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Conservation biology of wedgefishes (Family Rhinidae) and giant guitarfishes (Family Glaucostegidae)

Thesis submitted by

Brooke Minetta D'Alberto (she/her)

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Gurrumbilbarra and Thul Garrie Waja Country
Townsville, Queensland Australia

Acknowledgements of Country

Wadda Mooli
Hello, welcome, or goodbye
in Birrigubba language of the Bindal and Wulgurukaba people.

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Supervision:

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Dr Andrew Chin	James Cook University, Bebegu Yumba Townsville
Dr William White	CSIRO, nipaluna/Hobart
Dr Neil Hutchinson	James Cook University, Singapore

Additional collaborators:

Global FinPrint Project	https://globalfinprint.org/
Naomi Clark-Shen	James Cook University, Singapore; Dorsal Effect (NGO), Singapore
Kathy Xu	Dorsal Effect (NGO), Singapore
Grant Johnson	Northern Territory Fisheries, Garramilla/Darwin
Dr John Carlson	NOAA/National Marine Fisheries Service, Florida USA
Dr Sebastián Pardo	Dalhousie University, Nova Scotia Canada
Dr Madeline Green	CSIRO, nipaluna/Hobart

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Brooke D'Alberto on Minjerribah (North Stradbroke Island), Traditional lands of the Quandamooka People.

Copyright and collaboration

To the best of my knowledge and belief, the thesis contains no material previously published by any other person except where due acknowledgement has been made. Permission from external copyright holders and collaborators has been obtained when necessary.

Publications from this Research

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Thesis Abstract

Wedgefishes (Family Rhinidae) and giant guitarfishes (Family Glaucostegidae) from the Order Rhinopristiformes (also known as shark-like rays) are under intense anthropogenic pressures, mainly from overfishing driven by international trade of their fins, and habitat loss. Given the global concerns and the current substantial knowledge gaps for this group of species, this PhD thesis aimed to improve the understanding of the conservation biology of wedgefishes and giant guitarfishes. Specifically aiming to provide a synthesis of the use and values of batoids in the Indo-Pacific Ocean, investigate shark-like ray global distribution using baited remote underwater video surveys (BRUVS) on coral reefs, understand their interaction with coastal fisheries, determine the life history parameters of bottlenose wedgefish *Rhynchobatus australiae*, and estimate the maximum intrinsic rate of population increase to understand how these species might recover from population declines.

Global demands for products (e.g. meat, fins, and gill plates) has generated concerns for the population status of batoids, particularly in the Indo-Pacific region, which has the world's largest elasmobranch (shark and ray) catching and trading nations. To help understand the context in which conservation and management for this group is to be implemented, it is important to understand their ecological, economic, and cultural importance. In **Chapter Two**, I synthesised the existing literature on the uses and values of batoids, including their uses and derived products, as well as the cultural and economic values of the species, and identified knowledge gaps in order to provide a framework for future research. Batoids have an invaluable cultural link with humans throughout the Indo-Pacific region, and the loss of large, benthic elasmobranchs can have significant social, cultural, and economic impacts on the fishers and communities who depend on them. Elasmobranch fisheries provide a large proportion of income and/or protein for countless communities. In low-income nations, incentives for sustainable livelihoods to reduce fishing pressure and mortality for batoids needs to be a top priority if the recovery of batoid populations is to occur.

It is important to understand what factors shape species distribution patterns in order to identify areas where effective conservation and management strategies should be implemented. In **Chapter Three**, I investigated the distribution, and species diversity of wedgefishes, giant guitarfishes, and guitarfishes (Family Rhinobatidae) on coral reefs from ~18,000 BRUVS deployed globally for the Global FinPrint Project. Despite the extensive sampling effort, shark-like rays were only present on 0.006 – 0.369% of videos, and *R. australiae* was the most commonly observed wedgefish species. Sightings of wedgefish and giant guitarfish were higher around nations with management in place for rays (e.g. Australia), compared to other nations with no management for these rays (e.g. Indonesia). Zero inflated generalised linear model were used to determine the factors driving distribution for the wedgefish species, including the explanatory variables of depth, mean substrate relief, reef protection status, and total gravity. Depth and mean substrate relief were the most significant variables in predicting sightings. The shark-like rays in this study likely reflect not only their occasional use of coral reef habitats, but also their declines in populations in tropical environments from extensive fishing pressures.

There is one documented fishery that targets wedgefishes and giant guitarfishes, the Indonesian tangle-net fishery. In **Chapter Four**, I analysed market surveys data from multiple fisheries that landed at Muara Angke landing site in Jakarta, north-western Java. These surveys were conducted between 2001 and 2005, and recorded landed catch for tangle net fishery, including one frozen shipment from Benoa Harbour, Bali. In total 1,559 elasmobranchs (sharks and rays) were recorded, comprising 24 species of rays and nine species of sharks. The most abundant species landed were the pink whipray *Pateobatis fai* and *R. australiae*, the latter being the main target species. Catch composition varied based on differences in species catchability and may also be indicative of localized declines. The fishery was highly selective for larger sized individuals, while smaller size classes of many ray species, including the target species were also caught in other Indonesian fisheries, resulting in fishing pressure across all age classes. The decline of tangle net vessels in the fishery and the potential shift in catch composition in the Indonesian tangle net fishery, increase concerns about the status of shark-like rays and stingrays in Indonesia.

Despite the global distribution of wedgefishes, there is no species-specific life history information (age, growth, and maturity). In **Chapter Five**, I investigated the life history of *R. australiae*, purchased from two fishery ports in Singapore. A total of 48 samples were purchased between July 2018 – July 2019. Species identification was validated with mtDNA barcoding using the NADH2 region. Length of samples for females and males ranged from

506 – 1645 mm total length (TL), and ages ranged from 0 – 11 years. Two analytic approaches (frequentist and Bayesian) with multi-model analysis were conducted to estimate growth parameters. The Bayesian von Bertalanffy model was the best fitting growth model for the combined sexes with no difference in growth between sex (L_∞ = 3203.6 mm TL; L_0 = 507 mm TL; k = 0.05 yr-1), and an estimated theoretical longevity of 26 years. Females (A_{50} = 3.25 yr; L_{50} = 1014 mm TL) matured younger and at smaller sizes, than males (A_{50} = 5.03 yr; L_{50} = 1197 mm TL). This study provides the first species-specific life history results for *R. australiae*, suggesting that this species in Southeast (SE) Asian waters is relatively slow growing. This information will further the biological knowledge available for this Critically Endangered species and can be used to help design effective management and conservation measures.

The widespread declines of several shark-like rays raise concerns about their risk of extinction and if the populations can recover from over-exploitation. In **Chapter Six**, I used life history theory to estimate the maximum intrinsic rates of population increase (r_{max}) for nine species from four families of Rhinopristiformes to investigate if these species can recovery from declines. I used a modified Euler-Lotka model with four different natural mortality estimators. Estimates of mean r_{max}, across the different natural mortality methods, varied from 0.03 to 0.59 yr^{-1}, but generally increased with increasing maximum size. Comparing these estimates to r_{max} values for other species of chondrichthyans, the species *R. australiae*, giant guitarfish *Glaucostegus typus* and blackchin guitarfish *Glaucostegus cemiculus* were relatively productive, while most species from Rhinobatidae and Trygonorrhinidae had relatively low r_{max} values. If the demand for their high value products and excessive fishing mortality can be addressed, then population recovery for some species is possible but will vary depending on the species.

As there is limited information of wedgefish and giant guitarfish species, this thesis provides basic information on their distribution, interaction with fisheries, life history and how they might recover from population declines. In order to conserve these threatened species, improved fisheries management on a national and international scale and habitat preservation are needed. This important information will assist the understanding these critically endangered species and can be used to support management and conservation policies.

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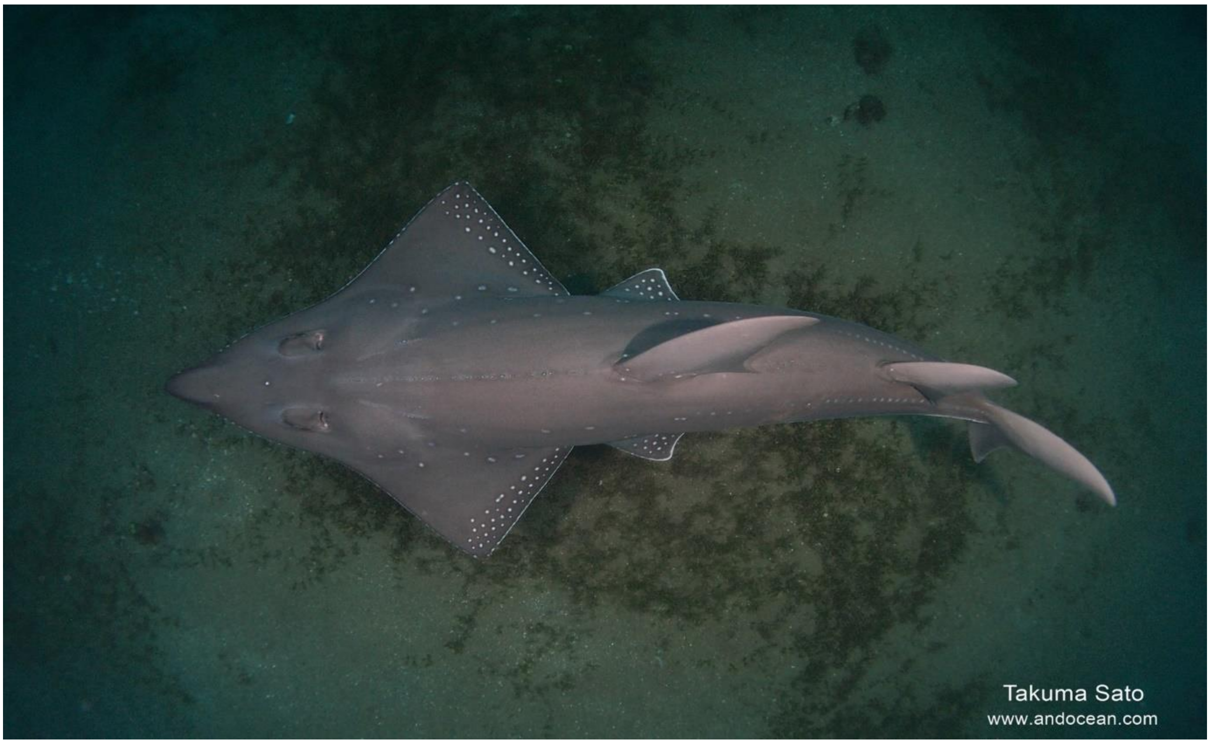
Glossary of Abbreviations and Acronyms

Term	Acronym
BRUVS	Baited remote underwater visual survey
BRD	By-catch reduction devices
CITES	Convention on International Trade in Endangered Species of Wild Flora and Fauna
CMS	Convention on the Conservation of Migratory Species of Wild Animals
FAO	United Nations Food and Agriculture Organisation
IPOA	International Plan of Action for Conservation and Management of Sharks
IUCN	International Union for Conservation of Nature
IUU	Illegal, unreported, and unregulated fishing
MMAF	Indonesian Ministry of Marine Affairs and Fisheries
NDF	Non-detriment finding for CITES
NGO	Non-governmental organisation
NPOA	National Plan of Action for the Conservation and Management of Sharks
SE Asia	Southeast Asia
SEAFDEC	Southeast Asian Fisheries Development Center
Sharks MoU	CMS The Memorandum of Understanding on the Conservation of Migratory Sharks
TRAFFIC	The Wildlife Trade Monitoring Network

Chapter One



General Introduction

This introductory chapter outlines the rationale for my research. In this chapter, I (1) reviewed the literature on wedgefishes and giant guitarfishes; (2) identified knowledge gaps for these families; and (3) discussed where my research fits into the overall elasmobranch literature.

Nature and extent to contribution

The chapter was written by the candidate, which was reviewed and edited by Prof. Simpfendorfer, Dr Andrew Chin, and Dr Neil Hutchinson.

1. General Introduction

Chondrichthyan fishes (sharks, rays, and chimeras) have a long and important history with humans throughout the world. Chondrichthyans have immeasurable and significant cultural value to communities that have developed over thousands of years of contact and experiences with marine and freshwater ecosystems (Rasalato, Maginnity & Brunnschweiler, 2010; Kitolelei et al., 2021). Coastal elasmobranch (sharks and rays) species provide vital food sources from products including meat and liver for centuries, demonstrating the invaluable link between humans and elasmobranchs through the practise of fishing and trade of products (Dent & Clarke, 2015). In modern times, chondrichthyans have retained these values and uses in many societies, with the development of global trade in the meat, fins, gill plates, cartilage, skin, and other products (Dent & Clarke, 2015). However, global fishing pressure has increased dramatically, driven by international demand of some chondrichthyan products, particularly meat and fins (Clarke, Milner-Gulland & Bjørndal, 2007). In the past three decades, the conservation status of many chondrichthyan populations has increasingly become a major environmental concern (Stevens et al., 2000; Dulvy et al., 2014a; Dulvy et al., 2017).

Over one-third of chondrichthyans species are currently facing substantial population declines (Dulvy et al., 2021). The susceptibility of many elasmobranch species to overfishing reflects their low biological productivity, which results from their life history characteristics of slow growth, late maturity, long generation times, and low fecundity (Cortés, 2000). The late maturing and low reproductive outputs of elasmobranchs translate to slow population growth rates and an increased sensitivity to elevated fishing mortality (Cortés, 2000). Overfishing is the direct cause of population decline for this group, which has intensified due to the rapid expansion of fisheries (Clarke et al., 2006), and the globalisation of trade (Clarke, Milner-Gulland & Bjørndal, 2007; Lack & Sant, 2009). The threat of overfishing is compounded by habitat loss and degradation (including from damage to habitats from fishing gear, development of coastlines, and natural system modifications and disturbance), and climate change that further increases the loss of habitats and declines in habitat suitability (Dulvy et al., 2021; Yan et al., 2021). Tropical and subtropical coastal species are disproportionately threatened by exploitation and habitat loss, particularly in waters of the longest standing and most intensive chondrichthyan fisheries in the world, including northern

Indian Ocean and Western Central and Northwest Pacific Oceans, from Pakistan to Japan, and as far east as Wallace line between Bali and Lombok (Dulvy et al., 2021).

Five of the seven most threatened chondrichthyan families worldwide belong to the superorder Batoidea (Dulvy et al., 2014a). This superorder comprises of over half of the chondrichthyan species diversity, with 633 of ~ 1170 valid species in 26 families (Compagno & Last, 1999; Aschliman et al., 2012; Last et al., 2016). The International Union for Conservation of Nature (IUCN) assessed a total of 611 batoid species, of which 36% (n = 220) are threatened with extinction (Dulvy et al., 2021; IUCN, 2021). The reported global chondrichthyan catch has been increasingly dominated by batoids (Dulvy et al., 2014a; Dulvy et al., 2021). This increase in reported batoid catches is likely the result of a number of causes, including improved catch reporting, declines in shark catches due to more stringent national and international regulations, and global declines of shark populations (Dulvy et al., 2014a; Davidson, Krawchuk & Dulvy, 2016). Batoids are mainly retained as by-products in trawl, bottom long line, purse seine, and gillnet fisheries (White & Dharmadi, 2007) but the catch of batoids in many of these fisheries is poorly documented. To date most of the scientific studies and conservation efforts have focused on the decline of shark populations (Myers & Worm, 2005; Ferretti et al., 2008; Ferretti et al., 2010). Until recently, there has been little attention to the declines in batoid populations despite them being among the most threatened groups of chondrichthyans (Dulvy et al., 2021).

The order Rhinopristiformes, also known as shark-like rays, is the most threatened order of marine fish (Kyne et al., 2020; Dulvy et al., 2021), and comprises seven families, i.e. giant guitarfish (Glaucostegidae), fanrays (Platyrhinidae), sawfish (Pristidae), wedgefish (Rhinidae), guitarfish (Rhinobatidae), banjo rays (Trygonorrhinidae) and panrays (Zanobatidae) (Last et al., 2016). These medium to large-sized, benthic, shark-like rays have a similar posterior morphology to sharks and are distributed in temperature to tropical waters on the insular and continental shelves (< 250 m depth) throughout the Indo-Pacific and Atlantic oceans (Last et al., 2016). The information available suggests that the shark-like rays are strongly associated with soft-bottom habitats such as sand, mud or gravel, and some species are often observed in areas adjacent to coral reefs (White et al., 2013a). The distribution of shark-like rays are highly variable, from broadly distributed species (e.g. bottlenose wedgefish *Rhynchobatus australiae* and giant guitarfish *Glaucostegus typus*) to those with very restricted and/or fragmented spatial distributions, e.g. clown wedgefish *Rhynchobatus cooki* known only from Java, Indonesia (Kyne, Rigby & Last, 2019), false shark ray *Rhynchorhina mauritaniensis* from a single location in the Eastern Central Atlantic (Banc d'Arguin of Mauritania) (Seret & Naylor, 2016). All five species of sawfishes, all six species of giant guitarfishes, nine out of 10 species of wedgefishes, 23 of 34 species of guitarfishes, and three of eight species of banjo rays are listed in a Threatened category (Critically Endangered, Endangered, or Threatened) on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (Dulvy et al., 2021; IUCN, 2021). These groups are extremely sensitive to overexploitation as a result of their large body size, slow life history strategy (Dulvy et al., 2014a), susceptibility to capture by multiple gears and use of inshore habitat in some of the world's most heavily fished coastal regions (Stobutzki et al., 2002; Jabado & Spaet, 2017; Moore, 2017; Jabado, 2018).

There is increasing evidence of historical and contemporary declines in landings and catch rates for shark-like rays of up to 80% throughout most of their ranges (Kyne et al., 2020), including Indonesia (Keong, 1996), South Africa (Diop & Dossa, 2011), Madagascar (Hopkins, 2011), Mozambique (Pierce et al., 2008), Tanzania (Schaeffer, 2004), Arabian Seas and surrounding region (Moore, 2017; Jabado, 2018), India (Mohanraj et al., 2009) and Brazil (Villwock de Miranda & Vooren, 2003). Indeed, *R. cooki* was believed to have been extirpated until it was recently recorded in a fish market in Singapore (Clark-Shen et al., 2019). While there are very few targeted fisheries for shark-like rays, the emerging information suggests that they are typically retained in commercial and artisanal fisheries as valuable by-products of opportunistic catch for their highly valued fins and good quality meat (Bizzarro et al., 2009a; Bizzarro et al., 2009b; Kyne et al., 2020). There is considerable concern that wedgefishes, guitarfishes, and giant guitarfishes are following a similar and predictable pattern of global decline as documented in the sawfishes (Moore, 2017). All five species of sawfish declined rapidly over 30 years throughout their range, driven by unregulated fisheries, the international fin trade, and delayed scientific attention (Simpfendorfer, 2005a; Thorburn et al., 2007; Dulvy et al., 2017). Yet despite a global conservation strategy (Harrison & Dulvy, 2014), restriction of international trade (i.e. listing on CITES Appendix I), and evidence that some species of sawfish have the ability to recover from fishing pressure in the foreseeable future (Carlson & Simpfendorfer, 2015), the recovery of the populations is projected to take at least several decades. Successful recovery of populations will require significant measures across local, regional, and global scales.

The magnitude of the declines and the subsequent conservation issues of wedgefish, giant guitarfish, and guitarfish has become a key focus for major international management conventions and agencies, such as Convention on International Trade in Endangered Species (CITES), Convention on the Conservation of Migratory Species of Wild Animals (CMS), and the Food and Agriculture Organization of the United Nations (FAO). All species of wedgefish and giant guitarfish were listed on the Appendix II of the CITES in 2019 (CITES, 2019b). For CITES Appendix II listed species, the international trade of wild specimens must be legal and sustainable, which is dependent on provisions such as the export is not detrimental to wild populations (demonstrated through a positive non-detriment finding, NDF), the specimens are legally sourced, and shipments are accompanied by export, import or re-export permits (Vincent et al., 2014). *Rhynchobatus australiae* and the common guitarfish *Rhinobatos rhinobatos* were listed on the Appendix II of CMS in 2017 (CMS, 2017). In addition, *R. australiae*, the whitespotted wedgefish *Rhynchobatus djiddensis*, the smoothnose wedgefish *Rhynchobatus laevis*, and *R. rhinobatos* are listed on Annex 1 of the CMS Memorandum of Understanding (MOU) on the Conservation of Migratory Sharks (CMS, 2018). The CMS Appendix II listing acts as a framework for the Range States (any Party [nation] that exercises jurisdiction over any part of the range of that migratory species) of the migratory species that have unfavourable conservation status, and requires international agreements (Lawson & Fordham, 2018). These international agreements provide a global platform and legal foundation for the conservation and sustainable use of internationally traded species (CITES), and migratory species and their habitat (CMS) (Vincent et al., 2014). Given the global concerns for this group of species and the importance of trade in their high-value fins, the use of international trade regulations through CITES listings may help achieve positive conservation outcomes (Ostrom et al., 1999; Vincent et al., 2014; Kyne et al., 2020). Despite the high exposure to fisheries, there is limited information available globally for shark-like ray species abundance and distribution, species specific interaction with fisheries, and biological information. Lack of species-specific information and data can negatively influence the establishment of effective management and conservation efforts.

To achieve population recovery for species exposed to fishing, managers and conservation practitioners need to understand their population status, risk exposure, and resilience to fishing pressure and other threats. This requires data on their biology and distribution, as well as fisheries catch composition (species, size classes and sex), changes in relative abundance, and the species-specific interactions with fisheries (Simpfendorfer et al., 2011; Jabado, 2018). There has been one published study that focused on the distribution of shark-like rays using baited remote underwater video surveys (BRUVS) that took place on the Great Barrier Reef (GBR) off eastern Australia (White et al., 2013b), while BRUVS studies in the Arabian Gulf have encountered shark-like rays on videos (Jabado et al., 2018; Jabado et al., 2021). These studies observed a very low abundance of shark-like rays and currently there is little information on the global distribution of shark-like rays on coral reefs. The majority of the global distribution information for these rays originates from fisheries dependent data, however, this data is limited as the fishery reports are grouped into nonspecific species codes or groupings, such as “wedgefish”, “guitarfish”, “rays” and “sharks” (Kyne et al., 2020). Thus, there is little information available on wedgefish and giant guitarfish species’ historical and contemporary interactions with fisheries. Quantifying the onset and extent of decline of these data-limited species is difficult, due to depletions occurring before independent scientific monitoring, and poor fisheries and trade reporting (Dulvy et al., 2016; Lawson et al., 2020). This resulted in little species-specific data, and lack of conservation awareness (Dulvy et al., 2016; Lawson et al., 2020).

Understanding a species’ ability to recover from declines is important for rebuilding depleted populations. This can be approximated through measuring the species’ population productivity, with one commonly used metric of productivity being the maximum intrinsic rate of population increase r_{max}, (Myers, Mertz & Fowlow, 1997). This parameter reflects the theoretical maximum growth rate of depleted populations in the absence of density-dependent regulation (Myers, Mertz & Fowlow, 1997). This inferential method can help to predict a species’ ability to recover from population declines, and provide the demographic basis for evaluating the sustainability of fisheries (Beddington & Kirkwood, 2005) and international trade, particularly for poorly monitored species with limited available life-history information (García, Lucifora & Myers, 2008; Pardo et al., 2018). However, assessing productivity requires accurate data about life history parameters (age, growth, and reproduction). While it is possible to use data from closely related species, the use of inaccurate surrogate information can reduce the accuracy of the demographic models and fisheries assessments (Chin et al., 2013; Smart et al., 2015; Cortes, 2016).

Currently there is very little information on the life history traits of wedgefishes and giant guitarfishes, and there are relatively high levels of uncertainty associated with the life-history parameters that are available for these families. For example, there are only two age and growth studies for wedgefishes and giant guitarfishes, one from the eastern coast of Australia for *R. australiae* and *G. typus* (White et al., 2014), and one from Central Mediterranean Sea for blackchin guitarfish *Glaucostegus cemiculus* (Enajjar, Bradai & Bouain, 2012). Neither study estimated age at maturity, nor aged individuals at the maximum sizes. The information on the reproductive biology for Rhinopristiformes is limited but is more available for species in the guitarfishes Rhinobatidae and Trygonorrhinidae families. For example, there is evidence that species such as shovelnose guitarfish *Pseudobatos productus*, Brazilian guitarfish *Pseudobatos horkelii*, and banded guitarfish *Zapteryx exasperata* employ embryonic diapause or delayed development (Marshall, White & Potter, 2007; Blanco-Parra, Márquez-Farías & Galván-Magaña, 2009; Waltrick, Awruch & Simpfendorfer, 2012), potentially as a result of unfavourable environmental conditions (Capapé, Ben Brahim & Zaouali, 1997) or sex segregation (Kyne & Bennett, 2002b). This demonstrates a substantial knowledge gap on the biology of these threatened rays, which can hinder the development of management and conservation efforts.

Given the global concerns for this these families, the importance of wedgefish and giant guitarfish fins in the international trade, and the current substantial knowledge gaps in the biology, distribution, and interaction with fisheries, the overarching aim of this thesis was to *improve scientific understanding of the global conservation biology of wedgefishes and giant guitarfishes*. The major goal of this thesis was accomplished by addressing five specific research aims:

1. Synthesise current knowledge on batoid species of the Indo-Pacific region, by compiling a checklist of species that occur within the region and review the uses of batoid products and cultural and economic values (**Chapter Two**).
2. Investigate the global distribution, species diversity, and abundance of shark-like rays (Order Rhinopristiformes) by analysing an existing global dataset from baited remote underwater videos systems (BRUVS) (**Chapter Three**).

3. Understand the impacts of inshore coastal fisheries on wedgefish and giant guitarfish with a case study of the Indonesian tangle-net fishery that targets large benthic batoids (**Chapter Four**).
4. Provide updated life history information for the bottlenose wedgefish *Rhynchobatus australiae* from Southeast (SE) Asia (**Chapter Five**).
5. Use life history theory and life history data from published literature to estimate the population productivity and intrinsic risk of extinction of nine species of shark-like rays, particularly within the context of other chondrichthyans (**Chapter Six**).

These findings will provide new and important information on the biology of wedgefishes and giant guitarfishes to inform future conservation. **Chapter Seven** will synthesise the information collected discuss the findings in the wider context and suggest directions of further research that should be taken, with particular emphasis on management. This thesis is organised as a series of sequential chapters written intended for publication in peer-reviewed journals (**Chapter Four** and **Chapter Six** are published) but reformatted to fit a thesis structure. Any repetition in the chapters will be limited to sections of the introduction and discussion. The information provided in this thesis has contributed to the listing of wedgefishes and giant guitarfishes on CITES Appendix II in 2019 and will continue to assist in the development of conservation and fisheries management for shark-like rays.

Chapter Two

Manuscript intended for publication associated with this chapter:

D'Alberto, B.M., et al. (Intended for publication) Batoids of the Indo-Pacific: a synthesis of their biological diversity, uses, values, with implications for conservation and recommendations for future research. Target journal: *Fish and Fisheries.*

Nature and extent to contribution of co-authors to the manuscript

The chapter was conceptualised by the candidate, with the assistance of Prof. Simpfendorfer and Dr. Chin. The candidate collated and analysed the literature. The chapter was written by the candidate, which was reviewed and edited by Prof. Simpfendorfer, Dr Andrew Chin, and Dr Neil Hutchinson.

2. Batoids of the Indo-Pacific: a synthesis of their biological diversity, uses and value, with implications for conservation and recommendations for future research

2.1 Introduction

Chondrichthyans (sharks, rays, and chimeras) have a long and important history with humans throughout the world. This group have immeasurable and significant cultural value to communities throughout the world. In ancient Egypt and Greek civilisations, rays featured prominently in mythology and medicine (Last et al., 2016; Koutroumpas, Lioumi & Vougiouklakis, 2020). In Ancient Mexico and Central America, stingray barbs were used as implements in ceremonial scarification, bloodletting and to pierce body areas like the tongue, nose, and ears (de Borhegyi, 1961). Stingrays and sawfishes have been documented in rock art in many nations of Aboriginal Australians, the oldest continuing culture in the world, with some rock art estimated to be over 12,000 years old (Brady, Bradley & Kearney, 2016; Finch et al., 2020). Chondrichthyans have also provided a vital food source from products including meat and liver for centuries, demonstrating the invaluable link between humans and elasmobranchs through the practise of fishing and trade of products (Dent & Clarke, 2015). In modern times, chondrichthyans have retained these values and uses in many societies, with the development of global trade in the meat, fins, gill plates, cartilage, skin, and other products (Dent & Clarke, 2015). However, global fishing pressure has increased dramatically and driven by high international demand and prices of chondrichthyan products, particularly for meat and fins (Clarke et al., 2007). In the past three decades, the conservation status of many chondrichthyan populations has increasingly become a major environmental concern (Stevens et al., 2000; Dulvy et al., 2014a).

Over one third of chondrichthyans are threatened by overfishing (Dulvy et al., 2021; IUCN, 2021). The global chondrichthyan catch has been increasingly dominated by batoids (Dulvy et al., 2014a; Dulvy et al., 2021). This increase is likely the result of a number of causes, including improved catch reporting, declines in shark catches due to stronger national and international regulations, and global declines of shark populations and improved catch reporting (Dulvy et al., 2014a). All parts of batoids are typically processed once landed, including fresh and dried meat, skin, vertebrae, fins, whole dried animals, intestines, liver and liver oil, rostrums of sawfishes and gill plates of mobulids (Haque, Biswas & Latifa, 2018). In addition to fishing pressure, shallow water and coastal habitats are under threat from anthropogenic pressures, such as coastal development and climate change (Dulvy et al., 2016), which can negatively impact batoid populations and slow any recovery from population declines. Batoids, like most chondrichthyans, have intrinsically low biological productivity, due to their slow growth rate, late maturity, long generation times, and low fecundity; and are therefore slow to recover from any population declines (Fowler, Reed & Dipper, 2002).

Batoids are widely distributed and found in freshwater, brackish, shallow coastal and deep-sea environments, and range considerably in size from the giant manta ray *Mobula birostris* which attains at least an eight-metre disc width (DW), to the finless sleeper ray *Temera hardwickii* considered the smallest batoid reaching a minimum of 15 cm total length (TL) (Aschliman et al., 2012; Last et al., 2016). Shallow water and coastal batoid species in particular are exposed to high levels of intense and expanding fishing pressure (Last et al., 2016; Dulvy et al., 2021), due to their strong association with soft bottom habitats in shallow (< 100 m depth) waters and this habitat is extensively fished by a range of gears, including gillnet, longline and trawls. Extensive declines in batoid populations have been reported , and are mainly the result of the rapid expansion of chondrichthyan catch in target and non-target fisheries (Clarke et al., 2006; Dulvy et al., 2014a), and the globalisation of trade (Clarke, Milner-Gulland & Bjørndal, 2007; Lack & Sant, 2009).

The Indo-Pacific region stands at the intersection of international trade routes, with approximately 40% of global exports coming from the region (Tertia & Perwita, 2018). For many nations in the Indo-Pacific region, coastal communities are more dependent on subsistence fisheries as a major source of protein and income than anywhere else in the world (Pomeroy et al., 2007; Pomeroy, 2012). Typically, most, if not all parts of elasmobranchs are used in these communities, with different body parts suppling different consumer groups nationally, or exported internationally (Haque, Biswas & Latifa, 2018). This high dependency, combined with a suite of management challenges, has depleted fish stocks, with 13 – 54.5% of stocks estimated to be fished at unsustainable levels in 2017 throughout the Indo-Pacific region (Silvestre et al., 2003; FAO, 2020). Demands for batoid products, including shark-like ray fins, meat and skin for leather has been reported to have increased over the years (**Chapter Four**) (Niedermüller et al., 2021), generating concerns of the population status of batoids in this region. Several high valued and commercially important batoid species have already experienced severe population declines due to fishing pressure (Dulvy et al., 2016; Moore, 2017; Haque, Leeney & Biswas, 2020; Kyne et al., 2020). Global conservation concerns have resulted in the utilisation of species listings under multilateral international trade (Convention of International Trade of Endangered Species, CITES) and conservation agreements (Convention on the Conservation of Migratory Species of Wild Animals, CMS). In addition, the development of international conservation and management action plans (e.g. International Plan of Action for Conservation and Management of Sharks [IPOA] with the United Nations Food and Agriculture Organisation [FAO]; and IUCN Species Specialist Commission [SSC] Shark Specialist Group [SSG] conservation strategies for sawfishes, mobulids and angel sharks) (Mundy-Taylor & Crook, 2013; Vincent et al., 2014; CITES, 2019b; IUCN SSG, 2022). These international agreements provide a global platform and driver for national protections (e.g. National Plan of Action for the Conservation and Management of Sharks, NPOA), and legal foundation for the conservation and sustainable use of internationally traded species (CITES), and migratory species and their habitat (CMS) to reduce fishing mortality of the listed species (Vincent et al., 2014; Lawson & Fordham, 2018).

The theoretical population productivity of some batoid species (such as *R. australiae* and *Glaucostegus cemiculus*) suggests that they have the biological capacity to recover relatively quickly from population declines (**Chapter Six**), whereas other batoids species, such as sawfishes, devil rays and manta rays have a lower biological productivity and may not recovery as quickly (Dulvy et al., 2014b; Pardo et al., 2016a; Pardo et al., 2016b; Pardo et al., 2018). Given the global concerns for this group of species and the importance of trade in their high-value fins, the use of international trade regulations through CITES listings may help achieve positive conservation outcomes (Ostrom et al., 1999; Vincent et al., 2014; Kyne et al., 2020). Successful recovery of populations will require significant conservation and management measures across local, regional, and global scales (Ostrom et al., 1999).

It is important to understand the ecological, economic, and cultural value of batoids in order to help understand the context in which conservation and management for this group is to be implemented. The ecological role and importance of batoids across taxa and different life stages was recently reviewed by Flowers, Heithaus & Papastamatiou (2020), expanding on other reviews, including the review of batoid nurseries by Martins et al. (2018). To date, there has been no systematic review of literature regarding the use of batoids and their importance to communities, culturally or economically, including the Indo-Pacific region (Last et al., 2016). Therefore, the overall objective of this review was to provide a synthesis of the current knowledge on batoid species of the Indo-Pacific region, specifically to (1) compile a checklist of species that occur within the region; (2) review uses of batoid products and cultural and economic values of these species; and lastly (3) to discuss the implications of this information for conservation and outline the goals for future research for batoids of the Indo-Pacific region.

2.2 Review Methods

Species lists from the Indo-Pacific region were generated from species distribution in Last et al. (2016). Species that were described and published after 2016 were included in the list, when possible. It is acknowledged that many species distributions are not complete and there may be batoid species that do occur in the Indo-Pacific region that are not included in Last et al. (2016). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species status was taken from their most recent species assessments (IUCN, 2021).

An academic literature search was conducted using a combination of following keywords in Web of Science, Google Scholar, and OneSearch: “batoid”, “elasmobranch”, “ray”, “stingray”, “skate”, “wedgefish”, “guitarfish”, “giant guitarfish”, “chondrichthyan”, “Asia”, “Indo-Pacific”, “Oceania”, “tourism”, “culture”, “traditional”, “ceremonial”, “leather”, “skins”, “fisheries”, “meat”. Literature deemed irrelevant to this review were excluded (e.g., elasmobranch parasitism, fresh-water research, etc). A separate search for grey literature was completed on Google using the same keywords, as well as on known relevant institutions’ report repositories, including FAO, Southeast Asian Fisheries Development Center (SEAFDEC), The Wildlife Trade Monitoring Network (TRAFFIC), IUCN, and Coral Triangle Initiative. This review does not include literature that is not in the English language, although this research is acknowledged to contain valuable information. Once papers were collected from searches, references were combed to identify more relevant literature.

2.3 Results

2.3.1 Batoids of the Indo-Pacific Region

All orders of batoids are found within the Indo-Pacific region: Order Rhinopristiformes (shark-like rays), Order Torpediniformes (electric rays), Order Rajiformes (skates), and Order Myliobatiformes (stingrays, eagle rays and mobulids) (Last et al., 2016). A total of 256 species from 23 families have been documented to occur in the region (**Table 2.1**). The most speciose order is Myliobatiformes, with the Family Dasyatidae being over half of the species in the order occurring in the Indo-Pacific region (**Table 2.1**). The most threatened order was the Rhinopristiformes, with 62% of the species listed in a threatened category (Critically Endangered, CR; Endangered, EN; or Vulnerable, VU) (IUCN, 2021). The most threatened families were Pristidae (sawfishes), Rhinidae (wedgefishes) and Glaucostegidae (giant guitarfishes), with 11 out of 12 species that occur in the region listed in a threatened category, and the remaining species is currently not evaluated (**Table 2.1**) (IUCN, 2021). The order Rajiformes had the most species listed as Least Concern (40%), as well as the most Data Deficient species (35%) (**Table 2.1**) (IUCN, 2021).

Table 2.1. Batoids of the Indo-Pacific Region. *n* refers to the number of species; International Union for Conservation of Nature (IUCN) Red List of Threatened Species status, CR Critically Endangered; EN Endangered; VU Vulnerable; NT Near Threatened; DD Data Deficient; NE Not Evaluated, https://www.iucnredlist.org/.

				IUCN Red List Status						
Order	**Family**	**Common name**	***n***	**CR**	**EN**	**VU**	**NT**	**LC**	**DD**	**NE**
Rhinopristiformes	Pristidae	Sawfishes	*4*	2	2	--	--	--	--	--
(Shark-like rays)	Rhinidae	Wedgefishes	*8*	6	--	1	--	--	--	1
	Rhinobatidae	Guitarfishes	*10*	--	--	2	1	1	4	2
	Glaucostegidae	Giant guitarfishes	*4*	4	--	--	--	--	--	--
	Trygonorrhinidae	Banjo rays	*4*	--	--	1	--	3	--	--
	Platyrhinidae	Fan rays	*4*	--	1	2	1	--	--	--
	Total		*34*	12	3	6	2	4	4	3
Torpediniformes	Narcinidae	Numbfishes	*12*	--	1	5	1	5	--	--
(Electric rays)	Narkidae	Sleeper rays	*5*	--	--	3	--	1	1	--
	Hypnidae	Coffin rays	*1*	--	--	--	--	1	--	--
	Torpedinidae	Torpedo rays	*5*	--	--	--	1	3	1	--
	Total		*23*	--	1	8	2	10	2	--

Rajiformes (Skates)	Rajidae	Skates	*49*	2	2	9	9	14	12	1
	Arhynchobatidae	Softnose skates	*36*	--	--	--	1	17	18	--
	Gurgesiellidae	Pygmy skates	*2*	--	--	--	--	1	1	--
	Anacanthobatidae	Legskates	*7*	--	--	--	--	5	2	--
	Total		*94*	2	2	9	10	37	33	1
Myliobatiformes (Stingrays, eagle rays and mobulids)	Hexatrygonidae	Sixgill stingrays	*1*	--	--	--	--	1	--	--
	Gymnuridae	Butterfly rays	*5*	1	1	2	--	1	--	--
	Dasyatidae	Stingrays	*60*	3	16	17	6	12	6	--
	Plesiobatidae	Giant stingarees	*1*	--	--	--	--	1	--	--
	Urolophiodae	Stingarees	*28*	1	1	4	2	18	2	--
	Myliobatidae	Eagle rays	*7*	--	2	2	1	2	--	--
	Aetobatidae	Pelagic eagle rays	*3*	--	1	2	--	--	--	--
	Rhinopteridae	Cownose rays	*3*	--	2	--	--	--	1	--
	Mobulidae	Devil rays	*6*	--	5	1	--	--	--	--
	Total		*114*	5	28	28	9	35	9	--
Grand Total			*265*	19	34	51	23	86	48	4

2.3.2 Value of Batoids

Traditional and Cultural values

Elasmobranchs have significant cultural value throughout the Indo-Pacific Region, with key species being of cultural and ecological importance to Indigenous communities (Hari et al., 2021; Kitolelei et al., 2021). Rays feature in many cultures throughout the Indo-Pacific and the world (Rasalato, Maginnity & Brunnschweiler, 2010; Drew, Philipp & Westneat, 2013; Macintyre & Dobson, 2017; Goetze et al., 2018; Kitolelei et al., 2021). Indigenous fishers developed their own traditional taxonomic classification systems for marine and freshwater resources. For example, the general term for wedgefish (*Rhynchobatus* spp.) in Fiji is *qio uluvai* that literally translates into a shark (*qio*) with a ray (*vai*) head (*ulu*) (Thaman, Fong & Balawa, 2008). In Bangladesh, sawfishes are known by many terms that are unique to sawfishes, with the most common name being *Karati Hangor* that translates into saw (*karat*) and shark (*hangor*) in Bangali, with other local names are dependent on the geographical regions (Hossain et al., 2015).

Indigenous communities have developed important knowledge systems (i.e. Traditional Ecological Knowledge; TEK) and relationships with marine and freshwater ecosystems, spanning thousands of years of daily contact and experiences with their environment (Rasalato, Maginnity & Brunnschweiler, 2010; Kitolelei et al., 2021). In Australia, elasmobranchs are an important part of many Aboriginal and Torres Strait Islander groups' culture, where they symbolise their connection to land and sea country. Batoids, mainly sawfishes and stingrays feature prominently in ancient and contemporary art of Aboriginal Australians. Marine rays such as giant guitarfish (*G. typus*), eagle ray (*Aetobatus narinari*), mobulid rays (*Mobula* spp.) and sawfishes (*Pristis* spp.) are important symbols for several clans of the *Anindilyakwa* people of Groote Eylandt as these rays helped to create the land in the Creation stories (McDavitt, 2005). The mangrove whipray *Urogymnus granulatus* is sacred to the *Gumatji* clan of the *Yolngu*, where it represents a metaphor for society, and represents fertility and cultural survival with the passing of lore from elders to the new generation (McDavitt, 2005). Sawfishes and sharks are believed to be connected with fertility of the land in Waiben (Thursday Island), northern Australia where *waiitutu kap* the sawfish dance is performed to insure the fertility of their fields (Baughman, 1948). In Zenadh Kes (Torres Strait Islands), many clans have a shark or ray totem, for example *Kaigas* (wedgefish, *Rhynchoabtus* spp.) or *Tapimal* (various stingrays) clans, while on island of New Guinea, there is a clan known as *Topinguros* (stingrays) (Baughman, 1948).

Stingrays also feature in Polynesian lore and Micronesia region. In Kiribati, one of their deities is *Nei de Tauahine*, a goddess who lives in the sea in the form of a stingray and believed to take shipwrecked marines on her broad back safely to shore (Baughman, 1948). In Federated States of Micronesia, member of the *Tipenway* clan whose totem is the stingray would carefully assist any stranded stingrays back to the water (Baughman, 1948). In Samoa, the stingray is the form of one of the household deities known as *Tangaloa* the god of heaves. In Samoa, Palau, and Marshall Islands there are districts where stingrays are held in reverence and were not to be eaten in those areas (Baughman, 1948). For several clans in Palau, the spotted eagle ray (*Aetobatus ocellatus*) is regarded as a demi-god that may not be harmed or taken, or misfortune, illness or death may befall the offender (Hari et al., 2021). In New Zealand, the Māori supernatural being *Punga* is the ancestor of sharks, rays, and lizards (Last et al., 2016). These examples demonstrate that batoids have strong cultural significance in many indigenous communities throughout the Indo-Pacific.

Fishing provides an important traditional livelihood throughout Indo-Pacific communities (Teh et al., 2007). Fishing can be an essential part of life as a key component of subsistence (e.g. catching fish for food for one's family), culture (e.g. use for ceremonies), part of a person's identity, and a source of income (Hari et al., 2021). For northern Aboriginal groups in Australia, such as *Yolngu* peoples, stingrays are a favourite food item, particularly the liver of young rays which tend to be more tender and succulent (Cherikoff & Brand, 1988). Aboriginal and Torres Strait Islander people hunt elasmobranchs seasonally, and if hunters harvested out of season, they could be punished by the group responsible for maintaining ritual relations with that species (Macintyre & Dobson, 2017). In Bangladesh, dried and fresh elasmobranch meat are consumed by the tribal people and non-Muslim groups (Hossain et al., 2015; Haque, Biswas & Latifa, 2018). In the Republic of Korea, the fermented meat of batoids (mainly skate and rays) is a traditional food that remains very popular with modern consumers (Dent & Clarke, 2015). For some communities elasmobranchs are not consumed for cultural reasons, such as *Noongar* peoples in southern Western Australia, stingrays and shark meat is considered repulsive (Macintyre & Dobson, 2017). For Islamic religion, elasmobranchs are prohibited (haram) and Muslims do not eat products from these animals, however these communities still catch and sell elasmobranch products (Hossain et al., 2015; Haque, Biswas & Latifa, 2018). Some nations across the South Pacific, such as Solomon Island communities, identify with the Christian Seventh Day Adventist religion (Central Intelligence Agency, 2021), where the beliefs prohibit the trade and consumption of elasmobranchs, as well as all fish without scales, shellfish, crustaceans, marine reptiles, cephalopods, and marine mammals (Sabetian, 2002). These cultural beliefs in turn influence how these communities interact with and use particular marine resources.

Western culture and attitudes towards elasmobranchs have been traditionally negative, particularly sharks which tend to symbolise predatory behaviour, greed, danger, and deceit (Whatmough, Van Putten & Chin, 2011). Western culture refers to the heritage of social norms, ethical values, traditional customs, and belief systems that originated from Europe, particularly nations whose history has been strongly impacted by European colonisation, such United States of America and Australia. There are few historical records of batoids in the Western culture. One record was from a manuscript on the origins of dragons, where it was hypothesised that European folklore of mythical dragons were influenced natural history literature and in the 11th Century, stingrays and moray eels were classified as marine dragons (Senter, Mattox & Haddad, 2016). While another other record was in early 17th century in Irish mythology, where it was thought that the *gae bolga* (spear) of the demigod Cú Chulainn was tipped by the caudal spines of a stingray (Pettit, 2015).

Fisheries and trade

The reported global production of sharks and batoids in 2016 was estimated to be 767,000 tonnes, with batoids accounting for approximately 36% of the recorded catch (FAO, 2019). Yet, this value is an underestimation of the magnitude of the total reported catches, as the FAO reports do not include discarded catch nor catch from illegal, unreported, and unregulated (IUU) fisheries (Pauly & Zeller, 2016). Batoids are rarely specifically targeted by commercial fisheries (with the exception of the tangle-net fishery in Indonesia – see **Chapter Four**), however they form a significant proportion of by-catch and by-product in numerous fisheries (Stobutzki et al., 2002; Brewer et al., 2006; Griffiths et al., 2013; Gilman et al., 2016; Campbell et al., 2020). For example, in the pelagic longline fisheries in Palau, the pelagic stingray *Pteroplatytrygon violcea* comprised over 8% of the recorded catch, with 99% of the catch discarded (Gilman et al., 2016). Batoids were the largest component of landed chondrichthyan catches in Malaysian, Thailand and Philippines fisheries (Keong, 1996; Teh et al., 2007). However, since 2005, the landed catch of batoids in Malaysia has been reported to have declined (Teh et al., 2007). A similar trend was observed for the batoids landings from gillnet bycatch in East Java, Indonesia, where annual landings have generally decreased since 2008 (Sjafrie, Oktaviyani & Kurniawan, 2020). Similar to shark-like rays, the population status of numerous tropical stingray species are likely declining in this region as inferred from decreasing landings and catch data (Sherman et al., 2020a).

The main trade of ray products across Indo-Pacific region are fins from shark-like rays, meat, skin, and gill rakers, while the by-products of rays include liver, internal organs, cartilage, and jaws/teeth (Dulvy et al., 2017; Wainwright et al., 2018; Sjafrie, Oktaviyani & Kurniawan, 2020; D'Alberto et al., 2021; Haque & Spaet, 2021; Niedermüller et al., 2021). These products are traded in domestic and international markets across the Indo-Pacific (Dent & Clarke, 2015; Haque, Biswas & Latifa, 2018). The main products and by-products are typically handled by different parties to be separated into international (e.g. meat, fins and gill plates) and domestic markets (e.g. meat, liver, internal organs, cartilage and jaws/teeth)

(Sjafrie, Oktaviyani & Kurniawan, 2020). In Bangladesh, there is a market for sawfish, wedgefish and giant guitarfish products that are typically landed as bycatch by artisanal fishers (Haque, Leeney & Biswas, 2020; Haque, Cavanagh & Seddon, 2021). Here sawfishes are not landed at official landing sites or local marketplaces (Haque, Leeney & Biswas, 2020). Instead, they are reported to be transported directly to private processing centers as soon as they are landed to be sold to specific buyers who deal in sawfish products, or separated into saleable products, including meat, skin and cartilage (Haque, Leeney & Biswas, 2020). Generally, the local consumption of ray products is smaller than the total landed catch, with the majority of the catch exported (Sjafrie, Oktaviyani & Kurniawan, 2020).

The international elasmobranch meat trade is currently valued at US$ 2.6 billion, which is significantly larger than the trade of fins valued at US$1.5 billion, yet until recently has received little attention (Niedermüller et al., 2021). Indonesia is the fourth largest exporter of batoid meat at 18,049 tonnes, with Argentina being the largest exported of batoid meat (81,601 tonnes)(Niedermüller et al., 2021). Malaysia is the fourth largest importer of batoid meat at 18,231 tonnes, with Korea being the largest importer of batoid meat (141,655 tonnes)(Niedermüller et al., 2021). Trade flow between Indonesia and Malaysia was the fifth largest of 10,084 tonnes (Niedermüller et al., 2021). Singapore imports large volumes of batoids in order to meet the demand for the local seafood. In Singapore, depending on the species, ray meat can fetch a high price of over US$18 per kilo (SGD$20) from wet markets (Clark-Shen et al., 2021). Whereas some species like the blue-spotted fantail ray *Taeniura lymma* are considered poor quality and sold at a lower price (Clark-Shen et al., 2021). Wedgefish meat at Singapore wet markets are sold for US$2 – 3 per kg (SGD$3 – 4), while the snouts are sold for approximately US$6 per kilo (SGD$10)(Clark-Shen et al., 2021).

Gill plates have been reported as an export trade from India, Indonesia, Sri Lanka, and Mozambique (Dent & Clarke, 2015). Gill plates in Sri Lanka can fetch up to US$190 per kilogram, depending on the mobulid species (Dent & Clarke, 2015). The market for mobulid ray plates is typically found in southern China, including Hong Kong (Wu, 2016). Gill rakers from unknown species sold in Hong Kong for between US$ 187 – 350 per kg, in 2016, (Wu, 2016).

Stingray leather has a long history in the international trade, yet there is little recent trade data available. A report of USA trade data from 1997 – 2001, recorded at least 10 main batoid species imported into the US, which comprised a small proportion of the all the fish leather imports. Over 99% of batoids were reportedly wild caught and sourced from Thailand (78%), Indonesia (12%), and the Philippines (7%), and then re-exported to Mexico (36%), Canada (25%) and France (11%) (Grey et al., 2006). The import of batoid products declined during the five year survey (average 29,900 stingray skins per year), while the value of the products increased (average worth of US$ 725,000) (Grey et al., 2006). In 2001 – 2005, ray skins were the second most valuable product from the Indonesian tangle net fishery (D'Alberto et al., 2021). In 2005, the reported values of 13 cm and 18 cm pieces of stingray leather were 25,000 IDR (= 59,543 IDR / 4.30 USD in 2021) and 35,000 IDR (= 83,360 IDR / 5.97 USD in 2021) (D'Alberto et al., 2021). Between 3,000 – 4,000 skins were estimated to be exported per month to the Philippines and Japan (D'Alberto et al., 2021). Products from the stingray leather include wallets and belts, which were reported to be sold for approximately 290,000 IDR (= 690,694 IDR / 49.50 USD in 2021) to 500,000 IDR (= 1,190,851 IDR / 85.33 USD in 2021) (D'Alberto et al., 2021). The increasing push for the commercialisation of batoid leather industry across the Indo Pacific, particularly in Indonesia (Sahubawa, Pertiwiningrum & Rahmadian, 2018; Sahubawa & Pertiwiningrum, 2020; Sahubawa, Atmoko & Sasongko, 2021) and India (Karthikeyan et al., 2009; Mardiah, Huda & Ahmad, 2010), raises concerns for the potential of increasing targeted fishing pressure on batoids.

Elasmobranch cartilage production has been reported in China, Japan, South Africa, the Sudan, USA, and Canada, and is believed to be more widespread with little documentation (Dent & Clarke, 2015; Cardeñosa, 2019). In Indonesian, dried elasmobranch vertebrae were reported to be worth 20,000 IDR kg^{-1} (= 50,717 IDR kg^{-1}/ US$ 3.63 kg^{-1} in 2021) and exported through an undisclosed port to Korea and Japan from Jakarta (**Chapter Four**). Historically, in the Indo-Pacific, large quantities of squalene oil were exported from Philippines to Japan and Korea between 1973 – 1994 (Cardeñosa, 2019). There have reports of sources of squalene for a number of Indo-Pacific nations (India, Indonesia, Malaysia, and New Zealand) either local or export uses of squalene (Dent & Clarke, 2015). However, there is little recent information available on the trade of squalene.

Tourism

Wildlife tourism has increased dramatically over the past four decades and it is the fastest growing section of tourism (Kuenzi & McNeely, 2008; O'Malley, Lee-Brooks & Medd, 2013). The estimated values for wildlife tourism can be significantly greater than those associated with harvesting wild populations (O'Malley, Lee-Brooks & Medd, 2013; Mustika, Ichsan & Booth, 2020). Tourism focuses on only a few (~18) elasmobranch species (Dulvy et al., 2017), with current elasmobranch tourism valued at approximately US$ 314 million annually (Cisneros-Montemayor et al., 2013). Elasmobranch tourism in Indonesia alone, estimated to engage an average 772,171 people annually, and the median total attributable expenditures in 2017 was USD $73.6 million and projected to be US$ 121.2 million by 2027 (Mustika, Ichsan & Booth, 2020). This high valued wildlife tourism can create economic incentives for protecting and sustainably managing marine ecosystems and species (Mustika, Ichsan & Booth, 2020). It can provide important auxiliary income to the destination nations and communities through expenditure on accommodation, food and transport, and tax revenue (Vianna et al., 2018). Batoids, in particular stingrays, eagle rays, devil rays and manta rays, are an important and valuable wildlife tourism attraction in many coastal communities in the tropical Indo-Pacific region (Gaspar, Chateau & Galzin, 2008; Semeniuk et al., 2009; DeLorenzo & Techera, 2019; Healy et al., 2020; Hari et al., 2021; Meyer et al., 2021).

Many ray wildlife tourism locations began from the offal discards of local fishers into waters, such as Hamelin Bay in southwest Western Australia and Moora in French Polynesia (Lewis & Newsome, 2003; Gaspar, Chateau & Galzin, 2008; DeLorenzo & Techera, 2019). Tourist operators often continue to use attractants (i.e. berley, bait, or food rewards) to attract, aggregate and/or positively reinforcing elasmobranchs natural aversion towards humans (Healy et al., 2020; Meyer et al., 2021). For example, the provisioning of pink whipray *Pateobatis fai* to certain shallow, inshore sandbars shas occurred on Moorea, French Polynesia since 1995, where up to 120 tourists can be present at the same time on one feeding spot (Gaspar, Chateau & Galzin, 2008). Visitors can touch and feed the rays in these locations, however, these interactions can lead to physiological changes in the stingrays. For example, causing sub-optimal body condition (Semeniuk et al., 2009). Manta ray watching tourism (*Mobula* spp.) at known aggregation sites is a popular and valuable activity, with an estimated global direct economic impact of US$140 million annually (O'Malley, Lee-Brooks

& Medd, 2013). Six out of the top ten nations that account for 93% of the global revenue are in the Indo-Pacific region, specifically Japan, Indonesia, Thailand, Australia, Federated States of Micronesia and Palau (O'Malley, Lee-Brooks & Medd, 2013). In 2013, swimming with manta rays brough US$6.8 million to the economy in Palau (Hari et al., 2021). Unregulated interactions with elasmobranchs (i.e. high number of boats in the vicinity and large volume of people in the water close to or touching rays) may cause the animal stress. Tourism operators in Palau are required to give guests an environmental briefing, while the feeding of wildlife is banned, and boat access is restricted at the main foraging and fish cleaning sites (common aggregation point for many species, including manta rays) (Barr & Abelson, 2019), to provide safety for the manta rays and tourists (Hari et al., 2021).

2.3.3 Uses of Batoids

Batoids are consumed globally and provide an important source of protein for many coastal communities (Griffiths et al., 2013; Hossain et al., 2015; Jeevanaraj et al., 2019). Batoids contain high levels of protein, mineral, vitamins, and omega-3 fatty acids (Jeevanaraj et al., 2019). The meat, shark-like ray fins, mobulid fin plates, and snouts of batoids are consumed either fresh, dried and/or salted depending on the dish.

Consumption

Meat

Stingrays, devil rays, manta rays, and skates are commercially valued for their large pectoral fins, referred to as 'wings' (Griffiths et al., 2013). Prior to sale, the bodies of batoids are usually discarded (i.e. "winged") and often skinned (Griffiths et al., 2013). This makes visual identification of species in markets almost impossible (Griffiths et al., 2013). Wedgefish and giant guitarfish meat have long been considered of high value and consumed locally in many counties of Indo-Pacific region, especially within Southeast (SE) Asia (Jabado, 2018).

Meat is typically sold fresh or preserved using methods such as drying, salting, and smoking. Fresh stingray wings and snouts of wedgefishes are considered a delicacy, particularly in Singapore and across Southeast (SE) Asia (Clark-Shen et al., 2021). Barbequed sambal stingray is a popular dish which can be found at hawker stalls at almost every food centre. Fish merchants at Singapore Fishery ports report that species from the genus *Maculabatis*, in particular *M. gerrardi* and sharpnose whipray *Maculabatis macruca* were the preferred species for this local delicacy, whereas fresh wedgefish meat was found to be sold in some supermarkets as 'shovelnose ray meat' (Clark-Shen et al., 2021). In Malaysia, the common dish '*Gulai Ikan Yu Perejang'* (Perejang shark curry), uses wedgefish meat and observed to be growing in demand, particularly in the eastern coast of West Malaysia. Another popular Malay dish is '*Sembam ikan'* which is charcoal/coconut shell grilled stingray (*ikan pari*) meat (Widayati, 2019).

Various nations in the Indo-Pacific region were found to have methods of preservation for batoid meat. Preservation of the meats prevents damage to the flesh and can increase the economic value of the product (Suprapto et al., 2021). In the Republic of Korea, fermented skate or ray meat is a very traditional and popular dish in the southern part of the nation that is eaten as sashimi or in a stew (Dent & Clarke, 2015). In Indonesia, salted elasmobranch meat is quite popular, and it is often given as a gift (Niedermüller et al., 2021). Stingrays, such as cowtail stingray *Pastinachus sephen* are popular species that are smoked in Indonesia, as smoked stingray has a long shelf life (up to nine days) (Swastawati et al., 2012; Suprapto et al., 2021). Smoked elasmobranch meat is sold to retailers in local markets in East Java for between US$0.16 – 0.25 per skewer of meat (Sjafrie, Oktaviyani & Kurniawan, 2020). Stingrays like whitespotted whipray *Maculabatis gerrardi* are processed into snack products such as fish crackers, fish floss, and *dendeng giling* (fish flakes), which is similar to beef jerky, by drying (Mardiah, Huda & Ahmad, 2010; Mardiah, Huda & Ahmad, 2012; Sjafrie, Oktaviyani & Kurniawan, 2020). The dried and flavoured wings of small skates are served as snacks in bars or sold in convenience stored in Republic of Korea and in Japan (Dent & Clarke, 2015).

Most elasmobranchs can have an elevated concentration of mercury (Hg) in their tissues (e.g. gills, muscle, and liver) that bio-accumulates in the marine food-chain. Coastal rural communities across the Indo-Pacific tend to consume higher amount of seafood than urban communities, therefore have a higher risk of Hg exposure (Jeevanaraj et al., 2019). For example, the pale-edged stingray *Dasyatis zugei* is one of the preferred fish species to eat in Malaysian communities (Jeevanaraj et al., 2016; Jeevanaraj et al., 2019). This demersal species can have medium (0.19 mg/kg total mercury THg) to high levels (0.71 mg/kg) of Hg within its muscle tissues (Jeevanaraj et al., 2016; Jeevanaraj et al., 2019). The consumption of tissues with Hg above the recommended levels (i.e. 0.50 mg/kg) can cause serious health risks for pregnant women and the developing fetus and sensitive populations, and should be warned to avoid consumption (Jeevanaraj et al., 2016; Jeevanaraj et al., 2019).

Shark-like ray fins

Shark fins (including the fins from shark-like rays) are consumed as high-value luxury soup, primarily in China, Japan, Singapore and Chinese communities in other nations (Dent & Clarke, 2015). Shark-fin soup is traditionally served as a token of respect and demonstration of status and power in Chinese folk custom (Fabinyi, 2012). The lucrative price and high demand for fins are the primary driver for catching and retaining elasmobranch in fisheries (Dent & Clarke, 2015). Shark-fins are graded and priced based on species and size (Dent & Clarke, 2015). The highest-grade fins are actually from two families of shark-like rays, the wedgefishes (Family Rhinidae) and giant guitarfishes (Family Glaucostegidae) (Hau et al., 2018). During market surveys in Indonesia in 2005, the quoted price for fins from sawfish, wedgefish and guitarfish was approximately 3 million IDR kg^{-1} wet weight (~ 7,145,108 IDR / $512 USD per kg in 2021 terms) (**Chapter Four**). Consumers prefer the higher prices and rare shark fins that were obtained without finning [the processing of removing the fins on board vessels and discarding the carcasses at sea](Fowler, Séret & Clarke, 2010; Zhou et al., 2021). Numerous nations in the Indo-Pacific region, such as Indonesia and Malaysia, Bangladesh, and Sri Lanka, capture shark-like rays and sharks to export the fins to several nations, including to Singapore and China where it is predominantly consumed (Hossain et al., 2015).

Shark-like ray heads

Wedgefish snouts are used in collagen soup, known as ‘steamed shark head’ in Singapore restaurants (Clark-Shen et al., 2021). Giant guitarfish snouts have been reported at several Bangladesh processing centres although the final export destination was unknown (Haque, Biswas & Latifa, 2018).

Other uses

Batoid livers from species including sawfish and mobulids, are regarded as good source of vitamin D (Cherikoff & Brand, 1988; Keong, 1996; Hossain et al., 2015). There are reports that elasmobranch cartilage is used to make flour in local communities in East Java Indonesia (Sjafrie, Oktaviyani & Kurniawan, 2020).

Batoid products are also used in for non-human consumption with cartilage and meats used in products such as pet food/treats, and fishmeal. Bycatch of batoids have been reported to be used to produce fish manure and animal feed (Haque, Biswas & Latifa, 2018; Cardeñosa, 2019; Bhagyalekshmi & Kumar, 2021). In India, the bulk catch of rays from trawl fisheries are considered trash, however these trash rays are used by small-scale factories to produce fish manure and animal feed (Bhagyalekshmi & Kumar, 2021). In neighbouring Bangladesh, the liver of rays are used in the fish feed industry (Haque, Biswas & Latifa, 2018). In East Java, Indonesia, ray entrails have been recorded as being sold to markets for catfish or crab feed (Sjafrie, Oktaviyani & Kurniawan, 2020). Traces of DNA of threatened shark species have been found in pet food (canned products, dry food, and treats) in the US (Cardeñosa et al., 2017; Cardeñosa, 2019). However, this was from a limited study and there this is a need for more research to have a better understanding of species composition, including if these widely used products contain traces of batoids.

Nutraceuticals

Batoid products have a long history of use as nutraceuticals [food extracts or derivatives that are said to exhibit a range of therapeutic health benefits (Espín, García-Conesa & Tomás-Barberán, 2007)], including uses in modern medicine (Pan et al., 2016; O'Malley et al., 2017; Koutroumpas, Lioumi & Vougiouklakis, 2020) and cosmetic products (Cardeñosa et al., 2017; Cardeñosa, 2019). For example, one of the first recordings of medicines for the purpose of extracting teeth in Ancient Greece (~ 1st Century A.D.), was the use of venom from stingray barbs from the common stingray *Dasyatus pastinaca*, as anaesthesia for their patients (Koutroumpas, Lioumi & Vougiouklakis, 2020). The use of batoid products for traditional medicinal use in the Indo-Pacific region is largely reported from southern China, Republic of Korea, and Bangladesh (Dent & Clarke, 2015; Hossain et al., 2015; Wu, 2016; Lawson et al., 2017).

Gill plates

Devil rays and manta rays are considered medicinal animals in southern China, where the gill plates (known as Peng Yu Sai, “Fish Gill of Mobulid Ray”) and brains are believed to have detoxification and anti-inflammatory functions, as well as being used to treat rashes, childhood measles, and boils (Wu, 2016; Lawson et al., 2017). The popularity of gill plates is thought to be limited to household consumption, as opposed to restaurants, hotels or caterers, as they are considered an ingredient for traditional health tonics (Wu, 2016). Historically, gill plates were not a part of Traditional Chinese Medicine, however over the past 15 years there have been efforts by traders and industry marketing to revive this remedy and demand for these products (Wu, 2016). In addition, toxicology research has suggested that there are health risks from consuming high levels of heavy metals in gill plates (Wu, 2016).

Batoid cartilage

Skate cartilage is consumed alongside shark meat in the Republic of Korea, as the cartilage is considered to have a comforting effect on those suffering from arthritis and other joint conditions (Dent & Clarke, 2015). Sawfishes are believed to have numerous medical properties in Bangladesh, where there is a belief that different parts of sawfishes have curative properties for different diseases and aliments (Hossain et al., 2015). Sawfish muscle is thought to produce medicine to cure cancer, heart disease, kidney disease, tuberculosis, tonsil problems, gangrene, wound healing and ulcers, whereas the liver and fat are thought to cure anaemia and influenza (Hossain et al., 2015). Sawfish ceratotrichia (fin needles), which are also the primary ingredient for shark-fin soup, were reported to be used in surgery as stitching thread as it can be absorbed by the body (Hossain et al., 2015). In addition, talisman vendors have been known to sell sawfish vertebrae with claims that it cures pain and all types of diseases and also protects the wearer from all evil harm (Hossain et al., 2015). These medicinal uses, as well as the high value of fins is thought to be driving the local market for sawfishes in Bangladesh (Hossain et al., 2015), and incentivises fishers and boat owners to retain sawfishes caught as bycatch, rather than releasing them (Haque, Leeney & Biswas, 2020).

In modern medicine, elasmobranch cartilage is a newly studied source of biomedical products, including collagen to regenerate damaged cartilaginous tissues and antioxidants (Pan et al., 2016; Atef & Ojagh, 2017; Seixas et al., 2020). Industrial exploitation of elasmobranchs for human consumption (i.e. meat and fins) for food results in substantial quantities of by-products such as skin and cartilage that is typically discarded. Studies on the extraction of biomedical products have suggested that discarded parts from fish processing industries would be a sustainable source (Pan et al., 2016; Atef & Ojagh, 2017; Seixas et al., 2020). However, this would also require effective management to ensure the sustainable exploitation and use of batoids.

Liver Oil

Elasmobranch livers contains many different oils, including squalene that is highly valuable in the cosmetics industry (Cardeñosa, 2019). It is used in a number of beauty products, such as moisturising cream, oils, lipstick, face powder, and mascara (Cardeñosa et al., 2017). Squalene can be obtained from plants (e.g. amaranth and olives) or animals (e.g. elasmobranch liver) sources, however most brands do not specify the source of the squalene in their products. While squalene mostly comes from deep-water shark species, DNA of threatened batoid species such as *Rhynchobatus* sp. have been detected in beauty products (Cardeñosa et al., 2017). This demonstrates that Critically Endangered batoid species are being used in the squalene trade.

Leather and accessories

The skin of stingrays or ‘shagreen’, is appreciated for the unique opulent, glossy surface created by the polished, calcified denticles within the structure of the leather. As it is highly durable, waterproof and can be dyed any colour, it is used to produce various leather products (e.g. bags, belts, wallets, and jewellery) that have a high economic value (Karthikeyan et al., 2009; Sahubawa, Pertiwiningrum & Rahmadian, 2018).

Ray skin has been used in Asia since at least the 13th century, primarily in Japanese weaponry and armour, where the grainy texture and water-resistant surface provided grip and decorations (Silverman, 2016). Raw ray skins were used by European craftsman from the 17th Century to decorate furniture, including cabinets and small chests (Silverman, 2016). The skins were likely to be imported from Japan, India and China with trade routes established in Thailand (Silverman, 2016). In 18th century Europe, French artisans created numerous items constructed of stingray skin, including snuff boxes, wig cases, and sheaths that were used exclusively by royalty including Louis X, demonstrating the popularity and exclusivity of this rare material (Silverman, 2016). It can be difficult to identify the ray species once the skin has been removed and processed, however the skins of species of Family Dasyatidae, which are wide spread throughout the Indo-Pacific region, have been documented primarily for products exported to Europe (Silverman, 2016).

Today, there is an increasing demand for stingray leather, driven by improvements in production and ability to mass produce products (Sahubawa & Pertiwiningrum, 2020). The trade routes for ray skin appear to have remained the same since the 17th Century, with the skins originating from tropical Indo-Pacific nations, including Indonesia, Republic of Korea, Thailand, and Bangladesh to be exported to Europe, Japan, Philippines, China, and USA for use in the production of luxury products (Grey et al., 2006; Haque, Biswas & Latifa, 2018). The most commonly used species come from the genera *Himantura, Maculabatis, Pastinachus, Pateobatis* and *Urogymnus*, with the Jenkins' whipray *Pateobatis jenkinsii* reported to be the most sought-after species due to the row of enlarged thorns which extend down the midline of the body and tail (**Chapter Four**). The skins used for leather products are typically waste from processing factories (Sahubawa, Pertiwiningrum & Rahmadian, 2018; Sahubawa & Pertiwiningrum, 2020; Sahubawa, Atmoko & Sasongko, 2021). In Indonesia, there has been a rise in demand for ray skin for leather products and increasing studies on the commercial development of ray leather to provide greater economic opportunities in coastal communities (Sahubawa, Pertiwiningrum & Rahmadian, 2018; Sahubawa & Pertiwiningrum, 2020; Sahubawa, Atmoko & Sasongko, 2021). Consumer preference surveys in Indonesia, indicate that consumers prefer wallets made from ray leather over cowhide products, due to the unique surface, shapes and colours, as well as being more affordable than the cowhide products (Sahubawa, Atmoko & Sasongko, 2021). A similar increase in demand has also been documented in Bangladesh and India (Haque, Biswas & Latifa, 2018; Haque & Spaet, 2021).

2.4 Discussion

The Indo-Pacific region has a long history of valuing batoids as important cultural figures, and the primary source of income and/or protein for countless communities. This region also contains the world's largest elasmobranch catching and trading nations (e.g. Indonesia, India, Republic of Korea, Malaysia) (Niedermüller et al., 2021). The rapid expansion of fisheries (that includes target and non-targeted elasmobranch catch) (Clarke et al., 2006) and the globalisation of trade (Clarke, Milner-Gulland & Bjørndal, 2007; Lack & Sant, 2009), has caused substantial declines in batoid populations, demonstrated by declines in reported catch rates and landings (Dulvy et al., 2021). Batoids are mostly retained as valuable by-catch and by-product in numerous fisheries, including small scale and subsistence fisheries (Stobutzki et al., 2002; Brewer et al., 2006; Griffiths et al., 2013; Gilman et al., 2016; Campbell et al., 2020; D'Alberto et al., 2021). Many Indo-Pacific batoid species have large geographical ranges that span multiple nations and jurisdictions increasing their interaction with numerous fisheries that negatively influences their extinction risk (Dulvy et al., 2017).

Overfishing is the largest threat to elasmobranch species, with fishing mortality being under-managed and unsustainable for many species (Vincent et al., 2014; Yulianto et al., 2018). The recovery of an overfished population can occur only when fishing mortality is reduced or in some cases halted completely (Myers & Worm, 2005; McAuley, Simpfendorfer & Hall, 2007; Ferretti et al., 2010). Only 22 of 104 (21.2%) Indo-Pacific batoid species listed in an IUCN threatened category (CR, EN or VU) have been listed on international agreements regulating the international trade (CITES) or conserving migratory species and their habitat (CMS) (**Table 2.2**). However, in some nations where national measures are adopted in an attempt to reduce elasmobranch fishing mortalities, often they can be insufficient (e.g. excessive quotas set higher than landed catch), haphazard (e.g. area/seasonal closure without overall catch limits), and/or poorly enforced and allowing excessive mortality (Harrison & Dulvy, 2014; Dulvy et al., 2017). Furthermore, some low-income nations can lack the capacity to implement and enforcement national legislation to meet their CITES and CMS commitments. Capacity building, improved trade monitoring and traceability, as well as awareness campaigns will be key to reduce fishing mortality, utilization, and trade (Clark-Shen et al., 2021). Reduction in fishing mortality will require practical fisheries measures and governance across local, national and global scales, and will need to factor the socio-economic drivers and mitigate negative impact to livelihood of communities (Ostrom et al., 1999; Booth, Squires & Milner-Gulland, 2019).

An increased push for the commercialisation of certain products (e.g. meat and leather industry) across the Indo-Pacific, particularly in Indonesia (Sahubawa, Pertiwiningrum & Rahmadian, 2018; Sahubawa & Pertiwiningrum, 2020; Sahubawa, Atmoko & Sasongko, 2021), Bangladesh (Haque, Biswas & Latifa, 2018; Haque & Spaet, 2021), India (Karthikeyan et al., 2009; Mardiah, Huda & Ahmad, 2010; Karthikeyan et al., 2011) and Republic of Korea (Dent & Clarke, 2015; Niedermüller et al., 2021), raises concern for the potential of increasing targeted fishing pressure on batoids, causing further population declines. Stingrays (Family Dasyatidae) are a valuable commodity for Indo-Pacific nations with products (meat, leather, etc.) sold in domestic markets and traded internationally, resulting in conservation concerns growing for species such as *M. gerrardi* and *M. macrura* (Clark-Shen et al., 2021). It is likely that stingrays are currently experiencing similar trends of declines to sawfishes, wedgefishes and giant guitarfishes, most of which are Critically Endangered (**Chapter Four**), where populations declined rapidly throughout their range, driven by unregulated fisheries, international demand for products and delayed scientific and

Table 2.2. Batoids of the Indo-Pacific that are listed (Y) on Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), Convention on the Conservation of Migratory Species of Wild Animals (CMS) and CMS The Memorandum of Understanding on the Conservation of Migratory Sharks (Sharks MoU). – indicates not listed in the international agreements.

Family	**Species**	**CITES**		**CMS**		
		Appendix I	**Appendix II**	**Appendix I**	**Appendix II**	**Sharks MoU**
Pristidae	*Anoxypristis cuspidata*	Y	--	Y	Y	Y
	Pristis clavata	Y	--	Y	Y	Y
	Pristis pristis	Y	--	Y	Y	Y
	Pristis zijsron	Y	--	Y	Y	Y
Rhinidae	*Rhina ancylostoma*	--	Y	--	--	--
	Rhynchobatus australiae	--	Y	--	Y	Y
	Rhynchobatus cooki	--	Y	--	--	--
	Rhynchobatus immaculatus	--	Y	--	--	--
	Rhynchobatus laevis	--	Y	--	--	Y
	Rhynchobatus palpebratus	--	Y	--	--	--
	Rhynchobatus springeri	--	Y	--	--	--
Glaucostegidae	*Glaucostegus typus*	--	Y	--	--	--
	Glaucostegus granulatus	--	Y	--	--	--
	Glaucostegus obtusus	--	Y	--	--	--
	Glaucostegus thouin	--	Y	--	--	--
Mobulidae	*Mobula alfredi*	--	Y	Y	Y	Y
	Mobula birostris	--	Y	Y	Y	Y
	Mobula eregoodoo	--	Y	Y	Y	Y
	Mobula mobula	--	Y	Y	Y	Y
	Mobula kuhlii	--	Y	Y	Y	Y
	Mobula tarapacana	--	Y	Y	Y	Y
	Mobula thurstoni	--	Y	Y	Y	Y

conservation attention (Thorson, 1982; Simpfendorfer, 2005a; Thorburn et al., 2007; Dulvy et al., 2016). The population status of numerous tropical stingray species have already reported substantial declines, inferred from decreases in grouped landings and catch data, and with little species-specific fisheries information available (Sherman et al., 2020a). Currently fisheries for stingrays are not regulated through national or regional species-specific fishing regulations. To avoid the same fate as sawfishes, wedgefishes and giant guitarfishes, precautionary national and international management and conservation actions for tropical stingrays is strongly recommended, which will be vital to maintain their populations.

The loss of large, benthic elasmobranchs can have significant social, cultural, and economic impacts on the fishers and communities who depend on them (Jaiteh, Loneragan & Warren, 2017). Coastal communities have an invaluable link with elasmobranchs in cultural traditions and art. An example of incorporating traditional values into fisheries management is in Palau, where commercial fishing of elasmobranchs is prohibited except for Palauan citizens who may land one elasmobranch per calendar day for traditional use or non-commercial purpose (Lawson & Fordham, 2018). Traditional ecological knowledge and Local Fishing Knowledge (LFK) is also an important source of information that can be utilised alongside fisheries data collection, which should be considered when implementing management measures (Sabetian, 2002; Kitolelei et al., 2021).

Fishers with few viable livelihood alternatives are likely to continue to catch elasmobranchs, selling derived products for economic gain and/or keeping the meat for protein needs (Jaiteh, Loneragan & Warren, 2017). The domestic market for elasmobranch products (e.g. meat, fins, leather etc.) throughout Indo-Pacific nations such as Indonesia, Bangladesh, Malaysia, and India, is likely to provide enough incentives for continued retention of batoids in local fisheries, regardless of international trade and conservation agreements that not apply to domestic trade (Booth et al., 2020; Mustika, Ichsan & Booth, 2020). For example, sawfishes have been protected in Bangladesh under national law since 2012 by the Wildlife (Conservation and Security) Act and listed under Appendix I for CITES since 2013, for which exports and imports of sawfish and derived products for commercial purposes are essentially prohibited (CITES, 2019a). Yet regular landings and international export of sawfish products from Bangladesh were documented in 2020, and will likely continue due to the lack of enforcement (Haque, Leeney & Biswas, 2020). Often fishers and traders in low-income nations, including throughout the Indo-Pacific region, are not aware of national and international legislation relating to catching and retaining of protected species (Haque, Leeney & Biswas, 2020). They can also be uninformed of the drivers behind fluctuating market prices for products (particularly shark fins), demonstrating fishers inability to access reliable information on relevant legislation and market trends (Jaiteh, Loneragan & Warren, 2017).

In low-income nations, incentives for sustainable livelihoods to reduce fishing pressure and mortality should be a top priority if recovery of populations is to occur (Jaiteh, Loneragan & Warren, 2017). Appropriate and economically viable incentives for livelihood alternatives for fishers will be required to address the issues of poverty and food security in resources dependent communities (MacKeracher et al., 2020). Using a precautionary and holistic risk-based approach like a mitigation hierarchy framework as proposed by Booth, Squires & Milner-Gulland (2019) would be highly beneficial for Indo-Pacific nations as it takes into the account the biological, social, and economic aspects of fisheries. This method has the capability of dealing with data paucity and could be used for any fishery that lands batoids. In addition, wildlife tourism has the potential to create alternative livelihoods and economic incentives for elasmobranch conservation across the Indo-Pacific region (Rusandi et al., 2019). Yet, this industry focuses on a few charismatic elasmobranch species (primarily manta rays and reef sharks) that are in locations accessible and well suited for tourism (Rusandi et al., 2019), while hundreds of species are landed by fishers across the region (Dulvy et al., 2017). Conservation interventions aimed at protecting elasmobranchs for tourism, may protect a few elasmobranch species more directly (e.g. marine protected areas, MPA), however it can have a more immediate detrimental impact on coastal livelihoods through displacing fishers from fishing grounds, while only protecting species that remain inside the MPA (Jaiteh et al., 2016b; Jaiteh, Loneragan & Warren, 2017). Any viable management options and regulations including wildlife tourism, will need to ensure that they are leading to noticeable conservation outcomes (Booth et al., 2020), as well as positive social and economic outcomes for communities (Booth, Squires & Milner-Gulland, 2019).

The evaluation of sustainability of fisheries and trade can be hampered by the lack of understanding of interaction with fisheries and life-history (e.g. age, growth, and maturity), demographic information and recovery rates (Skalski, Ryding & Millspaugh, 2005; Cortes, 2016). There is a considerable knowledge gap on batoids globally, on species life history, movement and distribution, species size and sex composition in landed catch, by-catch survivability and mortality rate, derived products and their trade routes and codes, any changes in market demand over time. Scientific advice and information on the monitoring of fisheries landings and supply chains of batoid species (ideally species-specific information) will be required to make management decisions for elasmobranch fisheries in SE Asia (Clark-Shen et al., 2021). To avoid the research-practitioner divide (failure to translate conservation assessments into actions that directly conserve species and habitats) scientific recommendations must be communicated and effectively translated to the relevant stakeholders, including governmental authorities, impacted communities and any conservation organisation in the area (Haque, Leeney & Biswas, 2020).

Chapter Three

Manuscript intended for publication associated with this chapter:

D'Alberto, B.M., et al. (Intended for publication) Like a drop in the ocean: Low abundance of rare and threatened shark-like rays on tropical coral reefs from global baited remote underwater videos stations (BRUVS) survey. Target journal: *Marine Ecology Progress Series.*

Nature and extent to contribution of co-contributors/authors to the chapter

The chapter was conceptualised by the candidate and Prof. Simpfendorfer. The data were collected by Global FinPrint Project. The data was cleaned, organised, and analysed by the candidate. The chapter was written by the candidate, which was reviewed and edited by Prof. Simpfendorfer, Dr Chin, Dr White, and Dr Hutchinson.

3. Like a drop in the ocean: Global survey reveals low abundance of rare and threatened shark-like rays on coral reefs.

3.1 Introduction

Coral reefs are marine biodiversity hotspots that provide millions of people with ecosystems services including food provisions and livelihood opportunities (Cinner et al., 2016). Yet, these productive and diverse ecosystems are under threat from anthropogenic stressors such as overfishing, pollution, habitat destruction, and climate change, which reduces the capacity of reefs to provide ecosystem services (Woodhead et al., 2019; Eddy et al., 2021). In the tropics and subtropics, coastal chondrichthyans (shark, ray and chimera) are also highly exposed to these anthropogenic stresses in the environment, with overfishing being the primary threat, followed by loss and degradation of habitat, climate change, and pollution (Dulvy et al., 2021). Many populations are in rapid decline as a result of chronic overfishing either from targeted and incidental catch (Dulvy et al., 2021). Chondrichthyans typically have low biological productivity (slow growth, late maturity, few offspring, and long generational times), which limits their ability to recover from population declines (Cortés, 2000; Fowler, Reed & Dipper, 2002). Conservation of threatened coastal elasmobranchs (sharks and rays) is an increasing priority on a global scale (Dulvy et al., 2014a; Kyne et al., 2020; Dulvy et al., 2021). As the rate of decline of many species accelerates, it is important to understand what factors shape their distribution and abundance patterns in order to implement effective conservation and management strategies.

Studies of coastal elasmobranch abundance and distribution have traditionally relied on fishing or capture of individuals, through fishery-dependent (e.g. commercial fisheries) and/or fishery-independent research (e.g. scientific surveys with capture of animals using gillnets and longlines) (Simpfendorfer et al., 2011). The capture and release of the animal for these studies can be stressful or lethal for the animal (Marshall et al., 2012; Bouyoucos et al., 2017; Whitney et al., 2021) and, given the increasing threatened status for many elasmobranchs, could add to the pressure’s species face (Gallagher et al., 2014). An alternative non-invasive method is to use video survey techniques like Baited Remote Underwater Video Surveys (BRUVS). BRUVS provide a standardised, non-extractive, method of surveying marine fauna and ecosystems to understand spatial distribution and abundance of species (Whitmarsh, Fairweather & Huveneers, 2016). The application of BRUVS provides opportunities to sample more efficiently across geographically wide areas with deployment of multiple units simultaneously and across wider depth ranges (Cappo, Speare & De'ath, 2004; Currey-Randall et al., 2020). As BRUVS are non-extractive, it is possible to record information on threatened and rare species without removing individuals from the population (Cappo et al., 2002), and as well as conduct surveys in fragile and protected habitats such as coral reefs (Dorman, Harvey & Newman, 2012), seagrass meadows (Whitmarsh et al., 2014), surf zones (Borland et al., 2017) and temperate rocky reefs (Williams et al., 2019). Numerous studies have focused on the distribution and abundance of sharks across large spatial scales in order to document species-specific habitat associations on coral reefs, and as well as quantify the effects and efficiency of marine protected areas (MPAs) (Espinoza et al., 2014; MacNeil et al., 2020; Jabado et al., 2021). Yet there are many other under studied taxa on coral reefs, such as shark-like rays that have considerable knowledge gaps regarding their population abundance and distribution, for which BRUVS may provide useful information.

The order Rhinopristiformes is one of the most threatened orders of marine fish (Kyne et al., 2020; Dulvy et al., 2021), and comprises seven families, i.e. giant guitarfish (Glaucostegidae), fanrays (Platyrhinidae), sawfish (Pristidae), wedgefish (Rhinidae), guitarfish (Rhinobatidae), banjo rays (Trygonorrhinidae) and panrays (Zanobatidae) (Last et al., 2016). These medium to large - sized, benthic, shark-like rays have a similar posterior morphology to sharks and are distributed in temperate to tropical waters on the insular and continental shelves (< 250 m depth) throughout the Indo-Pacific and Atlantic oceans (Last et al., 2016). They are strongly associated with soft-bottom habitats such as sand, mud or gravel, and some species are often observed in areas adjacent to coral reefs (White et al., 2013b). Wedgefish and giant guitarfish species are experiencing significant declines throughout their entire ranges (Kyne et al., 2020). All species of giant guitarfish and sawfishes, nine of 10 species (90%) of wedgefishes, and 23 of 34 species (67.7%) of guitarfish are listed as threatened on the International Union for Conservation of Nature’s (IUCN) Red List of Threatened Species (Kyne et al., 2020; Dulvy et al., 2021). They are very susceptible to overexploitation as a result of their large body size (Dulvy et al., 2014a), high catchability by multiple gear types (**Chapter Four**), and use of inshore habitat in some of the world's most heavily fished coastal regions (Stobutzki et al., 2002; White & Kyne, 2010; Jabado & Spaet, 2017). Shark-like ray distributions are highly variable, from broadly distributed species (e.g. *R. australiae* and *G. typus*) to those with very restricted and/or fragmented spatial distributions, e.g. clown wedgefish *Rhynchobatus cooki* known only from Java, Indonesia (Kyne, Rigby & Last, 2019), false shark ray *Rhynchorhina mauritaniensis* from a single location in the Eastern Central Atlantic (Banc d'Arguin of Mauritania) (Seret & Naylor, 2016). The majority of the global distribution information for these rays originates from fisheries dependent data (Kyne et al., 2020). There has been one published study that focused on the distribution of shark-like rays using BRUVS which took place on the Great Barrier Reef off eastern Australia (White et al., 2013b), while BRUVS studies in the Arabian Gulf have encountered shark-like rays on videos (Jabado et al., 2018; Jabado et al., 2021). These studies observed a very low abundance of shark-like rays and currently there is little information on the global distribution of shark-like rays on corals reef.

Quantifying the distribution patterns and species-specific habitat associations for shark-like rays will be key to assessing fishing exposure, and as well as implementing effective management responses (Jabado et al., 2021). The Global FinPrint Project (https://globalfinprint.org) conducted BRUVS deployments in tropical coral reef ecosystems world-wide to explore the relative abundance of coral reef associated elasmobranchs. The present study used data from this worldwide survey across 58 nations to investigate abundance patterns of shark-like rays on coral reefs. Specifically, the aims of this research were to identify global distribution, species diversity and abundance of these rare and threatened shark-like rays (Families Rhinidae, Glaucostegidae and Rhinobatidae) on coral reefs and investigate the environmental variables that could define and predict the distribution of these rays.

3.2 Material and Methods

3.2.1 Surveys

Field surveys were conducted from July 2015 to June 2018, according to the standard methodology as described below (MacNeil et al., 2020). The data analysed here also included a small number of BRUVS (16% of all sets) that were deployed in surveys prior to 2015. The surveys included 371 reefs from 58 nations in the Indian Ocean, Indo-Pacific Ocean, Central

Pacific Ocean, and Western Atlantic Ocean. “Nations” refers to the major jurisdiction, encompassing country, territory or large-scale division sampled, e.g., continental Australia was divided into the Pacific and Indian Ocean coasts, as well as Indian Ocean territories including the Cocos Keeling and Christmas Island, due to the distinctive jurisdictions of the country and biogeographic influences (Last & White, 2011; MacNeil et al., 2020). Each sampling site (referred to as a “reef”) consisted of a continuous reef area, approximately 10 km in length. The reefs selected for sampling were based on access through a local collaborator and the operational range of the vessel used for sampling. The survey aimed to include at least one reef per site with management levels in place, with reef protection status classified as whether the reefs were closed to fishing (closed), open to restricted fishing (restricted), or openly fished (open) (MacNeil et al., 2020). Human gravity (total gravity) was calculated per BRUVS deployment as the intensity of human impact based on population size, distance to the closest market, and reef accessibility (the nearest population, equal to the population of the nearest human settlement divided by the squared travel time between the reef site and the settlement) (Cinner et al., 2018).

Single camera and stereo (two camera) BRUVS were used. The BRUVS were comprised of a video camera (primarily GoPro HERO2, GoPro HERO3, GoPro Hero4 Silver, [https://www.gopro.com], or Sony CX7, and prior to July 2015 Sony Legria HF10, and Sony Handycam DCR-HC52 were used [www.sony.com]). The camera was fixed in a waterproof housing on a metal (stainless steel, aluminium, or rebar) frame, and set with a wide-angle view (~ 170° in air, 1920 x 1080 video format, and 30 frames per second). A bait arm was attached to the frame and extended 100 – 180 cm (mean 141.67 ± 11.41 cm SE) from the camera and within the frame of view. A rope and float were tied to the top of the frame to facilitate deployment, relocation and retrieval (**Figure 3.1**) (Harvey et al., 2018). The bait arm held a bait container (mesh bag, perforated PVC canister or wire cage, depending on location) with approximately 1 kg of bait. The type of bait (crushed, chopped, or whole) and fish species used, varied between sampling locations, and depended on the local availability of the bait. The preferred bait were oily fish species, such as pilchards (*Sardinella* spp.) or tuna (Tribe Thunnini) (Walsh, Barrett & Hill, 2017). Nearly all reefs were sampled with replicate BRUVS sets over a single period of < 10 days (mean BRUVS per reef = 39; range = 9 – 71) (MacNeil et al., 2020).

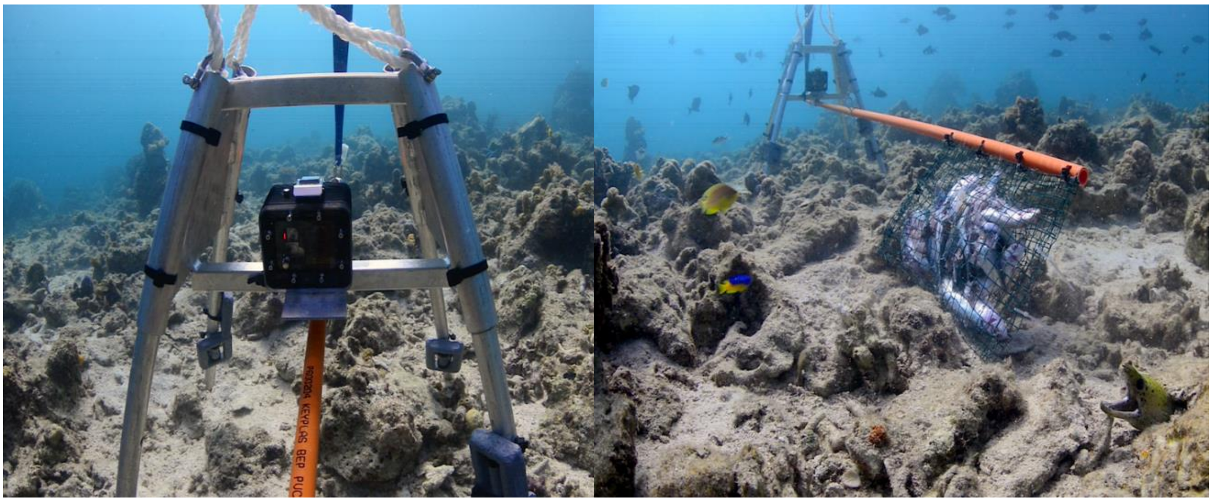


Figure 3.1. Baited remote underwater video survey (BRUVS) station deployed on seabed in reef habitat. BRUVS station comprises of a GoPro camera within an underwater housing on weighted metal frame, with a bait pole attached to attract predators, a current meter, and rope attached to surface float. Credit: Global FinPrint Project (https://globalfinprint.org/).

BRUVS sets were deployed during daylight hours (07:00 – 17:00) at depths between 1.5 to 50 m. A range of habitats were surveyed including fore reefs, reef flat, reef crest, reef slope, and lagoons. Up to six BRUVS were deployed at one time, and sets were retrieved after at least 70 minutes to ensure a standard 60 minutes of data collection from the time of settlement on the benthos. The depth of BRUVS deployment and sea surface temperature was recorded. Adjacent BRUVS were separated by a minimum distance of 500 m to reduce the overlap of bait plumes and the likelihood of elasmobranchs moving between replicates. The locations of replicate deployment were haphazard rather than random due to a lack of prior knowledge of the locations surveyed (i.e. bathymetry) (Goetze et al., 2018). In a single day, up to 24 BRUVS were deployed through multiple tidal states; fresh bait was used for each deployment.

3.2.2 Video analysis

Videos were viewed and scored in the FinPrint Annotator (v.1.1.44.0) or EventMeasure (www.seagis.com) to record the species present and the number of individuals observed (**Figure 3.2**). Each video was viewed by two independent, trained annotators. In the case of stereo BRUVS, only the left video was read for consistency. The maximum number of individuals observed of a species in a single frame of the video (*MaxN*) was recorded for each elasmobranch species in each video and was used as a measure of relative abundance (Sherman et al., 2018). Annotators marked the start and end time of the analysis, and the time of arrival for every elasmobranch that entered the screen throughout the video.

Three measurements were obtained from the BRUVS for this study, the *MaxN*, ‘soak time’, and ‘time to first sighting’. The ‘soak time’ was calculated as the minutes elapsed between the start time (when the BRUVS landed on the benthos) and the end time (the instant at which the BRUVS was hauled off the seabed). For standardisation among BRUVS, in instances where bait and/or bait bag was entirely removed from a BRUVS, the time at which this occurred was classified as the end time and marked completion of the soak. The ‘time to first sighting’ was the time elapsed between the start of the sampling period and the first record of a particular species in the field of view. A senior reviewer validated species identification and compared the two reads for each video in FinPrint Annotator. If there were differences between the two reads (e.g. different species identified and/or varying *MaxN*), then the video was read a third time by the senior reviewer, to determine which of the first two reads was correct to generate the final annotation.

Broad-scale habitat and vertical relief were analysed from a still reference image taken from the beginning of each BRUVS deployment video, using the online software BenthoBox (www.benthobox.com) from the Australian Institute of Marine Science. A 5 x 4 grid was overlaid on each image, and habitat and relief was classified within each rectangle using the Collaborative and Automated Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Althaus et al., 2015). Habitat was selected from the broad habitat types: hard corals, soft corals, sponges, zoanthids, macroalgae, turf algae, halimeda, seagrasses, unconsolidated (sand/rubble), and consolidated (rocky bottom). Visibility was estimated from the image in two-meter categories of 0-2m, 2-4m, 4-6m, 6-8m, 8-10m and 10+m. The relief, which describes the height and rugosity structure of the substrate, was estimated on a scale from 0-5: 0 being flat habitat with sandy and/or rubble substrate, with few features and < 45 slope, to 5 referring exceptional structural complexity, with numerous crevices and caves and/or vertical wall and ~ 90 slope. When a rectangle within the grid had 100% water and no substrate visible in the frame (i.e. set on the benthos and looking onto open water), it was classified as open water.

Figure 3.2. Photos of wedgefish species encountered on coral reefs on baited remote underwater video surveys (BRUVS) from the Global FinPrint Project: (**A**) bowmouth guitarfish *Rhina ancylostoma*; (**B**) bottlenose wedgefish *Rhynchobatus australiae*; (**C**) whitespotted wedgefish *Rhynchobatus djiddensis*; (**D**) smoothnose wedgefish *Rhynchobatus laevis*. Identifying spot patterns between the three *Rhynchobatus* species are circled in black.

3.2.3 Study Species

Species from the three shark-like ray families (Rhinidae, Glaucostegidae and Rhinobatidae) were identified using the information in Last et al. (2016). The key colour pattern difference used to differentiate species of wedgefishes was the pattern of white spots around the dark pectoral spot present (**Figure 3.2**). For example, in *R. australiae*, there is a line of three white spots located adjacent to the black pectoral spot, which can be faded or absent on some individuals (Giles et al., 2016; Last et al., 2016) (**Figure 3.2 B**). A global distribution range map was generated for each species in R using the 'ggplot2' package. The distribution raster files were downloaded from publicly available data published on the IUCN Red List (https://www.iucnredlist.org/).

3.2.4 Statistical analysis

To determine the environmental factors driving species distribution generalised linear models (GLM) with a zero inflated Poisson distribution were run using the glmmTMB R package (Brooks et al., 2017). Models included the explanatory variables of depth, mean substrate relief, reef protection status, and median total gravity per reef (Cinner et al., 2018; MacNeil et al., 2020). A zero inflated model was used due to the high percentage of zeros in the dataset. The reefs were assumed to be closed to fishing pressure when surveys were being conducted at the particular reef (MacNeil et al., 2008b). The reefs were nested with nations and the nations were nested within regions. Due to the small number of species sightings, the GLM used observations grouped by Family and was only able to run for the Family Rhinidae as there was insufficient data to run the GLM for the other two families. Residual diagnostics (test for normality, uniformity, outliers and dispersion) were conducted using the DHARMa package (Hartig, 2020). Models were generated using the backward stepwise selection method using an Analysis of Deviance Table (Type II Wald Chi-square tests) to determine which non-significant covariates should be removed from the model. This process was repeated until only significant covariates were left. Model performances were ranked using the Aikake Information Criterion (AIC) weights and the model with the lowest weight was considered the most appropriate (Burnham & Anderson, 2003).

3.3 Results

A total of 18,442 BRUVS were deployed globally across 371 reefs in 58 nations throughout the four regions. Shark-like rays were observed on 159 reefs in 22 nations (**Figure 3.3**). A total of 12 species were observed on the BRUVS globally, from six genera and three families (**Table 3.1**). Shark-like rays were very rare on the videos and only present on 0.006 to 0.369% of videos, with the highest *MaxN* = 1 for any one species (**Table 3.1**; **Figure 3.3**).

The average soak time for all deployments was 77.58 minutes (min) ± 23.2 min standard deviation (S.D.; *n* = 11,356; range: 2.32 – 272.65 min). Average time of first sighting for all shark-like ray species sighted was 31.58 ± 15:12 min (*n* =103, range = 1.48 – 59.35min). The average soak time of BRUVS deployments that sighted shark-like rays was 72.65 ± 10.88 min S.D. (*n* = 30; range = 50.87 – 98.23 min), which was not significantly different to the

Table 3.1. Summary of shark-like ray species (Order Rhinopristiformes) recorded on baited remote underwater video stations (BRUVS) on 371 tropical coral reefs in the Indian Ocean, Pacific Ocean, and Western Atlantic Ocean. The species conservation (status) of the species based on the International Union of Conservation of Nature's (IUCN) Red List of Threatened Species: CR Critically Endangered, EN Endangered, and VU Vulnerable; N – Number of BRUVS with a species, percentage (%) of videos with positive sightings (number of videos with species / total number of BRUVS deployed * 100), metrics of *MaxN* (maximum number of individuals of a species detected on a single frame) was used to describe the relative abundance: mean of the positive sets ± standard deviation (S.D.) and sum of *MaxN*; the minimum (min.), maximum (max.) and mean ± S.D. deployment depth (m) on positive sightings; minimum (min.), maximum (max.) and mean ± S.D. substrate relief on positive sightings; and minimum (min.), maximum (max.) and mean ± S.D. time of first arrival (min, minutes) on positive sightings.

Family	**Species**	**IUCN status**	***n***	**% positive sighting**	**Mean *MaxN* ± S.D.**	**Sum of *MaxN***	**Depth (m)**			**Mean substrate relief**		**Time of arrival (min)**		
							Min.	**Max.**	**Mean ± S.D.**	**Min. ± S.D.**	**Max. ± S.D.**	**Min.**	**Max.**	**Mean ± S.D.**
Rhinidae	*Rhina ancylostoma*	CR	4	0.026	1.0 ± 0	4	5.9	36.6	15.1 ± 14.4	0.00 ± 0.00	2.64 ± 0.5	26.05	51.48	39.12 ± 11.52
	Rhynchobatus australiae	CR	56	0.37	1.0 ± 0	56	1.5	40.0	14.8 ± 9.20	0.00 ± 0.00	4.63 ± 0.5	03.47	59.35	32.55 ± 15.15
	Rhynchobatus djiddensis	CR	11	0.073	1.0 ± 0	11	11.9	41.6	25.4 ± 10.5	0.00 ± 0.00	4.00 ± 0.0	04.37	56.80	27.80 ± 15.55
	Rhynchobatus laevis	CR	1	0.007	1.0 ± 0	1	16.8	--	--	1.00 ± 0.00	--	30.15	--	--
	Rhynchobatus spp.	--	19	0.13	1.0 ± 0	19	4.0	38.0	26.7 ± 8.06	0.00 ± 0.00	4.18 ± 0.8	01.80	56.45	30.48 ± 15.67
Rhinobatidae	*Acroteriobatus annulatus*	VU	1	0.007	1.0 ± 0	1	31.3	--	--	2.00 ± 0.00	--	32.28	--	--
	Acroteriobatus leucospilus	EN	1	0.007	1.0 ± 0	1	7.1	--	--	0.20 ± 0.42	--	22.35	--	--
	Pseudobatos lentiginosus	VU	1	0.007	1.0 ± 0	1	6.83	--	--	1.1 ± 0.32	--	23.73	--	--
	Pseudobatos percellens	EN	2	0.013	1.0 ± 0	2	15.1	20.42	17.7 ± 3.76	0.8 ± 0.42	1.00 ± 0.00	44.82	57.25	51.03 ± 08.78
	Rhinobatos hynnicephalus	EN	1	0.007	1.0 ± 0	1	16.6	--	--	0.00 ± 0.00	--	10.33	--	--
Glaucostegidae	*Glaucostegus typus*	CR	4	0.033	1.0 ± 0	4	2.8	32.5	13.1 ± 10.5	1.00 ± 0.00	3.00 ± 0.00	18.82	50.88	33.03 ± 14.88
	Total		101			101								

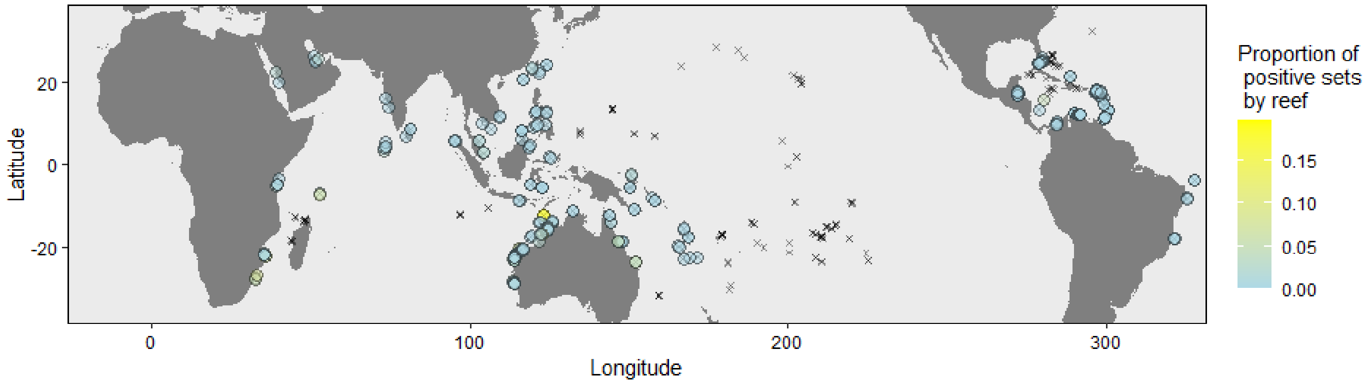


Figure 3.3. Combined proportion of positive sets for shark-like ray species (Family Rhinidae, Glaucostegidae and Rhinobatidae) sighted on 159 corals reefs from 22 nations on baited remote underwater video surveys (BRUVS), from July 2009 – 2017 (coloured circles on a scale from 0.00 in blue to 0.15 in yellow). The grey crosses indicate sets sampled where no shark-like rays were sighted.

overall soak time across all deployments (Two-sample T-Test with unequal variance, *df* = 30, *t value* = -2.46, *p* = 0.02).

Shark-like ray species were present on BRUVS at depths of 1.5 - 41.6 m and most frequently encountered at depths between 10 – 20 m (**Table 3.1**; **Figure 3.4**). Benthic habitats of the reefs where shark-like rays were most sighted had low mean relief (**Figure 3.5**) and were primarily dominated by unconsolidated benthic substrate (**Figure 3.2**).

Shark-like rays were primarily sighted at reefs that were either closed (*n* = 35) or had restricted fishing (*n* = 66), with only two observations of shark-like rays on reefs open to fishing. The primary type of fishing restriction used for elasmobranchs were size limits, bag limits, species retention restrictions, gear limitations, area restrictions and entrant restrictions i.e. licensing. Shark-like rays were sighted more frequently in nations with fisheries management in place for elasmobranchs, compared to nations with little to no management through reef protection. There was not sufficient positive sightings data of shark-like rays for the nation of sampling, total gravity, and protection status to influence the likelihood of observing shark-like rays on BRUVS and investigate these trends further.

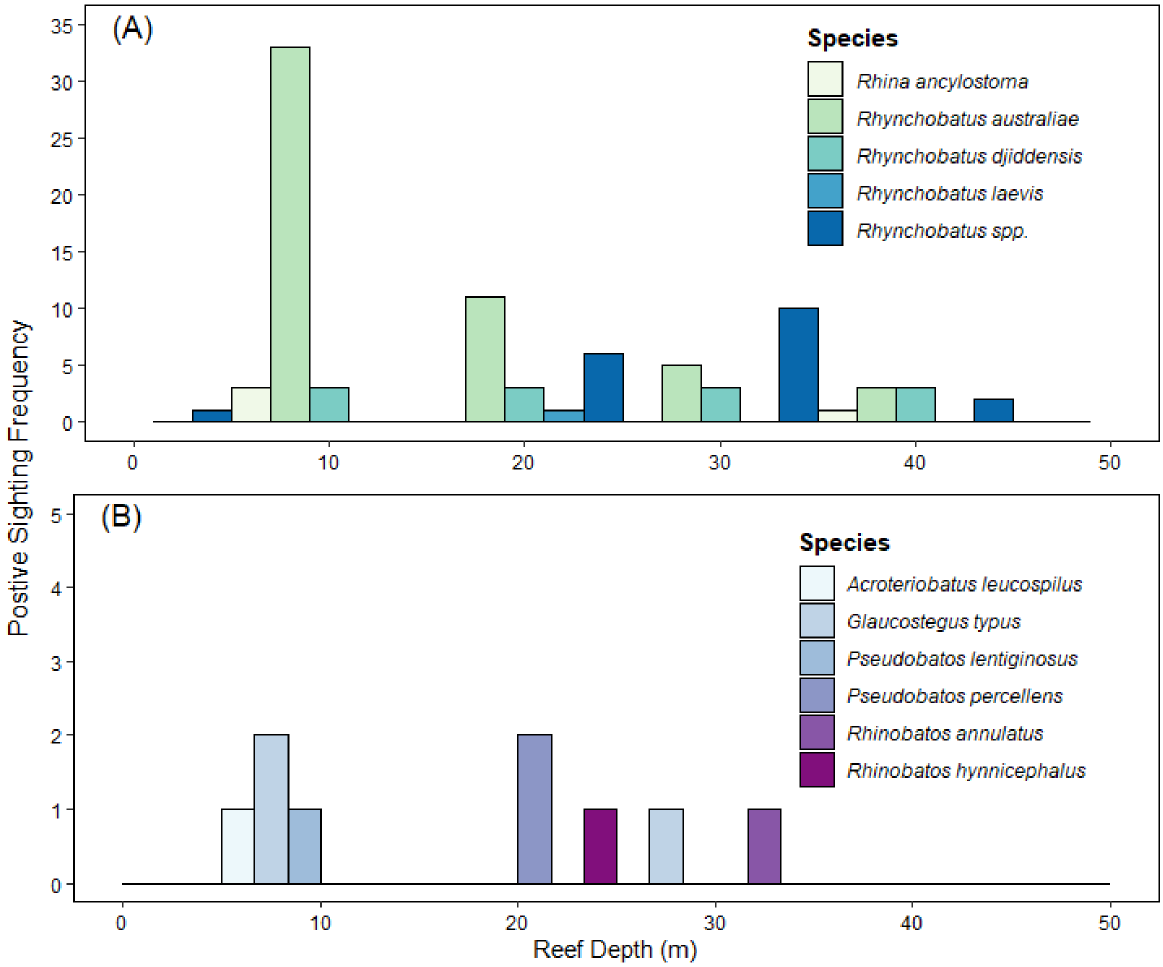


Figure 3.4. Frequency for the positive sightings by sampled reef depth (m, metre) for (**A**) for bowmouth guitarfish *Rhina ancylostoma*, bottlenose wedgefish *Rhynchobatus australiae*, whitespotted wedgefish *Rhynchobatus djiddensis*, smoothnose wedgefish *Rhynchobatus laevis*, and unidentified wedgefish *Rhynchobatus* spp; and (**B**) for lesser guitarfish *Acroteriobatus annulatus*, greyspot guitarfish *Acroteriobatus leucospilus*, freckled guitarfish *Pseudobatos lentiginosus*, Chola guitarfish *Pseudobatos percellens*, ringed guitarfish *Rhinobatos hynnicephalus*, and giant guitarfish *Glaucostegus typus* sighted on baited remote underwater video surveys (BRUVS) on tropical coral reefs surveyed by the Global FinPrint Project.

3.3.1 Species presence

Wedgefishes (Family Rhinidae)

Species from the Family Rhinidae were the most frequently sighted on the BRUVS, with 92 positive sightings. However, 19 sightings could not be identified to species level and were recorded as *Rhynchobatus* spp. (**Table 3.1**). Wedgefish species were observed at depths of 1.5 – 41.6 m, with an average depth of 18.7 ± 10.7 m S.D. The average time of arrival for rhinid species was 28.93 ± 17.17 min S.D. (n = 92; range = 1.8 – 59.35 min).

Rhina ancylostoma was sighted at three locations: once in the Maldives, once in Indonesia, and twice in Western Australia (**Table 3.1**; **Figure 3.6 A**). *Rhynchobatus australiae* was the most frequently sighted and widely distributed of the shark-like rays, with a total 56 sightings: three in Malaysia, 36 in Western Australia, three in Seychelles, two in Mozambique, one in Fiji, and two in the northern, three in central and six in southern Great Barrier Reef (**Table 3.1**; **Figure 3.6 B**). *Rhynchobatus djiddensis* was observed at two locations in the Indian Ocean, on four BRUVS at Ponta do Ouro reef in Southern Mozambique, and on seven BRUVS at iSimangaliso Wetland Park, St Lucia, South Africa (**Table 3.1**; **Figure 3.6 C**). *Rhynchobatus laevis* was sighted once in Qatar (**Table 3.1**; **Figure 3.6 D**).

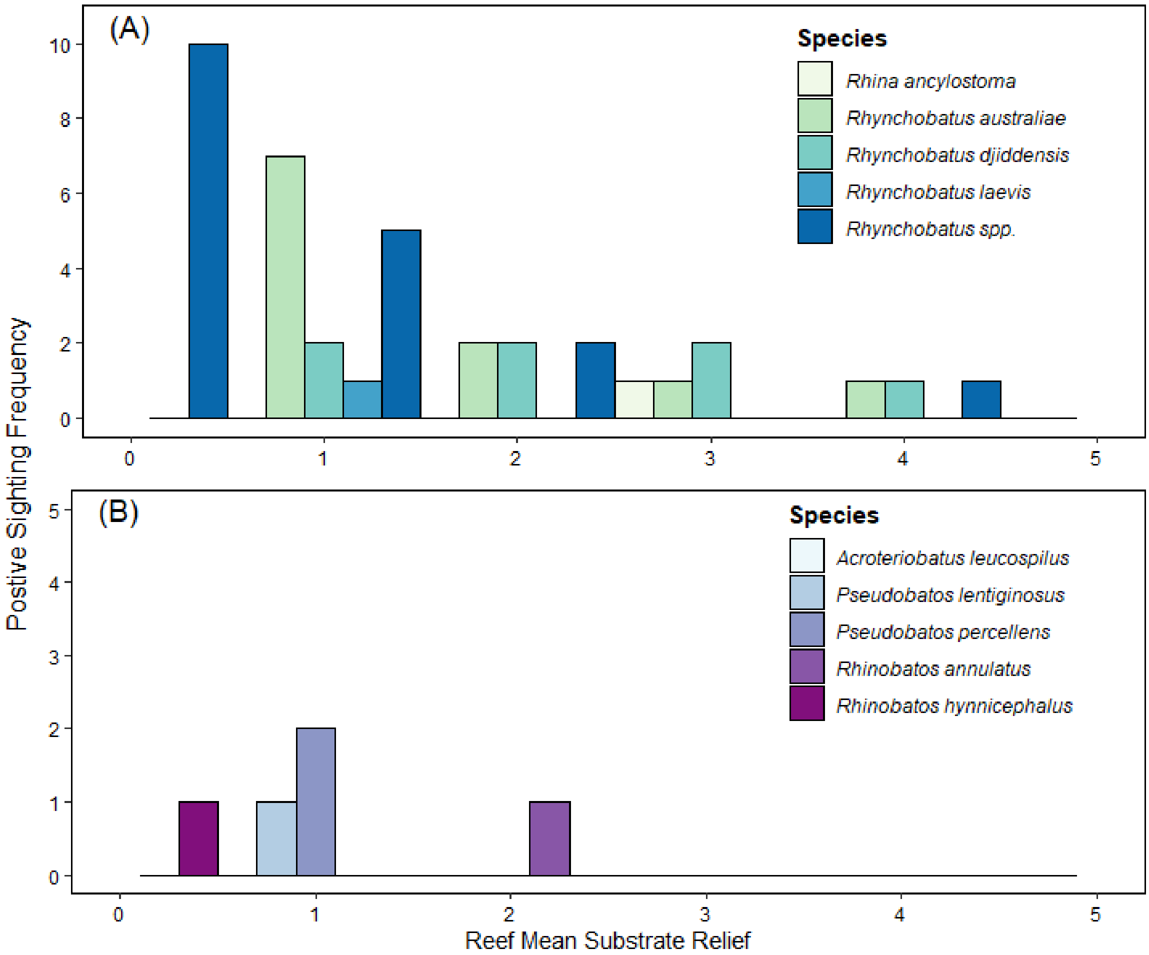


Figure 3.5. Frequency for the positive sightings by average substrate relief on sampled reefs for (**A**) for bowmouth guitarfish *Rhina ancylostoma,* bottlenose wedgefish *Rhynchobatus australiae,* whitespotted wedgefish *Rhynchobatus djiddensis,* smoothnose wedgefish *Rhynchobatus laevis,* and unidentified wedgefish *Rhynchobatus* spp; and (**B**) for lesser guitarfish *Acroteriobatus annulatus*, greyspot guitarfish *Acroteriobatus leucospilus,* freckled guitarfish *Pseudobatos lentiginosus,* Chola guitarfish *Pseudobatos percellens,* ringed guitarfish *Rhinobatos hynnicephalus,* and giant guitarfish *Glaucostegus typus* sighted on baited remote underwater video surveys (BRUVS) on tropical coral reefs surveyed by the Global FinPrint Project.

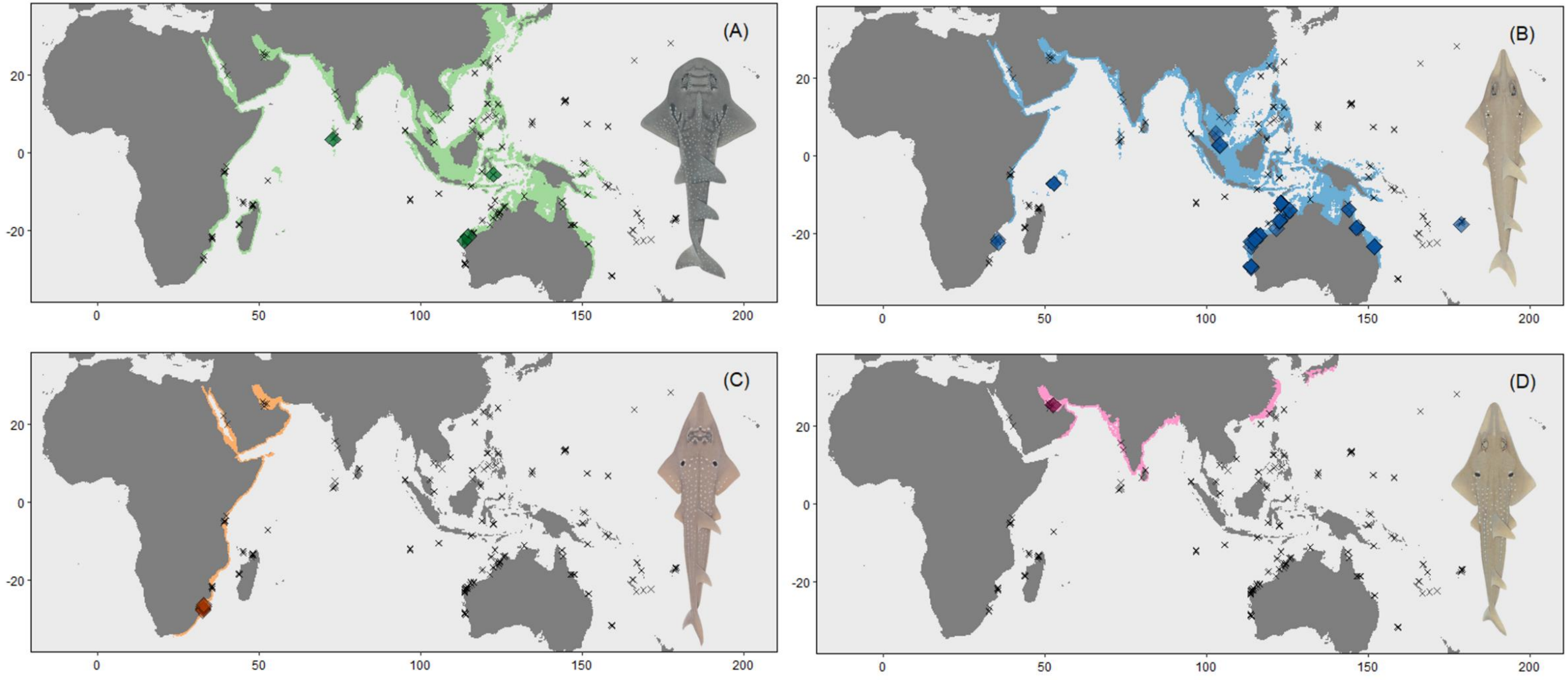


Figure 3.6. The global distribution of sightings of four species of wedgefish (Family Rhinidae) on coral reefs using baited remote underwater video surveys (BRUVS) from the Global FinPrint Project, (**A**) bowmouth guitarfish *Rhina ancylostoma* with the known distribution in green, (**B**) bottlenose wedgefish *Rhynchobatus australiae* with the known distribution in blue, (**C**) whitespotted wedgefish *Rhynchobatus djiddensis* with the known distribution in orange, (**D**) smoothnose wedgefish *Rhynchobatus laevis* with the known distribution in pink. Black crosses (X) denote sites surveyed with no sightings of the species, and coloured diamonds represent the respective species sightings on the BRUVS. Species illustrations were from Last et al. (2016).

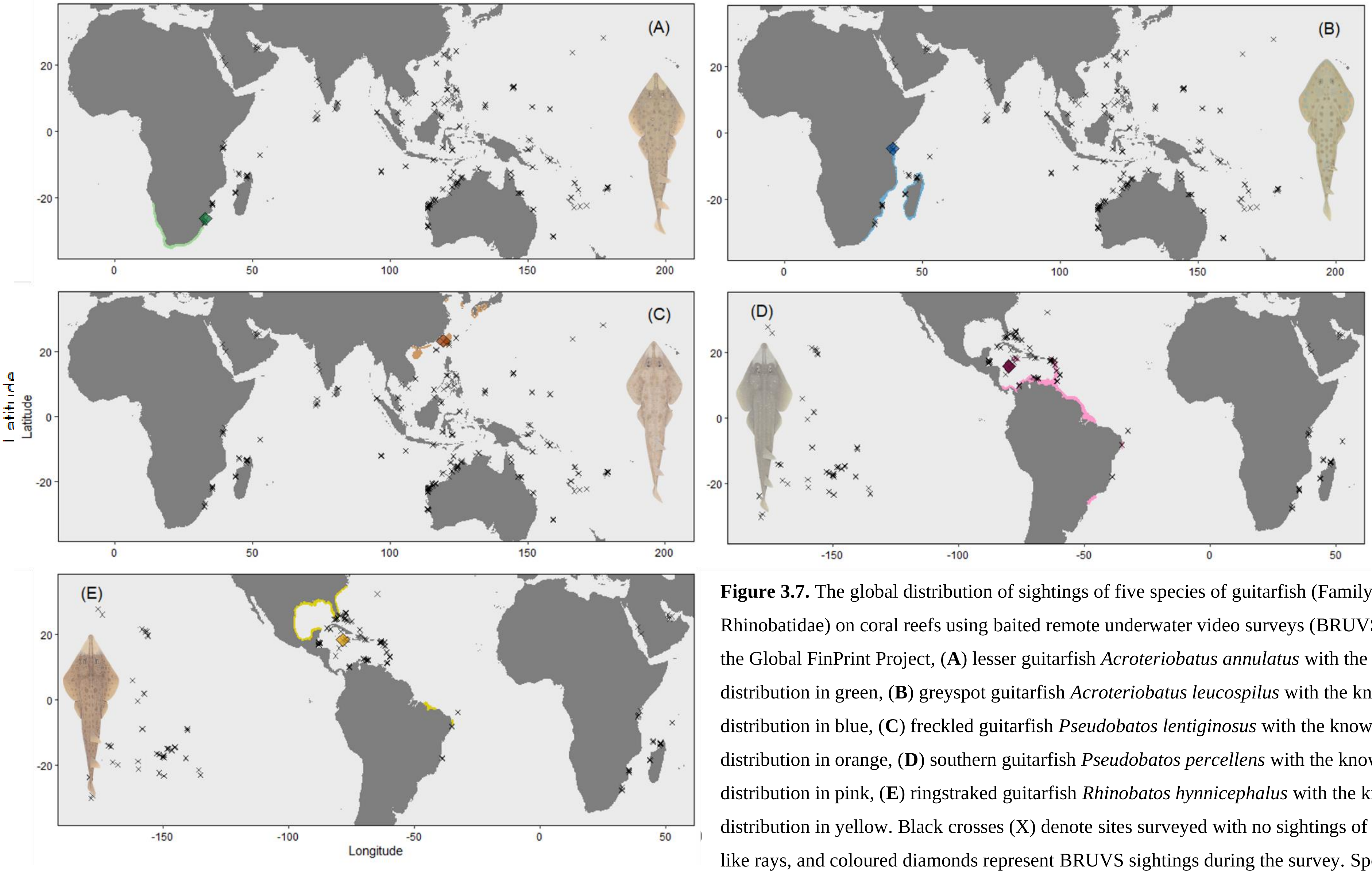


Figure 3.7. The global distribution of sightings of five species of guitarfish (Family Rhinobatidae) on coral reefs using baited remote underwater video surveys (BRUVS) from the Global FinPrint Project, (**A**) lesser guitarfish *Acroteriobatus annulatus* with the known distribution in green, (**B**) greyspot guitarfish *Acroteriobatus leucospilus* with the known distribution in blue, (**C**) freckled guitarfish *Pseudobatos lentiginosus* with the known distribution in orange, (**D**) southern guitarfish *Pseudobatos percellens* with the known distribution in pink, (**E**) ringstraked guitarfish *Rhinobatos hynnicephalus* with the known distribution in yellow. Black crosses (X) denote sites surveyed with no sightings of shark-like rays, and coloured diamonds represent BRUVS sightings during the survey. Species illustrations were from Last et al. (2016).

Guitarfishes (Family Rhinobatidae)

Species from the Family Rhinobatidae were sighted on six occasions, with a total of five species sighted globally (**Table 3.1**). The average depth guitarfish species were observed in was 16.2 ± 9.14 m S.D. (range = 6.83 – 31.3 m; **Figure 3.4 B**). The average time of arrival was 31.78 ± 16.93 min S.D. ($n = 6$; range = 10.33 – 57.25 min). They were observed only on low relief substates with a mean relief range of 0 – 2 (**Figure 3.5 B**).

Acroteriobatus annulatus was sighted once in Ponta do Ouro in Southern Mozambique (**Table 3.1**; **Figure 3.7 A**). *Acroteriobatus leucospilus* was observed once off Kisite-Mpunguti Marine National Park, southern Kenya (**Table 3.1**; **Figure 3.7 B**).
Pseudobatos lentiginosus was sighted once in Negril, Jamaica in 2016 (**Table 3.1**; **Figure 3.7 C**). *Pseudobatos percellens* was observed on two occasions in Cayo Serranilla, Colombia (**Table 3.1**; **Figure 3.7 D**). *Rhinobatos hynnicephalus* was sighted once in North Penghu, Taiwan (**Table 3.1**; **Figure 3.7 E**).

Giant guitarfishes (Family Glaucostegidae)

One species of giant guitarfish was observed globally: *G. typus*. This ray was only sighted in Western Australia on four BRUVS, at two reefs in Ningaloo and one reef in the Pilbara (**Figure 3.8**). The average time of arrival was 33.03 ± 14.88 min S.D. ($n = 4$; range = 18.82 – 50.88 min). *Glaucostegus typus* was observed at depths of 2.8 – 32.5 m (**Table 3.1**; **Figure 3.4 B**). They were observed only on low relief substates (**Table 3.1**) on macroalgae and unconsolidated substrate with sponges.

3.3.2 Factors affecting the presence of shark-like rays

Generalised linear models demonstrated that the environmental variables of deployment depth and mean substrate relief were the most significant factors in predicting sightings for wedgefish species (**Table 3.2**; **Figure 3.9**). While the sampling nation, reef protection status (whether the reef was open, restricted, or closed to fishing) and median total gravity did not affect the probability of encountering wedgefish species on coral reefs (**Table 3.2**).

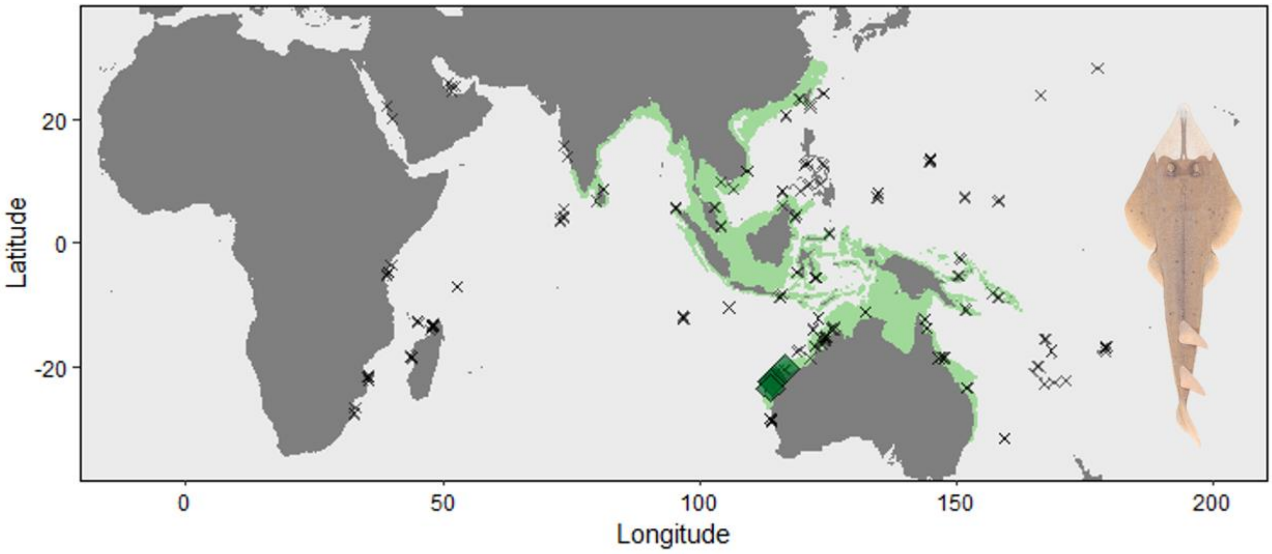


Figure 3.8. The global distribution of sightings of giant guitarfish *Glaucostegus typus* (Family Glaucostegidae), on coral reefs using baited remote underwater video surveys (BRUVS) from the Global FinPrint Project. Black x denotes sites surveyed but without the species sighted, the light green area is the known distribution of *G. typus* and the dark green diamonds are the sightings of *G. typus* on the BRUVS. Species illustrations were from Last et al. (2016).

Table 3.2. Summary of the Analysis of Deviance Table (Type II Wald Chi-square tests) for the zero inflated negative Poisson Generalised Linear Models (GLM) for predicting the *MaxN* of wedgefish (Family Rhinidae) on tropical coral reefs using baited remote underwater video surveys (BRUVS), and the Akaike's Information Criterion corrected for small sample sizes (AICc) performance of the three models used. The most appropriate model is highlighted in bold; where *df* is the degrees of freedom; Δ, the difference between AICc values; w, AICc weights. * refers to p value less than 0.05.

Model	**Variables**	**Chi-Square**	***df***	***p* value**	**AICc**	**Δ**	**w**
Model 1	Nations	38.7	21	0.0175*	478.5	9.22	0.01
(Full Model)	Protection Status	5.69	2	0.0579			
	Depth (scaled)	10.6	1	0.0011*			
	Mean Relief (scaled)	9.06	1	0.0026*			
	Median Total Gravity (scaled)	0.015	1	0.9039			
Model 2	Nations	31.9	21	0.0591	478.2	8.93	0.01
	Depth (scaled)	5.99	1	0.0143*			
	Mean Relief (scaled)	11.3	1	0.0008*			
Model 3	**Depth (scaled)**	**4.16**	**1**	**0.0415***	**469.3**	**0.00**	**0.98**
	Mean Relief (scaled)	**8.58**	**1**	**0.0034***			

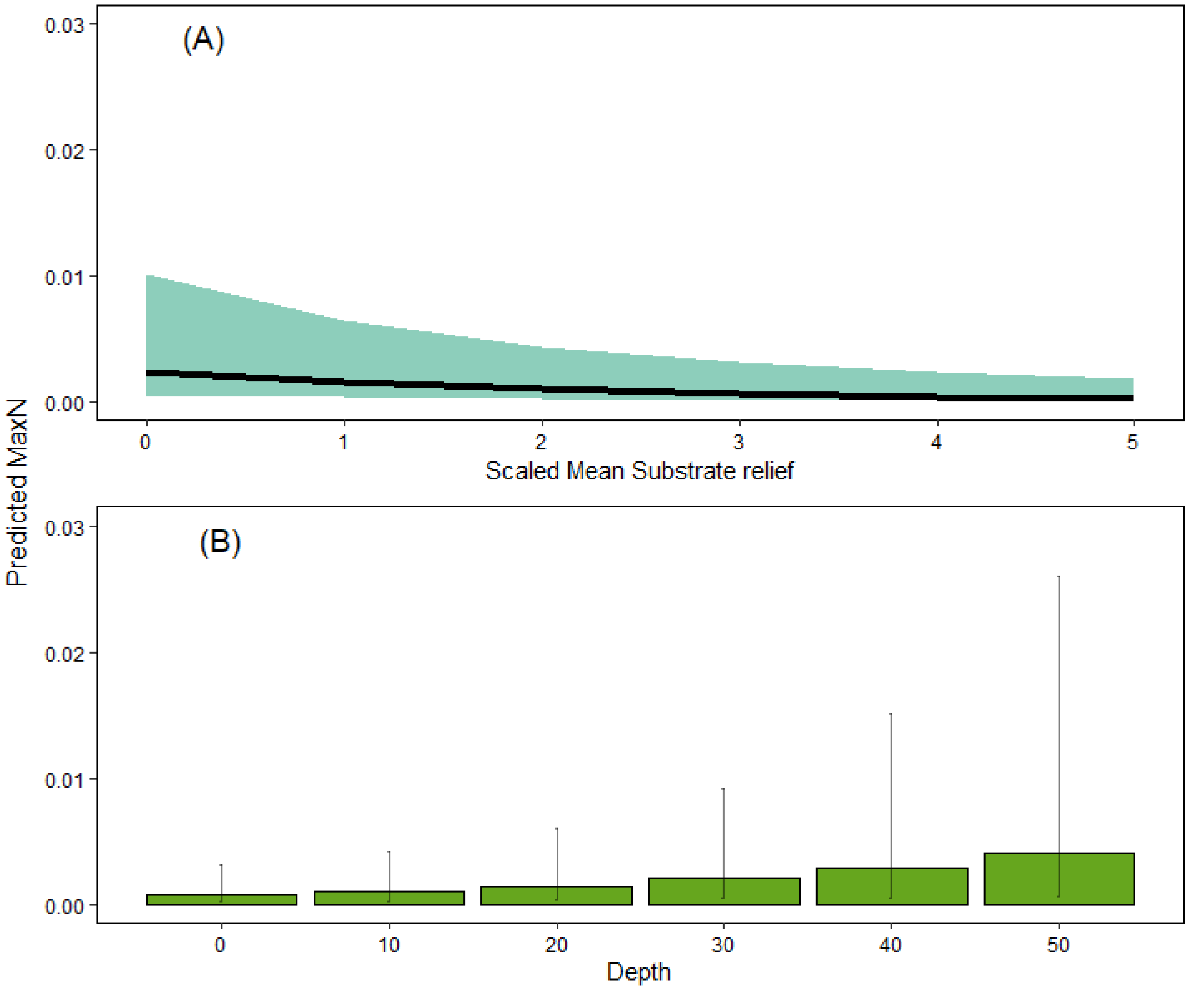


Figure 3.9. The predicted maximum number of individuals observed of a species in a single frame of the video *MaxN* as the measure for relative abundance for (**A**) scaled mean substrate relief and (**B**) depth for wedgefish species (Family Rhinidae) on coral reefs using data from baited remote underwater video surveys (BRUVS) from the Global FinPrint Project.

3.4 Discussion

Understanding species habitat associations over large spatial scales is crucial in order to reveal complex ecological processes within and across ecosystems, and to identify important areas for elasmobranch conservation (Espinoza et al., 2014; Jabado et al., 2018). Wedgefish, giant guitarfish, and guitarfish species occur in coastal and reef environments (White et al., 2013a; Last et al., 2016; Gaskins et al., 2020), yet shark-like ray species were rarely sighted on coral reef by BRUVS, despite the extensive global sampling efforts of this study. Wedgefishes are distributed primarily in the Indo-West Pacific Ocean from western Indian Ocean to Japan to eastern Australia (Last et al., 2016), and were the most observed Family of shark-like rays on coral reefs from BRUVS. The study confirms an eastward range extension of *R. australiae* to Ovalau, Fiji, as previously reported fisheries in Fiji by Glaus et al. (2015). Thaman et al. (2010) reported that *R. djiddensis* were uncommon in waters around Bellona Island in the southern Solomon Sea. This is likely a misidentification of *R. australiae* or *R. palpebratus*, which are distributed throughout Papua New Guinea and northern Australia, while *R. djiddensis* is restricted to Indian Ocean (Last et al., 2016). There have been sightings of wedgefish in New Caledonia from the citizen science platform iNaturalit (iNaturalist, 2021). Our observation of *R. australiae* off Fiji is the currently the furthest east known sighting of wedgefish in the Pacific Ocean, which may indicate that there are unknown populations of this species in the Pacific islands and/or a result of large-scale migrations. Research into the migration and population structure of wedgefishes will be required to understand the movements of wedgefishes between the Indo-Pacific and Central Pacific Oceans.

Globally, wedgefish species have been encountered across broad habitats, including coral reefs, seagrass meadows, and low relief areas e.g. sandy-muddy benthos (White et al., 2013a; Last et al., 2016). On coral reefs, the best predictors of occurrence for wedgefishes are low substrate relief and depth, especially greater than 20 m. Wedgefishes have been observed across a broader depth range than recorded in this study, supporting the GLM results that identifies depth as one of the environmental variables that has a significant effect on the occurrence of wedgefishes. This indicates that wedgefishes have a depth preference that could reduce their interactions with BRUVS on shallow coral reefs. For example, *Rhynchobatus* spp. have been observed on BRUVS at a depth of 87.5 m off eastern Australia (White et al., 2013a), juvenile *R. australiae* and *R. palpebratus* have been caught in trawls at depths of 100 m off northern Australia (D’Alberto unpublished data), and *R. ancylostoma* has been documented in open ocean between the African continent and the Seychelles in 4000 m depth (Forget & Muir, 2021). As a result of their large size and shark-like morphology, wedgefish species have strong swimming ability that would allow them to move between multiple habitats, including between coral reefs and across deep waters (Vaudo & Heithaus, 2011; White et al., 2013b; Forget & Muir, 2021). This use of pelagic environment may potentially contribute to the connectivity of some wedgefish species (e.g. *R. ancylostoma* and *R. australiae*) at large spatial scales and use of different depths (Forget & Muir, 2021). In addition, as shark-like rays are considered to have generalist diet (White, Platell & Potter, 2004; Basusta et al., 2007; Vaudo & Heithaus, 2011; do Carmo et al., 2015; Purushottama et al., 2020), different species may be taking advantage of common prey resources at various depths.

Unidentified wedgefishes were the second most observed shark-like ray on the global survey. Visual identification of wedgefishes is currently based on the shape of the snout with a need for a dorsal view of the head, and spot patterns on the pectoral fin and marking between the orbitals (Last et al., 2016). This complication in species differentiation is an ongoing issue that confounds efforts to quantify species-specific information on abundance and distribution. Misidentification of shark-like rays can be further compounded by ambiguity over the ranges of these species, as some species are rarer in landings and possibly have more of a restricted and/or fragmented spatial distribution than is currently reported. New species are also being described for shark-like rays, e.g. Papuan guitarfish *Rhinobatos manai* from New Ireland, Papua New Guinea (White, Last & Naylor, 2016), Austin's guitarfish *Rhinobatos austini* from the south western Indian Ocean (Ebert & Gon, 2017), Rangong guitarfish *Rhinobatos ranongensis* from the Andaman Sea and Bay of Bengal (Last, Seret & Naylor, 2019), spadenose guitarfish *Pseudobatos buthi* in the Gulf of California (Rutledge, 2019), Japanese wedgefish *Rhynchobatus mononoke* in southern Japan (Koeda et al., 2021), and Bangladeshi guitarfish *Glaucostegus younholeei* from the northern Bay of Bengal, Bangladesh (Habib & Islam, 2021). The newly described species were not observed on the BRUVS during this study and there is little information on their distribution and biology. Taxonomic confusion among species can compromise the sustainability of fisheries (both harvest and discards) and conservation related research (Garcia-Vazquez et al., 2012; Clark-Shen et al., 2021). The very rare observations of shark-like rays in this study likely reflect not only their occasional use of coral reef habitats, but also their declines in populations in tropical environments form extensive fishing pressures.

Only one species from Family Glaucostegidae was sighted on the global BRUVs survey on coral reefs. *Glaucostegus typus,* a widespread species in the Indo–West Pacific, including eastern Australia (Last et al., 2016; Kyne et al., 2019a), was the only glaucostegid species observed and was only observed on BRUVS in Western Australia. This is despite the deployment of BRUVS in the current study on coral reefs that have a documented population of *G. typus*, such as Orpheus Island and Heron Island on the Great Barrier Reef (White et al., 2013a; Kanno et al., 2019). *Glaucostegus typus* have been documented to display philopatric behaviour, where they have returned annually to use the same regions in Cleveland Bay, Townsville Australia, signifying site fidelity (White et al., 2013b). The lack of sightings of *G. typus* on coral reefs that were surveyed during this study, may also demonstrate the limited use of these habitats in addition to low population sizes, suggesting they are more likely to be found in habitats adjacent to coral reefs, including coastal lagoons, mangroves, seagrass beds, intertidal flats, and other soft bottom habitats. Newborn and juvenile *G. typus* are typically found in very shallow reef flats (10 – 16 cm depth), sandflats, intertidal habitats, and mangroves which are used as nursery areas, and may move into other habitats and/or deeper waters as they mature (White et al., 2013b; Cerutti-Pereyra et al., 2014; Freeman, 2019; Kanno et al., 2019; Gaskins et al., 2020). The nursery areas are thought to enhance feeding opportunities and provide protection from predation (Cerutti-Pereyra et al., 2014). These ecosystems are often shallow and have highly turbid waters (Farrugia, Espinoza & Lowe, 2011), which reduces the likelihood of observing animals on BRUVS that are limited to minimum deployment depth of 1 m (Whitmarsh, Fairweather & Huveneers, 2016). Along with wedgefishes, giant guitarfishes are facing extremely high risk of extinction due intense fishing pressure across their distribution (Kyne et al., 2020). The lack of sightings of this species is also likely to be demonstrative of low population sizes in various sampled locations where there is known intense fishing pressure, including across SE Asia.

Guitarfishes are considered inshore species, found in bays and estuaries (Borrell et al., 2011; Farrugia, Espinoza & Lowe, 2011; Jabado et al., 2018), and currently few to no records of species of this Family using coral reef habitats. Species of guitarfish were extremely rare on the BRUVS in the current study, with *A. annulatus*, *A. leucospilus*, *P. lentiginosus*, and *R. hynnicephalus* only observed on single occasions in reef ecosystems. Guitarfish species prey upon on coastal benthic organisms, mainly crustaceans like prawns, followed by demersal fishes and cephalopods, and this prey preference may help explain preferences for low relief, inshore habitats, and the limited use of coral reefs. Similar to the wedgefish, guitarfish species have a broader depth range than what was surveyed in the current study. For example, *Acroteriobatus variegatus* have been recorded at depths of 10 – 355 m (Nair & Lal Mohan, 1973; Last et al., 2016) and caught as bycatch in tuna hook and line fishery at depths of 110 – 130 m (Wilson et al., 2020). The very low number of observations in the deployment of shallow coral reef BRUVS of guitarfishes is unsurprising, as coral reefs are unlikely to be the preferred habitat. Given their habitat preference of inshore coastal waters with muddy substrates (Vaudo & Heithaus, 2009; Farrugia, Espinoza & Lowe, 2011; Pierce, Scott-Holland & Bennett, 2011; White et al., 2013a) and use of a broader depth, the focus on sampling efforts on coral reef habitats, including sandy reef lagoons could contribute to the lack of sightings for guitarfish and giant guitarfish species.

The spatial ecology (i.e. habitat use and preference, and movement) of elasmobranchs are typically driven by a suite of abiotic (e.g. water temperature, salinity, tide state, and dissolved oxygen) and biotic factors (e.g. prey availability, predator avoidance) (Schlaff, Heupel & Simpfendorfer, 2014). These factors can have varying levels of influence on species, sex, and ontogenetic stages (Schlaff, Heupel & Simpfendorfer, 2014). There have been only a few reports of the dietary preference for wedgefish species, with the main prey consumed for rhinid species being teleost fish, followed by crustaceans (e.g. prawns and crabs), cephalopods and polychaetes (Darracott, 1977; Devadoss, 1984; Raje, 2006; Purushottama et al., 2020). Ontogenetic shifts in diet have been documented for shark-like rays, with immature individuals having a more specialised diet (mainly crustaceans), and mature individuals moving to be more generalised (Blanco-Parra et al., 2012; Espinoza et al., 2013; Valenzuela-Quiñonez et al., 2018). Large wedgefish, giant guitarfish and sawfishes have been documented to consume stingrays (urobatid, myliobatid or dasyatid rays) based on embedded spines in jaws, demonstrating a different source of prey (Dean et al., 2017). Stable isotope analysis from samples in India have suggested that *R. ancylostoma* may have a more pelagic/epipelagic diet than previously thought (Borrell et al., 2011), which would open the possibility of feeding on larger, more mobile prey, and likely driving their habitat preference and distribution. The use of different depths and habitats in tropical environments is likely to reduce interspecific competition between shark-like ray families, likely reflecting diet preferences and prey availability, and therefore resource partitioning between the families.

Distinct seasonal differences have been documented to occur for elasmobranch abundances and habitat use in various ecosystems, including corals reefs (Sherman et al., 2020b). Temperature-mediated seasonal movements have been documented for shark-like rays (Gohar & Mazhar, 1964; Márquez-Farías, 2007; Farrugia, Espinoza & Lowe, 2011; Lessa & Vooren, 2016; Daly et al., 2021; Jordaan et al., 2021), which may be driven by suite of factors including, prey availability, predator avoidance, behavioural thermoregulation, and reproduction (Heupel, 2007; Schlaff, Heupel & Simpfendorfer, 2014). Off the east coast of

South Africa, *R. djiddensis* have been recorded to be more abundant in the inshore coastal areas (e.g. surf zones) of South Africa during warmer months (October – May), and migrate to warmer waters north during winter, likely for mating and reproduction (Daly et al., 2021; Jordaan et al., 2021). However, in the current study, BRUVS were deployed on coral reefs of central reef complex of iSimangaliso Wetland Park off St Lucia, South Africa in November, and this may have contributed to the low number of sightings of this species within its known distributions on coral reefs (**Appendix 3.1**). Similar trends have been observed for *G. typus* in Western Australia, where this species was more abundant in nearshore areas sand flats during the warmer months (September – May) and abundances decreased in colder months (June – August) (Vaudo & Heithaus, 2009). On the Great Barrier Reef, wedgefishes (species complex of *R. australiae* and *R. palpebratus*) were found to have a higher probability of being encountering on BRUVS during cooler months (June – August) (White et al., 2013a). Temperature and/or seasonal movement patterns could have contributed to the low number of sightings of shark-like ray species on the surveyed coral reefs in their known distribution (e.g. *R. djiddensis, R. australiae/R. palpebratus,* and *G. typus*).

Baited remote underwater video stations are an effective method for observing elasmobranchs (Santana-Garcon et al., 2014; Beer, 2015; De Vos et al., 2015; MacNeil et al., 2020; Sherman et al., 2020b), including shark-like rays (White et al., 2013a; Jabado et al., 2018). These non-extractive systems have access to greater depths and habitats for surveying diversity and abundance (De Vos et al., 2015). Yet, detection heterogeneity can occur in these underwater surveys and introduce bias into the data (MacNeil et al., 2008a). These survey biases can be a result of factors that are intrinsic to the species being observed i.e. physical traits, behaviour and life history, as well as the survey methodology itself (Colton & Swearer, 2010). The average soak time of this study, which is the amount of time a BRUVS is deployed on the seabed, was within the optimal range for sighting rare coral reef associated species (Currey-Randall et al., 2020). The metric for the relative abundance of organisms from BRUVS, *MaxN*, is considered a conservative estimate for abundance (Whitmarsh, Fairweather & Huveneers, 2016). The low *MaxN* for shark-like rays suggests that these rays are typically not found in large groups and/or at very high local abundances on coral reefs. It must be acknowledged that *MaxN* on single point of view BRUVS are likely an underestimation on abundance (Sherman et al., 2018) as more individual organisms may be present around the BRUVS but because they do not appear in the field of view at the same time, they remain unaccounted for. There has been minimal research into temporal movement and behaviour for shark-like rays, including habitat use and movements at night. Juvenile *G. typus* have been observed to be more commonly observed at around dusk and evenings (Cerutti-Pereyra et al., 2014; Gaskins et al., 2020). Any crepuscular or nocturnal behaviour was unable to be documented in this study as all BRUVS deployments were conducted during daylight hours, as well as any temporal (daily, seasonal, yearly) variations in shark-like ray movements and abundances. Temporal variations in movements may help explain the lack of sightings on coral reefs for shark-like rays during this current study. Research on the broad spatial and temporal scales will be required to help refine our understanding of variability in shark-like ray abundance and distributions, and the abiotic and biotic factors driving these patterns.

Overexploitation can be driven through high economic value of wildlife products, dense coastal populations in low-income countries, and weak and/or poor resourced governance (Sadovy de Mitcheson et al., 2018). The use of the inshore, shallow waters by shark-like rays results in these species being particularly vulnerable to coastal fishing activities (e.g. gillnets and trawls), as well as habitat modification and degradation (Jabado, 2018). Many species of shark-like rays are distributed over vast geographical ranges, crossing political borders, and interact with diverse fisheries in national and international waters. There are international trade restrictions in place for wedgefish and giant guitarfishes, as they are listed on the CITES Appendix II (CITES, 2019b). Sightings of wedgefish and giant guitarfish were observed to be higher around nations with national fisheries management in place for elasmobranchs through closure or restricted fishing of elasmobranchs (e.g. continental Australia, and South Africa), compared to other nations with no to little national management for elasmobranchs (e.g., Taiwan, Malaysia, and Indonesia). For example, in Australia, there is little fishing pressure for wedgefish and giant guitarfish and there are management controls in place in relation to commercial and recreational retention limits of this species, and use of bycatch reduction devices in trawl fisheries (Brewer et al., 2006). Australian waters represents a lifeboat for some species, including *R. australiae, R. palpebratus,* and *G. typus* (Kyne et al., 2020). The low number of sightings in Australian waters is likely due to the sampling methodology and habitat preference of shark-like rays, instead of indicating population declines. While wedgefish appear to have a limited use of coral reefs, the comparative lack of sightings of wedgefish and giant guitarfish on the BRUVS in SE Asia likely reflects the population declines have that been documented in this region (Kyne et al., 2020; D'Alberto et al., 2021). Despite being the most commonly landed wedgefish species in SE Asia (Giles et al., 2016), *R. australiae* was only observed on the BRUVS in Malaysia. A similar trend was observed for reef associated sharks using the same global dataset, where fishing protections were associated with substantially higher relative abundance of reef sharks, and depletions were strongly associated with socio-economic conditions (e.g. proximity and size of nearest market, poor governance and density of human populations) (MacNeil et al., 2020). There were vast differences in governance and fishing pressure between the countries sampled in this study, with differing levels of fishing effort and various gear types. With shark-like rays primarily sighted on reefs with some form of fisheries management, where they were classed as restricted (through gear type, species, or size/bag limits) or closed (spatially closed marine protected areas, MPA) to elasmobranch fishing, this suggests that management of fishing pressure and related factors (including fishing gear and effort) on coral reefs will also benefit shark-like ray populations.

Given the dire conservation status of these families there is a strong case for national protections, including species protection, by-catch mitigation, and harvest strategies. Spatial management is one tool that can be utilised to reduce fishing mortality and allow for population recovery of threatened species though protecting critical ecosystems and habitats (e.g. nurseries and feeding grounds) and reducing fishing mortality (Norse, 2010; Davidson & Dulvy, 2017; MacKeracher, Diedrich & Simpfendorfer, 2019). Large scale MPAs have been demonstrated to benefit reef associated elasmobranchs and other mobile species, if they are properly enforced from illegal fishing activities (Jacoby et al., 2020), and cover sufficient habitats and movement patterns of the species (e.g. over 10km for site-attached species and over 50km long for mobile species)(White et al., 2017a; Carlisle et al., 2019; Dwyer et al., 2020; Gallagher et al., 2021). Research on the spatial ecology of shark-like rays to identify critical areas (e.g. nursery or mating areas), the seasonality of their use, as well as the vulnerability of these habitats to localised anthropogenic impacts, is urgently required to allow quantifying the vulnerability of these species to overexploitation (Simpfendorfer et al., 2011; White et al., 2014; Yates et al., 2012), and to determine if and how MPAs will be beneficial to these threatened species.

3.5 Conclusion

This chapter is the first known study to examine the global abundance and distribution of wedgefishes, giant guitarfishes and guitarfishes on coral reefs using BRUVs. While the Global FinPrint Project survey itself was not designed to specifically sample shark-like rays and their preferred habitat (sandy substrates and coastal habitats), some shark-like rays were still observed and provided evidence of the extent of their use of coral reef habitats. The rare sightings of these threatened species on this extensive global survey likely reflects the global pressures on their population declines in coral reef environments, and in addition a function of the limited sampling in the preferred habitats for shark-like rays. Future studies should ensure that surveys include a wide range of depths from the shallows to depths of 100m to explore the depth preference of shark-like rays and focus on surveying low substrate relief areas. Additional research on spatial ecology and movement, potential sex/ habitat segregation for wedgefish will be a valuable contribution to our understanding of species distribution.

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3.6 Appendices

Appendix 3.1 Summary of the year and month of observation on baited remote underwater video survey (BRUVS) conducted by the Global FinPrint Project (https://globalfinprint.org/).by species and location, including site and region. The count refers to the total number of sightings per species per month for each site. The maximum number of individuals observed of a species in a single frame of the video (*MaxN*) for every species sighted was one.

Year	Month	Family	Species	Count	Site	Location	Region
2010	October	Rhinidae	*Rhynchobatus australiae*	1	Pilbara	Australia-Indian Ocean	Indian Ocean
2011	April	Rhinidae	*Rhynchobatus australiae*	4	Pilbara	Australia-Indian Ocean	Indian Ocean
2013	May	Rhinidae	*Rhynchobatus australiae*	1	Houtman Abrolhos	Australia-Indian Ocean	Indian Ocean
	September	Rhinidae	*Rhynchobatus australiae*	1	Kimberley	Australia-Indian Ocean	Indian Ocean
2014	May	Rhinidae	*Rhina ancylostoma*	1	Pilbara	Australia-Indian Ocean	Indian Ocean
			Rhynchobatus australiae	3	Pilbara	Australia-Indian Ocean	Indian Ocean
2014	October	Rhinidae	*Rhina ancylostoma*	1	Ningaloo	Australia-Indian Ocean	Indian Ocean
			Rhynchobatus australiae	4	Montebello Islands	Australia-Indian Ocean	Indian Ocean
			Rhynchobatus australiae	2	Ningaloo	Australia-Indian Ocean	Indian Ocean
2015	May	Rhinidae	*Rhynchobatus australiae*	3	Houtman Abrolhos	Australia-Indian Ocean	Indian Ocean
	August	Rhinidae	*Rhynchobatus australiae*	1	Kimberley	Australia-Indian Ocean	Indian Ocean
			Rhynchobatus australiae	1	Ningaloo	Australia-Indian Ocean	Indian Ocean
		Glaucostegidae	*Glaucostegus typus*	2	Ningaloo	Australia-Indian Ocean	Indian Ocean
	September	Rhinidae	*Rhynchobatus australiae*	4	Pilbara	Australia-Indian Ocean	Indian Ocean
		Glaucostegidae	*Glaucostegus typus*	2	Pilbara	Australia-Indian Ocean	Indian Ocean
	November	Rhinidae	*Rhynchobatus australiae*	2	Northern GBR 1	Australia-Pacific	Pacific

2016	January	Rhinidae	*Rhynchobatus australiae*	6	Ashmore	Australia-Indian Ocean	Indian Ocean
		Rhinidae	*Rhynchobatus spp.*	10	Ashmore	Australia-Indian Ocean	Indian Ocean
	February	Rhinidae	*Rhynchobatus australiae*	2	Alphonse	Seychelles	Indian Ocean
		Rhinidae	*Rhynchobatus spp.*	2	Alphonse	Seychelles	Indian Ocean
	March	Rhinidae	*Rhynchobatus australiae*	1	Ovalau	Fiji	Pacific
	April	Rhinidae	*Rhynchobatus australiae*	1	Alphonse	Seychelles	Indian Ocean
		Rhinobatidae	*Pseudobatos lentiginosus*	1	Jamaica	Jamaica	Western Atlantic
	May	Rhinidae	*Rhina ancylostoma*	1	Ari	Maldives	Indian Ocean
	July	Rhinidae	*Rhynchobatus australiae*	1	Central GBR	Australia-Pacific	Pacific
	August	Rhinidae	*Rhynchobatus australiae*	4	Kimberley	Australia-Indian Ocean	Indian Ocean
		Rhinidae	*Rhynchobatus australiae*	2	Central Mozambique	Mozambique	Indian Ocean
		Rhinidae	*Rhynchobatus spp.*	2	Central Mozambique	Mozambique	Indian Ocean
	September	Rhinidae	*Rhyncobatus laevis*	1	Eastern Qatar	Qatar	Indian Ocean
	October	Rhinidae	*Rhynchobatus australiae*	1	Kimberley	Australia-Indian Ocean	Indian Ocean
	November	Rhinidae	*Rhynchobatus djiddensis*	7	St Lucia	South Africa	Indian Ocean
2017	February	Rhinidae	*Rhynchobatus australiae*	2	Tioman	Malaysia	Coral Triangle
		Rhinidae	*Rhynchobatus spp.*	1	Tioman	Malaysia	Coral Triangle
	March	Rhinidae	*Rhynchobatus australiae*	1	Kuala Terrenganu	Malaysia	Coral Triangle
		Rhinidae	*Rhynchobatus spp.*	1	Northern Tanzania	Tanzania	Indian Ocean
	April	Rhinobatidae	*Rhinobatus hynnicephalus*	1	Penghu	Taiwan	Coral Triangle
	June	Rhinidae	*Rhynchobatus djiddensis*	2	Southern Mozambique	South Africa	Indian Ocean
	July	Rhinidae	*Rhina ancylostoma*	1	Bau Bau	Indonesia	Coral Triangle
		Rhinidae	*Rhynchobatus djiddensis*	3	Southern Mozambique	South Africa	Indian Ocean
		Rhinobatidae	*Acroteriobatus annulatus*	1	Southern Mozambique	South Africa	Indian Ocean
	September	Rhinidae	*Rhynchobatus spp.*	1	Kavieng	Papua New Guinea	Coral Triangle

		Rhinobatidae	*Pseudobatos percellens*	2	Cayo Serranilla	Colombia	Western Atlantic
	December	Rhinobatidae	*Acroteriobatus leucospilus*	1	Southern Kenya	Kenya	Indian Ocean
		Rhinidae	*Rhynchobatus spp.*	1	North Saudi	Saudi Arabia	Indian Ocean
2018	April	Rhinidae	*Rhynchobatus australiae*	2	Orpheus Island	Australia-Pacific	Pacific
	June	Rhinidae	*Rhynchobatus australiae*	5	Southern GBR	Australia-Pacific	Pacific
		Rhinidae	*Rhynchobatus spp.*	1	Southern GBR	Australia-Pacific	Pacific

Chapter Four

Manuscript associated with this chapter:

D'Alberto, B.M., White, W.T., Chin, A., Dharmadi, Simpfendorfer, C.A. (2021) Untangling the Indonesian tangle net fishery: describing a data-poor fishery targeting large, threatened rays (Order Batoidea). *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1-19. https://doi.org/10.1002/aqc.3754

Nature and extent to contribution of co-authors to the manuscript:

The chapter was conceptualised by the candidate, Prof. Simpfendorfer and Dr White. The data were collected by Dr. White and Dharmadi. The data was cleaned, organised, and analysed by the candidate. The chapter was written by the candidate, which was reviewed and edited by Prof. Simpfendorfer, Dr White, Dr Chin, and Dharmadi.

I dedicate this paper and chapter to the memory of 'Pak' Dharmadi, a leader and pioneer in shark and rays research and management in Indonesia.

4. Untangling the Indonesian tangle net fishery: describing a data-poor fishery targeting large, threatened rays (Superorder Batoidea).

4.1 Introduction

Rays (superorder Batoidea) are among the most threatened groups of chondrichthyans (sharks, rays, and chimaeras) (Dulvy et al., 2021; IUCN, 2021). Substantial declines in populations, catch rates and landings, as well as localized extinctions have been reported for several ray species (Moore, 2015). Declines in elasmobranch (shark and ray) populations are mainly the result of the rapid expansion of chondrichthyan catch in target and non-target fisheries (Clarke et al., 2006; Dulvy et al., 2021), and the globalisation of trade (Clarke, Milner-Gulland & Bjørndal, 2007; Lack & Sant, 2009). Recently, the global chondrichthyan catch has been increasingly dominated by rays (Dulvy et al., 2014a; Dulvy et al., 2021). This increase is likely the result of a number of causes, including improved catch reporting, declines in shark catches due to stronger national and international regulations, and global declines of shark populations (Dulvy et al., 2014a). Rays, like most chondrichthyans, have intrinsically low biological productivity, due to their slow growth rate, late maturity, long generation times, and low fecundity; and are therefore slow to recover from population declines (Fowler, Reed & Dipper, 2002). Due to their strong association with soft bottom habitats in shallow (< 100 m depth) tropical and temperate coastal waters, most ray species (excluding deep-sea skates) are exposed to high levels of intense and expanding fishing pressure (Last et al., 2016). Many ray species also play an important trophic role in soft sediment ecosystems as bioturbators (Kyne & Bennett, 2002a; White et al., 2013b; Flowers, Heithaus & Papastamatiou, 2020), and their coastal habitats are under threat from additional anthropogenic influences (Dulvy et al., 2016; Dulvy et al., 2021).

Wedgefish (Family Rhinidae, 11 species), and giant guitarfish (Family Glaucostegidae, six species), are large (~maximum size 300 cm total length, TL) benthic rays collectively referred to as shark-like rays (Last et al., 2016). They are found throughout the Pacific, Indian, and Atlantic-Mediterranean oceans in shallow, coastal waters (Last et al., 2016). Shark-like rays are mainly caught as bycatch in fishing gears such as trawl nets, pelagic and bottom set long lines, purse seine nets, and gillnets, and are typically retained as valuable by-products of opportunistic catch (Moore, 2017; Jabado, 2018). Shark-like ray fins are considered the highest grade in the international shark fin trade, which is likely the key driver for their retention in coastal fisheries (Keong, 1996; Wu, 2016; Hau et al., 2018). However, there are few documented targeted fisheries for these species (White & Dharmadi, 2007). Wedgefishes and giant guitarfishes are experiencing significant declines throughout their entire ranges (Kyne et al., 2020), and all but one species of wedgefish and giant guitarfish were classified as Critically Endangered on the IUCN Red List of Threatened Species in 2019 (Kyne et al., 2020). These species were listed under the CITES Appendix II in 2019 (CoP18), which aims to ensure that the international trade of products from wedgefish and giant guitarfish come from sustainable sources (CITES, 2019b).

Similar to the global decline of sawfishes and angel sharks (Dulvy et al., 2016; Lawson et al., 2020), depletion of wedgefish and giant guitarfish likely began many decades ago, driven by the incidental catch in fisheries and the high value of fins in the international trade (Keong, 1996; Clarke et al., 2006). Quantifying the onset and extent of decline of these data-limited species is difficult, due to depletions occurring before independent scientific monitoring, and poor fisheries and trade reporting (Dulvy et al., 2016; Lawson et al., 2020). This resulted in little species-specific data, and lack of conservation awareness (Dulvy et al., 2016; Lawson et al., 2020). Wedgefish and giant guitarfish have been inferred to have a higher-than-average population productivity compared to other chondrichthyans, and therefore can potentially recover from population declines more rapidly than other threatened species (**Chapter Six**). However, achieving this will require significant reductions in fishing mortality (**Chapter Six**). There is little information available on shark-like ray species’ historical and contemporary interactions with fisheries, which can hinder the development of management and conservation efforts.

Indonesia is the world’s largest contemporary elasmobranch fishing nation, accounting for ca. 13% of reported global elasmobranch catch (Blaber et al., 2009; Jaiteh, Loneragan & Warren, 2017). It is also the third largest exporter of shark fins in regards to quantity, with an average annual export of 1,235 tonnes, and the sixth largest in value, worth an average of US$10 million per year (Dent & Clarke, 2015). Elasmobranch meat is an important source of protein for communities in SE Asia (Ahmad et al., 2016), and a large volume of elasmobranch products, particularly stingrays, continue to be exported to regional markets such as

Singapore (Clark-Shen et al., 2021). In Indonesia, wedgefishes and guitarfishes are caught as bycatch in a variety of fisheries, but they are also specifically targeted in the tangle net fishery, with *R. australiae* the main target species. The fishery also lands stingrays and sharks as opportunistic catch (Keong, 1996; White & Dharmadi, 2007). This fishery uses large mesh (50 – 60 cm) bottom-set nylon gillnets, to capture large elasmobranchs by entanglement, on sandy or muddy substrates between 25 – 45 m depth (Amir, 1988). Fishing vessels in this fishery are typically refurbished 10 – 22 metre (30 – 40 tonnes) long wooden purse seine vessels (Amir, 1988). They have an approximate net load capacity of 15 tonnes, and are equipped with a diesel powered inboard engine and a small freezer to hold fins (Amir, 1988). In Indonesia, this fishery is referred to as "*jaring liongbun*" [= guitarfish gillnet] and/or "*jaring cucut*" [= shark gillnet]. The first records of this fishery are from Aru Island in the mid-1970s, from where the fishery rapidly expanded throughout Indonesian waters to Sumatra (Keong, 1996). It reached peak fishing capacity in 1987 with 500 active vessels and began operating at other ports, before declining to approximately 100 vessels in 1996 (Amir, 1988; Keong, 1996). Declines of *Rhynchobatus* spp. were reported to begin around 1992 according to local fishers that operate bottom set gillnets in the Aru-Arafura Sea (Jaiteh et al., 2016a). Dharmadi & Kasim (2010) reported that the number of tangle net vessels operating from Muara Angke decreased by half in a one-year period from 14 in 2008 to seven in 2009. The reductions in vessels operating in the tangle net fishery suggest that populations of the target species had declined and made the fishery economically unviable. The high value of wedgefish and giant guitarfish fins was a particularly strong driver for this fishery, with the fins worth approximately 1.5 times more than those from other species (Keong, 1996). More recently, high valued leather products from stingrays, which appear to be increasing in demand (Karthikeyan et al., 2009; Sahubawa, Pertiwiningrum & Rahmadian, 2018), have driven the retention of large stingrays. There is strong anecdotal evidence of declines of wedgefish and giant guitarfish in some areas of Indonesia as a result of this fishery (Amir, 1988; Keong, 1996). However, there are no catch and size composition data available for this fishery, and the fishery is poorly defined and little understood.

To achieve sustainable use of these species, managers and conservation practitioners need to understand their population status, risk exposure, and resilience to fishing pressure and other threats. This requires data on fisheries catch composition, changes in relative abundance, and their interactions with fisheries (Simpfendorfer et al., 2011; Jabado, 2018). The main aims of this chapter are to (1) examine the species, size, and sex composition of the landed catch of the Indonesian tangle net fishery at Muara Angke in 2001 – 2005 to provide an important historical context to document changes in abundance and species compositions over time, (2) and to examine the potential consequences of these trends for future fisheries management and species conservation. Information on the Indonesian tangle net fishery can be used to inform the basis for the development of local and international management plans and conservation action for threatened rays.

4.2 Materials and Methods

4.2.1 Muara Angke landing port surveys

This research presents an in-depth investigation of fisheries landings at one of the sites surveyed in 2001 – 2005 and reported on by White & Dharmadi (2007). Between April 2001 and December 2005, landed elasmobranch catches at the Muara Angke landing port (North Jakarta, Indonesia) (**Figure 4.1**) and the adjacent village (where post-landing processing of fish occurred) were recorded for the tangle net fishery. Landing port surveys at Maura Angke were conducted on 18 occasions, and for each visit the landing port was surveyed for 1 – 4 consecutive days, resulting in a total of 53 sampling days (**Appendix 4.1**).

Data on the nature of the products retained their use, value, and export destination were collected by fisheries officers from the Ministry of Marine Affairs and Fisheries (MMAF). The prices reported for these products have been converted to Indonesian Rupiah (IDR) in 2021 values to account for inflation (www.inflationtool.com; 1 IDR 2004 = 2.54 IDR 2021; 1 IDR 2005 = 2.38 IDR 2021), and to US Dollar (USD) prices using an online currency converter (www.xe.com/currencyconverter/; 1 USD = 13,957.10 IDR as of January 2021).

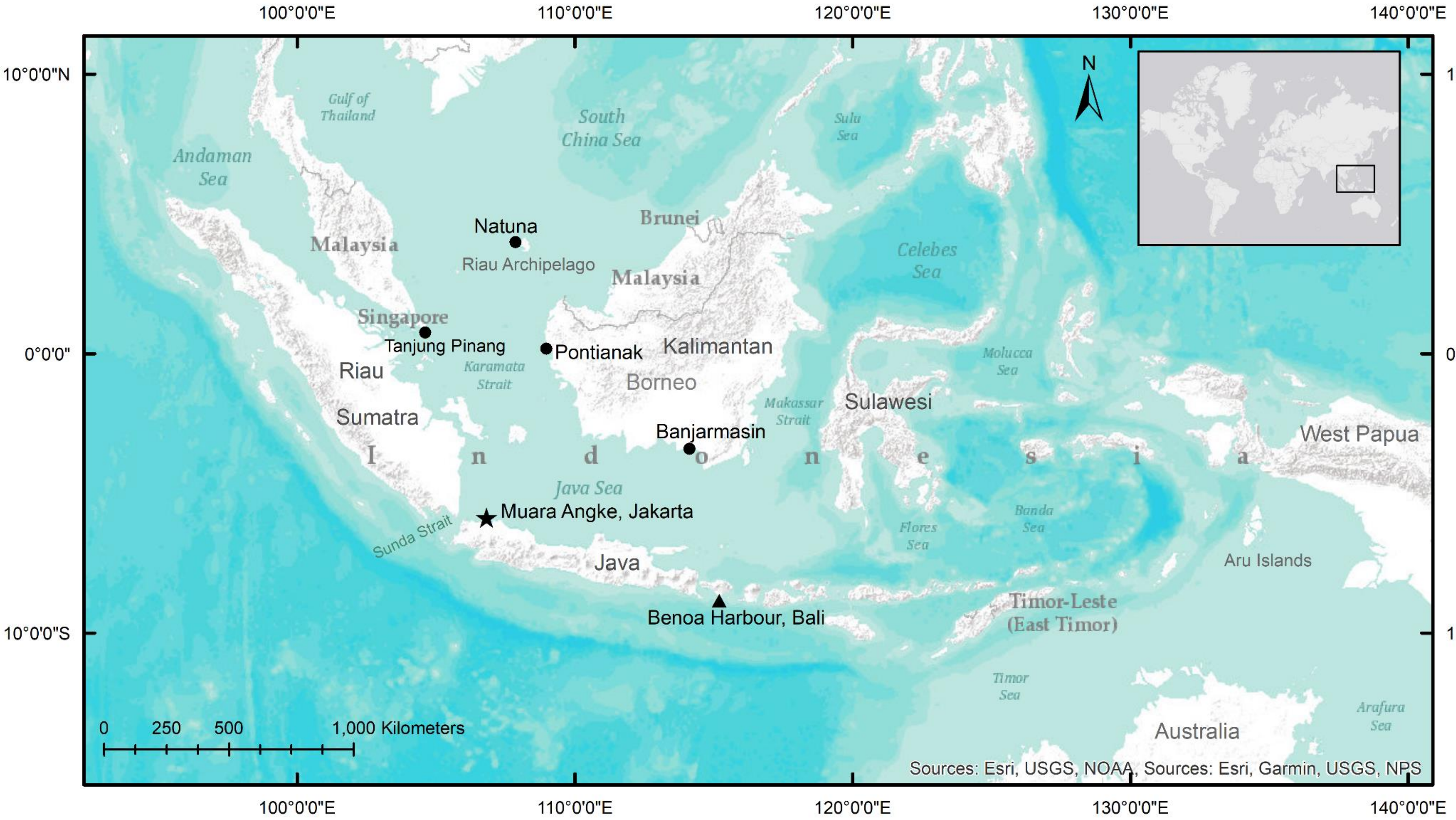

Figure 4.1. The location of the Muara Angke landing site and processing village in Jakarta (star), and Benoa Harbour, Bali (triangle), where the frozen shipment of landed catch was originally landed before relocated to processing village near Muara Angke, Indonesia. Other locations (circle) where tangle net vessels have been reported to fish are documented, including Natuna in Riau Archipelago, Tanjung Pinang off Sumatra, Pontianak, and Banjarmsain in Kalimantan. The map was created using ArcGIS software by Esri (Version 10.4.1; www.esri.com). Map Sources: Esri, USGS, NOAA, Garmin, NPS

Figure 4.2. Tangle net fishery catches at Muara Angke landing site, Jakarta Indonesia: (**A**) large bottlenose wedgefish *Rhynchobatus australiae* unloaded from tangle net vessels at the port; (**B**) large stingrays being processed at the adjacent village processing area; (**C**) drying ray skins which will be used to make stingray leather products such as wallets and belts; (**D**) wedgefish landings from Arafura Sea at the village processing area – *R. australiae* in centre of image highlighting the line of three white spots (yellow circle) diagnostic in this species. Photo credits: W.T.W.

The number of each species landed from a tangle net vessel was recorded. Due to the large number of landings and time constraints on each day surveyed, the number of specimens, biological data, and measurements could not be taken for all elasmobranchs present. Only specimens that could be accessed were surveyed, so randomized selection for sex/size was not possible. At the Muara Angke landing port, catch composition could only be recorded for a brief period while the vessels were being unloaded (**Figure 4.2 A, B**). After the catches were unloaded, elasmobranchs were taken to the adjacent village processing area, located less than a kilometre from the fishing port. Here the large elasmobranchs from the tangle net fishery were typically taken to one of the four processing 'houses' (**Figure 4.2 B**). Similar data could be obtained at the village processing area, often from the previous day's landings, but it was not possible to determine how many vessels they originated from if more than one vessel had landed in the previous two days. Species and size composition data were more readily collected during the unloading from the vessel at the fishing port. On days when catches were recorded in Muara Angke landing port, catches were not examined again in the village processing area. Due to the relatively low number of landings observed per trip, this issue was rarely encountered (**Appendix 4.1**). On one occasion, the landings from tangle net fishing vessels operating in the Banda and Arafura Seas that land at Benoa Harbour, Bali (**Figure 4.1**), were observed and recorded in the Muara Angke processing village. These catches arrived at the village processing area by freezer truck direct from Bali.

Often individual tangle net vessels would come into Muara Angke port once a month, and on three occasions it was possible to document the entire landed catch from four tangle net vessels. The entire landed catch from two of the four vessels were recorded at Muara Angke landing site on 17th July and 6th October 2004, and referred to as MA-SKR-170704, PV-PK-061004 respectively (**Table 4.1**). The landed catches from the vessels PV-KA-051005 and PV-UK-051005 were recorded on the same day 5th October 2005. The recorded catches for PV-KA-051005 and PV-UK-051005 were combined, as not all catch was able to be examined for PV-UK-051005 and assigned the vessel identifier code of PV-CC-051005 (**Table 4.1**).

Following the methods described above, catch composition of elasmobranchs from other fisheries were also recorded during the Muara Angke landing site surveys. This included landings from small-mesh gillnet (< 20 cm mesh size) fisheries, Java Sea and Arafura Sea trawl fisheries, the southern Java trammel net fishery, and various hand- and long-line fisheries, which were operating out of the landing ports surveyed [see White & Dharmadi (2007)]. This allowed the comparison of the size composition of species between the tangle net fishery and the other fisheries interacting with the same species. Similar to the tangle net fishery landings, only landed catch that could be accessed when a vessel was unloading was able to be surveyed, and randomized selection was not possible.

Table 4.1. Summary table of the recorded tangle net vessels landed in Muara Angke landing site and nearby processing village, Jakarta, Indonesia in April 2001 – December 2005, including a vessel identifier (Vessel ID), date of survey, type of sampling (partial landed catch, PC; total landed catch, TC), number (No.) of ray and shark species and specimens surveyed, the reported fishing grounds, and survey location (Muara Angke landing site, MA; the nearby processing village, PV).

Vessel ID	**Date of Survey**	**Type of Sampling**	**No. of ray species**	**No. of specimens**	**No. of shark species**	**No. of specimens**	**Reported fishing grounds**	**Survey Location**
MA-UK-040401	04/04/2001	PC	14	Unknown	3	Unknown	Unknown	MA
MA-UK-050401	05/04/2001	PC	5	11*	2	Unknown	Unknown	MA
MA-UK-150502	15/05/2002	PC	10	159	0	0	Unknown	MA
PV-BB-140802	14/08/2002	PC	15	197	2	3	Arafura and Banda Seas, shipped frozen from Benoa, Bali	PV
MA-UK-181002	18/10/2002	PC	9	69	0	0	Unknown	MA
PV-UK-090203	09/02/2003	PC	10	361	0	0	Unknown	PV
MA-SKR-170704	17/07/2004	TC	13	147	2	4	West Sumatra, Kalimantan, Riau Islands	MA
PV-UK-200704	20/07/2004	PC	1	49	0	0	Unknown	PV
MA-UK-210704	21/07/2004	PC	13	132	2	3	Unknown	MA
PV-PK-061004	06/10/2004	TC	12	106	4	5	Pontianak in Kalimantan	PV
MA-UK-160705	16/07/2005	PC	8	51	0	0	Unknown	MA
PV-KA-051005 (PV-CC-051005)ˆ	05/10/2005	TC	14	240	5	8	Kalimantan	PV
PV-UK-051005 (PV-CC-051005)ˆ	05/10/2005	PC					Unknown	PV
PV-UK-081205	08/12/2005	PC	1	4	1	2	Unknown	PV

* Only 11 specimens were recorded from 5 species of rays, no information on the remaining 6 species of rays and sharks were documented

ˆTwo tangle nets landed on same day, the landed catch was unable to be separate during the survey, and the landed catch was combined and assigned the ID of PV-C-2005. The number of species and specimens reflects the landed catch from both vessels.

4.2.2 Biological data

When possible, the disc width (from the two furthest points of the pectoral fins; DW) for the species of the Families Dasyatidae, Myliobatidae, Aetobatidae, Gymnuridae and Rhinopteridae, and total length (from the tip of the snout to the tip of the upper lobe of the caudal fin; TL) for the sharks and shark-like rays (Pristidae, Glaucostegidae and Rhinidae) were measured to the nearest 1 cm, and sex recorded. Occasionally, the removal of fins from these rays occurred following landing, and after measuring and weighing of specimens. When the shark-like rays were landed without fins, an estimated TL was recorded. Total weight (TW) of whole individuals (fins attached and not gutted) was recorded to the nearest g or kg (depending on the size of the individual), however, the vast majority of rays and sharks could not be weighed at the landing port. When large numbers of similar sized individuals were observed, measurements were taken from a subset of whole individuals that could be accessed, and used to estimate DW, TL and TW for the remaining unmeasured individuals. For specimens that were not weighed but had length measurements, the weight of individual specimens was calculated using the length to weight conversion equations (**Appendix 4.2**). For species where a length-weight equation was not available, the estimated weight was calculated using a conversion equation from a morphologically similar species (**Appendix 4.2**). In instances when the size of individuals for a particular species was not recorded, the weight was estimated using the average weight of the individuals for that species. Total landed weight was then determined for each species landed in the fishery. Details on the reproductive biology of each species recorded were previously reported in White & Dharmadi (2007).

4.2.3 Species identification

Species were identified using the keys in Carpenter & Niem (1998) and Last & Stevens (1994), with taxonomic nomenclature updated using Last et al. (2016) and Last & Stevens (2009). The identity of a subsample of *Rhynchobatus* species caught in the tangle net fishery was also further verified by genetic analysis (Giles et al., 2016), and from images that allowed examination of recently recognized colour pattern differences between species (Last et al., 2016). The key colour pattern difference used to differentiate *R. australiae* from its closest regional congeners was the pattern of white spots around the dark pectoral spot present in all but the largest individuals (**Figure 4.2 D**). In *R. australiae,* there is a line of three white spots located adjacent to the black pectoral spot, or its usual position if faded (Last et al., 2016). In two large pregnant females that possessed no white spots or black pectoral spots, due mainly to their poor condition, the typical *R. australiae* spot pattern was evident in late-term embryos allowing for confirmation of their identity. Sharpnose whipray *Maculabatis macrura* was only recently recognized as a valid species and distinct from whitespotted whipray *Maculabatis gerrardi* (Last et al., 2016), thus the data could not be retrospectively confirmed as being of either or both species. As these records could constitute either species, herein they are referred to as *M. gerrardi/macrura*.

4.2.4 Data analysis

Species composition of each landing was expressed as the percentage of the total number of individuals by both the number and weight for each species recorded at the landing port and processing village. Minimum, maximum, and mean ± standard error (S.E.) for DW, TL and TW are reported for each species. Size frequency histograms for the 10 most abundant species were produced.

4.3 Results

4.3.1 Species and size composition of the fishery

Across 18 sampling trips, totalling 53 survey days from April 2001 – December 2005, tangle net vessel landings were recorded at Muara Angke landing site eight times, and within the village processing area seven times, including one frozen shipment from Benoa Harbour, Bali from the Arafura or Banda Sea region (**Table 4.1**; **Appendix 4.1**). From discussions with a fleet manager, 13 vessels were reported to be operational in the tangle net industry in 2004, fishing in waters around Borneo, Sulawesi, West Papua and as far as the Arafura Sea (**Figure 4.1**). Only vessels that landed at Muara Angke landing site or processing village during the 2001-2005 surveys were sampled (**Table 4.1**).

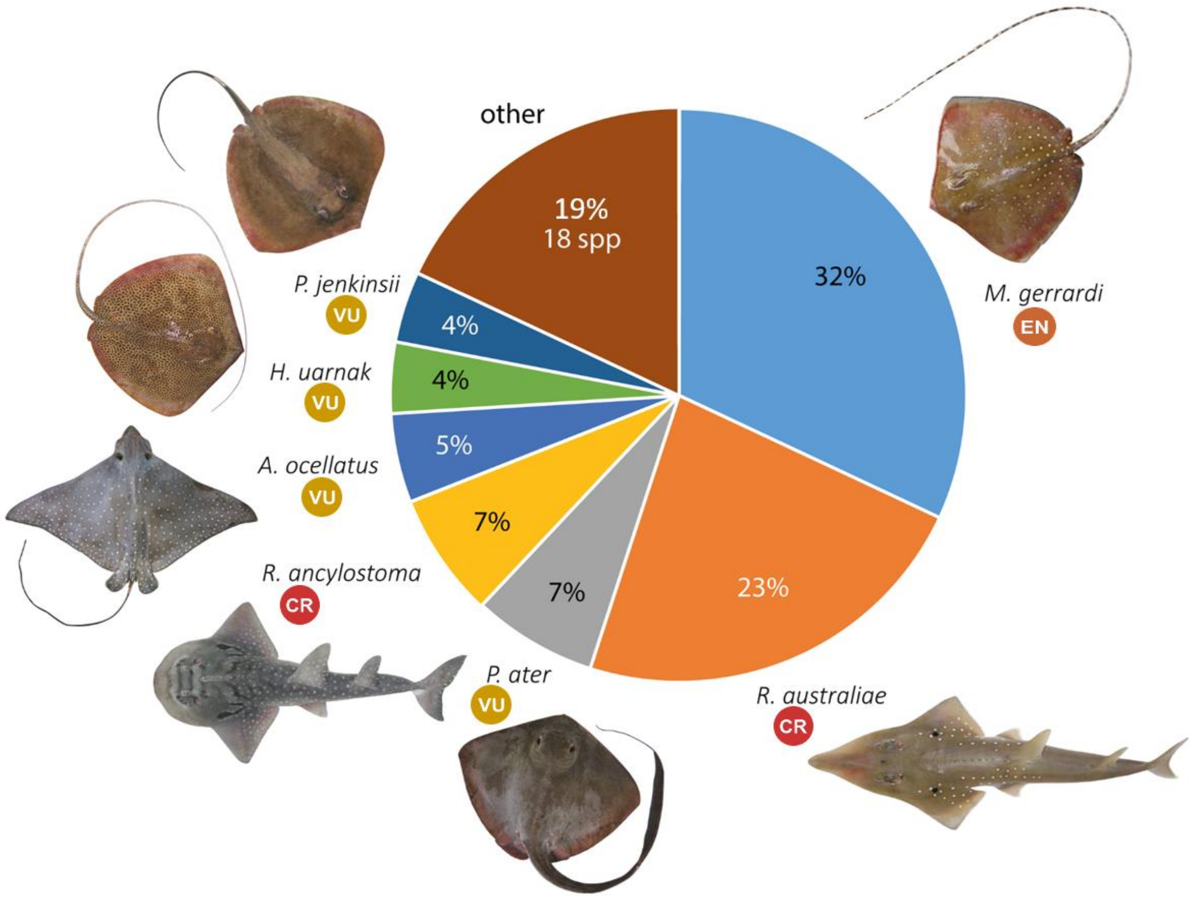

Figure 4.3. Overall species composition and percentage (%) of catch of the four Indonesian tangle net vessels (total *n* = 481), of which the landed catch was able to be fully documented from Muara Angke landing site, Jakarta Indonesia. *MA*-SKR-170704 landed on 7th July 2004; PV-PK-061004 landed on 16th October 2004; PV-CC-051005 (combined landed catch of PV-KA-051005 and PV-UK-051005) landed on 5th October 2005.The total landed catch from the four vessels consisted of whitespotted/sharpnose whipray *Maculabatis gerrardi /macrura*, *n* = 155, bottlenose wedgefish *Rhynchobatus australiae n* = 112, bowmouth guitarfish *Rhina ancylostoma n* = 32, spotted eagle ray *Aetobatus ocellatus n* = 25, Jenkins' whipray *Pateobatis jenkinsii n* = 18, coach whipray *Himantura uarnak n* = 17, and for the other species *n* = 90. The International Union for Conservation of Nature's (IUCN) Red List of Threatened Species status (as of 25th July 2022) are CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient. Photo credit: W.T.W.

A total of 1,559 elasmobranchs were recorded from tangle net fishery landings at Muara Angke landing port. These comprised 1,534 batoids (98.3% of the catch), of 24 species from seven families (**Table 4.2**). The most abundant Family was Dasyatidae, comprising 72.5% of the total number of elasmobranchs recorded, followed by the Family Rhinidae, which comprised 20.8% of total observed catch. Only 25 sharks were recorded from nine shark species from four families (**Table 4.2**). Of the species documented, eight ray species and eight shark species were recorded in low numbers (≤10 individuals). The number of individuals for clubnose guitarfish *Glaucostegus thouin* and pigeye shark *Carcharhinus amboinensis* were not documented due to logistics in accessing the samples.

Combining the total landed catch of the four Indonesian tangle net vessels for which the catch was fully documented from Muara Angke landing site revealed that the most abundant species was *M. gerrardi/macrura,* followed by *R. australiae,* broad cowtail ray *Pastinachus ater,* bowmouth guitarfish *Rhina ancylostoma,* spotted eagle ray *Aetobatus ocellatus,* coach whipray *Himantura uarnak,* and Jenkins' whipray *Pateobatis jenkinsii* (**Figure 4.3**).

Family Pristidae

Two largetooth sawfish *Pristis pristis* were recorded from the Benoa Harbour, Bali landings in August 2002 (**Table 4.1**). Information provided by the processors to one of authors (WW) indicated that they were caught in the Arafura or Banda Sea region (**Figure 4.1**). Both individuals were adult males and ca. 420 cm TL and had an estimated total landed weight of 220 kg (**Table 4.2**).

Family Glaucostegidae

Two species of giant guitarfish were recorded at Muara Angke landing site: *G. thouin*, and *G. typus*. The presence of *G. thouin* in the fishery was only recorded once in April 2001. However, due to the logistics of accessing these rays upon unloading from the vessel and the decayed state of some specimens, estimates of numbers or size were not collected for *G. thouin*, and it was unclear if it was a regular catch in the fishery. *Glaucostegus typus* were recorded on three occasions and of the 14 that were measured, seven were females, six males and one not sexed, with an estimated total landed weight of 386 kg (**Table 4.2**)

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Table 4.2. Species composition, number of individuals of a species observed (no.) and overall percentage (% by no.) of the landed elasmobranch catch by the tangle net fishery, and landed in Muara Angke landing site, Jakarta Indonesia in April 2001–December 2005. The observed maximum size (Max. size); observed mean (± S.E.) size (DW/TL cm), minimum (Min. weight) and maximum (Max. weight) and mean (± S.E.) estimated total weight (kg) are reported for each species, with the International Union for Conservation of Nature’s (IUCN) Red List of Threatened Species status (as of 25th March 2021). IUCN categories are CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient. Dashed lines indicate species presence was recorded in landings, but data was not able to be documented.

Family	Scientific name	Common name	IUCN Red List Category	Year Assessed	No.	% by No.	Min. size	Max. size	Mean Size	± S.E.	Min. weight	Max. weight	Mean Weight	± S.E.
Pristidae	*Pristis pristis*	Largetooth sawfish	CR	2013	2	0.128	--	420.0	--	--	--	220.3	--	--
Glaucostegidae	*Glaucostegus thouin*	Clubnose guitarfish	CR	2019	--	--	--	--	--	--	--	--	--	--
	Glaucostegus typus	Giant guitarfish	CR	2019	14	0.898	170.0	260.0	206.0	13.15	14.86	51.36	27.57	5.543
Rhinidae	*Rhina ancylostoma*	Bowmouth guitarfish	CR	2019	57	3.656	130.1	270.0	190.2	22.97	18.68	168.4	77.38	24.29
	Rhynchobatus australiae	Bottlenose wedgefish	CR	2019	238	15.27	190.0	300.0	282.1	4.662	30.21	118.7	100.9	4.181
	Rhynchobatus palpebratus	Eyebrow wedgefish	NT	2019	30	1.924	--	--	--	--	--	--	--	--
Dasyatidae	*Bathytoshia lata*	Brown stingray	LC*	2007	1	0.064	--	202.0	--	--	--	300.0		--
	Himantura leoparda	Leopard whipray	VU	2015	31	1.988	83.20	120.0	98.72	3.016	14.37	39.45	23.61	2.061
	Himantura uarnak	Coach whipray	VU	2015	57	3.656	42.60	147.6	99.50	6.204	4.015	69.83	28.57	4.189
	Himantura undulata	Honeycomb whipray	EN	2020	1	0.064	--	112.8	112.8	--	33.27	--	33.27	--
	Maculabatis astra	Blackspotted whipray	LC	2015	4	0.257	--	79.00	79.00	--	13.26	--	13.26	--
	Maculabatis gerrardi/macrura	Whitespotted whipray /Sharpnose whipray	ENˆ	2020	194	12.44	62.70	89.50	75.85	1.036	6.560	19.40	12.01	2.410
	Megatrygon microps	Smalleye stingray	DD	2015	1	0.064	--	174.8	--	--	--	111.3	--	--
	Pastinachus ater	Broad cowtail ray	VU	2020	199	12.76	86.00	149.0	114.3	2.618	15.74	71.67	37.98	2.332
	Pateobatis fai	Pink whipray	VU	2015	264	16.93	70.50	168.4	110.9	4.595	9.101	100.4	36.45	4.143
	Pateobatis jenkinsii	Jenkin's whipray	VU	2015	187	11.99	59.20	138.4	82.59	1.791	5.621	58.47	14.78	1.207
	Pateobatis uarnacoides	Whitenose whipray	EN	2020	125	8.018	51.70	118.8	91.23	4.206	3.869	38.38	20.42	2.390
	Taeniurops meyeni	Blotched stingray	VU	2015	51	3.271	62.80	164.0	116.8	5.332	6.615	93.37	40.25	4.713
	Urogymnus asperrimus	Porcupine ray	VU	2015	5	0.321	76.50	103.4	89.95	9.511	11.40	26.17	18.78	5.222
	Urogymnus granulatus	Mangrove whipray	VU	2015	10	0.641	97.20	141.0	118.8	6.300	22.07	61.55	39.72	5.728
Gymnuridae	*Gymnura zonura*	Zonetail butterfly ray	EN	2020	7	0.449	70.50	91.60	79.78	3.036	2.442	5.466	3.657	0.4433

Aetobatidae	*Aetobatus ocellatus*	Spotted eagle ray	VU	2015	45	2.886	108.9	214.4	138.6	3.994	19.37	135.4	41.43	4.151
Myliobatidae	*Aetomylaeus vespertilio*	Ornate eagle ray	EN	2015	11	0.706	146.2	240.0	187.5	17.157	45.11	187.1	100.6	26.66
Carcharhinidae	*Carcharhinus amboinensis*	Pigeye shark	DD	2005	--	--	--	--	--	--	--	--	--	--
	Carcharhinus obscurus	Dusky shark	EN	2018	2	0.128	--	--	--	--	--	--	--	--
	Carcharhinus leucas	Bull shark	NT	2005	2	0.128	--	--	--	--	--	--	--	--
	Carcharhinus limbatus	Common blacktip shark	NT	2005	6	0.385	--	--	--	--	--	--	--	--
Galeocerdidae	*Galeocerdo cuvier*	Tiger shark	NT	2018	4	0.257	--	--	--	--	--	--	--	--
Ginglymostomatidae	*Nebrius ferrugineus*	Tawny nurse shark	VU	2003	3	0.192	--	--	--	--	--	--	--	--
Hemigaleidae	*Hemipristis elongata*	Fossil shark	VU	2015	3	0.192	109.6	122.9	116.3	4.702	5.719	25.14	6.989	0.8984
Sphyrnidae	*Sphyrna lewini*	Scalloped hammerhead	CR	2019	3	0.192	--	175.4	175.4	--	--	--	25.14	--
	Sphyrna mokarran	Great hammerhead	CR	2019	2	0.128	--	--	--	--	--	--	--	--

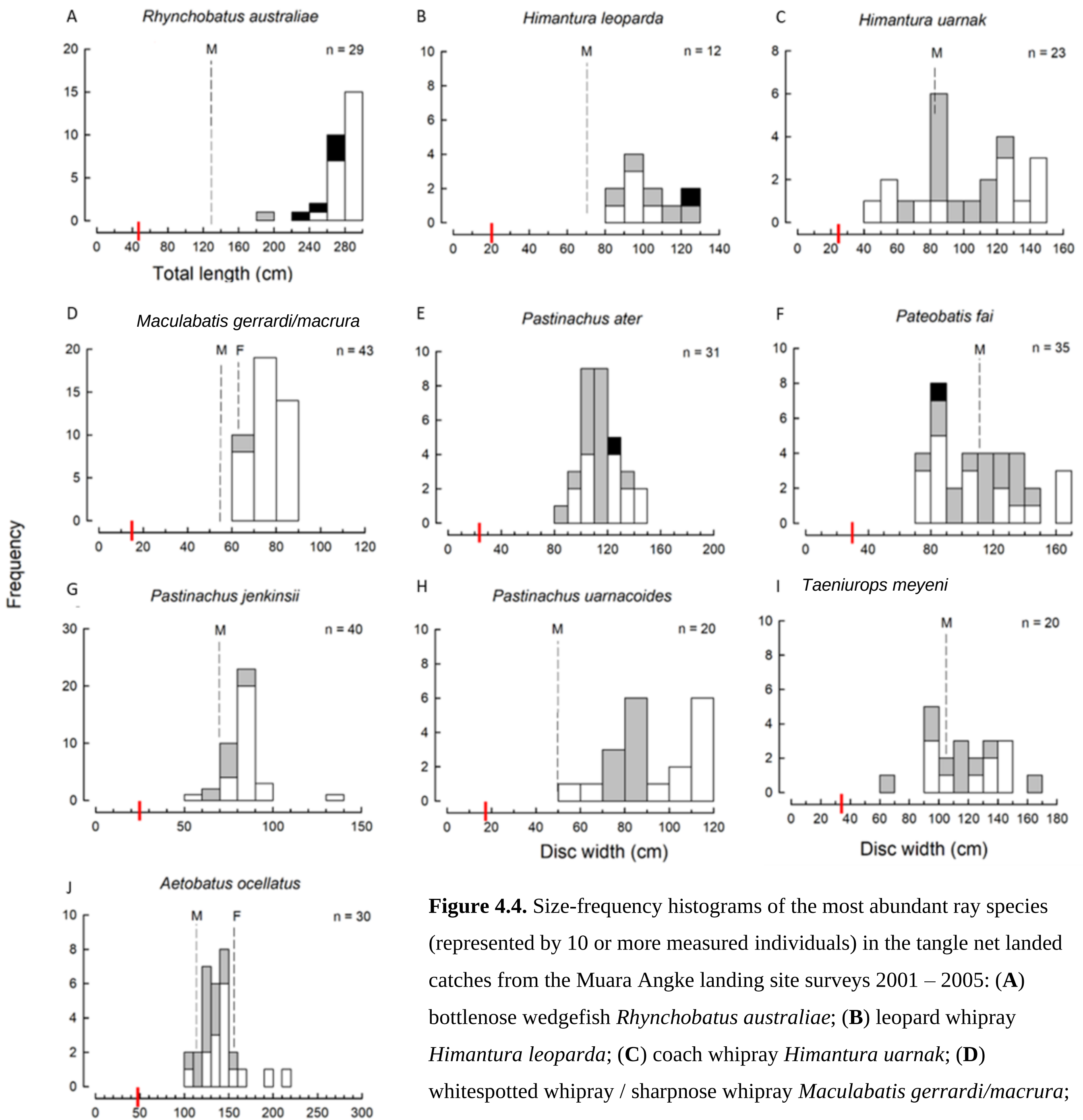

Figure 4.4. Size-frequency histograms of the most abundant ray species (represented by 10 or more measured individuals) in the tangle net landed catches from the Muara Angke landing site surveys 2001 – 2005: (**A**) bottlenose wedgefish *Rhynchobatus australiae*; (**B**) leopard whipray *Himantura leoparda*; (**C**) coach whipray *Himantura uarnak*; (**D**) whitespotted whipray / sharpnose whipray *Maculabatis gerrardi/macrura*; (**E**) broad cowtail ray *Pastinachus ater*; (**F**) pink whipray *Pateobatis fai*; (**G**) Jenkin's whipray *Pateobatis jenkinsii*; (**H**) whitenose whipray *Pateobatis uarnacoides*; (**I**) blotched stingray *Taeniurops meyeni*; (**J**) spotted eagle ray *Aetobatus ocellatus*. White bars denote females, grey bars males and black bars unsexed individuals; the total number (n) of individuals, size at birth (red solid line) and size at maturity (black dashed line; M, male; F, female) when known. The x-axis (size) extends to the maximum known size for each of the species. The species are placed in phylogenetic order from wedgefish through to eagle rays. Size at birth and size at maturity estimates are from Last et al. (2016)

Family Rhinidae

Three species of wedgefish were recorded: *R. ancylostoma*, the eyebrow wedgefish *Rhynchobatus palpebratus,* and *R. australiae*. *Rhina ancylostoma* were recorded on seven occasions over the sampling period (**Appendix 4.3**). The landed catch of *R. ancylostoma* comprised 15 females, 10 males, and 32 specimens counted but not sexed, with an estimated total landed weight of 4.4 tonnes (**Table 4.2**). Females ranged from 139 – 250 cm TL and 22.9 – 133.6 kg, and males ranged from 130 – 260 cm TL and 18.7 – 150.3 kg. One unsexed specimen was measured at 270 cm TL and 168 kg.

The main target species of the tangle net fishery, *R. australiae* comprised the largest component of wedgefishes and the second most abundant species recorded (**Table 4.2**; **Figure 4.3**). On one occasion, approximately 7.1 tonnes of *R. australiae* were landed from a single tangle net vessel. *Rhynchobatus australiae* was recorded on eight occasions (Table S3) with a total of 238 individuals with an estimated total landed weight of 24 tonnes, comprising 99 females, 18 males and 121 unsexed individuals (**Table 4.2**). A subset of 29 individuals were measured, the majority of which were females and approximately 300 cm TL (range: 120 – 300 cm TL; mean ± S.E.: 273.1 ± 7.95 cm TL) (**Figure 4.4 A**). Of that subset, 16 individuals of *R. australiae* were determined to be pregnant through internal examination and previously reported in White & Dharmadi (2007).

A subset of 16 samples from 100 *Rhynchobatus* spp. individuals landed in the tangle net fishery from the Benoa Harbour landings on the 14th August 2002 had their identifications confirmed by genetic analysis [see Giles et al. (2016)]. Of these, two were from landings at Muara Angke and identified as *R. australiae*, and the remaining 14 were from the Benoa Harbour landings and consisted of five *R. palpebratus* [reported as *R. palpebratus/ R.* cf *laevis* in Giles et al. (2016)] and nine *R. australiae.* A conservative ratio of *R. palpebratus* (31.25%, *n* = 5) to *R. australiae* (68.75%, *n* = 11) determined from the genetic analysis (30:70%) was used to estimate the species composition of the 100 *Rhynchobatus* spp. individuals recorded.

Rhynchobatus palpebratus was recorded on one occasion from landings in Benoa Harbour, with a total of 30 individuals but not sexed, measured, or weighed (**Table 4.2**).

Family Dasyatidae

Stingrays were present in every tangle net catch landed in Muara Angke. A total of 1,130 stingrays, with an estimated mass of 30.2 tonnes were recorded, comprising 14 species from eight genera (**Table 4.2**). The majority of the specimens caught of each species were near or at a larger size than their known size at maturity (**Figure 4.4**; **Appendix 4.4**). The most abundant stingray species were *P. fai* (*n* = 264; 9.6 tonnes;), *P. ater* (*n* = 199; 7.5 tonnes; **Figure 4.4 E**), *M. gerrardi/macrura* (n=194; 2.3 tonnes; **Figure 4.3**; **Figure 4.4 D**), *P. jenkinsii* (*n* = 187; 2.7 tonnes; Figure 3g), and whitenose whipray *Pateobatis uarnacoides* (*n* = 125; 2.5 tonnes; **Figure 4.4 H**). Other species that were recorded were the brown stingray *Bathytoshia lata*, leopard whipray *Himantura leoparda* (**Figure 4.4 B**), coach whipray *H. uarnak* (**Figure 4.4 C**), honeycomb whipray *Himantura undulata*, blackspotted whipray *Maculabatis astra*, smalleye stingray *Megatrygon microps*, blotched stingray *Taeniurops meyeni* (**Figure 4.4 I**), porcupine ray *Urogymnus asperrimus* and mangrove whipray *Urogymnus granulatus*. *Maculabatis astra* was only recorded from the single Benoa Harbour landing; this species is only present in the far eastern portion of Indonesia off West Papua and is allopatric from *M. gerrardi/macrura* (Last et al., 2016). Specimens of *H. leoparda, H. uarnak, P. fai, P. uarnacoides* and *T. meyeni* were close to their respective known maximum sizes (**Figure 4.4**)

Family Aetobatidae

One aetobatid species, *A. ocellatus*, was recorded in the tangle net fishery on eight occasions (**Appendix 4.3**). A total of 45 individuals were observed, with an estimated total landed weight of 1.8 tonnes (**Table 4.2**). These comprised 21 females, 22 males, and two unsexed specimens (**Table 4.2**). *Aetobatus ocellatus* specimens were mainly caught close to or at a greater size than the known size at maturity (**Figure 4.4 J**; **Appendix 4.4**).

Other families

Several other species from a range of families were recorded occasionally or in relatively small numbers. These included one species of Myliobatidae, the ornate eagle ray *Aetomylaeus vespertilio*, with an estimated landed catch of 1.1 tonnes. Specimens of *A. vespertilio* were all large and comprised five females (including one 160kg female), one male, and five unsexed individuals (**Table 4.2**). This species was only recorded occasionally (**Appendix 4.3**) and comprised a small proportion of the total landed catch. A single

Gymnuridae species was recorded, the zonetail butterfly ray *Gymnura zonura* with seven individuals recorded (**Table 4.2**). Sharks were a minor part of the catch and rarely observed. All of the shark species represented less than 1% of the total catch (**Table 4.2**). Of the small number of sharks taken in the fishery, the most commonly occurring in the catch were the common blacktip shark (*Carcharhinus limbatus*; *n* = 6), tiger shark (*Galeocerdo cuvier*; *n* = 4), and hammerheads (*Spyhrna* spp; *n* = 5) (**Table 4.2**; **Appendix 4.3**).

4.3.2 Products from the tangle net fishery

Data from MMAF indicated that the main products derived from the tangle net fishery catch were elasmobranch fins, leather made from ray skins, salted elasmobranch meat, and elasmobranch vertebrae. The most valuable product was fins from wedgefishes and giant guitarfishes. During the surveys in 2005, the quoted price for fins from sawfish, wedgefish and guitarfish was approximately 3 million IDR kg-1 wet weight (~ 7,145,108 IDR / $512 USD per kg adjusted for inflation in 2021). Any fins frozen on-board the tangle net vessels did not come through the Muara Angke landing site, but instead were directly exported through a different port to Hong Kong and Singapore.

Ray skins, used to produce leather products, were the second most valuable product from the fishery (**Figure 4.2 C**). The species primarily used were from the genera *Himantura, Maculabatis, Pastinachus, Pateobatis* and *Urogymnus*, which together were a large component of the landed catch during the market surveys. *Pateobatis jenkinsii* was reported to be the most sought-after stingray skin due to the row of enlarged thorns which extend down the midline of the body and tail. In 2005, the reported values of 13 cm and 18 cm pieces of stingray leather were 25,000 IDR (= 59,543 IDR / 4.30 USD in 2021) and 35,000 IDR (= 83,360 IDR / 5.97 USD in 2021). Between 3,000 – 4,000 skins were estimated to be exported per month to the Philippines and Japan. Products from the stingray leather include wallets and belts, which were reported to be sold for approximately 290,000 IDR (= 690,694 IDR / 49.50 USD in 2021) to 500,000 IDR (= 1,190,851 IDR / 85.33 USD in 2021), as well as bags. Estimated prices for bags were not available.

Ray meat, wedgefish in particular, was considered to be good quality. The meat from the elasmobranchs from the tangle net fishery was salted and dried due to the deteriorated condition upon arrival at the processing village. In 2004, in the Muara Angke processing village, the buying price for wedgefish and guitarfish meat was 4,000 – 5,000 IDR kg-1 (= 10,143 – 12,679 IDR kg-1/ 0.73 – 0.91 USD kg-1 in 2021). For stingrays, the meat was valued at between 2,000 – 3,500 IDR kg-1 (= 5,072 – 8,875 IDR kg-1/ 0.36 – 0.64 USD kg-1 in 2021). Salted meat was reported to be transported to West Java (Bandung, Bogor, Garut, Cianjur) and Central Java. Salted meat from wedgefish was reported to be sold for 10,000 – 12,000 IDR kg-1 (= 25,358 – 30,430 IDR kg-1/ 1.82 – 2.20 USD kg-1 in 2021), and for stingray meat 6,000 – 8,000 IDR kg-1 (= 15,215 – 20,287 IDR kg-1/ 1.09 – 1.45 USD kg-1 in 2021).

The cartilage, such as vertebrae, comprised a small part of the products from this fishery and the uses for these products were not recorded. In 2004, dried vertebrae were worth approximately 20,000 IDR kg-1 (= 50,717 IDR kg-1/ 3.63 USD kg-1 in 2021), which were then processed in Jakarta and exported through an undisclosed port to Korea and Japan.

4.3.3 Comparison of the size range of species from the tangle net fishery and other fisheries

The gill nets used in the tangle net fishery captured wedgefish and guitarfish over 130 cm TL, and stingrays over 50 cm DW (**Figure 4.5**), as a result of the large mesh size used (50 – 60 cm). The smallest recorded individual caught in this fishery was a *H. uarnak* of 42.6 cm DW and the largest recorded individual was a male *P. pristis*, estimated to be 420 cm TL. Meanwhile, smaller size classes (< 50 cm DW) for many ray species were captured in a range of fishing gears used in other fisheries operating in Indonesian waters during the 2001 – 2005 surveys, including trawl nets, hand- and long-lines, smaller mesh gillnets, and trammel nets (**Figure 4.5**). These other fisheries greatly increased fishing selectivity for some species. For example, all size classes of *R. australiae* were captured; neonates (~45 cm TL) were caught as bycatch in small mesh gillnets (**Figure 4.5 A**), while sub-adults (~90 – 130 cm TL) were captured in the Java Sea trawl fishery, and the larger mature individuals (> 170 cm TL) were taken in hand- and long-line fisheries (**Figure 4.5 A**).

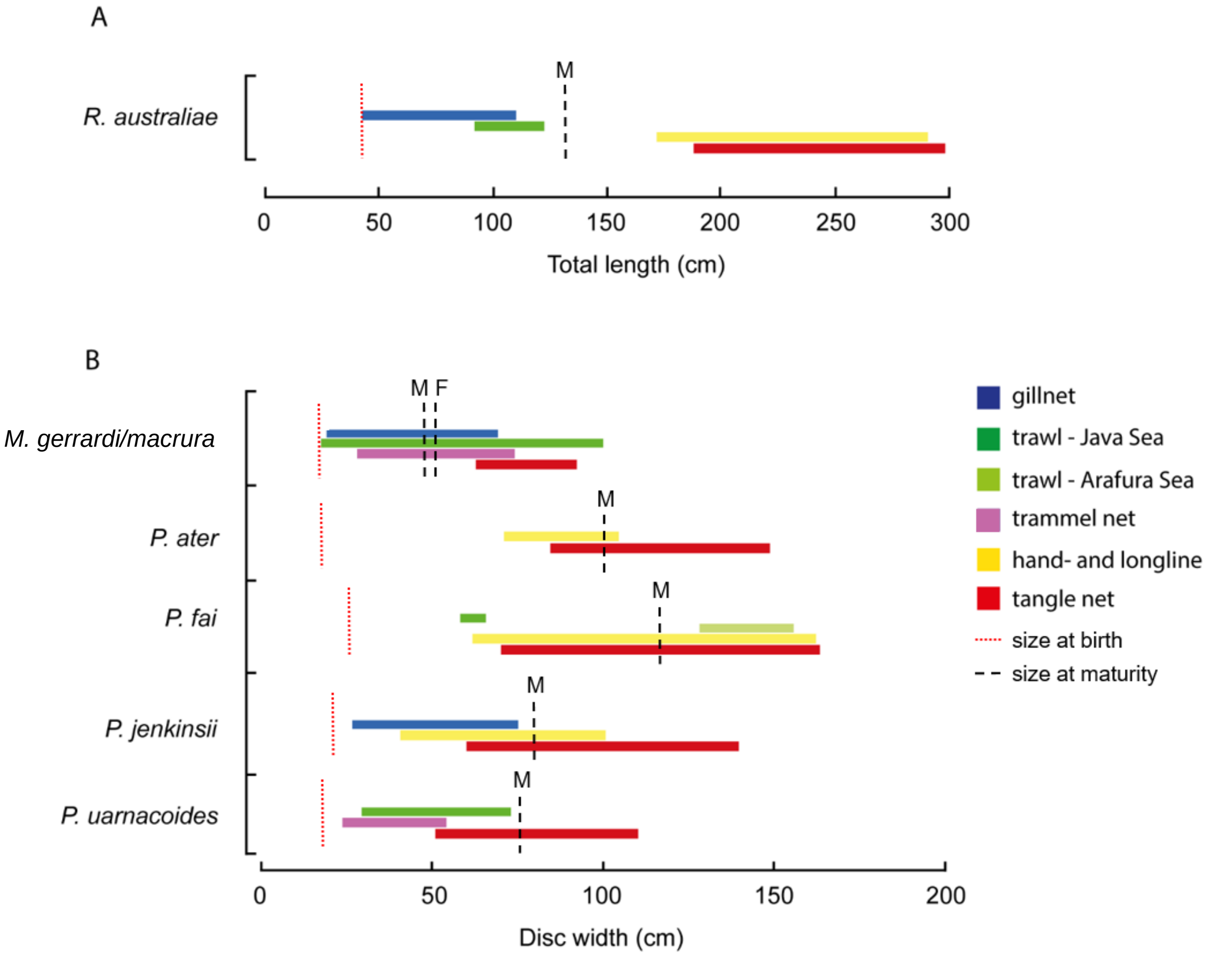

Figure 4.5. Comparison of the size ranges for the landed catches of (**A**) bottlenose wedgefish *Rhynchobatus australiae* using total length (TL cm) and (**B**) using disc width (DW cm) for whitespotted whipray / sharpnose whipray *Maculabatis gerrardi/macrura*, broad cowtail ray *Pateobatis ater*, pink whipray *Pateobatis fai*, Jenkins's whipray *Pateobatis jenkinsii*, and whitenose whipray *Pateobatis uarnacoides* caught in the small mesh gillnet (blue), Java Sea trawl fishery (dark green), Arafura Sea trawl fishery (light green), trammel net (purple), hand- and long-line (yellow) and tangle net (red) landed in Muara Angke landing site, Jakarta Indonesia. The size at birth (red dotted line) and size at maturity (black dashed line; M, male; F, female) are displayed from Last et al. (2016)

Similar trends are evident for several dasyatid rays, with life stages from neonates to sub-adults landed in other fisheries during the 2001 – 2005 market surveys (**Figure 4.5 B**). Catch of *M. gerrardi/macrura* was recorded from the small mesh gillnet fishery (neonates – mature adults; ~20 – 70 cm DW), the Java Sea trawl fishery (neonates – mature adults; ~20 – 100 cm DW), and the trammel net fishery off southern Java (juveniles – mature adults; ~30 – 70 cm DW) (**Figure 4.5 B**). *Pastinachus ater* was recorded in the hand- and long-line fisheries (~70 – 110 cm DW), compared to a typically larger size range of individuals landed in the tangle net fishery (~80 – 150 cm DW) (**Figure 4.5 B**). *Pateobatis fai* was recorded in the Java Sea trawl fishery (juveniles; ~60 – 70 cm DW), in the Arafura Sea trawl fishery (sub adults; ~139 – 160 cm DW) and hand- and long-line fisheries (juveniles to mature adults; ~65 – 160 cm DW) (**Figure 4.5 B**). *Pateobatis jenkinsii* was also exposed to fishing throughout all life stages, from small mesh gillnets (neonates – sub adults; ~25 – 75 cm DW), hand- and long-line fisheries (juveniles – mature adults; ~40 – 100 cm DW), as well as the tangle net fishery (juveniles – mature adults; ~60 – 140 cm DW) (**Figure 4.5 B**). Catch of *P. uarnacoides* was recorded in the Java Sea trawl fishery (juveniles to mature adults; ~30 – 60 cm DW), and in the southern Java trammel net fishery (juveniles to mature adults; ~25 – 55 cm DW) (**Figure 4.5 B**).

4.4 Discussion

Wedgefishes and giant guitarfishes face an extremely high risk of extinction (Kyne et al., 2020). While the status of populations and the exact extent of declines for wedgefish and giant guitarfish are uncertain, the currently available data suggest that global population declines are substantial (Diop & Dossa, 2011; Moore, 2017; Jabado, 2018; Kyne et al., 2020). This study advances our understanding of the data poor tangle net fishery in Indonesia, providing details on the species and size composition, and selectivity of the fishery for larger size classes. In doing so, the study provides an important historical context on the indications of significantly depleted populations for wedgefishes and giant guitarfishes in 2001 – 2005 and records the shift in target species to stingrays. Population declines were inferred from the declining catch rates of the target species, *R. australiae*, and the decline in the number of vessels operating in the tangle net fishery. The number of vessels in the fishery peaked at 500 vessels in 1987, and then rapidly declined to 100 vessels nine years later in 1996 (Keong, 1996). In 2004, from this study 13 vessels were recorded in the tangle net industry, while in 2008 14 vessels were reported to be operational in the fishery in Muara Angke (Dharmadi & Kasim, 2010). The number of vessels was reported to decline again by half to seven vessels from 2008 – 2009 (Dharmadi & Kasim, 2010), and the most recent information from 2017/2018 has recorded seven tangle net vessels active in Maura Angke (**Appendix 4.5**). This could indicate that current fishing effort (inferred from vessel numbers) has stabilized, but information on catch composition, fishing effort, and catch trends are needed to assess the status of stocks currently being exploited by the fishery. The significant reduction in the number of vessels operating in the fishery with the marked change in catch composition over the 31-year period (1987 – 2018), suggests that target species populations have declined, and the fishery became economically unviable. Over theses decades, it seems likely that the profits from the fins, salted meat and leather were insufficient to maintain the tangle net fishery in the face of the increasing operating costs and decreases in elasmobranch catches (Suzuki, 1997). The tangle net fishery was still operational as of July 2018 (**Appendix 4.5**), and the shift in target species from wedgefish to stingrays reported here suggests that the contemporary tangle net fishery may be reliant on the exploitation of stingrays for its viability and profitability, and opportunistically exploits the high valued wedgefish and guitarfish species when they are landed. However, there is no species-specific catch information for this fishery after 2005 and the landed catch was grouped under single labels such as ‘rays’, ‘sharks’, ‘wedgefish’ and ‘mixed’(**Appendix 4.5**). As such, contemporary catch composition and ongoing impacts on stingray populations remain poorly understood.

Opportunistic exploitation occurs when multiple species can be exploited in the same habitat (Branch, Lobo & Purcell, 2013). The most desirable and profitable species are targeted and depleted first, before exploitation switches to less desirable species, leading to overexploitation and harvesting to extinction of both the desired and less-desired species (Branch, Lobo & Purcell, 2013; Burgess et al., 2017). The apparent decline in wedgefish landings and the subsequent increase in stingray landed catches is an indication of the opportunistic exploitation in the fishery. Both groups are common demersal species in the Indo–West Pacific, and occupy similar habitats along inshore continental shelf waters to at least 60 m (Compagno & Last, 1999; White et al., 2006a). A decline or change in abundance of wedgefishes in these fishing grounds, would result in the stingrays that occupy the same habitat becoming the main target catch, with opportunities to retain the higher valued and critically endangered wedgefish and giant guitarfish species when they are encountered. The expansion of fishing grounds would also exacerbate the effects of the opportunistic exploitation as the fishery moves to new locations. The tangle net fishery originated in the eastern province of Maluku and spread throughout Indonesian waters to Java (Sunda Strait), Bali, Sumatra (Riau, Tanjung Pinang), Natuna/Riau Archipelago, Kalimantan (Pontianak to Banjarmasin), Sulawesi, West Papua and the Arafura Sea (**Figure 4.1**) (Keong, 1996; Dharmadi & Kasim, 2010). The changing of fishing grounds has likely led to the doubling of the reported trip lengths from 20 to 40 days to reach more-distant fishing areas (Keong 1996, Dharmadi and Kasim 2010), and potentially resulted in diminishing returns with increasing costs associated with longer trips (Jaiteh, Loneragan & Warren, 2017; Yulianto et al., 2018).

The information presented in this study indicates that the fishery was not sustainable, especially considering the expansion of fishing grounds with decline of tangle net vessels from 500 to seven, and the impacts of opportunistic exploitation of wedgefish on stingray populations.

There has been an increasing domestic demand for stingray leather in Indonesia over the past 40 years, with the development of a commercial market for stingray leather on the north coast of Central Java during the 1980s (Ibrahim, 2003). Prior to 1980, stingrays were discarded as bycatch in the tangle net fishery (Ibrahim, 2003; Sahubawa, Pertiwiningrum & Rahmadian, 2018), now they have been recorded as the main component of the landed catch in 2001 – 2005, and 2017 – 2018 (**Appendix 4.5**). The calcified denticles in stingray skin, such as in *P. jenkinsii*, results in a unique and attractive finish to the leather products (e.g. bags, belts, wallets, and jewellery), and have a high economic value (Karthikeyan et al., 2009; Sahubawa, Pertiwiningrum & Rahmadian, 2018). Additionally, stingrays remain a major fishery export from Indonesia with stingray meat being consumed throughout the region resulting in conservation concerns growing for species such as *M. gerrardi* and *M. macrura* (Clark-Shen et al., 2021). This targeted fishing pressure on the stingrays may also be causing population declines. It is likely that stingrays are experiencing similar trends of declines to shark-like rays, given the increasing pressure on stingrays as wedgefish have become less common. Similar to shark-like rays, the population status of numerous tropical stingray species are declining as inferred from decreasing landings and catch data, although there is little species specific fisheries information available (Sherman et al., 2020a). The loss of large, benthic elasmobranchs may have significant social, cultural, and economic impacts on the fishers and communities who depend on them (Jaiteh, Loneragan & Warren, 2017), as well as ecological consequences, altering important ecological processes such as predator-prey interactions and bioturbation from benthic feeding (Kyne & Bennett, 2002a; Flowers, Heithaus & Papastamatiou, 2020). The occurrence of large shark-like rays and stingrays and their high economic value has previously been used as justification for the continuation of the tangle net fishery (Amir, 1988). Given the current declining state of several batoid populations in SE Asia (IUCN, 2021), and the scale of Indonesia’s shark fishery (Jaiteh et al., 2016a), the contemporary catch of the tangle net fishery is likely not to be sustainable. However, the exact impact of the present-day tangle net fishery is unknown and requires detailed investigation, especially considering the impacts of other fisheries affecting different size classes, and the declines of batoid populations across SE Asia.

Length selective fishing mortality often drives a reduction in the catch length composition in heavily fished elasmobranch populations (Walker, 1998; Stevens et al., 2000). At the time of the landing site surveys in 2001 – 2005, several abundant species were landed close to their known maximum sizes. It can thus be inferred that the populations of wedgefishes, giant guitarfishes, and stingrays were experiencing length selective fishing mortality. It is expected that individuals from contemporary populations would be reaching a smaller maximum size and younger maximum age than previous generations due to fishing pressure (Thorson & Simpfendorfer, 2009). Sexual dimorphism is known to occur for numerous elasmobranch species, including *R. australiae, A. ocellatus* and *U. asperrimus* (Last et al., 2016), with females attaining a larger maximum size than males (White & Dharmadi, 2007). In the large-meshed tangle nets, larger sized female elasmobranchs are more likely to be captured than males. In the current study, the majority of *R. australiae, M. gerrardi/macrura,* and *P. uarnacoides* specimens were large females, with 16 individuals of *R. australiae* examined internally being pregnant (White & Dharmadi, 2007). The removal of large, breeding individuals from the population causes a reduction in the reproductive potential, resulting in rapid declines in these populations (Prince, 2005). The capture of large breeding females coupled with inferred population declines from decreasing number of tangle net vessels and reported landings data from 2017 – 2018, suggests that recruitment overfishing may have occurred for several species.

Recruitment overfishing occurs when the breeding stock size is reduced to a point where future recruitment declines strongly (Myers et al., 1994; Walters & Martell, 2004; Allen et al., 2013). This can be brought about through (a) a reduction of the number of young entering the population (capture of juveniles), and/or (b) indirectly through recruitment failure from environmental degradation, affecting the availability of resources and the size or suitability of nurseries, therefore further reducing the number of juveniles entering the population (Pauly, 1988). In fisheries where only adults or only the juveniles are caught, higher levels of fishing can be sustained (Simpfendorfer, 1999; Prince, 2005). The impact of other fisheries also likely contributed to these historical declines and may continue to affect contemporary fish stocks. When all age/size classes are fished, it is much more difficult to achieve sustainable outcomes. All life stages of these rays are experiencing fishing mortality from multiple fisheries in Indonesia. The smaller size classes for many of the species encountered in the tangle net fishery are also caught as bycatch or opportunistic catch in numerous other fisheries operating in Indonesian waters, i.e., trawls, hand- and long-lines, smaller mesh gillnets, and trammel nets. Recruitment overfishing substantially impacts the populations' productivity and may lead to collapse or prevent their recovery (Allen et al., 2013). Some species of wedgefish and giant guitarfish have a higher-than-average theoretical population productivity (i.e. recover at a faster rate from population declines) for chondrichthyans (**Chapter Six**). However, these species still have relatively low reproductive rates and long lifespans compared to teleost fish, and thus can only withstand modest to low levels of fishing mortality (Camhi et al., 1998; Musick, 1999; Cortés, 2000; Dulvy et al., 2014b). Combined with life history information, the magnitude of Indonesian chondrichthyan catches, and the knowledge of the effects of fisheries on large elasmobranch species that mainly takes adults (Prince, 2005; McAuley, Simpfendorfer & Hall, 2007; McAuley, Simpfendorfer & Wright, 2007), it is likely that these populations of rays are experiencing unsustainable levels of exploitation and have little potential for recovery without significant reductions in fishing mortality.

The sustainability of fisheries (both harvest and discards) and conservation-related research and management initiatives can be compromised by the misidentification of species (Garcia-Vazquez et al., 2012). Incorrect species identification is prevalent throughout multi-species fisheries where visual identification is challenging, and can lead to incidental overfishing, resulting in a higher risk of extinction for the misidentified species in the fishery (Metcalfe et al., 2007). While the latest available trade data from the Food and Agriculture Organization (FAO) do have separate trade categories for sharks, rays and skates, there is no genera- or species-specific information (Ramaschiello & Vannuccini, 2015). In SE Asia, *R. australiae* is the most commonly caught wedgefish species (Giles et al., 2016), yet due to similarities in morphology and identification issues, it is commonly confused with other large wedgefish species, in particular with *R. djiddensis, R. laevis* (Giles et al., 2016) and *R. palpebratus* (Compagno & Last, 2008). Historically, all four species of wedgefish have been referred to as 'white-spotted wedgefish' as the common name and/or *R. djiddensis* as the species name throughout the Indo-Pacific (Last et al., 2016). A recent clarification of species distributions has recognized that *R. djiddensis* is restricted to the Western Indian Ocean (Last et al., 2016).

A similar situation has occurred for *G. typus* and *Glaucostegus granulatus,* where records of the sharpnose guitarfish *G. granulatus* from the tangle net fishery in 1987, showed it constituted 4.6% of the total landed catch (Amir, 1988). This is likely to be a misidentification of *G. typus*, as prior to 2016, the range for *G. granulatus* was poorly described with no records to suggest that this species occurred in Indonesia, and is now known to only occur in the northern Indian Ocean between Myanmar and the Arabian/Persian Gulf (Last et al., 2016).

Misidentification of elasmobranchs can be further compounded by the ambiguity over the ranges of these species, as some species are rarer in landings and possibly have more of a restricted and/or fragmented spatial distribution. For example, the broadnose wedgefish *Rhynchobatus springeri* distribution overlaps with *R. australiae* off Java and Sumatra (Giles et al., 2016). The landed catches of small *Rhynchobatus* spp. during the 2001 – 2005 surveys could possibly have included this species, as the maximum known size for *R. springeri* is 213 cm TL (Last et al., 2016), compared to 300 cm TL for *R. australiae* (Last et al., 2016; Kyne et al., 2019b). The stingrays, *M. gerrardi* and *M. macrura* have overlapping distributions and differ in mostly subtle morphological characteristics (Last et al., 2016), thus without genetic identification, the two cannot be readily differentiated. However, our data could not be retrospectively confirmed as either or both species. As the catch records may comprise both *M. gerrardi* and *M. macrura*, the catch numbers must be used with caution. This complication in species differentiation is an ongoing issue that confounds efforts to quantify species-specific catch and consumption (e.g. Clark-Shen et al. (2021)). The lack of species-specific reporting was thought to have masked the known global declines for wedgefish and giant guitarfish throughout their distribution. From historical and contemporary records, there is evidence of population declines across all wedgefish and giant guitarfish species; however, the extent of declines for individual species are unknown due to the lack of species-specific time-series data (Kyne et al., 2019b). Species identification training for fisheries officials and observers, and the use of genetic identification such as *in-situ* DNA barcoding field kits (Booth et al., 2018), are some methods to address the lack of species-specific information and can help with law enforcement in Indonesia and SE Asia (Tillett et al., 2012).

Multi-species fisheries are complex social-ecological systems, and successful management will require multi-level governance (Ostrom et al., 1999). The Indonesian government is a signatory party of CITES, and it has taken important steps to implement international obligations under CITES and FAO National Plan of Action (NPOA) for the Conservation and Management of Sharks and Rays. It is working to regulate international trade originating from Indonesia through either full species protection (e.g. sawfishes, mobulids) or export controls. Appendix II-listed species can be landed and traded domestically, and there is no oversight by CITES unless the species is being exported internationally, which requires a positive Non-Detriment Finding. These measures would not necessarily affect the harvest and domestic use of these species, and do not cover the other 24 non – CITES elasmobranch species caught in the tangle net fishery. Currently there are no national or regional laws in Indonesia that specifically regulate the take and use of wedgefish, guitarfishes and stingrays (Rusandi et al., 2019). Scientific advice and information (e.g. monitoring of fisheries landings, supply chains) will be required to make management decisions for elasmobranch fisheries in SE Asia (Clark-Shen et al., 2021). Indonesia has complex fisheries supply and trade chains, from fishers to buyers to exporters, which have intricate interactions and different drivers occurring throughout the chain (Rusandi et al., 2019). To ensure the sustainable use of wedgefish, giant guitarfish and stingrays in Indonesia, management will be needed across multiple levels, from fisheries to exporters, with strategic and evidence-based methods (Booth et al., 2020). Improved trade monitoring and traceability, as well as awareness campaigns will be key to reduce fishing mortality, utilization, and trade (Clark-Shen et al., 2021).

Reducing fishing mortality must be directed at managing extraction as well as increasing the compliance and enforcement of trade regulations. For a targeted shark and ray fishery, technical management strategies that could be used to mitigate the risk of overfishing of stingrays, wedgefish and giant guitarfish in the tangle net fishery could involve gear restrictions, and spatial and temporal closures (Harry et al., 2011b; Yulianto et al., 2018). Given the size selectivity of the tangle net gear for larger animals, modifying the gear selectivity of the tangle net through the use of smaller mesh gill nets could reduce the capture of large, threatened rays. The tangle net fishery uses large mesh (50 – 60 cm) bottom-set nylon gillnets and using smaller mesh gill nets (e.g. < 45 cm) will likely reduce the capture of large and mature individuals of *R. australiae* and *M. gerrardi/macrura*. It would likely also reduce the fishing pressure on larger size classes of the other rays e.g. *P. ater, P. fai,* *P. jenkinsii,* and *P. uarnacoides.* Thus, adults will be subjected to the 'gauntlet effect' and effectively excluded, while juveniles are captured by the fishery (Simpfendorfer, 1999; Prince, 2005). This harvest strategy is considered an effective method to extract long-lived species (Simpfendorfer, 1999; Prince, 2005), provided that the fishing mortality on adults from other Indonesian fisheries remains low. Research on post release survival from different gear types such as smaller gillnets, trawls and longlines will be beneficial to understand the risks of certain gear types. Spatial and temporal closures (e.g. closure of breeding/nursery grounds) may be used to reduce fishing pressure on these rays. Marine protected areas (MPAs) are a widely used spatial tool for the protection of biodiversity, management of fisheries, and increasingly used as a strategy for conserving shark and ray populations (Davidson & Dulvy, 2017). Indonesia has committed to implement 30 million hectares of MPAs by 2030 and have already gazetted approximately 17 million hectares of MPAs as of 2021. However, it is unknown if the existing MPAs are in suitable locations for the conservation and protection of wedgefish and guitarfish. Identifying appropriate MPAs for these species will firstly require information on spatial ecology and movement, potential sex/ habitat segregation, and location of nursery areas. Secondly it will require the understanding of the socio-economic context and conditions of the local areas, including the capacity for enforcement, level of resource dependence and alternative livelihood options (MacKeracher, Diedrich & Simpfendorfer, 2019). Future research should examine the spatial ecology of wedgefish and, explore the role that MPAs can have on the conservation of wedgefish in Indonesia.

Managing the level of opportunistic catch and bycatch of wedgefish and rays in all fisheries will be difficult in Indonesia with limited fisheries management resources and capacity. Local and regional specific management will be required to address the overfishing of stocks, including potential reductions in fishing effort and fishing mortality (Vincent et al., 2014). Any viable management options and regulations will need to ensure that they are leading to noticeable conservation outcomes (Booth et al., 2020), as well as positive social and economic outcomes for fishers (Booth, Squires & Milner-Gulland, 2019). Appropriate and economically viable incentives for livelihood alternatives for fishers will be required to address the issues of poverty and food security in resources dependent communities (MacKeracher et al., 2020). Using a precautionary and holistic risk-based approach like a mitigation hierarchy framework as proposed by Booth, Squires & Milner-Gulland (2019) would be highly beneficial in Indonesia as it takes into the account the biological, social, and economic aspects of fisheries. This method has the capability of dealing with data paucity and could be used for the tangle net fishery. Regional management across multiple fisheries and life stages will be required to ensure the sustainability and conservation of wedgefish, giant guitarfish and stingrays that are being caught across a wide range of fisheries at all life stages.

4.5 Conclusion

There are concerns about the sustainability of the tangle net fishery and the population status of many of the ray species targeted. The potential increasing pressure on stingrays is also likely resulting in population declines and requires immediate investigation. Currently there is no known domestic management directly in place for this fishery. Several ray species landed in the tangle net fishery were also caught in other fisheries at different life stages, this will require management across multiple fisheries and life stages, instead of single fishery management, to ensure the sustainability and conservation of rays. This historical information was collected 20 years ago (2001 – 2005) and there are reports that the tangle net fishery remained active with seven operational vessels in 2018 down from a peak of 500 vessels historically. It would be expected then that 2001 – 2005 data already represents a significantly depleted population for wedgefish and giant guitarfish species in Indonesia. This continuing pressure will limit the ability of wedgefish to recover in the surrounding areas. Conservation measures were required for wedgefish populations and the tangle net fishery in Indonesia decades ago, and the results of this study emphasise the urgency for effective management for the conservation of these rays.

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Ethics Statement

All individuals examined in this study were landed from fisheries in Indonesia and were already dead upon inspection. Permission to undertake surveys in Indonesia was granted by the Research Centre for Fisheries Management and Conservation in Jakarta as part of collaborative projects funded by the Australian Centre for International Agricultural Research (ACIAR project codes FIS/2000/062 and FIS/2003/037).

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This research is dedicated to the memory of ‘Pak’ Dharmadi, a leader and pioneer in shark and ray research and management in Indonesia.

4.6 Appendices

Appendix 4.1. Dates of the landing port surveys conducted in the Muara Angke landing port, and the associated village processing area in Jakarta April 2001 – December 2005. Presence or absence of tangle net vessels at the landing port as recorded (Yes or No). The total number of species and specimens for rays and sharks per survey day are reported.

Date	Muara Angke	Village processing area	No. of ray species	No. of ray specimens	No. of shark species	No. of shark specimens
4/04/2001	**Yes**	No	14	Unknown	3	Unknown
5/04/2001	**Yes**	No	15	11*	2	Unknown
6/04/2001	No	No	--	--	--	--
27/06/2001	No	No	--	--	--	--
28/06/2001	No	No	--	--	--	--
11/07/2001	No	No	--	--	--	--
13/03/2002	No	No	--	--	--	--
14/03/2002	No	No	--	--	--	--
17/03/2002	No	No	--	--	--	--
20/03/2002	No	No	--	--	--	--
15/05/2002	**Yes**	No	10	159	0	0
16/05/2002	No	No	--	--	--	--
19/05/2002	No	No	--	--	--	--
20/05/2002	No	No	--	--	--	--
14/08/2002	No	**Yes**	15	197	2	3
15/08/2002	No	No	--	--	--	--
18/08/2002	No	No	--	--	--	--
18/10/2002	**Yes**	No	9	96	0	0
19/10/2002	No	No	--	--	--	--
31/01/2003	No	No	--	--	--	--
1/02/2003	No	No	--	--	--	--
9/02/2003	No	**Yes**	10	361	0	0
19/04/2004	No	No	--	--	--	--
21/04/2004	No	**Yes**[×]	--	--	--	--
22/04/2004	No	No	--	--	--	--
17/07/2004	**Yes**	No	13	147	2	4
18/07/2004	No	No	--	--	--	--
20/07/2004	No	**Yes**	1	49	0	0
21/07/2004	**Yes**	No	13	131	2	3
30/08/2004	No	No	--	--	--	--
31/08/2004	No	No	--	--	--	--
1/09/2004	No	No	--	--	--	--
4/10/2004	No	No	--	--	--	--
5/10/2004	No	No	--	--	--	--
6/10/2004	No	**Yes**	12	106	4	5
6/12/2004	No	No	--	--	--	--

7/12/2004	No	No	--	--	--	--
8/12/2004	No	No	--	--	--	--
23/01/2005	No	No	--	--	--	--
24/01/2005	No	No	--	--	--	--
13/03/2005	No	No	--	--	--	--
14/03/2005	No	No	--	--	--	--
15/03/2005	No	No	--	--	--	--
31/05/2005	No	No	--	--	--	--
1/06/2005	No	No	--	--	--	--
2/06/2005	No	No	--	--	--	--
15/07/2005	No	No	--	--	--	--
16/07/2005	**Yes**	No	8	51	0	0
4/10/2005	No	No	--	--	--	--
5/10/2005	**Yes**	**Yes**	14	239	5	8
7/10/2005	No	No	--	--	--	--
7/12/2005	No	No	--	--	--	--
8/12/2005	No	**Yes**	1	4	1	2
Total	8	7	--	1534	--	25

* Only 11 specimens were recorded from 5 species of rays, no information on the remaining 6 species of rays and sharks were documented

[x] No specimens were recorded on this day, informal interviews were conducted with the fishers on the price of fins, meat, and skins

Appendix 4.2. Length-weight relationship for the elasmobranch species caught in the Indonesian tangle-net fishery and landed in Muara Angke, Jakarta April 2001–December 2005.

Family	**Species**	***a***	***b***	R^2	**Source**
Pristidae	*Pristis pristis*	0.003	2.9985	0.949	Salini et al. (2007)
Glaucostegidae	*Glaucostegus thouini*	0.0046	2.9184	0.9797	White (2018)
	Glaucostegus typus	0.0046	2.9184	0.9797	White (2018)
Rhinidae	*Rhina ancylostoma*	0.008	3.012	0.9988	from length and weights in (Wallace, 1967; Gordon, 1992; Rajapackiam, Mohan & Rudramurthy, 2007)
	Rhynchobatus australiae	0.0045	2.9959	0.987	For *R. palpebratus* White et al. (2019)
	Rhynchobatus palpebratus	0.0045	2.9959	0.987	White et al. (2019)
Dasyatidae	*Bathytoshia lata*	--	--	--	Weight from Struhsaker (1969)
	Himantura leoparda	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Himantura uarnak	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Himantura undulata	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Maculabatis astra	0.0219	3.0471	0.9844	White et al. (2019)
	Maculabatis gerrardi	0.0219	3.0471	0.9844	White et al. (2019)
	Megatrygon microps	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Pastinachus ater	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Pateobatis fai	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Pateobatis jenkinsii	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Pateobatis uarnacoides	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Taeniurops meyeni	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
	Urogymnus asperrimus	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)

	Urogymnus granulatus	0.0728	2.7578	0.9737	For *H. australis* White et al. (2019)
Gymnuridae	*Gymnura zonura*	0.0050	3.078	0.977	White & Dharmadi (2007)
Aetobatidae	*Aetobatus ocellatus*	0.0276	2.87	0.98	for *A. ocellatus/narinari* Bassos-Hull et al. (2014)
Myliobatidae	*Aetomylaeus vespertilio*	0.0276	2.87	0.98	for *A. ocellatus/narinari* Bassos-Hull et al. (2014)
Carcharhinidae	*Carcharhinus amboinensis*	0.00194	3.27	0.986	Stevens & McLoughlin (1991)
	Carcharhinus obscurus	0.000032	2.7862	0.9649	Kohler, Casey & Turner (1996)
	Carcharhinus leucas	0.0111	2.923	0.908	(Compagno, 1984; Froese, Thorson & Reyes Jr, 2014)
	Carcharhinus limbatus	0.00251	3.125	0.989	Castro (1996)
Galeocerdidae	*Galeocerdo cuvier*	0.00141	3.24	--	Randall (1992)
Ginglymostomatidae	*Nebrius ferrugineus*	0.009006	2.911	0.988	Castro (2000)
Hemigaleidae	*Hemipristis elongatus*	0.00162	3.21	--	Stevens & McLoughlin (1991)
Sphyrnidae	*Sphyrna lewini*	0.00399	3.03	0.985	Stevens & Lyle (1989)
	Sphyrna mokarran	0.00123	3.24	0.991	Stevens & Lyle (1989)

Appendix 4.3. Temporal occurrence of elasmobranchs landed from tangle net vessels in Muara Angke landing site, Jakarta in April 2001–December 2005, over a total of 53 survey days, grouped by months that were surveyed

		2001			**2002**				**2003**		**2004**						**2005**						
Family	**Species**	Apr	Aug	Jul	Mar	May	Aug	Oct	Jan	Feb	Apr	Jul	Aug	Sep	Oct	Dec	Jan	Mar	May	Jun	Jul	Oct	Dec
Pristidae	*Pristis pristis*	--	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Glaucostegidae	*Glaucostegus thouini*	Y	--	--	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Glaucostegus typus	Y	--	--	--	--	--	--	--	--	--	Y	--	--	--	--	--	--	--	--	Y	--	--
Rhinidae	*Rhina ancylostoma*	Y	--	--	--	--	--	Y	--	--	--	Y	--	--	Y	--	--	--	--	--	Y	Y	Y
	Rhynchobatus australiae	Y	--	--	Y	--	Y	Y	--	--	--	Y	--	--	Y	--	--	--	--	--	Y	Y	--
	Rhynchobatus palpebratus	--	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Dasyatidae	*Bathytoshia lata*	--	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Himantura leoparda	Y	--	--	--	--	Y	--	--	Y	--	Y	--	--	Y	--	--	--	--	--	Y	Y	--
	Himantura uarnak	Y	--	--	Y	--	Y	--	--	Y	--	Y	--	--	Y	--	--	--	--	--	--	Y	--
	Himantura undulata	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	Y	--
	Maculabatis astra	--	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Maculabatis gerrardi/macrura	Y	--	--	Y	--	--	Y	--	Y	--	Y	--	--	Y	--	--	--	--	--	Y	Y	--
	Megatrygon microps	--	--	--	--	--	--	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	--	--
	Pastinachus ater	Y	--	--	Y	--	Y	Y	--	--	--	Y	--	--	Y	--	--	--	--	--	Y	Y	--
	Pateobatis fai	Y	--	--	Y	--	Y	Y	--	Y	--	Y	--	--	Y	--	--	--	--	--	--	Y	--
	Pateobatis jenkinsii	Y	--	--	Y	--	Y	Y	--	--	--	Y	--	--	Y	--	--	--	--	--	Y	Y	--
	Pateobatis uarnacoides	Y	--	--	--	--	Y	Y	--	Y	--	Y	--	--	Y	--	--	--	--	--	--	Y	--
	Taeniurops meyeni	Y	--	--	Y	--	Y	--	--	Y	--	Y	--	--	Y	--	--	--	--	--	--	Y	--
	Urogymnus asperrimus	Y	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Urogymnus granulatus	Y	--	--	Y	--	Y	--	--	Y	--	Y	--	--	Y	--	--	--	--	--	--	Y	--
Gymnuridae	*Gymnura zonura*	Y	--	--	--	--	--	Y	--	Y	--	Y	--	--	--	--	--	--	--	--	--	Y	--
Aetobatidae	*Aetobatus ocellatus*	Y	--	--	Y	--	Y	Y	--	--	--	Y	--	--	Y	--	--	--	--	--	Y	Y	--
Myliobatidae	*Aetomylaeus vespertilio*	Y	--	--	--	--	--	--	--	Y	--	Y	--	--	Y	--	--	--	--	--	--	--	--
Carcharhinidae	*Carcharhinus amboinensis*	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	Carcharhinus obscurus	--	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	Y	--
	Carcharhinus leucas	--	--	--	--	--	--	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	Y	--
	Carcharhinus limbatus	Y	--	--	--	--	Y	--	--	--	--	Y	--	--	Y	--	--	--	--	--	--	Y	--

	Galeocerdo cuvier	Y	--	--	--	--	Y	--	--	--	--	--	--	--	--	--	--	--	--	--	--	Y	--
Ginglymostomatidae	*Nebrius ferrugineus*	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	Y	--
Hemigaleidae	*Hemipristis elongatus*	--	--	--	--	--	--	--	--	--	--	--	--	--	Y	--	--	--	--	--	--	--	Y
Sphyrnidae	*Sphyrna lewini*	Y	--	--	--	--	--	--	--	--	--	Y	--	--	Y	--	--	--	--	--	--	--	--
	Sphyrna mokarran	Y	--	--	--	--	--	--	--	--	--	Y	--	--	Y	--	--	--	--	--	--	--	--
	Number of ray species	18	0	0	10	0	14	9	0	9	0	16	0	0	13	0	0	0	0	0	8	14	1
	Number of shark species	5	0	0	0	0	3	0	0	0	0	4	0	0	4	0	0	0	0	0	0	5	1
Total number of species observed		23	0	0	10	0	17	9	0	9	0	20	0	0	17	0	0	0	0	0	8	19	2

Appendix 4.4. Size at maturity (DW/TL cm) for species with length frequency data in the Indonesian tangle-net fishery and landed in Muara Angke, Jakarta April 2001–December 2005.

Species	Females	Males	Source
Rhynchobatus australiae	–	131	Compagno & Last (1999); White (2018)
Himantura leoparda	–	70 – 94	White & Dharmadi (2007); Last & Stevens (2009)
Himantura uarnak	–	82 – 84	Manjaji (2004); White et al. (2006b); White & Dharmadi (2007)
Maculabatis gerrardi	54	48	Manjaji (2004); White et al. (2006b); White & Dharmadi (2007)
Pastinachus ater	–	103	White (2018)
Pateobatis fai	–	108 – 122	White & Dharmadi (2007); Last & Stevens (2009)
Pateobatis jenkinsii	–	75 – 85	White & Dharmadi (2007); Last & Stevens (2009)
Pateobatis uarnacoides	–	76	Last & Compagno (1999); White et al. (2006b)
Taeniurops meyeni	–	100 – 110	White (2018)
Aetobatus ocellatus	100 – 110	130	Schluessel, Bennett & Collin (2010); Last et al. (2016)

Contemporary Muara Angke tangle net fishery: 2017 – 2018

Methods

Contemporary information on the tangle net fishery from the Muara Angke landing survey data were obtained from the Indonesian Centre for Fisheries Research, from 2nd January 2017 – 16th July 2018. The landed catch from every vessel, including vessels with no catch that landed at Muara Angke site was recorded in Bahasa Indonesia by the staff of the fish auction office for the Indonesian Centre for Fisheries Research. The date of arrival into the landing port, vessel, owner, fishing gear, total number of animals caught, and the main three species and landed catch caught per species in kilograms (kg) was recorded for each vessel. The data was translated to English by Dharmadi in 2018.

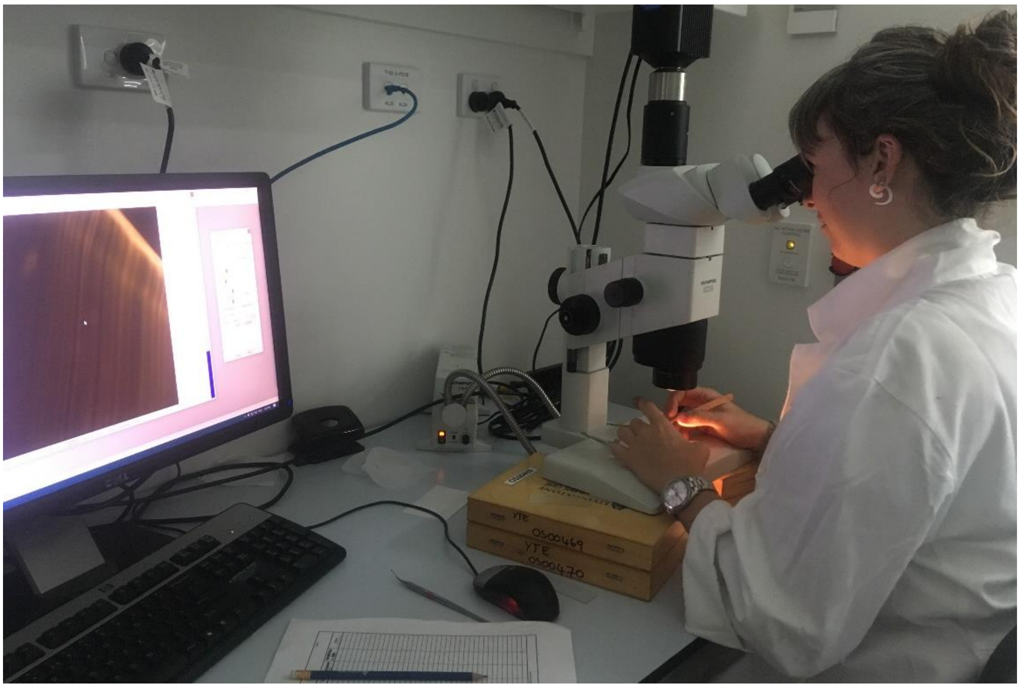
Results

A total of 198 vessel landings were recorded in the Muara Angke landing site during 2nd January 2017 to 16th July 2018. Of these landings, 14 were tangle net vessel landings from seven individual tangle net vessels (Table 4). The species are only recorded under single labels in Bahasa Indonesia of “yong bung/cucut liong bung” [=wedgefish/shark ray], “pari” [=rays], “cucut” [=sharks], “manyung” [=local catfish species, *Netuma* spp.] and ‘mix/mixed species’. Unidentified wedgefish species comprised a small component of the total landings for these tangle net vessels, with an estimated landed catch of 6 tonnes (Table 4). The majority of catch was recorded as rays with estimated landed catch of 43.9 tonnes, and unknown shark species were recorded once with 200 kg (Table 4). The local catfish species (*Netuma spp*.) was recorded from the tangle net landings, with an estimated catch of 5 tonnes, while unknown mixed species accounted for 8 tonnes (Table 4). No other data on species composition was recorded.

Appendix 4.5. Indonesian Capture Fisheries data on seven vessel landings from the tangle net fishery recorded at Muara Angke port in June 2017 – July 2018. The date of landing, vessel identifier (vessel ID) fishing gear, with main catch species, and landed catch weight (kilograms, kg) are reported. Dashed lines indicated no data was recorded. The species were recorded in Bahasa Indonesia, here they are reported in English with translation from Dharmadi. Source: Centre For Fisheries Research (2018)

Date of landing	Vessel ID	Species 1	Catch (kg)	Species 2	Catch (kg)	Species 3	Catch (kg)	Total
04/06/2017	SC-DA-040617	Rays	12,000	--	--	--	--	12,000
28/07/2017	HJ-OG-280717	--	--	--	--	--	--	--
13/09/2017	HJ-OG-130917	Rays	6,000	Mixed species	2,500	--	--	8,500
03/11/2017	BH-DA-031117	Rays	6,500	Mixed species	3,000	--	--	9,500
24/11/2017	KE-OG-241117	Rays	3,500	*Netuma spp.*	1,000	Mixed species	2,000	6,500
07/12/2017	KE-OG-071217	--	--	--	--	--	--	--
11/01/2018	KE-OG-110118	--	--	--	--	--	--	--
29/01/2018	HJ-OG-290118	Rays	4,500	Wedgefish spp 1	1,000	*Netuma spp.*	1,000	6,500
13/03/2018	BH-DA-130318	Rays	20,000	--	--			20,000
20/03/2018	KE-OG-200318	Sharks	200	*Netuma spp.*	1,000	Rays	3,000	4,200
29/03/2018	TS-HS-290318	--	--	--	--	--	--	--
06/06/2018	SC-DA-060618	--	--	--	--	--	--	--
26/06/2018	KE-OG-260618	Rays	5,900	*Netuma spp.*	2,000	--	--	7,900
07/07/2018	TS-HS-070718	Rays	2,503	Wedgefish spp 2	5,000	--	--	7,503

Chapter Five



Manuscript intended for publication associated with this chapter:

D'Alberto, B.M., Clark-Shen, N., Tingting, K.X., Green, M.E., Chin, A., Hutchinson, N., White, W. T., Simpfendorfer, C.A. (Intended for Publication) Back to basics: The life history of a critically endangered bottlenose wedgefish, *Rhynchobatus australiae* from SE Asia. Target journal: *Endangered Species Research.*

Nature and extent to contribution of co-contributors/authors to the chapter/manuscript

Study design was conceived by the candidate. Samples were collected in Singapore by Ms Xu, Ms Clark-Shen, and Dr Hutchison. Data for this chapter was processed and analysed by the candidate. The genetic analysis was conducted by the candidate and assisted by Dr Green. The candidate wrote the drafts of this chapter. Prof. Simpfendorfer, Dr Chin, and Dr Hutchinson helped with data interpretation and chapter edits.

5. Back to basics: Preliminary life history of the Critically Endangered bottlenose wedgefish *Rhynchobatus australiae* from Southeast Asia

5.1 Introduction

Accurately describing the life history parameters (age, growth, and reproduction) of a species is the foundation for understanding species biology, population dynamics and status. For species exposed to fishing, accurately characterising these parameters is important for fisheries stock assessment, and management and conservation, especially for long-lived, slow-growing, late-maturing and less-fecund species, such as elasmobranchs (sharks and rays) (Cortés, 2002). Coupled with knowledge of distribution, movement and abundance, this information can be used to predict how a species might respond to fishing pressure (Harry et al., 2011b), estimate sustainability of catches (Cailliet, 2015), estimate benefits of marine protected areas (Dwyer et al., 2020), and predict how quickly a species could recover from population declines (Dulvy et al., 2014b; D'Alberto et al., 2019).

Wedgefishes (Family Rhinidae) are among the most threatened marine taxa globally, with global populations experiencing substantial population declines from overfishing (Kyne et al., 2020). Wedgefishes are mainly caught as bycatch in fishing gears such as trawl nets, pelagic and bottom set long lines, purse seine nets, and gillnets, and are typically retained as valuable by-products of incidental catch (Moore, 2017; Jabado, 2018). The fins from wedgefish and giant guitarfish (Family Glaucostegidae) are classified as *Qun chi* in Hong Kong market, which is the highest classification due to high quality and texture of the fins (Hau et al., 2018). The high value of the fins in the international trade and the high-quality flesh in domestic markets are key drivers for their retention in coastal fisheries (Keong, 1996; Wu, 2016; Hau et al., 2018). To address concerns about the impact of the international trade, wedgefishes and giant guitarfishes were listed on Appendix II of the Convention of International Trade of Endangered Species of Wild Fauna and Flora (CITES) in 2019 (CoP18), which aims to ensure that the international trade of products from wedgefish come from sustainable sources (CITES, 2019b).

Singapore plays a significant role in the global trade through the importation and re-exportation of elasmobranch products and is a signatory Party of CITES (Boon, 2017; Clark-Shen et al., 2021). This small country is considered the second-largest importer and re-exporter of shark fins by value, which includes wedgefish and giant guitarfish fins (Boon, 2017). Singapore mainly relies on imports from neighbouring Asian countries to meet its seafood needs due to its small Exclusive Economic Zone and minor fishing fleet (total of 39 trawl vessels, including four off-shore) (Singapore Food Agency, 2019; Clark-Shen et al., 2021). The majority of the seafood supply originates from Indonesia and Malaysia (Boon, 2017), including large volumes of wedgefishes and giant guitarfishes (Choo et al., 2021; Clark-Shen et al., 2021). The fresh fillets or steak of wedgefish meat are sold at supermarkets, while cooked meat is sold in food centres (known as hawker centres)(Choo et al., 2021), including the wedgefish snout which is used in collagen soup (Clark-Shen et al., 2021).

Rhynchobatus australiae is a large (maximum reported size 323 cm total length, TL) (Faizah & Chodrijah, 2020) shark-like ray widespread throughout tropical and temperate waters in Indo – West Pacific Ocean from Mozambique to northern and eastern Australia [as far south as Ballina, NSW (Colefax et al., 2021)] and Fiji (Giles et al., 2016; Last et al., 2016)(**Chapter Three**). *Rhynchobatus australiae* are found primarily in soft benthos areas and most frequently at depths of 30 – 40m (White et al., 2013a) (**Chapter Three**). *Rhynchobatus australiae* is classified as Critically Endangered on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species, as it has experienced significant declines throughout its entire range (Kyne et al., 2019b). It is the most commonly caught wedgefish in SE Asia (Giles et al., 2016), yet due to similarities in morphology and identification issues, it is commonly confused with other large "look-alike" wedgefish species.

Historically, most species of wedgefish have been referred to as 'whitespotted wedgefish' and/or *R. djiddensis* throughout the Indo-Pacific, yet a recent clarification of species distributions has recognised that *R. djiddensis* is restricted to the Western Indian Ocean (Last et al., 2016). The similar morphological characteristics between wedgefish species have proved variable life history parameters in a study in the Great Barrier Reef (GBR) waters by White et al. (2014). White et al. (2014) estimated a growth completion rate of 0.40yr^{-1} using a two-parameter logistic growth function for *Rhynchobatus* spp. group, as these results were derived from an unresolved species complex with *R. australiae*, *R. palpebratus* and *R. laevis* along the eastern coast of Australia at the time of publication. Recent taxonomic revision has resolved this species complex, with *R. laevis* primarily found in the Arabian Sea and the Bay of Bengal in the Indian Ocean, and off China and Japan in the Western Pacific (Last et al., 2016). Meanwhile, further examination of data, including genetic analysis, associated with specimens examined by White et al. (2014) have demonstrated the Australian east coast samples were primarily *R. australiae* (D'Alberto et al., 2019). Upon re-analysis of the data using a three parameter frequentist multi-model growth analysis data from White et al. (2014) by D'Alberto et al. (2019), the growth completion rate for *R. australiae* was estimated to be 0.08 yr^{-1}, considerably slower than originally estimated, with the von Bertalanffy growth model as the most appropriate function. The estimated age at maturity of females and males was between 3 – 5 years old (D'Alberto et al., 2019). As a result of the early maturing, *R. australiae* has been inferred to have a higher-than-average population productivity compared to other chondrichthyans, and therefore can potentially recover from population declines more rapidly than other threatened species within the class (D'Alberto et al., 2019).

This study aimed to provide updated life history parameters for *R. australiae*, sourced from two fishery ports that import large volumes of wedgefishes in Singapore at Senoko Fishery Port (SFP) in north and Jurong Fishery Port (JFP) in the south (Clark-Shen et al., 2021). DNA barcoding was conducted to validate species identification, as morphological characteristics have proved variable in other studies (White et al., 2014). Due to the limited sample size and absences of large individuals, two modelling approaches were used, the frequentist growth model analysis and Bayesian growth models using Markov Chain Monte Carlo (MCMC) parameter estimation to account for uncertainty, and informative priors to improve the biological plausibility of growth estimates (Smart & Grammer, 2021). Accurate information on the life history of *R. australiae* can be used to inform the basis for the development of local and international management plans and conservation action for these threatened rays.

5.2 Material and Methods

5.2.1 Sample Collection

Samples were purchased by Singapore based enumerators (N.C.S. & K.X.T) from fish merchants at two government run facilities: Senoko Fishery Port (SFP) in the north (domestic fishing vessels) and Jurong Fishery Port (JFP) in the south (foreign fishing vessels)(Singapore Food Agency, 2019). Sampling was conducted twice per month in July, August, October and December 2018 and January, February, June, and July in 2019, during surveys reported in Clark-Shen et al. (2021). These ports receive whole, fresh products and are separate from the ports in Singapore that received dried goods such as dried shark fins. Local and regional fishing boats and trucks deliver seafood to the fishery ports during the early morning hours. For half of the survey period JFP was surveyed before SFP, and for half of the survey period SFP was surveyed before JFP to gain insights to the port activity at various times. The two ports were surveyed in the same morning between 00:30 and 04:00am (e.g. SFP from 00:30 to 01:30, and then JFP from 02:00 to 04:00). The country and port of origin recorded by the Singapore based enumerators was used to assign fishing countries and export points for wedgefish. The purchase prices were converted from Singapore Dollar (SGD) to US Dollar (USD) prices using an online currency converter (www.xe.com/currencyconverter/; 1 USD = 0.74 SGD as of October 2021).

The wedgefish collected were brought back to the laboratory and stored frozen until dissection. The wet weight (kg) and length measurements were recorded once the samples were thawed prior to dissections. Total length (TL; length from the tip of the snout to the furthest tip of the tail) was recorded for wedgefish sample with fins attached upon purchasing, as well as fork length (FL; length from the tip of the snout to the centre/fork of the tail) and pre-caudal length (PCL; length from the tip of the snout to the deepest part of the pre-caudal notch). For these specimens with dorsal, second dorsal and caudal fins removed prior to purchasing, the PCL was recorded and converted to total length using the following equation generated from the data collected in this study and unpublished data from northern Australia (D'Alberto, 2021) and Indonesia (White, 2021) (**Appendix 5.2**; **Appendix 5.3**):

$$TL = PCL \times 1.2175 - 13.305; r^2 = 0.99$$

A segment of the vertebral column (~10cm length) was removed from between the cranium and first dorsal fin, including a section of the cervical synarcual, which is a section of fused vertebral column located behind cranium (**Figure 5.1 A**), and stored frozen for subsequent age determination. Photographs were taken of each individual before processing.

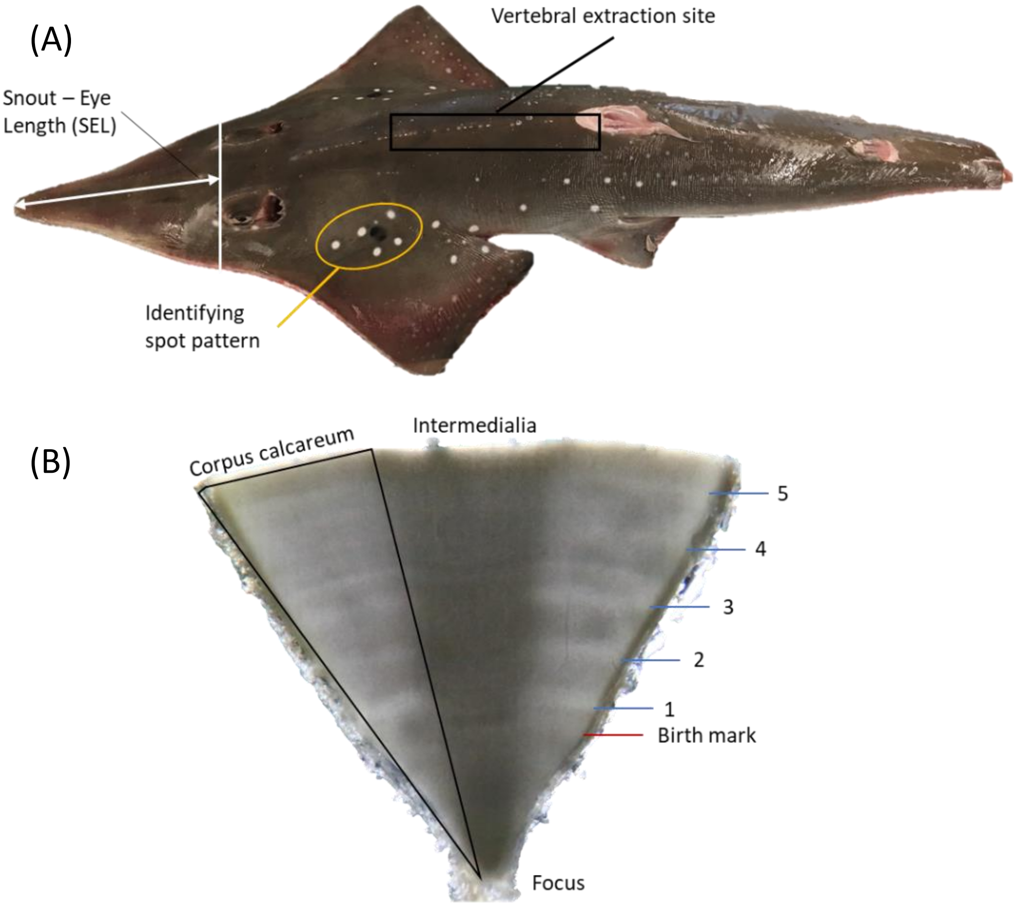


Figure 5.1. (**A**) Illustration of bottlenose wedgefish *Rhynchobatus australiae* highlighting the line of three white spots (yellow circle) diagnostic in this species, measurement of snout to eye length (SEL; white arrows) and location of the vertebral extraction site for age and growth analysis (black rectangle); (**B**) Photograph of a section vertebral centra for male *R. australiae*, aged to 5 years old at 96.6 cm total length (TL), sampled from Jurong Fishery Port in Singapore in July 2019. The location of the birth mark (red dash), corpus calcareum, focus, intermedialia, and estimated vertebral bands (blue dashes) are indicated.

5.2.2 DNA barcoding of tissue samples for species identification

Tissue samples for DNA barcoding were excised from the vertebral chord or remaining muscle around the vertebrae and preserved in 100% analytical-grade ethanol. DNA from vertebral chord or muscle samples was extracted using the DNeasy Blood & Tissue Kit (Qiagen, USA) following manufacturer’s instructions and with starting material of approximately 0.25 g. Genetic species identification was undertaken using the NADH2 region of the mitochondrial genome with primers ILEM (5'-AAG GAG CAG TTT GAT AGA GT-3') and ASMN (5'-AAC GCT TAG CTG TTA ATT AA-3') (Naylor et al., 2005). Polymerase chain reactions (PCRs) were undertaken in 25 mL volumes using Multiplex PCR kit (Qiagen, USA), 10 mM primers and DNA (15-25 ng). The PCR used the following thermocycler parameters; initial hold at 95°C/ 15 min, 30 cycles of 94°C/ 30 sec, 50°C/ 90 sec, 72°C/ 90 sec, followed by final extension of 72°C/ 10 min. Following PCR, products were cleaned with Agencourt AMPure magnetic beads (Beckman Coulter, Australia). Successfully amplified PCR products were sent to Australian Genome Research Facility (AGRF) for bi-directional Sanger sequencing. Forward and reverse sequences were assembled into consensus sequences using Geneious® Prime (Biomatters Ltd Auckland, New Zealand; http://www.geneious. com). Consensus sequences were aligned within Geneious and sequence identity was confirmed by using the BLAST module in Geneious against known and validated ND2 sequences of *R. springeri*, *R. palpebratus* and *R. australiae* provided by G. Naylor.

5.2.3 Vertebrae preparation and processing

Vertebral preparation and sectioning followed standard protocols detailed in Cailliet & Goldman (2004). After thawing, the haemal arch, neural arch, and muscle flesh were removed using a scalpel. Individual vertebral centra were separated and soaked in 5% sodium hypochlorite solution for up to 30 minutes to remove residual soft tissues. Centra were thoroughly rinsed under tap water and dried in an oven at 60 °C for 24 h (Simpfendorfer et al., 2000). The largest centra with no to minimal defects (e.g. scalpel cuts, staining) was selected to be sectioned. A low-speed rotary saw with twin diamond-tipped blades (Beuhler, Illionois, USA) was used to take longitudinal sections (400 µm thick) through the focus (centre of the vertebrae) of individual centra. The sections were mounted onto microscope slides using Crystal Bond adhesive (SPI supplies, Pennsylvania, USA) for analysis and storage. Centra that were too small to be loaded into the chuck of the sectioning saw were sectioned by hand sanding. Single centra were mounted onto a microscope slide using Crystal bond adhesive and sanded under 20mm of water towards the centre of the centrum using 400 grit wet and dry abrasive papers. Once one side was completed, the centrum was remounted and sanded again on the other side until the desired thickness was achieved (Simpfendorfer, 1993).

5.2.4 Age determination

Digital images of sectioned centra were taken under transmitted light using a Leica M165C dissecting microscope with a Canon EOS 6D (WG) digital camera. Samples were counted independently by three experienced readers (B.M.D., C.A.S. & A.C.) without any prior knowledge of the length or sex of the individual to minimise bias in the age estimates. The birth mark was identified by the change in angle of the inner margin of the corpus calcareum, demonstrating the transition from pre- to post-natal growth and was considered to be age zero (**Figure 5.1 B**). Age estimates were generated by counting the visible opaque bands in the corpus calcareum. The spacing and clarity of bands, inflections near the outside and inside edges of the corpus calcareum, and band continuity across the intermedialia were used to help distinguish true bands from checks (McPhie & Campana, 2009). Marginal increment analysis was conducted to validate the periodicity of the growth band pair formation, as samples were not able to be collected every month. Band pairs were assumed to be annual, based on the marginal increment analysis of a similar sized species of shark-like ray, *G. cemiculus* (Enajjar, Bradai & Bouain, 2012) (**Figure 5.1 A**). Section quality was rated on a scale of “0” (unreadable) to “4” (very clear banding), with quality being dependent on criteria such as band clarity along the corpus calcareum and closeness of the sagittal cut to the focus (McPhie & Campana, 2009).

Samples with differing counts between readers were re-examined collaboratively and a consensus age was agreed upon. If no consensus age could be agreed, then the samples were excluded from the analysis. Systematic bias of the growth band estimates between the three readers (first vs second, first vs third, and second vs third) was investigated with the unpooled Bowker’s tests of symmetry, using the ‘ageBias’ function in ‘R’ programme environment using the FSA package (R version 1.4.1717) (Ogle, Wheeler & Dinno, 2020). Pairwise age bias plots were generated for each iteration of reader estimates. Inter-reader precision was assessed using percentage agreement of samples for which all age estimates perfectly agree (PA), Chang’s coefficient of variation (CV), and average percentage error within a sample using mean as the divisor (APE), with the ‘agePrecision’ function in the FSA package (Ogle, Wheeler & Dinno, 2020).

5.2.5 Growth modelling

Due to the limited sample size and absences of large individuals, two model fitting approaches were applied to the length-at-age data, (1) a frequentist approach where models were fit using non-linear least squares, and (2) a Bayesian approach using Markov chain Monte Carlo simulation (MCMC). A multi-model framework was applied to the length-at-age data for three candidate growth functions chosen *a priori*: von Bertalanffy (VBGF), Gompertz, and logistic growth models (Thorson & Simpfendorfer, 2009; Smart et al., 2016). All models (**Table 5.1**) were fitted using frequentist and Bayesian approaches. The use of a multi-model framework generates the most robust growth estimates and avoided the possibility of using an inappropriate model, as the use of single model such as VBGF can bias growth estimations if it is unsuitable for the species' growth (Katsanevakis, 2006; Smart et al., 2016b).

Table 5.1. Model equations of the three candidate growth functions used to estimate the growth parameters of bottlenose wedgefish *Rhynchobatus australiae* collected at two Singapore Fish Markets, where L_t= length-at-age t; L_∞= asymptotic length; L_0 =length-at-age 0; *k*, g_{Log} and g_{Gom}= growth-completion coefficients of the respective models.

Model	Growth function equation	Reference
VBGF	$L_t = L_0 + (L_\infty - L_0)(1 - \exp(-kt))$	Von Bertalanffy (1938)
Logistic function	$L_t = \dfrac{L_\infty - L_0(\exp(g_{Log}))}{L_\infty + L_0(\exp(g_{Log} - 1))}$	Ricker (1979)
Gompertz function	$L_t = L_0\, e \ln(\frac{L_\infty}{L_0})(1 - e^{-g_{Gom}})$	Ricker (1975)

Frequentist approach

The frequentist growth curves were generated using the 'AquaticLifeHistory' package for the three growth models (Smart et al., 2019). Best-fit parameter estimates with standard error estimates were generated for all three candidate models using the 'nls' function in the 'R' programme environment (R version 1.4.1717) (R Core Team, 2021).

Model performance evaluation and selection was conducted using the Akaike's information criterion (*AIC*) with a small sample size bias correction algorithm (AIC_C). The use of sample size adjusted bias correction is recommended for sample sizes less than 200 (Zhu, Li &

Liang, 2009). This sample size bias algorithm provides a measure of model fit and complexity, allowing for simultaneous comparisons of growth models (Natanson et al., 2014). AIC_C was calculated as follows:

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

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

$$\Delta_i = AIC_{C,i} - AIC_{min}$$

Models that had the highest support had Δ values from 0 – 2, whereas models where Δ = 2-10 had substantially less support, and modes with little or no support had Δ values of > 10 (Burnham & Anderson, 2003). The probability of choosing the correct model from the set of candidate models was calculated using AIC weights (w) as:

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

A likelihood ratio test was used to determine if sexes should be modelled separately or combined (Kimura, 1980). This was performed for the best fitting model, using the method described by Haddon (2001), which was modified for the ‘R’ program environment (R Core Team, 2021). If a significant difference between male and female growth curves was detected for either data set, then separate growth curves were produced.

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

$$t_{max} = 7 \times ln(2 \div k)$$

where t_{max} is the longevity in years and k is the growth coefficient of the VBGF (Mollet, Ezcurra & O'Sullivan, 2002).

Bayesian approach

The Bayesian growth curves were created using the ‘BayesGrowth’ package (Smart & Grammer, 2021). The parameter estimates for asymptotic length (L_∞), length-at-birth (L_0) and growth-completion coefficient (k for VBGF, gG for Gompertz and gL logistic) for each growth model was estimated using the ‘Estimate_MCMC_growth’ wrapper function. Normally distributed priors were used for L_∞ (set at known maximum total length for females at 3230 mm TL and males 2950 mm TL) and L_0 (as length at birth is currently not recorded for this species and the smallest individual sampled was 506 mm a birth size of 500 mm was used). The standard errors for the L_∞ and L_0 priors was set at 100 mm and 131 mm, respectively. All models were fitted using a normal distribution with error denoted as σ. Non-informative priors were used for σ and the growth-completion coefficient parameters (*k* for VBGF, *gG* for Gompertz and *gL* logistic) to ensure that the priors for all three growth models were consistent.

The best fitting growth model was identified using the 'Compare_Growth_Models' function in the 'BayesGrowth' package (Smart & Grammer, 2021). This was conducted by using the 'Leave One Out' (*LOO*) cross validation analysis and Widely Application Information Criterion (*WAIC*). The leave-one-out-information criterion (*LOOIC*) and LOOIC weights (*LOOICw*) was calculated, of which the model with the lowest weights was selected to be the most appropriate growth model. These two functions are equivalent to Akaike's Information Criterion weights (*AICw*) (Akaike 1998) for frequentist model selection (Smart & Grammer, 2021). The growth curves for all three models were constructed using the 'Calculate_MCMC_growth_curve' function in the 'BayesGrowth' package (Smart & Grammer, 2021).

5.2.6 Reproductive biology

The internal reproductive condition and maturity were recorded for all samples. For males, clasper length was recorded in mm, from where the clasper joins the pelvic fin to the end of the clasper. Males were internally inspected for flowing sperm from the cloaca upon pressure applied to the seminal vesicle or presence of sperm in the clasper groove flowing freely (Stehmann, 2002). For females, the uterus condition was inspected internally (**Table 5.2**). The number of yolky ova present in the ovary were recorded, where the yolky ova have a distinct yellow colouration whereas non-yolky ova were white. The maximum ova diameter (MOD) for largest ova present in the ovary was measured to the nearest mm.

The maturity of each individual was staged using an index modified from Walker (2005) (**Table 5.2**). For males, the maturity was staged based on the clasper condition and the maturity stage of females was based on the uterus condition (**Table 5.2**). The maturity stage data was converted to a binary maturity category (immature = 0, mature = 1) for statistical analysis. Population estimates of length at maturity for produced for males and females using a logistic regression equation (Walker, 2005):

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

where $P(l)$ is the proportion of the population mature at total length (l) and P_{max} is the maximum proportion of mature individuals. The lengths that 50% (l_{50}) and 95% (l_{95}) of the population were mature were estimated using a generalised linear model (GLM) with a binomial error structure with a logit-link function in the 'R' program environment (R Core Team, 2021). Population estimates for age-at-maturity for the ages 50% (a_{50}) and 95% (a_{95}) were estimated using the same methods.

Table 5.2. Reproductive indices used for staging the maturity condition oviparous and viviparous cartilaginous fishes. Adapted from Walker (2005)

Organ	Index	Description	Binary maturity condition
Female Uterus	U = 1	Uteri uniformly thin and white tubular structure. Small ovaries and with no yolked ova	Immature
	U = 2	Uterus thin, tubular structure that is partly enlarged posteriorly. Small yolked ova developing in ovary	Immature
	U = 3	Uterus uniformly enlarged tubular structure. Yolked ova developing in ovary	Mature
	U = 4	Uterus enlarged with *in utero* eggs or embryos macroscopically visible – pregnant	Mature
	U = 5	Uterus enlarged, flaccid and distended tubular structure – post partum	Mature
Male Clasper	C = 1	Pliable with no calcification	Immature
	C = 2	Partly calcified	Immature
	C = 3	Rigid and fully calcified	Mature

5.3 Results

5.3.1 Sample composition

A total of 51 wedgefish specimens were purchased from JFP (n = 31) and SFP (n = 20) (**Appendix 5.1**) over eight trips. The majority of the wedgefish were imported from

Indonesia (*n* = 35), with four samples reported to have been imported from Malaysia, and 12 samples had unknown origins, therefore the sample will be referred to as the Southeast (SE) Asian population. Genetic sequencing confirmed that 49 of the specimens were *R. australiae* and two samples were eyebrow wedgefish *Rhynchobatus palpebratus*, which were excluded from the analysis (**Appendix 5.4**). One female *R. australiae* with its snout removed below the eyes, was excluded from the analysis due to concerns of the length conversions. In total, 28 females with a total length range of 506 – 1417 mm TL (**Figure 5.2 A**) and 20 males with a total length range of 512 – 1645 mm TL (**Figure 5.2 B**) were analysed for vertebral and maturity analysis. Thirty-nine wedgefish samples (81%; *n* = 48) had dorsal, second dorsal and caudal fins removed prior to the sample collection, with total length range of 631 – 1645 mm TL. Nine samples were whole with fins attached upon sample collection (19%) with length range of 506 – 1122 mm TL.

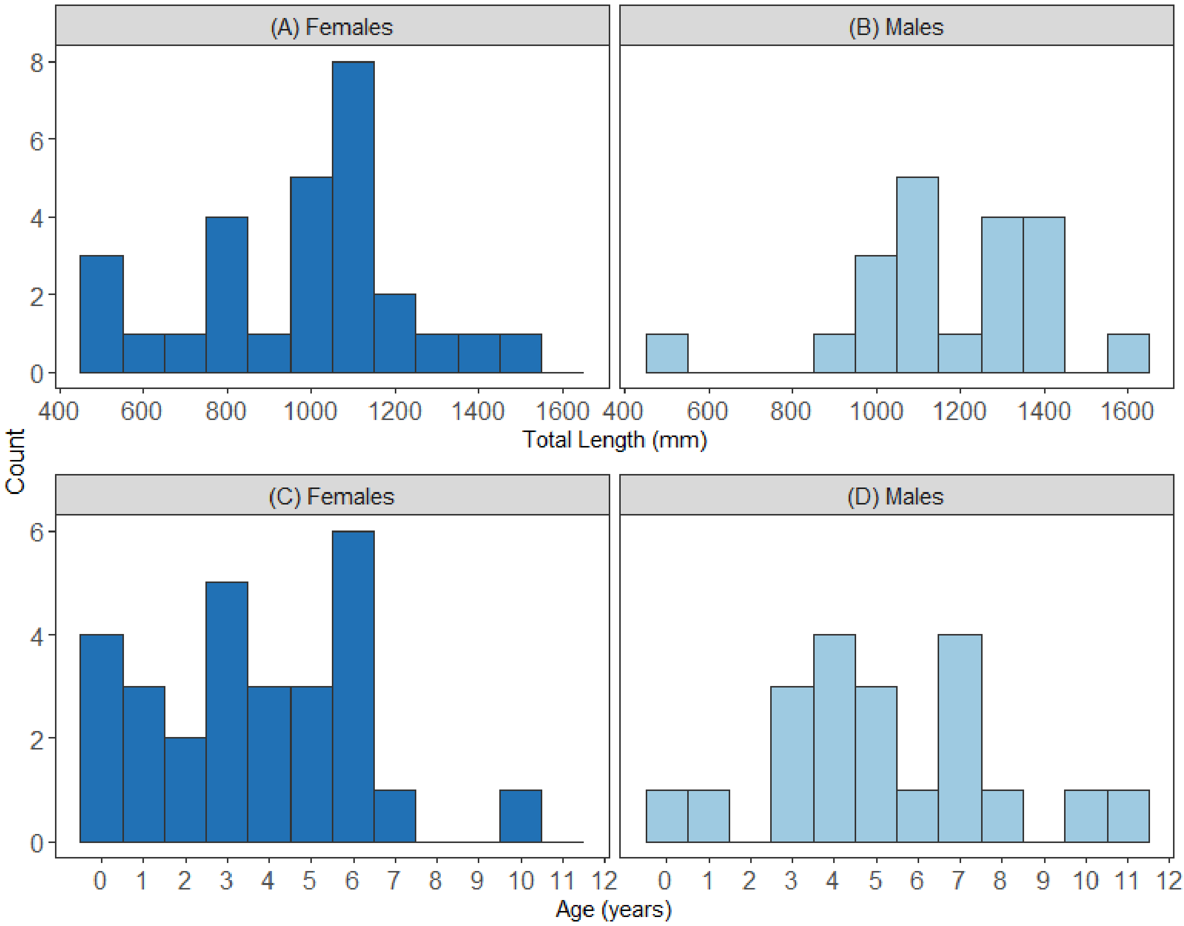


Figure 5.2. Sample composition of bottlenose wedgefish *Rhynchobatus australiae* for total length (mm TL) for (**A**) females and (**B**) males, and the estimated ages (years) for (**C**) females and (**D**) males, from two Singapore Fish Markets, sampled between October 2018 – August 2019

5.3.2 Age estimates

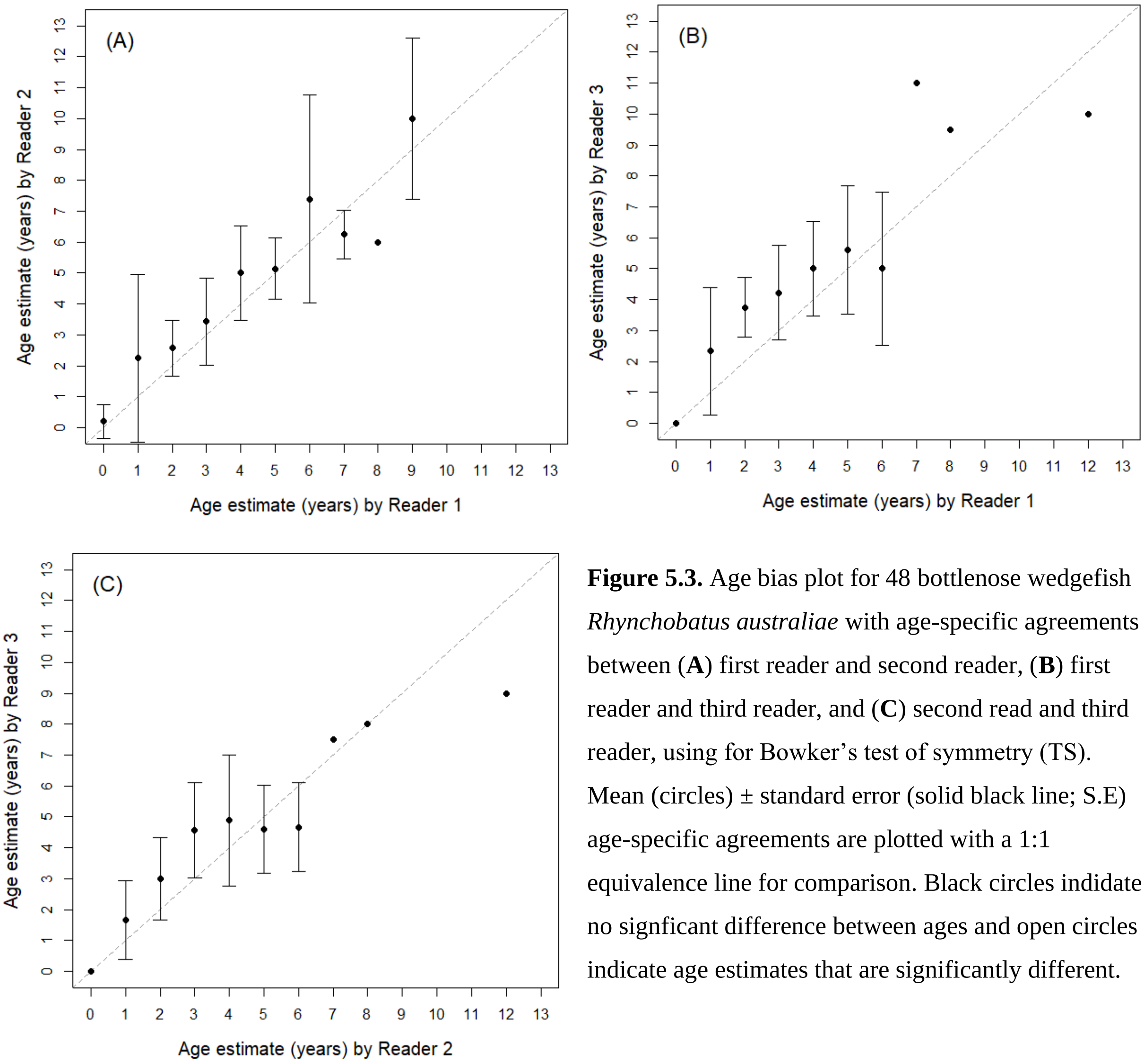


Figure 5.3. Age bias plot for 48 bottlenose wedgefish *Rhynchobatus australiae* with age-specific agreements between (**A**) first reader and second reader, (**B**) first reader and third reader, and (**C**) second read and third reader, using for Bowker's test of symmetry (TS). Mean (circles) ± standard error (solid black line; S.E) age-specific agreements are plotted with a 1:1 equivalence line for comparison. Black circles indidate no signficant difference between ages and open circles indicate age estimates that are significantly different.

The age estimates presented in this study are preliminary as the assumption of annual deposition of the growth band rings could not be verified by methods such as monthly increment analysis. Estimated ages for *R. australiae* ranged between 0 – 10 years for females (**Figure 5.2 C**) and 0 – 11 years for males (**Figure 5.2 D**). Across the three independent readers, there was no systematic bias of age estimates detected (Figure 3). Between Reader One and Two, the percentage agreement (PA ± 1 year) between readers was 25.5% with slight variation around the 1:1 line, as Reader 2 ageing older than Reader 1 (**Figure 5.3 A**). The average percentage error (APE) and Chang's coefficient of variation (CV) of the age estimates were 17.7% and 25.1%, respectively. No systematic bias was detected across the age range (Bowker's test of symmetry, *d.f.* = 18, χ^2 = 14.5, *p* = 0.69; **Figure 5.3 A**). Between Reader One and Three, the PA ± 1 year between readers was 24.5%. The APE and CV of the age estimates were higher than between Reader One and Two at 22.1% and 31.3%, respectively. There was no systematic bias was detected across the age range (Bowker's test of symmetry, *d.f.* = 21, χ^2 = 25.1, *p* = 0.24; **Figure 5.3 B**). Between Reader Two and Three, the PA ± 1 year between readers was 20.4%. The APE and CV of the age estimates were higher than between Reader One and Two at 21.4% and 30.3%, respectively. There was no systematic bias was detected across the age range (Bowker's test of symmetry, *d.f.* = 21, χ^2 = 20.0, *p* = 0.52; **Figure 5.3 C**). Comparing all three reader estimates together, the PA +1 was 10.2%, APE was 19.6%, and the average CV was 31.5%.

5.3.3 Growth modelling

The likelihood ratio test found no significant difference in growth completion rate for von Bertalanffy growth curves between females and males (χ^2 = 7.61, *p* = 0.055). However, there was a significant difference in growth completion rate between the two sexes for the Logistic growth curves (χ^2 = 9.33, *p* = 0.025) and Gompertz growth curve (χ^2 = 9.22, *p* = 0.026) based on the observed length-at-age data. On this basis growth models were produced for sexes combined and separately.

Frequentist approach

The von Bertalanffy growth model was the best fit for the observed length-at-age data based on the *AICc* weights (**Table 5.3**). A pronounced asymptote was not observed in growth curves from combined sexes, and the asymptotic length parameter was smaller than the known maximum length for *R. australiae* (**Figure 5.4 A**). The length at birth parameter was larger than the observed samples aged at zero years. The von Bertalanffy frequentist growth model estimated a growth completion rate of 0.14 yr^{-1}, and a theoretical longevity of 18.5 years (**Table 5.3**).

Separate growth curves for individual sexes were produced using the frequentist models. The von Bertalanffy growth model was the best fit for both female and male *R. australiae* (**Table 5.3**; **Figure 5.4**). Males were estimated to have a slower growth completion rate than females (**Table 5.3**; **Figure 5.4 B, C**). The estimated asymptotic length for females and males was estimated to be smaller than the known maximum length. A pronounced asymptote was not observed in growth curve for females, while there was a slight asymptote for the males

(**Figure 5.4 B, C**). The modelled sizes at birth for females and males was greater than the empirical size at birth of 512mm from this study (**Table 5.3**).

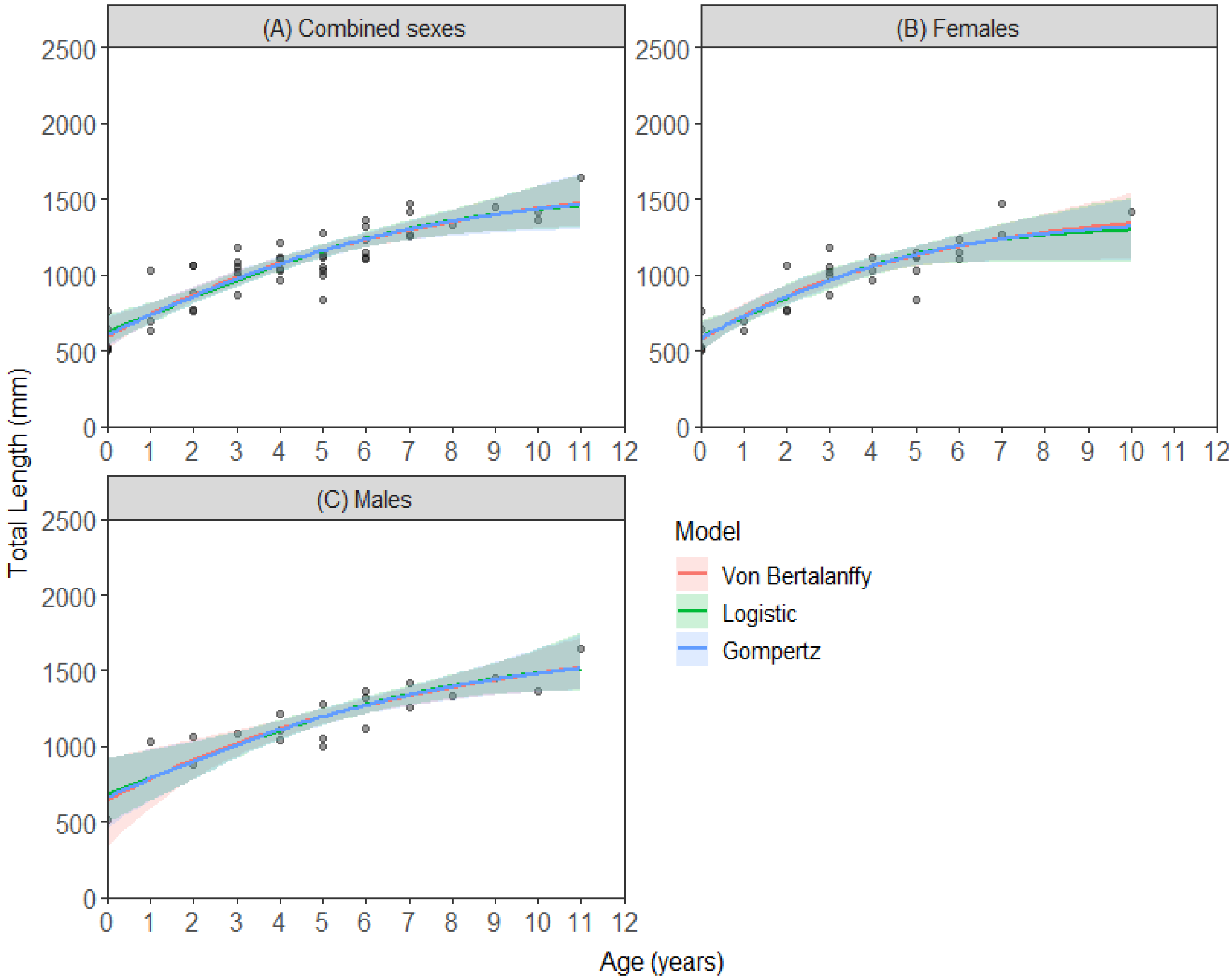


Figure 5.4. Multi-model length-at-age growth curves for bottlenose wedgefish *Rhynchobatus australiae* generated by the Frequentist growth modelling approach for (**A**) combined sexes (*n* = 48), (**B**) females (*n* = 28) and (**C**) males (*n* = 20), sampled from Senoko Fishery Port (SFP) and Jurong Fishery Port (JFP) in Singapore from September 2017 to September 2018, and January 2019 to January 2020.

Bayesian approach

Based on the LOOIC weights, the VBGF was the best performing model for the combined sexes (**Table 5.4**). The Bayesian VB growth function estimated a slower growth completion rate than the Frequentist VB growth function, and an older theoretical longevity estimate (**Table 5.4**). The multi model growth analysis using the Bayesian approach provided far more biologically realistic parameters than the frequentist growth functions (**Table 5.4**). When growth was analysed separately for each sex, similar to the frequentist results, the VBGF model was the most appropriate for both female and male *R. australiae* (**Table 5.4**). The growth completion coefficient estimates differed very slightly between sexes using the Bayesian approach (**Table 5.4**; **Figure 5.5**). Females were estimated to have a greater asymptotic length and slower growth completion coefficients than males. The length at birth estimates were similar for females and males and within the known documented range (**Table 5.4**; **Figure 5.5**; **Figure 5.6**). The results indicated that growth of wedgefish was relatively slow, taking four years to double in size from birth (~500 mm to 1000 mm).

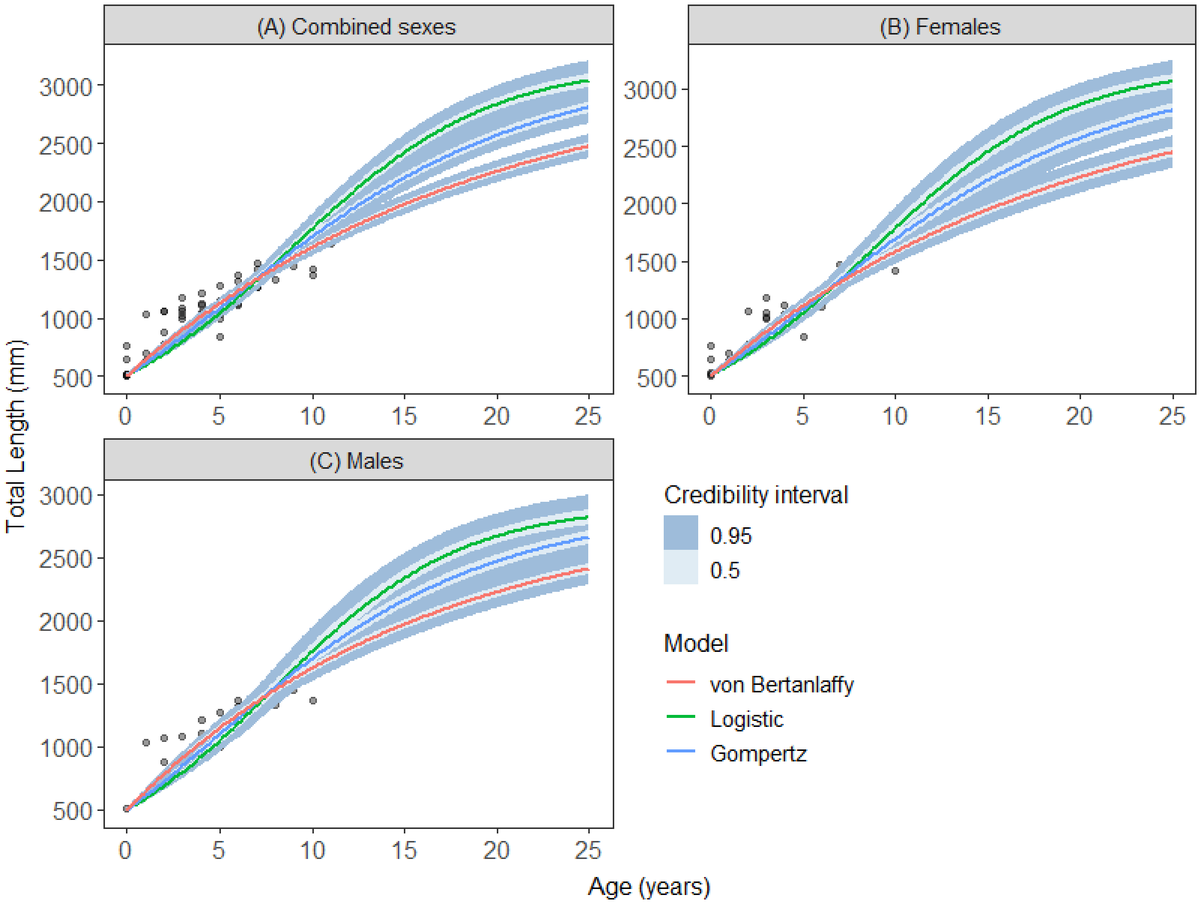


Figure 5.5. Multi-model length-at-age growth curves for bottlenose wedgefish *Rhynchobatus australiae* generated by the Bayesian growth modelling approach with a maximum age of 25 years, for (**A**) combined sexes, (**B**) females and (**C**) males, sampled from Senoko Fishery Port (SFP) and Jurong Fishery Port (JFP) in Singapore from September 2017 to September 2018, and January 2019 to January 2020.

Table 5.3. Summary of Frequentist model parameter estimates and Akaike's information criterion corrected for small sample size (AICc) performance of the three models used for the combined (females and males) and separate sexes observed length-at-age data (with removed outlier) for bottlenose wedgefish *Rhynchobatus australiae* from Singapore Fish Markets, sampled between October 2018 – August 2019. The best fitting model is highlighted in bold; VBGF, the von Bertalanffy growth function; *n*, sample size; *Δ*, difference between AIC_C values; *w*, AIC_C weights; L_∞, asymptotic length mm total length (TL); S.E., standard error; *k*, von Bertalanffy growth completion rate; *g*, Gompertz/Logistic growth completion rate; L_0, length-at-birth mm TL.

		Model Performance				**Model Parameter Estimates**						**Theoretical Longevity**
	Model	***n***	***AICc***	***Δ***	***w***	**L_∞ (mm TL)**	**± S.E.**	**k/g (yr^{-1})**	**± S.E.**	**L_0 (mm TL)**	**± S.E.**	
Combined	**VBGF**	**48**	**605.3**	**0.00**	**0.51**	**1711.9**	**240.1**	**0.14**	**0.05**	**597.8**	**48.0**	18.54
	Logistic	48	607.4	2.04	0.18	1535.5	121.2	0.30	0.06	628.0	44.3	
	Gompertz	48	606.3	1.00	0.31	1592.6	154.8	0.22	0.06	613.2	46.0	
Females	**VBGF**	**28**	**356.2**	**0.00**	**0.43**	**1471.2**	**233.8**	**0.19**	**0.09**	**577.1**	**56.1**	16.34
	Logistic	28	357.4	1.19	0.24	1325.3	116.9	0.41	0.12	591.7	53.8	
	Gompertz	28	356.7	0.55	0.33	1379.6	153.6	0.30	0.10	584.7	54.7	
Males	**VBGF**	**20**	**256.3**	**0.00**	**0.36**	**1781.7**	**358**	**0.13**	**0.08**	**649.1**	**99.6**	19.13
	Logistic	20	256.6	0.33	0.31	1615.2	185.9	0.27	0.09	684.7	88.8	
	Gompertz	20	256.5	0.20	0.33	1674.8	240.9	0.2	0.08	669	93.8	

Table 5.4. Summary of Bayesian model parameter estimates and leave-one-out-information criterion (LOOIC) performance of the three models used for the combined (females and males) and separate sexes observed length-at-age data with outlier removed for bottlenose wedgefish *Rhynchobatus australiae*. Samples were collected from Singapore Fish Markets, between October 2018 – August 2019. The LOOIC weight (w) values are similar to the Akaike Information Criterion weight (*AICw*) values and determine the most appropriate growth model, which is highlighted in bold; VBGF, the von Bertalanffy growth function; n, sample size; S.E., standard error; L_{∞}, asymptotic length mm total length (TL); *k*, von Bertalanffy growth completion rate; *g*, Gompertz/Logistic growth completion rate; L_0, length-at-birth cm TL; σ, sigma. Priors of L_0= 500 mm ± 10 mm were set for combined sexes, females, and males. Priors were set for combined sexes L_{∞}= 3230 mm ± 100 mm, for females were set as L_{∞} = 3230 mm ± 100 mm, and L_{∞} = 2950 mm ± 100 mm were set for males.

		Model Performance				**Model Parameter Estimates**								**Theoretical Longevity**
	Model	***n***	**LOOIC**	**± S.E.**	***w***	**L_{∞} (mm TL)**	**± S.E.**	***k/g* (yr^{-1})**	**± S.E.**	**L_0 (mm TL)**	**± S.E.**	***σ***	**± S.E.**	
Combined	**VBGF**	**48**	**618.2**	**12.4**	**1.00**	**3203.6**	**1.03**	**0.05**	**0.00**	**507.3**	**0.08**	**149.6**	**0.14**	25.82
	Logistic	48	647.8	11.4	0.00	3187.2	0.85	0.19	0.00	511.6	0.09	202.7	0.19	
	Gompertz	48	634.2	11.5	0.00	3189.5	0.91	0.11	0.00	510.1	0.09	176.7	0.17	
Females	**VBGF**	**28**	**361.6**	**9.2**	**0.98**	**3217.8**	**0.92**	**0.05**	**0.00**	**504.5**	**0.08**	**151.1**	**0.20**	25.82
	Logistic	28	375.8	7.7	0.00	3211.7	0.80	0.19	0.00	506.6	0.08	194.7	0.24	
	Gompertz	28	369.2	7.8	0.02	3212.2	0.84	0.11	0.00	505.8	0.08	173.6	0.22	
Males	**VBGF**	**20**	**261.1**	**9.04**	**0.98**	**2927.1**	**1.00**	**0.06**	**0.00**	**502.7**	**0.09**	**159.6**	**0.26**	24.55
	Logistic	20	276.4	8.33	0.00	2920.4	0.84	0.20	0.00	504.2	0.08	234.1	0.37	
	Gompertz	20	269.4	8.61	0.02	2919.9	0.91	0.12	0.00	503.8	0.09	196.5	0.32	

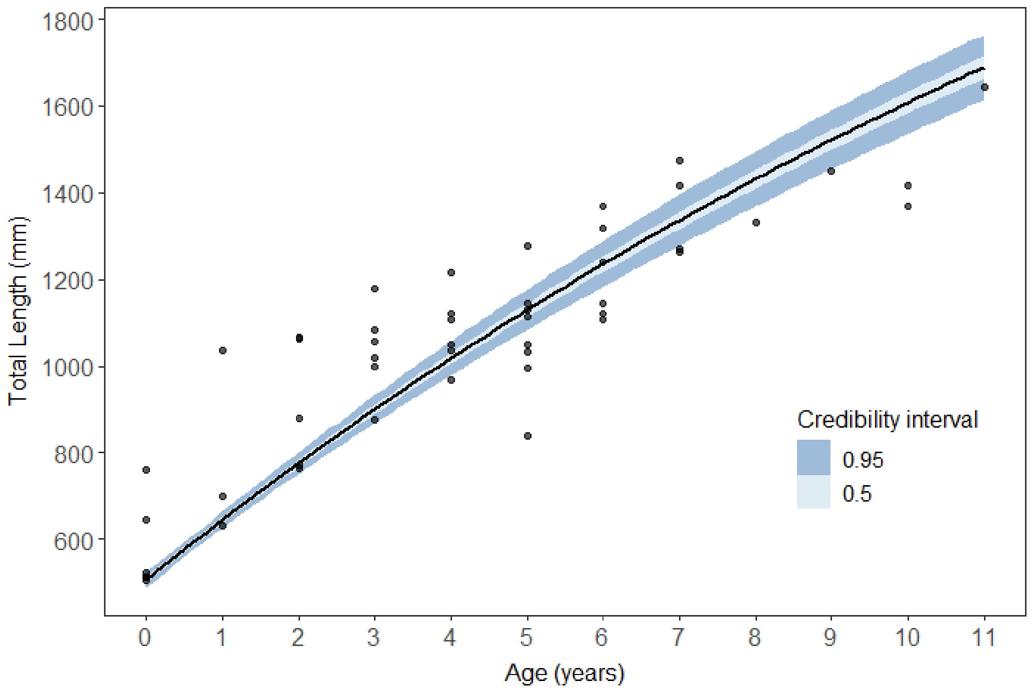


Figure 5.6. Observed length-at-age data until the oldest individual in the sample (11 years) with the Bayesian von Bertalanffy growth curve for combined sexes of bottlenose wedgefish *Rhynchobatus australiae*, sampled from Senoko Fishery Port (SFP) and Jurong Fishery Port (JFP) in Singapore from September 2017 to September 2018, and January 2019 to January 2020.

5.3.4 Reproductive biology

There were 12 and eight mature female and males respectively, as well as eight immature males and nine immature females in the samples. Five female *R. australiae* were observed to have ovum in their ovaries and were observed to be the maturity stage 4. The lengths of the mature females with ovum ranged from 1019 – 1473 mm TL. The mean maximum ovum diameter was 11.00 mm ± 2.86 S.E., ranging between 2 – 18 mm. The number of yolky ova in the ovaries ranges from 7 – 15. No embryos were observed.

The average length of fully calcified clasper length of male *R. australiae* was 212.6 ± 20.14 mm (*n* = 7; range = 165 – 292 mm). The average length for partially and non-calcified claspers were 120.6 ± 9.74 mm (*n* = 5; range = 94 – 145 mm) and 45.7 ± 20.7 mm (*n* = 3; range = 11 – 100 mm), respectively. For three male samples, the claspers had been removed prior to the sample being purchased and maturity was staged from internal dissections. The clasper calculation was not recorded for two samples, based on the clasper lengths (175 and 250 mm), these two samples were assumed to be mature individuals. Running sperm was observed for eight male samples and absent in nine samples. The internal gonad stage and running sperm was not recorded for six samples.

Maturity estimates

Female and male *R. australiae* were estimated to mature at different ages and lengths. The largest immature female was 1145 mm TL and estimated to be 5 years old, while the smallest mature female was 1019 mm TL with an estimated age of 3 years old. The mean (± S.E.) maximum likelihood estimates for length of maturity of L_{50} and L_{95} for females were estimated to be 1014.21 mm TL ± 52.99 S.E. and 1203.04 mm TL ± 93.68 S.E., respectively (**Figure 5.7A**). The mean age of maturity for A_{50} and A_{95} for females were 3.25 years old ± 0.56 S.E. and 5.58 years old ± 1.13 S.E., respectively (**Figure 5.7 B**).

The binomial logistic model for the male's age- and length at maturity data was not able to converge due to low sample size (n = 20) and a quasibinomial logistic model was conducted for the male maturity analysis, with a bin width of one year for age at maturity analysis, and 100 mm for the length at maturity analysis. The mean length of maturity estimates of L_{50} and L_{95} for males were estimated to be 1197.1 mm TL ± 0.05 S.E. and 1209.5 mm TL ± 0.15 S.E., respectively (**Figure 5.7A**). The mean estimates of A_{50} and A_{95} for males were 5.03 years old ± 0.0004 S.E. and 5.16 years old ± 0.0024 S.E., respectively (**Figure 5.7 B**).

5.3.5 Comparison of life history estimates

There was a difference in the growth completion rates of *R. australiae* from SE Asia, which was slower, compared to the population from the Great Barrier Reef (GBR), Australia estimated by D'Alberto et al. (2019) using the data from White et al. (2014) and assuming it represented *R. australiae* (**Table 5.5**). The life history parameter estimates from GBR population were generated using the Frequentist approach, while estimates in this study were generated using informative priors for L_∞ and L_0 in the Bayesian approach (**Figure 5.8**). The maximum observed age was similar between studies of 11 years age, however the maximum observed size of *R. australiae* were different between the studies (**Table 5.5**). Despite the difference in growth completion rates, the L_∞ estimates were similar between the two populations (**Figure 5.8**). The theoretical longevity of SE Asian population of *R. australiae* was greater than the theoretical longevity of the GBR population, due to the slower growth completion rate. The age at maturity estimates for females were similar between the two

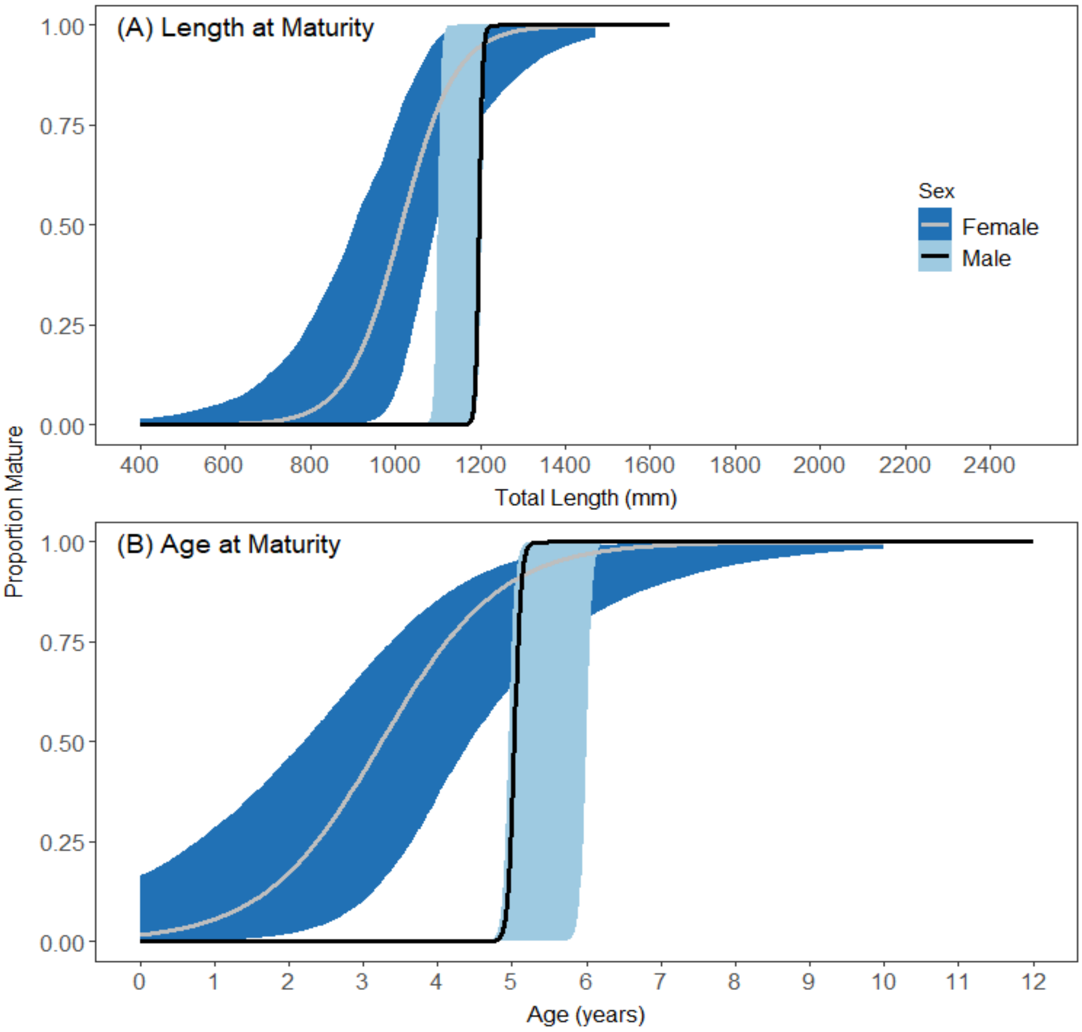


Figure 5.7. Maturity ogives for (**A**) length-at-maturity of females (*n* = 19) and males (*n* = 20) and (**B**) age-at-maturity of females and males for bottlenose wedgefish *Rhynchobatus australiae* sampled from Senoko Fishery Port (SFP) and Jurong Fishery Port (JFP) in Singapore from September 2017 to September 2018, and January 2019 to January 2020

population (**Table 5.5**). The size at birth were similar between the two populations (**Figure 5.8**; **Table 5.5**). The two populations of *R. australiae* from SE Asia and GBR had considerably slower growth compared to two giant guitarfish species (family Glaucostegidae) that have life history estimates available, *G. cemiculus* and *G. typus* (Capapé & Zaouali, 1994; Enajjar, Bradai & Bouain, 2012; White et al., 2014; D'Alberto et al., 2019). The age and length of maturity were similar between the wedgefish and giant guitarfish species (**Table 5.5**).

Table 5.5. Comparative life history parameters for bottlenose wedgefish *Rhynchobatus australiae* from Southeast (SE) Asia, sourced from Senoko Fishery Port (SFP) and Jurong Fishery Port (JFP) in Singapore and imported from Indonesia and Malaysia, *R. australiae* from eastern Australia, as well as similar species of blackchin guitarfish *Glaucostegus cemiculus* from central Mediterranean, and giant guitarfish *Glaucostegus typus* from eastern Australia. Where *n* is the sample size; observed maximum size in the study (L_{obsv}) in millimetres total length (mm TL); growth model of von Bertalanffy (VBGF), and logistic growth function (LOG) and the numbers indicating the number of parameters estimated: two parameters with fixed size at birth (-2), and standard three parameter model (-3); growth completion rate (k, year^{-1}), asymptotic total length (L_{∞}); length at birth (L_0); age at maturity in years (A_{mat}) for 50% of the population (A_{50}) and 95% of the population (A_{95}); length at maturity (L_{mat}) for 50% of the population (L_{50}) and 95% of the population (L_{95}); minimum (min.) and maximum (max.) reported litter size; maximum age/longevity (A_{max}) for observed samples (O_{max}) and theoretical estimates based on the von Bertalanffy growth completion rate (T_{max}).

Species	**Region**	**Sexes**	***n***	**L_{obsv} (mm TL)**	**Growth model**	**k (yr^{-1})**	**L_{∞} (mm TL)**	**L_0 (mm TL)**	**A_{mat} (yr)**		**L_{mat} (mm TL)**		**Litter size**		**A_{max} (yr)**		**References**
									A_{50}	**A_{95}**	**L_{50}**	**L_{95}**	**Min.**	**Max.**	**O_{max}**	**T_{max}**	
Rhynchobatus australiae	SE Asia (Indonesia - Malaysia)	Combined	48	1645	VBGF - 3	0.05	3204	505	--	--	--	--	--	--	11	26	Current Chapter
		Female	28	1473	--	--	--	--	3.3	5.6	1014	1203	--	--	10	--	
		Male	20	1645	--	--	--	--	5.0	5.2	1197	1209	--	--	11	--	
	Eastern Australia	Combined	47	2630	VBGF - 2	0.40	--	500	--	--	--	--	--	--	12	11	White et al. (2014)
					VBGF - 3	0.08	3178	525	3.0	6.0	--	--	--	--	12	22	D'Alberto et al. (2019)
Glaucostegus cemiculus	Central Mediterranean (southern Tunisia)	Female	247	2020	VBGF - 3	0.20	1987	265	5.1	--	1381	--	--	--	14	16	Enajjar, Bradai & Bouain (2012)
		Male	299	1680	VBGF - 3	0.27	1790	354	2.9	--	1118	--	--	--	10	14	
	Central Mediterranean (Southeast Tunisia)	Female	407	2300	--	--	--	300 - 350	--	--	1100	--	5	12	--	--	Capapé & Zaouali (1994)
		Male	390	1920	--	--	--	300 - 350	--	--	1000	--	--	--	--	--	
Glaucostegus typus	Eastern Australia	Combined	23	2840	VBGF - 2	0.15	--	400	--	--	--	--	--	--	--	18	White et al. (2014)
					VBGF - 3	0.06	4021	499	6.5	8.0	--	--	--	--	19	25	D'Alberto et al. (2019)

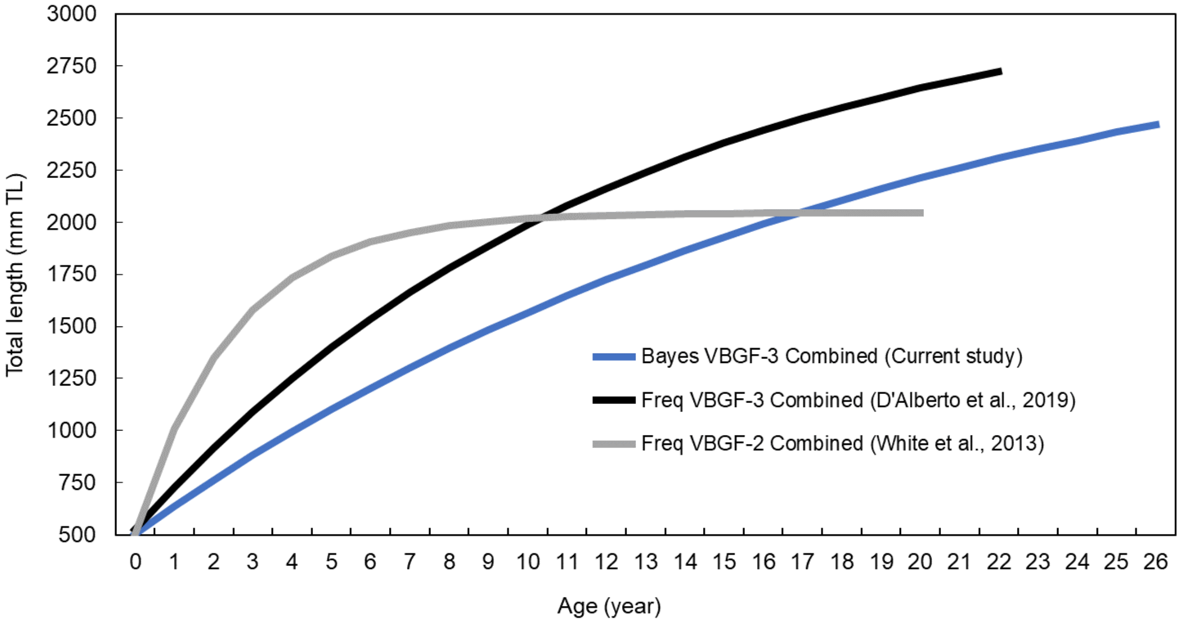


Figure 5.8. Comparison of growth completion rates for the combined sexes (female and male) bottlenose wedgefish *Rhynchobatus australiae* between two populations, Southeast Asia from this current study using a Bayesian (Bayes) three parameter von Bertalanffy growth function (VBGF-3; blue solid line), and eastern Australia from D'Alberto et al. (2019) using a frequentist (Freq) three parameter von Bertalanffy growth function (black solid line), and frequentist two parameter von Bertalanffy growth function (VBGF-2; grey solid line) from White et al. (2014).

5.4 Discussion

Overestimation of growth rates is a serious concern for fisheries management , as it can lead to the overharvesting of species (Smith et al., 1995; Harry, 2018). *Rhynchobatus australiae* in this study were estimated to have a slower growth competition rate (k = 0.05 yr $^{-1}$), compared to estimated growth completion rate (k = 0.08 yr $^{-1}$) of the population from GBR by D'Alberto et al. (2019). The longevity of SE Asian *R. australiae* were similar to the estimated longevity of 24 years to *R. djiddensis* off the eastern coast of South Africa, based on tag-recapture growth analysis (Jordaan et al., 2021). The different methodology and yet similar longevity between *R. australiae* and *R. djiddensis* suggest similar growth completion rate estimates presented in this study. Species with a growth completion rate of < 0.10 yr^{-1} tend to be particularly vulnerable to population decline (Cailliet & Goldman, 2004). Overexploitation could be driving the slow growth rate in the SE Asian population of *R. australiae,* and this population may be more likely to be more vulnerable to population declines and overharvesting than the GBR population.

Female *R. australiae* from SE Asia in the current study were estimated to mature at a younger age and smaller length than males. This is unusual for elasmobranchs as females typically mature at an older age than males (Cortés, 2000). This could also be a sampling artefact as the male samples may have originated from a different population with an older age at maturity than the female samples in this study. This could be likely; however this hypothesis was not able to be investigated as the samples were sourced from fish markets with little information on the exact fishing location, and therefore sampling population. *Rhynchobatus australiae* was also estimated to mature at a younger age between 3 – 6 years old for both sexes. This is considerably younger than 50% of the maximum age (~12 years for *R.australiae*) that is a typical relationship for sharks between age at maturity and maximum age (Cortés, 2000). While this pattern is unusual, similar patterns are evident for other Rhinopristiformes. Early maturity for both female and males are also reported for *G. typus* and *G. cemiculus* (**Table 5.5**), as well as for the largetooth sawfish *Pristis pristis* (Capapé & Zaouali, 1994; Enajjar, Bradai & Bouain, 2012; White et al., 2014; D'Alberto et al., 2019; Kyne et al., 2021). This suggest that the life history generalisations for maximum age and age at maturity by Cortés (2000) may not always apply to members of the Rhinopristiformes, and requires further investigation.

A positive relationship has been found between litter size and maternal size in elasmobranchs, which suggests that larger individuals have more uterine space available to carry a larger litter size and/or larger sized pups (Kyne et al., 2021). Wedgefishes are lecithotrophic viviparous, with a reported litter size between 7 – 19 pups (Last et al., 2016; Mull, Yopak & Dulvy, 2020). This litter size is likely an underestimation as shark-like ray species are known to often prematurely abort embryos under stress (e.g. capture in fishing gear (Adams et al., 2018)). The estimates of early maturity of SE Asian *R. australiae* support the findings from D'Alberto et al. (2019) on the theoretical modelling of the maximum intrinsic rate of population for *R. australiae*. The early maturity of *R. australiae* suggest that this species may be relatively productive, as a result of earlier maturity, large litter sizes and large size at birth, compared to other chondrichthyans, and therefore have a greater chance of recovery from population declines (D'Alberto et al., 2019). Nevertheless, the reproductive estimates of the current study must be viewed with caution due to the limited number of samples, especially in the larger length classes, and mature male samples in this study. Across all rhinid species, reproductive parameters are generally poorly defined, where the age and size at maturity, litter size and reproductive periodicity are unknown for most species (Last et al., 2016). Life history patterns and correlations, like those presented in Cortés (2000) have not been investigated for batoids. Therefore, it is unknown if the earlier maturity is a unique trait to wedgefishes and giant guitarfishes, to other ray species, or a result of inaccurate age estimates. There is crucial reproductive data missing for all rhinids, particularly from the larger length classes, in terms of estimated length/age of maturity, litter sizes, pregnancy length and reproductive periodicity.

Growth parameters differ substantially between the two modelling approaches used in this study. The largest sample in this study was a 1473 mm TL, while *R. australiae* has been recorded to have a maximum total length of 3230 mm TL in eastern Indonesia (Faizah & Chodrijah, 2020). The frequentist approach considerably underestimated L_∞, of approximately half the reported maximum size of *R. australiae*, leading to an overestimated growth completion rate and size at birth for the von Bertalanffy frequentist model (Goldman, 2005; Cailliet et al., 2006; Smart et al., 2016b). White et al. (2014) and D'Alberto et al. (2019) used the frequentist modelling approach with larger length classes, and yet used different models, von Bertalanffy two parameter model with fixed size at birth to 500 mm TL (White et al., 2014), and von Bertalanffy standard three parameter model (D'Alberto et al., 2019). Using a two-parameter growth model through fixing the L_∞ or L_0 parameters normally results in serious biases in the remaining parameters and should be avoided in growth modelling (Pardo, Cooper & Dulvy, 2013; Smart & Grammer, 2021). Therefore the growth parameters presented by White et al. (2014) are considered to be an overestimation, as using the standard three parameter growth model with the same data by D'Alberto et al. (2019) produced a substantially slower growth completion rate. The two-parameter logistic growth completion rate $g_{Log} = 0.41$ yr $^{-1}$for *R. australiae* by White et al. (2014) cannot be directly compared to the growth completion coefficient to other models. However, the Bayesian growth modelling approach used in this study can overcome the limitations of missing larger length classes and the resulting biases in the estimation of the growth completion rate. This approach applies the known biological traits of a species as explicit components of a growth model with informative priors, but does not fix the L_∞ or L_0 parameters which can seriously bias the remaining parameters (Pardo, Cooper & Dulvy, 2013; Smart & Grammer, 2021). The Bayesian approach provided a more biologically realistic estimate of the asymptotic length, closer to the maximum reported size, and a smaller size at birth. This method has the ability to account for missing older individuals in the sample (Smart & Grammer, 2021), as older individuals are often under sampled due to gear selectivity or age truncation (McAuley et al., 2006; McAuley, Simpfendorfer & Wright, 2007; Smart et al., 2017). The Bayesian approach is an especially useful growth modelling technique for Critically Endangered species where collection of samples across all length classes can be difficult, or even the removal of individuals from the populations can be detrimental.

Biased size- or age-distributions in the sample can reduce the accuracy of life history parameters and can be caused by sampling data from different areas and/or with size selective gear types (Thorson & Simpfendorfer, 2009). The sample size of this study was a quarter of the sample size for age and growth studies recommend by Thorson & Simpfendorfer (2009). However, the recommended sample size can be unrealistic for many rare and threatened species that have low population sizes or fragmented distributions. The sample size and composition can be also influenced by gear selectivity (Thorson & Simpfendorfer, 2009), as well as imposed permitting restrictions to collect scientific samples (Simpfendorfer et al., 2008). The GBR samples in White et al. (2014) were collected from a commercial gillnet fishery and fisheries independent longline survey. There were larger individuals in the GRB studies, with the largest individual sampled (2630 mm TL) being smaller than reported maximum size of *R. australiae.* The lack of the larger size classes would have highly influenced the growth parameters, leading to an overestimation of the frequentist growth completion rate reported by D'Alberto et al. (2019) (Thorson & Simpfendorfer, 2009). As the samples in the present study were imported from Indonesia and Malaysia, the type of gear used as well as fishing location is unknown, demonstrating a substantial knowledge gap on spatial distribution or sex/size segregation of rhinids in SE Asia. There is evidence of population separation between Australian and SE Asian populations based on genetic analysis (Giles et al., 2016), and there may be intra-specific variation in life history traits, occurring due to regional differences in environment (e.g. water temperature and prey availability), population density and exploitation.

The misidentification of species and the use of inaccurate surrogate information can have a significant effect on calculations of life history parameter estimates (Smart et al., 2016a). Imprecise parameters may ultimately compromise stock assessments and the sustainability of fisheries as well as impacting conservation-related research and management initiatives

(Garcia-Vazquez et al., 2012). In Senoko and Jurong Fishery Ports, rhinids are landed in fresh condition with the majority of samples finned and on some occasions, snouts removed prior to sale (Clark-Shen et al., 2021). In some fishery ports across SE Asia, rhinids are often landed in poor and degraded condition, which results in visual species identification especially difficult (D'Alberto et al., 2021). The identification of rhinid species, either in person or from photographs, is complicated as the useable morphological features such as spot patterns, snout shape, and fin morphology can be difficult to distinguish from “look-alike” or cryptic species (Giles et al., 2016; Last et al., 2016). The visual characteristic used to differentiate *R. australiae* from its closest regional congeners (e.g. *R. palpebratus, R. springeri,* and *R. cooki*) is the pattern of white spots around the dark pectoral spot, with *R. australiae* typically having a line of three white spots located adjacent to the black pectoral spot (Last et al., 2016). However, these identifying spots for *R. australiae* can be faded or absent, especially in larger individuals (White & Dharmadi, 2007; Giles et al., 2016). Genetic sequencing for this study confirmed that all but two samples were *R. australiae,* whereas the two samples excluded from the analysis were visually distinct to other *R. australiae* samples and were genetically identified as *R. palpebratus.* The distribution of *R. australiae* overlaps with *R. palpebratus* in Papua New Guinea and northern Australia (Last et al., 2016). The presence of *R. palpebratus* in the two Singapore fish markets, where the majority of rhinid species were imported from Indonesia and Malaysia, indicates that either the individuals originated from waters around Papua New Guinea, or the range for this species is broader than previously documented and requires further investigation. Interestingly, despite the extensive distribution overlap in SE Asia with *R. australiae*, *R. springeri* was not observed during the surveys in this current study, which may be a result of the survey period. *Rhynchobatus springeri* were recorded at JFP and SFP during the market surveys conducted in Clark-Shen et al. (2021), which covered a greater time period between September 2017 – September 2018 and January 2019 – January 2020. The overlapping ranges of rhinid species has compounded the misidentification of these rays, especially as some species are rarer in landings and possibly have more of a restricted and/or fragmented spatial distribution.

Globally, populations of *R. australiae* are in steep decline, driven by extensive fishing pressure , especially within the SE Asian region (Kyne et al., 2020). During surveys reported in Clark-Shen et al. (2021), from which the samples of this current study originated, over half of *R. australiae* (65%) imported into JFP and SFP reportedly originated from Indonesia

(Sumatra and Riau Islands including Batam Island, Bintan Island, Kijang, Moro Island, Panjung), followed by unknown location (29%) and Malaysia (5.7%; Johor and Pahang) (Clark-Shen et al., 2021). All samples in this study were fresh, indicating recent capture and importation of the wedgefishes. Indonesia is the second highest producer of capture fisheries globally and elasmobranchs are primarily reported to be caught incidentally as by-products in commercial and artisanal fisheries such as trawls, small and large mesh gillnets, purse seines, longlines and handlines (White & Dharmadi, 2007; Dharmadi, Fahmi & Satria, 2015), with the expectation of the tangle net fishery that targets shark-like rays (D'Alberto et al., 2021). These fisheries, capture wedgefishes and other large ray species across different life stages, meaning there is little refuge from fishing pressure in Indonesian waters (D'Alberto et al., 2021). Currently there are no national or regional laws in SE Asian nations that specifically regulate the take of wedgefish (Rusandi et al., 2019; Choo et al., 2021; Clark-Shen et al., 2021), with the exception of the Philippines which automatically provides national protection of CITES listed species, of which wedgefishes and giant guitarfishes were listed on CITES Appendix II in 2019 (Republic of the Philippines, 2014; CITES, 2019b). Nevertheless, CITES Appendix II-listed species can still be landed and traded domestically, as CITES regulations apply only to international trade (Vincent et al., 2014). If traded internationally the species being exported requires a positive Non-Detriment Finding from the exporting country (Vincent et al., 2014). Thus the knowledge of the origin of the wildlife product is paramount for the enforcement of the regulations for CITES Appendix II species. Clark-Shen et al. (2021) reported that the occurrence of wedgefish in Singapore markets in 2020 may have required that landings from Indonesia or Malaysia be accompanied by the appropriate documentation and approvals in order to comply with CITES. Indonesia is a signatory to CITES and has complex fisheries supply and trade chains, from fishers to buyers to exporters, which have intricate interactions and different drivers occurring throughout the chain (Rusandi et al., 2019). However, the efficacy of conservation measures such as CITES in SE Asian fisheries presents a significant and complex challenge. Further research is needed to assess the efficacy of CITES listings on the trade of wedgefish and other CITES listed species in Singapore and across SE Asia, and this should include the human dimensions of shark and ray fishing and trade as it is these factors that may shape conservation outcomes (Jaiteh, Loneragan & Warren, 2017; Booth, Squires & Milner-Gulland, 2019).

5.5 Conclusion

High-income nations, such as Singapore, are in a strong position to act on the sustainability of the seafood that they source. Scientific advice and information, e.g. monitoring of fisheries landings and supply chains, and examining the effect of the CITES listings on the imports of wedgefish and other CITES listed species) will enable more informed management strategies to be developed for elasmobranch fisheries in SE Asia (Clark-Shen et al., 2021). Such measures could include spatial/seasonal protection, and limit or ban on retention in recreational fisheries for shark-like rays. These measures will depend upon identifying important habitats and movements patterns of wedgefishes, fishing locations across SE Asia, as well as effective enforcement of the regulations in the respective nations. Any approaches to ensure the sustainability of seafood and also reduce the demand for shark-like rays, will need to consider the socio-economic implications for the supply regions (Booth, Squires & Milner-Gulland, 2019), and complement efforts for sustainable exploitation of non-threatened species for the benefit of local fishing communities. The life history parameters of *R. australiae* suggest this species caught in SE Asian waters is slower growing than populations in eastern Australia, and so more vulnerable to population declines. *Rhynchobatus australiae* mature at an earlier age and smaller length than other similar size elasmobranchs, which contributes to the productivity of the populations, despite a slow growth completion rate. There is a need for further investigation into the differences in life history parameters to determine if variations are related to methodological differences or potential intra-specific variations.

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Ethics Statement

All individuals examined in this study were purchased from public fishery ports in Singapore and were dead upon collection. No specific permits or ethics were required to purchase the samples, prior to the closures to public from COVID-19 pandemic. The samples were imported into Australia under DAFF Permit Number 002424804, preceding to the enforcement of the CITES Appendix II listing on 26th November 2019.

5.6 Appendices

Appendix 5.1. Summary of the sample trips to the two Fishery Ports and the cost of the wedgefish samples purchased. Size class indicates the estimated size at collection at the fishery ports; sample type if the animal was whole, tailed, or trunked; fins attached (yes or no) if samples had dorsal, second dorsal and caudal fins removed prior to the sample collection; fishery port sampled Senoko Fishery Port (SFP) and Jurong Fishery Port (JFP); import country from the casual discussions from the fish merchants; individual purchase cost of samples if available; combined total purchase cost for samples that were purchased together; -- indicate information was not recorded/available.

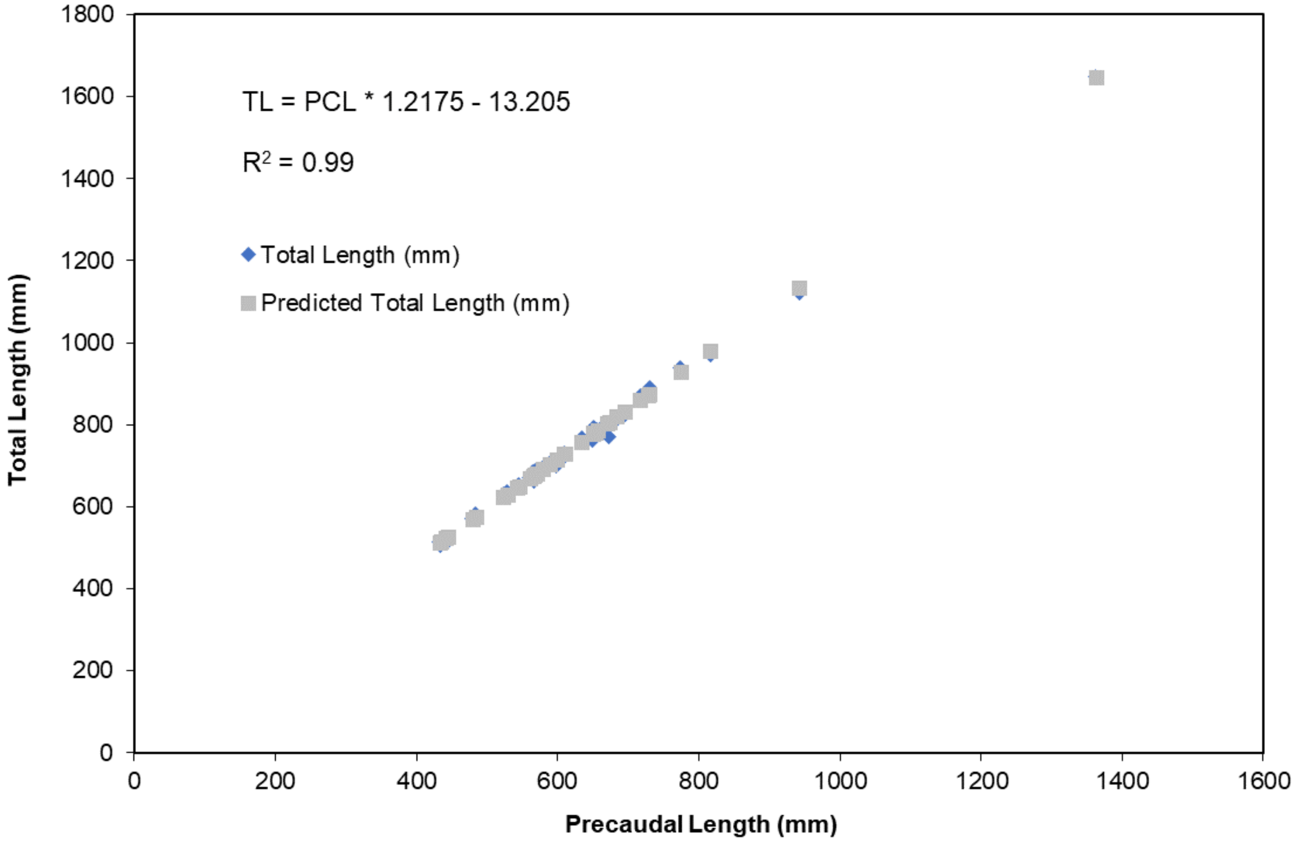
Sample	Trip Code	Day	Month	Year	Sex	Size Class	Sample Type	Fins Attached	Fishery Port	Import Country	Individual Sample Cost $USD	Combined Sample Cost $USD
1	SIN_T01_Jul_2018	22	July	2018	F	>90	Whole	No	JFP	--	--	11.13
2	SIN_T01_Jul_2018	22	July	2018	F	>90	Tailed	No	JFP	--	--	
3	SIN_T01_Jul_2018	22	July	2018	M	>90	Tailed	No	SFP	Indonesia	16.92	--
4	SIN_T01_Jul_2018	22	July	2018	F	>90	Tailed	No	SFP	Malaysia	--	11.87
5	SIN_T01_Jul_2018	22	July	2018	F	>90	Whole	Yes	SFP	Malaysia	--	
6	SIN_T01_Jul_2018	22	July	2018	F	>90	Whole	Yes	SFP	Malaysia	--	
7	SIN_T01_Jul_2018	22	July	2018	F	>90	Whole	Yes	SFP	Malaysia	--	
8	SIN_T02_Jul_2018	28	July	2018	M	<100	Tailed	No	SFP	Indonesia	32.65	--
9	SIN_T02_Jul_2018	28	July	2018	M	--	Tailed	No	JFP	Indonesia	--	19.59
10	SIN_T02_Jul_2018	28	July	2018	F	--	Tailed	No	JFP	Indonesia	--	
11	SIN_T02_Jul_2018	28	July	2018	M	<100	Tailed	No	JFP	Indonesia	33.39	--
12	SIN_T02_Jul_2018	28	July	2018	M	<100	Tailed	No	JFP	Indonesia	--	89.05
13	SIN_T02_Jul_2018	28	July	2018	M	<100	Tailed	No	JFP	Indonesia	--	
14	SIN_T02_Jul_2018	28	July	2018	F	>90	Tailed	No	JFP	Indonesia	--	
15	SIN_T03_Oct_2018	20	October	2018	--	>90	Tailed	No	JFP	Indonesia	--	161.77
16	SIN_T03_Oct_2018	20	October	2018	--	>90	Tailed	No	JFP	Indonesia	--	
17	SIN_T03_Oct_2018	20	October	2018	--	>90	Tailed	No	JFP	Indonesia	--	
18	SIN_T03_Oct_2018	20	October	2018	--	>90	Tailed	No	JFP	Indonesia	--	
19	SIN_T03_Oct_2018	20	October	2018	--	>90	Tailed	No	JFP	Indonesia	--	
20	SIN_T03_Oct_2018	20	October	2018	--	>90	Tailed	No	JFP	Indonesia	--	

21	SIN_T04_Dec_2018	1	December	2018	--	>90	Tailed	No	JFP	--	--	130.6
22	SIN_T04_Dec_2018	1	December	2018	--	>90	Tailed	No	JFP	--	--	
23	SIN_T04_Dec_2018	1	December	2018	--	<100	Tailed	No	JFP	--	--	
24	SIN_T04_Dec_2018	1	December	2018	--	<100	Tailed	No	JFP	--	--	
25	SIN_T04_Dec_2018	1	December	2018	--	<100	Whole	Yes	JFP	--	5.34	--
26	SIN_T05_Jan_2019	1	January	2019	--	<100	Tailed	No	JFP	--	23.72	--
27	SIN_T06_Feb_2019	23	February	2019	--	<100	Tailed	No	JFP	--	7.42	--
28	SIN_T06_Feb_2019	23	February	2019	--	>100	Tailed	No	JFP	--	77.92	--
29	SIN_T06_Feb_2019	23	February	2019	--	>100	Tailed	No	JFP	--	--	57.14
30	SIN_T06_Feb_2019	23	February	2019	--	>100	Tailed	No	JFP	--	--	
31	SIN_T07_Jun_2019	22	June	2019	--	>100	Whole	Yes	JFP	Indonesia	14.47	--
32	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	183.29
33	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
34	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
35	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
36	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
37	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
38	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
39	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
40	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
41	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
42	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
43	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
44	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
45	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	SFP	Indonesia	--	
46	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	JFP	Indonesia	--	48.08
47	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	JFP	Indonesia	--	
48	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	JFP	Indonesia	--	
49	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	JFP	Indonesia	--	
50	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	JFP	Indonesia	2.97	--
51	SIN_T08_Jul_2019	27	July	2019	--	--	--	--	JFP	Indonesia	89.05	--

Appendix 5.2. Data for the length conversion analysis for bottlenose wedgefish *Rhynchobatus australiae*, with information on the sex (F, female; M, male), total length in millimetres (mm TL); fork length (FL); precaudal length (PCL); sample location; predicted total length using the conversion equation TL = PCL * 1.2175 - 13.205 and the calculated residuals; -- indicate information was not recorded/available.

Species	Sex	TL (mm)	FL (mm)	PCL (mm)	Sample location	Predicted TL (mm)	Residuals	Reference
Rhynchobatus australiae	F	524	480	444	northern Australia	527.2732709	-3.27327	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	571	521	479	northern Australia	569.8864334	1.11357	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	583	531	484	northern Australia	575.9740281	7.02597	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	632	577	523	northern Australia	623.4572664	8.54273	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	638	582	529	northern Australia	630.7623799	7.23762	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	650	603	543	northern Australia	647.807645	2.19236	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	653	600	545	northern Australia	650.2426828	2.75732	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	661	611	566	northern Australia	675.8105804	-14.8106	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	670	618	560	northern Australia	668.5054668	1.49453	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	684	623	570	northern Australia	680.6806561	3.31934	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	686	630	565	northern Australia	674.5930614	11.4069	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	687	632	568	northern Australia	678.2456182	8.75438	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	696	641	579	northern Australia	691.6383264	4.36167	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	707	647	589	northern Australia	703.8135158	3.18648	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	721	660	609	northern Australia	728.1638944	-7.16389	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	730	670	610	northern Australia	729.3814133	0.61859	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	769	705	634	northern Australia	758.6018676	10.3981	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	789	721	656	northern Australia	785.3872841	3.61272	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	790	724	653	northern Australia	781.7347273	8.26527	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	792	721	651	northern Australia	779.2996894	12.7003	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	806	741	670	northern Australia	802.4325491	3.56745	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	814	736	684	northern Australia	819.4778141	-5.47781	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	826	765	695	northern Australia	832.8705223	-6.87052	D'Alberto (2021) Unpublished data

Rhynchobatus australiae	F	870	789	717	northern Australia	859.6559388	10.3441	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	883	806	728	northern Australia	873.048647	9.95135	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	F	889	798	730	northern Australia	875.4836849	13.5163	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	M	940	859	774	northern Australia	929.0545178	10.9455	D'Alberto (2021) Unpublished data
Rhynchobatus australiae	--	1648	--	1363	Indonesia	1646.173168	1.82683	White (2021) Unpublished data
Rhynchobatus australiae	F	969	894	816	Indonesia	980.1903129	-11.1903	This study
Rhynchobatus australiae	F	763	728	650	SE Asia	778.0821705	-15.0822	This study
Rhynchobatus australiae	F	772	731	673	Malaysia	806.0851059	-34.0851	This study
Rhynchobatus australiae	M	512	492	442	Malaysia	524.838233	-12.8382	This study
Rhynchobatus australiae	F	506	488	434	Malaysia	515.0980816	-9.09808	This study
Rhynchobatus australiae	F	513	483	433	Malaysia	513.8805627	-0.88056	This study
Rhynchobatus australiae	F	700	650	598	SE Asia	714.7711861	-14.7712	This study
Rhynchobatus australiae	M	1122	1030	942	SE Asia	1133.597698	-11.5977	This study



Appendix 5.3. Linear relationship for bottlenose wedgefish *Rhynchobatus australiae,* between the pre-caudal length and total length measurements to convert pre-caudal length measures to predicted total length using the conversion equation TL = PCL * 1.2175 - 13.205.

Appendix 5.4. The results of the genetic sequencing for the species identification for wedgefish samples collected from two fish markets in Singapore. The sequencing was compared to three species, bottlenose wedgefish *Rhynchobatus australiae*¸ broadnose wedgefish *Rhynchobatus springeri* and eyebrow wedgefish *Rhynchobatus palpebratus*. A match of over 99% (in bold) indicated the species identification. Three samples did not have conclusion genetic species identification (*) and were visually identified by an elasmobranch taxonomic expert (W.T.W) as *R. australiae*.

		Percentage match to species		
Species Code	**ID Number**	***R. australiae***	***R. springeri***	***R. palpebratus***
WSG	138214	**99.3**	95.7	95.6
WSG	138215	**99.4**	95.6	95.4
WSG	138216	**99.6**	95.4	95.3
WSG	138217	**99.4**	95.6	95.1
WSG	138218	**99.6**	95.7	96.0
WSG	148530	**98.9**	95.7	97.9
WSG	148531	**99.0**	95.4	95.7
WSG	148532	**99.1**	95.9	95.7
WSG	148533	**99.3**	96.0	97.1
WSG	148534	**99.1**	95.8	96.9
WSG	148535	**99.6**	95.7	95.3
WSG	148536	96.2	97.2	**99.1**
WSG	148537	**100.0**	96.0	95.6
WSG	148539	**99.5**	95.8	96.9
WSG	148541	**99.1**	95.6	95.7
WSG	148542	**99.1**	95.6	95.4
WSG	148543	**99.2**	96.1	97.1
WSG	148545	**99.1**	96.6	95.7
WSG	148548	**99.5**	95.8	95.3
WSG	148549	**99.6**	95.7	95.3
WSG	148550	**99.6**	95.7	95.3
WSG	148551	**99.5**	95.8	96.9
WSG	148552	**99.3**	96.0	95.6
WSG	148553	**99.2**	96.0	95.1
WSG	150337	**99.4**	96.6	95.5
WSG	150338	**99.3**	95.8	95.8

WSG	195072	**99.4**	95.7	95.4
WSG	195074	**98.7**	96.3	96.2
WSG	195075	**99.1**	95.8	96.9
WSG	195076	**99.4**	95.6	95.4
WSG	195077	**99.3**	95.4	95.6
WSG	195078	95.7	97.5	**99.1**
WSG	195079	**99.3**	95.9	95.3
WSG	195080	**99.0**	95.7	95.9
WSG	195081	**99.1**	95.6	95.6
WSG	195082	**99.3**	95.8	95.5
WSG	195083	**99.6**	95.7	95.3
WSG	195084	**99.6**	95.4	95.3
WSG	195085	**99.6**	95.8	95.2
WSG	195086	**99.6**	95.7	95.3
WSG	195087	**99.4**	95.6	95.4
WSG	195088*	**96.6**	96.3	96.4
WSG	195089*	**97.2**	96.4	96.7
WSG	195090*	**96.7**	96.6	96.7
WSG	195091	**99.4**	95.6	95.4
WSG	198597	**99.0**	95.9	96.9

Chapter Six

Manuscript associated with this chapter:

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Nature and extent of author contribution

Study design was conceived by the candidate and all co-authors. Data for this chapter was collected by the candidate. The model was created by Dr Pardo, and data was analysed by the candidate. The candidate wrote the drafts of this chapter. Prof. Simpfendorfer, Dr Carlson, Dr Pardo helped with data interpretation and reviewed the chapter. The candidate would like to thank Charlotte Heacock for assisting in the data collection.

Cover Image

Dr. Conner Gervais

6. Population productivity of shark-like rays (Order Rhinopristiformes): inferring the likelihood of recovery

6.1 Introduction

Over a third of chondrichthyan (sharks, rays and chimeras) populations have an elevated risk of extinction for marine organisms (Dulvy et al., 2014a; Dulvy et al., 2021), raising significant ecological and conservation concerns (Stevens et al., 2005; Heithaus et al., 2008; Ferretti et al., 2010). Chondrichthyans, generally have low biological productivity (slow growth, late maturity, few offspring, and long generational times), which limits their ability to recover from population declines (Cortés, 2000; Fowler, Reed & Dipper, 2002). Declines of chondrichthyan populations are typically the result of the rapid expansion of fisheries (Clarke et al., 2006; Oliver et al., 2015; Dulvy et al., 2017) and the globalisation of trade (Clarke, Milner-Gulland & Bjørndal, 2007; Lack & Sant, 2009), and can be exacerbated by habitat degredation (Knip, Heupel & Simpfendorfer, 2010). Compared to other chondrichthyans, larger elasmobranchs (sharks and rays, Subclass Elasmobranchii) have some of the lowest intrinsic rates of population increase (Dulvy et al., 2014b; Pardo et al., 2016a), and as a result are unlikely to sustain high levels of fishing pressure before population collapse (Holden, 1973; Holden, 1974; Stevens et al., 2000; Smith, Cailliet & Cortés, 2008).

The order Rhinopristiformes is one of the most threatened orders of marine fish (Dulvy et al., 2014a; Moore, 2017), and comprises five families: sawfish (Pristidae), giant guitarfish (Glaucostegidae), wedgefish (Rhinidae), guitarfish (Rhinobatidae) and banjo rays (Trygonorrhinidae) (**Table 6.1**) (Last et al., 2016; Moore, 2017). These large rays are strongly associated with soft-bottom habitats in shallow (< 100 m) tropical and temperate coastal waters (Kyne & Bennett, 2002a; White et al., 2013b; White et al., 2013a), resulting in high exposure to intensive and expanding fisheries (Kyne et al., 2020). These coastal habitats are under threat from anthropogenic influences including coastal development and climate change, which is also a significant threat for these rays (Sommerville & White, 2010; Harrison & Dulvy, 2014). They are very susceptible to overexploitation as a result of their large body size (Dulvy et al., 2014a), high catchability by multiple gear types (**Chapter**

Four), and use of inshore habitat in some of the world's most heavily fished coastal regions (Stobutzki et al., 2002; White & Kyne, 2010; Jabado & Spaet, 2017).

There is increasing evidence of historical and contemporary declines in landings and catch rates for wedgefishes, giant guitarfishes, guitarfishes and banjo rays (herein collectively referred to as shovelnose rays), of up to 80% throughout most of their ranges (Kyne et al., 2020), including Indonesia (Keong, 1996), South Africa (Diop & Dossa, 2011), Madagascar (Hopkins, 2011), Mozambique (Pierce et al., 2008), Tanzania (Schaeffer, 2004), Arabian Seas and surrounding region (Moore, 2017; Jabado, 2018), India (Mohanraj et al., 2009) and Brazil (Villwock de Miranda & Vooren, 2003). Many species of shovelnose rays are facing a high to extremely high risk of extinction (Vooren et al., 2006; Lessa & Vooren, 2016; Kyne et al., 2020). While there are very few directed fisheries [e.g. Indonesian tangle-net fishery (**Chapter Four**)] for shovelnose rays, they are typically retained in commercial and artisanal fisheries as by-products for their highly valued fins and good quality meat (Bizzarro et al., 2009a; Bizzarro et al., 2009b; Kyne et al., 2020). Wedgefish and giant guitarfish fins are considered the highest-grade fins (Keong, 1996; Clarke et al., 2006; Compagno & Last, 2008; Harrison & Dulvy, 2014). The reported declines of landings and catches of shovelnose rays are likely to be primarily driven by the international shark fin trade as they are prevalent in fin trading hubs such as Hong Kong (Fields et al., 2018) and Singapore (Boon, 2017; Wainwright et al., 2018). There is considerable concern that shovelnose rays, in particular wedgefishes and giant guitarfishes, are following a similar pattern of global decline as the sawfishes (Moore, 2017; Kyne et al., 2020). All five species of sawfish declined rapidly over 30 years throughout their range, driven by unregulated fisheries, the interational fin trade, and delayed scientific attention (Thorson, 1982; Simpfendorfer, 2005a; Thorburn et al., 2007; Dulvy et al., 2016). Yet despite a global conservation strategy (Harrison & Dulvy, 2014), restriction of international trade (i.e. listing on Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES] Appendix I), and evidence that some species of sawfish have the ability to recover from fishing pressure (Carlson & Simpfendorfer, 2015), the recovery of the populations is projected to take at least several decades. Precautionary management and conservation of shovelnose rays is therefore vital to maintain their populations.

Currently, fisheries for shovelnose rays are not regulated through national or regional species-specific fishing regulations. The magnitude of declines in landings in heavily fished regions, and the subsequent conservation issues have attracted the focus of major international management conventions and agencies, such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS; *R. australiae* and *Rhinobatos rhinobatos* listed on the Appendix II) (CMS, 2017), the non-binding CMS Memorandum of Understanding on the Conservation of Migratory Sharks (CMS Sharks MoU; *R. australiae, R. djiddensis, R. laevis,* and *R. rhinobatos* listed on Annex 1) (CMS, 2018), and CITES (families Rhinidae and Glaucostegidae listed on Appendix II) (CITES, 2019b). For CITES Appendix II listed species, the international trade of wild specimens must be legal and sustainable, which is dependent on provisions such as the export is not detrimental to wild populations (through a positive NDF), the specimens are legally sourced, and shipments are accompanied by export, import or re-export permits (Vincent et al., 2014). While the CMS Appendix II listing acts as a framework for the Range States (any Party [nation] that exercises jurisdiction over any part of the range of that migratory species) of the migratory species that have unfavourable conservation status, and requires international agreements (Lawson & Fordham, 2018). These international agreements provide a global platform and legal foundation for the conservation and sustainable use of internationally traded species (CITES), and migratory species and their habitat (CMS) (Vincent et al., 2014). Given the global concerns for this group of species and the importance of trade in their high-value fins, the use of international trade regulations through CITES listings may help achieve positive conservation outcomes (Ostrom et al., 1999; Vincent et al., 2014; Kyne et al., 2020). Successful recovery of populations will require significant measures across local, regional and global scales (Ostrom et al., 1999). However, management and conservation efforts can be hampered by the lack of understanding of life-history (e.g. age, growth, and maturity), demographic information, and recovery rates.

Understanding the ability of species to recover from declines following implementation of management measures is important for rebuilding depleted populations. This can be approximated through measuring the species' population productivity using various demographic techniques such as rebound potential models (Au & Smith, 1997; Au, Smith & Show, 2015; Hutchings & Kuparinen, 2017), age or stage structured life-history tables and matrix models (Caswell, 2001; Cortés, 2002), and demographic invariant methods (Niel &

Lebreton, 2005; Dillingham, 2010). These demographic techniques utilise the known relationships between life-history traits and demography, known as the Beverton-Holt dimensionless ratios (Dulvy & Forrest, 2010) that can be used to infer a species' life-history traits based on known parameters (Frisk, Miller & Fogarty, 2001; Dulvy et al., 2004; Reynolds et al., 2005). One commonly used metric of productivity is the maximum intrinsic rate of population increase r_{max}, which reflects the theoretical maximum growth rate of depleted populations in the absence of density dependent regulation (Myers, Mertz & Fowlow, 1997). This method can help to infer and understand a species ability to recover from population declines, and provide the demographic basis for evaluating the sustainability of fisheries (Beddington & Kirkwood, 2005) and international trade, particularly for poorly monitored species with limited available life-history information (García, Lucifora & Myers, 2008; Pardo et al., 2018). The maximum intrinsic population rate of population increase has previously been estimated for *Pseudobatos horkelii* and *Pseudobatos productus* as a part of multi-species comparison (García, Lucifora & Myers, 2008; Pardo et al., 2016b), however there has not been a comprehensive analysis on the population productivity for shovelnose rays.

The aim of this chapter was to use life-history data and theory to estimate the population productivity for shovelnose rays. The focal families studied were wedgefishes, giant guitarfishes, guitarfishes and banjo rays, while the sawfishes were excluded as they have been previously assessed in detail (Dulvy et al., 2016). The population productivity of these rays was compared to available productivity estimates of 115 other shark and ray species.

6.2 Materials and Methods

6.2.1 Life-history data collection

A literature search was conducted for all species from the four families of shovelnose rays to provide data for estimation of population productivity using peer reviewed scientific manuscripts and taxonomic grey literature. An academic literature search was conducted using a combination of following keywords in Web of Science, Google Scholar, and OneSearch: "life history", "wedgefish", "giant guitarfish", "guitarfish", shovelnose ray", "banjo ray", "age", "growth", "maturity", "reproduction", "Rhinidae", "Glaucostegidae", "Rhinobatidae", and "Trygonorrhinidae". A separate search for grey literature was completed on Google using the same keywords, as well as on known relevant taxonomic reference books, including Last et al. (2016) Rays of the World. This review does not include literature that is not in the English language, although this research is acknowledged to contain valuable information.

Life-history information required for analyses consisted of age at maturity (α_{mat}, range of years), maximum age (α_{max}, in years), range of litter size (in number of female pups), sex ratio, breeding intervals (i, years), and von Bertalanffy growth coefficient (k, year^{-1}). Out of the four families, with a total of 57 species, only nine species had enough published life-history information to estimate r_{max} (**Table 6.1**).

Table 6.1. The nine species of shovelnose rays included in this study, their threat status on the International Union of Conservation of Nature's (IUCN) Red List of Threatened Species, and whether the species are listed on the appendixes of CITES, and/or CMS, and the CMS Sharks MOU (MOU). IUCN categories are CR, Critically Endangered; EN, Endangered; VU, Vulnerable; LC, Least Concern; DD, Data Deficient.

Family	**Species**	**IUCN**	**Year**	**CITES**	**Year**	**CMS**	**Year**
Rhinidae	*Rhynchobatus australiae*	CR	2019	Appendix II	2019	Appendix II/ MOU Annex 1	2017 2018
Glaucostegidae	*Glaucostegus cemiculus*	CR	2019	Appendix II	2019	-	-
	Glaucostegus typus	CR	2019	Appendix II	2019	-	-
Rhinobatidae	*Acroteriobatus annulatus*	LC	2006	-	-	-	-
	Pseudobatos horkelii	CR	2007	-	-	-	-
	Pseudobatos productus	NT	2014	-	-	-	-
	Rhinobatos rhinobatos	EN	2007	-	-	Appendix II/ MOU Annex 1	2017 2018
Trygonorrhinidae	*Zapteryx brevirostris*	VU	2006	-	-	-	-
	Zapteryx exasperata	DD	2015	-	-	-	-

The three parameter von Bertalanffy growth rate was estimated for *G. typus* using extracted length at age data from White et al. (2014) (see **Appendix 6.1** for methods). This was done as White et al. (2014) only reported the two parameter von Bertalanffy growth rate for this species, where the size at birth parameter (L_0) is fixed to an empirically estimated length (Fabens, 1965) and substantially biases the growth estimates (Pardo, Cooper & Dulvy, 2013; Smart et al., 2016b). For *G. typus* and *Z. brevirostris* the age at maturity was back-calculated using:

$$Age_x = \frac{\left(ln(L_\infty - TL_x) - ln(L_\infty) - (k * t_0)\right)}{-k}$$

Table 6.2. Life-history values and sources used to estimate maximum intrinsic rate of population increase (r_{max}) for the nine species of shovelnose rays studied: including the maximum size (L_{max} in centimetres total length, cm TL), lower, upper and mean (standard deviation, S.D.) values of the age at maturity (A_{mat}, years), lower and upper values for litter size, breeding interval (i, years), lower and upper annual reproductive output of females (b), lower and upper values for von Bertalanffy growth coefficient (k, year^{-1}), the observed, and lower (T_{lower}) and upper (T_{upper}) and mean (S.D.) values of theoretical maximum age (α_{max}, years). See S1 Table in S1 Appendix for re-estimated k parameter for *Glaucostegus typus*.

	L_{max}	**α_{mat} (yr)**				**litter size**		**i**	**b**		**k (yr^{-1})**		**A_{max} (yr)**					
Species	**(cm TL)**	**lower**	**upper**	**mean**	**± S.D.**	**lower**	**upper**	**(yr)**	**lower**	**upper**	**lower**	**upper**	**O_{max}**	**T_{lower}**	**T_{upper}**	**mean**	**± S.D.**	**References**
Rhynchobatus australiae	329	3.00	6.00	4.50	0.450	7	19	1	3.5	9.5	0.050	0.400	12.0	11.3	25.8	16.78	0.76	White et al. (2014); Last et al. (2016); **Chapter Five**
Glaucostegus cemiculus	290	2.89	6.50	4.70	0.680	5	24	1	2.5	12	0.200	0.275	14.0	13.9	16.1	14.67	0.50	Capapé & Zaouali (1994); Seck et al. (2004); Ali, Saad & Kurbaj (2008); Enajjar, Bradai & Bouain (2012); Last et al. (2016)
Glaucostegus typus	270	6.50	8.00	7.25	0.245	5	24	1	2.5	12	0.040	0.150	19.0	18.1	27.4	22.74	0.16	White & Dharmadi (2007); White et al. (2014); Last et al. (2016)
Acroteriobatus annulatus	140	2.30	2.80	2.55	0.080	2	10	1	1.0	5.0	0.240	0.240	7.00	14.8	14.8	12.23	1.30	Rossouw (1984); Last et al. (2016)
Pseudobatos horkelii	140	7.00	9.00	8.00	0.300	4	12	1	2.0	6.0	0.194	0.194	28.0	16.3	16.3	22.17	1.86	Casselberry & Carlson (2015); Last et al. (2016)
Pseudobatos productus	170	7.00	8.40	7.70	0.200	1	10	1	0.5	5.0	0.016	0.240	33.8	14.8	33.8	33.80	3.50	Timmons & Bray (1998); Downton-Hoffman (2007); Márquez-Farías (2007); Last et al. (2016)
Rhinobatos rhinobatos	185	2.20	4.10	3.15	0.350	1	14	1	0.5	7.0	0.134	0.310	18.9	13.1	18.9	18.92	1.00	Abdel-Aziz, Khalil & Abdel-Maguid (1993); Ismen, Yıgın & Ismen (2007); Başusta et al. (2008); Last et al. (2016); Lteif et al. (2016a); Lteif et al. (2016b); Newell (2017)
Zapteryx brevirostris	66	7.71	11.5	9.61	0.700	1	8	1	0.5	4.0	0.110	0.130	10.0	19.1	20.3	16.48	1.55	Gonzalez (2004); Barbini, Lucifora & Hozbor (2011); Colonello, Garcia & Menni (2011); Last et al. (2016); Carmo, Fávaro & Coelho (2018)

Zapteryx exasperata	103	5.41	9.65	7.53	0.800	2	13	1	1.0	6.5	0.144	0.174	22.6	17.1	18.4	19.85	0.80	Villavicencio-Garayzar (1995); Blanco-Parra, Marquez-Farias & Galvan-Magana (2009); Blanco-Parra, Márquez-Farías & Galván-Magaña (2009); Last et al. (2016); Cervantes-Gutiérrez, Tovar-Ávila & Galván-Magaña (2018)

where Age_x is age at time x, TL_x is total length (cm TL) at time x, L_∞ is the asymptotic length (cm TL), t_0 is the length at time zero, and k is the von Bertalanffy growth coefficient. The age at maturity for *G. typus* was estimated using the estimated size at maturity (Last et al., 2016) and growth coefficient (White et al., 2014). There is no reported litter size for *G. typus*, thus we assumed it had the same litter size and breeding interval as *Glaucostegus cemiculus* to calculate annual reproductive output. For *R. australiae*, *Acroteriobatus annulatus*, *Zapteryx exasperata* and *Z. brevirostris,* the breeding interval was assumed to be one year, based on other similar species as there was no information available (**Table 6.5**).

6. 2.2 Estimation of maximum intrinsic population growth rate, r_{max}

Maximum intrinsic rate of population increase was estimated using an unstructured derivation of the Euler-Lotka model. This model accounts for juvenile survivorship that depends on age at maturity and species-specific natural mortality, and incorporates uncertainty within the parameters through Monte Carlo simulation (Cortes, 2016; Pardo et al., 2016b). Requirements of this model are estimates of three biological parameters: annual reproductive output, age at maturity, and natural mortality. This model is founded on the principle that a breeding female only has to produce one mature female in her lifetime to ensure a stable population (Charnov & Schaffer, 1973; Myers & Mertz, 1998; Simpfendorfer, 2005b; Charnov & Zuo, 2011):

$$l_{\alpha_{mat}} b = e^{r_{max} \alpha_{mat}} - e^{-M} (e^{r_{max}})^{\alpha_{mat}-1}$$

where $l_{\alpha_{mat}}$ is survival to maturity in the absence of fishing and is calculated as $l_{\alpha_{mat}} = (e^{-M})^{\alpha_{mat}}$, b is the annual rate of production of females, α_{mat} is the age of maturity and M is instantaneous natural mortality. The annual reproductive output of females was calculated as $b = 0.5l/i$, where l is litter size (in number of males and females) and i is breeding interval (in years). Annual reproductive output estimates were derived from uniform distributions constrained by the minimum and maximum litter sizes published in the literature (**Table 6.2**). If the litter sex ratio was unknown, it was assumed to be 1:1. Age at maturity estimates were derived from normal distributions with means and standard deviations (S.D.) calculated from the available ages at maturity published in the literature for each species (**Table 6.2**). Normal distributions were truncated to be positive, using the standard deviations to be within “reasonable biological bounds”. The von Bertalanffy growth coefficients (*k)* for each species were derived from uniform distributions ranging between the minimum and maximum published values (**Table 6.2**). As the observed maximum age may not reflect the longevity of the species (Natanson et al., 2018), the theoretical maximum age (T_{max}) was calculated using minimum and maximum k reported for each species in the literature, using the following the formula (Fabens, 1965):

$$T_{max} = 7 \times ln(2/k)$$

Maximum age (α_{max}) estimates were derived from a normal distribution using the mean and S.D., calculated from the observed maximum age reported in the literature, minimum theoretical maximum age (T_{lower}) and maximum theoretical age (T_{upper}). As there was no current consensus on the best indirect method to estimate the instantaneous natural mortality, it was estimated using four common methods, Jensen's First mortality estimate (Jensen, 1996), modified Hewitt and Hoeing estimator (Hewitt & Hoenig, 2005), Frisk's estimator (Frisk, Miller & Fogarty, 2001), and reciprocal of the lifespan (Dulvy et al., 2004) (**Table 6.3**).

Table 6.3. Natural mortality (*M*) methods used to estimate maximum intrinsic rate of population increase in this study, where α_{mat} is age at maturity in years, α_{max} is maximum age in years, and k is the von Bertalanffy growth coefficient in year^{-1}.

Method	Equation	References
Jensen's First Estimator	$M = 1.65/\alpha_{mat}$	Jensen (1996)
Modified Hewitt & Hoeing Estimator	$M = 4.22/\alpha_{max}$	Hewitt & Hoenig (2005)
Frisk's Estimator	$M = 0.4/k$	Frisk, Miller & Fogarty (2001)
Reciprocal of lifespan	$M = 1/(\alpha_{mat} + \alpha_{max}/2)$	Pardo et al. (2016b)

Monte Carlo simulation was used to account for uncertainty of input parameters. The annual reproductive output and age at maturity were highly uncertain parameters, while the natural mortality was estimated indirectly, which can result in additional uncertainty (Dulvy et al., 2014b). Model parameters were drawn from their respective distributions iteratively 20,000 times (Pardo et al., 2018). To incorporate uncertainty into *M*, for each iteration the values for α_{mat}, α_{max} and k were drawn from their respective distributions, and used to estimate natural mortality for the four natural mortality estimators, which in turn is required to estimate r_{max} (Pardo et al., 2018). In each iteration, the r_{max} equation was solved using the *nlminb* optimisation function by minimising the sum of squared differences. This range of r_{max} values was generated to encompass the widest range of plausible life histories and should therefore include the true parameter values. Median and mean r_{max} values and standard deviation were calculated.

Scenarios were investigated where uncertainty was only incorporated into a single parameter. Values of one parameter were drawn from its distribution, while the remaining parameters were set as deterministic by using the median values of their respective distributions. This was done for the age at maturity, annual reproductive output, and natural mortality. The M value was set as deterministic in the other scenarios, even when the parameters used to estimate M were being drawn from distributions.

6.2.3 Comparison of shovelnose ray r_{max} estimates among chondrichthyans

Median r_{max} of the nine shovelnose ray species were compared to all available estimates using values by Pardo et al. (2016b) to incorporate survival to maturity, including an additional 13 species (**Appendix 6.2**). Following the method described above, the median r_{max} was calculated for the additional species for which life-history information was available, including great hammerhead *Sphyrna mokarran,* smooth hammerhead *Sphyran zygaena,* common thresher shark *Alopias vulpinus,* reef manta ray *Mobula alfredi,* giant manta ray *Mobula birostris,* Chilean devilray *Mobula tarapacana,* bentfin devil *Mobula thurstoni,* blackspotted whipray *Maculabatis astra,* speckled maskray *Neotrygon picta,* narrow sawfish *Anoxypristis cuspidata,* dwarf sawfish *Pristis clavata,* smalltooh sawfish *Pristis pectinata,* and green sawfish *Pristis zijsron* (**Appendix 6.2**). These species were added to increase the sample size, and to include more ray species in the analysis. The reciprocal of the lifespan natural mortality method was chosen to estimate the natural morality to compare to values generated by Pardo et al. (2016b) as that was the method used in their study. The r_{max} estimates for *Pseudobatos horkelii* and *Pseudobatos productus* were updated with the values from this study for the comparison. The age at maturity (years), maximum age (years), growth rate (k, years^{-1}) and maximum size in centimetres (cm) were plotted against the r_{max} estimates for 115 chondrichthyan species, including the nine species of shovelnose rays. Maximum sizes were TL for all species except for Myliobatiformes, where the disc width (DW) was used (García, Lucifora & Myers, 2008; Dulvy et al., 2014b). All models and figures were built in the R version 3.4.1 (R Core Team, 2021).

6.3 Results

6.3.1 Estimation of maximum intrinsic population growth rate, r_{max}

Estimates of maximum intrinsic rate of population increase for the nine species of shovelnose rays varied considerably among species, between families, and by the method of estimating natural mortality, ranging from 0.19 to 0.73 year^{-1} (25% - 95% quantiles) (**Table 6.5**). There was a high level of uncertainty in the annual reproductive output and age at maturity across all species (**Figure 6.1**). Uncertainty in the natural mortality values was low (**Figure 6.1**), but it resulted in high uncertainty in the r_{max} estimates, which was highly influenced by the natural mortality estimator (**Figure 6.2**; **Table 6.5**).

The ranges of r_{max} for each species were relatively large as a result of the high uncertainty in the life-history parameters and method of estimating natural mortality (**Figure 6.2**). *Acroteriobatus annulatus* and *R. rhinobatos* had the largest range of r_{max}, regardless of the natural mortality estimation method used (**Figure 6.2**; **Table 6.5**). *Pseudobatos horkelii* and *P. productus* had the smallest range of r_{max} (**Figure 6.2**; **Table 6.5**). Frisk's estimator, Maximum Age and Lifespan methods produced similar r_{max} estimates for each species, with 7% or less difference between mean values (**Figure 6.2**; **Table 6.5**). The lowest r_{max} values from every species were generated using the Jensen's First estimator and modified Hewitt and Hoeing's methods. These methods estimated negative r_{max} values for *A. annulatus*, *P. horkelii,* and *Z. brevirostris* (**Figure 6.2**; **Table 6.5**). *Zapteryx brevirostris,* the smallest species in the study, had one of the lowest estimates of r_{max}, across of natural mortality methods (**Table 6.5**).

As the age at maturity decreased, the estimates of r_{max} increased for the nine species of shovelnose rays (**Figure 6.3 A**). The species with the highest median estimates of r_{max}, *R. australiae*, *G. cemiculus*, *R. rhinobatos* and *A. annulatus* had the youngest age at maturity, while *Z. brevirostris* had the oldest age at maturity and lowest median estimate for r_{max} (**Figure 6.3 A**). The estimates of r_{max} increased as the number of female offspring produced annually increased (**Figure 6.3 B**). *Rhynchobatus australiae* and *G. cemiculus* had the highest annual reproductive output and r_{max}, while *G. typus* had lower r_{max} estimates but the same annual reproductive output as the two species (**Figure 6.3 B**). *Rhinobatos rhinobatos, P. horkelii* and *Z. exasperata* had similar estimates of annual reproduction, yet *R. rhinobatos*

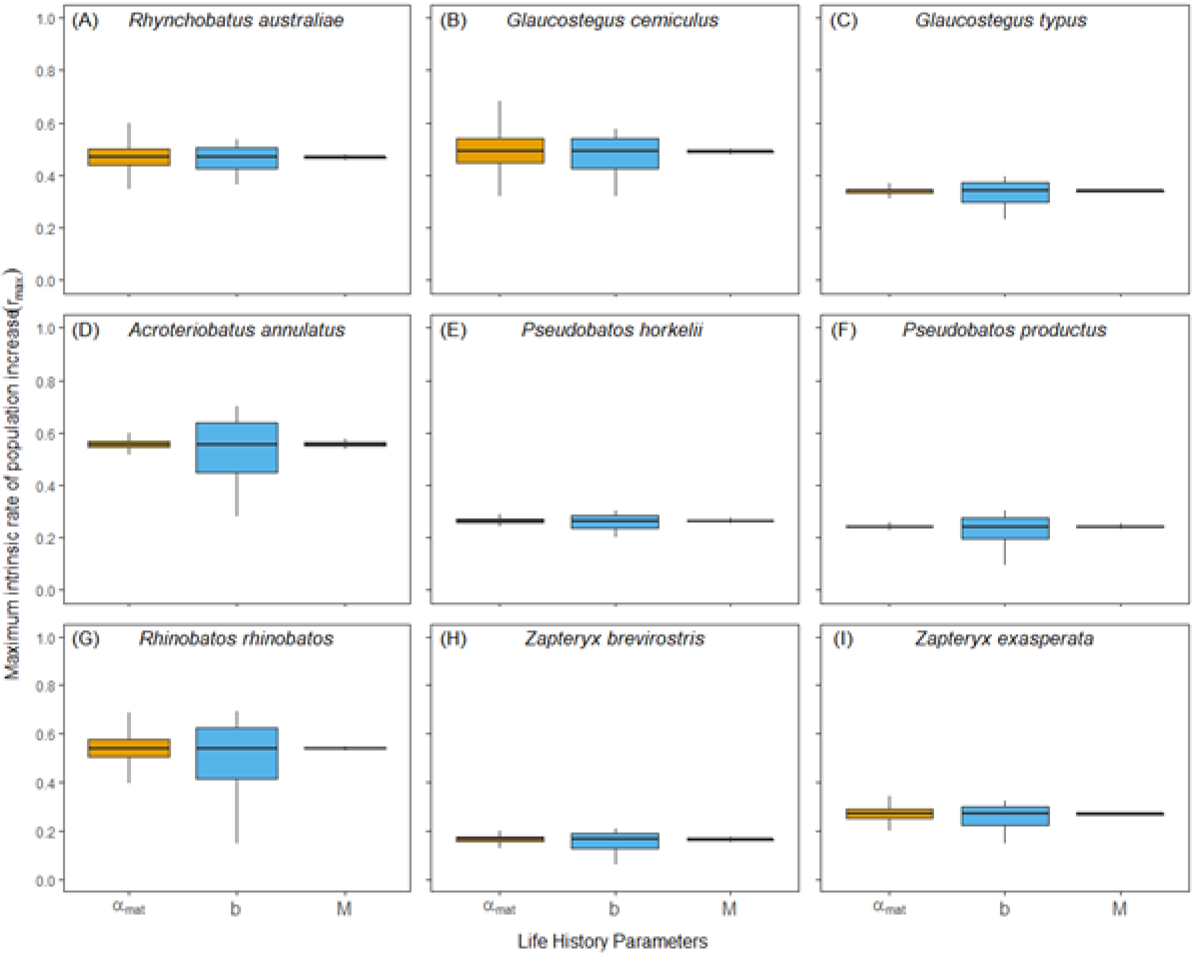

Figure 6.1. Predicted values of maximum intrinsic rate of population increase (r_{max}) for nine shovelnose ray species when including uncertainty in age at maturity (αmat, first/orange boxplot), annual reproductive output (b, middle/blue boxplot), and reciprocal of the lifespan natural mortality estimator (M, last/grey boxplot). Species are (**A**) bottlenose wedgefish *Rhynchobatus australiae*, (**B**) blackchin guitarfish *Glaucostegus cemiculus*, (**C**) giant guitarfish *Glaucostegus typus*, (**D**) lesser guitarfish *Acroteriobatus annulatus*, (**E**) Brazilian guitarfish *Pseudobatos horkelii*, (**F**) shovelnose guitarfish *Pseudobatos productus*, (**G**) common guitarfish *Rhinobatos rhinobatos*, (**H**) shortnose guitarfish *Zapteryx brevirostris*, and (**I**) banded guitarfish *Zapteryx exasperata*. Boxes indicate median, 25 and 75% quantiles, whereas the lines encompass 95% of the values (2.5 and 97.5% quantiles). For plots incorporating uncertainty with other natural mortality methods, see **Appendix 6.3**, **Appendix 6.4** and **Appendix 6.5**.

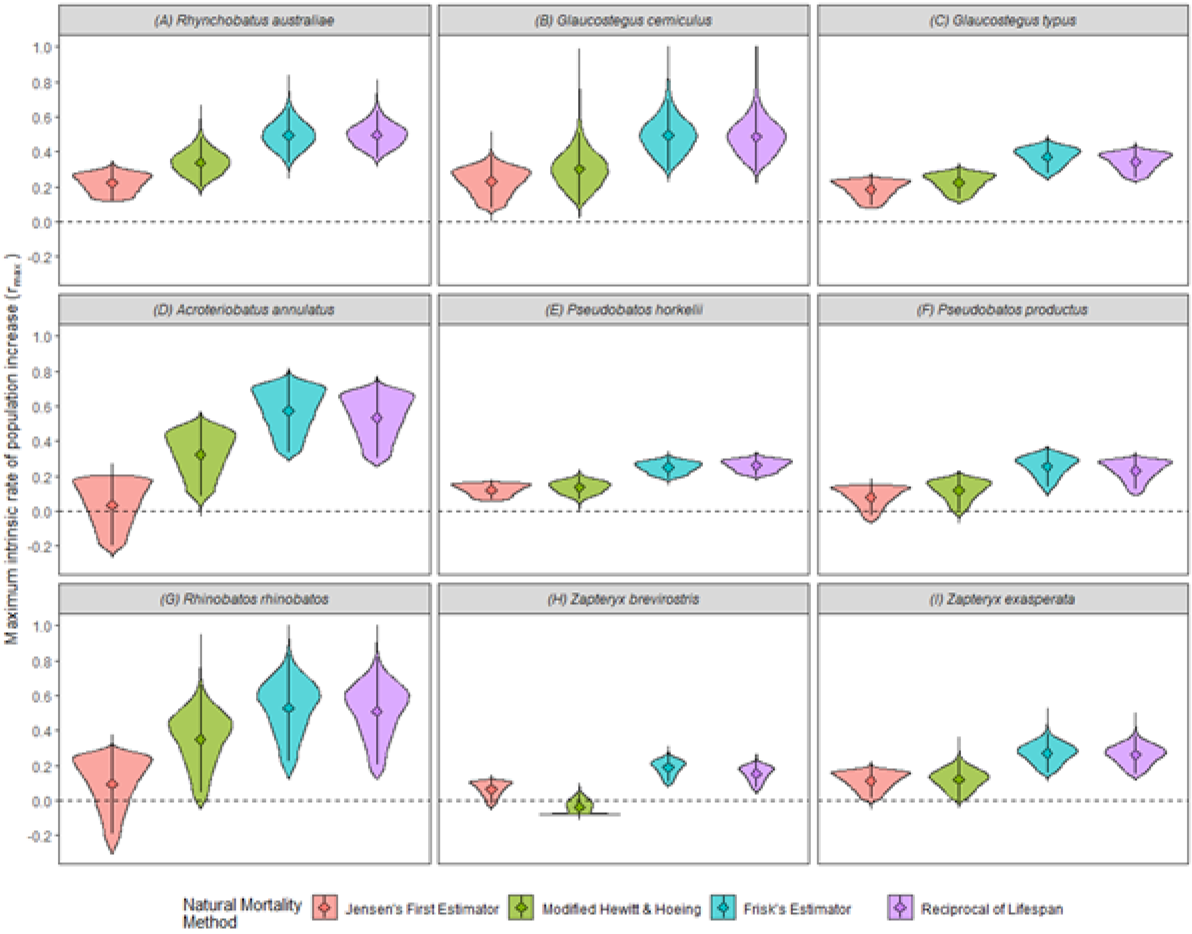

Figure 6.2. The range of maximum intrinsic rate of population increase (r_{max}, year^{-1}) for nine species of shovelnose rays, obtained with four different methods of estimating the instantaneous natural mortality: Jensen's First Estimator (red), modified Hoeing & Hewitt's Estimator (yellow), Frisk's Estimator (green), and Reciprocal of lifespan (blue). Means (triangle) and standard deviation (black line) are presented for each method. Species are (**A**) bottlenose wedgefish *Rhynchobatus australiae*, (**B**) blackchin guitarfish *Glaucostegus cemiculus*, (**C**) giant guitarfish *Glaucostegus typus*, (**D**) lesser guitarfish *Acroteriobatus annulatus*, (**E**) Brazilian guitarfish *Pseudobatos horkelii*, (**F**) shovelnose guitarfish *Pseudobatos productus*, (**G**) common guitarfish *Rhinobatos rhinobatos*, (**H**) shortnose guitarfish *Zapteryx brevirostris*, and (**I**) banded guitarfish *Zapteryx exasperata*. Values below the black dashed line indicate implausible r_{max} estimates.

had a higher estimate of r_{max} than *P. horkelii* and *Z. exasperata* (**Figure 6.3 B**). *Zapteryx brevirostris* had the lowest annual reproductive output and r_{max} estimate (**Figure 6.3 B**). Maximum rate of population growth increased with maximum size of the species (**Figure 6.4 A**). The largest species (i.e. *R. australiae*, *G. cemiculus* and *G. typus*) were estimated to have a higher maximum rate of species was the result of the high mean annual reproductive outputs, large size at birth and an early age at maturity (**Figure 6.4 B**, **C**). The smallest species, *Z. exasperata* and *Z. brevirostris,* had the lowest annual reproductive output and size at birth in relation to their maximum size (**Figure 6.4 B, C**).

6.3.2 Comparison of shovelnose ray r_{max} estimates to other chondrichthyans

The maximum intrinsic rate of population increase estimates of the chondrichthyans ranged from 0.04 to 1.39 yr^{-1}. The average r_{max} estimate was 0.30 yr^{-1}, which was considered to be a medium rate of population increase for chondrichthyans (n = 20; 17.4% of species) (**Figure 6.5**; **Table 6.4**). Of the superorder Batoidea, 35.4% of species (n = 17) have a high r_{max} values and high population productivity, 22.9% of species (n = 11) were classified as a medium population productivity, and 41.7% of species (n = 20) have a low r_{max} estimates (**Table 6.4**). For the superorder Selachimorpha (including the order Chimaeriformes), 19.4% of species have a theoretical high population productivity estimate (n = 13), 13.4% species were classified as medium population productivity (n = 9), and 67.2% of species were classified with a low population productivity (n = 45) (**Table 6.4**).

Table 6.4. Summary of the maximum intrinsic rate of population increase (r_{max}) for 115 chondrichthyans, grouped by superorders Selachimorpha (including order Chimaeriformes) and Batoidea (rays, skates and mobulids), calculated with the reciprocal of lifespan natural mortality estimator (**Appendix 6.2**). The r_{max} estimates are grouped into high (r_{max} value greater than the average of 0.3 yr^{-1}), medium (equal to the average r_{max} estimate) and low (lower than the average r_{max} estimate) where n refers to the number of species, and % refers to the percentage within the group.

	All species		**Selachimorpha**		**Batoidea**	
r_{max} estimate	*n*	%	*n*	%	*n*	%
High	30	26.1	13	19.4	17	35.4
Medium	20	17.4	9	13.4	11	22.9
Low	65	56.5	45	67.2	20	41.7
Total	**115**	**100**	**67**	**100**	**48**	**100**

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Table 6.5. Maximum intrinsic rates of population increase estimates (r_{max}, year^{-1}) for nine species of wedgefishes, guitarfishes, and banjo ray, using four estimators of natural mortality. The mean (± standard deviation S.D.) and 25% and 95% quantiles of r_{max} values are reported for each species and natural mortality estimator.

	Jensen's First estimator				**Hewitt & Hoeing's estimator**				**Frisk's estimator**				**Reciprocal of lifespan estimator**			
Species	**25%**	**Mean**	**± S.D.**	**95%**	**25%**	**Mean**	**± S.D.**	**95%**	**25%**	**Mean**	**± S.D.**	**95%**	**25%**	**Mean**	**± S.D.**	**95%**
Rhynchobatus australiae	0.18	0.22	0.050	0.30	0.29	0.34	0.069	0.46	0.44	0.50	0.077	0.63	0.45	0.49	0.067	0.61
Glaucostegus cemiculus	0.17	0.23	0.074	0.34	0.23	0.30	0.103	0.48	0.42	0.49	0.103	0.67	0.42	0.49	0.100	0.66
Glaucostegus typus	0.15	0.18	0.046	0.24	0.19	0.22	0.047	0.28	0.34	0.37	0.048	0.44	0.31	0.34	0.047	0.41
Acroteriobatus annulatus	-0.05	0.03	0.116	0.19	0.23	0.28	0.119	0.49	0.48	0.57	0.117	0.73	0.45	0.52	0.117	0.69
Pseudobatos horkelii	0.09	0.12	0.029	0.16	-0.11	0.13	0.035	0.25	0.23	0.25	0.032	0.29	0.24	0.26	0.031	0.31
Pseudobatos productus	0.04	0.08	0.053	0.14	0.08	0.12	0.055	0.19	0.22	0.25	0.056	0.33	0.19	0.23	0.053	0.30
Rhinobatos rhinobatos	0.00	0.10	0.143	0.27	0.25	0.35	0.153	0.57	0.43	0.53	0.154	0.75	0.41	0.51	0.152	0.73
Zapteryx brevirostris	0.04	0.06	0.040	0.11	-0.08	-0.04	0.038	0.03	0.16	0.19	0.042	0.25	0.13	0.16	0.041	0.21
Zapteryx exasperata	0.07	0.11	0.049	0.17	0.08	0.12	0.057	0.21	0.23	0.27	0.057	0.36	0.22	0.26	0.056	0.34

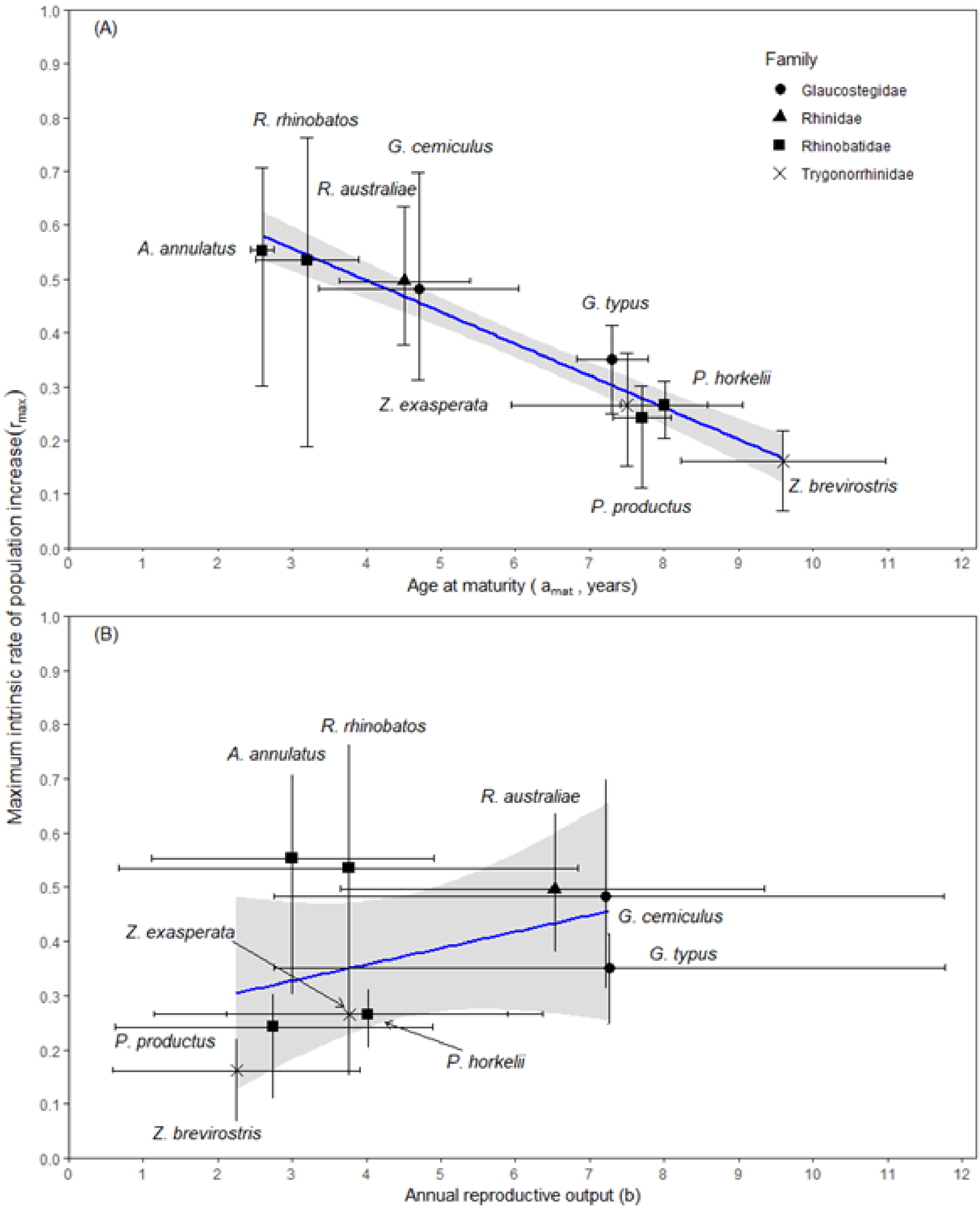

Figure 6.3. Maximum intrinsic rate of population increase (r_{max}) for the nine species of shovelnose rays in relation to the (**A**) age at maturity (a_{mat}, years) and (**B**) annual reproduction rate of females (b). The black lines encompass 95% of the values (2.5 and 97.5% quantiles). The reciprocal of lifespan natural mortality estimator to estimate r_{max}. The shapes represent the four families; black circles represent the giant guitarfishes, Family Glaucostegidae; black triangles signify the wedgefishes, Family Rhinidae; black squares represent guitarfishes, Family Rhinobatidae; and black crosses are banjo rays, Family Trygonorrhinidae.

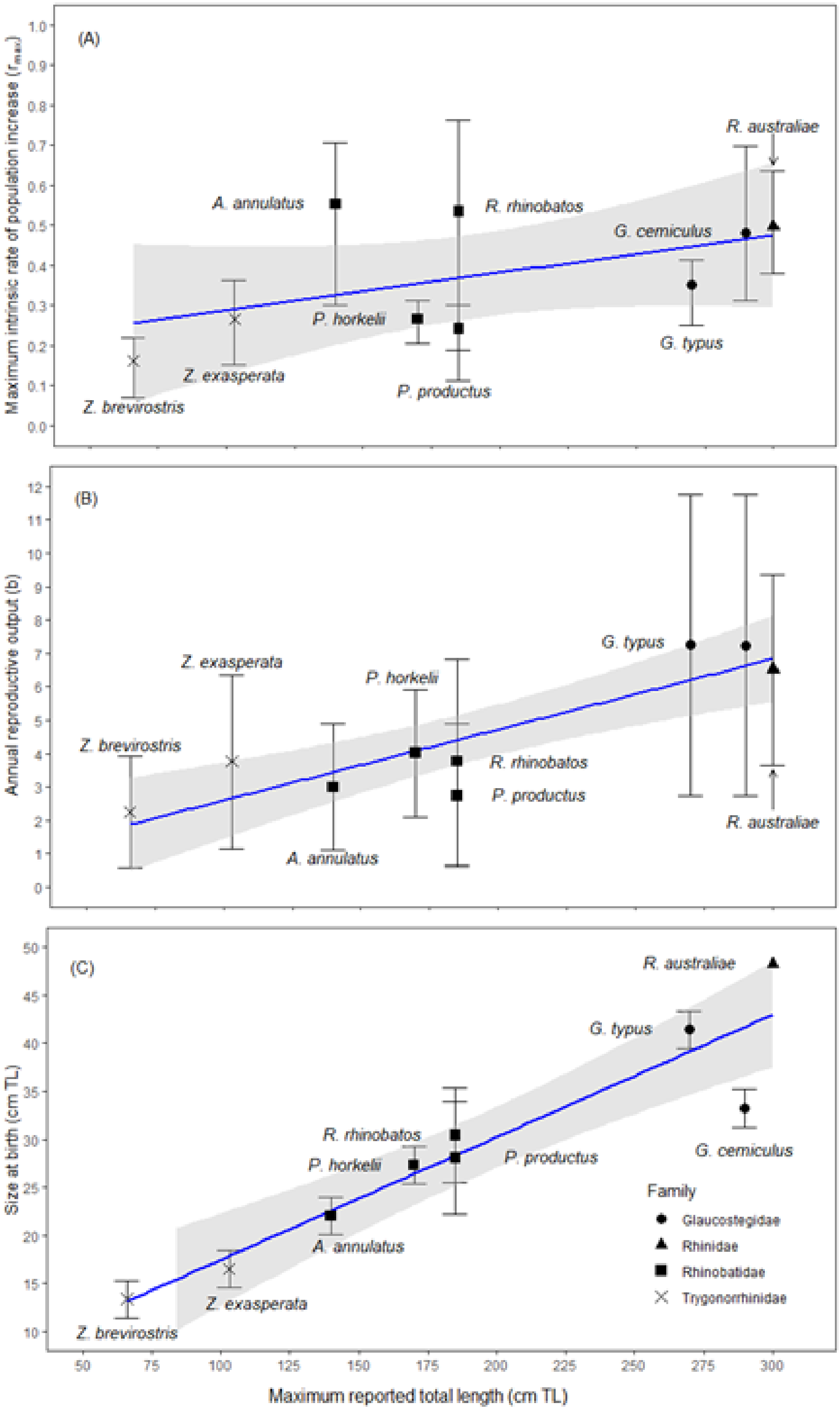

Figure 6.4. Maximum size (cm TL) for the nine species of shovelnose rays in relation to the (**A**) median maximum intrinsic rate of population increase (r_{max}, yr^{-1}) using the reciprocal of lifespan to estimate natural mortality, (**B**) annual reproduction rate of females (*b*), and (**C**) size at birth (cm TL). The black lines encompass 95% of the values (2.5 and 97.5% quantiles). The shapes represent the four families; black circles represent the giant guitarfishes, Family Glaucostegidae; black triangles signify the wedgefishes, Family Rhinidae; black squares represent guitarfishes, Family Rhinobatidae; and black crosses are banjo rays, Family Trygonorrhinidae.

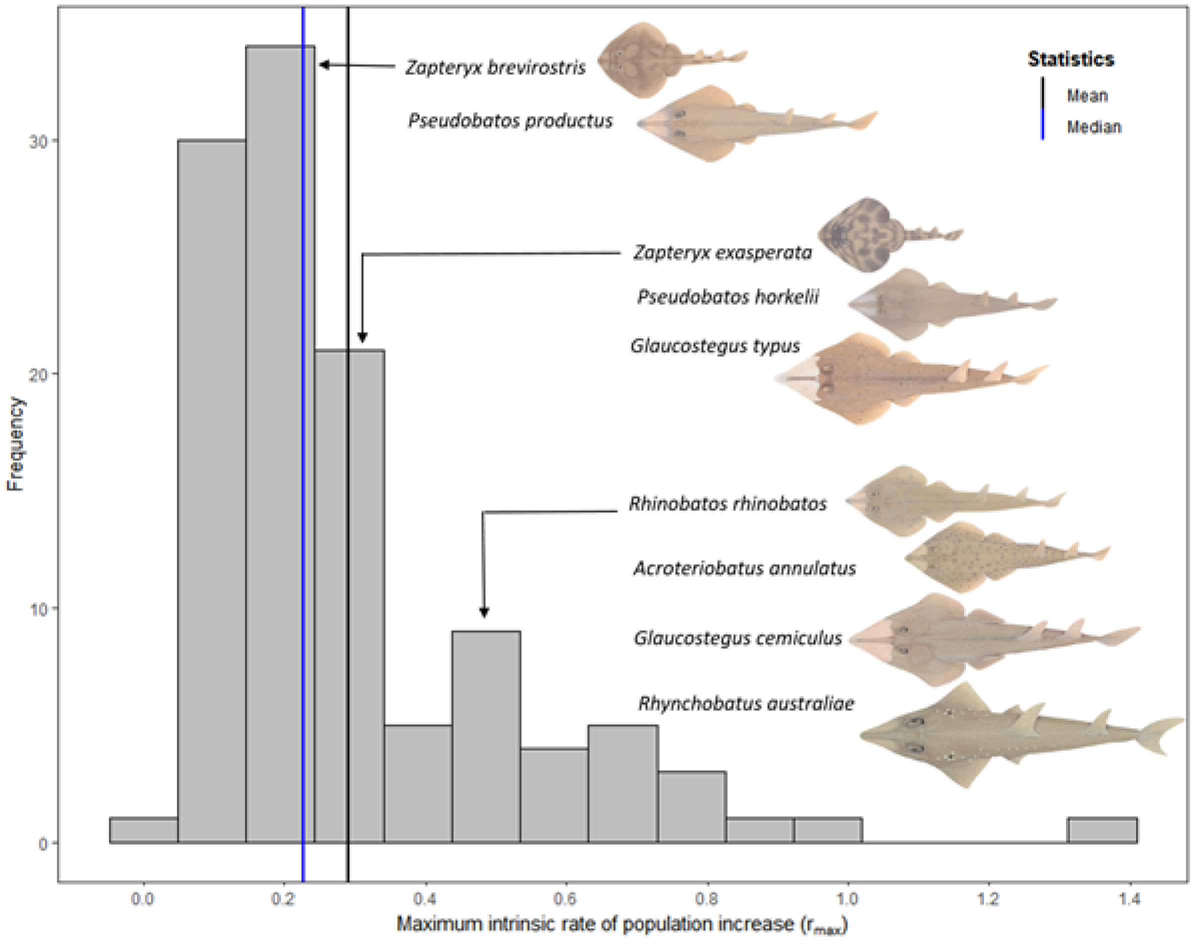

Figure 6.5. Maximum intrinsic rate of population increase (r_{max}) for 115 chondrichthyans, including the nine shovelnose ray species, which are displayed on the figure and grouped by their rmax r_{max}. The reciprocal of lifespan natural mortality estimator was used to estimate r_{max}. Black line denotes the mean (r_{max} = 0.30), and blue line represents the median (r_{max} = 0.23). Species illustrations are from Last et al. (2016).

Compared to the other chondrichthyans species, *Z. brevirostris* and *P. productus* have a below average r_{max} estimates, while *Z. exasperata*, *P. horkelii*, and *G. typus* have medium r_{max} estimates, and *R. rhinobatos*, *A. annulatus*, *G. cemiculus*, and *R. australiae* have a higher-than-average r_{max} estimates (**Figure 6.5**; **Table 6.5**). *Rhynchobatus australiae*, *G. cemiculus* and *G. typus* had relatively high r_{max} estimates, compared to species with similar maximum sizes (**Figure 6.6 A**). *Pseudobatos horkelii*, *P. productus* and *Z. exasperata* had mid-range estimates of r_{max} compared to species of a similar maximum size (**Figure 6.6 A**). *Acroteriobatus annulatus* and *R. rhinobatos* had relatively high r_{max}, while *Z. brevirostris* had a lower r_{max} when compared to similar maximum sized species (**Figure 6.6 A**). The majority of the largest chondrichthyan species for which r_{max} are available are all listed on CITES and CMS, however they are not the least productive species (**Figure 6.6 A**). *Acroteriobatus annulatus*, *G. cemiculus* and *R. australiae* mature at the youngest ages and had higher estimates of r_{max}, compared to the other Rhinopristiformes and chondrichthyans (**Figure 6.6 B**). *Acroteriobatus annulatus*, *R. rhinobatos, G. cemiculus* and *R. australiae* are among the chondrichthyans species with the lowest maximum age estimates, and hence high r_{max} (**Figure 6.6 C**). *Glaucostegus typus, Z. exasperata, P. horkelii* and *P. productus* have mid-range maximum ages compared to other species, while *Z. brevirostris* had a lower r_{max} estimate compared to other species with a similar maximum age (**Figure 6.6 C**). *Acroteriobatus annulatus*, *R. rhinobatos, G. cemiculus* and *R. australiae* have relatively higher r_{max} estimates compared to species with similar annual reproductive output. *Zapteryx exasperata, P. horkelii* and *P. productus* are estimated to have a mid-range annual reproductive estimate, compared to species with similar r_{max} (**Figure 6.6 D**). *Glaucostegus typus* has a relatively high r_{max} estimate compared to species with similar annual reproductive output, while *Z. brevirostris* has a low r_{max} estimate compared to species with similar annual reproductive output (**Figure 6.6 D**). *Acroteriobatus annulatus, R. rhinobatos, G. cemiculus* and *R. australiae* have fast somatic growth and a high r_{max} in comparison to the other chondrichthyan species (**Figure 6.6 E**). *Glaucostegus typus, Z. exasperata* and *P. horkelii* have a mid-range r_{max} compared to species with similar growth rates, while *P. productus* and *Z. brevirostris* have a lower r_{max} compared to other species with similar growth rates (**Figure 6.6 E**).

6.4 Discussion

Typically, large-bodied marine animals are associated with factors of vulnerability, such as lower intrinsic rate of population growth, late maturity, and dependence on vulnerable habitat, while smaller-bodied species are linked to factors providing resilience, including faster population growth and early maturity (Smith, Au & Show, 1998; García, Lucifora & Myers, 2008; Dulvy et al., 2014a). The productivity of shovelnose rays was similar to four sawfish species, which despite their large size (ranging from 318 – 700 cm TL) have been estimated to have a relatively high productivity for elasmobranchs (Carlson & Simpfendorfer, 2015). The positive relationship between maximum size and maximum intrinsic rate of population growth for seven out of nine shovelnose ray species in this study is unusual among elasmobranchs (Dulvy, Sadovy & Reynolds, 2003). This relationship is being driven by the positive relationship between body size and litter size, as the litter size increases with the maximum size of these rays. These findings for these species contrast other multi-species

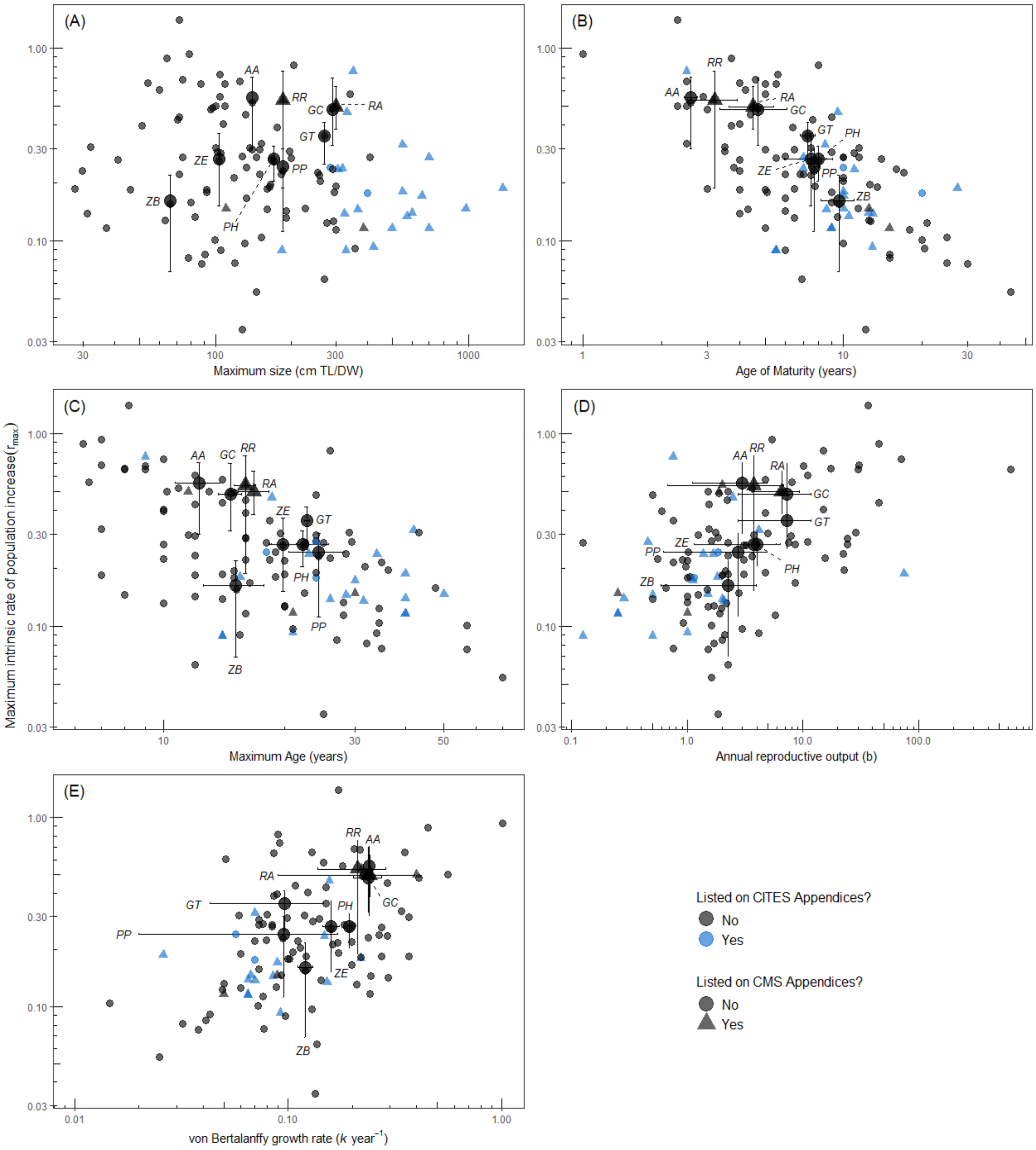

Figure 6.6. Maximum intrinsic rate of population increase (r_{max}) estimates for 115 chondrichthyans, including nine shovelnose ray species compared with (**A**) maximum size (cm TL/DW), (**B**), age at maturity (α_{mat} years), (**C**) maximum age (α_{max}, years), (**D**) annual reproductive output *b*, (**E**) the von Bertalanffy growth coefficient (*k*, year^{-1}). The nine shovelnose ray species labelled are: RA, bottlenose wedgefish *Rhynchobatus australiae;* GC, blackchin guitarfish *Glaucostegus cemiculus*; GT, giant guitarfish *Glaucostegus typus*; AA, lesser guitarfish *Acroteriobatus annulatus;* PH, Brazilian guitarfish *Pseudobatos horkelii*; PP, shovelnose guitarfish *Pseudobatos productus;* RR, common guitarfish *Rhinobatos rhinobatos*, ZB, shortnose guitarfish *Zapteryx brevirostris;* ZE, banded guitarfish *Zapteryx exasperata*. The black lines encompass 95% of the values (2.5 and 97.5% quantiles). The median r_{max} value is reported, using the reciprocal of the lifespan method to estimate natural mortality. All axes are on a logarithmic scale. Species that are listed on CITES Appendix I or II are represented in blue, species listed on CMS Appendix I or II are represented as triangles. Species that are listed on neither CITES or CMS are indicated as grey circles.

comparative studies, such as Dulvy et al. (2014b), where the maximum intrinsic rate tends to decrease with increasing maximum size. *Acroteriobatus annulatus* and *R. rhinobatos* did not fall within this positive relationship due to their young age at maturity, fast somatic growth, and high annual reproductive output (Last et al., 2016). While body size has been used to predict extinction risk in elasmobranchs, with the larger species predicted to be most at risk of extinction (Dulvy et al., 2014a), this may not be the case for some shovelnose rays. Additionally, other studies have found little (Frisk, Miller & Fogarty, 2001; García, Lucifora & Myers, 2008) to no correlation (Cortés, 2000) between body size and rate of population increase. The relationship between body size and rate of population growth has been hypothesised to be the result of correlations between body size and other more influential life-history traits such as age at maturity and litter size (Blueweiss et al., 1978; Purvis et al., 2000).

The estimates of r_{max} are sensitive to increasing variation in age at maturity (Pardo et al., 2018). The early maturity of shovelnose rays, particularly compared to other species of similar size, as well as the increasing litter size with increasing body size, help to explain the relatively high r_{max} estimates for this group. The larger body size of wedgefishes and giant guitarfishes allows these species to produce numerous and large offspring in relation to their maximum size. In contrast, the guitarfishes and banjo rays have smaller birth size and smaller litters relative to their maximum size. Larger offspring will likely have a greater survival probability than the smaller offspring of species with a similar r_{max} (Pardo et al., 2018). For long-lived species, juvenile survival is a key contributor to the population growth rate (Frisk, Miller & Fogarty, 2001). While the model used in this study incorporates juvenile survival, it also assumes that juvenile mortality is equal to adult mortality (Pardo et al., 2016b). Juveniles, as well as neonates (age 0) tend to have higher mortality rates than adults (Cushing, 1975), which then can vary with local differences in habitat (Heupel & Simpfendorfer, 2011). This assumption of equal mortality is likely to result in conservative estimates of M (Pardo et al., 2016b). The differential neonate and juvenile mortality among species was not accounted for in this model, but should be the focus of further study (Pardo et al., 2018).

Natural mortality, referring to the death of individuals in the population from natural causes such as predation, disease and old age (Simpfendorfer, 2005b), is one of the most important parameters in fisheries and conservation modelling, yet it is one of the hardest to estimate (Dulvy et al., 2004; Then et al., 2014; Hoenig et al., 2016). While in some models uncertainty in the natural mortality parameter has little influence on r_{max} (Pardo et al., 2018), different estimators can have substantial effects on r_{max} values (Then et al., 2014). Frisk's estimator and Reciprocal of life span are more suited for elasmobranchs, given they have relatively high juvenile survival (Frisk, Miller & Fogarty, 2001; Pardo et al., 2016b). Considering juvenile mortality, r_{max} estimates produced by these two natural mortalities suggest these estimators are more plausible and may be the more appropriate methods for elasmobranchs. In contrast the Jensen's First Estimator (Jensen, 1996) and the modified Hewitt and Hoeing method (Hewitt & Hoenig, 2005) were explicitly designed for adult mortality and systematically resulted in negative value of r_{max} for five out of the nine species of shark-like ray species. The biologically implausible estimates were also demonstrated in Pardo et al. (2016b), and are likely the consequence of overestimating natural mortality (e.g. > 0.1 year^{-1}) for these species, particularly when the annual reproductive output is low (e.g. $b < 5$) and age at maturity is high (Pardo et al., 2016b; Pardo et al., 2018). It is therefore likely that Jensen's First Estimator and the modified Hewitt and Hoeing are less appropriate methods of estimating natural mortality for chondrichthyans. There is considerable debate as to which empirical model should be used to estimate adult natural mortality, as there are numerous and diverse approaches using life-history information to estimate this parameter (Kenchington, 2014; Hoenig et al., 2016). However, identifying, or improving the best indirect estimator would require data-intensive methods, such as catch data to analyse catch curves, mark re-capture experiments, virtual population analysis, or fully integrated stock assessments (Kenchington, 2014). These methods all require extensive prior knowledge of the biology of the species that is lacking for many chondrichthyan species. Presenting the results from multiple natural mortality estimators provides a better understanding of the uncertainty associated with the maximum intrinsic rate of population increase.

The greatest obstacle to accurately estimate r_{max} and natural mortality is the accuracy of the biological information used (Cortes, 2016). The use of inaccurate surrogate information can reduce the accuracy of the demographic models (Chin et al., 2013; Smart et al., 2015; Cortes, 2016). Of the 56 species across the four families of shovelnose rays, only nine species had sufficient information to estimate their maximum intrinsic rate of population increase, and with relatively high levels of uncertainty associated with the life-history parameters and small sample sizes. For example, there were only two age and growth studies for wedgefishes and giant guitarfishes, one from the eastern coast of Australia for *R. australiae* and *G. typus* (White et al., 2014), and one from Central Mediterranean Sea for *G. cemiculus* (Enajjar, Bradai & Bouain, 2012). Neither study estimated age at maturity, nor aged individuals at the maximum sizes. Given that the age at maturity is a pivotal parameter when estimating r_{max}, yet highly uncertain for all shovelnose rays examined, these estimates must be taken with caution. Furthermore, numerous reviews have reported sampling biases and failures in ageing protocols, including lack of validation (Cailliet et al., 2006; Cailliet, 2015) that often result in overestimation or underestimate of age and growth parameters (Harry, 2018). As there has been no validation studies in the ages of wedgefishes, guitarfishes, and banjo rays, the maximum ages for these species are likely to be underestimated, while the age at maturity estimates could also be inaccurate. This can lead to inaccurate estimates of natural mortality and r_{max} (Gedamke et al., 2007; Cortes, 2016). The information on the reproductive biology for Rhinopristiformes is limited but is more available for species in the guitarfishes Rhinobatidae and Trygonorrhinidae families. For example, there is evidence that species such as *P. productus, P. horkelii*, and Z. *exasperata* employ embryonic diapause or delayed development (Marshall, White & Potter, 2007; Blanco-Parra, Márquez-Farías & Galván-Magaña, 2009), potentially as a result of unfavourable environmental conditions (Capapé, Ben Brahim & Zaouali, 1997) or sex segregation (Kyne & Bennett, 2002b). Simpfendorfer (1992) hypothesised that diapause allowed another elasmobranch species (*Rhizoprionodon taylori*) to have larger litter sizes than other similar sized species in the same family (Carcharhinidae). Capture-induced parturition (premature birth or abortion) during sampling is possible for elasmobranchs and can result in the underestimation of litter sizes (Adams et al., 2018). As possibility of diapause and capture induced parturition was not able to be taken into account during this study, the breeding interval and annual reproductive output may be inaccurate, and it could result in an inappropriate maximum intrinsic rate of population growth. Directing research efforts to obtain data from more species, as well as improving the accuracy of life-history parameters for data-poor species, such as age at maturity and annual reproductive output, would be the most pragmatic option to improve the accuracy of r_{max} for shovelnose rays.

Measuring the population productivity allows for a greater understanding of the species' ability to recover from declines and provides the demographic basis for evaluating the sustainability of fisheries and trade (Skalski, Ryding & Millspaugh, 2005; Cortes, 2016). The unregulated fishing pressure that most shovelnose ray species currently experience is likely unsustainable (Moore, 2017; Jabado, 2018). Yet, there are minimal regional and national level management by countries within the ranges of shovelnose rays. To reduce fishing mortality, conserve populations and allow for recovery, a suite of management measures will be required including species protection, spatial management, bycatch mitigation, and harvest strategies (Kyne et al., 2020). International trade of highly-valued fins is considered a major driver of over-exploitation for shovelnose rays (Ostrom et al., 1999; Kyne et al., 2020) and the use of trade controls through CITES listings may be an effective way to encouraging better management of shovelnose ray species. In 2019, the wedgefishes (Rhinidae) and giant guitarfishes (Glaucostegidae) were listed on the CITES Appendix II (Cardeñosa et al., 2018). Any Parties that wish to export products from these rays, requires an NDF, which provides evidence that the populations that supply the trade are sustainable. In addition, CITES, unlike many other international agreements, has the capacity to enforce its actions through a Review of Significant Trade and possible trade suspensions, in conjunction with national-level enforcement and compliance measures (Vincent et al., 2014). The recent CITES Appendix II listing provides an opportunity to gather information through the CITES database, which holds all permitted exports, re-exports, and imports of Appendix II species. As other commercially important elasmobranch species are listed on CITES, a number of capacity building tools are available for Parties for the implementation and enforcement of elasmobranchs on Appendices, including an elasmobranch specific information portal (CITES, 2019a), and a new species identification guide for wedgefishes and giant guitarfishes (Jabado, 2019). International agreements such as CITES and CMS are only one step needed to reduce threats of these species in international trade, recover populations, ensure sustainable resource use, and are designed to be complementary to existing national and regional management (Vincent et al., 2014). Fisheries are complex social-ecological systems, and successful management will require significant improvements in governance across local, global and regional scales (Ostrom et al., 1999). After the enactment of national and international management measures to reduce fishing mortality, the theoretical maximum intrinsic rate of population increases of some species of shovelnose rays (i.e. *R. australiae, G. cemiculus, G. typus*), suggests that they have the biological capacity to recover relatively quickly from the reported population declines.

6.5 Conclusion

Using current life-history data, incorporating uncertainty in parameters, and considering juvenile mortality, this study provides the first analysis into the population productivity for nine species from four families of Rhinopristiformes. Compared to other chondrichthyans, the larger wedgefish and giant guitarfishes were found to be potentially productive species, while the smaller guitarfishes and banjo rays were less productive. The maximum intrinsic rate of population increases varied with the different natural mortality estimator, yet it also appears to increase with increasing maximum size for the four families, which is counter to most studies of shark populations. There was considerable uncertainty in the age at maturity and annual reproductive output for all species. There is a need for better life-history information for these data-poor species, as there was only nine of out 56 species with sufficient life-history information. We recommend presenting the results from multiple natural mortality estimators to provide a greater understanding of the uncertainty for the maximum intrinsic rate of population increase. It appears that wedgefishes and giant guitarfishes could, theoretically, recover from population depletion faster than guitarfishes and banjo rays, if fishing mortality is kept low. Extensive regional, national, and international fisheries management strategies, including the regulation of international trade through CITES, will be required to address the overfishing of these species, and may help to achieve positive conservation outcomes. The results of this study provide guidance to help implement management and conservation measures, while highlighting the lack of information available for these species.

Acknowledgements

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6.6 Appendices

Re-estimating the three parameter von Bertalanffy growth rate of *Glaucostegus typus* from White et al. (2014)

Method

Published observed and back calculated length at age data was extracted from the (White et al., 2014) Figure 4 for combined sexes of *G. typus* using the program, Data Thief (Tummers, 2006). Male and female samples were combined in the study and therefore, the estimates for combined sexes are presented here. The extracted length at age for the observed and back calculated data was fitted to the three parameter von Bertalanffy growth model [VBGF, (von Bertalanffy, 1938)] in the R statistical environment (R Core Team, 2021) as:

where L_t is length at age t, L_0 is length at age 0, L_∞ is asymptotic length, and k is the von Bertalanffy growth rate. The model was fitted using the biologically relevant length at birth parameter (L_0), instead of the time at size zero parameter (t_0). Parameter estimates were estimated using non-linear least-square regression methods. The standard errors for the parameter estimates were calculated using bootstrapping method with the ‘nlstools’ package in R.

Results

The extracted ages for *G. typus* ranged from 0 – 18 years. Length estimates ranged from 51 – 286 cm TL. The data points extracted from the Figure 4 for the *G. typus* observed data was greater than reported in text of 23 samples (Table1). Given the considerable uncertainty associated with this data, the lowest *k* value was used as the minimum *k* estimated in the model for G. *typus* (**Appendix 6.1**).

Appendix 6.1 Summary of the three parameter von Bertalanffy estimates for the observed length-at-age data and back calculated data for *G. typus*, from Eastern Australia. Length-at-age was extracted from White et al. (2014), using the program Data Thief (Tummers, 2006). *n* refers to the sample size, L_∞ the asymptotic length (± standard error S.E. in centimetres total length, cm TL), *k* is the von Bertalanffy growth parameter (S.E. ± year^{-1}) and L_0 is the size at birth (± S.E. cm TL).

	n	L_∞ (± S.E. cm TL)	*k* (± S.E. year^{-1})	L_0 (± S.E. cm TL)
Observed data	60	402.1 ± 123.9	0.059 ± 0.031	49.85 ± 11.34
Back calculated data	101	500.8 ± 108.5	0.040 ± 0.129	39.16 ± 5.912

Appendix 6.2. Maximum intrinsic rate of population increase (r_{max}) estimates, life-history values and sources used to estimate r_{max} for all chondrichthyan species in the comparison analysis. The natural mortality method used was the reciprocal of the lifespan method. Included is whether the species are listed on the appendixes of Convention of International Trade of Endangered Species (CITES, yes or no) and/or Convention on the Conservation of Migratory Species of Wild Animals (CMS, yes or no). The values included are the maximum size (L_{max} in centimetres total length/disk width, cm TL/DW), von Bertalanffy growth coefficient (k, year^{-1}), age at maturity (α_{mat}, years), reported maximum age (α_{max}, years), litter size (l), breeding interval (i, years), annual reproductive output of females (b). The r_{max} estimates are grouped into high (r_{max} value greater than the average of 0.3 yr $^{-1}$), medium (equal to the average r_{max} estimate) and low (lower than the average r_{max} estimate). The '--' indicates parameter was not available from literature.

Superorder	**Order**	**Family**	**Species**	**CITES**	**CMS**	**L_{max} (cm TL/DW)**	***k* (yr^{-1})**	**α_{mat} (yrs)**	**α_{max} (yrs)**	**average lifespan**	***l***	***i* (yrs)**	***b***	**r_{max}**	**Classification**	**Source**
Selachimorpha	Carchariniformes	Carcharhinidae	*Carcharhinus acronotus*	No	No	132.4	0.27	3.8	19	11	3.9	2.0	0.98	0.2	Low	Pardo et al. (2016b)
			Carcharhinus amblyrhynchos	No	No	190.0	0.29	6.0	12	9.0	4.1	2.0	1.03	0.1	Low	Pardo et al. (2016b)
			Carcharhinus brachyurus	No	No	275.0	0.05	21	35	28	17	2.0	4.15	0.1	Low	Pardo et al. (2016b)
			Carcharhinus brevipinna	No	No	294.1	0.10	9.0	19	14	8.5	2.0	2.13	0.2	Low	Pardo et al. (2016b)
			Carcharhinus cautus	No	No	133.0	0.19	6.0	16	11	4.2	2.0	1.05	0.2	Low	Pardo et al. (2016b)
			Carcharhinus falciformis	Yes	Yes	305.0	0.15	11	23	17	6.5	2.0	1.63	0.2	Low	Pardo et al. (2016b)
			Carcharhinus galapagensis	No	No	300.0	0.17	7.8	15	11	8.7	2.0	2.13	0.2	Low	Pardo et al. (2016b)
			Carcharhinus isodon	No	No	159.6	0.24	4.3	8.0	6.2	4.0	2.0	1.00	0.1	Low	Pardo et al. (2016b)

Carcharhinus leucas	No	No	300.2	0.07	18	28	23	9.9	2.0	2.48	0.1	Low	Pardo et al. (2016b)
Carcharhinus limbatus	No	No	191.0	0.21	6.5	10	8.3	4.6	2.0	1.15	0.1	Low	Pardo et al. (2016b)
Carcharhinus longimanus	Yes	No	285.0	0.06	10	18	14	6.1	2.0	1.53	0.2	Low	Pardo et al. (2016b)
Carcharhinus obscurus	No	No	357.2	0.04	21	34	27	10	3.0	1.67	0.1	Low	Pardo et al. (2016b)
Carcharhinus plumbeus	No	No	226.5	0.09	11	22	17	7.9	2.0	1.98	0.1	Low	Pardo et al. (2016b)
Carcharhinus porosus	No	No	12.08	0.07	6.0	24	15	4.5	1.0	2.25	0.3	Medium	Pardo et al. (2016b)
Carcharhinus signatus	No	No	260.0	0.11	10	32	21	11	2.0	2.78	0.2	Low	Pardo et al. (2016b)
Carcharhinus sorrah	No	No	151.8	0.34	2.5	7.0	4.8	3.1	1.0	1.55	0.3	Medium	Pardo et al. (2016b)
Carcharhinus tilstoni	No	No	196.0	0.14	3.5	12	7.8	3.0	1.0	1.50	0.3	Medium	Pardo et al. (2016b)
Galeocerdo cuvier	No	No	410.0	0.18	10	23	16	32	2.0	7.88	0.3	Medium	Pardo et al. (2016b)
Isogomphodon oxyrhynchus	No	No	160.0	0.12	6.5	20	13	5.0	2.0	1.25	0.2	Low	Pardo et al. (2016b)
Negaprion brevirostris	No	No	293.6	0.06	13	20	16	7.4	2.0	1.85	0.1	Low	Pardo et al. (2016b)
Prionace glauca	No	No	341.8	0.15	5.0	14	9.5	30	1.0	15.0	0.6	High	Pardo et al. (2016b)
Rhizoprionodon taylori	No	No	78.40	1.01	1.0	7.0	4.0	4.5	1.0	2.25	0.9	High	Pardo et al. (2016b)
Rhizoprionodon terraenovae	No	No	108.9	0.56	2.3	10	6.3	4.4	1.0	2.20	0.5	High	Pardo et al. (2016b)

Scyliorhinidae	*Scyliorhinus canicula*	No	No	71.00	0.15	7.6	12	9.8	46	1.0	22.8	0.4	High	Pardo et al. (2016b)
Sphyrnidae	*Sphyrna lewini*	Yes	Yes	331.0	0.16	9.5	19	14	20	1.0	10.1	0.5	High	Pardo et al. (2016b)
	Sphyrna mokarran	Yes	Yes	550.0	0.07	8.5	42	25	6.0	2.0	1.50	0.3	Medium	Stevens & Lyle (1989); Harry et al. (2011a); **Chapter Six**
	Sphyrna tiburo	No	No	104.0	0.18	2.9	6.5	4.7	10	1.0	5.00	0.6	High	Pardo et al. (2016b)
	Sphyrna zygaena	Yes	No	400.0	0.07	20	24	22	17	1.0	8.63	0.2	Low	White et al. (2017b); **Chapter Six**
Triakidae	*Furgaleus macki*	No	No	150.0	0.37	6.5	12	9.0	19	2.0	4.75	0.3	Medium	Pardo et al. (2016b)
	Galeorhinus galeus	No	No	164.5	0.11	13	36	24	25	3.0	4.15	0.2	Low	Pardo et al. (2016b)
	Mustelus antarcticus	No	No	175.0	0.08	6.4	16	11	16	1.0	8.0	0.4	High	Pardo et al. (2016b)
	Mustelus californicus	No	No	125.0	0.22	2.5	9.0	5.8	9.5	1.0	4.75	0.7	High	Pardo et al. (2016b)
	Mustelus canis	No	No	132.0	0.29	4.4	16	10	9.5	1.0	4.75	0.5	High	Pardo et al. (2016b)
	Mustelus henlei	No	No	100.0	0.23	2.5	13	7.8	4.5	1.0	2.25	0.5	High	Pardo et al. (2016b)
	Mustelus lenticulatus	No	No	137.0	0.12	7.5	20	14	11	1.0	5.35	0.3	Medium	Pardo et al. (2016b)
	Mustelus manazo	No	No	107.0	0.12	4.0	10	7.0	7.5	1.0	3.75	0.4	High	Pardo et al. (2016b)
	Mustelus mustelus	No	No	164.0	0.06	14	24	19	12	1.0	5.75	0.2	Low	Pardo et al. (2016b)
	Triakis semifasciata	No	No	145.0	0.07	10	25	18	15	1.0	7.50	0.3	Medium	Pardo et al. (2016b)

Hexanchiformes	Hexanchidae	*Notorynchus cepedianus*	No	No	291.0	0.29	16	29	22	89	2.0	22.1	0.2	Low	Pardo et al. (2016b)
Lamniformes	Alopiidae	*Alopias pelagicus*	Yes	Yes	365.2	0.08	8.6	29	19	2.0	1.0	1.00	0.1	Low	Cailliet et al. (1983); Smith et al. (2008); Gervelis & Natanson (2013); **Chapter Six**
		Alopias superciliosus	Yes	Yes	422.0	0.09	13	21	17	2.0	1.0	1.00	0.1	Low	Pardo et al. (2016b)
		Alopias vulpinus	Yes	Yes	573.0	0.15	11	32	21	1.2	2.0	0.28	0.1	Low	Pardo et al. (2016b)
	Cetorhinidae	*Cetorhinus maximus*	Yes	Yes	980.0	0.07	10	50	30	6.0	3.0	1.00	0.1	Low	Pardo et al. (2016b)
	Lamnidae	*Carcharodon carcharias*	Yes	Yes	600.0	0.06	13	40	26	6.0	2.0	1.50	0.1	Low	Pardo et al. (2016b)
		Isurus oxyrinchus	No	Yes	385.0	0.05	15	21	18	13	3.0	2.08	0.1	Low	Pardo et al. (2016b)
		Lamna ditropis	No	No	257.3	0.17	7.5	20	14	4.5	1.0	2.25	0.2	Low	Pardo et al. (2016b)
		Lamna nasus	Yes	Yes	324.3	0.07	13	26	20	4.0	1.0	2.00	0.1	Low	Pardo et al. (2016b)
	Carchariidae	*Carcharias taurus*	No	No	269.5	0.14	6.9	12	9.5	2.0	2.0	0.50	0.1	Low	Pardo et al. (2016b)
Orectolobiformes	Rhincodontidae	*Rhincodon typus*	Yes	Yes	1370	0.03	27	40	34	300	2.0	75.0	0.2	Low	Pardo et al. (2016b)
Squaliformes	Centrophoridae	*Centrophorus granulosus*	No	No	128.0	0.13	12	25	19	1.0	2.0	0.25	0.0	Low	Pardo et al. (2016b)
		Centrophorus squamosus	No	No	145.0	0.03	44	70	57	8.1	2.5	1.62	0.1	Low	Pardo et al. (2016b)
		Centroselachus crepidater	No	No	99.50	0.07	20	57	39	6.0	2.0	1.50	0.1	Low	Pardo et al. (2016b)
		Deania calcea	No	No	119.0	0.08	25	35	30	13	4.0	1.63	0.1	Low	Pardo et al. (2016b)
	Dalatiidae	*Dalatias licha*	No	No	182.0	0.19	6.8	18	13	12	3.0	2.00	0.2	Low	Pardo et al. (2016b)

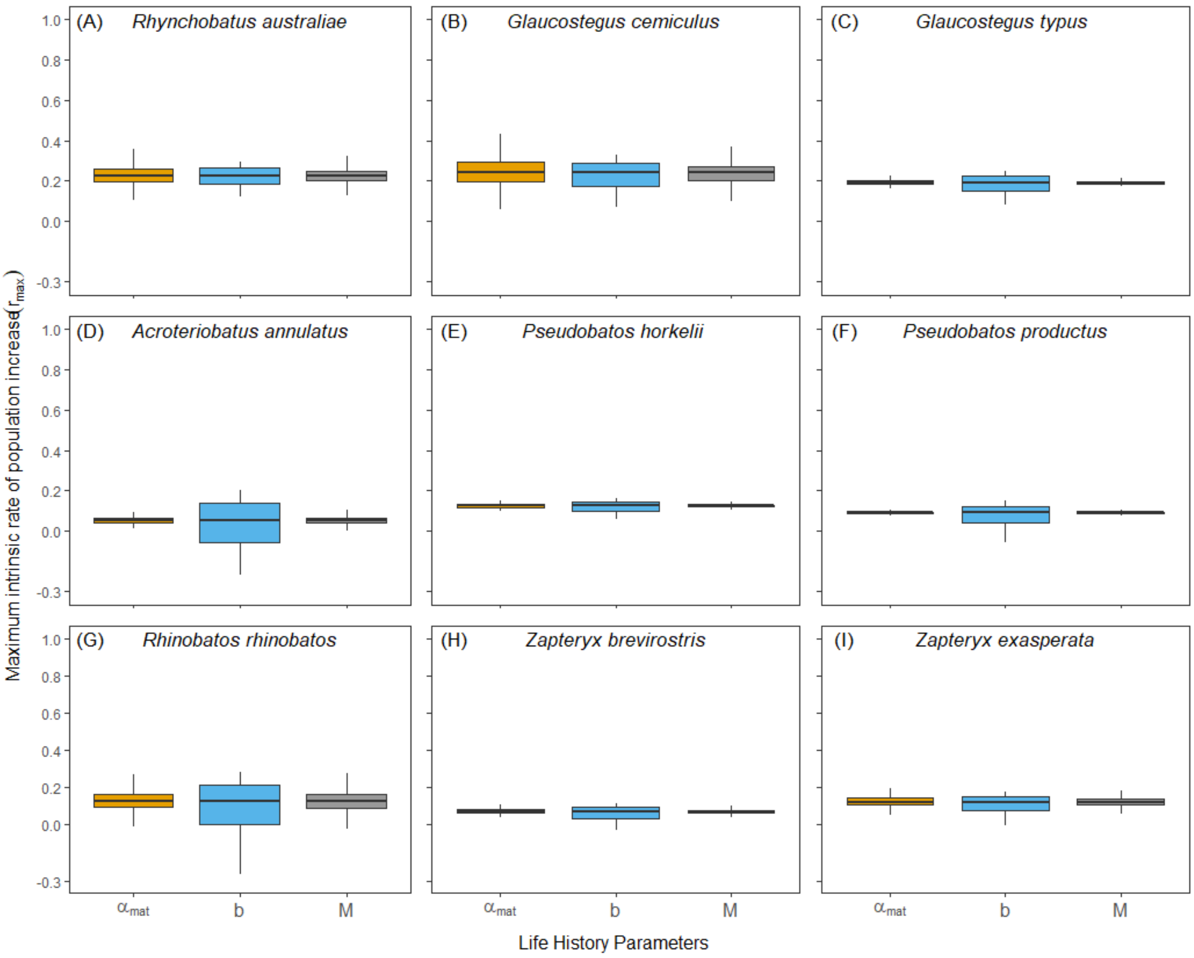
		Etmopteridae	*Etmopterus granulosus*	No	No	88.00	0.04	30	57	44	11	3.0	1.83	0.1	Low	Pardo et al. (2016b)
			Etmopterus spinax	No	No	46.00	0.22	5.0	7.0	6.0	6.8	2.0	1.70	0.2	Low	Pardo et al. (2016b)
		Squalidae	*Squalus acanthias*	No	Yes	110.0	0.09	12.5	30	21	8.0	2.0	2.00	0.1	Low	Pardo et al. (2016b)
			Squalus blainvillei	No	No	92.00	0.10	5.1	15	10	4.0	2.0	1.00	0.2	Low	Pardo et al. (2016b)
			Squalus megalops	No	No	78.20	0.03	15	32	24	3.0	2.0	0.75	0.1	Low	Pardo et al. (2016b)
			Squalus mitsukurii	No	No	91.00	0.04	15	27	21	3.6	2.0	0.90	0.1	Low	Pardo et al. (2016b)
	Squatiniformes	Squatinidae	*Squatina californica*	No	No	118.0	0.16	10	35	23	6.0	1.0	3.00	0.2	Low	Pardo et al. (2016b)
			Squatina dumeril	No	No	152.0	0.02	25	34	30	4.0	1.0	2.00	0.1	Low	Pardo et al. (2016b)
			Squatina guggenheim	No	No	92.00	0.28	4.0	12	8.0	5.5	3.0	0.92	0.2	Low	Pardo et al. (2016b)
			Squatina occulta	No	No	131.0	0.13	10	21	16	6.0	4.0	0.75	0.1	Low	Pardo et al. (2016b)
Holocephalimorpha	Chimaeriformes	Callorhinchidae	*Callorhinchus capensis*	No	No	60.00	0.05	4.2	12	8.1	22	1.0	11.0	0.6	High	Pardo et al. (2016b)
			Callorhinchus milii	No	No	97.00	0.22	4.5	15	9.8	13	1.0	6.50	0.5	High	Pardo et al. (2016b)
		Chimaeridae	*Chimaera monstrosa*	No	No	74.00	0.08	12	29	21	22	1.0	11.0	0.3	Medium	Pardo et al. (2016b)
Batoidea	Myliobatiformes	Dasyatidae	*Hypanus americanus*	No	No	200.0	0.20	5.5	18	12	4.2	1.0	2.10	0.3	Medium	Pardo et al. (2016b)
			Dasyatis chrysonota	No	No	71.90	0.07	7.0	10	8.5	6.2	1.0	3.10	0.2	Low	Pardo et al. (2016b)

	Hypanus dipterurus	No	No	83.00	0.05	9.5	28	19	2.0	1.0	1.00	0.1	Low	Pardo et al. (2016b)
	Dasyatis pastinaca	No	No	51.00	0.09	3.7	10	6.9	6.2	1.0	3.10	0.4	High	Pardo et al. (2016b)
	Maculabatis astra	No	No	80.00	0.07	9.0	48	28	1.0	1.0	0.50	0.2	Low	Jacobsen & Bennett (2011); Rigby (2016); **Chapter Six**
	Neotrygon picta	No	No	32.00	0.08	3.5	43	23	1.0	1.0	0.50	0.3	Medium	Jacobsen & Bennett (2010); Pierce et al. (2015); **Chapter Six**
	Pteroplatytrygon violacea	No	No	96.00	0.41	3.0	24	14	4.5	1.0	2.25	0.5	High	Pardo et al. (2016b)
Mobulidae	*Mobula alfredi*	Yes	Yes	500.0	0.06	9.0	40	25	0.4	1.5	0.13	0.1	Low	Dulvy et al. (2014b); **Chapter Six**
	Mobula birostris	Yes	Yes	700.0	0.06	9.0	40	25	0.4	1.5	0.13	0.1	Low	Dulvy et al. (2014b); **Chapter Six**
	Mobula tarapacana	Yes	Yes	328.0	--	5.5	14	9.8	0.5	1.0	0.25	0.1	Low	Cuevas-Zimbrón et al. (2013); Dulvy et al. (2014b); **Chapter Six**
	Mobula thurstoni	Yes	Yes	183.0	--	5.5	14	9.8	0.5	1.0	0.25	0.1	Low	Walls et al. (2016) ; **Chapter Six**
Aetobatidae	*Aetobatus flagellum*	No	No	150.0	0.11	6.0	16	11	3.5	1.0	1.75	0.2	Low	Pardo et al. (2016b)
Myliobatidae	*Myliobatis californicus*	No	No	140.0	0.10	5.0	24	25	3.8	1.0	1.90	0.3	Medium	Pardo et al. (2016b)
Rhinopteridae	*Rhinoptera bonasus*	No	No	104.8	0.09	6.0	16	11	1.0	1.0	0.50	0.1	Low	Pardo et al. (2016b)
Urolophidae	*Trygonoptera mucosa*	No	No	36.90	0.24	5.0	16	11	1.1	1.0	0.55	0.1	Low	Pardo et al. (2016b)

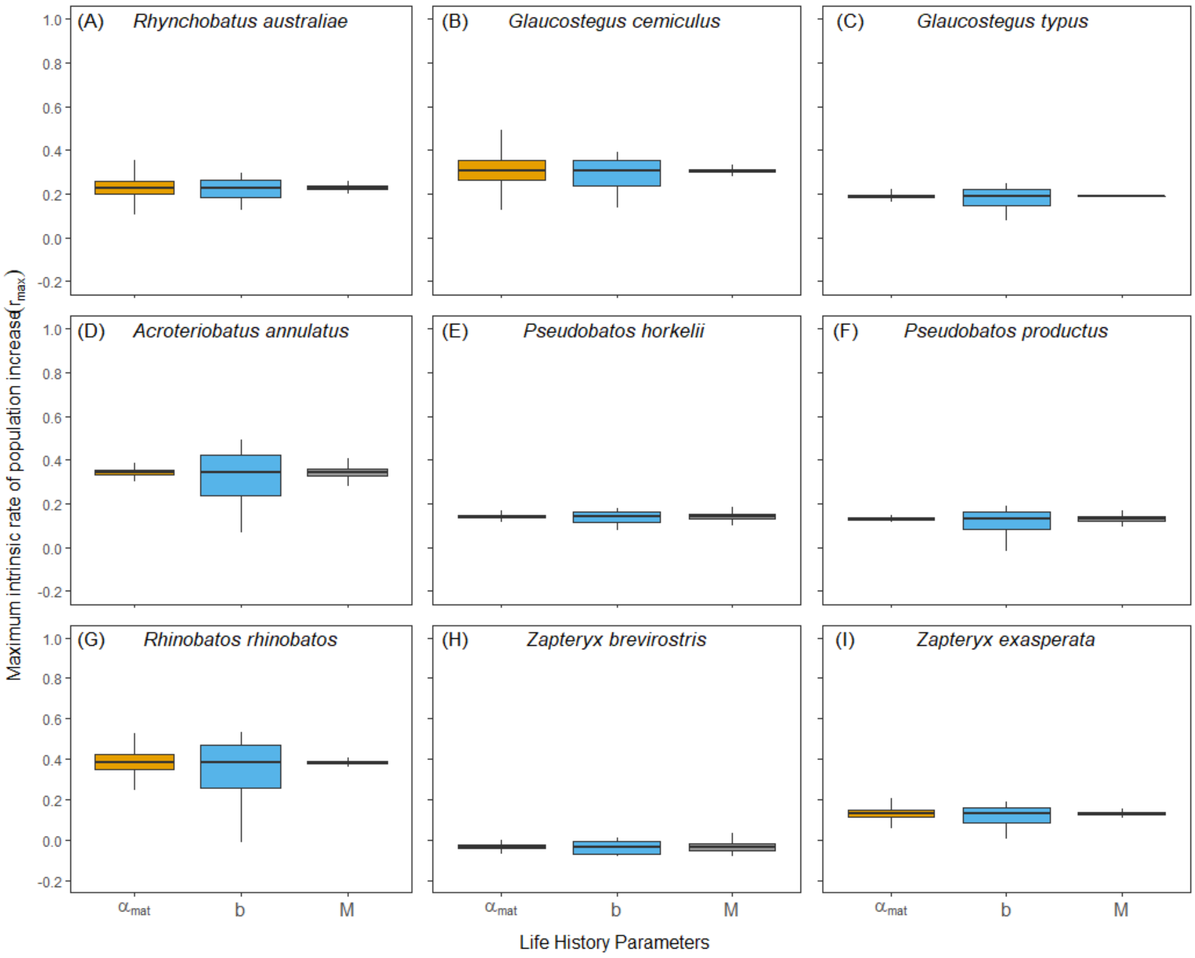
		Trygonoptera personata	No	No	31.10	0.14	4.0	14	9.0	1.2	1.0	0.60	0.1	Low	Pardo et al. (2016b)
		Urolophus lobatus	No	No	27.70	0.37	3.0	14	8.5	1.3	1.0	0.65	0.2	Low	Pardo et al. (2016b)
		Urolophus paucimaculatus	No	No	29.80	0.24	4.0	12	8.0	2.5	1.0	1.25	0.2	Low	Pardo et al. (2016b)
Rajiformes	Rajidae	*Amblyraja radiata*	No	No	105.0	0.13	11	16	14	31	1.0	15.5	0.3	Medium	Pardo et al. (2016b)
		Dipturus chilensis	No	No	168.0	0.08	14	23	18	48	1.0	24.1	0.3	Medium	Pardo et al. (2016b)
		Dipturus trachydermus	No	No	253.0	0.08	17	26	22	48	1.0	24.4	0.2	Low	Pardo et al. (2016b)
		Leucoraja erinacea	No	No	54.00	0.35	4.0	8.0	6.0	30	1.0	15.0	0.7	High	Pardo et al. (2016b)
		Leucoraja naevus	No	No	72.00	0.11	9.0	14	12	90	1.0	45.0	0.4	High	Pardo et al. (2016b)
		Leucoraja ocellata	No	No	100.0	0.06	12	29	20	35	1.0	17.5	0.3	Medium	Pardo et al. (2016b)
		Raja asterias	No	No	64.00	0.45	3.7	6.3	5.0	73	1.0	36.5	0.9	High	Pardo et al. (2016b)
		Beringraja binoculata	No	No	203.9	0.09	8.0	26	17	1260	1.0	630	0.8	High	Pardo et al. (2016b)
		Raja brachyura	No	No	109.0	0.13	5.5	8.0	6.8	90	1.0	45.0	0.7	High	Pardo et al. (2016b)
		Raja clavata	No	No	104.4	0.09	5.6	10	7.8	142	1.0	71.0	0.7	High	Pardo et al. (2016b)
		Raja microocellata	No	No	87.50	0.08	5.0	9.0	7.0	56	1.0	28.8	0.6	High	Pardo et al. (2016b)
		Raja miraletus	No	No	71.70	0.17	2.3	8.2	5.3	61	1.0	30.5	1.4	High	Pardo et al. (2016b)
		Raja montagui	No	No	74.00	0.20	4.6	7.0	5.8	60	1.0	30.0	0.7	High	Pardo et al. (2016b)

Rhinopristiformes	Glaucostegidae	*Glaucostegus cemiculus*	No	No	290.0	0.24	4.7	15	9.7	7.2	1.0	7.27	0.5	High	Capapé & Zaouali (1994); Seck et al. (2004); Ali, Saad & Kurbaj (2008); Enajjar, Bradai & Bouain (2012); Last et al. (2016); **Chapter Six**
		Glaucostegus typus	No	No	270.0	0.09	7.3	23	13	7.3	1.0	7.23	0.4	High	White & Dharmadi (2007); White et al. (2014); Last et al. (2016); **Chapter Six**
	Pristidae	*Anoxypristis cuspidata*	Yes	Yes	350.0	--	2.5	9.0	--	6.2	1.0	3.10	0.8	High	Dulvy et al. (2016) **Chapter Six**
		Pristis clavata	Yes	Yes	318.0	--	7.0	34	--	1.8	2.0	0.46	0.2	Low	Dulvy et al. (2016) ; **Chapter Six**
		Pristis pectinata	Yes	Yes	550.0	0.22	10	16	13	3.0	2.0	0.75	0.2	Low	Dulvy et al. (2016) ; **Chapter Six**
		Pristis pristis	Yes	Yes	656.0	0.09	10	30	20	7.3	2.0	1.83	0.2	Low	Pardo et al. (2016b); **Chapter Six**
		Pristis zijsron	Yes	Yes	700.0	--	7.0	24	--	3.0	2.0	0.75	0.3	Medium	Dulvy et al. (2016) ; **Chapter Six**
	Rhinidae	*Rhynchobatus australiae*	No	Yes	300.0	0.24	4.5	17	8.0	7.0	1.0	6.47	0.5	High	White et al. (2014); Last et al. (2016) ; **Chapter Six**
	Rhinobatidae	*Acroteriobatus annulatus*	No	No	140.0	0.24	2.6	12	6.8	3.0	1.0	2.99	0.6	High	Rossouw (1984); Last et al. (2016) ; **Chapter Six**
		Rhinobatos horkelii	No	No	170.0	0.19	8.0	22	15	4.0	1.0	4.02	0.3	Medium	Casselberry & Carlson (2015); Last et al. (2016) ; **Chapter Six**
		Rhinobatos productus	No	No	185.0	0.09	7.7	24	16	3.0	1.0	2.77	0.2	Low	Timmons & Bray (1998); Downton-Hoffman (2007);

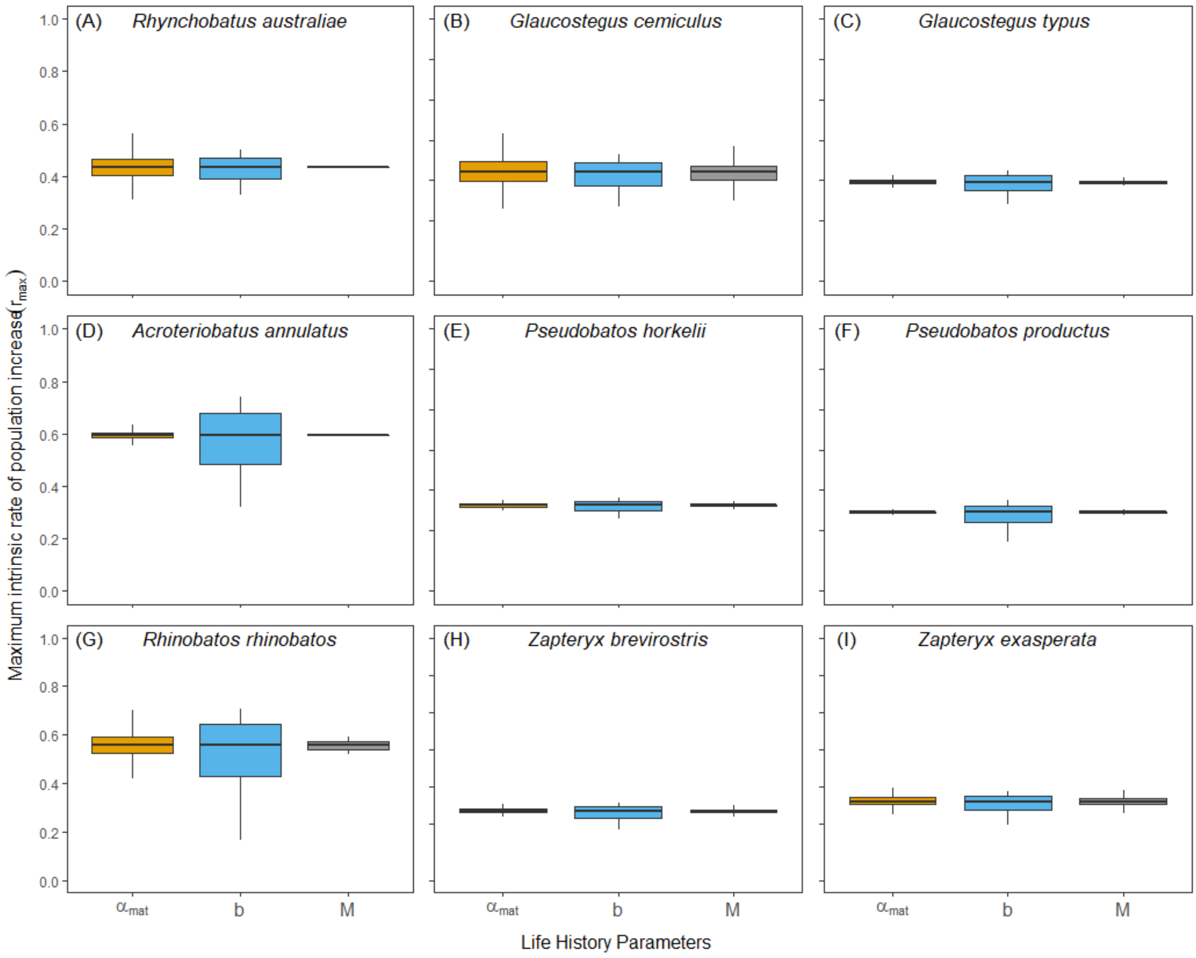
															Márquez-Farías (2007); Last et al. (2016) ; **Chapter Six**
		Rhinobatos rhinobatos	No	Yes	185.0	0.21	3.2	16	12	3.8	1.0	3.72	0.5	High	Abdel-Aziz, Khalil & Abdel-Maguid (1993); Ismen, Yıgın & Ismen (2007); Başusta et al. (2008); Last et al. (2016); Lteif et al. (2016a); Lteif et al. (2016b); Newell (2017) ; **Chapter Six**
	Trygonorrhinidae	*Zapteryx brevirostris*	No	No	66.00	0.12	9.6	15	12	2.0	1.0	2.25	0.2	Low	Pardo et al. (2016b) ; **Chapter Six**
		Zapteryx exasperata	No	No	103.0	0.16	7.5	20	14	4.0	1.0	3.73	0.3	Medium	Pardo et al. (2016b) ; **Chapter Six**
Torpediniformes	Torpedinidae	*Tetronarce californica*	No	No	102.0	0.07	9.0	16	13	17	1.0	8.50	0.3	Medium	Pardo et al. (2016b)
		Torpedo marmorata	No	No	63.00	0.09	13	20	16	11	3.0	1.83	0.1	Low	Pardo et al. (2016b)
		Torpedo torpedo	No	No	41.00	0.27	4.0	10	7.0	3.4	1.0	1.70	0.3	Medium	Pardo et al. (2016b)



Appendix 6.3. Predicted values of maximum intrinsic rate of population increase (r_{max}) for nine shovelnose ray species when including uncertainty in age at maturity (α_{mat}, first/orange boxplot), annual reproductive output (b, middle/blue boxplot), and Jensen's natural mortality estimator (M, last/grey boxplot). Species are (**A**) bottlenose wedgefish *Rhynchobatus australiae*, (**B**) blackchin guitarfish *Glaucostegus cemiculus*, (**C**)giant guitarfish *Glaucostegus typus*, (**D**) lesser guitarfish *Acroteriobatus annulatus*, (**E**) Brazilian guitarfish *Pseudobatos horkelii*, (**F**) shovelnose guitarfish *Pseudobatos productus*, (**G**) common guitarfish *Rhinobatos rhinobatos*, (**H**) shortnose guitarfish *Zapteryx brevirostris*, and (**I**) banded guitarfish *Zapteryx exasperata*. Boxes indicate median, 25 and 75% quantiles, whereas the lines encompass 95% of the values (2.5 and 97.5% quantiles).



Appendix 6.4. Predicted values of maximum intrinsic rate of population increase (r_{max}) for nine shovelnose ray species when including uncertainty in age at maturity (α_{mat}, first/orange boxplot), annual reproductive output (*b*, middle/blue boxplot), and modified Howitt & Hewitt's natural mortality estimator (*M*, last/grey boxplot). Species are (**A**) bottlenose wedgefish *Rhynchobatus australiae*, (**B**) blackchin guitarfish *Glaucostegus cemiculus*, (**C**)giant guitarfish *Glaucostegus typus*, (**D**) lesser guitarfish *Acroteriobatus annulatus*, (**E**) Brazilian guitarfish *Pseudobatos horkelii*, (**F**) shovelnose guitarfish *Pseudobatos productus*, (**G**) common guitarfish *Rhinobatos rhinobatos*, (**H**) shortnose guitarfish *Zapteryx brevirostris*, and (**I**) banded guitarfish *Zapteryx exasperata*. Boxes indicate median, 25 and 75% quantiles, whereas the lines encompass 95% of the values (2.5 and 97.5% quantiles).



Appendix 6.5. Predicted values of maximum intrinsic rate of population increase (r_{max}) for nine shovelnose ray species when including uncertainty in age at maturity (α_{mat}, first/orange boxplot), annual reproductive output (b, middle/blue boxplot), and Frisk's natural mortality estimator (M, last/grey boxplot). Species are (**A**) bottlenose wedgefish *Rhynchobatus australiae*, (**B**) blackchin guitarfish *Glaucostegus cemiculus*, (**C**)giant guitarfish *Glaucostegus typus*, (**D**) lesser guitarfish *Acroteriobatus annulatus*, (**E**) Brazilian guitarfish *Pseudobatos horkelii*, (**F**) shovelnose guitarfish *Pseudobatos productus*, (**G**) common guitarfish *Rhinobatos rhinobatos*, (**H**) shortnose guitarfish *Zapteryx brevirostris*, and (**I**) banded guitarfish *Zapteryx exasperata*. Boxes indicate median, 25 and 75% quantiles, whereas the lines encompass 95% of the values (2.5 and 97.5% quantiles).

Chapter Seven

Chapter Summary:

In this final chapter, I discuss core findings of my research in the context of their overall contribution to understanding the biology, distribution, habitat preference and recovery potential for these Critically Endangered species. I finalise this discussion by identifying areas of future research and providing recommendations for future research to for wedgefishes and giant guitarfishes to improve their conservation and management.

Nature and extent to contribution

The chapter was written by the candidate, which was reviewed and edited by Prof. Simpfendorfer, Dr Neil Hutchinson and Dr William White.

7. General Discussion

Elasmobranchs have long and important history with humans, with immeasurable and significant value to many cultures, and also as a vital source of protein and income through the fishing and trade of products (Rasalato, Maginnity & Brunnschweiler, 2010; Dent & Clarke, 2015; Kitolelei et al., 2021). Global fishing pressure for elasmobranchs has increased dramatically, driven by international demand of some chondrichthyan products, particularly for meat and fins (Clarke, Milner-Gulland & Bjørndal, 2007). Wedgefishes and giant guitarfishes face an extremely high risk of extinction and extensive regional, national, and international fisheries management strategies will be required to address the overfishing of these species. This present study contributes new information on the conservation biology of wedgefishes and giant guitarfishes and provides valuable information for the conservation and management of these species.

Firstly, I demonstrated that, in the Indo-Pacific region, batoids have significant uses (consumption, pharmaceutical and accessories) and values (cultural and traditional, tourism, and fisheries and trade). This synthesis of knowledge helps to inform on the drivers of retention of batoids (including shark-like rays) in global fisheries (**Chapter Two)**. To understand the abundance and distribution of shark-like rays on coral reefs, I analysed an extensive global BRUVS dataset that revealed sightings of shark-like rays were rare and likely reflects their preference of other habitats and global pressures on their population declines on coral reefs (**Chapter Three**). To help understand the impacts of coastal fisheries on shark-like rays, I provided an historical insight on the catch composition (species, size classes and sex) of data-poor Indonesian tangle net fishery that targets shark-like rays and recorded the shift in target species to tropical stingrays (Family Dasyatidae) as abundance declined (**Chapter Four**). I then estimated age, growth, and maturity parameters for *R. australiae* from SE Asia, to inform the basis for demographic analysis for the development of local and international management plans and conservation action for these threatened rays (**Chapter Five**). Finally, using life history information, I conducted a population productivity analysis to estimate the theoretical maximum intrinsic rate of population increase to understand their recovery potential once management measures are implemented (**Chapter Six**).

In this chapter, I will (1) briefly discuss findings from this thesis regarding the conservation and management of wedgefishes and giant guitarfishes, as well as other threatened batoids, and (2) suggest directions that further research should be taken. These topics are followed by a short concluding remark.

7.1 Implications for the management and conservation for batoids

Wedgefishes and giant guitarfishes are the most imperilled marine fish families globally and face an extremely high risk of extinction in the wild (Kyne et al., 2020). Demand for elasmobranch products, including the high valued fins and meat of wedgefishes and giant guitarfishes will continue to drive and incentivise the targeting and retention of these species in both small- and large-scale fisheries (**Chapter Two** and **Chapter Four**) (Kyne et al., 2020; Dulvy et al., 2021). The preferred habitats of wedgefish and giant guitarfish are exposed to intensive levels of fishing pressure (**Chapter Four**), and habitat loss and degradation in coastal ecosystems (shallow soft bottom habitats including areas in coral reefs) (**Chapter Three**) can further compound population declines. Current levels of fishing mortality for wedgefish and giant guitarfish are unsustainable. Yet the population productivity for some species has been estimated to be relatively high (*R. australiae, G. typus*, and *G. cemiculus*) based on life history information (**Chapter Five**), indicating their ability to rebound at a faster rate than other elasmobranch species (**Chapter Six**). Urgent action is required to stop further population declines and allow for recovery.

International concern for the substantial decline of wedgefish and giant guitarfish populations has led to a number of listings on multilateral and international trade and conservation agreements in an attempt to prevent further loss of species and eventually assist with population recovery. The recovery of an overfished population can occur only when fishing mortality is reduced, or in some cases halted completely (Myers & Worm, 2005; McAuley, Simpfendorfer & Hall, 2007; Ferretti et al., 2010). Reducing fishing mortality must be directed at managing and reducing fishing pressure as well as increasing the compliance and enforcement of trade regulations. The use of trade controls through Appendix II of CITES is an important method to reduce the incentives to retain these species in fisheries and encourage national management of the species. Yet, Appendix II-listed species can be landed and traded domestically, and there is no oversight by CITES unless the species is being exported internationally. Therefore, national, and regional protection measures will be imperative to wedgefish and giant guitarfish recovery, given the extensive domestic fisheries and trade for batoids, particularly throughout SE Asia.

The currently level of global fishing pressure on wedgefishes and giant guitarfishes is at an unsustainable level. No-take catch regulations will need to be the goal for fisheries management to ensure the species survival in the wild and allow for population recovery before any form of sustainable fishery these species can be considered. This will need multiple management approaches, at international, national, and regional levels. Currently there are only a few national management measures in place for wedgefishes and giant guitarfishes (Kyne et al., 2020). National fisheries management strategies that could be used to manage wedgefish and giant guitarfish populations can include by-catch reduction measures, size and catch limits, gear restrictions, and spatial and temporal closures.

Understanding the fate and discard survival in terms of at-vessel mortality from fishing gear and bycatch-reduction devices (BRD) and post release survival of threatened species will assist with the benefits of non-retention management measures (Ellis, McCully Phillips & Poisson, 2017). By-catch reduction devices have been demonstrated to reduce the number of wedgefishes as bycatch in prawn trawl fisheries (Stobutzki et al., 2002). In the Australian northern prawn fishery, the number of individuals of *R. australiae* [identified as *R. djiddensis* prior to the taxonomic revision, with *R. djiddensis* distributed only in the Indian Ocean (Last et al., 2016)] decreased after the implementation of a type of BRD, turtle exclusion device (Stobutzki et al., 2002). In addition, trawls with BRDs caught fewer larger individuals and *R. australiae* was estimated to have relatively high estimate survival rate (90%) compared to most elasmobranchs in the fishery after being released alive (Stobutzki et al., 2002). Implementing BRD in trawl fisheries that interact with wedgefish and giant guitarfish throughout their range will assist in reducing the fishing pressure, however there can be significant challenges in the implementation of BRDs, such as fishers incentives and socio-economic impacts on the fishers and fisheries (Campbell & Cornwell, 2008). Spatial and temporal closures (e.g. closure of breeding/nursery grounds) of fisheries can be used to reduce fishing pressure on these rays. Gear restrictions can be implemented along with spatial and temporal closures to minimize the interactions with wedgefish and giant guitarfish, for example restricting the use of benthic nets or trawls in key habitats during pupping seasons (Gupta et al., 2020). Marine protected areas (MPAs) are a widely used spatial tool for the protection of biodiversity, management of fisheries, and increasingly used as a strategy for conserving shark and ray populations (Davidson & Dulvy, 2017). These management measures will require data on the critical habitats and the spatio-temporal variation of their use of different habitats. The degree of connectivity between populations across the Indo-Pacific is unknown, if animals regularly move from areas with low fishing pressure (e.g. Australia) to areas of high fishing pressure (e.g. Indonesia), these countries must be able to jointly manage these species (Kyne et al., 2020). Some species of wedgefishes and giant guitarfishes are listed under CMS Appendices, which can help to provide a framework of the joint management of these species (CMS, 2018; Lawson & Fordham, 2018).

Importantly, any viable management options and regulations will need to ensure that they are leading to noticeable conservation outcomes (Booth et al., 2020), as well as positive social and economic outcomes for fishers (Booth, Squires & Milner-Gulland, 2019). Appropriate and economically viable incentives for livelihood alternatives for fishers will be required to address the issues of poverty and food security in resources dependent communities (MacKeracher et al., 2020).

Unseen declines - First sawfish, then wedgefish, and now stingrays?

Similar to the global decline of sawfishes and angel sharks (Dulvy et al., 2016; Lawson et al., 2020), depletion of wedgefish and giant guitarfish went unnoticed for decades until recently (Moore, 2017; Jabado, 2018; Kyne et al., 2020), driven by the incidental catch in fisheries and the high value of fins in the poorly documented international trade (Keong, 1996; Clarke et al., 2006). Conservation and management measures have lagged behind exploitation in the shark-like rays (Kyne et al., 2020), and a similar pattern is now likely occurring for large tropical stingrays, particularly throughout the Indo-Pacific region. The increased demand for batoid products and the commercialisation of batoid meat and leather industries as revealed in **Chapter Two**, and the shift in target species from wedgefishes to stingrays in Indonesia documented in **Chapter Three,** raises alarm bells for tropical stingrays. Shark-like rays (sawfishes, wedgefishes and giant guitarfishes) and large stingrays occupy similar habitats in coastal waters. The increasing pressure on stingray populations in these habitats is likely as a result of depleted population of shark-like rays, resulting in the stingrays that occupy the same habitat becoming the main target catch, with opportunities to retain the higher valued and Critically Endangered species when they are encountered (**Figure 7.1**), known as opportunistic exploitation (Branch, Lobo & Purcell, 2013; Burgess et al., 2017). Opportunistic exploitation occurs when multiple species can be exploited in the same habitat, where the most desirable and profitable species are targeted and depleted first, before exploitation switches to less desirable species, leading to overexploitation and harvesting to extinction of both the desired and less-desired species (Branch, Lobo & Purcell, 2013; Burgess et al., 2017). Opportunistic exploitation can also occur simultaneously with the serial depletion phenomenon, where the harvesters successively exploit, deplete, and finally abandon traditional fishing grounds with increasing distance from the harbor and economical importance of the species. The expansion of fishing grounds would also exacerbate the effects of the opportunistic exploitation as the fishery moves to new locations.

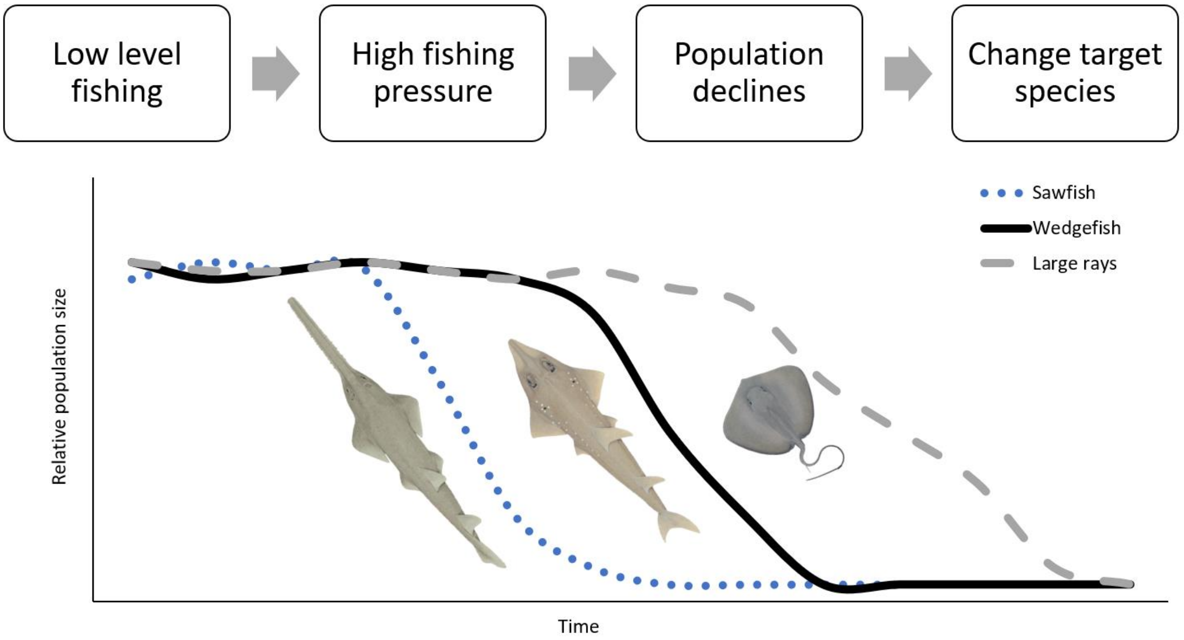


Figure 7.1. Conceptual diagram of the "opportunistic exploitation" of sawfishes (Family Pristidae; blue dotted line), wedgefishes (Family Rhinidae; black solid line) and large tropical stingrays (Family Dasyatidae; grey dashed line) in coastal fisheries in the Indo-Pacific Ocean. Opportunistic exploitation occurs when multiple species can be exploited in the same habitat, where the most desirable and profitable species are targeted and depleted first, before exploitation switches to less valuable species, leading to overexploitation and harvesting to extinction of both the desired and less-desired species. Sawfishes were abundant but were easily entangled in gear and they experienced high fishing pressure for their fins and rostrum throughout their distribution. As the sawfish populations declined, the fishing pressure for large wedgefish and giant guitarfish increased. Once the wedgefish and giant guitarfish populations declined, fishing pressure increased/switches for stingrays and the fisheries retain the highly valuable shark-like rays when they are caught.

For tropical stingrays, the outlook is bleak with recent IUCN assessments revealing that there are decreasing population trends occurring for 74% of species (*n* = 67 of 91 species), with unknown population trend for 18% of species (*n* = 16), stable populations for 8% of species (*n* = 7) and one species experiencing an increase in populations (bluespotted fantail ray *Taeniura lymma*) (IUCN, 2021). Most batoid families all face common problems of unsustainable fishing pressure driven by the high demand of product. To avoid the label as the most imperilled marine fish families, researchers, conservation practitioners, and managers need to look ahead using the precautionary principle to prevent population declines and ensure stingrays do not face the fate as wedgefishes, giant guitarfishes and sawfishes.

7.2 Considerations for future research

While this thesis addresses important gaps in the literature, there are many areas to direct future research, which can further inform management and conservation plans for threatened batoids, particularly for shark-like rays and tropical stingrays. The following areas of suggested future research can be applied to both shark-like rays and stingrays.

Distribution and important habitats

It is important for shark-like ray conservation to identify critical areas (e.g. nursery, mating areas, feeding grounds etc.), the seasonality of their use, as well as the vulnerability of these habitats to localized anthropogenic impacts. Habitat loss and degradation can further compound population declines and hinder recovery efforts for the species if important habitats are not protected. The extensive BRUVS survey on coral reefs in **Chapter Three** provided evidence of habitat preferences that can help to direct future studies. Future research on shark-like ray distributions and habitats could focus on:

- Dedicated BRUVS projects to further investigate habitat preference on soft substrate areas across a wider depth range than the surveys in **Chapter Three**, as well as conducting repeated surveys within a season and between multiple years to observe any seasonal differences in abundance.
- Using citizen science to assist with the understanding of the distribution and habitat preferences of shark-like rays. Collaboration with tourism industry such as dive centres that located in the known ranges of shark-like rays may be able to provide information and important sightings data. For example, the Wolf Rock Dive Centre in Queensland

regularly observes *R. australiae* and *R. ancylostoma* (personal communication, Wolf Rock Dive Centre) and would be able to provide an opportunity to collect data and science communication on the threatened species.

- Identification of nursery areas for wedgefish in Australia in order to provide habitat protections. The Australian populations of shark-like rays are considered "life-boats" and provide important opportunities to be able to conduct research which may not be possible in other locations due to the extensive population declines. The presence of young of year/juvenile *R. australiae* and *R. palpebratus* (length range = 436 – 1170 mm TL; D'Alberto unpublished data) caught in trawls at depths of 100 m in northern Australia could be an indication of deep-water nurseries and breeding grounds and requires further investigation.
- Once the preferred habitats have been identified, research on large- and small-scale spatial ecology and movement can be conducted using to understand the biotic and abiotic drivers of their habitat preference and will be a valuable contribution to our understanding of species distribution and assist with any design and implementation of spatial protections.

Population structure and movement

It is crucial to understand population and stock structure and connectivity of threatened shark-like ray, particularly across international borders as the extent to which these stocks are shared will likely require joint management efforts between governments. This information will assist in informing fisheries and ecological risk assessments to inform relevant fisheries and conservation management strategies, including scales need to implement spatial protections.

- The population structure and sex-specific connectivity of wedgefish can be investigated using a multifaceted approach of genetic techniques, stable isotope analysis and parasitology. This can unveil genetic variation in shark-like ray populations, movements and migrations, stock structure and any site fidelity and/or natal philopatry.
- Biotic (e.g. predation risk, intra- and inter-specific competition, prey abundance) and abiotic (e.g. temperature, salinity, oxygen levels) drivers of movement patterns, as well as trophic levels. This information would assist to predict shark-like ray ecological responses to habitat degradation and climate change.

Life history parameters

There is a need for better life history information for these data-poor species, as there is limited species-specific information, with high levels of uncertainty associated with the life-history parameters that are available (**Chapter Five** and **Chapter Six).** There are likely density dependent population changes induced by fishing pressure occurring for shark-like ray populations, which can have a varying effect on the asymptotic length, growth, and maturity parameters. Therefore, there is a need for monitoring of population-specific life history parameters so that wider demographic analyses can be accurate. Generating life history information for Critically Endangered species can be difficult as it traditionally these data have been collected through lethal sampling for research purposes and scientific levels of harvest may pose a threat to some populations (e.g. SE Asia wedgefish populations). Yet without this information, effective management and conservation strategies are more difficult to design (Heupel & Simpfendorfer, 2010). This is the fine balance for life history research, of using lethal and non-lethal sampling techniques (e.g. mark and recapture, genetic techniques) to define life history parameters. Collecting samples for future life history projects could include but not limited to:

- Collaborating with aquariums that house shark-like rays to gather *in-situ* observations of growth, maturity size, litter size and gestation length, while considering that aquariums cannot accurately reflect marine ecosystems
- Collaborating with local sustainable fisheries in areas where populations are stable (e.g. Australia) to retain bycatch species caught in gear to be used for life history analysis (e.g. Northern Finfish Trawl Fishery with Northern Territory Fisheries)
- Purchasing samples at local fish markets or processing units where local researchers can gather length data along with a sample of vertebrae, or whole specimens (**Chapter Five**). This approach will require good relationships with local fishers and fish market stalls to gather information on where the specimens were caught and also it will be important to not increase the fishing demand for the species of interest.

Post release mortality

There is a need to better understand the survivorship of discarded fishes, particularly for species of conservation concern. The survival rate of *R. australiae* was estimated to be higher than other elasmobranchs (~90%) caught as bycatch in prawn trawls. This estimate was derived from on-board observer data that recorded whether individuals were dead or alive when landed on the deck (Stobutzki et al., 2002). Currently there has been no published focused research on the discard survival and post release mortality for wedgefishes and giant guitarfishes, revealing an important knowledge gap. Future research projects could include:

- Collaborating with local sustainable fisheries in areas where populations are stable (e.g. Australia) to investigate bycatch mortality and post release survival (e.g. Northern Finfish Trawl Fishery with Northern Territory Fisheries) through methods such as acoustic or archival tagging
- Mark and recapture program using recreational fisher as a citizen science program

Fisheries assessment and trade regulations

Species specific fisheries information (e.g. monitoring of fisheries landings, supply chains) will be required to make management decisions for elasmobranch fisheries. Directed research in the following will be highly beneficial to management and conservation strategies

- Contemporary catch composition of the Indonesian tangle net fishery and information on the fishing locations for the fishery
- Investigation into impacts of fisheries on stingray populations in the Indo-Pacific region
- Assess the efficacy of CITES listings on the trade of wedgefish and giant guitarfish, and product traceability, including genetic identification such as in-situ DNA barcoding field kits to help with law enforcement in Indonesia and South-East Asia
- Drivers and socio-ecological dimensions of batoids in fisheries as these factors that will assist with the positive conservation outcomes.

Avoiding publish, then perish for species of conservation concern

A final caveat of this thesis and any conservation-based research in general, regardless of the conservation status of marine species, is that research itself will not prevent population declines and meet the needs of conservation practitioners and managers to make evidence-based decisions (Haque, Leeney & Biswas, 2020). This thesis has been driven by the need to provide impartial scientific information for the species proposals of two families of shark-like rays (Rhinidae and Glaucostegidae) to be listed under Appendix II of CITES (**Chapter Three, Chapter Four** and **Chapter Six**). However, the listing on multilateral trade agreements is only the first step in the regulation of shark-like ray products to assist with population recovery of threatened species. Any future scientific research and the resulting recommendations must be communicated and effectively translated to the relevant stakeholders and to those who can implement on-the-ground actions that will positively impact the recovery of the species and/or habitats (Haque, Leeney & Biswas, 2020). A collaborative approach involving researchers, communities, government institutions, and other conservation practitioners will be essential.

7.3 Concluding statement

Overall, this thesis has laid a foundation of understanding shark-like rays in terms of their global distribution, interaction with coastal fisheries, preliminary life history traits and estimates of population recovery potential. Wedgefish and giant guitarfish are currently facing dire circumstances, in order for the species to recover from substantial population declines, numerous national and international management actions plans are required. The information provided in this thesis has contributed to the listing of wedgefishes and giant guitarfishes on CITES Appendix II in 2019 and will continue to assist in the development of conservation and fisheries management for shark-like rays. There is hope for wedgefish and giant guitarfish, given that some species have a higher theoretical biological capacity to recover from population declines. Yet this relies on the significant reduction (ideally halt) on fishing mortality and demand of shark-like ray products, as well as spatial habitat protection. While there are still areas of uncertainty, findings from this thesis have highlighted questions that require more information to resolve. Addressing the identified knowledge gaps will further our understanding of the biology and ecology of wedgefishes and giant guitarfishes across important habitats. It will be vital that this information and any further research is to be effectively communicated to relevant stakeholders, including governmental authorities, impacted communities and any conservation organisations in the area to avoid the researcher-practitioner divide, and therefore have a direct and meaningful impact on the conservation of these threatened species.

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