlo simulations were applied to a range of shark species; large whaler sharks (maximum size > 2.5m TL) typically had mean λ of 1.02 – 1.06 yr^{-1} when the populations were unfished (Cortés 2002). The unfished populations of *C. albimarginatus* and *C. limbatus* corresponded to this as they both had a mean λ of 1.07 yr^{-1}. Previous demographic studies on large whaler sharks that also included *F* found similar results to the present study. Life table analyses performed on silky sharks (*C. falciformis*) estimated that $r = 0.05$ yr^{-1} ($\lambda = 1.05$ yr^{-1}) when the population was unfished. However, the population declined as *F* approached 0.5 (Beerkircher et al. 2003). Similarly, sandbar shark (*C. plumbeus*) populations in the US were determined to increase at a rate of 1.3 % per year when unfished but declined when low levels of *F* were applied across all age-classes (Cortés 1999). When a range of fishing strategies were examined, it was determined and that large juveniles (100 – 150 cm TL) were the most vulnerable life stage (Cortés 1999). However, if harvest was limited to only YOY *C. plumbeus* then this age-class could be fished sustainably at low levels (Cortés 1999).

The exclusive harvest of juveniles through gauntlet fisheries has been demonstrated as one of the most sustainable management strategies for shark fisheries (Prince 2005). It relies on the principle that when *M* is high for juvenile age-classes, it can be replaced by *F* without affecting the population growth (Cortés et al. 2012). As long as only the juveniles are harvested, the breeding stock is protected and can replace the young sharks taken by the fishery. The most successful example of this strategy is the dusky shark (*C. obscurus*) gillnet fishery in Western Australia (WA) (Simpfendorfer 1999b, McAuley et al. 2007). *Carcharhinus obscurus* had a low *r* of 0.04 yr^{-1} ($\lambda = 1.04$ yr^{-1}) and an

$F_{CRITICAL}$ of 0.04 yr^{-1} when all age-classes were exposed to fishing (Simpfendorfer 1999b). However, when fishing was limited to YOY, up to 64 % ($F_{CRITICAL}$ = 1.04 yr^{-1}) could be harvested before the population would decline (Simpfendorfer 1999b). The present study determined that a similar strategy could be applied for *C. albimarginatus* and *C. limbatus* as up to 69% ($F_{CRITICAL}$ = 1.18 yr^{-1}) and 38% ($F_{CRITICAL}$ = 0.48 yr^{-1}) of YOY, respectively can be harvested without population declines until density dependent effects begin to manifest. However, with this management strategy it is imperative that fishing be limited to these age-classes (Simpfendorfer 1999b, McAuley et al. 2007). If the juveniles and adults were also caught by the fishery (even at low levels) then a gauntlet strategy would fail and the population would decline.

In addition to examining a gauntlet fishery scenario, this study examined the efficacy of protecting the juvenile age-classes to maintain sustainable harvest levels. This management strategy can be particularly effective for small and productive shark species (Simpfendorfer 1999a) but less effective for large less productive shark species (Cortés 1998). The AAFC analysis in this study demonstrated that a stable population would not occur for either species unless all immature age-classes were protected from fishing. Given that *C. albimarginatus* and *C. limbatus* mature at 14.8 and 7.6 years respectively (Chapter 4 and Chapter 6), a large portion of the population would need to be protected for this management strategy to succeed. However, catches of *C. limbatus* from Indonesia show that the majority of landed individuals were juveniles (White 2007). Similarly, the age-classes included in Chapter 6 show that mostly immature *C. albimarginatus* were caught by PNG longline fisheries. Delaying harvest until these species mature to achieve sustainable F levels would potentially maximise conflict with fishers and would also risk recruitment overfishing (Cortés 1998). Therefore, management strategies that focus on protecting immature age-classes would likely be ineffective and difficult to regulate for both populations.

While both species had similar life history and demographic estimates, subtle differences in management are required to maintain sustainable harvest levels. *Carcharhinus albimarginatus* could sustain higher levels of YOY and juvenile harvest than *C. limbatus.* This is due to *C. albimarginatus* having higher reproductive values (left eigenvector; v) across age-classes. Reproductive values define the relative contribution to future population growth that an individual in a particular age-class is expected to make (Morris and Doak 2002). Therefore, as YOY and younger juvenile age-classes contribute little to future population growth, these individuals can sustain moderate harvest through gauntlet fishing without detriment to the population. As *C. albimarginatus* has higher v across its adult age-classes, it is able to replace harvested age-classes at a greater rate than *C. limbatus* – sustaining higher levels of F. Therefore, when only the YOY are fished, *C. albimarginatus* can sustain an F of 1.18 yr^{-1} (U = 0.69 yr^{-1}) while *C. limbatus* can sustain an F of 0.48 yr^{-1} (U = 0.38 yr^{-1}), until density dependent effects occur. While both species have different growth profiles (Chapter 4 and Chapter 6), a maximum size limit of 100 cm TL would restrict fishing to age-classes that can sustain higher levels of F for both species. This size limit would encapsulate individuals up to an age of 3 for *C. limbatus* and 5 for *C. albimarginatus*, thus allowing for an increased $F_{CRITICAL}$ of 0.17 yr^{-1} and 0.25 yr^{-1}, respectively.

The harvest strategies presented in this study demonstrate with appropriate management, both *C. albimarginatus* and *C. limbatus* can be fished without their populations declining. Critically though, only limited information is available on either species stock status, posing a serious challenge for stock assessments (Brooks et al. 2010). A current F is required to determine whether a stock has been overfished, and an estimate of biomass or a time series of relative abundance is needed to evaluate overfishing criteria (Cortés et al. 2012). Furthermore, a lack of catch information from artisanal and subsistence fisheries will provide challenges in estimating these analytical reference points and provide difficultly in scaling sustainable harvest levels (Brooks et al. 2010). For a gauntlet fishery to be sustainable, the older age-classes must be protected from fishing (Simpfendorfer 1999b, Prince 2005). Total protection of older age-classes can be a difficult task even in well managed fisheries (McAuley et al. 2007). Subsequently, restricting fishing effort to the necessary length-classes may prove difficult in developing nations where subsistence and artisanal fisheries are complex, dispersed and difficult to monitor and manage. With this in mind, the most conservative approach to sustaining both populations would be to the limit F on the young adults and first breeders by implementing a maximum size limit of 100 cm TL. This precautionary measure is warranted as mature individuals require the greatest protection (Cortés et al. 2012). The target level of *F* for these age-classes should also be set at a conservative level which is lower than the maxima provided by this study as some uncertainty still exists around these demographic parameters. Further studies that attempt to directly estimate *M* would be beneficial as this vital rate was the most uncertain for these species and had the most influence over the matrix analyses. Therefore, a better understanding of *M* can lead to more robust assessments being undertaken. Once more detailed data on catch, fishing effort and species abundance on the fisheries are available, the results of this study can be combined with other derived analytical reference points. This will then determine if these populations have been overfished and establish the best approach to ensure they are harvested sustainably into the future.

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Chapter 8

General Discussion

8.1 Conclusions and Implications

Many species of sharks and rays are long lived, late maturing and have very low fecundity (Musick 1999). These traits have often propagated views that shark fisheries are largely unsustainable (Holden 1974). The life histories of many shark species mean that they can be easily overfished (Musick et al. 2000). However, it is important not to overlook the fact that many shark species are fished sustainably and have been for some time. Good examples of this come from the gummy shark fishery in Australia (Walker 1998), rig in New Zealand (Francis 2003), and several species of large whaler sharks (genus: *Carcharhinus*) in the US (Cortés et al. 2002, SEDAR 2012). The key to developing these sustainable fisheries was a good understanding of the species life histories and determining fishing strategies that would allow them to be harvested at sustainable levels (Walker 1998). The life history and demographic estimates produced by this dissertation provide baseline information that can be used to assess the shark stocks of Indonesia and Papua New Guinea (PNG). While aspects of the regions shark fisheries are still poorly understood, knowledge of the susceptibility of various species to fishing provides useful information towards the management of these fisheries until more detailed fisheries information becomes available.

Estimates of age and growth are the most important piece of life history information as they are used to determine the schedule of events throughout a species life time. Accurate length-at-age estimates are therefore necessary to add age-structure to a variety of fisheries models. Additionally, the growth parameters derived from length-at-age analysis (Asymptotic length [L_∞] and growth completion parameters [k, g_{Gom} and g_{log}]) are needed to facilitate further analyses such as mortality estimation or yield per recruit analysis (Beverton and Holt 1957, Pauly 1980). Despite this importance, the process of estimating age and growth information has historically been very diverse. A review by Cailliet et al. (2006) on age and growth studies for elasmobranchs provided standardisation to many aspects such as terminology and laboratory protocols. However, the one aspect of this field that continued to differ between studies was the approach to growth modelling. Chapter 2 addressed this by providing a comprehensive analysis of growth modelling approaches for elasmobranchs using empirical estimates from the literature – culminating in a best practice approach to standardise this field of study. These results indicated that using a multi-model approach that incorporated *AIC* and multi-model inference would provide the most robust estimates possible for a given set of data. Improvements to the resulting growth estimates were greatest at age-zero. This has important implications for elasmobranchs that are caught in gauntlet fisheries (where fishing effort is focused on juvenile age-classes) where accurate estimates of early growth are required to understand the age classes that are being harvested. However, the most interesting finding was that the long held hypothesis that certain candidate growth models (VBGF, Gompertz, logistic, etc.) would better suit certain taxa (sharks or batoids) or different reproductive modes was disproved (Cailliet and Goldman 2004). Therefore, a multi-model approach is required as the most appropriate model cannot be known until several candidate models have been fit to the data and compared.

This dissertation provides numerous outputs that can advance the field of age and growth studies for elasmobranchs. The newly defined best practice approach from Chapter 2 was applied to chapters 4, 5 and 6 to determine age and growth data for three species of whaler sharks from the Indo-Pacific: *Carcharhinus limbatus*, *C. amblyrhynchos* and *C. albimarginatus*. While the approach outlined in Chapter 2 maximised the accuracy of resulting growth estimates, issues remained with samples from all three species that needed to be addressed to produce accurate age and growth estimates. *Carcharhinus limbatus* and *C. albimarginatus* both required back-calculation techniques to overcome a small sample size and a lack of juveniles in their samples. This under sampling of the younger age classes occurred either due to longline gear selectivity which caught predominantly adult age-classes or that fishing did not take place in areas where juveniles occur (White et al. 2008). However, back-calculation techniques are well suited to this situation as they can account for missing juvenile age classes (Goldman et al. 2012, Smart et al. 2013). Therefore, these age classes were effectively accounted for *C. limbatus* and *C. albimarginatus* in Chapters 4 and 6, respectively. *Carcharhinus amblyrhynchos* (Chapter 5) did not require back-calculation due to an adequate sample being attained that produced biologically plausible growth estimates. However, one issue that arose in Chapter 5 was the occurrence of several species misidentifications. Accurate species identification has been previously highlighted as an issue for data collected by fisheries observers in tropical shark fisheries (Tillett et al. 2012). This is due to the large diversity of whaler sharks caught in the Indo-Pacific region and the similarities that some of these species have to one another (White et al. 2006). This was overcome in Chapter 5 with these results highlighting the need for accurate species identification when collecting samples for life history studies. This is a serious issue as population declines have occurred when inaccurate life history estimates led to overfishing, especially when incorrect age estimates were used in population models (Beamish and McFarlane 1995). Therefore, a key recommendation of this dissertation was the inclusion of digital cameras as part of observer sampling kits. This will provide an effective way to verify the identifications of specimens prior to their inclusion in life history analyses

There has been considerable conservation concern for *C. amblyrhynchos* as previous studies have highlighted it's susceptibility to population declines at low levels of fishing pressure (Robbins et al. 2006, Hisano et al. 2011). In PNG, *C. amblyrhynchos* constituted 11 % of the shark longline fishery catch (Kumoru 2003b) and also formed an important (yet unquantified) component of artisanal catches (Teh et al. 2014). However, only limited life history information was available for this species prior to the current research (Robbins 2006). The results of Chapter 5 demonstrated that the growth of the PNG population was slightly faster than the Australian population (Robbins 2006) and that both sexes matured earlier in the PNG population. This is an important outcome as previous demographic analyses performed on *C. amblyrhynchos* have shown that populations on the Great Barrier Reef (GBR) were declining (λ = < 1) even when the population was unfished (Robbins 2006, Robbins et al. 2006, Hisano et al. 2011). Therefore, it's possible that previous life history studies have underestimated its productivity as from a life history perspective a species should not have a declining population unless there is some non-natural source of mortality (such as fishing or habitat degradation). The exception to this is if the population size is close to unfished levels and is therefore at equilibrium (Gedamke et al. 2007). Furthermore, recent studies on the GBR have shown that *C. amblyrhynchos* populations are increasing in unfished marine protected areas (Espinoza et al. 2014).

Natural mortality (*M*) is likely to be the confounding parameter in previous demographic studies on *C. amblyrhynchos* (Robbins 2006, Hisano et al. 2011). Some scepticism exists around the process of indirectly estimating *M* based on other life history traits (Kenchington 2014). It's therefore possible that the reef associated ecology of *C. amblyrhynchos* means that it suffers less mortality than other species with similar life history characteristics from which many *M* estimation techniques were derived. Additionally, *C. amblyrhynchos* have a small litter size for a whaler shark species of its size (Robbins 2006). Therefore, a combination of low fecundity and overestimated *M* may lead to underestimated and pessimistic demographic estimates. The results of Chapter 5 predict a rate of productivity that is higher than these previous studies. Therefore, it's likely that future demographic analyses based on the results of Chapter 5 may provide more realistic information on the population status of the Indo-Pacific and Australian populations. However, future research will need to address the likely inadequacy of standard approaches to indirectly estimating *M* for *C. amblyrhynchos*.

The life history of *C. limbatus* had been studied extensively in other regions as this species has a circumglobal distribution (Branstetter 1987, Killam and Parsons 1989, Wintner and Cliff 1996, Carlson et al. 2006). However, these previous studies determined that regional differences occurred between populations. Therefore, despite a wealth of research having been conducted on *C. limbatus*, none of these life history estimates were suitable to use as surrogates for assessing the Indo-Pacific population. The results of Chapter 4 identified that the Indo-Pacific population grow larger, mature later and live longer than their US conspecifics (Branstetter 1987, Killam and Parsons 1989, Carlson et al. 2006). As such using this life history information from the US populations would have overestimated the productivity of the Indo-Pacific population. This could have potentially led to management strategies that would have resulted in overfishing. The demographic results of this species demonstrated that its relatively low productivity produced a slow population growth rate (λ) when the population was unfished (Chapter 7). Subsequently, even low levels of fishing pressure ($F =$

0.1) produced a declining population if all age classes were exposed to harvest. Therefore, this dissertation has demonstrated that this species could be easily overfished and requires population specific management

Silvertip sharks (*C. albimarginatus*) are one of the most under-represented whaler shark species in the scientific literature. Prior to this dissertation, only limited life history information was available which included preliminary data on litter sizes and maturity (Stevens 1984, White 2007). This paucity of data was caused by their patchy Indo-Pacific distribution (Ebert et al. 2013) and occurrence in remote areas which made them difficult to study. However, *C. albimarginatus* was caught regularly by artisanal fisheries in PNG as well as in commercial fisheries that operated around coral reefs (Kumoru 2003b). Therefore, this dissertation was able to collect sufficient samples that could be used to provide preliminary life history estimates for this population. This information was important as it now facilitates upcoming population assessments that will inform management. Preliminary assessments were undertaken in Chapter 7 which incorporated the results Chapter 6 as well as other life history studies (Stevens 1984, White 2007) to produce static demographic assessments. Chapter 6 identified that this species has low productivity which was predominantly caused by an age-at-maturity of 14.8 years for females. This low productivity resulted in demographic results that demonstrate its inability to withstand even low levels of fishing mortality ($F = 0.1$) and that when unfished it's population growth rate (λ) was 7% per year (Chapter 7).

The demographic estimates produced for *C. limbatus* and *C. albimarginatus* provide useful information that can be used in management. Chapter 7 identified that both species could successfully be harvested using a gauntlet fishery strategy – where F is focused on the youngest age-classes leaving the breeding stock intact to replenish these age-classes each year. This fishing strategy has been effectively applied in several shark fisheries and is viewed as the most sustainable way to harvest shark species with low productivity (Walker 1998, Simpfendorfer 1999b, Prince 2005). Chapter 7 identified that if a maximum size limit of 100 cm TL were imposed, up to 16% and 22% of this size class to be harvested for *C. limbatus* and *C. albimarginatus,* respectively, until density dependent effects begin to manifest. However, this strategy is dependent on completely excluding mature age-classes from fishing – a difficult task for many fisheries (McAuley et al. 2007).

The success of gauntlet fisheries is reliant on fishing gears that selectively catch younger age classes or fishing in areas where juveniles do not occur (Prince 2005). Both *C. limbatus* and *C. albimarginatus* are caught in artisanal and subsistence fisheries in PNG (Fig. 8.1) and Indonesia (White 2007) which are difficult to monitor and manage (Teh et al. 2014). If inshore artisanal fisheries operate using gill nets with mesh sizes less than 165 mm, then it is likely that the majority of their catch would be sharks less than 150 cm TL (Harry et al. 2011) – especially as inshore habitats function as nursery areas which adults emigrate from. Therefore, inshore species such as *C. limbatus* could likely be harvested sustainably by implementing a gauntlet fishery through gear restrictions. However, *C. albimarginatus* are rarely caught in gill nets as this fishing gear is impractical in reef environments as it easily becomes entangled on the substrate. Therefore, *C. albimarginatus* are caught using line fishing techniques which are less size selective. Artisanal fishers have developed specialised techniques for catching *C. albimarginatus* as this species is aggressive when fishing with bait and can easily be targeted (Fig. 8.2). These techniques typically catch larger individuals as it is selective towards the larger, more aggressive individuals (J. Smart unpublished data). Consequently, a gauntlet fishery may be difficult to implement for this species as the younger individuals are difficult to target and are rarely caught (as demonstrated by the sample used in Chapter 6). Given that predominantly adult *C. albimarginatus* are caught in this manner, gauntlet fishing would likely be difficult to implement. A better management solution would be to educate fishers on the importance of limiting F on the adults and mature breeders.

Photograph credit: W. White

Figure 8.1: Evidence of a) *Carcharhinus limbatus* and b) *Carcharhinus albimarginatus* in artisanal catches in PNG. The dorsal fin pictured in b) was genetically verified to be *C. albimarginatus* (W. White and S. Appleyard, unpublished data).

Figure 8.2: Fishers from Fisherman's Island, Central Province, Papua New Guinea demonstrate the gear they use to target *Carcharhinus albimarginatus* when line fishing from small vessels. The gear consists of a large un-submersible float connected to a circle hook via a wire leader. This gear is deployed when *C. albimarginatus* are attracted to the activities of line fishers. The float is left unattached to the vessel and is used to exhaust the shark once it's hooked. The fishers follow the float in their vessel and retrieve the shark once it is exhausted. This method can be used to catch larger individuals.

Coral reef associated shark species such as *C. amblyrhynchos* and *C. albimarginatus* may be more susceptible to exploitation that inshore species such as *C. limbatus*. Currently, the most sustainable approach to exploiting shark species with low productivities is to use gillnets to target juvenile length-classes (Simpfendorfer 1999b, Prince 2005). As coral reef associated species are rarely taken in gillnets, successfully implementing a gauntlet fishery may not be possible and therefore they are more likely to be overfished. Previous research on *C. amblyrhynchos* has demonstrated that this species can easily be overfished due to its low productivity (Robbins et al. 2006, Hisano et al. 2011). Chapter 7 also demonstrated that *C. albimarginatus* can also be easily overfished, especially if large individuals are caught by fisheries. Given these findings it is likely future management on these species should focus on their conservation rather than determining sustainable fishing strategies. Marine protected areas (MPAs) may provide the best solution as populations of *C. amblyrhynchos* have been demonstrated to increase in areas closed to fishing in the GBR (Espinoza et al. 2014). For species such as *C. albimarginatus*, the best MPA framework would involve protecting reefs that have higher abundances of this species rather than establishing a single large MPA (Espinoza et al. 2015b). This strategy could be implemented in PNG as *C. albimarginatus* catches are specific to certain regions in northern provinces (Kumoru 2003b). Therefore, establishing MPA’s in areas such of these may be the best strategy to limit further population declines.

Knowledge of a species life history and population structure is crucial for both conservation and effective fisheries management. This dissertation has elucidated on the life histories of *C. limbatus* and *C. amblyrhynchos* in the Indo-Pacific and has provided the first life history estimates for *C. albimarginatus*. Determining whether the populations of these species have declined is not possible due to a lack of time series abundance data (Cortés et al. 2012). However, inferences can be made from the demographic analyses performed in Chapter 7 and by Robbins (2006) which indicate that population declines have likely occurred for all three species. From this research it is evident that all three species require population management otherwise population declines will continue. The recent closure of the longline fishery will allow these populations an opportunity to recover in PNG.

However, further management may be needed in order to conserve these species. This will have to be balanced carefully with the food security needs of the region.

8.2 Future Research

Generating appropriate life history estimates is possible from small sample sizes (Chapter 4; 6, Smart et al. 2013). The life history estimates generated for *C. limbatus* and *C. albimarginatus* are an important step towards understanding their populations in the Indo-Pacific. However, large sample sizes are more ideal, especially for large shark species that typically have more variation in growth than smaller species. Additionally, larger sample sizes increase the likelihood that candidate growth models will produce divergent fits to one another – potentially increasing the accuracy of resulting growth estimates (Chapter 2). Collecting maximum size individuals should be a future priority as these individuals can have the most influence on resulting growth models (Haddon 2001). Missing younger age classes can have the same influence on growth models. However, these size classes can be accounted for through back-calculation whereas larger individuals cannot. The lack of asymptotic growth that occurred for *C. albimarginatus* (Chapter 6) was most likely caused by the absence of older individuals in the sample. These individuals can be difficult to encounter as they are the rarest demographic of the population – especially for exploited populations where fishing may prevent many individuals from reaching maximum age (Taylor and Methot 2013). As maximum size individuals were not included in the *C. albimarginatus* sample (Chapter 6) it is possible that future studies that include these individuals may demonstrate an asymptotic growth profile and an updated maximum age for the species.

Validating annual growth band deposition would also be beneficial for both *C. limbatus* and *C. albimarginatus*. Age validation can be undertaken using three techniques: 1) chemical mark and recapture, 2) bomb radiocarbon assays, and 3) marginal increment analysis (Goldman et al. 2012). All three of these techniques have prerequisites which precluded them from being performed in this dissertation. Chemical mark and recapture methods require at least one individual to be captured after being at liberty for more than one year. This can be impractical in regional and developing nation fisheries where the chances of recovering tagged individuals is low. However, this technique was applied with some success for *C. amblyrhynchos* – demonstrating that this species has annual growth band deposition (Robbins 2006). Marginal increment analysis requires samples are caught in each month of the year. While this was not achieved in this dissertation, continued sampling in the Indo-Pacific region may be able to achieve this. Bomb radio carbon assays typically require individuals that were born in a period where ocean levels of Δ^{14}C were high after nuclear testing (~1955-1970) (Andrews et al. 2011). This has been performed for several shark species with individuals born within this time range (Campana et al. 2002, Kneebone et al. 2008, Passerotti et al. 2010). However, more recent studies have not been able to use recent samples as they only included individuals born after this period (Andrews et al. 2011). As neither *C. limbatus* or *C. albimarginatus* are likely to have individuals this old, historical specimens would need to be used which are rare for these species. Recent developments have overcome this pre-requisite for bomb radio carbon dating by using Δ^{14}C reference datasets from corals that were still valid until 2004 (Andrews et al. 2013). Should similar Δ^{14}C reference data become available in the Indo-Pacific then future work could possibly use this approach to validate the ages of local shark species.

This dissertation has the ability to act as the foundation for a greater number of species assessments from the region. Sufficient life history data is available for several species from the Indo-Pacific (e.g. White 2007, Hall et al. 2012, Drew et al. 2015, D'Alberto et al. in press) which can be included in the Leslie matrix models outlined in this dissertation. By incorporating Monte Carlo simulations into these models, any remaining uncertainty around specific parameters can further be accounted for. Future research should therefore focus on applying these techniques for species that are at risk of overfishing and of concern to management. Ideally more comprehensive stock assessment models such as delay difference and surplus production models should be conducted in order to account for the historical effects of exploitation (Bonfil 2004). This would require a time-series data on species specific catches and indices of abundance – both of which are difficult to attain for marine species and are rarely available for sharks (Cortés et al. 2012, Cortés 2016, Dillingham et al. 2016). The ability to conduct these assessments will depend on the quality of data that has been collected by regional management authorities. However, given that the National Fisheries Authority (NFA) of PNG has been engaged with the shark longline fishery since the 1990’s through observer and log book programs (Kumoru 2003b), there is potential for more comprehensive fisheries and population assessments to be conducted in the future.

Indo-Pacific artisanal fisheries still remain largely unquantified which needs to be addressed. Marine resources play a crucial role in food security in both Indonesia and PNG (White and Kyne 2010) and the reliance on fisheries is expected to grow rapidly. The artisanal sector is the dominant component of fisheries in Indonesia; accounting for 80% of the total catch (Thia-Eng et al. 1997). Therefore, artisanal catches must be considered when determining species specific population management as many species will interact most with this sector. Information on catch compositions and fishing effort will be important to management and has been provided for Indonesian fisheries through an ACIAR project and its associated outputs (ACIAR 2004, White 2007, White and Dharmadi 2007, White et al. 2008, Blaber et al. 2009). However, little of this information is currently available for PNG. As subsistence catches make up two thirds of PNG’s unreported catch (Teh et al. 2014), a priority must be placed on better understanding the extent, impacts and dynamics of regional fisheries. In PNG, it is anticipated that the fish supply required to satisfy nutrition needs will increase by 64% by 2030 (Bell and Kronen 2009). Therefore, fishing pressure is expected to grow in coastal communities and will require greater effort by management authorities to ensure sustainability in the artisanal and subsistence sectors (Teh et al. 2014). The paucity of data on PNG’s shark fisheries is currently being addressed by an Australian Centre for International Agricultural Research (ACIAR) funded project: “Sustainable management of the shark resources of Papua New Guinea: socioeconomic and biological characteristics of the fishery”. This project aims to better understand the aspects of PNG’s shark fisheries and will eventually form the basis of management decisions. This dissertation has formed a part of this project and its results will be included in advice that is given to the local PNG management authority – the NFA.

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