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THE BIOLOGY AND ECOLOGY OF CARCHARHINIFORM SHARKS IN THE GULF OF PAPUA PRAWN TRAWL FISHERY

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For the degree of
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Statement of sources

Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

19th November 2019

Signed Date

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Google Scholar uses the phrase “stand on the shoulder of giants” which is originally attributed to the philosopher Bernard of Charters. This saying for me sums up my journey through this PhD candidature. For this thesis to finally be put together it has taken the support and might of many giants in my life and I pay tribute to them here.

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Contribution of others to the thesis

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Publications arising from this thesis

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Other co-authored publications not directly related to this thesis

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Grant, M. I., Smart, J. J., White, W. T., Chin, A., Baje, L. & Simpfendorfer, C. A. 2018. Life history characteristics of the silky shark *Carcharhinus falciformis* from the central west Pacific. *Marine and Freshwater Research,* 69**,** 562-573, 10.1071/MF17163.

Smart, J. J., Chin, A., Baje, L., Tobin, A. J., Simpfendorfer, C. A. & White, W. T. 2017. Life history of the silvertip shark *Carcharhinus albimarginatus* from Papua New Guinea. *Coral Reefs,* 36**,** 577-588, 10.1007/s0033.

White, W. T., Baje, L., Sabub, B., Appleyard, S. A., Pogonoski, J. J. & Mana, R. R. 2017. *Sharks and rays of Papua New Guinea,* Canberra Australian Centre for International Agricultural Research

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D'Alberto, B. M., Chin, A., Smart, J. J., Baje, L., White, W. T. & Simpfendorfer, C. A. 2016. Age, growth and maturity of oceanic whitetip shark *Carcharhinus longimanus* from Papua New Guinea. *Marine and Freshwater Research,* 68**,** 1118-1129, 10.1071/MF16165.

Smart, J. J., Chin, A., Baje, L., Green, M. E., Appleyard, S. A., Tobin, A. J., Simpfendorfer, C. A. & White, W. T. 2016. Effects of including misidentified sharks in life history analyses: A case study on the grey reef shark *Carcharhinus amblyrhynchos* from Papua New Guinea. *PloS one,* 11**,** e0153116.

White, W. T., Appleyard, S. A., Sabub, B., Kyne, P. M., Harris, M., Lis, R., Baje, L., Usu, T., Smart, J. J. & Corrigan, S. 2015. Rediscovery of the threatened river sharks, *Glyphis garricki* and *G. glyphis*, in Papua New Guinea. *PloS one,* 10**,** e0140075.

Abstract

The elasmobranch fauna of Papua New Guinea (PNG) and its interaction with fisheries has been poorly studied in the past. Fisheries generally adversely impact elasmobranchs due to their low productivity life histories. Without fishery and region specific data on elasmobranchs the impact on their populations cannot be fully understood and subsequent development of appropriate fisheries management and conservation measures cannot be achieved. The objectives of this thesis were to address some of these data gaps for the Gulf of Papua Prawn Fishery (GoPPF) in PNG through the assessment of biological and ecological parameters of species caught as bycatch and the development of an ecological risk assessment for all elasmobranch species caught in the fishery.

The ecological component of this work focused on the feeding relationships among the Australian blackspot shark *Carcharhinus coatesi*, the milk shark *Rhizoprionodon acutus* and the Australian sharpnose shark *Rhizoprionodon taylori*. *Rhizoprionodon acutus* had a more specific diet compared to the other species, feeding almost exclusively on teleosts while *C. coatesi* and *R. taylori* had more diverse diets that had greater overlap. The limited sampling in this study did not fully characterise the diets of the three species, however, it does provide the first empirical evidence of trophic relationships between these sympatric sharks and their prey for the Gulf of Papua.

The biology of *R. taylori* and *C. coatesi* was investigated through determination of their age, growth and maturity. Ages were determined from vertebrae samples. Length at age data were fitted to several models in a multi-model information theoretic approach to determine which model provided the best fit. Maturity was analysed using logistic regression of maturity categories recorded from samples combined with size and age data. These studies provide an understanding of the growth rate and pattern of each species and the length and age which males and females of each species reach reproductive maturity.

To assess the biology of *R. taylori,* 186 samples were collected comprising 131 females (31-66 cm TL) and 55 males (31-53 cm TL). The lack of small individuals close to the size at

birth made fitting of growth curves more difficult, two methods (fixed length at birth and additional zero aged individuals) accounting for this were trialled. The von Bertalanffy growth model provided the best fit to the data when used with a fixed length-at-birth (L_0 = 26 cm TL). Males (L_∞= 46 cm TL, k = 3.69 yr^{-1}, L_{50} = 41.7 cm TL and A_{50} = 0.5 years) grew at a faster rate and matured at smaller sizes and younger ages than females (L_∞ = 58 cm TL, k = 1.98 yr^{-1}, L_{50} = 47.0 cm TL and A_{50} = 0.93 years). However, none of the methods to account for the lack of small individuals fully accounted for this phenomenon, and hence the results remain uncertain. Despite this, the results reaffirm the rapid growth of this species and suggest that the Gulf of Papua population may grow at a faster rate than Australian populations. *Rhizoprionodon taylori* is possibly well placed to withstand current fishing pressure despite being a common bycatch species in the GoPPF. However, further research needs to be undertaken to estimate other key life history parameters to fully assess the population status of this exploited shark species.

Carcharhinus coatesi is a similar small bodied coastal shark to *R. taylori* but some differences were observed in its growth and maturity parameters. The von Bertalanffy growth model also fit the data best for *C. coatesi*; parameters were L_0 = 40.6 cm ± 0.8, L_∞ = 74.8 cm ± 2.1, k = 0.33 year^{1} ± 0.06. Length-at-maturity analysis indicated that males reach maturity at L_{50} = 66.3 cm (CI: 63.8, 71.4) and L_{95} = 71.6 (C1: 64.6, 74.2) cm while females matured at L_{50} = 71.4 cm (CI: 61.5, 72.01) and L_{95} = 72.5 cm (CI: 62.7, 74.0). Age-at-maturity estimates showed that both males (A_{50} = 5.1 years (CI: 4.6, 7.1), A_{95} = 6.4 years (CI: 5.1, 7.2) and females (A_{50} = 5.3 years (CI: 3.5, 8.7) and A_{95} = 7.4 (CI: 3.6, 8.8) years) reach maturity at about the same age, but in comparison to other small bodied carcharhinids, *C coatesi* has slower growth in early life stages and reaches maturity at a later age. This biological trait along with a small litter size indicates that the population of *C. coatesi* in the Gulf of Papua may be more susceptible to decline as a result of fishing.

An Ecological Risk Assessment (ERA) was conducted to estimate the susceptibility of species caught in the fishery and the potential for a species to recover from population declines due to fishing if they occur. Of the 39 elasmobranch species encountered as bycatch in the fishery 10 were classified as being at low risk, 26 subjected to medium risk and 3 at high risk. The species at high risk were the Australian blackspot shark *C. coatesi*, the

eyebrow wedgefish *Rhynchobatus palpebratus* and the blackspotted whipray *Maculabatis astra*. This is the first ERA conducted for this fishery. The findings provide fishery managers with information to implement an ecosystem-based approach to managing the fishery to reduce bycatch and improve the sustainability of the GoPPF.

This thesis has provided new information on the diet, age, growth, maturity and the potential risk of species suffering population declines from being caught in the GoPPF. These outcomes have implications for fisheries management and conservation of species in PNG and the surrounding regions. The areas of study begin to address current data gaps for this fishery and also set the foundation for future work to improve fisheries management and protect the survival of species through conservation measures in PNG.

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Chapter 1 General Introduction

Elasmobranchs (sharks and rays) are a subclass of Chondrichthyes (cartilaginous fishes) that have lived for more than 420 million years (Simpfendorfer and Dulvy, 2017). Elasmobranchs inhabit a variety of habitats but the majority of species are marine dwelling (Musick et al., 2004). As predators, sharks and rays are functional members of food chains that impede the population growth of their prey through direct feeding and by inducing anti-predator behaviour (Heithaus et al., 2008). The effect on prey communities is dependent on size, where large sharks in particular with few natural predators function as apex feeders with a strong top down influence on prey populations (Stevens et al., 2000). Smaller sized sharks and rays are regarded as meso-predators that provide an intermediate link between top and lower trophic levels (Kinney et al., 2011, Heupel et al., 2014).

In recent times, many elasmobranch populations have faced drastic population declines due to anthropogenic factors, in particular increasing global fisheries (Dulvy et al., 2014). The vulnerability of these fishes stems from the inability of their populations to regenerate within short time frames to compensate for the consistent loss of individuals harvested through fishing (Herndon et al., 2010). This is attributed to biological traits such as slow growth, late maturity and small litter sizes that are common among elasmobranch species (Stevens et al., 2000, Smith et al., 1998). It is now estimated that up to a quarter of all known elasmobranch species face some level of threat to their survival (Dulvy et al., 2014). Therefore there is growing international concern focused on the protection of these species (Camhi et al., 2009) and the possible ecological ramifications of the absence of strong predatory roles that elasmobranchs exert in aquatic food webs (Grubbs et al., 2016).

Improving the sustainability of fisheries is an important step in addressing the steady decline in elasmobranch populations. This requires fishery specific data on catches of sharks and rays and information about their taxonomy, life history and ecology. In particular, life history information is crucial to fisheries management because it provides fundamental biological characteristics such as the growth rate, size and age at first maturity, periodicity of reproduction, the number of young produced, and maximum age (Gallucci et al., 2006). Such information then forms the basis for wider demographic analyses which can estimate the risks of extinction (Pardo et al., 2016b) and be used in ecological risk assessments where full scale stock assessments are lacking (Braccini et al., 2006). Noting that life history traits can differ among populations of the same species in different localities (Lombardi-Carlson et al., 2003, White, 2007a) it is imperative to determine population and region specific parameters to provide more accurate management advice. An understanding of the ecological traits of species on the other hand further enhances knowledge of ecosystem processes (Barría et al., 2015) and is also a precursor for assessing the level of risk a fishery poses to vulnerable species. Ecological species information is vital for managing fisheries from an ecosystem perspective which is a management approach in line with modern practices of responsible fisheries (Astles et al., 2006).

The acquisition of fishery-specific data varies worldwide but generally many fisheries remain data poor despite many years of operation especially pertaining to bycatch (Barker and Schluessel, 2005). Although there are fisheries based on commercially valuable sharks and rays, a large portion of elasmobranch mortality is often caught incidentally and regarded as bycatch (Dulvy et al., 2008, James et al., 2016) . These are often ignored in standard data collection practices (Clarke et al., 2013), which means that in many instances fisheries managers do not know what species are caught and the rates at which they are exploited. Given the vulnerability of elasmobranch life histories it is possible that in regions of high fishing pressure many elasmobranch populations may have been overfished without detection. The lack of quantitative information on which to base fisheries management decisions is more severe in developing countries (Fuentes and de Leon Corral, 1997) and data collection in these regions will have potentially significant benefit for developing future management actions.

Papua New Guinea (PNG) is a developing nation located in a region of high marine biodiversity (Allen, 2008), including elasmobranchs (White et al., 2017b). In PNG, elasmobranchs have cultural, food security and socio-economic value through fisheries. Sharks and rays support livelihoods through subsistence and semi-economic fishing in coastal communities across 14 maritime provinces. Coastal fishers actively target elasmobranchs for their fins to be sold to domestic buyers and eventually reach international markets (Sabetian and Foale, 2006) while the meat from some more palatable species is sold locally. Sharks were also targeted in a dedicated shark longline fishery that ceased operation in mid-2014 (Usu et al., 2015, Smart et al., 2016a). In addition, a large proportion of elasmobranchs are harvested as bycatch in the industrial tuna longline, purse seine and trawl fisheries. Despite the varied uses of elasmobranch resources in PNG, there remains a paucity of research (White et al., 2015) to underpin improving and strengthening fishery management practices for the stocks that are impacted. In an effort to address this severe lack of information, recent research has been conducted on elasmobranch life history (Smart et al., 2017a, D'Alberto et al., 2016), demography (Smart et al., 2017b) and population connectivity (Green et al., 2019) for key species encountered mainly in the tuna and shark longline fisheries. However, there is a need for similar work to be done with respect to the coastal and trawl fisheries.

The Gulf of Papua Prawn Fishery (GoPPF) is currently the only trawl fishery operating in PNG, supplying domestic and international markets with wild caught prawns. Trawling operations are concentrated in the inshore areas of the Gulf of Papua (GoP) and capture a variety of bycatch in the trawl nets, including elasmobranchs. Despite a 40 year history of the fishery, the species composition of elasmobranch bycatch has only recently been established (White et al., 2019). Trawl fisheries, particularly in regions of high bio-diversity such as PNG, impact a wide range of species due to the gear type and the method of fishing used (Oliver et al., 2015). This scenario, alongside poor data collection on bycatch, leaves scarce information to assess the sustainability of impacted populations. Therefore, this research was aimed at further advancing investigations into the biology and ecology of common bycatch species, and the sustainability of elasmobranch bycatch in the GoPPF. In order to achieve these aims, this thesis comprises a literature review and four main data chapters: Chapters 2 and 3 focus on the ecological component of this thesis. Chapter 2 is a literature review on research that has contributed to the understanding of resource partitioning in elasmobranchs while Chapter 3 explores the dietary overlap of three sympatric shark species. Chapters 4 and 5 examine life history of two of the three key shark species that are most commonly captured in the GoPPF and were featured in Chapter 3; and to investigate the effect of the fishery on the entire range of elasmobranch bycatch in the fishery, Chapter 6 is an ecological risk assessment to identify species that are most at risk from impact of commercial prawn trawling in the Gulf of Papua.

Chapter 2 Resource partitioning in elasmobranchs: a review

2.1 Introduction

The ecological niche of one organism overlaps with another when they use the same resources that are available to them in the environment. The interaction becomes competitive when shared resources are limited (Krebs, 2009) which can lead to the decline in population size and eventual extinction of a species (Schoener, 1974). A theory originally postulated by Gregory Gause implies that species cannot co-exist for long periods if they use very similar resources (Schoener, 1974). However, in nature great numbers of species are able to co-exist and seemingly share resources. Resource partitioning is recognised as a mechanism used to circumvent the harmful consequences of competition and enable co-existence, maintaining biodiversity in terrestrial and aquatic systems (Chesson, 2000). In general, the dimensions across which the use of resources can be divided are food, habitat, and time. An early review of resource partitioning studies on fish revealed that partitioning is most likely to occur by trophic differences, followed by space use and finally temporal separation (Ross, 1986).

Earlier studies of resource partitioning conducted on fish species were based on teleost species and largely ignored elasmobranchs (sharks and rays) (Ross, 1986) though they play a key role in shaping the structure of marine ecosystems (Heithaus, 2004). Their ecological roles as top-level and meso-predators is understood on a general level but are still being defined in variable contexts (Heupel et al., 2014). Furthermore, the direct feeding interactions of elasmobranchs and the indirect consequences of their presence such as inducing behavioural changes in prey species is yet to be fully investigated (Heithaus et al., 2008). The decline of elasmobranch populations due to various anthropogenic effects can lead to ecosystem shifts in the diversity and abundance of marine species which results in further changes in the food web. Over the past three decades there has been a gradual increase in the number of studies focused on the ecology of elasmobranchs which has also integrated assessments of resource partitioning. Ultimately these studies provide an understanding of the role of elasmobranchs in ecosystems (Simpfendorfer et al., 2011) and enable changes in communities as a result of declining elasmobranch populations to be predicted (Shipley et al., 2018).

Knowledge of elasmobranch resource use patterns aids in conservation planning and the management of fisheries from an ecosystem perspective (Munroe et al., 2014, Bethea et al., 2004). Studies have focused on dietary, spatial and temporal partitioning using a range of methods to focus on a single species, sympatric elasmobranchs, or groups of co-occurring elasmobranch and non-elasmobranch species. The extent of resource use overlap in food consumption or space use indicates the level of competition for resources. While this body of work has contributed to a more in-depth understanding of elasmobranch interactions across the various resource use planes individually, it has also revealed that the ecology in this group of fishes is dynamic and resource partitioning across all scales are interrelated to maintain co-existence of species. This chapter reviews the existing literature on resource partitioning in elasmobranchs with the following objectives: (1) describe resource partitioning identified among elasmobranchs (2) outline the methods used in studies (3) identify gaps and avenues for future research.

2.2 Article selection and outcome

Key words were used to identify studies that directly examined the occurrence of resource partitioning or inferred resource partitioning from characterisation of diets or spatial use patterns. The key search terms included elasmobranch, shark, rays and partitioning. Criteria for including a paper in this review included work that examined the diets, habitat use and seasonal patterns of habitat use of elasmobranchs as well as studies that discussed the main methodology used in fish resource partitioning studies. A total of 56 studies were identified (Table 2-1). The greatest proportion (38%) of studies were focused on sharks. Studies on rays made up only 24% of the included papers, and the remainder of studies focused on co-occurring sharks and rays (23%) and elasmobranchs and other sympatric species (16%). The majority of studies focused on characterising trophic traits of species and dietary partitioning. Habitat information was dominated by the determination of nursery areas and space use within these sites. The occurrence of partitioning or potential for it was recorded in the majority of studies with a minimal number of investigations not finding any evidence.

Table 2-1: List of studies on elasmobranch resource partitioning

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
Heupel et al. (2019)	North East Coast Australia	Examine space use, movement and habitat use of sharks in a coastal bay to determine niche partitioning.	Acoustic telemetry	Tropical nearshore embayment	6			Spatial partitioning
Shiffman et al. (2019)	Florida	Hypothesise that similar prey availability and overlap of study species ranges the relative isotopic niche area and core isotopic niche overlap and other trophic interactions would remain constant across different habitats.	Stable isotope analysis	Bay and reef	11			Dietary partitioning between two species at one habitat but not observed at a neighbouring different habitat where both species were also present.
Curnick et al. (2019)	British Indian Ocean Territory	Examine resource partitioning and seasonal variation in resource use.	Stable isotope analysis	Reef	2			Temporal dietary partitioning.
Shipley et al. (2018)	Bahamas	Hypothesise that resource partitioning of food enables co-occurrence of species in relatively high abundance which will be	Stable isotope analysis	Benthic	1	2		Possible dietary or food partitioning among rays.

Study	Location	Objective	Method	Habitat	Shark species	Ray species	Other species	Outcome: Type of partitioning exhibited
		shown in a diverse range of trophic resource pools.						
Valls et al. (2017)	Mediterranean	Investigate the trophic relationship of elasmobranch and cephalopods to determine feeding strategies and resource partitioning.	Stomach content and stable isotope analysis.	Deep sea	5	18	cephalopod	Food partitioning
Gallagher et al. (2017)	Southeastern USA	Investigated inferred trophic position, isotopic niche overlap and patterns of resource use and compared this to abundance information from the study area.	Stable isotope analysis, estimates of abundance and occurrence from empirical shark surveys	Bay	3			No resource partitioning in prey rich area but possible selective feeding overtime.
Bangley and Rulifson (2017)	North Carolina USA	Investigate habitat use incorporating set time in a fishery - independent sampling to also focus on transition from diurnal to nocturnal periods to account for potential temporal effects on habitat preferences and resource partitioning among elasmobranchs.	Multi-gear fishery independent surveys.	Estuarine	9	4		Temporal partitioning among three species and spatial partitioning among two species.
Gracan et al. (2017)	continental shelf of the Adriatic Sea	To determine the diet, feeding ecology and trophic position.	Fishery dependent sampling, sharks collected from	Continental shelf	2			Seasonal dietary partitioning

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
			commercial trawlers.					
Matich et al. (2017a)	Florida Everglades	Investigate if abundant large bodied species (aquatic reptiles, elasmobranchs, marine mammals and teleost fishes) partition resources and habitat in low productivity environment.	Stable isotope analysis, acoustic telemetry, visual surveys, published diet and life history demographic information.	Estuary	1		alligators, 2 teleosts and bottlenose dolphins	Potential dietary and seasonal habitat use.
Matich et al. (2017b)	French Polynesia	Test the hypothesis that niche segregation occurs in response to potential completion for food resources between co-occurring shark species within their nursery habitats.	Stable isotope analysis.	Coral reef lagoon	2			Dietary partitioning only when both species are present one area.
Amariles et al. (2017)	Colombian Pacific	Examine feeding habits and trophic relationships between species and evaluate trophic overlap or partitioning.	Stomach content analysis	Coastal region	2			Dietary partitioning
Estupinan-Montano et al. (2017)	Malpelo Island, Colombia	Describe trophic ecology.	Stable isotope analysis	Coastal	2			Dietary and habitat partitioning.

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
Shaw et al. (2016)	South Carolina, USA	Examine the trophic ecology of estuarine dependent predatory fish, analyse dietary niche overlap and infer potential prey.	Stable isotope analysis	Bay or estuary area	6	1	3 teleost	Dietary partitioning
Pardo et al. (2015)	Moreton Bay, Australia	Investigate dietary partitioning between species.	Stomach content analysis	Intertidal flat		3		Dietary partitioning
Raoult et al. (2015)	Tasmania, Australia	Test the hypothesis that species will feed on different prey at different trophic levels to reduce overlap and competition despite similar morphology.	Stable isotope analysis	Coastal	2			Dietary partitioning - species feed at different trophic levels.
Varghese et al. (2014)	India, Arabian Sea	To understand prey species composition, trophic level, diet overlap and trophic organisation.	Stomach content analysis	Pelagic	2	1	9 other pelagic species	Temporal partitioning though diurnal and nocturnal feeding to avoid competition
Szczepanski and Bengtson (2014)	Delaware Bay, USA	Examine diet and analyse how feeding habits may change temporally and ontogenetically.	Stomach content analysis and, fisheries independent trawl surveys.			1		Ontogenetic dietary partitioning
Bornatowski et al. (2014b)	Brazil	Analyse and compare the diet of co-occurring species.	Stomach content analysis from fishery landings.	Coastal bay		4		Dietary partitioning through differing diets.

Study	Location	Objective	Method	Habitat	Shark species	Ray species	Other species	Outcome: Type of partitioning exhibited
Kiszka et al. (2014)	Southwestern Madagascar	Assess the trophic relationships, isotopic niche breath and overlap as well as ontogenetic variation in trophic interactions.	Stable isotope analysis	Coastal	3	1		Possibly diet and habitat partitioning also by size and sex.
Tillett et al. (2014)	Northern Australia	Determine degree of dietary overlap, differences in type and proportion of prey among species, determine if prey type increases with maturity and correlates with adult feeding patterns and analyse if dietary partitioning occurs by sex.	Stomach content analysis	Gulf area	3			Possible spatial and temporal partitioning among juveniles, and possible dietary differences.
O'Shea et al. (2013)	Western Australia	Feeding biology and dietary preferences were examined in order to determine if sympatric species partition diets according to the degree of overlap in occupied habitats, so that species with differences in spatial and temporal scales will have the lowest diet overlap.	Stomach content and sediment analysis.	Coral reef lagoon		5		Diet partitioning for one species, the other four species may partition resource use by time and space (habitat).
Taylor and Bennett (2013)	Moreton Bay, Australia	Identify species composition and sex ratio to determine size at birth and timing of parturition. To identify size related patterns of occurrence and determine extent to which shark assemblage varies among months and seasons.	Commercial gillnet catches and fishery independent surveys.	Bay	13			Temporal partitioning

Study	Location	Objective	Method	Habitat	Shark species	Ray species	Other species	Outcome: Type of partitioning exhibited
Tilley et al. (2013)	Belize	Determine the ecological niche of a species and compare it to other sympatric elasmobranchs.	Stable isotope analysis	Reef atoll	2	1		Dietary partitioning among two shark species.
Heithaus et al. (2013)	Shark Bay, Western Australia	Investigate trophic positions and isotopic niches, overlap of isotopic niches among species, relationship between body size and relative trophic position and possibility for individual dietary specialisation.	Stable isotope analysis	Inshore bay	11	1	1 (dolphin)	Trophic resource partitioning based on non-overlapping stable isotope results.
Navarro-Gonzalez et al. (2012)	Mexico	Describe and analyse feeding habits and dietary similarities.	Stomach content analysis			6		
Vaudo and Heithaus (2012)	Western Australia	Investigate residency patterns of species and diel-patterns of habitat use to test the hypothesis that individuals spend more time in near-shore microhabitats, left the sandflats during the night and spent less time on the sand flats during the cold seasons.	Acoustic telemetry	Shallow mud flat in bay.		4		No apparent temporal or spatial partitioning.
Barbini and Lucifora (2012)	Southwestern Atlantic	Analyse inter-specific relationship in diets between two morphologically similar species.	Stomach content analysis	Coastal zone		2		Both species exhibited different dietary traits and therefore partitioned food resources.

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
Rogers et al. (2012)	South Australia	Examine, quantify and compare diets of pelagic sharks in a continental shelf region and adjacent gulf regions.	Stomach content analysis	Pelagic	5			Potential dietary partitioning. Specialised diet in one species.
Jacobsen and Bennett (2012)	Northeastern Australia	Describe diets and examine intra and inter specific differences in diet compositions.	Stomach content analysis	Coastal temperate and tropical waters.		3		Possible dietary partitioning linked to differences in prey proportion among species, size and morphology.
Yick et al. (2011)	Australia	Describe the diet and assess the level of dietary resource partitioning.	Stomach content analysis	Bay		2		Dietary partitioning through specialisation on different prey taxa despite feeding on similar prey.
Dale et al. (2011)	Kanehoe Bay, Hawaii	Quantify the foraging ecology and habitat use and evaluate the extent of ecological interactions.	Stomach content analysis and bulk amino acid stable isotope analysis.	Marine bay	1	1		Dietary partitioning

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
Speed et al. (2011)	Northwestern Australia	Hypothesise that aggregations are due to reproductive purposes and use of site as nursery area, species and size classes partition by space use and time, species use site as a refuge through diel patterns of attendance and species show long term site fidelity.	Acoustic telemetry and visual census.	Inshore bay	4			No evidence of partitioning.
Vaudo and Heithaus (2011)	Shark Bay, Western Australia	Examine the trophic niches of a nearshore elasmobranch community.	Stomach content and stable isotope analyses.	Marine bay	2	11		No clear evidence of differences in diets but attribute co-existence and high diversity to individual specialisation.
Sommerville et al. (2011)	Southwestern Australia	Examine similarities in diets of species and how this change with body size and season.	Stomach content analysis	Coastal region	1	3		Diets change seasonally and intra-and inter-specific differences in diets facilitate co-existence through food partitioning.
Kinney et al. (2011)	Cleveland Bay, QLD, Australia	Assess the extent of dietary partitioning within and established shark nursery.	Stable isotope analysis	Bay	7		3 teleost species	Dietary partitioning occurring among species

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
								in the communal nursery.
Taylor et al. (2011)	South-eastern Queensland, Australia	Identify catch composition and seasonal differences at different beaches.	Gillnets	Coastal beaches	17	8		Spatial and seasonal partitioning.
Abrantes and Barnett (2011)	Southern Tasmania, Australia	Determine differences in stable isotope composition between sites to assess connectivity between areas and to use SIA, SCA and tracking data to assess intra-population differences in diet and movement patterns.	Stomach content and stable isotope analyses and electronic tracking.	Coastal and offshore	1			Possible diet and habitat partitioning.
Bethea et al. (2011)	Florida, USA	Quantify diet and feeding ecology to understand resource partitioning.	Stomach content and stable isotope analyses.	Bays	2			Dietary partitioning
Powter et al. (2010)	South-eastern Australia	Determine if there is sex-based and or ontogenetic differences in diet, dentition and head morphology.	Stomach content analysis	Coastal temperate waters	1			Dietary partitioning
Vaudo and Heithaus (2009)	Shark Bay, Western Australia	Spatial and temporal variation in abundance and species composition and examine size distribution and macro-habitat preference among common species.	Visual surveys and capture methods.	Marine bay	1	10		No clear evidence of resource partitioning.

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
Whitty et al. (2009)	Fitzroy River, Australia	Test the hypothesis that juveniles are able to move through shallow runs to enable upstream migration and that morphological differences in size and age class will mean they will be ontogenetic differences in habitat use.	Acoustic tracking	River		1		Spatial partitioning
Saidi et al. (2009)	Tunisa	Describe food composition in relation to predator size and season, determine prey diversity and compare with studies from different locations.	Stomach content and stable isotope analysis.	Gulf	1			Ontogenetic food partitioning
DeAngelis et al. (2008)	US Virgin Islands	Assess species diversity and relative abundance, determine if area is a nursery habitat and assess if habitat partitioning is occurring.	Bottom longline and hand-gear sampling.		5	1		Habitat partitioning and temporal partitioning of space use.
Marshall et al. (2008)	South-eastern Queensland, Australia	To determine if inter-specific dietary differences occurred through ontogeny and if dietary resources partitioning occurred between species.	Stomach content analysis	Demersal		2		Dietary partitioning but other factors could also play a role.
Taylor and Bennett (2008)	Moreton Bay, South-eastern Queensland, Australia	Study trophic relationship between the Australian weasel shark and cephalopods.	Stomach content analysis	Bay	1		cephalopods	Specialisation on cephalopods to reduce competition with other sharks.

Study	Location	Objective	Method	Habitat	Shark species	Ray species	Other species	Outcome: Type of partitioning exhibited
Treloar et al. (2007)	South-eastern Australia	Comparative feeding ecology and trophic levels.	Stomach content analysis	Continental shelf and slope		6		Dietary partitioning among both continental shelf and slope species.
Wiley and Simpfendorfer (2007)	Florida, USA	Document co-occurring species of elasmobranchs, examine the environmental and habitat factors that influence occurrence and distribution as well as examine movement.	Longline, rod and reel and gillnet.	Gulf and estuaries	4			Habitat partitioning due to environmental characteristics.
Navia et al. (2007)	Colombia	Quantify and compare diet and trophic interactions.	Stomach content analysis	Coastal and oceanic	1	4		Possible temporal and habitat partitioning among rays.
Papastamatiou et al. (2006)	Hawaii	Quantify and compare diets and geographical depth distributions to determine resource partitioning and or competition.	Shark control program data and Stomach content analysis.	Marine	4			Spatial separation possibly based on competition.
Pikitch et al. (2005)	Belize	Assessment of species diversity, use of reef system by early life stages, species and age specific patterns of abundance in reef macro habitats and demographic population structure of early life characteristics.	Longline sampling, gillnet, seine, drumline and opportunistic market surveys.	Reef and atoll	10	3		Habitat and depth partitioning.

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
Simpfendorfer et al. (2005)	Florida, USA	Examine distribution and investigate habitat partitioning and the environmental parameters that may influence distribution.	Longline surveys	Estuaries	1			Size based habitat partitioning influenced by salinity.
White and Potter (2004)	Western Australia	Test hypotheses that the area is used as a nursery area, use of habitat is partitioned, species have more affinity to vegetated regions then non-vegetated areas and composition of species that use the area change over time.	Gillnets	Inshore bay area	5	4	12 teleosts	Spatial and dietary partitioning.
White et al. (2004)	Western Australia	Test hypotheses that food partitioning is occurring, different feeding habits and morphology will facilitate differences in diets, species occurring mostly over seagrass will have different diet, diets changes with body size, main prey will be most abundant crustaceans and prey composition will change throughout the year.	Stomach content analysis	Inshore bay area	3	1		Dietary partitioning that could also be related to habitat.
Bethea et al. (2004)	Apalachichola Bay, Florida, USA	Describe and quantify diet to calculate diet overlap, habitat overlap and investigate prey size-predator size relationship.	Stomach content analysis and catch data.	Inshore bay area	4			Spatial and temporal partitioning.
Brickle et al. (2003)	Falkland Islands	Examine ontogenetic shifts in diet and dietary overlap among species.	Stomach content analysis.	Demersal		3		Dietary partitioning

Study	**Location**	**Objective**	**Method**	**Habitat**	**Shark species**	**Ray species**	**Other species**	**Outcome: Type of partitioning exhibited**
								and depth partitioning
Platell and Potter (2001)	Western Australia	Compare dietary compositions to analyse inter specific differences to assess potential resource petitioning, also to analyse dietary differences in relations to ontogeny, phylogeny, mouth morphology and feeding behaviour.	Stomach content analysis	Temperate coastal		4	14 teleosts	Dietary and depth partitioning among species.
Platell et al. (1998)	Southwestern Australia	Determine if species are partitioned by habitat, type of food and if there is interspecific competition.	Stomach content analysis	Temperate coastal		4		Combination of diet and habitat partitioning.

2.3 Development of methodologies to study resource partitioning

Ecology is as an empirical study (Krebs, 1989) and multivariate in nature, with many facets contributing to defining the ecological niche of a species (Munroe et al., 2014). To understand the resource use patterns of elasmobranchs across dietary, habitat, and temporal planes, a number of methods have been used either separately or in combination.

Dietary partitioning has been the most widely studied form of resource partitioning among elasmobranchs. Earlier work that addressed the diets of co-occurring elasmobranchs used stomach content analysis (McEachran et al., 1976, Platell et al., 1998). This has since become a common feature of dietary resource partitioning studies. Stomachs are extracted and dissected to identify prey items to the lowest possible taxon and comparisons are made either within members' of one species or among species to assess the level of diet overlap from which competition is inferred (Wetherbee et al., 2012). However, stomach content analysis does have its drawbacks, the method has been criticised for; providing only a narrow view of what is fed on at the point of sampling and not a broader view of diet over time (Hussey et al., 2012, MacNeil et al., 2005), the predominance of indigestible hard parts (for example from cephalopods beaks and crustacean exoskeletons) that may overestimate the prevalence of certain prey in the diet (Kim et al., 2012), occurrence of empty stomachs particularly in sharks resulting from regurgitation during capture (Cortés, 1997), as well as the need for large sample sizes to adequately characterise diet which means the mortality of large number of individuals. However, some studies that carried out stomach content analysis were able to access large sample sizes by obtaining samples from the bycatch of various fisheries (Rogers et al., 2012, Barbini and Lucifora, 2012, Bornatowski et al., 2014b), or used gastric lavage (Frisch et al., 2016).

More recently stable isotope analysis has been used in the study of elasmobranchs ecology and resource partitioning. The method has been hailed as a low cost and non-lethal option compared to the acquisition and examination of actual stomachs from dead animals (Shiffman et al., 2012). In addition, stable isotope analysis provides an indication about longer term trophic ecology compared to stomach content analysis. Essentially stable isotope analysis is based on the process of examining the levels of carbon and nitrogen isotopes in the tissues of consumers that can be related directly to the isotopes of their prey (Kinney et al., 2011). One of the key strengths of stable isotope analysis is its capability to investigate both dietary and habitat use patterns (Hussey et al., 2012). Over the last 10 years the use of this method has steadily increased, however issues of caution that may affect stable isotope values and consequently the interpretation of results are also prevalent. For instance isotopic values may be influenced by the presence of urea and lipid in samples (Gallagher et al., 2017), changes or fluctuations in the isotopic signatures of base prey in space and over time may also cause variation in carbon and nitrogen isotopic values in consumers (Shiffman et al., 2019). Though stable isotope analysis provides an indication of average resource use trends, the interpretation of stable isotopes values in isolation from other trophic data can lead to erroneous conclusions, and interpretations from stable isotope analysis should not be extrapolated to the wider ecosystem without complementary stomach content and movement data which provide empirical evidence that can validate or enhance findings (Gallagher et al., 2017, Shiffman et al., 2019, Abrantes and Barnett, 2011).

Capture methods are often used to study the use of resources in time and space. Fishery independent surveys have been used to capture species at various sites and depths, while some studies have used data from shark control programs (Papastamatiou et al., 2006, Taylor et al., 2011). Tag recapture was also used as a means to investigate habitat use (Wiley and Simpfendorfer, 2007). The development of electronic devices (e.g. acoustic, data storage and satellite tags) to monitor the movement of individual animals has become widely used to study aquatic animals and provides more fine scale data on the habitat use of some elasmobranch (Donaldson et al., 2014). The majority of studies that use acoustic tracking have been done on sharks while the habitat use patterns of rays have been largely inferred from stable isotope analysis and catch information (Table 2-1).

The need for an integrated approach to studying elasmobranch resource use has been recognised in earlier work (White et al., 2004). Various studies have used complementary data sets using a combination of methods such as both stable isotope and stomach content analysis to determine trophic ecology (Bethea et al., 2011, Vaudo and Heithaus, 2011) or the inclusion of catch data (Gallagher et al., 2017, Papastamatiou et al., 2006) and spatial data to determine both dietary and spatial partitioning (Abrantes and Barnett, 2011). Complementary published stomach content information has also been valuable to validate the results of stable isotope analysis (Matich et al., 2017a). The development of methodologies that can provide a broader assessment of resource use patterns and the improved ability to track the movement of species over time and space has provided researchers with a greater ability to understand and monitor the ecology of elasmobranchs which when coupled with life history and population information is valuable for conservation and management efforts.

2.4 Dietary partitioning

Dietary partitioning is likely to occur among elasmobranchs where species co-exist in a given area (Wetherbee et al., 2012). The majority of studies on elasmobranch resource partitioning have focused on this aspect. Dietary partitioning has been detected among sharks (Bethea et al., 2004, Hussey et al., 2012, Rogers et al., 2012), skates (Treloar et al., 2007, Barbini and Lucifora, 2012), stingrays (Bornatowski et al., 2014b, Pardo et al., 2015, Platell et al., 1998, Platell and Potter, 2001) and species assemblages of sharks and rays (Dale et al., 2011, Kiszka et al., 2014, White et al., 2004, Sommerville et al., 2011, Heithaus et al., 2013) as well as in feeding interactions with other non-elasmobranch species (Kinney et al., 2011, Platell and Potter, 2001).

Interspecific dietary differences occur at varying levels. The same range of prey may be consumed but relative proportions among species differs (Platell et al., 1998). White et al. (2004) found that three shark species fed predominantly on teleosts, however the species composition of prey was different for each shark species. In other instances there was more specialisation in diets where the prey item constituting the largest portion of each diet was different (Bornatowski et al., 2014b, Sommerville et al., 2011). For example dietary patterns of two sympatric rays were found to be markedly different feeding on benthic crustaceans and polychaetes, respectively (Yick et al., 2011). Furthermore similar co-existing species have diversified their diets to the point where they feed at different trophic levels (Amariles et al., 2017, Raoult et al., 2015).

Ontogenetic food partitioning or the change in diets with growth and maturity among members of the same species has also been widely detected in elasmobranchs (Barbini and

Lucifora, 2012, Sommerville et al., 2011). Morphological traits such as dentition and gape size develop with growth and enable the capture of larger prey (Powter et al., 2010) and can facilitate adults and juveniles to feed at different trophic levels to partition food resources (Amariles et al., 2017). For instance, adults and juveniles of the Australian weasel shark *Hemigaleus australiensis* feed on different prey (Taylor and Bennett, 2008). Prey release by adult members of population when diet changes occur may ensure that there is food supply for young immature individuals and therefore increase the likelihood of survival (Ebert, 2002). However, dietary partitioning between sexes of the same species is rare among elasmobranchs, as Kiszka et al. (2014) was the only study that detected potential intra-specific niche partitioning among sexes.

Prey abundance may be a major contributing factor to the presence of competition for food between co-occurring species (Bornatowski et al., 2014b). However, few studies have directly measured prey abundance and diversity (Pardo et al., 2015, Gutteridge et al., 2011). Competition is mainly inferred from dietary overlap where sharks and rays with more specialised diets that have little overlap are presumed to be partitioning resources based on the limitation of prey. Conversely, a high dietary overlap can mean that prey is not limited (Heithaus et al., 2013) or that there is direct competition for prey. The availability of prey may also vary temporally and spatially. Curnick et al. (2019) found dietary partitioning between two shark species was only seasonal due to the influx of prey at certain times of the year while differences in diurnal and nocturnal feeding patterns can partition food among co-occurring species (Varghese et al., 2014). Further information on prey abundance, diversity and distribution will improve the current understanding of elasmobranch feeding ecology.

2.5 Spatial and temporal partitioning

In studies where attempts to investigate dietary partitioning showed a lack of distinction in diets, inferences are made to spatial or temporal partitioning as the likely cause of co-existence (O'Shea et al., 2013, Bethea et al., 2004, Tillett et al., 2014, Navia et al., 2007). Though stomach content and stable isotope analysis have both provided indirect indication of potential spatial and temporal partitioning (Kiszka et al., 2014, Varghese et al., 2014).

More empirical evidence of elasmobranch habitat use patterns from catch records and movement data suggest that substrate type, competition, abiotic factors, and asynchronous seasonal behaviour are factors that influence habitat partitioning. Elasmobranchs, particularly juveniles, have been observed to have an affinity to vegetated areas compared to unvegetated zones possibly due to the provision of nutrition and shelter from predators (White and Potter, 2004, DeAngelis et al., 2008). Behavioural inter-specific avoidance of competition was exhibited in sharks (Papastamatiou et al., 2006, Bangley and Rulifson, 2017, Heupel et al., 2019). Competition avoidance can also lead to asynchronous seasonal behaviour. For example one species of shark was found to remain in cooler waters when all other co-occurring species had migrated to warmer regions (Taylor and Bennett, 2013). Physiological tolerance to salinity and temperature have also determined distribution of sharks in nursery areas (Simpfendorfer et al., 2005, Bangley and Rulifson, 2017). Additionally a study on juvenile sawfish found that habitat was partitioned by different aged cohorts with regard to temperature and light regimes due to lunar phases (Whitty et al., 2009).

2.6 Interrelationship between resource use axes

Dietary and habitat partitioning may occur together to facilitate co-existence. For example four species of rays occurring across a 200 km area in Western Australia partitioned both food and space (Platell et al., 1998). White et al. (2004) also documented that both food and habitat was partitioned among an array of 14 species of elasmobranchs in Shark Bay, Australia. A study conducted on five species of sympatric stingrays found that only one species had a specialised diet implying food partition while the other four species were likely to employ habitat partitioning as a survival strategy that reduces competition (O'Shea et al., 2013).

The inter-relationship between habitat use and diet is complex and requires further investigation as studies are often focused on a single species or location (Shiffman et al., 2019). Pardo et al. (2015) suggested that large-scale sampling may overlook microhabitat partitioning which could cause the dietary differences observed among species. A similar view was provided by Marshall et al. (2008) in explaining the reason behind the significant dietary differences of sympatric urolophid rays. Bornatowski et al. (2014b) found evidence of dietary partitioning but suggested that further study of spatial and temporal distribution should also be conducted. Conversely, the movement patterns of elasmobranchs may not always reflect resource use and wider data sets including dietary information is needed to verify observations (Heithaus et al., 2013). This emphasises the need for integrated studies across all resource axes (White et al., 2004).

Recent studies show more evidence of the dynamics of elasmobranch resource partitioning. For example the feeding habits of two juvenile shark species were compared in habitats where they both existed and where only one species was present; dietary partitioning only occurred where both species were present and competing for resources (Matich et al., 2017b). Furthermore, habitat type can play a significant role, an assemblage of elasmobranchs present in distinct habitats that were in close proximity to each other partitioned resources only in one habitat type (Shiffman et al., 2019). Therefore fine-scale assessment of resource use is important to identify variability and generalisations should be avoided (Shiffman et al., 2019).

2.7 Future work

The segregation of resource use occurs according size, sex, morphology, and behaviour of a species or by social interactions such as competition, and also is influenced by abiotic environmental elements. The current body of work has been built upon characterisations of food or space use by elasmobranchs to document more complex and changing patterns in interactions between species. Despite these advancements there are knowledge gaps that remain in understanding elasmobranch ecology from the standpoint of resource partitioning. These include: (1) a lack of studies conducted in tropical areas that support a large diversity of elasmobranchs as well as other fish species and marine taxa, (2) literature on spatial and temporal use of resources is more limited than dietary information, though stable isotope analysis improves the understanding of habitat use, more empirical movement data is needed to accurately represent the space use of many species, particularly rays, (3) the extent to which abiotic factors influence species distribution needs more attention, particularly in light of other driving factors such as climate change and the impact of development in coastal habitats, (4) the resource use patterns of elasmobranchs in coastal and nearshore areas is more common in literature, however further work in pelagic and deep-water species is needed to develop a better understanding of species ecology in these habitats. Finally, the high variability of ecosystem function, habitats, and species interactions requires more integrated assessments of species ecology utilising multiple complementary data sets to arrive at a more accurate representation of resource use patterns and the factors that play a critical role in influencing the outcomes.

Chapter 3 Dietary overlap of carcharhinid sharks in the Gulf of Papua

3.1 Introduction

Fisheries are a major contributor to the decline of shark populations (Dulvy et al., 2014) that function mainly as top and middle order predators in marine ecosystems (Heupel et al., 2014). Concern for the survival of these populations has also highlighted that the flow on effects of low predator abundance on the ecosystem remain largely unknown, partly due to the paucity of ecological information for specific regions (Ferretti et al., 2010). Therefore, establishing an understanding of the ecology of species, and their contributions to ecosystem processes (Bornatowski et al., 2014a), is a crucial element in predicting the outcomes of population declines and potential species loss. Assessing the ecosystem impacts of fisheries in order to set appropriate management and conservation guidelines requires information from both target and non-target (bycatch) species (Pikitch et al., 2004).

Characterising the dietary traits of sharks from stomach content analysis provides empirical evidence of the trophic linkages in the food chain (Cortes, 1999). This information can be incorporated into ecosystem models to aid fisheries management endeavours (Rogers et al., 2012). Furthermore feeding patterns indicate diet specialisation, which helps understand the vulnerability of predators and the breadth of ecosystem impacts from their decline. Specialised feeders have a narrow range of prey and may be more vulnerable to perturbations that may directly impact food availability while generalist feeders may be more resilient to environmental changes (Munroe et al., 2014, Simpfendorfer et al., 2001). The level of diet overlap among similar sympatric species is an indirect measure of competition among species when food resources are limited, and also provides an indication of potential resource partitioning among species (Wetherbee et al., 2012). Dietary studies have shown that potential competition for food can influence the differential distribution of similar shark species (Papastamatiou et al., 2006) while evidence of resource partitioning as a possible means to alleviate competition is common in sharks (Wetherbee et al., 2012). Dietary investigations thus provide a preliminary view of complex and dynamic ecological interactions that require integrated datasets (White et al., 2004), and monitoring diets over time can gain an understanding of the ecology of a species and its role in the overall function of the ecosystem.

Small-bodied coastal sharks are generally considered to be meso-predators that connect the lower and top trophic levels of the food chain (Heupel et al., 2014) and are also common in fisheries bycatch (Stobutzki et al., 2002). The Australian blackspot shark *Carcharhinus coatesi*, the milk shark *Rhizoprionodon acutus* and the Australian sharpnose shark *Rhizoprionodon taylori* are small-bodied coastal sharks that are frequently caught as bycatch in the Gulf of Papua Prawn Fishery (GoPPF) in Papua New Guinea (White et al., 2019). The life histories of *C. coatesi* and *R. taylori* indicate that the populations of each species may be impacted differently by the fishery based on growth and biological productivity (Baje et al., 2018, Baje et al., 2019). However, the ecology of these sympatric sharks has not been investigated in the Gulf of Papua, and their ecological roles are not well understood. Using samples caught in the fishery this study aimed to characterise the diets of *C. coatesi*, *R. acutus* and *R. taylori* and estimate the level of dietary overlap to assess if competition and partitioning of food resources occurs among these species in the Gulf of Papua. We hypothesise that the diets of these species will be different based on the occurrence of resource partitioning.

3.2 Methods

3.2.1 Study site

The Gulf of Papua, situated on the south coast of Papua New Guinea (Fig 3.1), is a region comprised of extensive mangrove and estuarine areas with high riverine input. Waterways from high altitude areas of PNG drain into the Gulf forming several major river systems, the largest of which is the Fly River in the West. North Eastward of the Fly River are the Kikori and Purari rivers along with several other systems. These areas provide major nursery grounds for penaeid prawn species which eventually recruit into the Gulf of Papua prawn trawl fishery (Evans et al., 1997). The region experiences two main seasons: the North-West monsoon from November to March each year and the South-East monsoon winds that occur from April to October (Moore and MacFarlane, 1984).

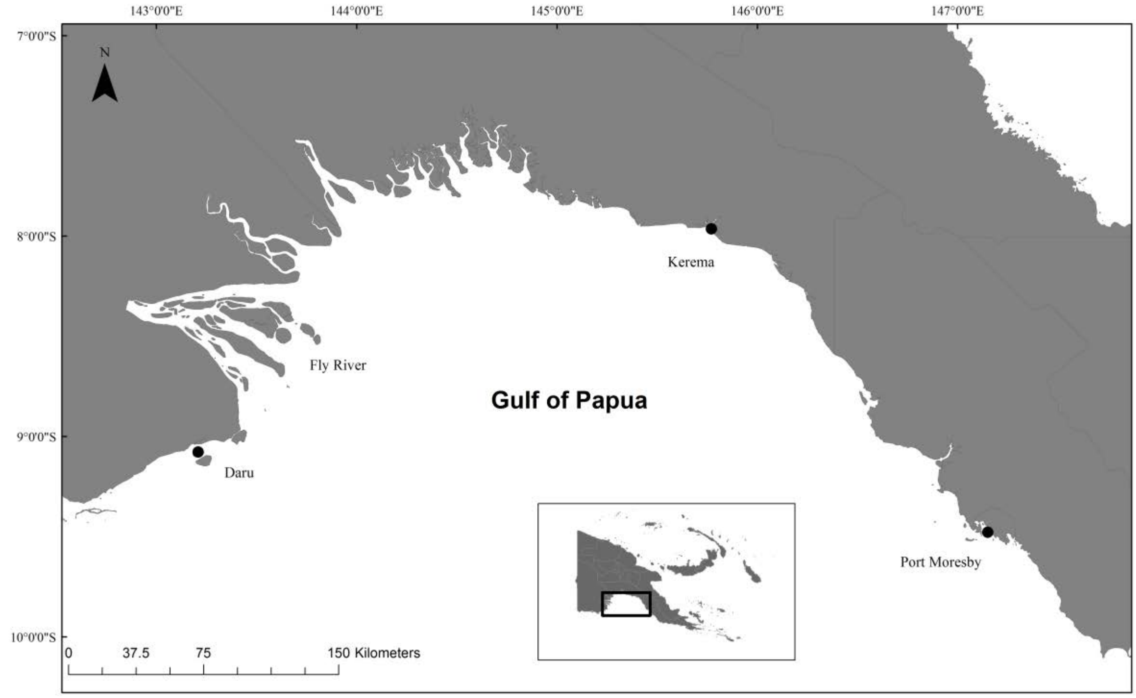

Figure 3-1: The Gulf of Papua situated in the south of Papua New Guinea.

3.2.2 Sampling and sample preservation

Fishery observers were deployed on seven prawn trawl fishing trips between June 2014 and August 2015 to collect shark bycatch samples. Samples were kept whole and frozen on board. In a laboratory, sharks were thawed, total length (TL) measured to the nearest ± 1 cm, sex recorded and stomachs excised. The level of fullness was estimated and graded as: an empty stomach = 0, 25% full =1, 50% full = 2, 75% full = 3 and 100% full = 4 was recorded for each sample, contents from each stomach were removed, fixed in 10% formalin and transferred to 70% ethanol for preservation. Each set of stomach contents were weighed and examined to identify the number and type(s) of prey to the lowest possible taxa. The level of digestion was classified using a grading system from 1–5 based on the amount of body tissue of the prey remaining as follows: 100–80% was classified as stage 1, 80–61% was classified as stage 2, 60–41 % stage 3, 40–21% stage 4 and 20–1% stage 5 (Simpfendorfer 1993). In order to detect if the sample size was sufficient to adequately describe diets, a cumulative prey curve was produced using the specaccum function of the 'vegan' package (Oksanen et al., 2013) in R (R Core Team, 2015).

3.2.3 Dietary indices

To assess the importance of each prey item in the diet of the three shark species the percent frequency of occurrence (% FO) and the percent by number (%N) were calculated. The former is the number of times a prey category is present in one or more stomachs expressed as a percentage of the total number of stomachs containing food while the latter is the number of each prey category found in each stomach expressed as a proportion of the total number of prey for all stomachs of a particular species (Hyslop, 1980). The state of digestion and mastication in most of the samples meant that prey items could not be adequately identified and separated therefore volumetric and gravimetric methods were not carried out.

3.2.4 Dietary overlap

Dietary overlap, which is a measure of the level of similarity in the diets between shark species, was measured using the simplified Morisita index (Krebs, 1989):

$$CH = \frac{2\Sigma_i^n \, p_{ij}\, p_{ik}}{\Sigma_i^n p_{ij}^2 + \Sigma_i^n \, p_{ik}^2}$$

where CH = Simplified Morisita index of overlap between two species with values ranging from 0 (no overlap) to 1 (complete overlap).

p_{ij} = the proportion prey in species *i* that is of the total prey categories used by species *j*

p_{ik} = Proportion prey i is of the total prey categories used by species k.

n = total number of prey categories.

3.2.5 Multivariate analysis

Samples were initially randomised and pooled within each species to minimise the large number of zeros and improve the effectiveness of the analyses (Sommerville et al., 2011). The resulting new samples comprised stomach contents from 4 or 5 individuals of the same species randomly pooled together. The percentage by number (%N) was calculated for each prey item in each sample and entered into Primer-E (Plymouth Routines in Multivariate Ecological Research) version 7.0. 13 (Clarke and Gorley, 2015). Prior to further analysis the data were subject to square-root transformation followed by creation of a Bray Curtis resemblance matrix. To test for differences in dietary composition among sex, species and season Analysis of Similarities (ANOSIM) was conducted. Similarities of Percentages (SIMPER) was also used to identify the components that typified the diets of each shark species. Non-metric Multidimensional Scaling (nMDS) ordination was used to produce plots to visualise the dietary composition based on species, size and season. To test for the multivariate variability in the diet of each species Multivariate Dispersion (MVDISP) was conducted. To assess if the diets of the three shark species undergo changes with respect to growth, samples were grouped into 10 cm size classes and randomly pooled into groups of 4 or 5 samples in the data preparation stage. Column graphs were constructed to demonstrate any change in the composition of diets with respect to increasing size and an nMDS ordination plot was also used to visualise the level of similarity in diets between different size classes.

3.3 Results

3.3.1 Size ranges and sample size

Total lengths recorded were similar among species and ranged from 31–76 cm TL for *R. taylori*; 31–84 cm TL for *R. acutus*; and 35–79 cm TL for *C. coatesi* (Fig 3-2). A total of 177 stomachs were sampled of *R. taylori*, 83 of *R. acutus*, and 122 of *C. coatesi*. The cumulative prey curve for all three species did not appear to reach asymptote, indicating a larger sample size would be required to fully characterise the diets (Fig 3-3). The number of stomachs containing prey was high with few empty stomachs encountered for each species (Table 3-1).

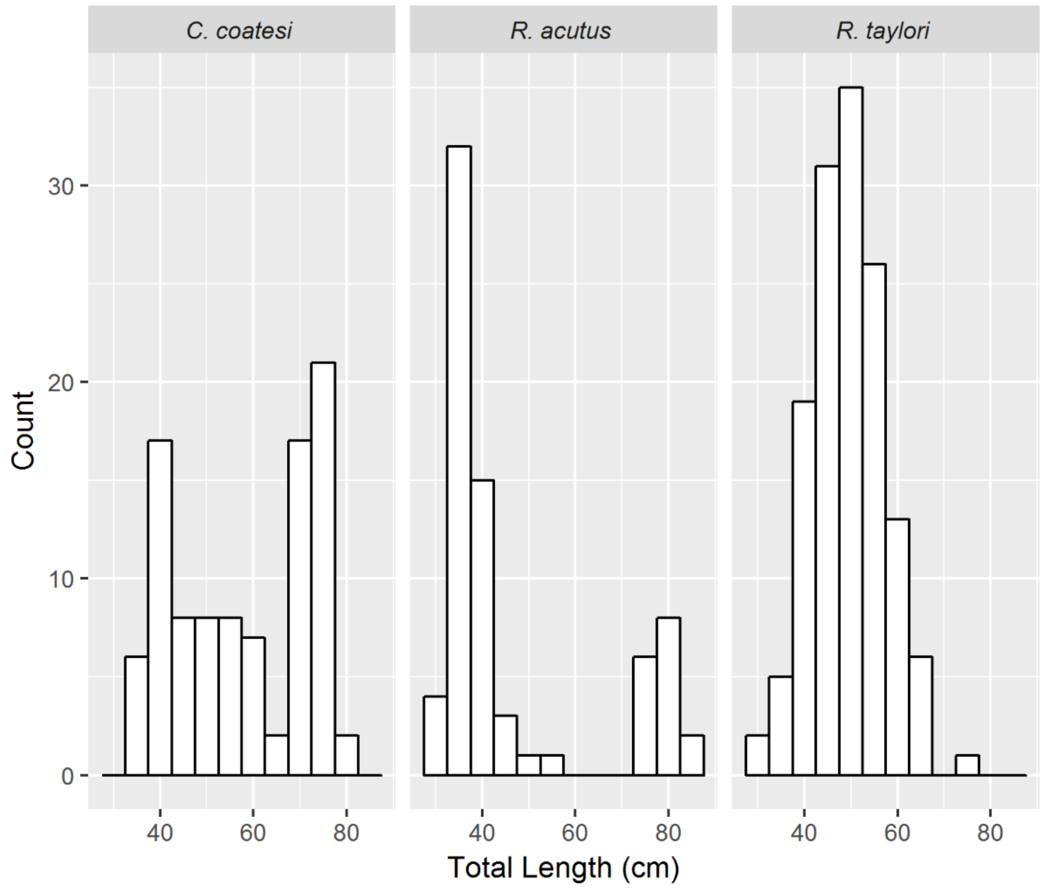

Figure 3-2: Length frequency of *Carcharhinus coatesi*, *Rhizopriondon acutus* and *Rhizoprionodon taylori* caught in the Gulf of Papua prawn trawl fishery and used for stomach content analysis

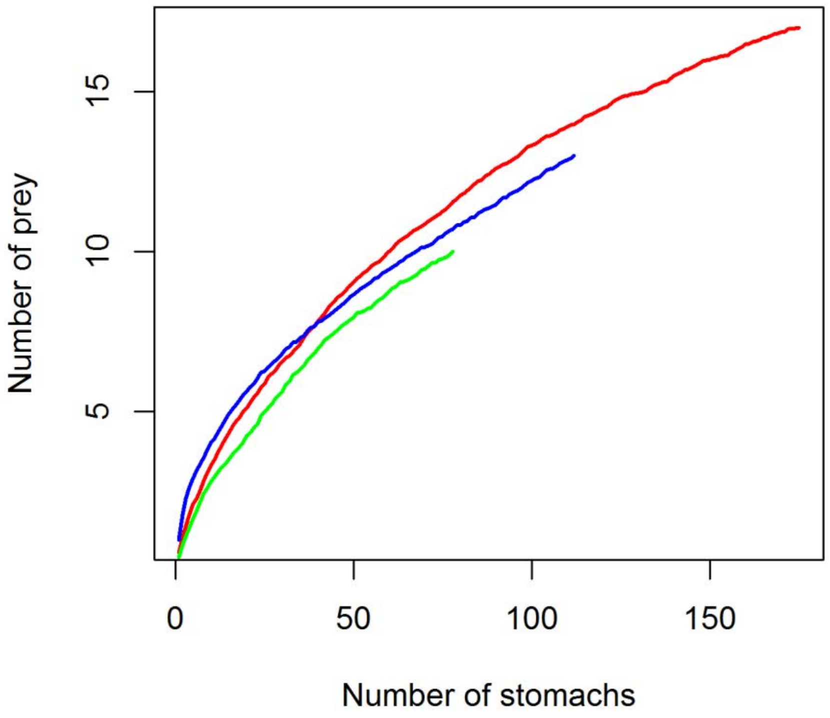

Figure 3-3: Cumulative prey curves for *Carcharhinus coatesi* (blue) *Rhizoprionodon acutus* (green) and *Rhizoprionodon taylori* (red) from the Gulf of Papua.

3.3.2 Main prey types and proportions in diet

Teleosts, crustaceans and molluscs were observed as the main prey groups, with sixteen teleost families, three crustacean families and two families of molluscs identified. The proportion of individual %FO and %N of each teleost family was low, not exceeding 5% owing to mastication and the process of digestion that resulted in only a small number of individual fishes being identified. Of the 16 families of teleosts observed only 3 families: Haemulidae, Engraulidae and Trichiuridae appeared in the diet of all three shark species. Other families were only shared between two of the species, for example Leiognathidae was only present in the stomach contents of *R. acutus* and *C. coatesi*. However, distinctively the families Pegasidae, Fistulariidae and the eel families Muraenesocidae and Ophichthidae, were only present in the diet of *C. coatesi*. The proportion of unidentified teleosts was high for all species (Table 3-1).

The presence of crustaceans in the diet, %FO and %N of Penaeidae was high for all species, but particularly prevalent in the diet of *C. coatesi* (54.5 %FO). Stomatopoda were also more common in the diet of *C. coatesi* (23.14%FO and 7.51%N) compared to *R. taylori* (11.61%FO and 5.36 N) while being absent in the diet of *R. acutus*. Similarly, with respect to crabs there was a higher %FO and %N in the diet of *C. coatesi* (7.44% FO and 2.15 % N) compared to *R. taylori* (1.29 % FO and 0.59% N) and *R. acutus* (1.33% FO and 0.5% N). Molluscs played a lesser role in the diet of the all three species, *R. acutus* (2.67% FO and 0.99% N) consumed fewer cephalopods than *R. taylori* (7.74 % FO and 5.06% N) and *C. coatesi* (5.78 % FO and 6.22 %N) while Gastropoda were only found in the stomach contents of *R. taylori* (Table 3-1).

Table 3-1: Percent frequency of occurrence (% FO) and percent by number (% N) of prey categories found in the stomachs of *Rhizoprionodon taylori*, *Rhizoprionodon acutus* and *Carcharhinus coatesi* in the Gulf of Papua

Prey categories	*R. taylori*		*R. acutus*		*C. coatesi*	
	%FO	%N	%FO	%N	%FO	%N
Teleostei						
Sciaenidae	3.1	0.6	2.7	2.0	-	-
Labridae	1.6	0.3	-	-	-	-
Mullidae	1.6	0.3	-	-	-	-
Haemulidae	3.1	0.89	1.3	2.0	1.65	0.43
Engraulidae	1.55	0.3	2.67	0.99	0.83	0.215
Nemipteridae	1.29	0.6	-	-	-	-
Gobiidae	1.94	0.89	-	-	0.83	0.22
Synodontidae	1.29	0.6	1.33	0.5	-	-
Terapontidae	1.29	1.2	2.67	1.0	-	-
Trichiuridae	0.65	0.3	2.67	0.5	0.83	0.22
Carangidae	0.65	0.3	-	-	-	0.22
Leiognathidae	-	-	4.00	1.99	4.13	1.07
Pegasidae	-	-	-	-	0.83	0.22
Fistulariidae	-	-	-	-	0.83	0.22
Muraenesocidae	-	-	-	-	1.65	0.43
Ophichthidae	-	-	-	-	0.83	0.22

Unidentified eel	-	-	-	-	0.83	0.24
Unidentified teleost	56.77	45.24	77.33	77.11	54.5	44.42
Crustacea						
Penaeidae	36.77	27.68	25.33	10.95	51.24	33.05
Stomatopoda	11.61	5.36	-	-	23.14	7.51
Crab	1.29	0.59	1.33	0.5	7.44	2.15
unidentified crustacean	6.45	3.57	1.33	0.5	-	-
Mollusca						
Cephalopoda	7.74	5.06	2.67	0.99	5.78	6.22
Gastropoda	1.29	0.89	-	-	-	-
Other unidentified	20.15	4.17	1.33	0.5	7.44	2.15
No. of stomachs analysed	177		83		128	
No. of stomachs with food	155		75		121	
No. of empty stomachs	22		8		7	

3.3.3 Diet Overlap

The Morisita Index of Similarity calculated for each pair of species showed high overlap for all species. The highest overlap was between *R. taylori* and *C. coatesi* ($C_H = 0.99$) with less overlap between the diets of *R. taylori* and *R. acutus* ($C_H = 0.85$) and *R. acutus* and *C. coatesi* ($C_H = 0.82$).

3.3.4 Multivariate analyses

3.3.4.1 Intraspecific dietary comparison

Dietary data for males and females were pooled for subsequent analysis as there was no significant difference between sexes (*P* = 0.4, *R*= 0.039). A one-way ANOSIM indicated a significant difference among the diets of *R. taylori*, *R. acutus* and *C. coatesi* (*P*= 0.1, *R*= 0.181). Similarities of percentages (SIMPER) showed that the main groups that typified the diets of *R. taylori* and *C. coatesi* were unidentified teleosts and penaeid prawns, while unidentified teleosts typified the diet of *R. acutus*. The pairwise tests between species showed a significant difference in dietary compositions of *R. acutus* and *R. taylori* (*P* = 0.2*, R* = 0.243) and *R. actus* and *C. coatesi* (*P* = 0.1, *R* = 0.479). However, there was no significant difference in dietary compositions between *R. taylori* and *C. coatesi* (*P* > 0.05, *R* = 0.28). The multivariate dispersion (MVDISP) analysis showed that *R. taylori* had the highest dispersion of 1.17, followed by *C. coatesi* with 0.81 and *R. actus* with 0.53. The nMDS ordination plot of the dietary compositions of the three shark species showed that *R. taylori* has a broad diet that overlaps with *C. coatesi* and also with *R. acutus*. Samples of *R. acutus* appeared in the bottom left of the plot and did not overlap with *C. coatesi* (Fig 3-4).

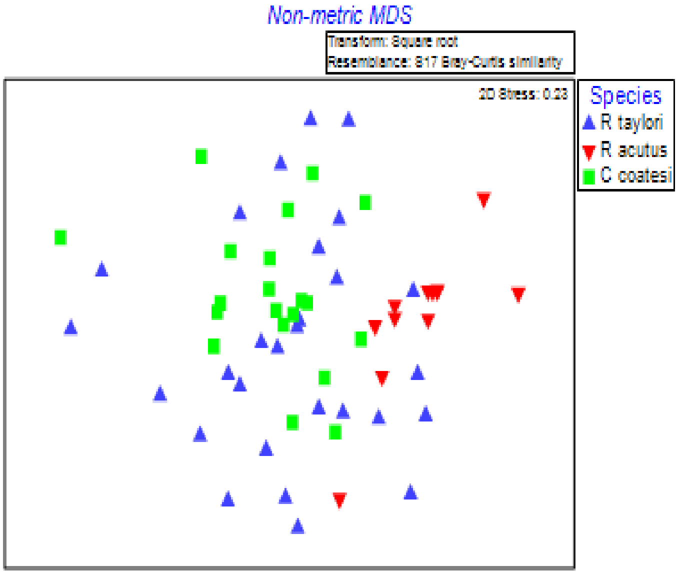

Figure 3-4: non-Metric multidimensional scaling ordination of dietary composition by number (%N) of *Rhizoprionodon taylori*, *Rhizoprionodon acutus* and *Carcharhinus coatesi* in the Gulf of Papua.

3.3.4.2 Dietary comparison by season

A one-way ANOSIM testing between North-West Monsoon and South East Monsoon periods did not detect a significant result (*P* >0.05, *R* = -0.002) indicating there was no difference in the diets of all three species between seasons. The nMDS ordination of diets sampled in different seasons showed that the majority of South East Monsoon samples overlapped with North West Monsoon indicating similarity (Fig 3-5).

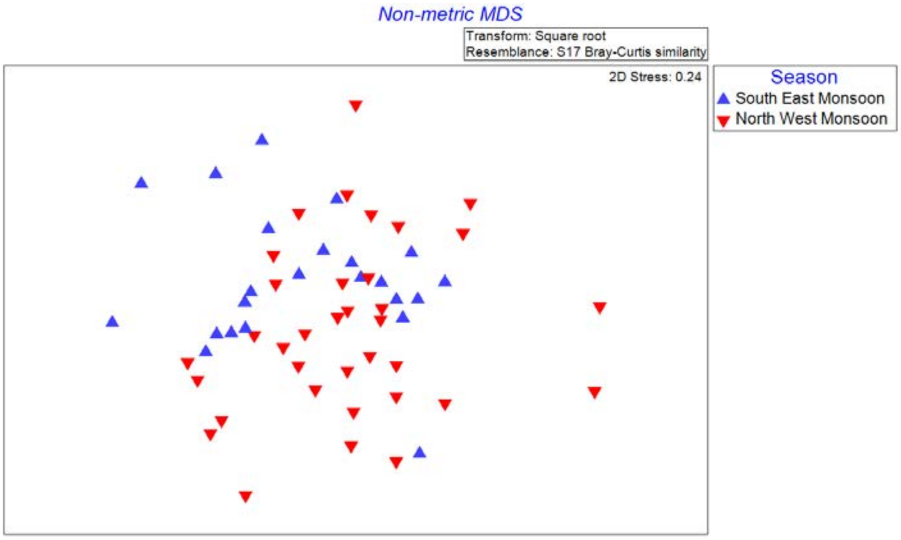

Figure 3-5: non-Metric multidimensional scaling ordination of dietary composition by number (%N) according to North-west monsoon and South-east monsoon periods that occur in the Gulf of Papua.

3.3.4.3 Dietary composition among size classes

Comparison of diet composition among size classes for each species showed that *R. taylori* has a fairly consistent diet with respect to proportions of different dietary components. Cephalopods were not consumed by the smallest size class and there may be a reduction in the consumption of penaeid prawns in the largest sizes class with a possible increase in the consumption of teleosts. *Rhizoprionodon acutus* consumes large proportions of teleosts in all size classes and may consume less crustaceans and cephalopods with increasing size. *Carcharhinus coatesi* had a marked decrease in teleost consumption with increasing size accompanied by an increase in the consumption of crustaceans particularly penaeid prawns (Fig 3-6).

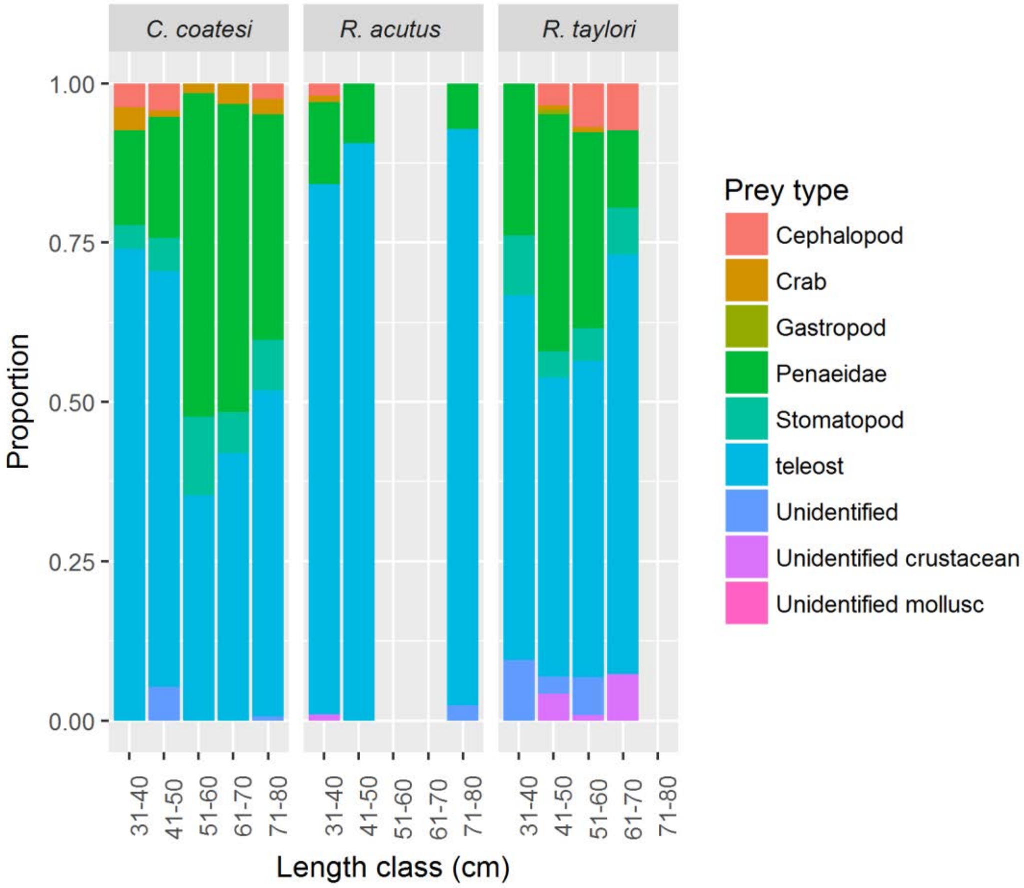

Figure 3-6: Composition of the diets of *Carcharhinus coatesi*, *Rhizoprionodon acutus* and *Rhizoprionodon taylori* according to different size classes.

The nMDS ordination plot of size classes showed a more pronounced difference among species, with the vast majority of the samples of *R. taylori* and *C. coatesi* clustering on the left of the plot and well separated from the majority of *R. actus* samples on the right. Among *R. taylori* and *C. coatesi* cluster the 41–50 cm size class and the 51–60 cm size class were more dispersed, while distinctively the largest size class (71–80 cm) of *C. coatesi* appeared to the left of the plot and the largest size class (61–70 cm) of *R. taylori* was situated away from the main group of samples indicating less similarity. For *R. acutus* the 51–60 cm and 61–70 cm size classes were not available due to a lack of samples. However, there was some separation among the 41–50 cm, 71–80 cm and the 31–40 cm size classes (Fig 3-7).

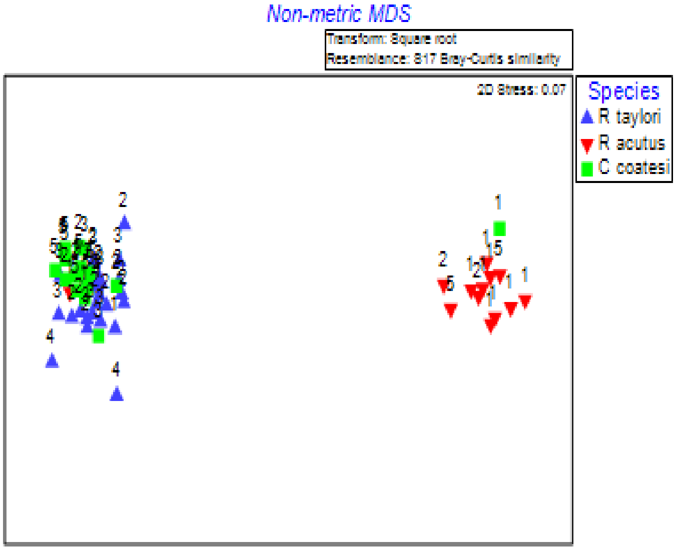

Figure 3-7: non-Metric multidimensional scaling ordination of dietary composition by number (%N) of size classes of *Rhizoprionodon taylori* (1), *Rhizoprionodon acutus* (2) and *Carcharhinus coatesi* (3) in the Gulf of Papua.

3.4 Discussion

Many shark species are considered to be generalist feeders (Munroe et al., 2014) and have been observed to feed in a density-dependent manner (Salini et al., 1992). The small-bodied carcharhinids studied here feed at similar trophic levels (Cortes, 1999), therefore where they co-occur competition for food resources can arise if prey are limited. This study shows that teleosts, crustaceans and molluscs make up the majority of prey in the diets of *C. coatesi*, *R. acutus* and *R. taylori*. There are noticeable differences in the diet of these species that may facilitate co-occurrence. Teleosts and greater proportions of crustaceans were found in the diet of *R. taylori* and *C. coatesi* while the diet of *R. actus* consisted predominantly of teleost with other prey categories being much less important. Stevens and McLoughlin (1991) found similar predominant prey types for all three species in northern Australia, however the relative amounts of prey differed from this study. Furthermore the findings of this study align with the classification of *R. taylori* as dietary generalist due to its broad diet breath (Munroe et al., 2015b) and additionally a predominance of teleosts in the diet of *R. acutus* (Ba et al., 2013).

Resource partitioning in elasmobranchs is a common occurrence (Wetherbee et al., 2012) and can occur in different ways. Co-occurring similar species that have high spatial overlap may partition resources by consuming different proportions of prey available to them (Platell et al., 1998, White et al., 2004). Significant dietary differences and low level of similarity indicate that *R. acutus* partitions food resources with *C. coatesi* by feeding predominantly on teleosts and reducing consumption of crustaceans, molluscs and other groups. The greater reliance of *R. acutus* on teleosts has been noted in previous studies in Australia and Africa

(White et al., 2004, Stevens and McLoughlin, 1991, Ba et al., 2013). *Rhizoprionodon acutus* also occupies a broader depth range (White et al 2017) which may provide a larger foraging area. There was high dietary overlap and no clear partitioning between *C. coatesi* and *R. taylori* however, noticeably *C. coatesi* consumed a few prey groups that were not observed in the *R. taylori* diet, further sampling would be needed to investigate these differences as the cumulative prey curves for all species indicated that the sample size was not sufficient to fully describe diets.

Apart from interacting with a wide range of bycatch species, including elasmobranchs, trawl fisheries also contribute to the disturbance of the benthic environment and provide or expose unnatural sources of food (Dayton et al., 1995) for opportunistic feeders, which can impact community structure (Kaiser and Spencer, 1994). Sharks have been observed to scavenge on discarded trawl catch (Hill and Wassenberg, 1990). The typical diet of inshore sharks is mainly made up of teleosts, crustaceans and molluscs (White et al., 2017b) captured in trawl grounds (Stobutzki et al., 2002). The comparison of diets from fishery independent sampling may be an option for future work to explore the impact of trawling on the diets of common bycatch species which may investigate possible changes to the benthic community structure.

Volumetric and gravimetric (bulk) descriptions of diets have been consistently included with other measures to produce compound indices and have been the preferred measure on which to conduct multivariate analysis. However, practically assessing stomach contents to achieve bulk measures of diets is associated with the difficulty of sorting through masticated and partially digested prey items that are separated into many pieces or loose tissue which makes it impossible to know which prey item they belong to or if they are part of a separate prey item altogether. Thus, the inclusion of bulk dietary measures introduces inherent errors linked to the difficulty in identifying and quantifying prey items (Baker et al., 2014). The absence of a bulk measure of the diet meant that a compound index (e.g. percent index of relative importance) was not calculated for this study. Compound indices have been recommended as a standard practice (Cortés, 1997, Brown et al., 2012, Hyslop, 1980), however, they have been found to have little significance, as opposed to considering separate dietary measures individually (Baker et al., 2014), particularly for demersal species (Macdonald and Green, 1983).

The patterns of predation in tropical inshore areas are driven by habitat type and abiotic factors which influence the species composition of predator and prey species (Salini et al., 1998). The Gulf of Papua presents a unique system within PNG that historically hosts a wide array of marine resources (Pernetta and Hill, 1981). The biodiversity and ecological dynamics of this region remain to be fully explored. The stomach content analyses used in this study provided a preliminary understanding of the diet of small-bodied carcharhinids though a larger sample size will be needed to fully characterise the diets of these species because of the high prey diversity and high proportion of unidentifiable stomach contents. This study is also limited in its use of current methodology that could provide a more in-depth assessment of diets through a finer level of prey identification. Recent approaches for dietary analysis have included the use of a combination of different methods alongside stomach content analysis such as stable isotope analysis and molecular techniques to identify prey (Matley et al., 2018). Future work in the region should consider employing such methods as well as understanding the spatial resource use patterns to draw a clearer picture of the food web and ecosystem use.

Chapter 4 Age, growth and maturity of the Australian sharpnose shark *Rhizoprionodon taylori* from the Gulf of Papua

4.1 Introduction

A general view on the life history characteristics of sharks assumes slow growth, late maturity, and a low number of offspring resulting in populations that have low intrinsic rates of population growth and are highly vulnerable to overfishing (Stevens et al., 2000, Smith et al., 1998). However, not all shark species share these characteristics. In particular, small-bodied carcharhinids such as the milk shark *Rhizoprionodon acutus* and the sliteye shark *Loxodon macrorhinus* are characterised by relatively rapid growth and early maturity resulting in higher population turnover rates (Gutteridge et al., 2013, Harry et al., 2010). Fast population turnover rates for these species make them potentially more resilient to fishing (Goldman et al., 2012), although sustainable shark catch is mostly associated with the development of science-based fisheries management (Simpfendorfer and Dulvy, 2017).

The Australian sharpnose shark *Rhizoprionodon taylori* is a small carcharhinid species known to have one of the fastest growth rates of all shark species (Cortés, 2004, Simpfendorfer, 1993). Initial studies suggested it grows rapidly in the first year of life, on average increasing to 140% of its length-at-birth, and attains a maximum length of only 67 and 97 cm TL respectively in different locations in Australia (Simpfendorfer, 1993, Taylor et al., 2016). Maturity is reached after only one year with a litter of 1–10 pups produced every year following maturity (Simpfendorfer, 1992, Simpfendorfer, 1993). *Rhizoprionodon taylori* is also one of the few elasmobranch species that can halt embryonic development (diapause), possibly to facilitate increased litter sizes (Waltrick et al., 2012, Simpfendorfer, 1992).

Occurring only in southern New Guinea and tropical and sub-tropical nearshore waters of Australia from Carnarvon in Western Australia to Moreton Bay in southern Queensland, it is a locally abundant species often incidentally caught in trawl and gillnet fisheries (Harry et al., 2011b, Last and Stevens, 2009).

All known biological information about *R. taylori* has been established from populations in Australia (Simpfendorfer, 1992, Simpfendorfer, 1993, Simpfendorfer, 1999, Stevens and McLoughlin, 1991, Simpfendorfer, 1998, Taylor et al., 2016). Recent trawl fisheries data from Papua New Guinea (PNG) confirm that *R. taylori* is also frequently caught as bycatch in the Gulf of Papua (GoP) (NFA unpublished data). Prawn trawling has occurred in the area since the late 1960's and bycatch levels can comprise up to 85% of the total catch (Matsuoka and Kan, 1991). However, the effect of trawling on the sustainability of bycatch populations cannot be properly assessed without determining species compositions and locally relevant biological parameters.

Life history traits can differ for populations in separate localities (Lombardi-Carlson et al., 2003, White, 2007b). The GoP is in close proximity to the northern coast of Australia. However, *R. taylori* has been observed to maintain residency in embayments and nearshore habitats, travelling short distances and rarely moving greater than 100 km within 6 months to one year (Munroe et al., 2015a). These limited movements mean that there may be differences in the life history of this species between the GoP and other regions. These differences need to be investigated since variations in size at birth and length-at-maturity could affect fisheries risk assessments and have already been documented between different locations in Australia (Stevens and McLoughlin, 1991, Simpfendorfer, 1992, Taylor et al., 2016).

Age and growth studies provide essential information for wider population analyses such as stock assessments (Cortés et al., 2012). Growth parameters for *R. taylori* were determined by Simpfendorfer (1993) prior to the development and use of multiple growth models within an information theoretic framework, which is now the recommended approach for age and growth studies (Smart et al., 2016b, Goldman et al., 2012). This study used the more contemporary multi-model approach to determine growth and maturity parameters for *R. taylori* in the GoP. The specific aims were: (1) to determine the age, growth and maturity of *R. taylori*; (2) compare life history parameters to previous work to determine if the use of the multiple model approach substantially changed the outcomes; and (3) examine spatial variation in life history of this species. This study also contributes new knowledge from a data poor region that can be used to inform fisheries management and conservation in PNG.

4.2 Materials and methods

4.2.1 Sample collection

This work is a collaboration with the National Fisheries Authority (NFA), the government agency responsible for managing commercial fisheries and implementing fisheries research in PNG. Fishery observers were stationed on board prawn trawlers and collected sharks that were caught as bycatch and discarded. The sharks collected for this study had already suffered mortality in the process of fishing and no sharks were intentionally sacrificed for the study. All sampling procedures were allowed by the NFA and in line with James Cook University, Animal Ethics approval A2310 obtained prior to the commencement of the study. Sampling did not involve endangered or protected species. No further permits were required by relevant authorities.

Commercial trawling in the GoP occurs between Parama Island in the West, just south of the mouth of the Fly River, and the border of the Central and Gulf Provinces in the East (Fig 4-1). Trawl fishing is permitted all year round throughout the GoP except in a section of the Gulf between Iokea and Cape Blackwood which is closed to fishing between the 1st of December and the 31st of March, a measure put in place to protect the growth and survival of prawn recruits (Evans et al., 1997). Samples of *R. taylori* were collected on commercial vessels from June 2014 to August 2015. Whole samples were kept frozen and brought ashore at the end of each trip for confirmation of identification and processing. In a laboratory samples were defrosted, total length (TL) measured, and sex recorded. For each individual, maturity was also determined using an index modified from (2005a). Reproductive organs were examined and categorised according to the developmental stage of the ovaries and uteri in females, and claspers in males. Females were categorised into one of five stages and males into one of three stages (Table 4-1). A section of the vertebral column from beneath the first dorsal fin was retained and stored frozen for subsequent age determination (Cailliet and Goldman, 2004, Goldman et al., 2012).

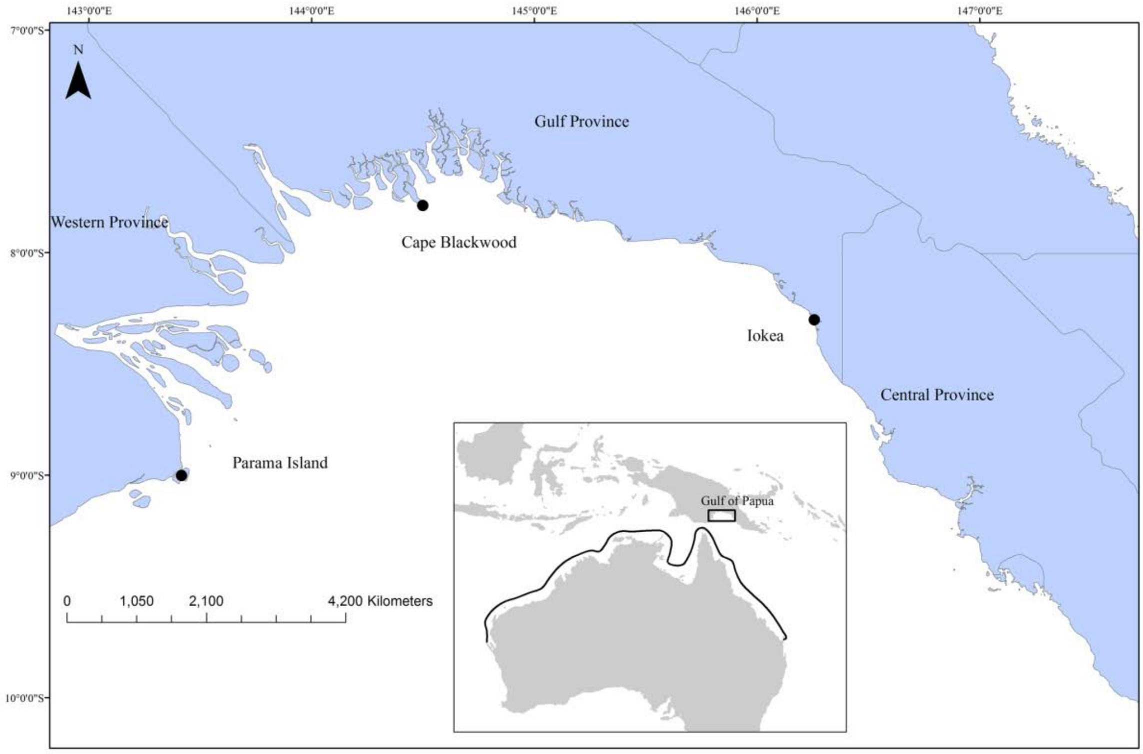

Figure 4-1: The Gulf of Papua is situated along the southern coast of Papua New Guinea. The insert shows the distribution of *Rhizoprionodon taylori* in Australia.

Table 4-1: The maturity of male and female samples were determined by the state of the uteri and ovaries in females, and claspers in males. Maturity stages were assigned a binary category for statistical analysis.

Female stage		**Description**	**Binary category**
1	Immature	Uteri very thin, ovaries small and without yolked eggs.	0
2	Maturing	Uteri slightly becoming enlarged at one end, ovaries becoming larger and small yolked eggs developing.	0
3	Mature	Uteri large along entire length, ovaries containing some large yolked eggs.	1
4	Pregnant	Uteri containing embryos or large eggs.	1
5	Post-partum	Uteri very large but without embryos.	1
Male stage		**Description**	**Binary category**
NC	Not Calcified	Clasper very short not extending past the pelvic fin tip.	0
PC	Partially Calcified	Claspers longer, extending past the pelvic fin tip, not entirely hard, still flexible.	0
FC	Fully Calcified	Claspers long, hard along almost the entire length.	1

4.2.1 Vertebrae preparation

Vertebrae processing and ageing followed protocols described by Cailliet et al. (2006). Frozen vertebrae were thawed and any excess tissue was removed using a scalpel. Vertebrae were separated into individual centra and immersed in 4% sodium hypochlorite solution for 3 – 5 minutes to clean remaining soft tissue from the small sized vertebrae. The centra were then rinsed using water and dried in an oven at 60 °C for 24 hours. A single centrum was selected from each individual and mounted on a microscope slide using Crystal bond adhesive (SPI supplies, Pennsylvania, USA). To achieve the desired thickness of < 400 µm the vertebrae was sanded towards the centre of the centrum using 400-1200 grit wet and dry abrasive paper. After one side was complete the centrum was remounted and sanded again on the other side until the desired thickness was achieved (Simpfendorfer, 1993).

4.2.2 Age determination

To estimate the age of each individual, mounted sections of vertebrae were observed using a dissecting microscope. Growth increments appeared as a pair of alternating wide opaque band and a narrow translucent band, referred to as a band pair (2006, Goldman et al., 2012). The birthmark was identified where there was an obvious change in angle along the corpus calcareum. Subsequent band pairs that spanned from one side of the corpus calcareum to the other side were interpreted to represent annual growth (Cailliet and Goldman, 2004, Goldman et al., 2012). The age of each individual was estimated as the number of band pairs present after the birthmark. The annual deposition of bands for this species has been validated using marginal increment analysis and size frequency data by (1993).

Precision and bias

Visual estimation of age from vertebrae is an approach which may include some level of bias (Cailliet and Goldman, 2004). To minimise bias two readers estimated ages separately. The first reader conducted an initial read of all vertebrae followed by a second experienced reader. Both readers had no prior knowledge of the sex or size of individuals. Final ages were the result of a consensus process between the readers – where counts were different readers examined the section and agreed on a final age. Where differences could not be resolved, those centra were removed from the analyses. To assess the precision of counts the average percent error (APE) (Beamish and Fournier, 1981), Chang's coefficient of variation (CV) (Chang, 1982) and percent agreement (PA ± 1 year) (Cailliet and Goldman, 2004) were used. Bowker's test of symmetry was used to estimate bias between readers (Bowker, 1948). Analyses were carried out using 'FSA' package version 0.8.11 in the R program environment version 3.2.2 (R Core Team, 2015).

4.2.3 Partial ages

For a species that reproduces seasonally, and the period of parturition is known, it is possible to assign partial ages and therefore improve age estimation (Smart et al., 2013). The pupping season for *R. taylori* was observed in January in Queensland (Simpfendorfer, 1993). In this study the largest embryo (22 cm TL) was caught in the month of December, confirming a similar timing in the GoP. Partial ages were calculated by choosing a birth date of 15th of January and determining the total number of days between this date and the date of capture which was then divided by the number of days in a year. This value was added to the number of full annual band pairs for each individual to give the final age. For example, samples aged at 1 year caught on the 17th of June and 30th of August, respectively, were given partial ages of 1.39 and 1.62 years.

4.2.4 Growth model fitting

The growth of *R. taylori* was modelled using a multi-model approach. This method incorporated the Akaike Information Criterion (AIC) (Akaike, 1973) which selected the best model fit based on the lowest AIC value (Smart et al., 2016a). Preference for the use of multiple growth models over an *a priori* approach, using only the von Bertalanffy growth model (VBGM) is standard methodology in elasmobranch growth literature (Smart et al., 2016b). The multi-model approach is considered to provide better growth estimates as it avoids model mis-specification and biases compared to the use of a single model (Cailliet et al., 2006, Thorson and Simpfendorfer, 2009, Smart et al., 2016b). The lack of small juveniles in the sample, and their likely very rapid growth required a variety of approaches to determine the most suitable growth parameters. Three candidate models were used: VBGM, logistic model, and Gompertz model (Table 4-2). However, because of the limited data from very young individuals three approaches to fitting the models was used: (1) standard three-parameter growth models, (2) versions of the growth models with a fixed length-at-birth (which ensured that models accounted for the rapid early growth; two-parameter version) (Harry et al., 2011a), and (3) three-parameter models with four hypothetical aged zero individuals (L_0 = 26 cm TL) added to the sample in order to provide a reference point for the model given that aged zero individuals were absent from the sample (Smart et al., 2013). Separate growth models were constructed for males, females, and combined sexes.

Table 4-2: Equations of the three growth functions used in the multi model approach

Model	Growth function
von Bertalanffy	$L(t) = L_0 + (L_\infty - L_0)(1 - e^{(-kt)})$
Logistic	$L(t) = \dfrac{L_\infty L_0 (g_{(\log)} t)}{L_\infty + (L_0\, e^{(g_{(\log)} t - 1)})}$
Gompertz	$L(t) = L_\infty\, e^{(-L_0\, e^{(-g_{(gom)} t)})}$

The three-parameter models estimated length-at-birth (L_0), asymptotic length (L_∞) and the different growth coefficients for each respective model; k indicates the relative growth rate of the VBGM model while $g_{(log)}$ and $g_{(gom)}$ represent alternative sigmoidal growth of the Gompertz and logistic models (Katsanevakis and Maravelias, 2008). The two-parameter models incorporated a fixed known value for length-at-birth and thus the models only estimated the asymptotic length and the growth coefficients. Umbilical scars were not recorded in this study which meant that a length-at-birth for *R. taylori* in the GoP was not identified but could be estimated using other data available from the sample as well as published information. In this study the smallest free swimming individuals were 31 cm (TL) and largest embryos were 22 cm (TL) observed in December (a month prior to pupping). The literature estimates of length-at-birth are 25–30 cm (Stevens and McLoughlin, 1991) from northern Australia and 22–26 cm in north eastern Australia (Simpfendorfer, 1993). A possible estimate for the length-at-birth would therefore be 22–30 cm, however in the GoP *R. taylori* are still embryos at 22 cm and are possibly born at a larger size. The midpoint between 22 and 30 cm (26 cm) was chosen because this value was within the length-at-birth range suggested by both previous studies and was biologically plausible given embryo sizes in the GoP. Growth models were fit using the ‘nls’ function, multi-model analysis was conducted using the ‘MuMIn’ package version 1.15.6 (Barton, 2016) and bootstrapped confidence intervals were produced using the ‘nlstools’ package version 1.0-2 (Baty et al., 2015) in the R program environment version 3.2.2 (R Core Team, 2015).

As the sample size was less than 200, the AIC_C, a size adjusted bias correction, was used (Zhu et al., 2009) :

$$AIC_C = AIC + \frac{2k(k+1)}{n-k-1}$$

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 that has the lowest AIC_C value (AIC_{min}) was chosen as the best fit for the data. The AIC difference (Δ) was calculated for each model (i = 1-3) and used to rank the remaining models as follows:

$$\Delta_i = AIC_{Ci} - AIC_{min}$$

Models were ranked according to the value of Δ. Values from 0-2 were considered to have the strongest support, less support was given to values between 2-10 and the least support for Δ values > 10 (Anderson and Burnham, 2002). The AIC weights were calculated by the expression:

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

To test if there were differences in the growth curves for males and females, a likelihood ratio test was carried out (Kimura, 1980). This was conducted on the model with the best fit based on the AIC_C results for the sexes combined. The method used to carry out the likelihood ratio test was described by (Haddon, 2001) and incorporated into the R program environment version 3.2.2 (R Core Team, 2015) for this analysis.

4.2.5 Maturity

The maturity stage data was converted to a binary maturity category (immature = 0 or mature =1) for statistical analyses (Table 4-1). The length-at-maturity was estimated for both males and females using logistic regression (Walker, 2005a) :

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

where P (l) is the proportion mature at TL, l and P_{max} is the maximum proportion of mature individuals. The lengths of which 50 and 95% of the population are mature (l_{50} and l_{95}) were estimated using a generalised linear model (GLM) with a binomial error structure and a logit-link function using the 'psyphy' package version 0.1-9 (Knoblauch, 2014) and the 'FSA' package version 0.0.11 (Ogle, 2016) in the R program environment version 3.2.2 (R Core Team, 2015). Age-at-maturity was determined by substituting length with age. A_{50} and A_{95} were the ages at which 50 and 95% of the population reached maturity.

4.3 Results

4.3.1 Age determination

In total 186 individuals were collected: 131 females and 55 males. Males ranged in size from 31–53 cm (TL) and females from 31–66 cm (TL). The majority of sharks were aged between 0 and 1 years (i.e. birthmark was present but not fully formed 1st band pair) (Fig 4-2). Final partial ages ranged from 0.2 to 4.6 years. The oldest female was 64 cm (TL) and aged at 4.6 years. The oldest male was 51 cm (TL) and aged at 3.6 years.

The measures of variability around the determination of ages were high compared to other elasmobranch ageing studies (Campana, 2001, Natanson et al., 2007, Gutteridge et al., 2013). The Average Percent Error (APE), Chang's CV and PA ± 1 year were 29.1%, 41.1% and 62.4%, respectively. Higher variability will be experienced when ageing short lived species as small differences in band pair counts can produce inflated error estimates in comparison to longer lived species (Simpfendorfer, 1993). Bowker's test for symmetry (df = 8, $x^2 = 16.4$, $P = 0.037$) indicated some systematic bias between readers. The age bias plot (Fig 4-3) showed that this bias was associated with reader 1 estimating younger counts of band pairs at 3 and 4 years relative to reader 2. The use of consensus counts to produce final ages overcame this ageing bias.

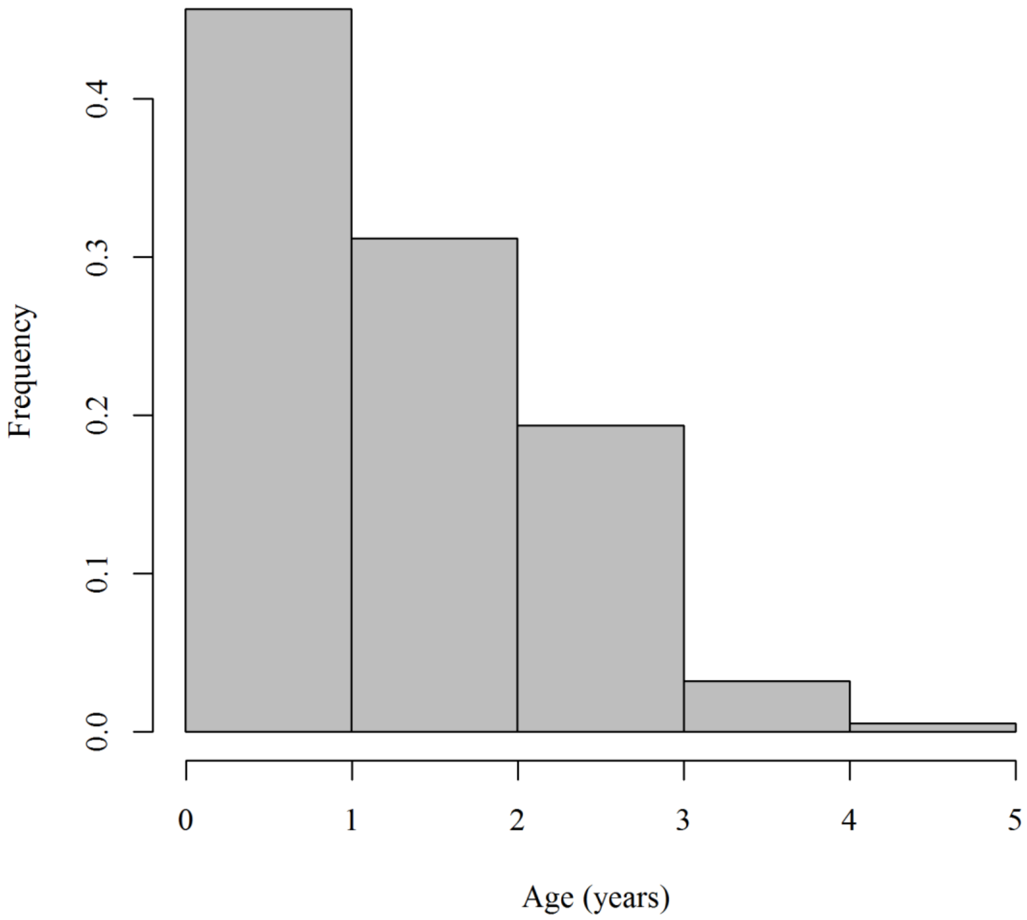

Figure 4-2: Frequency histogram of samples for each age class.

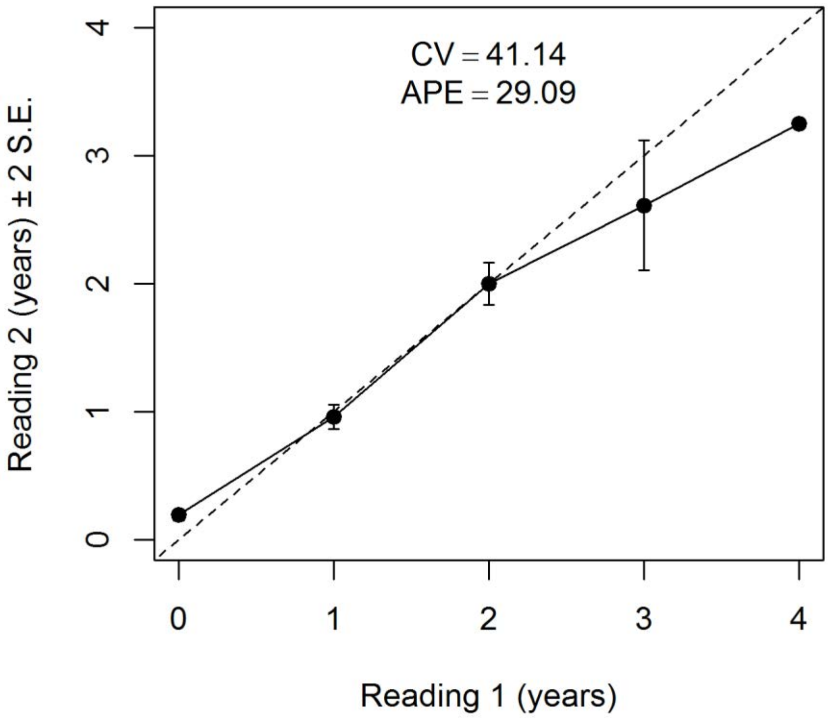

Figure 4-3: Age bias plot showing agreement between two independent readers. The PA ± 1 year was 62.4%, APE was 29.1 and Chang's coefficient of variation (CV) was 41.1%.

4.3.2 Growth model fitting

Without data from small new born animals three-parameter models were unsuitable as the projected length-at-birth values were too high and biologically unreasonable for *R. taylori* (37– 38 cm) (Table 4-3).The three-parameter models with the four added size at birth individuals had similar AIC weights for combined and individual sexes (Table 4-4). All three candidate models had similar weights in the three-parameter models. Neither of the three-parameter approaches accurately represented the early growth of *R. taylori*, over-estimating the size at birth. Amongst the two-parameter models the VBGM performed best as neither logistic and Gompertz models had Δ values < 2, although there was some weak support for the Gompertz model for males ($w = 0.24$) (Table 4-5). The two-parameter models projected much higher growth completion rates (k, $g_{(log)}$, $g_{(gom)}$) than three-parameter models however, the fixed length-at-birth value were more realistic. Thus, it is likely that none of the fitting approaches produced accurate estimates of all three parameters. However, the two-parameter VBGM is recommended to describe the growth of *R. taylori* in the GoP (Fig 4-4), with a growth estimate (k) of 1.27 for both sexes combined (Table 4-5). A likelihood ratio test showed significant difference (df = 3, $x^2 = 23.3$, $P = 3.5$) in the VBGM fit between males and females which demonstrated that sexes should be modelled separately. The error estimates for the male VBGM parameters were much higher than for females, indicating much greater level of uncertainty, probably because of the smaller sample size.

Table 4-3: Summary of results from the multi model approach incorporating Akaike's information Criterion (AIC) using three-parameter versions of models.

Sex	**Model**	**n**	**AIC_C**	**Δ**	**W (%)**	**L_0(±SE)**	**L_∞(±SE)**	**k(±SE)**	**$g_{(log)}$(±SE)**	**$g_{(gom)}$(±SE)**	**RSE**
Combined	VB3	186	1129.06	0.53	0.29	37.89±1.27	74.34±12.98	0.25±0.14			4.96
	Logistic	186	1128.53	0	0.38	38.17±1.11	66.92±6.0		0.50±0.14		4.96
	Gompertz	186	1128.78	0.25	0.33	38.03±1.18	69.65±8.21			0.38±0.14	4.96
Male	VB3	55	306.3	0.17	0.32	38.48±1.50	58.89±15.72	0.31±0.37			3.72
	Logistic	55	306.13	0	0.35	38.51±0.76	55.71±8.90		0.51±0.20		3.71
	Gompertz	55	306.22	0.09	0.33	38.50±1.44	57.00±11.41			0.41±0.37	3.72
Female	VB3	131	801.08	0.29	0.31	38.03±1.90	71.08±10.55	0.31±0.17			5.04
	Logistic	131	800.8	0	0.36	38.53±1.35	66.30±5.79		0.55±0.15		5.04
	Gompertz	131	800.93	0.13	0.33	38.30±1.74	68.17±7.46			0.43±0.17	5.04

n is the sample size, AIC_C is the small-sample bias adjusted from the Akaike's Information Criteria, Δ is the difference in AIC_C values between models, w (%) are the AIC_C weights, L_0 and L_∞ are the length-at-birth and asymptotic length in cm respectively, k is the growth completion rate in (year^{-1}) for the VB3, $g_{(log)}$ and $g_{(gom)}$ are the growth parameters for Logistic and Gompertz functions respectively, SE is the standard error of each growth parameter and RSE is the residual standard error for the models.

Table 4-4: Summary of results from the multi model approach incorporating Akaike's information Criterion (AIC) using three-parameter versions of models with four hypothetical aged zero individuals.

Sex	**Model**	**n**	**AIC_C**	**Δ**	**W (%)**	**L_0(±SE)**	**L_∞(±SE)**	**k(±SE)**	**$g_{(log)}$(±SE)**	**$g_{(gom)}$(±SE)**	**RSE**
Combined	VB3	190	1166.85	0	0.45	35.12±1.32	63.88±4.03	0.48±0.14			5.15
	Logistic	190	1168.21	1.96	0.23	35.98±1.14	61.75±2.87		0.73±0.15		5.16
	Gompertz	190	1167.59	0.73	0.32	35.59±1.22	62.65±3.33			0.60±0.14	5.16
Male	VB3	57	330.66	0	0.39	34.55±1.87	50.42±2.57	1.01±0.43			4.19
	Logistic	57	331.28	0.62	0.28	35.28±0.92	50.41±2.47		1.17±0.25		4.21
	Gompertz	57	331.01	0.35	0.33	34.96±1.76	50.44±2.53			1.08±0.44	4.2
Female	VB3	133	819.85	0	0.44	34.91±1.96	63.77±3.92	0.53±0.17			5.17
	Logistic	133	821.06	1.21	0.24	36.22±1.38	62.27±3.04		0.77±0.15		5.20
	Gompertz	133	820.51	0.66	0.32	35.64±1.8	62.92±3.41			0.65±0.18	5.19

n is the sample size, AIC_C is the small-sample bias adjusted from the Akaike's Information Criteria, Δ is the difference in AIC_C values between models, w (%) are the AIC_C weights, L_0 and L_∞ are the length-at-birth and asymptotic length in cm respectively, k is the growth completion rate in ($year^{-1}$) for the VB3, $g_{(log)}$ and $g_{(gom)}$ are the growth parameters for Logistic and Gompertz functions respectively, SE is the standard error of each growth parameter and RSE is the residual standard error for the models.

Table 4-5: Summary of results from the multi model approach incorporating Akaike's information Criterion (AIC) using two parameter versions of growth models with a fixed length-at-birth for *Rhizoprionodon taylori* from the Gulf of Papua.

Sex	**Model**	**n**	**AIC_C**	**Δ**	**W (%)**	**L_∞(±SE)**	**k(±SE)**	**$g_{(log)}$(±SE)**	**$g_{(gom)}$(±SE)**	**RSE**
Combined	VB2	186	1193.71	0	0.99	55.95±0.95	1.27±0.11			5.54
	Logistic	186	1213.08	19.38	0	54.41±0.75		2.12±0.14		5.83
	Gompertz	186	1203.61	9.9	0.01	55.07±0.82			1.67±0.13	5.68
Male	VB2	55	336.13	0	0.64	46.11±0.9	3.69±0.68			4.44
	Logistic	55	339.47	3.34	0.12	45.08±0.77		6.73±1.23		4.57
	Gompertz	55	338.1	1.97	0.24	45.52±0.82			5.04±0.92	4.52
Female	VB2	131	830.37	0	0.96	57.78±1.12	1.17±0.12			5.40
	Logistic	131	842.88	12.52	0.00	56.08±0.84		1.98±0.15		5.66
	Gompertz	131	836.6	6.23	0.04	56.8±0.94			1.55±0.13	5.53

n is the sample size, AIC_C is the small-sample bias adjusted from the Akaike's Information Criteria, Δ is the difference in AIC_C values between models, w (%) are the AIC_C weights, L_∞ is the asymptotic length in cm, k is the growth completion rate in ($year^{-1}$) for the VB2, $g_{(log)}$ and $g_{(gom)}$

are the growth parameters for logistic and Gompertz functions respectively, SE is the standard error of each growth parameter and RSE is the residual standard error for the models.

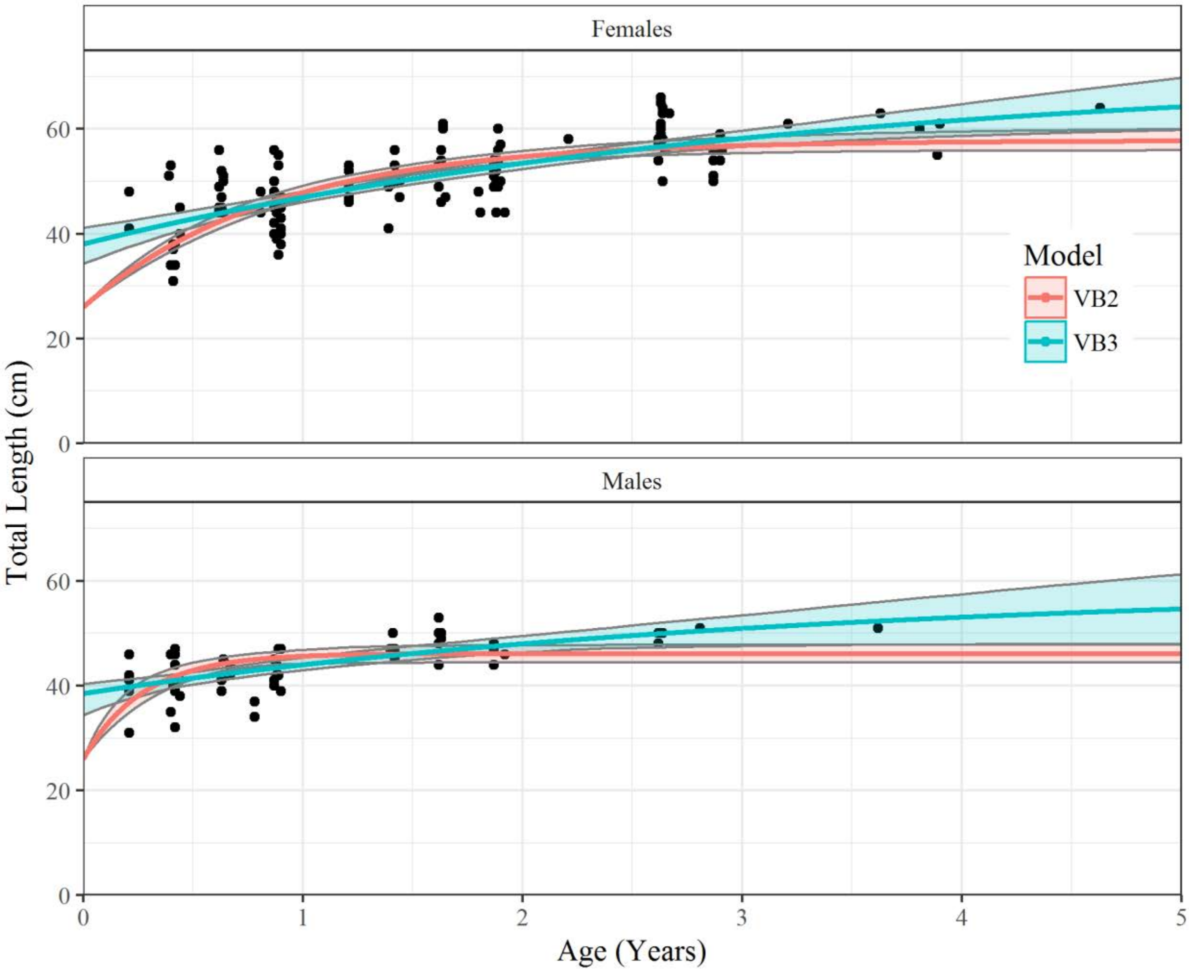

Figure 4-4: Two (VB2) and three parameter (VB3) length-at-age curves for female and male *Rhizoprionodon taylori* from the Gulf of Papua fitted with 95% bootstrapped confidence intervals.

4.3.3 Maturity

Maturity estimates for male and female *R. taylori* differed slightly. Females grew larger than males, and males matured earlier in terms of both length and age (Fig 4-5). The smallest mature female was 42 cm (TL) and lengths at maturity L_{50} and L_{95} were 47.0 cm (TL) ± 0.68 S.E. and 53.5 cm TL ± 1.2 S.E. The A_{50} and A_{95} were 0.93 years ± 0.1 S.E. and 2.95 years ±

0.4 S.E., respectively for females. The smallest mature male was 39 cm (TL). The L_{50} and L_{95} for males were 41.7 cm (TL) ± 0.8 S.E. and 47.2 cm (TL) ± 1.5 S.E while the ages at maturity A_{50} and A_{95} were 0.5 years ± 0.2 S.E. and 2.2 years ± 0.6 S.E.

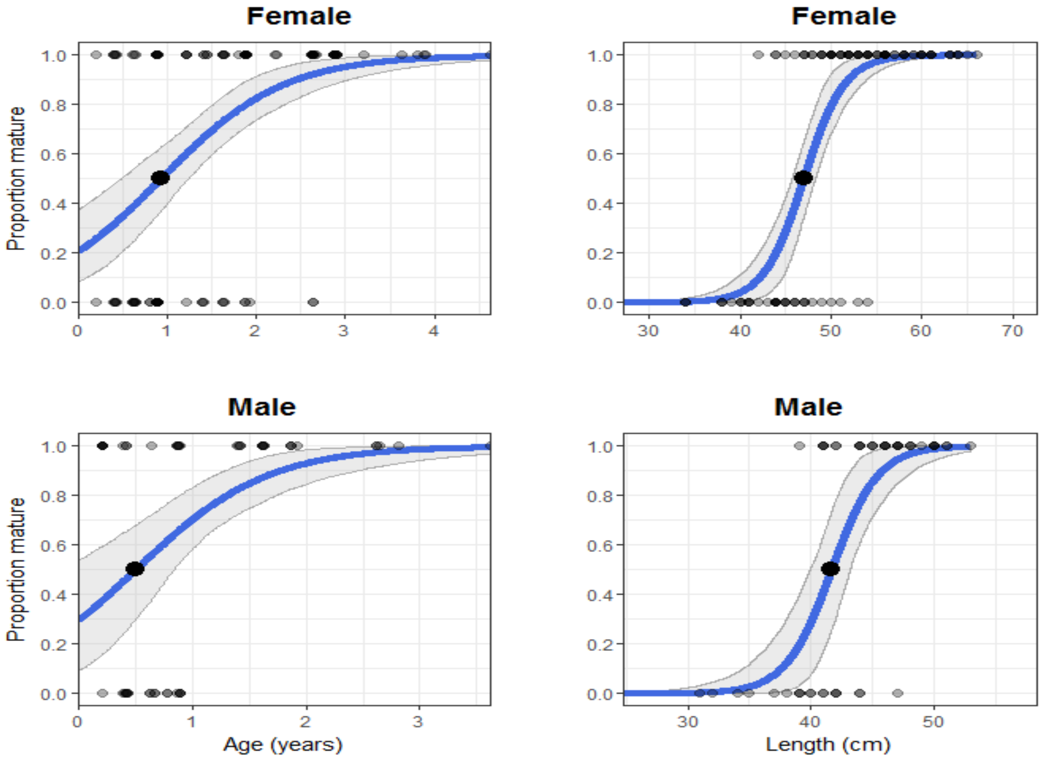

Figure 4-5: Age and length-at-maturity ogives for female and male *Rhizoprionodon taylori* from the Gulf of Papua. The large points on the curve represent the length and age at which 50% of population reaches maturity. 95% bootstrapped confidence intervals are indicated with shaded areas.

4.4 Discussion

The results of this study reaffirm the very rapid growth and maturity of *R. taylori* in comparison to the majority of chondrichthyan species. For sharks, von Bertalanffy growth completion rates (*k*) >1, as seen in *R. taylori* are rare and indicate very rapid growth compared to other species, most of which reach much larger maximum sizes. For example *Isurus oxyrinchus* (*k* = 0.052 year^{-1}) and *Carcharhinus plumbeus* (*k* = 0.040 year^{-1}) (Bishop et al., 2006, McAuley et al., 2006) both have much lower growth completion rates and as a result take many years before they reach maturity. Small bodied coastal shark species such as *Rhizoprionodon terraenovae* (*k* = 0.5 year^{-1}) and *Rhizoprionodon acutus* (*k* = 0.63 year^{-1} for females, *k* = 0.94 year^{-1} for males) (Loefer and Sedberry, 2003, Harry et al., 2010) generally exhibit more rapid growth. *Rhizoprionodon taylori* has the fastest known growth completion rate for a shark species gaining more than 100% of its body size in the first year of life (Simpfendorfer, 1993).

The growth completion rate of female *R. taylori* from the two-parameter model fitting (*k* = 1.165 year^{-1}) in the GoP is similar to that previously found in Australia (*k* =1.013) (Simpfendorfer, 1993). The elevated growth completion rate (k=3.69 y^{-1}) for males predicted by the model had a high level of error and so remains to be resolved by further research. The two-parameter VBGM produced reduced L_∞ estimates for both males and females. While the three parameter VBGMs estimated reasonable values for L_∞ for both sexes, the L_0 projected by the model was well beyond the size at birth previously reported for this species and outside the ranges expected from the GoP data. The addition of hypothetical zero aged animals provided little improvement in the value of L_0 for *R .taylori* despite its utility in other species (Smart et al., 2013). Given the linkage between the parameters in growth models the true values of growth completion parameters lie between those estimated by the two and three parameter models. Based on the biological implausibility of size at birth projected by the three-parameter VBGM it cannot be considered to model the growth of *R. taylori* in the GoP. Similarly the two-parameter VBGM has its drawbacks however does provide growth estimates that are within reason particularly for females, but further investigation is warranted given the large confidence intervals around k for males and the large differences between males and females. Factors that may have influenced this outcome are; methodological differences between this study and Simpfendorfer (1993) who fitted growth curves by eye, the relatively small number of males in the sample and the model being constrained by fixing the length-at-birth. Fixing models by selecting a single length-at-birth value has been discouraged because of variations in the actual birth size (Pardo et al., 2013).

Two-parameter models are recommended under stringent conditions where: there is limited data for smaller juveniles, low sample sizes, and where the length-at-birth cannot be estimated from the study population but can be deduced from a representative population in the same geographic region (Thorson and Simpfendorfer, 2009). The lack of data from younger *R. taylori* close to the length-at-birth posed a problem that is usually solved by back calculation (Smart et al., 2013). However, this could not be done because much of the growth of *R. taylori* occurs prior to the first year of life and there are no growth bands deposited during this period that can be used to track their growth. In addition, although the AIC values indicated that the three-parameter models provided a better fit the projected length-at-birth values were not biologically realistic. For these reasons, the use of two-parameter models in this study was considered to provide the best way to ensure that biologically plausible parameters were produced.

The rapid growth of juvenile *R. taylori* is relatively unique and alternative methods to improve model fitting could be explored beyond the scope of this study. The information theoretic approach has a limited capacity to include variations in individual growth since only a single value of L_0 was used. Bayesian modelling on the other hand is less sensitive to missing data and can account for variation in individual growth (Siegfried and Sanso, 2006, Baum et al., 2003). Bayesian frameworks have been used to set informative priors of L_0 rather than fixing a specific value (Siegfried and Sanso, 2006, Pardo et al., 2016a). Alternatively, since early growth of *R. taylori* is somewhat linear but levels off after maturity a biphasic Lester model could be suitable as a surrogate approach to approximate growth parameters in the different stages of growth (Wilson et al., 2018).

The maturity estimates for *R. taylori* in the GoP showed that males matured within 6 months of birth while females reached maturity as they approached 12 months of age. The only other age-at-maturity estimates for *R. taylori* were observed by Simpfendorfer (1993) and although the female age-at-maturity observed in the GoP corresponds to this study, the males in the GoP appear to reach maturity within half the time noted in Queensland. Length-at-maturity estimates for the GoP showed that males also matured at smaller sizes then females. The length at which both 50% of males and females in the GoP reached maturity resembled data from north and western Australia recorded by Stevens and McLoughlin (1991) which were smaller than that observed by Simpfendorfer (1993) and Taylor et al. (2016). These findings highlight latitudinal variation for this species suggesting length-at-maturity increases with higher latitudes. The underlying reasons for latitudinal variation in life history traits have been attributed to differences in water temperature (Yamaguchi et al., 2000, Lombardi-Carlson et al., 2003).

It is important to correctly determine age in sharks as errors can lead to inaccurate projections of parameters such as age-at-maturity which can have a sizable impact on population models

(Loefer and Sedberry, 2003), and stock assessments. Achieving accuracy and precision in vertebral ageing relies on the clarity of growth markings and the ability of the readers to identify and differentiate growth bands. Several studies focused on small shark species have noted difficulties in detecting the correct number of growth bands particularly on the edge of the vertebrae, where bands are deposited very close to each other and as a consequence maximum age may be underestimated (Gutteridge et al., 2013, Loefer and Sedberry, 2003). Furthermore as temperate seasonality may influence the deposition of growth bands (Goldman et al., 2012), they appear more pronounced in temperate sharks as opposed to tropical sharks where seasonality is limited. For instance the appearance of check marks in the GoP vertebrae were not as pronounced as that observed by Simpfendorfer (1993).

Assumptions on annual growth band deposition for *R. taylori* were made in this study because validation was not possible due to logistic constraints. The annual periodicity of band formation for *R. taylori* in northern Queensland was verified by Simpfendorfer (1993) based on marginal increment analysis and length frequency data. This assumption has strong support given the geographic proximity of this study, and annual band formation being the typical pattern observed in carcharhinid sharks (Harry et al., 2013, Simpfendorfer et al., 2002).

Partial ages were calculated to improve the estimation of age and overall growth model projections. This method is suited to sharks with seasonal patterns of reproduction where mating and parturition occur at specific times of the year, rather than asynchronous species. *Rhizoprionodon taylori* undergoes a seven month period of diapause where embryonic development at the blastodermic disc stage is suspended (Simpfendorfer, 1992). Regardless of this, the reproductive cycle of *R. taylori* appears to be seasonal as mating occurs only once a year from late January to early February (Simpfendorfer, 1992). The fertilised eggs then enter a state of diapause until September, after which active growth of the embryos recommences until parturition in January (Simpfendorfer, 1992, Waltrick et al., 2012).

The rapid growth and early onset of maturity in small-bodied sharks has been hypothesised to be a survival strategy to counter high levels of predation experienced by a species (Branstetter, 1990). Small bodied sharks are an important intermediate link in the food chain as they are often preyed upon by larger predators (Heupel et al., 2014). A study on *R. acutus* by Harry et al. (2010) also noted that high natural mortality experienced by a species may be balanced by early maturity. Certainly in the GoP *R. taylori* may experience high natural mortality as their small size and slower swimming capacity would render them a common prey for larger predators (Branstetter, 1990). Furthermore, the high level of bycatch from the Gulf of Papua trawl fishery (Matsuoka and Kan, 1991) places some level of fishing mortality on the *R. taylori* population. High levels of natural and fishing mortality may account for their very young age-at-maturity.

Commercial trawling has taken place in the GoP for over forty years. At the onset of this fishery, as many as 30 vessels were licensed. The total number of vessels and fishing effort has fluctuated over the years peaking at 95 000 trawl hours in 1989 before decreasing when effort control measures were introduced (Evans et al., 1995). Currently only six vessels are actively trawling in the GoP. Rapid growth and early maturity are biological characteristics associated with the ability of a species to withstand fishing pressure (Smith et al., 1998), therefore it is probable that *R. taylori* in the GoP are better placed to withstand current fishing levels than other shark species.

The foundations of managing fish stocks and attaining sustainable fisheries rely upon accurate biological data of fish populations (Cailliet and Goldman, 2004, Heupel and Simpfendorfer, 2010). Until recently, information for sharks in PNG has been scarce (White et al., 2015, D'Alberto et al., 2016, Smart et al., 2016a, Smart et al., 2017a). This study is one of the first attempts to determine biological parameters of a small-bodied, commonly caught carcharhinid species in PNG. However, further work is needed to provide critical biological data for population assessments as well as to understand the ecological functions of shark species in order to fine tune management and conservation measures to suit the PNG context. Advancement in elasmobranch research in PNG will also address important data gaps for the Indo-Australasian region which supports the highest diversity of sharks globally (White and Kyne, 2010).

Chapter 5 Age, growth and maturity of the Australian blackspot shark *Carcharhinus coatesi* in the Gulf of Papua.

5.1 Introduction

In recent years many species of chondrichthyans have faced large declines in population size leading to concerns about their conservation status (Dulvy et al., 2014). The main causes of declines are the effects of harvesting through various fishing practices, as well as habitat degradation, pollution and other factors (Dulvy et al., 2017, Stevens et al., 2000). The need to make fishing more sustainable and less ecologically damaging is urgent given the widespread declines, but these efforts are hampered by the lack of taxonomic and fundamental life history information for many species in vast regions of the world (Frisk et al., 2001). Without an understanding of basic biological parameters such as reproductive and growth characteristics of a species it is difficult to carry out stock assessments and understand population dynamics, which are needed to improve management for threatened and exploited shark stocks (Simpfendorfer et al., 2011).

Small bodied sharks that typically grow to a maximum length of less than one meter are commonly caught in coastal areas by a range of fishing gears, including gillnets and trawls that target other species (Cortés, 2002, Stobutzki et al., 2002, Harry et al., 2011a). This group of sharks have relatively fast growth, and thus are thought to be more resilient to fishing pressure than larger, slower growing shark species (Smith et al., 1998). Despite this general understanding it is also known that the biology of a single shark species can differ between localities within its range (Taylor et al., 2016, White, 2007b). Region or population specific information is therefore required to produce more accurate stock assessments (Smart et al., 2015) and improve fisheries management.

The Australian blackspot shark (*Carcharhinus coatesi*) is a common small-bodied carcharhinid shark found throughout northern Australia and Papua New Guinea (Amariles et al., 2017). Taxonomic uncertainty led to earlier mis-identification of this species in Australia as *Carcharhinus dussumieri* (white cheek shark) (Stevens and McLoughlin, 1991, Stobutzki et al., 2002, Last and Stevens, 2009). However, recent taxonomic work combined with molecular techniques distinguished *C. coatesi* as a separate species (White, 2012). Stevens and McLoughlin (1991) established biological information for this species in Australia and preliminary age and growth assessments of *C. coatesi* were conducted by Smart et al. (2013) from the Great Barrier Reef region, Australia. However, there have been no studies of *C. coatesi* in Papua New Guinea despite it being a common bycatch in commercial trawl fishing.

The Gulf of Papua prawn trawl fishery (GoPPF) has been in existence for over four decades and total levels of bycatch of all species (including sharks) varies between 60–85% by weight of the overall catch (Matsuoka and Kan, 1991, Evans et al., 1995). Despite the large composition of bycatch there has been little research to identify, quantify and determine the biology and life history of bycatch species in order to understand the broader ecological impact of the trawl fishery in the Gulf of Papua (GoP). In an effort to address these data gaps, and subsequently provide fishery managers with local information, this study aimed to: (1) present new information about the age, growth and maturity of *C. coatesi* in the Gulf of Papua, and (2) compare this information with previous work in north-eastern Australia to investigate any regional variation in life history.

5.2 Materials and methods

The Gulf of Papua is a semi enclosed body of water on the southern side of PNG covering an area of over 50,000 km^2 (Wolanski et al., 1995). Several major rivers flowing from the interior of PNG converge on the gulf. The larger Fly River is located in the north-west and several other rivers occur eastward (Fig 3-1). Extensive mangrove swamps and estuarine areas line the coastline providing important habitat and nursery areas which support a diverse array of aquatic life (Pernetta and Hill, 1981). Several commercially valuable crustacean species (mostly penaeid prawns) occur in the region and are harvested via the GoPPF (Gwyther, 1982).

Fishery observers were deployed on seven prawn trawl fishing trips between June 2014 and August 2015 to collect shark bycatch samples and data. Sharks that had suffered fishing mortality were kept whole, frozen on board and brought back to shore. In the laboratory sharks were thawed, total length (TL) measured, and sex and maturity recorded. Maturity stages were assessed by inspecting the appearance and development of the ovaries and uteri in females and the claspers in males based on Walker (2005a) that categorizes five reproductive stages ranging from immature to post parturition in females and three stages in males. A binary category was assigned to maturity for estimating the size at maturity reached (Table 1). A section of the vertebrae beneath the first dorsal fin was extracted and kept frozen for further preparation to determine the age of the sharks.

Table 5-1: The maturity of male and female samples were determined by the state of the uteri and ovaries in females, and claspers in males. Maturity stages were assigned a binary category for statistical analysis.

Female stage		**Description**	**Binary category**
1	Immature	Uteri very thin, ovaries small and without yolked eggs.	0
2	Maturing	Uteri slightly becoming enlarged at one end, ovaries becoming larger and small yolked eggs developing.	0
3	Mature	Uteri large along entire length, ovaries containing some large yolked eggs.	1
4	Pregnant	Uteri containing embryos or large eggs.	1
5	Post-partum	Uteri very large but without embryos.	1
Male stage		**Description**	**Binary category**
NC	Not Calcified	Clasper very short not extending past the pelvic fin tip.	0
PC	Partially Calcified	Claspers longer, extending past the pelvic fin tip, not entirely hard, still flexible.	0
FC	Fully Calcified	Claspers long, hard along almost the entire length.	1

5.2.1 Vertebrae preparation

Protocols described by Cailliet et al. (2006) were used to prepare vertebrae for ageing. Frozen vertebrae were thawed, excess tissue was removed using a scalpel, and the sample separated into individual centra. All centra from an individual shark were placed in separate vials and immersed in 4% sodium hypochlorite solution to remove any remaining soft tissue. Vertebrae were immersed for up to five minutes depending on size. The centra were then rinsed with water and dried in an oven at 60°C for 24 hours. Vertebrae large enough to be sectioned were mounted onto a low speed circular saw (Beuhler, Illinois USA) and a section approximately 400 µm was cut using two diamond tip blades. Each section was attached onto a microscope slide using Crystal Bond adhesive (SPI supplies, Pennsylvania, USA). Centra that were too small to be adequately held by the chuck of the circular saw were mounted on a microscope slide using the same adhesive and were sanded towards the centre on either side using 400-1200 grit wet and dry abrasive paper. After one side was complete each centrum was remounted and sanded again on the other side to achieve the desired thickness (Simpfendorfer, 1993).

5.2.2 Age determination

Mounted sections of vertebrae were examined using a dissecting microscope. Growth increments appeared as wide and narrow bands. The wide band was usually opaque while the narrow band was translucent and together were referred to as a band pair as recommended by Cailliet et al. (2006). The birthmark was identified as an obvious change in angle along the inner margin of the corpus calcareum. Complete band pairs that could be seen from one side of the corpus calcareum to the other side were assumed to represent annual growth (Cailliet and Goldman, 2004) (Fig. 5-1). The age of each shark was indicated by the number of band pairs present after the birth mark. *Carcharhinus coatesi* has no distinct breeding season (Stevens and McLoughlin, 1991) so to account for aseasonal parturition of 0.5 years was added to each individual age following Harry et al. (2010). Annual growth band deposition could not be verified using marginal increment analysis because sampling was not carried out consistently in each month of the year due to logistical issues. However, it was assumed that *C. coatesi* deposited bands annually based on evidence in literature that supports annual growth band deposition for sharks belonging to the family Carcharhinidae (McAuley et al., 2006, Chin et al., 2013, Harry et al., 2013, Barreto et al., 2011).

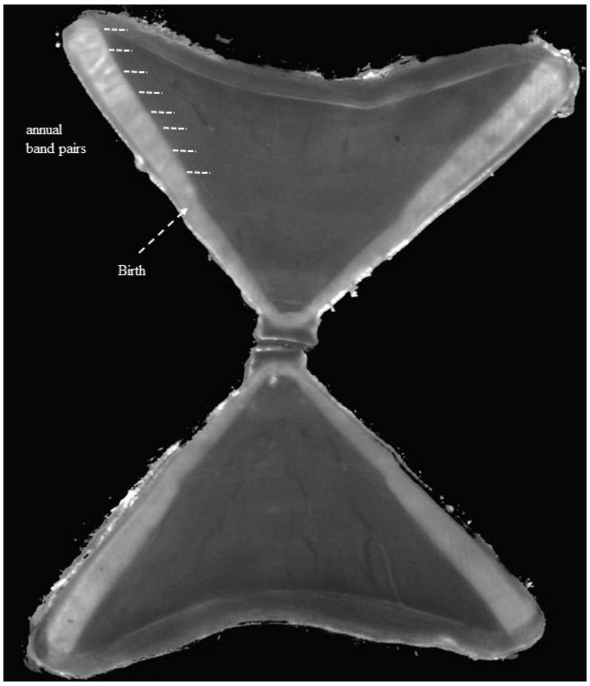

Figure 5-1**:** Cross-section of a *Carcharhinus coatesi* vertebral centrum viewed under a microscope. Birthmark and annual band pairs indicate, 8 years of age.

5.2.3 Precision and bias

The appearance of growth band pairs differs between species and may be affected by the light source and method of preparation (Cailliet and Goldman, 2004). In addition, readers may also interpret growth bands differently from each other. To reduce variability and bias, independent age readings were carried out by two separate readers without knowledge of the size and sex of individual sharks. Readers then compared their results and a consensus read was conducted in any instance where counts differed. Samples were excluded from further analysis where an agreed age could not be reached. The precision of the counts was analysed using average percentage error (APE) (Beamish and Fournier, 1981), Chang's coefficient of variation (CV) (Chang, 1982) and percentage agreement (PA ± 1 year) (Cailliet and Goldman, 2004). Bias between readers was calculated using Bowker's test of symmetry (Bowker, 1948). Analyses were carried out using 'FSA' package (Ogle, 2016) in the R program environment (R Core Team, 2015).

5.2.4 Growth model fitting

A multi-model approach was used to determine the growth of *C. coatesi* by assessing the level of fit between several candidate models as opposed to only the von Bertalanffy growth model (VBGM). The traditional *a priori* use of the VBGM to fit length-at-age data is now being replaced by the multi-model approach which has been recommended as best practice in recent elasmobranch growth studies (Smart et al., 2016b). The multi-model approach uses the Akaike Information Criterion (AIC) (Akaike, 1973) to rank performance of each candidate model thereby indicating the model with the best fit to the length at age data. When all models perform similarly a Multi Model Inference approach calculates model averaged parameters based on Akaike weights from each respective model (Katsanevakis and Maravelias, 2008). The use of the multi-model approach minimises the risk of model-misrepresentation and associated biases (Cailliet et al., 2006, Thorson and Simpfendorfer, 2009, Smart et al., 2016b).

Three candidate models were used: the VBGM, logistic model, and Gompertz model (Table 5-2). The models estimated length at birth (L_0), the asymptotic length (L_∞) and growth coefficient (k). Growth models were fit using the 'nls' function, multi-model analysis was conducted using the 'MuMIn package'(Barton, 2016) and bootstrapped confidence intervals were produced from 1000 bootstraps using the 'nlstools package' (Baty et al., 2015) in the R program environment (R Core Team, 2015).

As the sample size was less than 200, the AIC_C, a size adjusted bias correction, was used (Zhu et al., 2009) :

$$AIC_C = AIC + \frac{2k(k+1)}{n-k-1}$$

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 that has the lowest AIC_C value ($AIC_{\min}$) was chosen as the best fit for the data. The AIC difference (Δ) was calculated for each model (i = 1-3) and used to rank the remaining models as follows:

$$\Delta_i = AIC_{CI} - AIC_{min}$$

Models were ranked according to the value of Δ. Values from 0-2 were considered to have the strongest support, less support was given to values between 2-10 and the least support for

Δ values > 10 (Anderson and Burnham, 2002). The AIC weights were calculated by the expression:

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

To test if there were differences in the growth curves for males and females, a likelihood ratio test was carried out (Kimura, 1980). This was conducted for all candidate models included in the analysis. The method used to carry out the likelihood ratio test was described by Haddon (2001) and incorporated into the R program environment for this analysis.

Table 5-2: Equations of the three growth functions used in the multi model approach

Model	Growth function
von Bertalanffy	$L\,(t) = L_0 + (L_\infty - L_0)\,(1\text{-}exp\,(-kt))$
Logistic	$L\,(t) = \frac{L_\infty L_0 (g_{log} t)}{L_\infty + L_0 (exp(g_{log} t) - 1)}$
Gompertz	$L(t) = L_\infty\, exp\,(-L_0\, exp\,(-g_{gom}\, t))$

5.2.5 Maturity

The maturity stage data was converted to a binary maturity category (immature = 0, or mature =1) for statistical analyses. The length-at-maturity was estimated for both males and females using logistic regression (Walker, 2005b):

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

where $P(l)$ is the proportion mature at TL, l and P_{max} is the maximum proportion of mature individuals. The lengths of which 50 and 95% of the population are mature (L_{50} and L_{95}) were estimated using a generalised linear model (GLM) with a quasi-binomial error structure and a logit-link function based on 4 cm length bins in the 'R' program environment (R Core Team, 2015). Age-at-maturity was calculated using the same process as length-at-maturity by substituting length with age. The age at which 50 and 95% of the population were mature were designated as A_{50} and A_{95} respectively.

5.3 Results

A total of 115 *C. coatesi* were used in this study, 81 males and 34 females. Males ranged in size from 33–79 cm TL, and females from 35–75 cm TL. The majority of samples were smaller sized juveniles. Only three pregnant females were observed each having two embryos. The maximum embryo size was 12 cm, but they were not full term.

5.3.1 Age determination

The average per cent error was 9.93% and Chang's coefficient of variation was 14.05%, which were relatively low in comparison to other studies on small bodied carcharhinids (Smart et al., 2013, Harry et al., 2010, Gutteridge et al., 2013). Percent Agreement ± 1 year between readers was 58.7% reflected some level of disagreement between readers. The age bias plot (Fig. 5.2) showed that bias was associated more so with ages greater than six years. However, the Bowker's test of symmetry (df = 23, x = 30.13, P = 0.14) indicated that bias was not significant between readers. The maximum ages were the same for both sexes at 10.5 years. The oldest male measured 76 cm TL while the oldest female was 73 cm TL.

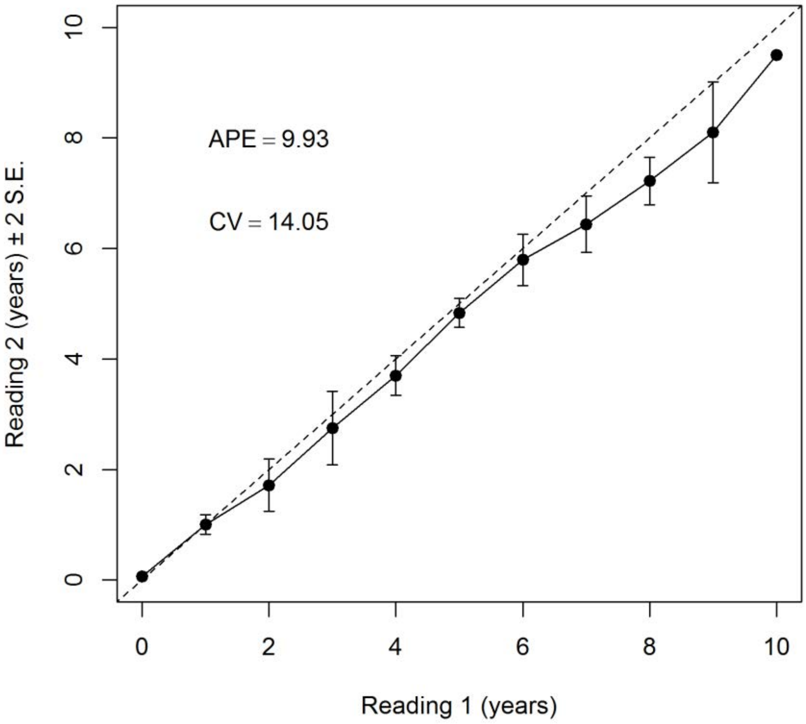

Figure 5-2**:** Age bias plot showing agreement between two independent readers. The percentage agreement_1 year was 58.7%, Average Percentage Error was 9.93% and Chang's coefficient of variation was 14.05%.

5.3.2 Growth model fitting

The AICc values were similar for all candidate models. All models (Table 3) had a Δ of < 2 and w < 0.9. The length-at-birth (L_0) were 40.61 ± 0.81 SE, 40.86 ± 0.08 SE, 40.74 ± 0.81 SE for the VBGM, logistic and Gompertz models respectively. The asymptotic length were also very similar (VBGM = 74.84 ± 2.05 SE; logistic = 73.70 ± 1.56 SE and Gompertz = 74.17 ± 1.75 SE) and the growth completion rates k, $g_{(log)}$ and $g_{(gom)}$ were 0.33 ± 0.06 yr^{-1}, 0.48 ± 0.07 yr^{-1}, 0.40 ± 0.06 yr^{-1}. Given that all models produced almost identical growth estimates it was therefore not necessary to perform model averaging (Table 3). The VBGM (Fig.5-3) model was however chosen to describe the growth of *C. coatesi* given its wide use in literature. Sexes were combined because the likelihood ratio test showed no significant difference between sexes for all three models (VBGM $df = 3, \chi^2 = 3.78, P = 0.29$; logistic $df = 3, \chi^2 = 4.05, P = 0.26$; Gompertz $df = 3, \chi^2 = 3.90, P = 0.27$).

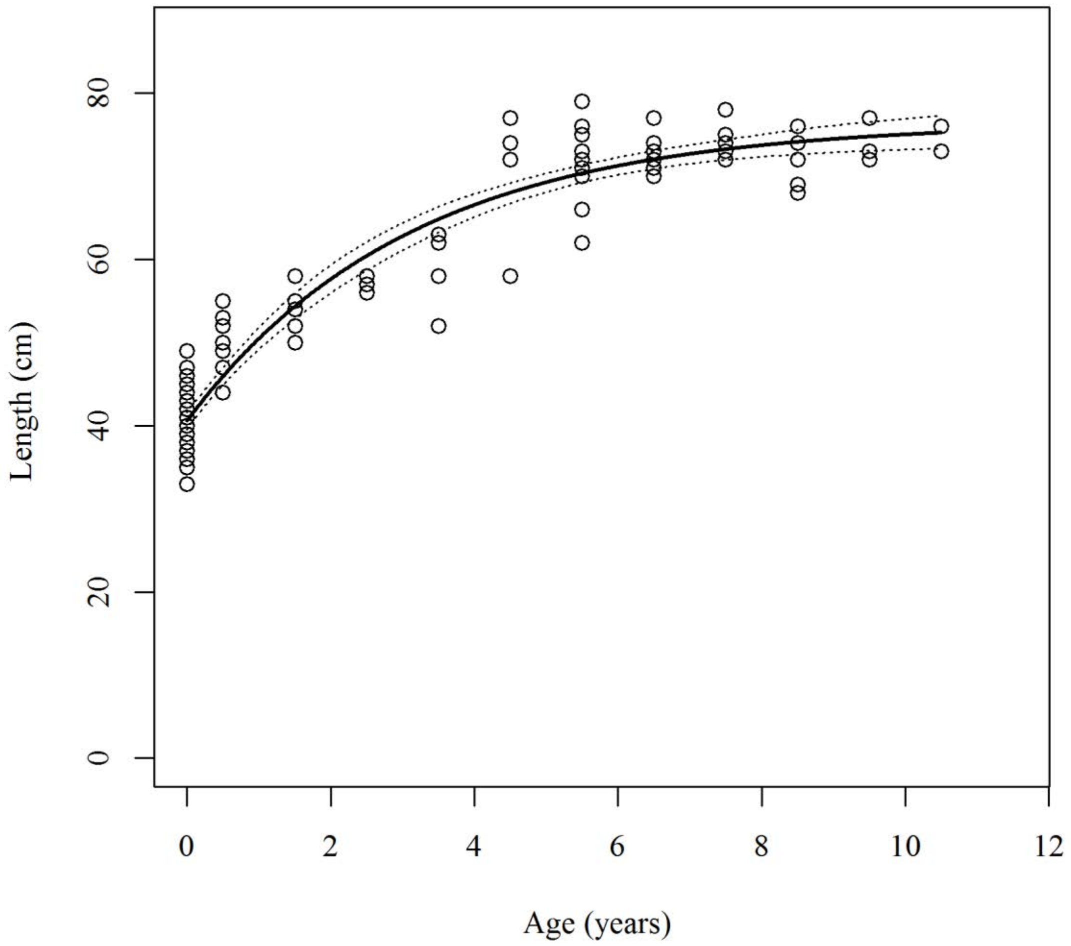

Figure 5-3: Length-at-age curve for *Carcharhinus coatesi* from the Gulf of Papua with both sexes combined fitted with a three-parameter von Bertalanffy growth model (solid line) and 95% bootstrapped confidence intervals (dotted lines).

Table 5-3: Summary of results from the multi model inference framework (MMI) incorporating Akaike's Information Criterion (AIC). n is the sample size, AIC_C is the small-sample bias adjusted Akaike's Information Criteria, Δ is the difference in AIC_C values between models, w (%) are the AIC_C weights, L_0 and L_∞ are the length-at-birth and asymptotic length in cm respectively, k is the growth completion rate in ($year^{-1}$) for the VBGM, $g_{(log)}$ and $g_{(gom)}$ are the growth parameters for Logistic and Gompertz functions respectively, SE is the standard error of each growth parameter and RSE is the residual standard error for the model.

Model	n	AIC_C	Δ	W (%)	L_0(±SE)	L_∞(±SE)	k(±SE)	$g_{(log)}$(±SE)	$g_{(gom)}$(±SE)	RSE
VBGM	115	729.84	0	0.42	40.61±0.81	74.84±2.05	0.33±0.06			5.65
Logistic	115	730.8	0.97	0.26	40.86±0.08	73.70±1.56		0.48±0.07		5.67
Gompertz	115	730.31	0.47	0.33	40.74±0.81	74.17±1.75			0.40±0.06	5.66

5.3.3 Maturity

The size at which 50 and 95% of individuals became sexually mature showed that males attained maturity at L_{50} = 66.3 cm (CI: 63.8, 71.4) and L_{95} = 71.6 cm (C1: 64.6, 74.2). Females reached maturity at L_{50} = 71.4 cm (CI: 61.5, 72.0) and L_{95} = 72.5 cm (CI: 62.7, 74.0) (Fig. 5-4). Age-at-maturity estimates indicate that males (A_{50} = 5.1 years (CI: 4.6, 7.1), A_{95} = 6.4 years (CI: 5.1, 7.2)) and females (A_{50} = 5.3 years (CI: 3.5, 8.7) and A_{95} = 7.4 (CI: 3.6, 8.8) years reach maturity at about five years of age (Fig. 5-5). A large proportion of individuals in the sample were in the first year of life or had not reached maturity (Fig. 5-6).

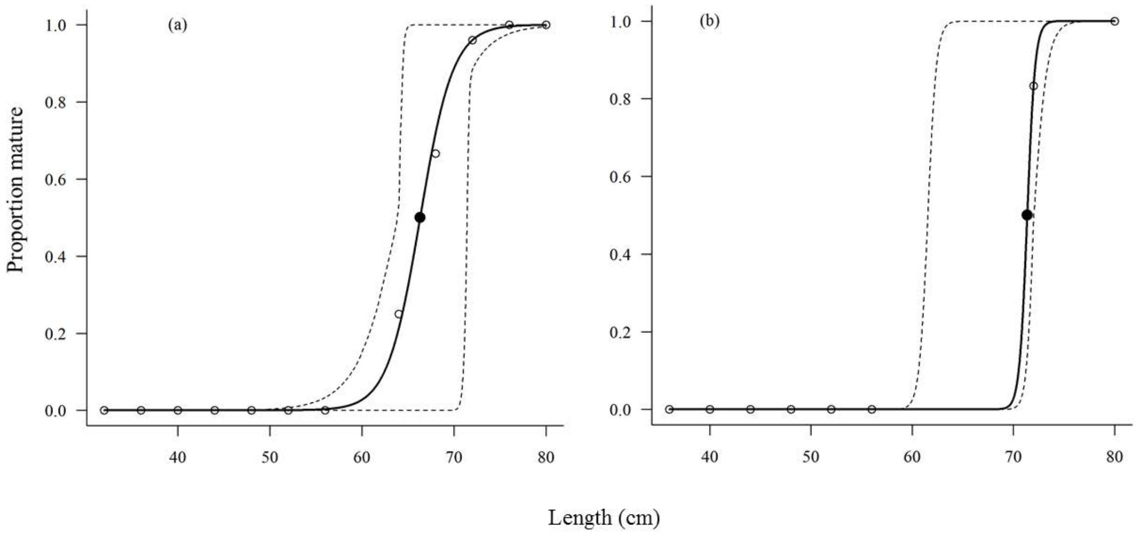

Figure 5-4: Length-at-maturity ogives for (a) male and (b) female *Carcharhinus coatesi* from the Gulf of Papua. The shaded points represent the length at which 50% of the population reaches maturity. The 95% confidence intervals are indicated with dashed lines.

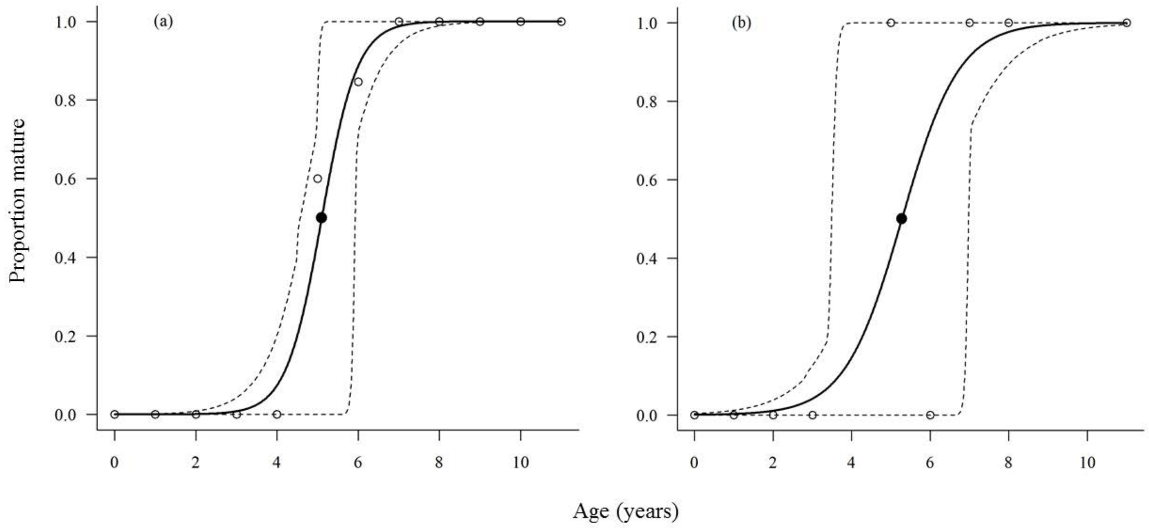

Figure 5-5: Age-at-maturity ogives for (a) male and (b) female *Carcharhinus coatesi* from the Gulf of Papua. The shaded points represent the ages at which 50% of the population reach maturity. The 95% confidence intervals are indicated with dashed lines.

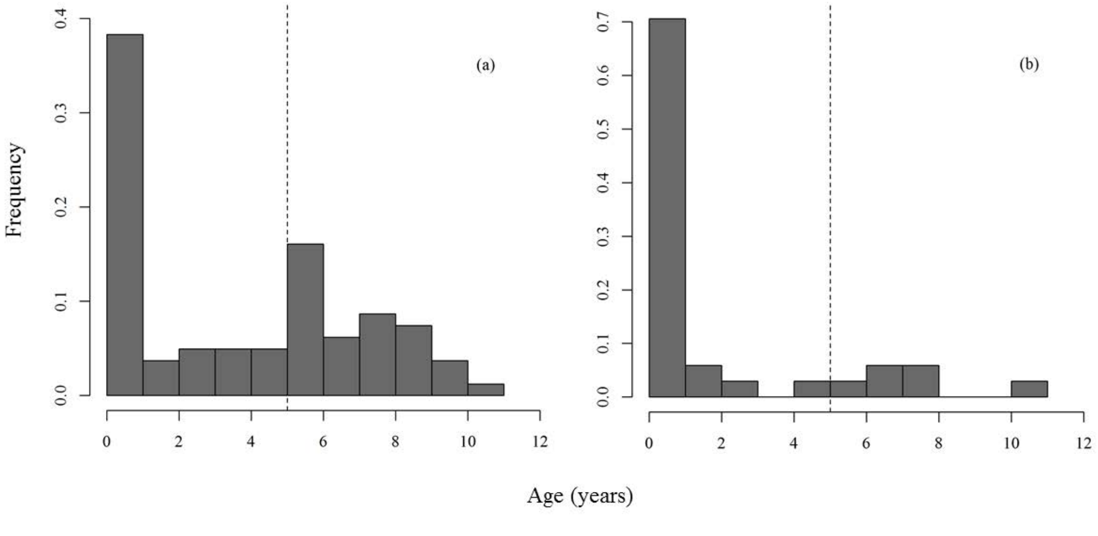

Figure 5-6: Age frequency of individual *Carcharhinus coatesi* sampled. The dotted lines indicated age-at-maturity for (a) males and (b) females.

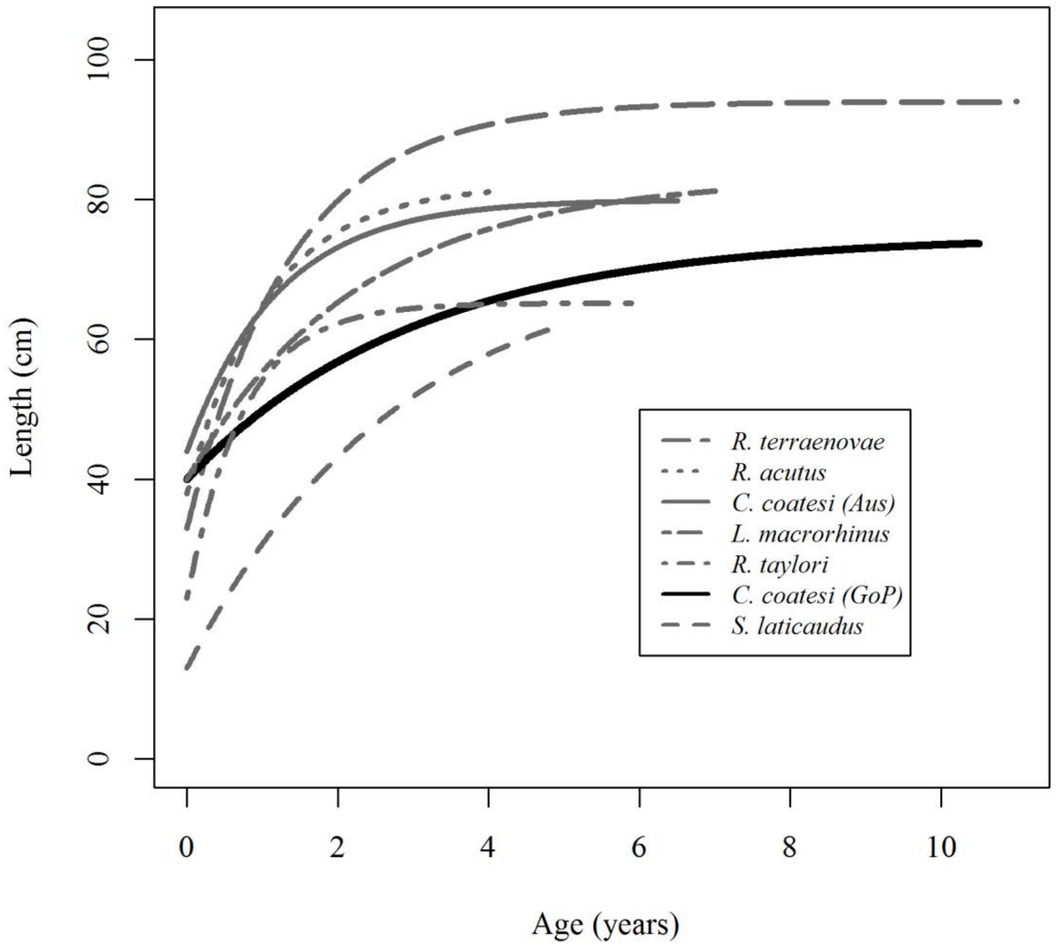

Figure 5-7: von Bertalanffy growth curves of small-bodied carcharhinids. Data sources: *Rhizoprionodon terraenovae* (Loefer and Sedberry 2003), *Rhizoprionodon acutus* (Harry et al. 2010), *Carcharhinus coatesi* (Aus) (Smart et al. 2013), *Loxodon macrorhinus* (Gutteridge et al. 2013), *Rhizoprionodon taylori* (Simpfendorfer 1993), *Scoliodon laticaudus* (Nair 1976).

5.4 Discussion

The Australian blackspot shark is a small but relatively fast growing species of shark. Studies in Australia show that on the Great Barrier Reef coast it has a growth completion rate of 0.83 yr^{-1} and reaches a maximum age of 6.5 years (Smart et al., 2013), while the maximum length is 88 cm in the Northern Territory (Stevens and McLoughlin, 1991). The results of this study demonstrate that the life history of *C. coatesi* in the waters of southern Papua New Guinea was somewhat dissimilar. The von Bertalanffy growth completion rate was lower (0.33 yr^{-1}), maximum age higher (10.5 years) and maximum length smaller (79 cm). These differences occurred despite the size at birth and maximum size being similar between these areas. Such intra-specific variation in life history traits is often reported in sharks (Lombardi-Carlson et al., 2003, Taylor et al., 2016, Gutteridge et al., 2013) and can be the result of a range of factors, including local selection pressures, differences in methodology, differential effects of fishing or latitudinal variation in environmental conditions.

The Carcharhinidae is the most diverse family of sharks with over 50 species (White and Sommerville, 2010), and show a variety of growth patterns. The largest species of this group is the tiger shark *Galeocerdo cuvier* which can grow to over five meters in length, reaching maturity after 12 years of age (Holmes et al., 2015) and has a von Bertalanffy growth completion rate of $k = 0.08$ yr^{-1}. Another species the silky shark *Carcharhinus falciformis,* attains a total length over two meters, takes over 10 years to reach maturity and grows at a rate of $k = 0.066$ yr^{-1} (Hall et al., 2012). The blue shark *Prionace glauca* has a maximum length of about three meters, and fully matures after six years growing at a rate of $k = 0.12$ yr^{-1}(Jolly et al., 2013). Meanwhile, small bodied carcharhinids that reach less than one meter have much higher growth rates ranging from $k = 0.18$ yr^{-1} for *Loxodon macrorhinus*

(Gutteridge et al., 2013) to k = 1.33 yr^{-1} (Simpfendorfer, 1993). Small bodied coastal carcharhinids usually grow rapidly after birth (Fig. 5-7) and reach maturity within one to two years (Smart et al., 2013, Loefer and Sedberry, 2003, Harry et al., 2010, Gutteridge et al., 2013, Nair, 1976). The variability in the life history of the carcharhinid sharks demonstrates that they have evolved highly diverse life histories, despite their common ancestry, to become one of the most important groups of predators in the ocean.

Validating ages particularly in older age classes has proven to be problematic in age and growth literature and consequently the underestimation of ages is prevalent (Harry, 2017). Vertebral ageing indicated that *C. coatesi* grows to more than 10 years in the GoP. Reader precision was relatively high with no significant bias detected, however difficulty in determining ages on older individuals was evident. Bands deposited towards the edge of the vertebrae can be difficult to distinguish because of close proximity to each other reflecting slower growth later in life. Therefore, it is possible that ages may be underestimated for older individuals that have reached their maximum size but are still depositing growth band pairs. This has been observed in other studies on small bodied sharks (Gutteridge et al., 2013, Loefer and Sedberry, 2003, Huveneers et al., 2013). Growth band pairs are associated with seasonality in temperate waters (Cailliet and Goldman, 2004). Therefore, a lack of seasonality in the tropics may affect the clarity and readability of band pairs (Fig. 5-1) and thus the overall estimation of age. Though, there is some uncertainty surrounding the correlation of band pair deposition as a reference for age, the formation of band pairs is more consistent in smaller sharks (Natanson et al., 2018) and therefore likely to predict age more accurately. Future work should focus on age validation of this species incorporating other datasets where possible such as tag-recapture or length data (Harry, 2017).

The slower growth completion rate of *C. coatesi* compared to other small carcharhinids may be a trade-off with the larger size at birth. The size at birth is relatively large, at about half the maximum observed size, and for individuals often >50% of the mothers length. This relatively large size at birth is uncommon in sharks, with most less than 30% of maximum size (Cortés, 2000). By increasing the size at birth survival rates of newborns will be higher (Heupel et al., 2007) and so the very rapid growth seen in species with very small sizes at birth is not required (Fig. 5-7). These very rapid growth rates in other species are believed to reduce the time that young sharks are subject to high levels of predation. A consequence of this trade-off is that litter sizes (such as those observed in *C. coatesi*; normally only 2 per litter) are much smaller than these other species with smaller sizes at birth e.g. *R. taylori*: litters 1-10, size at birth 25 cm (Simpfendorfer, 1993); *R. terraenovae:* litters 1-8, size at birth 28 cm (Loefer and Sedberry, 2003) and *Scoliodon laticaudus:* litters 6-18, size at birth 14 cm (Devadoss, 1979). The consequences of these trade-offs amongst small carcharhinids should be further investigated using demographic models to understand how these strategies may be affected by fishing and how they contribute to sustainability.

This study provides the first age-at-maturity estimates for *C. coatesi*. Whereas other small bodied carcharhinids (≤ 1 m) take 1–2 years to mature (Harry et al., 2010, Gutteridge et al., 2013, Simpfendorfer, 1993, Carlson and Baremore, 2003), both male and female *C. coatesi* attain sexual maturity at about five years of age. Delayed age-at-maturity combined with a small litter size (Stevens and McLoughlin, 1991) suggests that this species may be less productive and less able to sustain fishing pressure than other small carcharhinids, but demographic models should be investigated to confirm this hypothesis. Length-at-maturity analysis indicated that males attain maturity at sizes smaller than females, unlike northern

Australia where both sexes reach maturity at the same length (Stevens and McLoughlin, 1991). This is consistent with shark life history patterns that show males tend to grow faster though reach maximum sizes that are smaller than females (Cortés, 2000). Given that the number of females in the sample was low the confidence intervals reported for female size and age-at-maturity were wide, estimates should be treated as preliminary and be further investigated with additional sampling.

Fishing on coastal shark populations has led to several population declines (Dulvy et al., 2014). This could potentially cause changes in life history parameters in heavily fished populations. Carlson and Baremore (2003) recorded a higher growth rate and reduced age-at-maturity in *R. terraenovae* after more than a decade of intense fishing, noting increased fishing pressure and a reduction in stock size over this time as potential drivers for changing growth patterns. The extent to which biological traits of *C. coatesi* may have changed due to the effects of fishing in the GoP over four decades remains unknown due to the lack of data on previous abundance and bycatch data over time and previous life history information. Historical records over a 19 year period (1974 -1993) of the GoPPF indicate that fishing effort had varied over time, being at its lowest in 1975 (17,000 trawl hours) and peaked in 1989 (95,000 trawl hours) (Evans et al., 1997). In 2011 eight vessels were actively fishing with an overall effort of 14,000 trawl hours (Suuronen et al., 2013) currently only six vessels are in operation. The total amount of bycatch taken in the fishery is expected to have fluctuated in proportion with fishing effort, and in recent years total bycatch may be at lower levels given that effort appears to have decreased. The current growth and maturity information for *C. coatesi* gathered in this study implies that although it is a reasonably fast growing species, it may be more vulnerable to fishing pressure than other small carcharhinids (Baje et al., 2018) due to its older age-at-maturity and lower litter size. As such, increases in exploitation may differentially have greater effects on the population compared to other small carcharhinid species.

Sustainable fisheries management relies on an understanding of the biology of both targeted fish stocks for commercial markets and those that are taken as bycatch. In order to carry out wider demographic and stock assessment analysis, as well as ecological risk assessments, determining local life history parameters is fundamental. Research on bycatch species have been overlooked, especially in the Indo Pacific (Molina and Cooke, 2012), but are increasingly needed for a more holistic approach to managing fisheries in view of wider sustainability concerns (Pikitch et al., 2004). This study highlights the case of *Carcharhinus coatesi* that is potentially more vulnerable to population decline in the event of increased fishing pressure in the GoP due to its life history characteristics. The information provided here can be used to assess the ecological consequences of trawl fishing in the GoP and evaluate the conservation status of *C. coatesi*. Further research should be encouraged in regions of high biodiversity where fishing regularly occurs as population declines and the threat of extinction may easily go unnoticed in the absence of quantitative data (Edgar et al., 2005).

Chapter 6 Ecological Risk Assessment of elasmobranchs caught in the Gulf of Papua prawn fishery

6.1 Introduction

Managing fisheries in data poor circumstances is a problem faced by fisheries managers worldwide (Pilling et al., 2009). This creates high levels of uncertainty around management decisions and thus the sustainability of fish stocks (Jabado et al., 2018). The recent advent of Ecosystem-based Fisheries Management (EBFM) further intensifies the need for additional information to assess the broader impact of a fishery. One area of EBFM focus is the impact on bycatch species (Pikitch et al., 2004). In many fisheries, fisheries monitoring and assessment are often only focused on key commercial species while bycatch are ignored because they are often discarded due to low economic value (Stevens et al., 2000). Therefore, information on bycatch is still lacking for many fisheries worldwide (Lewison et al., 2011). Without an understanding of the taxonomy, life history, ecology, and exploitation rates of bycatch species, the potential ecological impact of a fishery cannot be fully ascertained.

One method that has been developed to assist fisheries management processes in addressing bycatch issues is Ecological Risk Assessment (ERA). An ERA can have different forms, but all predict the relative vulnerabilities of fish stocks to fisheries harvest (Gallagher et al., 2012) or other potential threats (Chin et al., 2010). Depending on the availability of data, an ERA can be quantitative, semi-quantitative or qualitative, or a combination of these (Stobutzki et al., 2001, Hobday et al., 2011, Braccini et al., 2006). An advantage of qualitative and semi-quantitative ERAs is that they can be used when there is limited species-specific data (Hordyk and Carruthers, 2018). Ultimately conducting an ERA allows fisheries managers to prioritise monitoring, research, and management on the most vulnerable species at risk of over-exploitation (Zhou and Griffiths, 2008).

World-wide declines in elasmobranch populations has propagated international concern for this group of fishes (Dulvy et al., 2017). Approximately a quarter of all sharks and rays are listed as threatened with extinction by the International Union of Conservation of Nature (IUCN) (Dulvy et al., 2014). While there are some fisheries that target shark populations that can be sustainably harvested (Simpfendorfer and Dulvy, 2017) a large proportion of elasmobranch mortality due to fishing globally is attributed to being captured as bycatch from various fisheries (Oliver et al., 2015). Typically, information on elasmobranchs caught as bycatch is lacking, therefore ERAs are a key method to assess their vulnerability to exploitation. ERAs featuring elasmobranchs have steadily increased over the last 20 years (Gallagher et al., 2012). However despite the emergence of this work and the ongoing call for the implementation of EBFM, such assessments are still lacking for the majority of fisheries worldwide, especially in developing countries (Pitcher et al., 2009).

Trawl fisheries employing the use of non-selective gears are responsible for large quantities of bycatch (Stobutzki et al., 2001, Oliver et al., 2015). In regions of high biodiversity the potential impact of such a fishery can be extensive (Stevens et al., 2000). The island of New Guinea is one of the world's most species-rich zones that also supports a high diversity of elasmobranchs, and consequently the highest proportion of threatened elasmobranch species in the Indo-Australasian region (White and Kyne, 2010). Papua New Guinea (PNG) occupies the eastern half of New Guinea. A commercial prawn trawl fishery operates in the south of PNG within the Gulf of Papua. The fishery historically takes high levels of bycatch, making up 65-85% of the total catch by weight (Evans et al., 1995). The fishery is managed under the Gulf of Papua Prawn Fishery Management Plan in accordance with the Fisheries Management Act of PNG (www.fisheries.gov.pg). The management plan also emphasises the importance of research on bycatch species, and does not allow the finning of sharks and rays (National Fisheries Authority, 2008), however a full assessment of the species composition and quantity of bycatch has not been conducted since the inception of the fishery in the late 1960s. Recent work in PNG has identified an array of elasmobranch species that are caught in the Gulf of Papua prawn fishery (GoPPF) (White et al., 2017b). The aim of this study was to conduct an ERA of these species to inform fisheries management and conservation for these species in PNG and the region more broadly.

6.2 Methods

6.2.1 Sample collection

Between June 2014 and August 2015, National Fisheries Authority (NFA) observers were deployed on seven trips on-board one of five commercial trawl vessels in the Gulf of Papua. To ensure proper taxonomic identification, whole specimens of sharks and rays were collected. In instances where the specimen was too large to be kept, digital photographs and genetic samples were taken. In a laboratory the identification was verified, and disc width (DW) or total length (TL) ± 1 cm, weight, sex, and maturity were recorded. Based on the information collected over the five trips, the total number, weight, size range and catch per unit effort (elasmobranchs caught per hour) of each species was calculated (White et al., 2019).

6.2.2 Ecological Risk Assessment

To assess the sustainability of each species, the method devised by Stobutzki et al. (2001) and subsequently used by Stobutzki et al. (2002) specifically on elasmobranch bycatch was used. This semi-quantitative method subjects fishery data and relevant species-specific information from published literature to a specific set of criteria and is suited for data poor fisheries such as the GoPPF (Hordyk and Carruthers, 2018). The criteria assess: (1) susceptibility, which is the likelihood that a species will be caught by the fishery, and (2) its potential to recover from population decline (Table 6-1).

6.2.2.1 Susceptibility of being caught by the fishery

For the GoPPF both susceptibility and recovery potential were assessed by 5 separate criteria: water column position, survival or post capture mortality, distribution, diet, and depth range. Information about the ecology of species was obtained from White et al. (2017b). Each criterion was assessed as follows;

Water column position: The position a species usually occupies in the water column can make it more susceptible to capture by otter trawl, especially if this overlaps with the areas where fishing occurs. Vessels in the GoPPF fish relatively close to shore and target bottom-dwelling crustaceans. Species that were more demersal in nature were considered to be more likely to interact with trawl gear then those that primarily occur in mid-water or at the surface.

Post-capture mortality or survival: Information regarding the survival of bycatch after capture in the GoPPF is limited, there are reports of most bycatch being dead when the catch is landed on the vessels and finning of larger elasmobranchs. However, further monitoring of bycatch fate is needed. Nevertheless, until such data are available, post-release survival is considered here based on animal size with previous studies and risk assessments suggesting that larger individuals have a greater chance of survival (Stobutzki et al., 2002). Therefore for this criterion, the total mean length at capture for each species was used as an indicator of survivability. The range of the total overall mean length of species measured using TL or DW was calculated separately and divided into thirds. We assumed that smaller species were more susceptible to suffer mortality than larger species and ranked each species accordingly.

Distribution: For this criterion the distribution of each species within the Gulf of Papua was considered. The likelihood of a species having a restricted or more widespread distribution was determined from their habitat preferences in literature. Species with a more widespread distribution may be less susceptible to the fishery.

Diet**:** Species that have the tendency to feed on crustaceans were more likely to be caught in the fishery compared to species that did not.

Depth range**:** Vessels in the GoPPF fish at depths of 6-37 m, based on this, elasmobranchs that occupied depths and habitats outside of this depth range were considered to be less susceptible to capture.

6.2.2.2 Recovery potential

The probability of breeding, maximum size, removal rate, annual fecundity and mortality index were the criteria used to measure the recovery potential for each species. Biological information was extracted from White et al. (2017b). Each criterion was assessed as follows;

Probability of breeding**:** The reproductive potential of a species varies based on life history characteristics. The danger posed to a population will vary if a fishery captures its most successful spawners which may differ based on age class for each species (Gallucci et al., 2006). The proportion of individuals caught as adults and juveniles and the size at maturity were compared based on White et al. (2019).

Maximum size**:** Species that attain large sizes are generally slower growing and potentially have slower rates of recovery (Frisk et al., 2001). The range of total maximum sizes for elasmobranchs measured using total length (TL) or disc width (DW) respectively was calculated and divided into thirds.

Annual fecundity**:** Species that produced more pups annually may have a greater potential to recover from the effects of fishing. The average number of pups that a female produces each year was multiplied by the number of times breeding occurs in a year. Where there was no information it was assumed that breeding occurred once a year. The gestation period where available was also used as an indicator of the frequency of breeding. The range of annual fecundities was divided into thirds to assign ranks.

Removal rate**:** Species with a higher proportion of biomass removed may have slower recovery rates. The percentage of weight of a species as a proportion of the total catch composition by weight for all elasmobranchs caught was calculated for each species. The range of the proportion of catch composition by weight for all species was calculated and divided into thirds to assign ranks.

Mortality index**:** Species with a high mortality index will be slow to recover from the effects of fishing. In the absence of biological parameters that are often used to calculate mortality it is derived by the following formula (Stobutzki et al., 2002);

$$\text{Mortality index} = (L_{max} - L_{ave}) / (L_{ave} - L_{min})$$

Where L_{max} = the maximum length

L_{ave} = the mean length at capture in the fishery and

L_{min} = the smallest length caught

6.2.3 Analysis of criteria

A rank was allocated for each criteria (Table 6-1). A rank of 3 reflected the greatest risk while a rank of 1 represented the lowest level of risk. Each criteria was assigned a weight based on Stobutzki et al. (2002) as the GoPPF is a similar fishery. A weighted average was calculated across all criteria to provide overall scores for susceptibility and recovery potential, respectively. These were then graphically represented, the recovery potential on the x-axis and susceptibility on the y-axis. Consequently the point of lowest risk is when susceptibility = 1 (lowest susceptibility) and recovery potential = 1 (highly productive). Following Tobin et al. (2010) the Euclidian distance was calculated between where each species was situated on the plot to the point of lowest risk (1,1). The range of Euclidean distances from the point of lowest risk was categorised into different levels of risk form low to very high (Table 6-2). A partial correlation was also conducted to assess the independence of each criterion.

Table 6-1: The criteria used to assess and assign ranks for each criteria considered under susceptibility and the potential to recover from the effects of fishing.

Criteria	Weight	Species-specific information (%)	Rank		
			1	2	3
Susceptibility					
Water column position	3	100	Benthopelagic or pelagic	not applicable	Benthic
Survival (post capture mortality)	3	100	The total mean length at capture is > 200 cm (TL)	Total mean length at capture greater than 100 cm but less than 200 cm (TL)	The total mean length at capture is less than 100 cm (TL)
Survival (post capture mortality)	3	100	Total mean length at capture is greater than 137.33 cm (DW)	Total mean length at capture is greater than 68.67 but less than or equal to 137.33 cm (DW)	Total mean length of capture is less than 68.67 cm (DW)
Distribution	3		Have a greater habitat preference and distribution beyond trawl zones	Distribution may overlap with trawled areas	Highly Likely to inhabit trawl zones
Diet	2	100	Feed on pelagic organisms and does not feed on crustaceans or demersal prey.	Have the tendency to feed on crustaceans but not exclusively because the species feeds on a broad range of prey.	Known to feed exclusively on crustaceans and demersal prey.
Depth Range	1	100	Existing within trawl depth of 6 -38 m	not applicable	Existing beyond trawl depth range
Recovery					
Probability of breeding	3	100	Higher proportion caught after reaching maturity.	Similar proportions caught as adults and juveniles.	Higher proportion caught before reaching maturity
Maximum size	3	100	Maximum disc width < 203.33 cm	203.33 <Maximum disc width< 376.66	Maximum disc width > 376.66 cm
Maximum size	3	100	Maximum total length < 271.3 cm	Maximum total length is greater than 271.3 but less than 474.66 cm	Maximum total length > 474.66 cm

Removal rate	3	100	3.08 ≤ removal rate	3.08 > removal rate ≤ 6.15	Removal rate is > 6.15
Annual fecundity	1	46	Annual fecundity is greater than 17 per year	Annual fecundity is greater than 9 per year but less than or equal to 17 per year	Annual fecundity ≤ 9 per year
Mortality index	1	100	Mortality index ≤ 20.59	Mortality index is greater than 20.59 but less than 42.12	Mortality index > 42.12

Table 6-2: Range of Euclidean distances and corresponding level of risk.

Euclidean distance	**Level of Risk**
0.00 – 0.99	Low
1.00 -1.99	Medium
2.00 – 2.99	High
> 3.00	Very High

6.3 Results

6.3.1 Elasmobranch species encountered in the fishery

From the 7 trips a total of 2030 individuals were recorded from 39 elasmobranch species (White et al., 2019). Sixteen shark species from 5 families and 23 ray species across 9 families were observed from the catch (Table 6-3). The Carcharhinidae (12 species) and Dasyatidae (11 species) were the most diverse families of shark and ray, respectively. All other families had between one and three species. The most commonly caught species, were the coastal sharks *Rhizoprionodon taylori, Carcharhinus coatesi, Rhizoprionodon acutus, Sphyrna lewini* (juveniles) and *Hemigaleus australiensis*; and rays *Gymnura australis* and *Maculabatis astra*. (Table 6-4).

Partial correlation of productivity and susceptibility criteria showed that all criteria were below r = 0.7 which meant that the effect of other criteria influencing the correlation between a pair of criteria was minimal (Table 6-5). The global IUCN Red List status of each species range from Least Concern (n = 11) to Critically Endangered (n = 1), with 13 threatened (i.e. Vulnerable, Endangered Critically Endangered). Three were Data Deficient and two were Not Evaluated. In terms of risk, 10 of 39 species were assessed to be at low risk. These were mostly mid-water species including the bull shark which has a very extensive habitat preference and therefore having lower susceptibility to the fishery. The majority of species (26 species) are at medium risk (Table 6-6). These are species with a higher susceptibility but relatively high to low recovery potential. Only three species are considered to be facing high risk under present fishery conditions, these are the Australian blackspot shark (*Carcharhinus* *coatesi*), the eyebrow wedgefish (*Rhynchobatus palpebratus)* and the blackspotted whipray (*M. astra)*, all of which had relatively high catch rates and the lowest recovery potential compared to all other species (Fig 6-1).

Table 6-3: Elasmobranch species taken as bycatch in the Gulf of Papua prawn trawl fishery.

Family	**Species**	**Common name**
Hemiscylliidae	*Chiloscyllium punctatum*	Brownbanded bambooshark
Stegostomatidae	*Stegostoma fasciatum*	Zebra shark
Hemigaleidae	*Hemigaleus australiensis*	Australian weasel shark
Carcharhinidae	*Carcharhinus amblyrhynchoides*	Graceful shark
	Carcharhinus amboinensis	Pigeye shark
	Carcharhinus brevipinna	Spinner shark
	Carcharhinus coatesi	Australian blackspot shark
	Carcharhinus fitzroyensis	Creek whaler shark
	Carcharhinus leucas	Bull shark
	Carcharhinus limbatus	Common blacktip shark
	Carcharhinus macloti	Hardnose shark
	Carcharhinus sorrah	Spottail shark
	Carcharhinus tilstoni	Australian blacktip shark
	Rhizoprionodon acutus	Milk shark
	Rhizoprionodon taylori	Australian sharpnose shark
Sphyrnidae	*Eusphyra blochii*	Winghead shark
	Sphyrna lewini	Scalloped hammerhead shark
	Sphyrna mokarran	Great hammerhead shark
Pristidae	*Anoxypristis cuspidata*	Narrow sawfish

	Pristis pristis	Largetooth sawfish
Rhinidae	*Rhina ancylostoma*	Shark ray
	Rhynchobatus palpebratus	Eyebrow wedgefish
Glaucostegidae	*Glaucostegus typus*	Giant guitarfish
Gymnuridae	*Gymnura australis*	Australian butterfly ray
Dasyatidae	*Hemitrygon longicauda*	Merauke stingray
	Himantura australis	Australian whipray
	Himantura leoparda	Leopard whipray
	Maculabatis astra	Blackspotted whipray
	Megatrygon microps	Smalleye stingray
	Neotrygon annotata	Plain maskray
	Neotrygon picta	Speckled maskray
	Pastinachus ater	Broad cowtail ray
	Pateobatis fai	Pink whipray
	Pateobatis hortlei	Hortle's whipray
	Urogymnus acanthobothrium	Mumburarr whipray
Myliobatidae	*Aetomylaeus caeruleofasciatus*	Bluebanded eagle ray
Aetobatidae	*Aetobatus ocellatus*	Spotted eagle ray
Rhinopteridae	*Rhinoptera neglecta*	Australian cownose ray
Mobulidae	*Mobula alfredi*	Reef manta ray

Table 6-4: The abundance, percentage of total elasmobranch catch, size range and maximum known size of species caught in the GoPPF from all sampling trips.

Family	Species	No.	Percent by number	Weight (kg)	Weight (%)	Size range (cm)	Size at maturity (cm)	maximum size (cm)
Hemiscylliidae								
	Chiloscyllium punctatum	74	3.65	34.35	0.79	18–88 TL	65	132 TL
Stegostomatidae								
	Stegostoma fasciatum	10	0.49	21.00	0.48	39–186 TL	147	235 TL
Hemigaleidae								
	Hemigaleus australiensis	118	5.81	40.00	0.92	21–90 TL	60	110 TL
Carcharhinidae								

	Carcharhinus amblyrhynchoides	1	<0.1	4.50	0.10	87 TL	110	178 TL
	Carcharhinus amboinensis	3	0.15	15.20	0.35	89–95 TL	195	280 TL
	Carcharhinus brevipinna	20	0.99	88.80	2.03	79–158 TL	190	300 TL
	Carcharhinus coatesi	192	9.46	201.94	4.62	33–88 TL	70	88 TL
	Carcharhinus fitzroyensis	18	0.89	94.50	2.16	66–123 TL	80	135 TL
	Carcharhinus leucas	3	0.15	66.05	1.51	85–192 TL	220	340 TL
	Carcharhinus limbatus	11	0.54	20.10	0.46	55–91 TL	165	250 TL
	Carcharhinus macloti	19	0.94	35.20	0.81	38–90 TL	69	110 TL
	Carcharhinus sorrah	3	0.15	15.60	0.36	96–100 TL	90	160 TL
	Carcharhinus tilstoni	8	0.39	33.80	0.77	54–139 TL	105	200 TL
	Rhizoprionodon acutus	148	7.29	117.27	2.69	31–86 TL	68	100 TL
	Rhizoprionodon taylori	597	29.41	356.55	8.16	30–68 TL	40	68 TL
Sphyrnidae								
	Eusphyra blochii	86	4.24	164.67	3.77	37–159 TL	138	186 TL
	Sphyrna lewini	133	6.55	162.60	3.72	40–171 TL	155	350 TL
	Sphyrna mokarran	2	0.10	20.30	0.46	119–150 TL	210	600 TL
Pristidae								

	Anoxypristis cuspidata	11	0.54	190.30	4.36	02–215 TL	200	350 TL
	Pristis pristis	1	<0.1	126.40	2.89	349 TL	260	656 TL
Rhinidae								
	Rhina ancylostoma	2	0.10	52.80	1.21	120–165 TL	150	270 TL
	Rhynchobatus palpebratus	60	2.96	401.87	9.20	43–234 TL	103	262 TL
Glaucostegidae								
	Glaucostegus typus	5	0.25	96.52	2.21	39–240 TL	150	284 TL
Gymnuridae								
	Gymnura australis	154	7.59	149.81	3.43	26–77 DW	35	94 DW
Dasyatidae								
	Hemitrygon longicauda	25	1.23	9.41	0.22	12–31 DW	Unknown	31 DW
	Himantura australis	13	0.64	402.68	9.22	52–140 DW	112	183 DW
	Himantura leoparda	19	0.94	180.93	4.14	38–104 DW	70	140 DW
	Maculabatis astra	134	6.60	293.73	6.73	22–76 DW	44	92 DW
	Megatrygon microps	1	<0.1	80.00	1.83	~180 DW	Unknown	222 DW
	Neotrygon annotata	35	1.72	15.29	0.35	12–30 DW	22	30 DW

	Neotrygon picta	1	<0.1	0.11	<0.1	14 DW	17	32 DW
	Pastinachus ater	3	0.15	50.57	1.16	80–100 DW	96	200 DW
	Pateobatis fai	3	0.10	140.00	3.21	67–170 DW	112	170 DW
	Pateobatis hortlei	32	1.58	79.57	1.82	16–112 DW	100	112 DW
	Urogymnus acanthobothrium	3	0.15	84.00	1.92	100–114 DW	110	161 DW
Myliobatidae								
	Aetomylaeus caeruleofasciatus	46	2.27	25.08	0.57	20–52 DW	43	59 DW
Aetobatidae								
	Aetobatus ocellatus	5	0.25	45.10	1.03	66–107 DW	100	300 DW
Rhinopteridae								
	Rhinoptera neglecta	29	1.43	293.2	6.7	37–140 DW	115	140 DW
Mobulidae								
	Mobula alfredi	1	<0.1	145.8	3.3	220 DW	300	550 DW

Table 6-5: Partial correlation of criteria used in the study.

	Water Column Position	Post Capture Mortality	Distribution	Diet	Depth Range
Water Column Position	1				
Post Capture Mortality	-0.149	1			
Distribution	0.540	0.287	1		
Diet	0.649	-0.175	0.618	1	
Depth Range	-0.374	-0.108	-0.087	0.111	1

	Probability of breeding	Maximum size	Removal Rate	Annual Fecundity	Mortality Index
Probability of breeding	1				
Maximum size	0.084	1			
Removal Rate	-0.410	-0.032	1		
Annual Fecundity	-0.116	-0.445	-0.008	1	
Mortality Index	-0.101	0.487	-0.212	-0.143	1

6.3.2 Assessment of risk

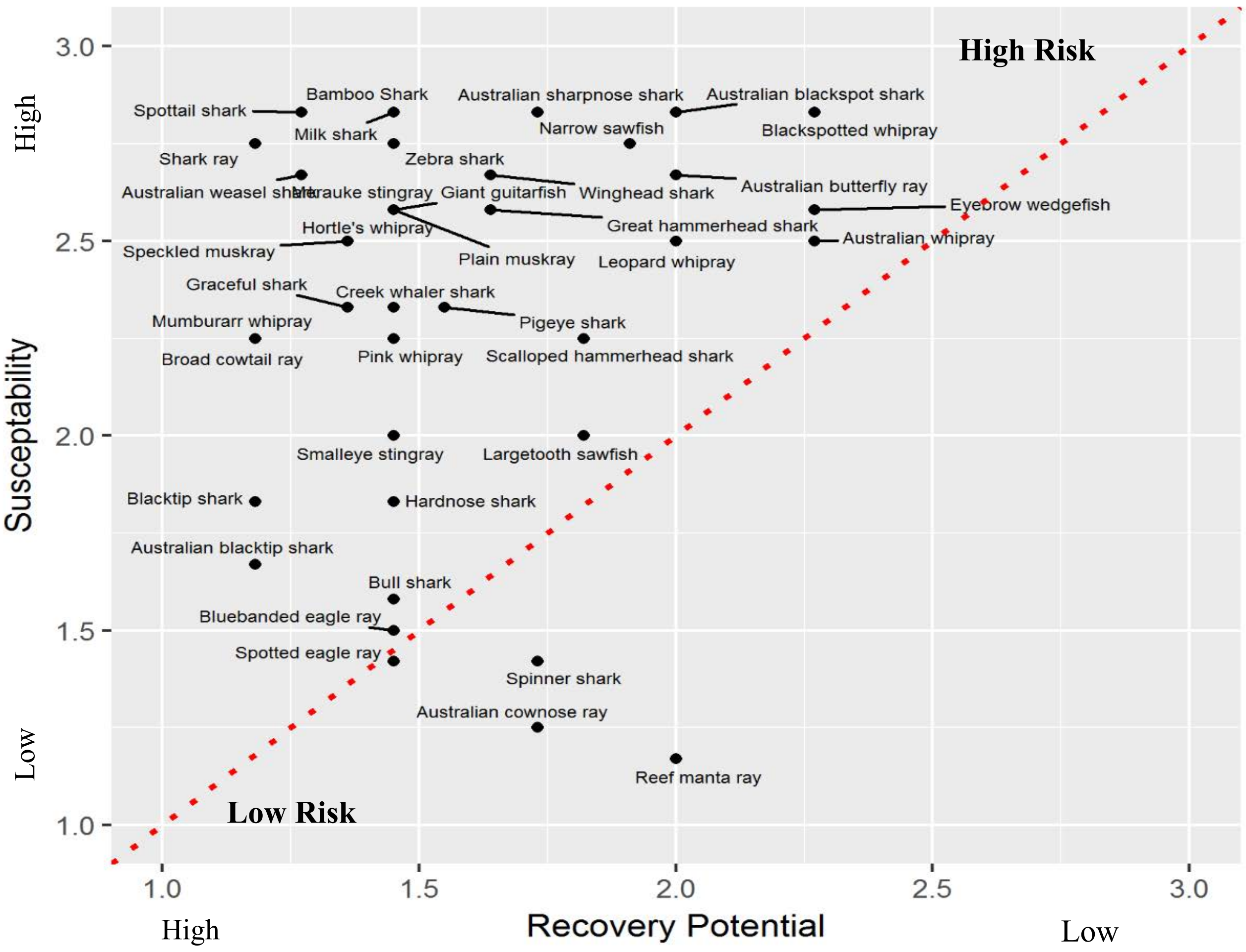

Figure 6-1: Ecological Risk Assessment of elasmobranch species caught in the GoPPF based on the susceptibility of each species to the fishery and their estimated potential to recover from the effects of fishing.

Table 6-6: The Euclidean distance from the point of lowest risk to each species, the associated level of risk and the IUCN status of elasmobranch bycatch caught in the GoPPF.

Species	**Common name**	**Euclidean Distance**	**Risk level**	**IUCN Status**
Aetobatus ocellatus	Spotted eagle ray	0.62	low	VU
Aetomylaeus caeruleofasciatus	Bluebanded eagle ray	0.68	low	LC
Carcharhinus tilstoni	Australian blacktip shark	0.69	low	LC
Carcharhinus leucas	Bull shark	0.74	low	NT
Rhinoptera neglecta	Australian cownose ray	0.77	low	DD
Carcharhinus brevipinna	Spinner shark	0.84	low	NT
Carcharhinus limbatus	Common blacktip shark	0.85	low	NT
Carcharhinus macloti	Hardnose shark	0.95	low	NT
Mobula alfredi	Reef manta ray	1.01	medium	VU
Megatrygon microps	Smalleye stingray	1.10	medium	DD
Pastinachus ater	Broad cowtail ray	1.26	medium	LC
Urogymnus acanthobothrium	Mumburarr whipray	1.26	medium	NE
Pristis pristis	Largetooth sawfish	1.29	medium	CR
Pateobatis fai	Pink whipray	1.33	medium	VU
Carcharhinus amblyrhynchoides	Graceful shark	1.38	medium	NT
Carcharhinus fitzroyensis	Creek whaler shark	1.41	medium	LC
Carchahinus amboinenesis	Pigeye shark	1.44	medium	DD
Sphyrna lewini	Scalloped hammerhead shark	1.49	medium	EN
Neotrygon picta	Speckled maskray	1.54	medium	LC
Glaucostegus typus	Giant guitarfish	1.65	medium	VU

Hemitrygon longicauda	Merauke stingray	1.65	medium	NE
Neotrygon annotata	Plain maskray	1.65	medium	NT
Pateobatis hortlei	Hortle's whipray	1.65	medium	VU
Haemigaleus australensis	Australian weasel shark	1.69	medium	LC
Sphyrna mokarran	Great hammerhead shark	1.71	medium	EN
Rhina ancylostoma	Shark ray	1.76	medium	VU
Eusphyra blochii	Winghead shark	1.78	medium	EN
Himantura leoparda	Leopard whipray	1.80	medium	VU
Stegostoma fasciatum	Zebra shark	1.81	medium	EN
Carcharhinus sorrah	Spottail shark	1.85	medium	NT
Chiloscyllium punctatum	Bamboo Shark	1.89	medium	NT
Rhizoprionodon acutus	Milk shark	1.89	medium	LC
Gymnura australis	Australian butterfly ray	1.94	medium	LC
Himantura australis	Australian whipray	1.97	medium	NE
Anoxypristis cuspidata	Narrow sawfish	1.97	medium	EN
Rhizoprionodon taylori	Australian sharpnose shark	1.97	medium	LC
Rhynchobatus palpebratus	Eyebrow wedgefish	2.03	high	NE
Carcharhinus coatesi	Australian blackspot shark	2.09	high	NE
Maculabatis astra	Blackspotted whipray	2.23	high	LC

6.4 Discussion

ERAs of prawn trawls have detected high numbers of elasmobranchs that are subjected to bycatch in tropical regions, with demersal batoids most often being the most at risk to this form of fishing (Stobutzki et al., 2002) as well as some coastal sharks (Clarke et al., 2018). Particularly low productivity species that are most susceptible to interact with fishing gear are most vulnerable to over-exploitation (Hobday et al., 2011). This study found that of the 39 elasmobranchs caught in the fishery only 3 species were at high risk, two demersal batoids and one coastal shark species. The majority of elasmobranchs were ranked as having medium risk. However, the results are based on irregular sampling and further monitoring of bycatch rates over time may show that the risk level for some of these species may change. In addition, future increases in fishing effort could elevate some species to a higher risk category, such as the hammerhead sharks *Sphrna lewini* and *Eusphyra blochii*. Of particular concern also is the narrow sawfish *Anoxypristis cuspidata* which is considered to be Endangered on the IUCN Red List. The Gulf of Papua was assessed to still have higher numbers of sawfish compared to depleted populations in other regions of the world (White et al., 2017a) which could mean that encounters with the fishery could be more prevalent than reported here.

The inshore shark species *R. taylori* and *C. coatesi* were the most commonly caught species in the GoPPF with the total number of *R. taylori* far exceeding all other species caught. *Rhizoprionodon taylori* is a prolific breeder and possibly better placed to withstand current fishing effort (Baje et al., 2018, Simpfendorfer, 2003). In contrast, this thesis (Chapter 5) has shown that *C. coatesi* has a slower growth rate and matures later than other small-bodied carcharhinid sharks and overall has a lower biological productivity. Thus, the population of

C. coatesi may be more negatively impacted by the fishery. The assessment conducted in this study are semi-quantitative but also highlight the importance of population-specific biological data which greatly aids the interpretation of risk, and the development of more quantitative risk assessments based on species-specific life history data and estimates of population productivity (Cortés et al., 2010).

Turtle Excluder Devices (TEDs) and bycatch reduction devices (BRDs) are extensions and modifications of trawl gear used to prevent unintentional catch (Eayrs, 2007). The use of these devices can be configured to suit a specific fishery (Duarte et al., 2019). For example, a combination of both TED and BRD use has proven to be effective in minimising the catch of skates in Suriname, South America (Willems et al., 2016). TEDs were trialled in the GoPPF in 1988 and 1989 to limit the capture of finfish and showed that the catch specific species and larger size ranges could be considerably reduced (Matsuoka and Kan, 1991, Kan, 1991), but TEDs have not yet been adopted in this fishery. Studies in Australia have shown that though the capture of smaller individuals remains high (Stobutzki et al., 2002), TEDs are successful at preventing the capture of large elasmobranchs (Brewer et al., 2006) and have reduced the mortality of species when introduced (Griffiths et al., 2006). The sustainability of the following species improved after the introduction of TEDs in the Griffiths et al. (2006) study of the Northern Prawn Fishery in Australia: *R. acutus*, *Chiloscyllium punctatum*, *Carcharhinus coatesi*, *Carcharhinus sorrah* and *Anoxypristis cuspidata.* A similar result would be expected for the GoPPF along with a reduction in the capture of larger sharks and rays if TEDs and BRDs are eventually introduced.

The protection of threatened populations requires a management approach that takes into account the combined impact of different fisheries on a population. Additional fishing pressure independent of the GoPPF may also increase the total risk from fisheries on some populations. Coastal fishing by local communities is common in the Gulf of Papua for subsistence and semi-economic activities, this has the potential to increase with emerging fisheries activities. However, at present it is considered to be low given the low human population density in the area (White et al., 2017a). Vessels in the PNG tuna longline fishery also fish in the Gulf and capture adult hammerhead sharks and other pelagic species that are not common in the GoPPF (White et al., in press). Therefore, pelagic species that may have a low risk level in the GoPPF may be more susceptible to other fisheries.

The ERA provides a broad method to determine the sustainability of bycatch species. Where fishery specific data is limited, assumptions are often made in a precautionary manner or based on information from other similar fisheries such as the case here. Other data that improve risk assessments are based around the fate of species when caught, post capture handling, release and mortality. Understanding the fate of a species or specific size classes that are able to survive capture can lead to safe handling procedures and the eventual release of individuals with some chance of survival (Ellis et al., 2017). Implementation of these approaches reduce the overall risk rating of species to which they are applied.

This study is a first attempt at assessing the ecological risk to elasmobranch bycatch in the GoPPF. Approximately 30% of all shark and ray species that have been recorded in PNG (White et al., 2017b), are caught in the fishery, of the 39 species encountered, 16 are endemic to the Gulf of Papua and northern Australia. The high diversity and endemism as well as the regular capture of immature size classes indicate that the Gulf of Papua is an important breeding and potentially a nursery area, and therefore is an important area for conservation of threatened elasmobranchs in PNG. ERAs require a wide suite of data including life history, ecology of species, catch and operational information of the fishery and potential survival post capture. Part of this information has recently been established for elasmobranchs in the Gulf of Papua (White et al., 2017b), however further monitoring of bycatch rates is needed to improve assessments in future. The reduction of bycatch through the introduction of TEDs and BRDs in the GoPPF is also needed to reduce fishing pressure on a number of threatened species.

Chapter 7 General Discussion

The Gulf of Papua Prawn Fishery (GoPPF) licenses vessels to fish for a number of commercially valuable crustaceans in Papua New Guinea. Fishing grounds extend across the Gulf all year round except for a demarcated area closed to fishing for a three month period between December and March each year (National Fisheries Authority, 2008). The fishery has undergone a decrease in size from accommodating a foreign fleet of up to 30 vessels to presently being reserved for partnerships with national operators, with only 15 licences issued (Evans et al., 1995) however only 6 to 7 vessels are actually actively fishing. The stocks exploited by the fishery (mostly penaeid prawns) were considered to be under-developed (Kompas and Kuk, 2008) and past research has focused mostly on the potential yield and factors affecting that (Gwyther, 1982, Evans et al., 1997); but little attention has been given to the large proportion of bycatch generated by the fishery (White et al., 2019, Evans et al., 1995, Matsuoka and Kan, 1991).

This thesis covered aspects of the biology and ecology of elasmobranch bycatch in the GoPPF and developed an Ecological Risk Assessment (ERA) to evaluate the potential effects on the species caught. The ecological component of this study included an analysis of the diet of the three most abundant shark species taken in the fishery (White et al., 2019): the Australian sharpnose shark (*Rhizoriopodon taylori*), the Australian blackspot shark (*Carcharhinus coatesi*) and the milk shark (*Rhyzoprionodon acutus*). Chapter 3 considered competition and resource partitioning among these sympatric species. In Chapters 4 and 5 biological attributes of *R. taylori* and *C. coatesi* were investigated. The age, growth and maturity studies provided an assessment on the likely ability of two of the most common elasmobranch bycatch species to sustain fishing pressure. The ERA in Chapter 6 utilised both biological and ecological data along with fishery information to provide an assessment of all other of elasmobranchs caught in the GoPPF. This final output of this work is highly relevant to the role and functions of the National Fisheries Authority (NFA) as a fisheries management body and the Conservation and Environment Protection Authority (CEPA) of Papua New Guinea dealing with matters of environment and conservation. Both organisations require this information to aid in decision making processes. Furthermore, in broader terms the results of this work are also significant for regional and global assessments of sharks and rays as it provides some of the first information on the effects of prawn trawl bycatch in poorly studied areas of the equatorial Pacific.

The diet research in Chapter 3 includes the first empirical data of trophic ecology of the three shark species studied (*C. coatesi, R. acutus* and *R.taylori*). In a region where the impact of mining and proposed coastal developments have been discussed for many years (Hettler et al., 1997, Campbell, 2011), such ecological data may be considered as baseline information relevant to environmental or ecological impact assessments in the future, especially with regard to projects that impact the inshore coastal zones. Moreover, gaining an understanding of the ecological attributes of species serve an important role in examining the potential impacts of fisheries through mapping of ecosystem processes (Link et al., 2002).

A general model of the life history of small-bodied shark species consists of rapid growth in early life stages reaching maturity at in just 1-3 years (Smart et al., 2013, Gutteridge et al., 2013). However, the age, growth and maturity parameters for *R. taylori* and *C. coatesi* from the GoP (Chapters 4 and 5) show that such biological traits are not common among all small bodied coastal carcharhinids, highlighting the variability of life history traits among whaler sharks (Cortés, 2000). The life history of *C. coatesi* in the GoP deviates from most other small-bodied coastal carcharhinids including *R. taylori*, having a slower growth rate, reaching maturity at a later age with relatively low fecundity. This therefore increases its risk of over exploitation as observed in the ecological risk assessment conducted in Chapter 6. Differences in life history characteristics can be attributed to evolutionary trade-offs to ensure greater survivability (Reynolds et al., 2001) and latitudinal variation (Lombardi-Carlson et al., 2003, Parsons, 1993, Taylor et al., 2016). Another possible contributing factor could be density dependent population changes induced by fishing pressure, differences in asymptotic length, growth and maturity have been observed in populations exposed to fishing over time (Carlson and Baremore, 2003, Sosebee, 2005, Coutré et al., 2013). There is, therefore, a need for monitoring of population-specific life history parameters so that wider demographic analyses are accurate because of the important gear management implications that they can have (Fujiwara, 2012, Heino et al., 2013).

The risk assessment conducted in Chapter 6 is a significant development as it is the first ERA conducted for a small local fishery in PNG. Using available data, a preliminary assessment of risk was established for each elasmobranch bycatch species encountered in the GoPPF. This study is a concerted effort to apply an ecosystem based fisheries management approach (EBFM) to the GoPPF that has been managed to date largely from a target species perspective with little effort to enforce the reduction of bycatch (Kan, 1991, Matsuoka and Kan, 1991). Importantly the study identifies potential areas of data collection that will allow future ERAs to be more quantitative (Zhou and Griffiths, 2008, Cortés et al., 2010) in nature and therefore more robust.

This longstanding issue of bycatch is prevalent in many fisheries (Oliver et al., 2015) and contributes to the wastage of a wide range of taxa including fish, mammals and birds (Davies et al., 2009, Read et al., 2006, Wallace et al., 2010, Lewison et al., 2014). Approaches to dealing with the problem of bycatch have been proposed (Lewison et al., 2011, Crowder and Murawski, 1998) and standards (Kirby and Ward, 2014) have been developed for some regions, and work is ongoing as more fisheries management organisations take on an EBFM approach (Caddy and Mahon, 1995). However the vast majority of fisheries worldwide remain deficient in bycatch data relating to fishery operations, catch rates and specific biology and ecology of species (Soykan et al., 2008). This is a major limiting factor to the implementation of EBFM which aims to improve the sustainability of fisheries and minimise impacts to the wider environment (Dayton et al., 1995, Pikitch et al., 2004). The need to address this data gaps remain critical (Molina and Cooke, 2012) in light of the current global threat to many marine species, including a large number of sharks and rays (Davidson et al., 2016, Dulvy et al., 2014). Therefore, the studies conducted here cumulatively provide the foundations for further development of the EBFM approach for the GoPPF alongside increasing the knowledge of how marine species are exploited in the region for better decisions to be made in terms of safe guarding the survival of species.

Papua New Guinea's strategic plan "Vision 2050" (Ambang, 2012) states the intent to develop the county's resources including marine resources for further economic gain. Consequently, one of the four pillars of PNG's constitution declares that development should be achieved in a sustainable manner while fostering the protection of the natural environment (Constitution of the Independent State of Papua New Guinea). To practically achieve these overarching goals requires focused research, while the need for building and strengthening PNG's research capacity has been recently recognised at a policy level (Forsyth, 2015) there is still a functional disconnect between PNG research institutions to address the data needs of specific government sectors including fisheries, as such the pressing need for evidence-based decision making remains. The work presented in this thesis begins to address requirements under the Fisheries Management Act of PNG and the Gulf of Papua Prawn trawl fishery management plan that recognise the importance of information on bycatch and to operate the fishery with minimal impacts to the wider marine environment.

International concern for the drastic decline of elasmobranch stocks has led to a number of organisations taking steps to prevent further loss of species (Cavanagh et al., 2008, Clarke et al., 2014). In 1999 member countries of the United Nations (UN) agreed that a National Plan of Action for Sharks (NPOA) will be drafted by members as a voluntary obligation. A number of countries have progressed this which outlines the steps that will be taken at a national level from improving data collection and research, management, education and consultation with stakeholders (Davis and Worm, 2013). To date Papua New Guinea has not developed an NPOA for sharks, but management and conservation of their shark and ray fauna would likely benefit from the development of such a plan. Papua New Guinea is now in a much stronger position to start to formulate its national plan through the NFA as leading national body as a result of this research and other recent elasmobranch studies as part of an ACIAR funded research collaboration between NFA, CSIRO, JCU and UPNG (D'Alberto et al., 2016, Smart et al., 2016a, Smart et al., 2017a, White et al., 2017a, Grant et al., 2018).

The International Union for the Conservation of Nature (IUCN) conducts assessments to characterise the level of threat to a species and hence its risk of extinction. These assessments require a broad range of information including the biology, ecology and utilisation of species (https://www.iucnredlist.org/). Country specific information is important for species with wide geographic distributions as depending on the likely status of stocks and level of exploitation a specific risk category can be assigned for the same species in different regions which then indicates specific management and conservation strategies. The assessments are also equally important for the conservation of endemic species and potentially shared stocks, especially between the GoP and northern and north-eastern Australia where there is a high degree of faunal similarity. The extent to which these stocks are shared will likely require joint management efforts but requires more study to fully understand.

The Convention on Illegal Trade of Endangered Species of Wild Flora and Fauna (CITES) regulates the trade of endangered species as a complementary measure for management and conservation (Vincent et al., 2014). Countries that are signatory to the Convention have to ensure that the import and export of species listed under CITES must follow a licensing system to regulate the international trade of specimen (https://www.cites.org). Several species caught in the GoPPF are listed under CITES, all three hammerhead species (Sphyrnidae), devilrays (Mobulidae) and all species of the families Rhinidae and Glaucostegidae are listed in Appendix II while sawfishes (Pristidae) are listed in Appendix I. The possibility that fins from some of these species enter the shark fin trade out of PNG in an unregulated manner is highly likely and a matter of concern given the endangered status of these species (White et al., 2017a, Vieira et al., 2016). This presents further tasks of monitoring and enforcement to be put in place by the NFA to aid in conservation efforts. The development of non-detrimental findings (NDF) is also a procedural CITES requirement for member nations if there is to be legal export of Appendix II listed species. This documentation serves as proof that any specimen transported has been collected in a manner that poses no risk to the survival of a species. However for PNG and the wider Oceania region the progress of such procedures is limited by the paucity of data surrounding the utilisation of species (Simpfendorfer, 2014). The information contained in this thesis will also contribute directly to this data need.

With a unique geography PNG is situated in a region of high biodiversity including a wide range of elasmobranch species composition especially in the GoP. In its present state the GoPPF is a relatively small however without addressing issues surrounding bycatch, any future increases in fishing effort will be detrimental to species already facing high levels of risk. Modern approaches to fisheries management incorporate reference points based on population parameters to develop a harvest strategy. The underlying basis for this is data on the life history and ecology of impacted species (Caddy and Mahon, 1995). The potential for PNG to develop management of its fisheries to better standards can be realised through focused research to address data gaps. It is hoped that the work presented in this thesis begins to situate the importance of ongoing PNG specific fisheries science as a fundamental basis for management and conservation decisions and strategies for the country moving forward.

7.1 Future research

The studies presented here are a baseline for future work to be carried out on the bycatch of the GoPPF and the elasmobranch fauna of southern PNG more generally. Aspects of biology and ecology of only three species (*C. coatesi*, *R. acutus* and *R. taylori*) were investigated, along with a risk assessment suited to data poor conditions for the range of elasmobranch bycatch. To address the uncertainties that still exist there is scope for further work which could include the following; (1) studies to determine both biological (life history) and ecological aspects (diet and trophic ecology) of species caught in the fishery, particularly those that are caught in considerably high numbers such as the bamboo shark (*Chiloscyllium punctatum*), Australian weasel shark (*Hemigaleus australiensis*), eyebrow wedgefish (*Rhynchobatus palpebratus*), Australian butterfly ray (*Gymnura australis*) and the blackspotted whipray (*Maculabatis astra*), (2) studies focused on spatial ecology (movement, migration and habitat use) to provide a better understanding of susceptibility to the fishery, (3) monitoring of bycatch catch rates and fishery operations to improve understanding of temporal changes in bycatch composition, (4) investigate the fate of bycatch species to determine where survivability can be improved either through gear changes or handling practices, (5) develop gear modifications for the introduction of TEDs and BRDs to reduce the overall bycatch in the fishery, (6) assess the degree to which shark and ray stocks are shared between PNG and Australia to develop joint management and conservation efforts if necessary and (7) determine the taxonomy of cryptic and unknown species to account for biodiversity. These potential areas of research can be supported by continued sampling and monitoring by fishery observers and independent research where possible. In general, the research format used here and specific methodologies have a direct application to other fisheries in PNG and can be used to assess the sustainability of other impacted stocks.

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