Grant, Michael Ian (2021) *Conservation of non-marine elasmobranchs.* PhD Thesis, James Cook University.

Conservation of Non-Marine Elasmobranchs

Thesis submitted by Michael Ian Grant | BSc., Hons. (James Cook University)

For the degree of

Doctor of Philosophy

Centre for Sustainable Tropical Fisheries and Aquaculture

College of Science and Engineering

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“*Unfortunately, freshwater elasmobranchs are not well known biologically, and have been little studied in terms of fisheries management and conservation. Although freshwater elasmobranchs were known for the past few centuries, their dire plight has only been recognized in the past three decades. Only a handful of researchers… have paid much attention to their problems*.”

Leonard V. Compagno and Sid F. Cook,

Shark News, Vol 3, pp 4, 1995

Statement of the Contribution of Others

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Significant overall contribution

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List of Publications Directly Arising from Thesis

Grant, M. I., Kyne, P. M., Simpfendorfer, C. A., White, W. T., and Chin, A. 2019. Categorising use patterns of non-marine environments by elasmobranchs and a review of their extinction risk. Reviews in Fish Biology and Fisheries, 29: 689-710. DOI: 10.1007/s11160-019-09576-w

Grant, M. I., White, W. T., Amepou, Y., Baje, L., Diedrich, A., Ibana, D., Jogo, D. J., Jogo, S., Kyne, P. M., Li, O., Mana, R., Mapmani, N., Nagul, A., Roeger, D., Simpfendorfer, C. A., and Chin, A.. 2021. Local knowledge surveys with small-scale fishers indicate challenges to sawfish conservation in southern Papua New Guinea. Aquatic Conservation: Marine and Freshwater Ecosystems, 31: 2883-2900. DOI: 10.1002/aqc.3678

Grant, M. I., White, W. T., Amepou, Y., Appleyard, S. A., Baje, L., Devloo-Delva, F., Feutry, P., Ibana, D., Jogo, D. J., Jogo, S., Kyne, P. M., Mana, R., Mapmani, N., Nagul, A., Roeger, D., Simpfendorfer, C. A., and Chin, A. 2021. Papua New Guinea: A Potential Refuge for Threatened Indo–Pacific River Sharks and Sawfishes. Frontiers in Conservation Science, 2. DOI: 10.3389/fcosc.2021.719981

List of Other Publications During Candidature

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

Baje, L., Smart, J. J., **Grant, M. I**., Chin, A., White, W. T., and Simpfendorfer, C. A. 2019. Age, growth and maturity of the Australian blackspot shark (*Carcharhinus coatesi*) in the Gulf of Papua. Pacific Conservation Biology, 25: 403-412. DOI: 10.1071/PC18069

Grant, M. I., Smart, J. J., Rigby, C. L., White, W. T., Chin, A., Baje, L., and Simpfendorfer, C. A. 2019. Intraspecific demography of the silky shark (*Carcharhinus falciformis*): implications for fisheries management. Ices Journal of Marine Science, 77: 241-255. DOI: **10.1093/icesjms/fsz196**

Smart, J. J., White, W. T., Baje, L., Chin, A., D'Alberto, B. M., **Grant, M. I**., Mukherji, S., Simpfendorfer, C. A.. 2020. Can multi-species shark longline fisheries be managed sustainably using size limits? Theoretically, yes. Realistically, No. Journal of Applied Ecology. 10.1111/1365-2664.13659, 57: 1847-1860. DOI: 10.1111/1365-2664.13659

Kyne, P. M., Davies, C.-L., Devloo-Delva, F., Johnson, G. J., Amepou, Y., **Grant, M. I**., Green, A., Gunasekara, R. M., Harry, A. V., Lemon, T., Lindsay, R., Maloney, T., Marthick, J., Pillans, R. D., Saunders, T., Shields, A., Shields, M., and Feutry, P. 2021. Molecular analysis of newly-discovered geographic range of the threatened river shark Glyphis glyphis reveals distinct populations. Report to the National Environmental Science Program, Marine Biodiversity Hub. Charles Darwin University and CSIRO.

Kyne, P. M., Oetinger, M., **Grant, M. I**., and Feutry, P. 2021. Life history of the Critically Endangered largetooth sawfish: a compilation of data for population assessment and demographic modelling. Endangered Species Research, 44: 79-88. DOI: 10.3354/esr01090

Raoult, V., **Grant, M. I**., Barbosa Martins, A. P., Feitosa, L. M., Braccini, M., Cardeñosa, D., Carlson, J., et al. 2021. Assigning shark fin origin using species distribution models needs a reality check. Biology Letters, 17: 20200907. DOI: 10.1098/rsbl.2020.0907

International Union for the Conservation of Nature (IUCN) publications

Grant, M. I., Mizrahi, M. i., and Mather, R. 2022. A step towards contextualising the conservation of non-marine elasmobranchs within the global freshwater biodiversity crisis. Shark News, 4: 38-46.

Grant, M. I., Rigby, C.L., Bin Ali, A., Fahmi, Hasan, V & Sayer, C. 2021. *Fluvitrygon kittipongi*. *The IUCN Red List of Threatened Species* 2021: e.T161719A124533257. **https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T161719A124533257.en**.

Grant, M. I., Rigby, C. L., Bin Ali, A., Fahmi, Hasan, V & Sayer, C. 2021. *Fluvitrygon oxyrhynchus*. *The IUCN Red List of Threatened Species* 2021: e.T44185A2993563. **https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T44185A2993563.en**.

Grant, M. I., Rigby, C.L., Bin Ali, A., Fahmi, Hasan, V & Sayer, C. 2021. *Fluvitrygon signifer*. *The IUCN Red List of Threatened Species* 2021: e.T39411A2924238. **https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T39411A2924238.en**.

Grant, M. I., Rigby, C. L. & Sayer, C. 2021. *Hemitrygon laosensis*. *The IUCN Red List of Threatened Species* 2021: e.T39407A124411226. **https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T39407A124411226.en**.

Grant, M. I., Rigby, C., Mizrahi, M., and Sayer, C. 2021. *Makararaja chindwinensis*. *The IUCN Red List of Threatened Species* 2021: e.T161698A124530183. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T161698A124530183.en.

Grant, M. I., Rigby, C. L., Bin Ali, A., Fahmi, Haque, A. B., Hasan, V., and Sayer, C. 2021. *Urogymnus polylepis*. *The IUCN Red List of Threatened Species* 2021: e.T195320A104294071. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T195320A104294071.en.

Kyne, P. M., Rigby, C. L., Cheok, J., Darwall, W. R. T., **Grant, M. I**., and Simpfendorfer, C. A. 2021. *Glyphis garricki*. *The IUCN Red List of Threatened Species* 2021: e.T42712A68624151. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T42712A68624151.en.

Kyne, P. M., Rigby, C. L., Darwall, W. R. T., **Grant, M. I**., and Simpfendorfer, C. A. 2021. *Glyphis glyphis*. *The IUCN Red List of Threatened Species* 2021: e.T39379A68624306. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T39379A68624306.en.

Rigby, C. L., Derick, D., Dulvy, N. K., **Grant, M. I**., and Jabado, R. W. 2021. *Glyphis gangeticus*. *The IUCN Red List of Threatened Species* 2021: e.T169473392A124398647. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T169473392A124398647.en.

Sherman, C. S., Bin Ali, A., Bineesh, K. K., Derrick, D., Dharmadi, Fahmi, Fernando, D., **Grant, M. I.**, Haque, A. B., Maung, A., Seyha, L., Tanay, D., Utzurrum, J. A. T., Vo, V. Q. & Yuneni, R. R. 2021. *Pastinachus ater*. *The IUCN Red List of Threatened Species* 2021: e.T70682232A124550583. **https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T70682232A124550583.en**.

Sherman, C.S., Derrick, D., Dharmadi, **Grant, M. I**. & Sianipar, A. 2021. *Hemitrygon longicauda*. *The IUCN Red List of Threatened Species* 2021: e.T104110247A104112674. **https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T104110247A104112674.en**.

Conference and meeting presentations

Grant, M. I. Informing research priorities for non-marine elasmobranchs in Indonesia. 3rd Indonesian Shark & Ray Symposium, Virtual Conference, March 2021

Grant, M. I., White, W. T., Amepou, Y., Appleyard, S. A., Baje, L., Devloo-Delva, F., Feutry, P., Ibana, D., Jogo, D. J., Jogo, S., Kyne, P. M., Mana, R., Mapmani, N., Nagul, A., Roeger, D., Simpfendorfer, C. A., and Chin, A. Papua New Guinea: A Potential Refuge for Threatened Indo–Pacific River Sharks and Sawfishes. Oceanic Chondrichthyan Society, Virtual Conference, November 3–4 2020.

Grant, M. I., Kyne, P.M., Simpfendorfer, C.A., White, W.T. and Chin, A. Categorising habitat use patterns of elasmobranchs in non-marine environments and a review of their extinction risk. International Congress of Conservation Biology, Kuala Lumpur, Malaysia, July 2019.

Abstract

Over one-third of chondrichthyan species (sharks, rays, and chimaeras) are threatened with extinction on the International Union for the Conservation of Nature Red List of Threatened Species (hereafter 'IUCN Red List'). The greatest pressure to all threatened chondrichthyans is overfishing, with habitat degradation being a secondary pressure for some species. However, chondrichthyan research and conservation effort is heavily focused on marine environments. Consequently, elasmobranchs (sharks and rays) that occur in non-marine environments (freshwater and estuaries with salinities ≤ 30 ppt) are poorly studied and their conservation status and the primary pressures to their populations are not well understood. Presently, there is global concern for the deterioration of freshwater environments, which is leading significant declines in freshwater biodiversity. The issue for elasmobranchs that occur in non-marine environments is that the present paucity of information on their populations limits our ability to contextualise their conservation status within the global 'freshwater biodiversity crisis'. While it is understood that populations of elasmobranchs in non-marine environments are facing extinction risks (i.e. IUCN Red List status of species), there are still fundamental knowledge gaps concerning which species occur in non-marine environments (i.e. which species are full- or part-time residents), overall trends of extinction risk, primary pressures to their populations, and life history characteristics and habitat use requirements of species. With most non-marine elasmobranchs occurring in remote regions of developing nations, conservation research is logistically challenging, although efforts are needed to understand local population pressures in order to safeguard these species into the future. The present dissertation aims to: 1) review the present state of knowledge of non-marine elasmobranchs and review their extinction risk, and; 2) apply a range of field and analytical methods that will develop new information on species distribution, life history, uses and values to local resource users, present and emerging threats, and population status. To accomplish the second aim, this dissertation focused on non-marine elasmobranch species in Papua New Guinea (PNG) and northern Australia.

Due to a range of impediments including unresolved taxonomy, lack of fisheries data, and poor public perception, our knowledge of elasmobranchs in non-marine environments has lagged behind marine species. This dissertation refined previous categorisations of elasmobranchs that occur in non-marine environments by reviewing the timing and duration of freshwater (≤ 5ppt) and/or estuarine (>5 to ≤ 30 ppt) habitat use throughout each species' life history. Five categories were identified describing elasmobranchs in non-marine environments: 1) freshwater obligates (43 spp.); 2) euryhaline generalists (10 spp.); 3) estuarine generalists (19 spp.); 4) non-marine transients; 5) non-marine vagrants. Criteria for species inclusion is provided for all categories, and species lists are presented for categories 1–3. Euryhaline and estuarine generalists had the highest number of species that are threatened with extinction on the IUCN Red List of Threatened Species (50% and 65%, respectively), and freshwater obligate species have a very high portion of Data Deficient and Not Evaluated species (77%). The refinement of non-marine elasmobranch categories will aid in our understanding of elasmobranchs that occur in non-marine environments, helping facilitate more strategic conservation and management initiatives. Research on the biology of elasmobranchs and their interactions with humans in non-marine environments are suggested, as this will lead to better availability of information for conservation and management.

Sawfishes (Pristidae) are considered to be among the most threatened families of non-marine elasmobranchs, and understanding their interactions with people, and their uses and values, are critical to conservation. This dissertation used interviews with local fishers to investigate the presence of sawfishes in southern PNG and their interactions, uses, and values with small-scale fishers. A range of sawfish size classes are still encountered throughout coastal and estuarine waters in southern PNG, with juvenile largetooth sawfish *Pristis pristis* additionally reported in the freshwater reaches of all rivers surveyed. Reports of large size classes in estuarine and marine environments provide an optimistic outlook that sawfish populations persist throughout southern PNG. Most fishers that catch sawfishes retain them for various uses including consumption, and for sale of meat, fins, and occasionally rostra. Negative population trends including decreases in catch frequency and/or size classes were reported by 66% of interviewees, with the largest declines being reported in the Kikori River. The increasing technical capacity of small-scale fishers, their preference for gillnetting, and the emerging market for teleost swim bladder (a high value fishery product), present a major ongoing threat to sawfishes in southern PNG. Furthermore, the tendency of fishers to kill or remove rostra from entangled sawfish results in high fishing mortality regardless of any use by the fisher. This dissertation indicates that considerable community engagement will be necessary to effect any legislative actions or increased enforcement on international trade regulations for sawfishes in PNG. This is due to traditional land and waterway ownership values throughout PNG, and the local perception of sawfishes as a traditional resource, rather than an animal of intrinsic biodiversity value as perceived by global conservationists. Future research should consider exploring culturally appropriate conservation initiatives that are likely to achieve engagement and participation from local fishers.

The conservation of threatened elasmobranchs in tropical regions is challenging due to high local reliance on aquatic and marine resources, which often translates to intensive fishing pressure. Due primarily to fishing pressure, river sharks (*Glyphis*) and sawfishes have experienced large population declines in the Indo–Pacific. PNG may offer a refuge for these species, as human population density is low, and river shark and sawfish populations are thought to persist. However, few data are available on these species in PNG, and risk posed by small-scale fishers is poorly understood. This dissertation explores elasmobranch catches in small-scale fisheries in riverine and coastal environments in the East Sepik (northern region), Gulf, and Western Provinces (southern region) of PNG. Surveys were conducted over a period of weeks to months in each region, during the dry season across seven field trips between 2017 to 2020. A total of 783 elasmobranchs encompassing 38 species from ten families were observed. River sharks contributed to 29.4% (the northern river shark *Glyphis garricki*, 23.0%; the speartooth shark *Glyphis glyphis*, 6.2%; *Glyphis* sp., 0.2%) of observations in the southern region, while sawfishes contributed to 14.8% (Narrow sawfish *Anoxypristis cuspidata*, 7.8%; *P. pristis,* 7.8%) and 20.3% (*A. cuspidata*, 8.5%; dwarf sawfish *Pristis clavata*, 1.5%; *P. pristis*, 9.9%; green sawfish *Pristis zijsron*, 0.2%; *Pristis* sp., 0.3%) in the northern and southern regions, respectively. River sharks were commonly caught by small-scale fishers in lower riverine environments in southern PNG, while sawfishes were generally less common and mainly observed through dried rostra. The primary threat to river shark and sawfish populations is their capture by small-scale fishers targeting teleosts for swim bladder. Persisting populations of river sharks and sawfishes indicate that PNG is the second known nation with viable populations of multiple species in the Indo–Pacific. However, populations are declining or at high risk of decline, and fisheries management and conservation are required to realise the potential of PNG as a long-term refuge.

While river sharks and some sawfishes inhabit riverine environments, their long-term habitat use patterns in rivers are poorly known. This dissertation investigated the diadromous movements of the northern river shark (*Glyphis garricki*), speartooth shark (*Glyphis glyphis*), narrow sawfish (*Anoxypristis cuspidata*), and the largetooth sawfish (*Pristis pristis*) using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) on vertebrae to recover elemental ratios over an individual's lifetime. Elemental ratios for the bull shark (*Carcharhinus leucas*) and a range of inshore and offshore stenohaline marine species were also measured to assist in interpretation of results. Ba was found to be an effective indicator of freshwater, while Sr and Li were effective indicators of marine water. The relationship between Ba and Sr was consistently inverse. Juveniles of both river shark species had prolonged use of upper estuarine environments, while adults appear to mainly use lower estuarine environments rather than marine. In comparison, a wide range of freshwater, estuarine, and marine environments were observed for *C. leucas*. For *P. pristis*, decreases in Sr:Ba at the end of the pre-natal growth zone indicated that parturition likely occurs in freshwater. There was limited evidence of prolonged riverine habitat use for *A. cuspidata*. The results of this study suggest that elemental-environment relationships observed in teleost otoliths are also applicable to a wide range of elasmobranch species. A greater understanding of processes that lead to element incorporation in vertebrae, and relative concentrations in vertebrae with respect to the ambient environment, will improve the applicability of elemental analysis to inform life history movements of elasmobranchs into the future.

In the conservation assessment of euryhaline generalist elasmobranchs, both non-marine and marine pressures need to be considered. The largetooth sawfish *Pristis pristis* is Critically Endangered due to severe depletion of populations throughout its global distribution. Northern Australia is regarded as the only long-term refuge for *P. pristis*. However, the viability of *P. pristis* in Australia has never been investigated and there are concerns that populations are declining. This dissertation used Population Viability Analysis (PVA) to determine the recovery potential and extinction risk of *P. pristis* under various scenarios examining non-marine and marine anthropogenic and environmental pressures within the Queensland Gulf of Carpentaria, Northern Territory, and Western Australian fisheries management jurisdictions. Due to ambiguities in reproductive biology of *P. pristis*, four natality schedules were used to construct Lefkovitch matrix models for use in PVA. Population growth was highest when *P. pristis* reproduced annually and litter size increased with maternal size ($\lambda = 1.14$ year^{-1}), and lowest when reproduction was biennial with a constant mean litter size ($\lambda = 1.05$ year^{-1}). PVA results across the 12 scenarios considered had a high level of variability between natality schedules and jurisdictions. Population growth was generally positive in Western Australia and Northern Territory, while the highest extinction probabilities occurred in the Queensland Gulf of Carpentaria. Management approaches focused on lowering commercial fisheries mortality produced the most positive population responses. However, severe population declines occurred in all scenarios for the biennial mean litter size natality schedule (at least -53%), and scenarios of additional crocodile mortality (at least -55%). This indicates that extinction risk of the metapopulation may be high, although more informed data are required. Research on 1) reproductive biology, 2) dynamics of juvenile recruitment and survival, and 3) mitigation or improved post-release survival from commercial fishery interactions, are most urgently needed. Continued building of knowledge for management and conservation purposes will help rebuild *P. pristis* populations in Australia and secure its status as a globally important long-term refuge.

Through categorising habitat use patterns of non-marine elasmobranchs and reviewing their extinction risk, this dissertation has underlined the conservation concern for these species globally. This dissertation has also applied a range of inter-disciplinary field survey methods, analytical approaches to informing life history and habitat use, and a population model able to incorporate non-marine and marine environmental pressures, to improve our understanding of non-marine elasmobranch populations in PNG and northern Australia. The approaches to conservation research of non-marine

elasmobranchs outlined in this dissertation now provides opportunity for their application to other species across the global tropics.

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Chapter 1

Introduction

There are ~1240 extant chondrichthyan species (sharks, rays, and chimaeras) globally (W. White pers comm 5/12/2021). They are found throughout a diverse range of environments and latitudes including in rivers, coastal and continental shelves, open ocean and deep sea habitats, and in polar regions (Ebert et al., 2013; Last et al., 2016). Within these environments, chondrichthyans occupy predatory trophic niches, with most species being meso- or apex predators (Stevens et al., 2000). A general trait of chondrichthyans are their ‘slow’ life histories (Musick, 1999). Most chondrichthyan species grow slowly, reach maturity at a late age, have low fecundity, long gestation times, reproductive periodicities that span up to 3 years, and exhibit considerable longevity (Musick, 1999; Cortés, 2000). Collectively, these life history traits make chondrichthyan species susceptible to population declines and protract the time needed for population recovery following depletion.

Globally, humans have had a large and prolonged historic impact on marine and aquatic environments. Human uses of these environments include fisheries harvest, mineral resource extraction, transportation, sewage and waste disposal, and modification for development purposes. Owing to these human uses, the International Union for the Conservation of Nature’s Red List of Threatened Species (hereafter, ‘IUCN Red List’) estimates that over one-third of chondrichthyan species are threatened with extinction (categorized as Critically Endangered, Endangered, or Vulnerable) (Dulvy et al., 2021). Of these pressures, the greatest pressure to threatened chondrichthyan species is overfishing, (67.3% spp., inclusive of incidental capture), followed by environmental degradation (31.2% spp.), climate change (10.2% spp.), and pollution (6.9% spp.) (Dulvy et al., 2021). These pressures are present throughout riverine (Compagno and Cook, 1995), coastal and continental shelf (Dulvy et al., 2016; e.g. Macneil et al., 2020), open ocean (Dulvy et al., 2008; Pacoureau et al., 2021), and deep sea (Simpfendorfer and Kyne, 2009; Finucci et al., 2020) environments.

The loss or depletion of chondrichthyans from local and regional ecosystems can have flow-on ecological and social effects. Firstly, chondrichthyans play an important ecological role as either 'top down' predators, meso-predators, or lower order consumers and in turn, contribute to overall ecosystem health (Stevens et al., 2000; Heithaus et al., 2008). Overharvest of chondrichthyan species can lead to changes in lower order trophic species assemblages and population densities (e.g. Dulvy et al., 2004; Heithaus et al., 2008; Polovina et al., 2009), although due to the complex nature of marine food webs, the severity of broader ecosystem effects of predator loss can be difficult to define (Heupel et al., 2014; Bierwagen et al., 2018). Secondly, chondrichthyans are important to economic and cultural livelihoods in many global regions (e.g. Dent and Clarke, 2015; Vieira et al., 2017; Haque et al., 2021). Globally, chondrichthyans are primarily used for human consumption and sale, with meat and fin being the main products (Okes and Sant, 2019), while liver oil, skins, gill rakers, or other curios (e.g. sawfish rostra) are usually secondary uses (e.g. McDavitt and Charvet-Almeida, 2004; Finucci et al., 2020; Booth et al., 2021b). The high reliance on fishery resources in many nations creates challenges for chondrichthyan conservation, as species protections and 'fishing bans' may have unforeseen negative economic and cultural consequences that undermine conservation efforts (Jaiteh et al., 2017; Booth et al., 2021c; Castellanos-Galindo et al., 2021). These challenges are most pronounced in developing nations, where coastal communities lack alternative livelihood options to fisheries or access to alternative protein sources (Ban et al., 2009; White and Kyne, 2010). Additionally, negative human relationships with chondrichthyans can also create challenges for conservation, particularly in the context of 'human-shark' conflicts such as depredation or negative shark interactions that are perpetuated in media (Ostrovski et al., 2021; Simpfendorfer et al., 2021). Despite these challenges, conservation efforts are required to rebuild chondrichthyan populations globally (Simpfendorfer et al., 2011a).

Chondrichthyan research and conservation effort is heavily focused on marine environments. Consequently, non-marine elasmobranchs (sharks and rays that occur in riverine environments including freshwater and estuaries) are poorly studied and their general biology and conservation status is not well understood (no chimaeras occur in riverine environments) (Lucifora et al., 2015). A lack of information on tropical riverine environments and the species that use them is not restricted to elasmobranchs. Marine environments also receive a disproportionately larger amount of conservation research and attention compared to freshwater environments for teleost fish (Darwall et al., 2011; He et al., 2021). Teleost fishes have remarkable diversity in freshwater environments, with over half of all described teleost species occurring in freshwater (Fricke et al., 2021). There is significant concern for the status of freshwater vertebrate species globally, with population declines estimated to be far more severe than observed for marine or terrestrial taxa (WWF, 2018). The largest population declines, including several extinctions, have occurred for freshwater megafauna (>30 kg body mass), with declines of 88% occurring from 1970–2012 (He et al., 2019). Recently, there have been numerous publications highlighting the dire state of freshwater environments, the declining population status of species that use them, and concern for the future (e.g. Vörösmarty et al., 2010; Collen et al., 2014; Sills et al., 2018; WWF, 2018; Dudgeon, 2019; He et al., 2019; Reid et al., 2019; Tickner et al., 2020; Harper et al., 2021; He et al., 2021; Su et al., 2021). The major pressures from fisheries (Ainsworth et al., 2021), ornamental harvest (Reid et al., 2013), invasive species (Vilizzi et al., 2019), pollution (Tuholske et al., 2021), barriers to water flow (Grill et al., 2019), vegetation and land repurposing (Gardner et al., 2018), climate change (Lennox et al., 2019), mining related resource extraction (Maus et al., 2020), and general human reliance's of riverine systems (Fedele et al., 2021) are all contributing factors, often occurring in combination. Furthermore, many of these threats are not present, or not as severe, in marine environments where most of our understanding of elasmobranch conservation biology comes from. This limits our ability to properly assess the level of threat that non-marine elasmobranchs are exposed to.

A persistent challenge to understanding which elasmobranch species are vulnerable to riverine pressures is the lack of information about which species rely on riverine environments to complete their life cycle. At least 56 elasmobranch species are thought to occur in freshwater environments, representing ~5% of the global chondrichthyan fauna (Lucifora et al., 2015). Freshwater elasmobranchs are dominated by the neotropical stingrays, Potamotrygonidae, that occur throughout major river systems of South America (Thorson et al., 1983). In West Africa and Asia, there are additionally a small number of freshwater stingrays, Dasyatidae. Meanwhile, some species are able to transit between freshwater and marine environments (i.e. termed 'euryhaline' species). This adaption has occurred in only a few species across three families Whaler sharks (Carcharhinidae), Dasyatidae, and sawfishes (Pristidae). Finally, there is an unquantified number of elasmobranchs that may occur in freshwater, though are more commonly found in estuaries and marine environments. For these species, associations with riverine environments are poorly understood which limits our ability to properly appraise their vulnerabilities to riverine pressures.

The most widely accepted categorisation of freshwater use by elasmobranchs was provided by Compagno and Cook (1995), with four categories identified:

1. Obligate freshwater: *species confined to freshwater*
2. Euryhaline: *species that readily penetrate far into freshwater but also regularly occur in inshore marine waters*
3. Brackish-marginal: *species confined to brackish water only*
4. Marginal: *coastal shelf species that penetrate freshwater in estuaries or river mouths but were not found far from the sea*

While these categories provide a useful guide to the range of associations between riverine environments and different elasmobranch species, they lack an informative underlying context regarding the ecological or reproductive reasons for why species are assigned into each category. The lack of environmental use context was due to a general paucity of species-specific information available at the time, as noted by Compagno and Cook (1995). Within the literature concerning non-marine elasmobranchs, historic ambiguities in species distributions and taxonomy restricted understanding (Faria et al., 2013; Li et al., 2015), while information on life history and ecology remain absent for most species. This lack of information is highlighted by more than half of freshwater species being historically listed as Data Deficient on the IUCN Red List (Dulvy et al., 2014; Lucifora et al., 2015). Collectively, for species that use, or are thought to use, riverine environments, there remains a lack of understanding on 1) why they use them; 2) their life history and ecological characteristics; and, 3) their conservation status.

Despite the lack of available information, there is significant conservation concern for non-marine elasmobranchs (Lucifora et al., 2015). River sharks (*Glyphis* spp.) and sawfishes (Pristidae) are two groups that underline the present conservation concern. All species in these groups are listed as threatened on the IUCN Red List, with most listed in high-risk categories (Critically Endangered or Endangered). The Ganges river shark *Glyphis gangeticus* is only rarely observed within its historic southern Asia range (Jabado et al., 2018; Haque and Das, 2019), and has not been observed in northern Borneo since the late 1990s (Manjaji-Matsumoto et al., 2016). Meanwhile, the northern river shark *Glyphis garricki* and the speartooth shark *Glyphis glyphis* are restricted to remote regions of northern Australia (e.g., Thorburn and Morgan, 2004; Pillans et al., 2009; Lyon et al., 2017). These two species were recently re-documented in Papua New Guinea (PNG), along with the first adult *G. glyphis* specimen scientifically recorded (White et al., 2015). Similarly, all sawfishes have undergone significant population declines and are now presumed to be extinct in half (46/90) of the nations they formally occurred in (Yan et al., 2021). Today, sawfishes are regarded among the most threatened vertebrate families globally (Dulvy et al., 2016).

The high extinction risk observed across river shark and sawfish species is almost certainly due to their reliance on riverine and shallow inshore habitat in tropical regions that are typically densely populated by humans (Compagno and Cook, 1995). This makes them highly susceptible to fisheries and development (including construction of barriers to water flow and mangrove deforestation) in tropical river basins and coastlines. Today, viable river shark and sawfish populations only appear to be found in tropical regions with low human population density (e.g., northern Australia), or in nations with significant fisheries protections and conservation effort (e.g., southern Florida, United States). Many obligate freshwater ray species, however, are restricted to densely populated tropical nations and lack refuges or effective species protections. For example, the Chindwin cowtail ray *Makararaja chindwinensis* is a Data Deficient species known from only two observed specimens in a tributary of the Ayeyarwady River in Myanmar (Grant et al., 2021a). With Myanmar supporting one of the world's largest per-capita inland fisheries (Soe et al., 2020), there is immense conservation concern for this species. Tropical developing nations face immense challenges in gathering data on non-marine elasmobranchs to inform conservation management, as in-country research capacity and prioritization of threatened species conservation is low. Consequently, there are numerous logistical challenges to effectively study populations and implement realistic conservation and management initiatives.

Presently, there is an urgent need to gather the information required to understand the conservation status of non-marine elasmobranchs in the context of drastic biodiversity declines and increasing human pressures. This dissertation aimed primarily to:

1) review the present state of knowledge for non-marine elasmobranchs and their extinction risk (Chapter 2)

2) apply a range of inter-disciplinary field and analytical methods to develop new information on species' distributions, life history, local uses and values, present and emerging threats, and population trends.

To accomplish the second aim, this dissertation focused on non-marine elasmobranch species in Papua New Guinea (PNG) and northern Australia. Chapter 3 used local knowledge surveys to understand the distribution, population trend, and local uses and values of sawfishes to small-scale communities in PNG to inform locally appropriate conservation approaches. Chapter 4 focused on small-scale fisheries catch in PNG, to assess the local fisheries threat posed to non-marine elasmobranchs. Chapter 5 applied elemental analysis techniques to vertebrae from a range of non-marine elasmobranch species collected during field studies in Chapter 4, and from previous studies in northern Australia, to understand their long-term habitat use patterns in riverine environments. Finally, Chapter 6 used a population viability analysis model to assess a range of riverine and marine pressures on *P. pristis* in northern Australia to inform future conservation management requirements and identify research priorities. The intention is that each of the methods applied herein can be used in broader global regions to further our understanding of non-marine elasmobranchs in the interest of their conservation.

Chapter 2

Categorising use patterns of non-marine environments by elasmobranchs and a review of their extinction risk

2.1 Introduction

Elasmobranchs (sharks and rays) that use non-marine environments (salinities < 30 ppt, McLusky, 1993) during critical stages of their life history are one of the most poorly understood and threatened groups of vertebrates (Compagno and Cook, 1995; Dulvy et al., 2014). Elasmobranchs occurring in these environments may be obligate freshwater species or euryhaline species (Lucifora et al. 2015). Approximately 56 (~5%) of all elasmobranch species are known to regularly occur in low salinity environments (Lucifora et al., 2015). Most of these species are rays from the families Potamotrygonidae (neotropical stingrays) and Dasyatidae (stingrays) that reside exclusively in freshwater throughout their entire life history. Meanwhile, only a few elasmobranchs are euryhaline, able to transition between marine and freshwater environments for prolonged periods e.g. bull shark (*Carcharhinus leucas*) and largetooth sawfish (*Pristis pristis*). Almost all freshwater and euryhaline elasmobranchs occur across tropical latitudes with a few species also extending marginally into temperate zones such as *C. leucas* and green sawfish (*Pristis zijsron*), while the Maugean skate (*Zearaja maugeana*) occurs exclusively in temperate waters of Tasmania, southeastern Australia (Compagno and Cook, 1995; Compagno, 2002).

With most elasmobranchs that use non-marine environments occurring in tropical latitudes, they have been exposed to a range of anthropogenic pressures associated with the higher levels of human population growth in tropical regions (Smith, 2003; Collen et al., 2014). Fisheries pressure (mostly commercial but also artisanal and recreational) is the primary threat to elasmobranchs in freshwater and estuarine environments (Lucifora et al., 2015; Kyne and Feutry, 2017; Lucifora et al., 2017). River engineering, habitat destruction, and pollution also pose considerably greater threat to elasmobranchs in non-marine environments, compared to species that use only marine environments (Compagno and Cook, 1995; White and Kyne, 2010; Dulvy et al., 2014; Lucifora et al., 2016). Elasmobranchs are inherently susceptible to population decline due to low productivity, which includes slow growth, late age-at-maturity, longevity, low fecundity, low natural mortality, and often protracted breeding cycles (Cortés, 2000). These ‘slow’ life history traits are particularly unfavourable in spatially-confined freshwater and estuarine environments, where population size is inherently constrained (Ballantyne and Robinson, 2010).

Temporally, freshwater and estuarine environments are much more variable in their physical parameters (e.g. temperature, salinity, turbidity, dissolved oxygen, water flow) compared to marine environments (McLusky, 1993; Pinto and Marques, 2015). Furthermore, it is likely that fluctuations in these physical parameters will become more frequent and severe with climate change (Lennox et al., 2019). Unlike their marine counterparts, elasmobranchs in freshwater and estuarine environments cannot always readily escape unfavourable environmental and anthropogenic pressures (Compagno and Cook, 1995). Nor have they evolved strategies such as rapid growth, short life cycles or the ability to aestivate or breath air in order to outlast unfavourable environmental conditions like some teleost fishes (Compagno, 2002).

In recent decades, significant concern has been raised about the status of freshwater and euryhaline elasmobranch populations (Dulvy et al., 2014; Lucifora et al., 2015). Many species have become increasingly threatened and rapid local extinctions have been observed in regions of dense human population (Dulvy et al., 2014; Dulvy et al., 2016; Moore, 2017). Of the 33 freshwater species identified in Dulvy et al. (2014) (a grouping which includes obligate freshwater and euryhaline species), 12 are listed as threatened with extinction on the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (‘the Red List’) (IUCN 2018). The conservation status of euryhaline elasmobranchs indicates they have the highest susceptibility to negative anthropogenic pressures. This is likely because they move between freshwater and marine environments during their life history, thereby increasing potential for exposure across a range of environments (Compagno and Cook, 1995). Sawfishes (Pristidae) for example, are one of the most threatened marine vertebrate families with all five species assessed as either Critically Endangered or Endangered on the IUCN Red List (Dulvy et al., 2016). Similarly, river sharks of the genus *Glyphis*, also assessed as either Critically Endangered or Endangered, have seemingly disappeared from river systems throughout Asia and are now only reliably found in northern Australia (Li et al., 2015). Both these species groups are known to use non-marine environments during their life histories, and high exposure to anthropogenic pressures has been attributed to their threatened status.

Conservation and management of freshwater and euryhaline elasmobranch populations is impeded by several factors (Compagno, 2002). Firstly, a lack of information on their exploitation by fisheries targeting more commercially viable crustacean and teleost species (Compagno and Cook, 1995). Secondly, artisanal and subsistence fisheries dominate regions where most species occur, and collection of biological data at fish landing and market sites can be difficult as shark and ray landings are often quickly consumed, finned, and portioned for sale (Appleyard et al., 2018; Feitosa et al., 2018; Fluet-Chouinard et al., 2018). Thirdly, poor taxonomic resolution within key taxa (i.e. Dasyatidae, *Glyphis,* Potamotrygonidae, and Pristidae), has impeded collection of reliable biological data and confused species distributions (both geographically and their temporal occurrence in freshwater, estuarine, and marine environments) (Compagno and Cook, 1995; Rosa et al., 2010; Faria et al., 2013; White et al., 2017). Lastly, elasmobranchs have had a poor reputation in non-marine environments as they can be dangerous to humans and cause damage to fishing gear, generally reducing interest in implementing conservation and management (Castello, 1975; Thorson, 1987; da Silva et al., 2015). Due to these factors, biological research on elasmobranchs in non-marine environments has generally lagged behind studies on their marine counterparts.

The adaptation, distribution, duration, and timing of use of freshwater, estuarine, and marine environments throughout the life history of most species remain poorly understood. Apart from the obligate freshwater potamotrygonid rays, there is generally a poor understanding about which species remain in a freshwater environment throughout their life history and those that are euryhaline, only occurring in freshwater during particular stages of their life history. Similarly, for estuarine environments, a number of species are commonly observed in lower salinity waters of estuaries but are also often observed in marine environments. There is presently a lack of distinction between species that routinely use estuarine environments for critical parts of their life history (e.g. nursery areas) and predominantly marine species that may only be transient and are otherwise intolerant of prolonged exposure to non-marine salinities (Compagno and Cook, 1995; Last, 2002). Given the heightened susceptibility of elasmobranchs to adverse anthropogenic and environmental pressures in non-marine environments, it is important to understand how different species are temporally distributed in these environments throughout their life history. Identifying species, or groups of species, that may be more susceptible to anthropogenic threats based on their frequency of occurrence and reliance on particular non-marine environments will lead to more integrated and strategic conservation and management regimes (Compagno and Cook, 1995; Simpfendorfer et al., 2011a).

This study aims to review the biology and ecology of elasmobranchs that are known to occur in non-marine environments and to clear distinguish between species that require a non-marine environment within their life history from those that do not. Previous categorisations of elasmobranchs that occur in non-marine environments (i.e. Thorson et al., 1983; Compagno and Cook, 1995; Last, 2002; Martin, 2005) are refined with updated categories and species lists compiled. The conservation status of these species in each category were also compiled from the IUCN Red List, and future research directions are discussed.

2.2 Previous categorisations of elasmobranchs found in non-marine environments

There have been limited attempts to systematically categorise the elasmobranch species known from non-marine environments (i.e. Thorson et al., 1983; Compagno and Cook, 1995; Last, 2002; Martin, 2005). The first attempt was proposed by Thorson et al. (1983) who presented two sets of criteria; the first criterion ranked species into eight categories based on their osmoregulatory ability to alter urea concentrations within their blood in response to the ambient environment. The second criterion related to the functionality of the rectal gland. In the absence of detailed studies of many species' physiology, only a small number of species could be accurately assigned to a category, and most of these were Atlantic species based on Thorson's earlier works (e.g. Thorson et al., 1973; Thorson, 1976; Gerst and Thorson, 1977; Thorson et al., 1978; Thorson, 1983). Furthermore, these two categorisation systems were exceptionally convoluted in describing euryhaline elasmobranchs, with the 'urea' criteria suggesting six, and the 'rectal gland' criteria three, different categories into which the osmoregulatory physiology of euryhaline elasmobranchs could be placed. These systems also lacked a life history context regarding the habitat use and reproductive requirements of species within each category, rather only stating their physiological osmoregulatory tolerance to lower salinities. This restricted their use and application to conservation and management as these categorisations did not explain the importance that particular non-marine environments may have to the life history of the elasmobranchs that occur in them.

The most widely accepted categorisation of freshwater and euryhaline elasmobranchs, was proposed by Compagno and Cook (1995). They divided the known and 'thought to be' freshwater and euryhaline species at the time, into four categories:

1. obligate freshwater: *species confined to freshwater;*

2. euryhaline: *species that readily penetrate far into freshwater but also regularly occur in inshore marine waters;*

3. brackish-marginal: *species confined to brackish water only; and,*

4. marginal: *coastal shelf species that penetrate freshwater in estuaries or river mouths but were not found far from the sea*.

Assignment of species into these categories was based on distribution and regularity of occurrence data rather than physiological ability specific to certain osmoregulatory features as used by Thorson et al. (1983). This provided a vastly improved system for categorising freshwater and euryhaline elasmobranchs as species with little biological study could be categorised based on their occurrence within particular salinity ranges alone. Compagno and Cook (1995) listed 29 obligate freshwater species, 14 euryhaline species, and 1 brackish marginal species, and stated there were "*at least 26 marginal and possibly marginal species, with considerable uncertainty to which category some species belong to*" (p.66).

With the paucity of life history information and unresolved taxonomic issues at the time, clear distinctions between categories, their criteria, and the species that fit them could not be made. Like Thorson et al. (1983) these categorisations lacked a life history context to the habitat use and reproductive requirements of species within each category. For example, the criteria given for the '*Euryhaline*' category does not consider a reproductive or ecological context to a particular non-marine environment within their life history, rather it only implies that populations of these species are distributed across marine and freshwater environments. Meanwhile, the criteria given for the '*Marginal*' category might imply these species are also euryhaline but do not venture as far up rivers as the '*Euryhaline*' species do. Within the species listed in these two categories by Compagno and Cook (1995) and later by Compagno (2002), Last (2002), and (Martin, 2005), there was no clarity provided between species that use a freshwater and/or brackish (estuarine) environment during their life history and those which may only transiently occur in lower salinity waters. Furthermore, Compagno and Cook (1995) did not define the salinity ranges for freshwater, brackish, and marine environments.

The resulting confusion was demonstrated by Martin (2005), whose refinements largely corresponded with those originally proposed by Compagno and Cook (1995). The attempt by Martin (2005) to modify the definition of '*Brackish marginal*' to "*…common in brackish to freshwater habitats…*" (p.1052) suggests that species in this group could also be classified as '*Euryhaline*' as most species listed in this category are predominately marine. The categorisations presented by Martin (2005) resulted in three categories with criteria implying that species could be found in freshwater to marine environments with still limited ecological or reproductive context provided to distinguish between species in each category. Aside from species that exclusively reside in freshwater, there is currently no clear distinction between how different groups of species use non-marine environments during their life history. This makes consistent and accurate allocation of species to categories difficult.

Since the publication of the above-mentioned categorisation schemes, there have been notable studies on the occurrence, physiology, taxonomy, reproductive biology, and ecology for elasmobranch species that occur in non-marine environments. Some of these studies have provided life history (e.g. Charvet-Almeida et al., 2005; Morgan et al., 2011; Charvet et al., 2018), population structure and distribution (e.g. Faria et al., 2013; White et al., 2015; Lucifora et al., 2016), movement (e.g. Collins et al., 2008; Almeida et al., 2009; Heupel et al., 2010), and osmoregulatory physiology (e.g. Tam et al., 2003; Pillans et al., 2005) information for many of the species originally listed in each category by Compagno and Cook (1995). Given this improvement in the availability of relevant data, better differentiations between how some elasmobranchs use non-marine environments throughout critical parts of the life history can now be made. The categories originally proposed by Compagno and Cook (1995) can be refined to improve the accuracy, precision and consistency between categories and their criteria. A revised, more informed, categorisation would aid in our understanding of elasmobranchs that occur in non-marine environments and will help facilitate more strategic conservation and management initiatives.

2.3 Refinement of categories

This study refines the categorisation of elasmobranchs that occur in non-marine environments proposed by Compagno and Cook (1995) by considering how different groups of elasmobranch species interact with non-marine environments throughout critical parts of their life history. Previous listings of elasmobranchs in non-marine environments (Compagno and Cook, 1995; Compagno, 2002; Last, 2002; Martin, 2005), taxonomic guides (e.g. Ebert et al., 2013; Last et al., 2016a; Last et al., 2016b), and primary literature were used to identify species that are known or suspected to use non-marine environments. Following this, primary literature and IUCN Red List assessments (IUCN, 2018) were reviewed to determine their non-marine habitat use (or not). Species were then grouped into categories based on the type of environment (i.e. freshwater, estuarine, or marine, Table 2.1) that critical life history stages including parturition, nursery areas, and mating were identified to occur in. Five categories describing elasmobranchs in non-marine environments are proposed: 1) freshwater obligates; 2) euryhaline generalists; 3) estuarine generalists; 4) non-marine transients; and, 5) non-marine vagrants (Table 2.2). Notably, only the first three categories rely on non-marine environments, and the distribution of these species was then grouped into eight continental regions including North and Central America, South America, West Africa, East Africa, The Arabian/Persian Gulf (hereafter referred to as ‘The Gulf’), South Asia, Southeast Asia, and Oceania (regions are defined in Figure 2.1). The IUCN Red List category of each species was also collated to assess trends in extinction risk for each non-marine environment use category and continental region.

Table 2.1 The salinity range of freshwater, estuarine, and marine environments. Adapted from McLusky (1993).

Environment type	**Salinity range (ppt)**
Freshwater	0 – ≤5
Estuarine	>5 – ≤30
Marine	>30

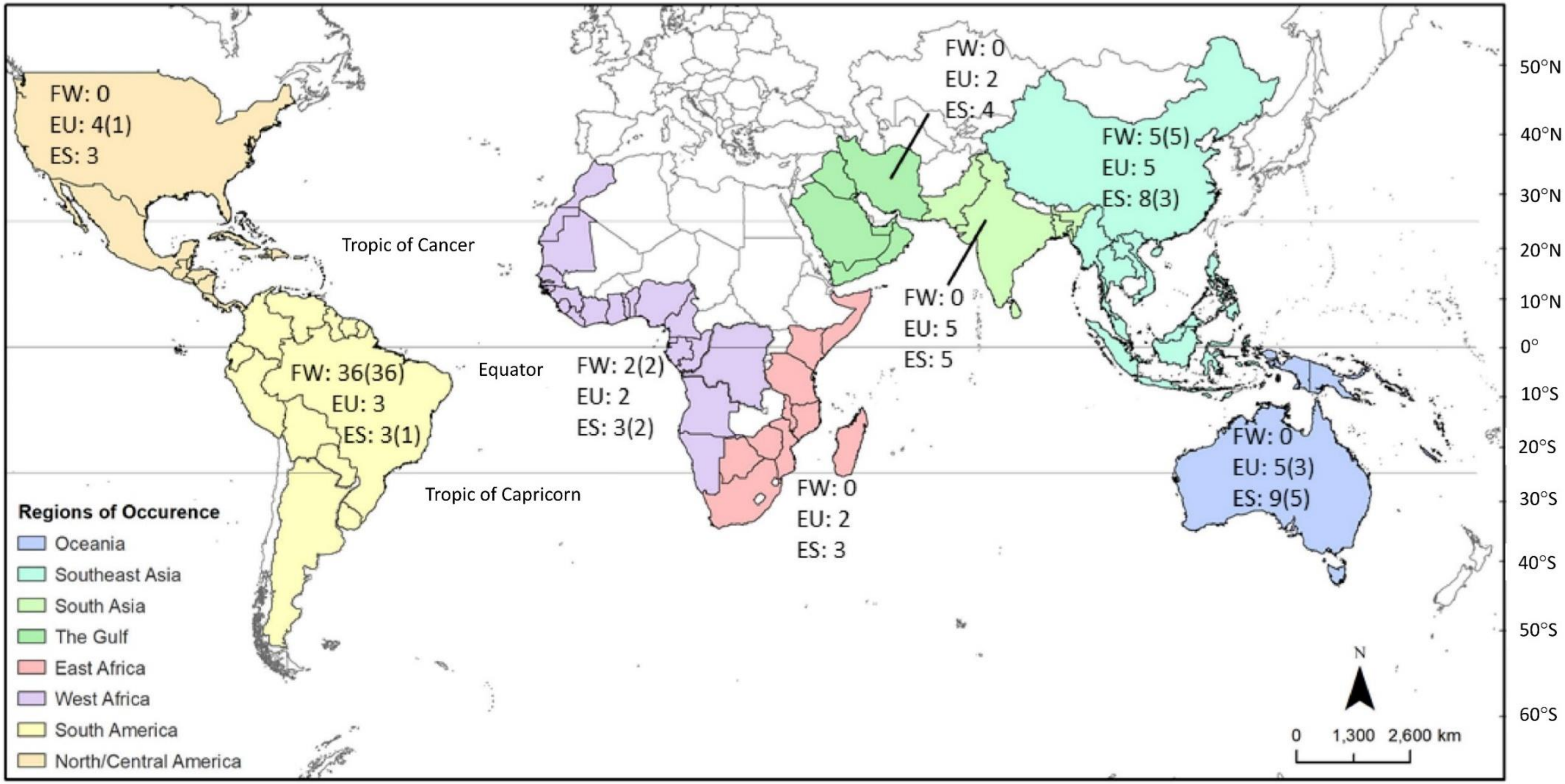


Figure 2.1 Distribution of freshwater obligates (FW), euryhaline generalists (EU), and estuarine generalists (ES) in each continental region. The total number of species in each category is shown and the number of those that are endemic to the region is shown in parentheses.

Table 2.2 Categories describing elasmobranch occurrence in non-marine environments and their criteria.

Category	Criteria	Environment type(s) that life history stages occur in
Freshwater obligate	Complete the entirety of their life history in freshwater and carryout all of their reproductive and ecological functions in freshwater exclusively.	Freshwater
Euryhaline generalist	Encountered throughout a range of salinities (freshwater to marine); are physiologically capable of prolonged exposure to environments ranging from freshwater to marine; characteristically use freshwater and/or estuarine environments for a life stage, typically for parturition and/or nursery areas.	Freshwater, estuarine, and marine
Estuarine generalist	Commonly occur in environments ranging from estuarine to marine; are physiologically capable of penetrating into lower salinity waters of estuaries for prolonged periods, though cannot withstand prolonged exposure in freshwater; characteristically use estuarine environments for a life stage, typically as nursery areas.	Estuarine and marine
Non-marine transients	May occur in non-marine environments intermittently, though carry out all aspects of their life history in marine waters; not considered to be physiologically capable of prolonged exposure to estuarine or freshwater environments.	Marine
Non-marine vagrants	Have no identifiable biological association with non-marine environments throughout their life history; not expected to occur in a non-marine environment; not considered to be physiologically capable of prolonged exposure to estuarine or freshwater environments.	Marine

2.3.1 Freshwater obligates

Freshwater obligate species complete their entire life history in freshwater. Potamotrygonid rays of South America (36 spp.) are the dominant family, while seven species of dasyatid rays inhabiting the tropical rivers of Southeast Asia and West Africa are also included (Table 2.3). These dasyatids spend their entire life history in freshwater, but unlike potamotrygonids maintain low levels of urea as an osmolyte within their blood chemistry (Tam et al., 2003; Ip et al., 2005; Otake et al., 2005; Ballantyne and Robinson, 2010). The loss of the ability to synthesise and retain urea in potamotrygonids is presumably due to their prolonged historic isolation within South American river basins (Thorson et al., 1983). While some of the dasyatids listed here may make irregular excursions outside of freshwater although there is little evidence that they persist or carry out part of their life history in higher salinity waters. For example, white-edge whipray (*Fluvitrygon signifer*) has been demonstrated to survive in brackish water (20 ppt) for at least two weeks in the laboratory, though has not been observed outside of freshwater environments in the wild (Tam et al., 2003; Wong et al., 2013). Furthermore, some potamotrygonid species including the ocellate river stingray (*Potamotrygon motoro*), smooth-back stingray (*Potamotrygon orbignyi*), and the whitespotted freshwater stingray (*Potamotrygon scobina*) are reported occasionally in estuarine water at the mouth of the Amazon River (Almeida et al., 2009). These movements are presently only considered to be transient and there is limited evidence that populations of these species use environments other than freshwater at all critical stages of their life history hence, they are here categorised as obligate to freshwater systems.

Table 2.3 List of freshwater obligate species, their IUCN Red List of Threatened Species category and distribution (continental regions defined in Figure 2.1). EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated (no species are listed as CR, Critically Endangered).

Species	**Common name**	**IUCN Red List category**	**Distribution**
Potamotrygonidae (36)	**Neotropical stingrays**		
Heliotrygon gomesi	Gomes' round ray	NE	South America
Heliotrygon rosai	Rosa's round ray	NE	South America
Paratrygon aiereba	Discus stingray	DD	South America
Plesiotrygon iwamae	Antenna ray	DD	South America
Plesiotrygon nana	Dwarf antenna ray	NE	South America
Potamotrygon adamastor	Adamastor's freshwater stingray	NE	South America
Potamotrygon albimaculata	Tapajós freshwater stingray	NE	South America
Potamotrygon amandae	Amanda's freshwater stingray	NE	South America
Potamotrygon amazona	Amazons freshwater stingray	NE	South America
Potamotrygon boesemani	Suriname freshwater stingray	NE	South America
Potamotrygon brachyura	Giant freshwater stingray	DD	South America
Potamotrygon constellata	Rough freshwater stingray	DD	South America
Potamotrygon falkneri	Paraná freshwater stingray	DD	South America
Potamotrygon garmani	Garman's freshwater stingray	NE	South America
Potamotrygon henlei	Henle's freshwater stingray	LC	South America
Potamotrygon histrix	Porcupine freshwater stingray	DD	South America
Potamotrygon humerosa	False reticulate freshwater stingray	NE	South America
Potamotrygon jabuti	Pearl freshwater stingray	NE	South America
Potamotrygon leopoldi	Xingu freshwater stingray	DD	South America
Potamotrygon limai	Madeira freshwater stingray	NE	South America
Potamotrygon magdalenae	Magdalena freshwater stingray	NT	South America
Potamotrygon marinae	French Guiana freshwater stingray	DD	South America
Potamotrygon marquesi	Marques's freshwater stingray	NE	South America
Potamotrygon motoro	Ocellate freshwater stingray	DD	South America
Potamotrygon ocellata	Marajó freshwater stingray	DD	South America
Potamotrygon orbignyi	Reticulate freshwater stingray	LC	South America
Potamotrygon pantanensis	Pantanal freshwater stingray	NE	South America

Potamotrygon rex	Great freshwater stingray	NE	South America
Potamotrygon schroederi	Schroeder's freshwater stingray	DD	South America
Potamotrygon schuhmacheri	Rosette freshwater stingray	DD	South America
Potamotrygon scobina	Whitespotted freshwater stingray	DD	South America
Potamotrygon signata	Parnaíba freshwater stingray	DD	South America
Potamotrygon tatianae	Tatiana’s freshwater stingray	NE	South America
Potamotrygon tigrina	Tiger freshwater stingray	NE	South America
Potamotrygon wallacei	Wallace’s freshwater stingray	NE	South America
Potamotrygon yepezi	Maracaibo freshwater stingray	DD	South America
Dasyatidae (7)	**Stingrays**		
Fluvitrygon kittipongi	Roughback whipray	EN	Southeast Asia
Fluvitrygon oxyrhynchus	Marbled whipray	EN	Southeast Asia
Fluvitrygon signifer	White-edge whipray	EN	Southeast Asia
Fontitrygon garouaensis	Smooth whipray	VU	West Africa
Fontitrygon ukpam	Thorny whipray	EN	West Africa
Hemitrygon laosensis	Mekong stingray	EN	Southeast Asia
Makararaja chindwinensis	Chindwin cowtail ray	DD	Southeast Asia

2.3.2 Euryhaline generalists

There are 10 species of elasmobranchs that fit the criteria of euryhaline generalist. Four are carcharhinid sharks including *C. leucas* and all three extant members of the genus *Glyphis*, and six are rays including *P. pristis*, Bennett's stingray (*Hemitrygon bennettii*), two *Hypanus* spp. and two *Urogymnus* spp. (Table 2.4). Generally, adults of these species may be encountered in any salinity environment, although juveniles are typically found in very low salinities or freshwater (Thorburn et al., 2003; Thorburn and Rowland, 2008; Pillans et al., 2009; Morgan et al., 2011). Populations of *P. pristis* and *C. leucas* in the Río San Juan region of Central America may occupy the freshwater lacustrine environment of Lake Nicaragua for long periods of time throughout their life history (Thorson, 1971; Thorson, 1982). Similarly, a population of Atlantic stingray (*Hypanus sabinus*) occurs exclusively in the freshwater environments of Lake Jesup, Florida, USA (Piermarini and Evans, 1998), while other populations of this species use marine environments of the Northwest Atlantic, frequenting freshwater rivers on a seasonal (Schwartz, 1995), or may persist year-round in estuaries and marine environments (Ramsden et al., 2017), depending on latitude. *Hemitrygon bennettii* has not been observed in freshwater in South Asia (Muktha et al., 2019), although this species is reported in the freshwaters of the Pearl River in China (Zhang et al., 2010). All 10 species occur in tropical and subtropical waters with the exception of *C. leucas,* which also extends into temperate regions. Juveniles of euryhaline generalists are rarely observed in marine environments, as they tend to move upstream into freshwater or lower salinity environments following birth (Thorson et al., 1973; Thorson, 1982; Pillans et al., 2005; Pillans et al., 2009). This may be a facultative behaviour related to predator avoidance away from large coastal sharks, decreased ecological competition from other marine species, or possible preference of physical environmental conditions such as light, temperature, and salinity (Simpfendorfer et al., 2005; Whitty et al., 2008; Whitty et al., 2009; Whitty et al., 2017). However, juveniles of the longnose stingray (*Hypanus guttatus*) contradict this trend as they only occur in higher salinity estuarine and coastal marine environments, while only adults occur in both freshwater and marine environments (Thorson, 1983; Yokota and Lessa, 2007; Barrios-Garrido et al., 2017).

Table 2.4 List of euryhaline generalist species, their IUCN Red List of Threatened Species category and distribution (continental regions defined in Figure 2.1). CR, Critically Endangered; EN, Endangered; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated (no species are listed as VU, Vulnerable; or NE, Not Evaluated).

Species	**Common name**	**IUCN Red List category**	**Distribution**
Carcharhinidae (4)	**Whaler sharks**		
Carcharhinus leucas	Bull shark	NT	Global
Glyphis gangeticus	Ganges river shark	CR	South Asia, Southeast Asia
Glyphis garricki	Northern river shark	CR	Oceania
Glyphis glyphis	Speartooth shark	EN	Oceania
Pristidae (1)	**Sawfishes**		
Pristis pristis	Largetooth sawfish	CR	Global
Dasyatidae (5)	**Stingrays**		
Hemitrygon bennettii	Bennett’s stingray	DD	South Asia, Southeast Asia
Hypanus guttatus	Longnose stingray	DD	North and Central America, South America
Hypanus sabinus	Atlantic stingray	LC	North and Central America
Urogymnus dalyensis	Freshwater whipray	LC	Oceania
Urogymnus polylepis	Giant freshwater whipray	EN	South Asia, Southeast Asia

There is no indication that juveniles of euryhaline generalists are physiologically restricted to particular salinity environments. Studies on *C. leucas* in the Brisbane River, eastern Australia, indicated that juveniles tolerate a significantly higher osmotic pressure gradient in freshwater compared to marine, despite their preferential use of lower salinity environments as nursery areas (Pillans and Franklin, 2004; Pillans et al., 2005). In the Caloosahatchee River, Florida, USA, acoustic tracking of *C. leucas* indicated that juveniles migrate up and down stream presumably to reside within particular salinity ranges, although this may have unidentified ecological benefits (Simpfendorfer et al., 2005; Heupel and Simpfendorfer, 2008; Heupel et al., 2010). However, *C. leucas* is noted to occupy lower salinity areas of the Caloosahatchee River compared to other elasmobranchs that frequent higher salinity areas closer to the river mouth e.g. smalltooth sawfish (*Pristis pectinata*) and the bonnethead shark (*Sphyrna tiburo*) (Heupel et al., 2006; Simpfendorfer et al., 2011b). Therefore, unlike other elasmobranchs that may frequently occur in estuarine areas, species listed here as euryhaline generalists are those that additionally occur in low salinity areas of estuaries and freshwater at some point during their life history.

2.3.3 Estuarine generalists

Estuarine generalists consist of 19 ray species from five families (Table 2.5). These species are generally found in low salinity areas of estuaries as juveniles, while adults more typically occur in marine environments. Unlike species of the euryhaline generalist category, estuarine generalist species do not occur in freshwater environments for prolonged periods. This suggests they are unable to physiologically cope with freshwater environments. An example of an estuarine generalist is the Mumburarr whipray (*Urogymnus acanthobothrium*). Juveniles of this species have only been recorded in brackish (estuarine) water of rivers in Northern Australia, while large mature individuals have been observed in coastal marine environments around Northern Australia and Papua New Guinea (Last et al., 2016c). Similarly, both the daisy stingray (*Fontitrygon margarita*) and the pearl stingray (*Fontitrygon margaritella*) occur in estuarine and shallow inshore environments in heavily fished areas of West Africa, but are not reported in freshwater catches (Compagno and Roberts, 1984; Séret, 1990). Other estuarine generalists such as the tubemouth whipray (*Urogymnus lobistoma*) and *Z. maugeana* may spend their whole life cycle in estuaries, never penetrating into freshwater or marine environments (Manjaji-Matsumoto and Last, 2006; Treloar et al., 2017). All pristid species, except *P. pristis*, are estuarine generalists as juveniles are consistently recorded in estuarine nursery areas although adults are generally more frequently observed in marine environments (Taniuchi, 2002; Thorburn et al., 2008; Morgan et al., 2011; Poulakis et al., 2011; Simpfendorfer et al., 2011b; White et al., 2017a). The physiology of species regarded here as estuarine generalist has not been specifically studied and no data exist to explicitly describe the osmoregulatory differences between estuarine generalists and other euryhaline or steno-marine elasmobranchs. Identification of estuarine generalists is potentially clouded by the extensive array of elasmobranchs that may occur in estuarine systems transiently. However, unlike transient species, estuarine generalists are dependent on estuaries for part, or all, of their life history stages.

Table 2.5 List of estuarine generalist species, their IUCN Red List of Threatened Species category and distribution (continental regions defined in Figure 2.1). CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated.

Species	Common name	IUCN Red List category	Distribution
Dasyatidae (12)	**Stingrays**		
Fontitrygon colarensis	Colares stingray	VU	South America
Fontitrygon margarita	Daisy whipray	EN	West Africa
Fontitrygon margaritella	Pearl whipray	DD	West Africa
Hemitrygon fluviorum	Estuary stingray	VU	Oceania
Himantura australis	Australian whipray	NE	Oceania
Himantura uarnak	Coach whipray	VU	East Africa, The Gulf, South Asia, Southeast Asia
Hypanus say	Bluntnose stingray	LC	North and Central America, South America
Pastinachus ater	Broad cowtail ray	LC	East Africa, The Gulf, Oceania, South Asia, Southeast Asia
Pastinachus solocirostris	Roughnose cowtail ray	EN	Southeast Asia
Pateobatis hortlei	Hortle's whipray	VU	Oceania
Urogymnus acanthobothrium	Mumburarr whipray	NE	Oceania
Urogymnus lobistoma	Tubemouth whipray	VU	Southeast Asia
Pristidae (4)	**Sawfishes**		

Anoxypristis cuspidata	Narrow sawfish	EN	The Gulf, Oceania, South Asia, Southeast Asia
Pristis clavata	Dwarf sawfish	EN	Oceania, South Asia, Southeast Asia
Pristis pectinata	Smalltooth sawfish	CR	North and Central America, South America, West Africa
Pristis zijsron	Green sawfish	CR	East Africa, The Gulf, Oceania, South Asia, Southeast Asia
Rajidae (1)	**Hardnose skates**		
Zearaja maugeana	Maugean skate	EN	Oceania
Rhinidae (1)	**Wedgefishes**		
Rhynchobatus springeri	Broadnose wedgefish	VU	Southeast Asia
Rhinopteridae (1)	**Cownose rays**		
Rhinoptera bonasus	Cownose ray	NT	North and Central America, South America

2.3.4 Non-marine transients

Non-marine transients do not directly or consistently use a non-marine environment during their life history. Non-marine transients generally occupy inshore coastal habitats and are often observed in the sheltered marine waters of bays, lagoons, and lower reaches of river systems (Salini et al., 1990; Harasti et al., 2017). Short excursions into lower salinity environments may allow these species to exploit these resources but avoid the osmoregulatory stress induced by prolonged exposure to lower salinities. Non-marine transients include numerous species, mostly from the shark families

Carcharhinidae (whaler sharks), Orectolobidae (wobbegongs), Sphyrnidae (hammerhead sharks), Squatinidae (angel sharks), and Triakidae (hound sharks); and the ray families Aetobatidae (pelagic eagle rays), Arhynchobatidae (softnose skates) Dasyatidae, Glaucostegidae (giant guitarfishes), Myliobatidae (eagle rays), Narcinidae (numbfishes), Rhinobatidae (guitarfishes), and Torpedinidae (torpedo rays). For example, juvenile pigeye sharks (*Carcharhinus amboinensis*) are common within and around river and creek outflows throughout tropical Australia and East Africa, although they display avoidance of freshwater during periods of high freshwater-flow and resulting low salinity plumes associated with rainfall (Knip et al., 2011a; Knip et al., 2011b). Although individuals of this species are suspected to enter non-marine environments, data indicate *C. amboinensis* populations do not complete significant periods of their life cycle in non-marine environments as a range of size classes are commonly captured in inshore coastal marine areas (Bass et al., 1973; Cliff and Dudley, 1991; Stevens and McLoughlin, 1991). Similar habitat use patterns around estuaries have been observed for numerous elasmobranchs including the angular angel shark (*Squatina guggenheim*) (Colonello et al., 2006), lemon shark (*Negaprion brevirostris*) (Yeiser et al., 2008), scalloped hammerhead (*Sphyrna lewini*) (Brown et al., 2016), *S. tiburo* (Heupel et al., 2006), shovelnose guitarfish (*Pseudobatos productus*) (Márquez-Farías, 2007), and to a lesser extent, the white shark (*Carcharodon carcharias*) (Harasti et al., 2017). Movement studies on these species indicate that coastal marine habitats adjacent to river outflows are important for particular life stages of non-marine transients as they may provide nursery areas (Heupel et al., 2006; Heupel et al., 2007; Wiley and Simpfendorfer, 2007; Harasti et al., 2017; Martins et al., 2018). However, there is presently no evidence that they penetrate lower salinity waters of estuaries for prolonged periods, nor at consistent parts of their life history. Thus, they are considered transient in non-marine environments.

2.3.5 Non-marine vagrants

All other marine species that have reported occurrences in non-marine environments and do not fit the criteria of non-marine transient are considered non-marine vagrants. Accounts of vagrancy in elasmobranchs are rarely reported, and furthermore the term ‘vagrant’ has not previously been properly defined within elasmobranch literature. Last (2002) proposed a list of 41 species that were categorised as “*Marine species – vagrant in brackish/freshwater*” in Australia, whereby vagrant species were defined in the context of his categorisations as “*marine species that are known from but which are rarely recorded from estuaries*” (p. 185–187). However, this definition of vagrant is only applicable to vagrancy in estuaries by marine species, and therefore is not suitable for use in other scenarios of vagrancy. Furthermore, this definition of vagrant by Last (2002) did not capture the key concept of vagrancy, i.e. an individual is found outside the known distribution of its species (Norton, 1998; Lees and Gilroy, 2014). For example Duffy et al. (2017) reported what was likely a single individual whitetip reef shark (*Triaenodon obesus*) observed four times over a 12 month period at reefs in temperate New Zealand, despite the closest known population’s distribution being 598 km away in tropical waters of southern Fiji. Under the definition provided by Last (2002) this account would not fit the term vagrant, although under traditional definitions of the term (i.e. Norton, 1998; Lees and Gilroy, 2014), this is clearly an example of vagrancy. Therefore, in order to resolve confusion around the term within elasmobranch literature, this study defines vagrant to better encompass all scenarios of vagrancy, and also to provide a definition more comparable with other taxa e.g. birds (Lees and Gilroy, 2014), plants (Norton, 1998), marine mammals (de Bruyn et al., 2006):

> *An individual found outside of the known distribution of its species, with no apparent biological context.*

Under this definition, a non-marine vagrant is an individual of a coastal, shelf, or pelagic species that has no identifiable biological association with non-marine environments throughout its life history. The distributions of populations of these species are not considered to extend into, nor be adjacent to non-marine environments, though individuals of these species may very occasionally have anomalous sightings in lower salinities. This contrasts to non-marine transient species, where a) there is an ecological context to their occurrence in non-marine environments; and, b) their distribution is adjacent, or encroaches into, non-marine environments. Factors leading to vagrancy have not been studied specifically for elasmobranchs but likely causes include abnormal weather and ocean current conditions driving species out of their ‘normal’ marine distribution. Under our present understanding of non-marine vagrant species, the conservation of non-marine environments likely has little importance to their populations.

2.4 Discussion of categories

This review has identified five categories of elasmobranchs, three of which require a non-marine environment as part of their life history: freshwater obligates, euryhaline generalists, and estuarine generalists. The two remaining categories are marine species that can occur in non-marine environments, and are defined as non-marine transients and non-marine vagrants. This refinement builds on the categories originally proposed by Compagno and Cook (1995) to provide clearer distinctions between groups of species that require non-marine environments throughout their life histories. Primarily, clarity has been provided in how species in each category use non-marine environments throughout their life history, and the range of their non-marine environment use. The new categorisation also quantifies salinity profiles of each habitat type, allowing species to be more accurately categorised. This categorisation system thus provides an applicable and informative framework for applying conservation and management strategies to elasmobranchs that occur in non-marine environments. For most species however, further information is still required on fundamental aspects of their life history traits, movement and habitat use patterns, and demographic attributes in order to better understand the conservation and management requirements of their populations. Due to the lack of information for some species, or groups of species, these proposed categorisations are intended to provide a ‘testable baseline’ from which our understanding of how elasmobranchs interact with non-marine environments throughout their life histories can improve.

The categories presented here share some similarities with the guild approach (see Elliott et al., 2007; Potter et al., 2015) used to classify teleost fishes interactions with estuaries. However, teleost fishes are vastly more specious than elasmobranchs and they have numerous different life history strategies and trophic roles, each with complex and various arrays of associated habitat use behaviours not observed within elasmobranchs (e.g. planktonic larval phases and semelparity). Furthermore, the physiology of teleost fishes allows them to more easily adapt to non-marine environments throughout various stages of their life history (Ballantyne and Robinson, 2010). Collectively, this necessitates a more intricately structured categorisation system to accomodate all the different ways that teleost fish interact with non-marine environments (Elliott et al., 2007). In contrast, elasmobranchs that occur in non-marine environments are relatively uniform in their life history strategy. They are all live bearing (except for *Z. maugeana*), all produce small litter sizes of well-developed young, reproductive seasonality often spans of several months, they generally have well defined nursery areas, and they occupy similar ecological trophic roles. Therefore, a simpler approach can be taken to categorise their habitat use patterns. While it is true that some elasmobranchs listed in this review could be allocated into existing categories of teleost fishes (e.g. *C. leucas* may be amphidromous using the guild approach of Elliott et al. (2007)), the simpler structure of the present categorisations are more compatible with the limited information available for most elasmobranchs that occur in non-marine environments.

There are still some discrepancies within the present categorisations, and it is likely that an improved understanding of these species will result in future alterations and/or subsequent categories. Within the euryhaline generalist category for example, some species have populations that remain in freshwater environments for longer portions of their life history than others. Thorson (1976) noted a range of *P. pristis* size classes, including reproducing females persisting in Lake Nicaragua and suggested that this freshwater system may support the ecological and reproductive necessities of this species. Similarly, Lake Jesup, Florida, USA, contains a closed freshwater population of *H. sabinus* (Piermarini and Evans, 1998). The only factor separating these *P. pristis* and *H. sabinus* populations from dasyatids in the freshwater obligate category is that these species also have conspecifics that use and persist in estuarine and marine environments at particular life history stages (Schwartz, 1995; Whitty et al., 2017). On the other end of the spectrum in the euryhaline category, *H. guttatus* may require higher salinities in juvenile age classes while only adults seem able to persist in freshwater. Hence, it is plausible that a category of elasmobranchs is included that sits between the potamotrygonid rays that are physiologically obligate to freshwater and euryhaline species that require access to marine environments. Such a category might include species that can complete their whole life history within freshwater, though are still capable of osmoregulation in higher salinities (i.e. non-obligate freshwater species). This category would include the freshwater dasyatids (and possibly some potamotrygonids e.g. *P. motoro*) and euryhaline species that have a population(s) that complete their life cycle exclusively within freshwater (i.e. *H. sabinus*). However, considering the information currently available on the environmental distribution and osmoregulatory physiology of these species throughout their life histories, their conservation requirements do not diverge from those of the present freshwater obligate or euryhaline generalist category. Therefore, the dasyatid rays that reside exclusively in freshwater are categorised with the potamotrygonid rays as their conservation and management concerns only freshwater environments. Similarly, euryhaline species with sub-populations that may be able to reside exclusively in freshwater are categorised with other species that occur from freshwater to marine environments as conservation and management of all of the populations of these species concerns environments ranging from freshwater to marine.

Knowledge gaps in the distribution of species throughout their respective life histories are a common theme in historic and present understanding of elasmobranchs in non-marine environments. The estuarine generalist category for example is a group of rays that have been overlooked in all previous categorisation attempts (Thorson et al., 1983; Compagno and Cook, 1995; Martin, 2005). These species were regarded as either 'euryhaline' or 'marginal' by Compagno and Cook (1995), although almost no life history and movement information existed on these species at the time. It is only with recent studies that they have been separated here on the basis that populations of these species are noted to consistently use lower salinity waters of estuaries (generally as nurseries) within their life histories e.g. *P. clavata* was previously listed as 'Marginal' by Compagno and Cook (1995) although, presently it is categorised as an estuarine generalist as juveniles are considered to use low salinity estuarine areas as nurseries

(Peverell, 2005; Morgan et al., 2011). Therefore, the conservation and management of these species should focus on estuarine and marine environments. It is likely that the species listing of this category will be subject to change over time as there is generally a lack of information on the life history and movement patterns of estuarine generalist species [and possible estuarine generalist species not included here e.g. Atlantic chupare (*Styracura schmardae*) and the daggernose shark (*Isogomphodon oxyrhynchus*)] and furthermore, no studies on their osmoregulatory physiology are presently available.

2.5 Constraints to elasmobranchs in non-marine environments

From this review, only 72 (5.8%) of total chondrichthyan species (~1250) were identified to use a non-marine environment within their life history. This provides an update on the number of species previously considered to use non-marine environments (freshwater and euryhaline species) by Lucifora et al. (2015) (56 spp.). In comparison, 47–53% of teleost species (~15,000) occur in freshwater either fulltime or at critical parts of their life history (Reid et al., 2013). The potamotrygonid rays of South America are the most specious family to occur in non-marine environments. They adapted to freshwater by vicariant processes, following marine incursions on the South American continent, and have subsequently speciated throughout many of South America's northern and central river systems (Kirchhoff et al., 2017). However, it is less clear what factors have led a small number of dasyatid rays to colonise freshwater on differing continents and why so few chondrichthyan species have adapted to use non-marine environments in general.

The higher incidence of teleost species adapting to non-marine environments is likely due to differences in osmoregulatory physiology between chondrichthyans and teleosts that originate from their marine origins (Ballantyne and Robinson, 2010). Unlike teleosts, chondricthyans in marine environments regulate their osmotic balance through the retention of nitrogenous compounds (urea and tri-methyl amine oxide [TMAO]). This increases their blood osmolarity to that of saltwater reducing their requirement to actively intake water (Thorson et al., 1973). While this strategy of osmo-conformation through retention of nitrogenous compounds is well suited to marine environments, it results in a significantly higher net metabolic offset in maintaining homeostasis in lower salinities (Thorson et al., 1973; Pillans and Franklin, 2004; Pillans et al., 2005). Despite this offset, euryhaline generalist and estuarine generalist species (and possibly freshwater obligate dasyatid rays) still use non-marine environments at critical parts of their life history.

A pattern that has emerged from the present review is that most euryhaline and estuarine generalist species tend to occur at their lowest salinity environment as juveniles. Nursery areas are important for most elasmobranch species (Heupel et al., 2007; Martins et al., 2018). They generally increase survivorship and fitness of juvenile age classes through decreased predation and offer beneficial abiotic and biotic conditions and features (Heupel et al., 2007). Typical elasmobranch nursery habitats include shallow coastal inshore areas, embayments, river mouths, seagrass and algae beds, coastal lagoons and rocky/coral reefs (Martins et al., 2018). However, many elasmobranch species may co-occur within these habitats (Castro, 1993; Simpfendorfer and Milward, 1993) and interspecific competition may be high (Kinney et al., 2011; Heupel et al., 2019). Thus, species that can access nursery environments further up rivers eliminate interspecific competition for resources and may lower predation risk, thereby resulting in higher survivorship than if they persisted around river mouths or coastal inshore areas. This may have been a driving factor in the historic colonisation of freshwater and estuarine environments by elasmobranchs.

Ballantyne and Robinson (2010) suggested three stages of freshwater colonisation from marine environments by elasmobranchs: i) estuarine species transiently enter freshwater; ii) species remain in freshwater for prolonged periods (or their whole life) though still maintain functional osmoregulatory organs; and, iii) species reside in freshwater exclusively and lose the ability to osmoregulate in higher salinities. These stages of evolutionary colonisation align well with the categories proposed in this review. Estuarine generalist species allign with stage i and the potamotrygonid rays represent stage iii, while species fitting the definition of stage ii include the euryhaline generalist species and also dasyatid rays from the freshwater obligate category. The observation that estuarine and euryhaline species tend to occur in lower salinity areas as juveniles, supports the model of gradual colonisation of freshwater proposed by Ballantyne and Robinson (2010). It is reasonable that over time juveniles may adapt to persisting in these lower salinities for longer periods if immediate ecological needs are met. However, high variability in physical parameters of non-marine environments create challenges for elasmobranchs with their prolonged life histories (Compagno and Cook, 1995; Frisk et al., 2001). Slow growth, late ages of sexual maturation, and small litters of live young (only a single elasmobranch with life history stages in non-marine environments, *Z. maugeana*, is oviparous (Treloar et al., 2017)) make elasmobranchs susceptible to density-independent environmental factors such as periods of drought and flooding, or adverse changes in water quality associated with sporadic flow regimes (Mills and Mann, 1985; Lozano et al., 2019). Only 29 species appear to occur in estuarine environments for prolonged periods within their life history. Furthermore, *U. lobistoma* and *Z. maugeana* are the only species that reside solely within estuaries for the duration of their life histories. The small number of elasmobranchs identified in this review that persist in estuaries for a life history stage supports the suggestion of Kirchhoff et al. (2017) that estuarine waters are an evolutionary bottleneck in elasmobranch adaptation to freshwater from marine environments. Once they have colonised freshwater environments, Kirchhoff et al. (2017) suggest these species actually have speciation rates equal to their marine counterparts.

2.6 Conservation status and distribution

Elasmobranch populations have declined globally due to adverse anthropogenic influence and exploitation of aquatic and marine environments (Dulvy et al., 2014; Davidson et al., 2016). Freshwater and estuarine environments have been subject to an increased intensity of adverse anthropogenic influences due to their accessibility to humans for resource exploitation (Compagno and Cook, 1995; Darwall et al., 2011; Collen et al., 2014), and may also be at most risk from climate change impacts

(Chin et al., 2010). Consequently, elasmobranchs that use or require access to these environments within their life history have increased susceptibility to population decline**.**

Over half (51%) of elasmobranch species within the freshwater obligate, euryhaline, and estuarine generalist categories identified in this review are either assessed as Data Deficient or are Not Evaluated against the IUCN Red List Categories and Criteria (Table 2.6). Of those with sufficient data available for assessment, 25 (74%) are classified as threatened with extinction (IUCN Red List categories CR, EN, VU). Of the 10 freshwater obligate species that have been assessed, seven are threatened with extinction, raising serious concern about the present state of the Data Deficient (16 spp.) and Not Evaluated (17 spp.) species within this category. Estuarine generalist species have the highest proportion of species that are threatened with extinction (65%), while euryhaline generalists contain the most species with an elevated extinction risk with 50% classified as either CR (3 spp.) or EN (2 spp.) (Table 2.6). Furthermore, an undescribed *Glyphis* species known from Borneo and Bangladesh has only four documented observations (Li et al., 2015) and is also likely to be threatened with extinction due to its occurrence in areas of very high human population density and consequential inshore and riverine fishing pressure.

The distribution pattern of species that require a non-marine environment within their life history raises concern, as there is a high level of endemism to regions (regions specified in Figure 2.1). These high rates of endemism reflect the dependency of non-marine environments during the life history of these species as it likely restricts their movement between neighbouring river systems and furthermore, ocean basins to other regions. Overall, 81% (58/72 spp.) are endemic to a region with just 14 species found in two or more regions, and only *C. leucas* and *P. pristis* are found throughout all regions (Figure 2.1). Rates of endemism in each category are: 100% (43/43) for freshwater obligates; 40% (4/10) for euryhaline generalists; and, 58% (11/19) for estuarine generalists. It should be noted that *P. motoro* has been introduced into a reservoir in the upper Seletar River in Singapore (Ng et al., 2010), while *P.*

motoro, *Potamotrygon leopoldi*, and *P. orbignyi* have been reported from freshwater systems in China (Xiong et al., 2015), presumably due to releases from the ornamental industry. These 'distributions' have not been included in the present review as the validity of their establishment in these regions is complex (see Ng et al., 1993) and further verification of the viability of their populations is needed (Xiong et al., 2015).

Table 2.6 Number of species in each IUCN Red List of Threatened Species category (IUCN 2018). CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated. Threatened comprises CR, EN, and VU.

Category	Species	CR	EN	VU	NT	LC	DD	NE	Threatened
Freshwater Obligate	43	0	6	1	0	3	16	17	7 (16%)
Euryhaline Generalist	10	3	2	0	1	2	2	0	5 (50%)
Estuarine Generalist	19	2	5	6	1	2	1	2	13 (65%)
Total	**72**	**5**	**13**	**7**	**2**	**7**	**19**	**19**	**25 (35%)**

More than half of all freshwater, euryhaline, and estuarine species occur in South America, although this is mainly comprised of freshwater obligates with 36 (84%) of the world's 43 freshwater species found in the region (Figure 2.1). This is largely consistent with global diversity patterns of other freshwater vertebrate taxa (Collen et al., 2014). Other regions of high species density include Southeast Asia (18 spp.) and Oceania (14 spp.). In Southeast Asia and Oceania, 44% and 57% of species are endemic, respectively. Although no obligate freshwater species occur in the Oceania region, it is a centre of diversity for euryhaline and estuarine elasmobranchs. Five of the ten euryhaline generalist species listed are found in the region, three of which are endemic. Additionally, nine estuarine generalist species are found here also, with five of these endemic (Figure 2.1). West Africa also represents a smaller pocket of freshwater and estuarine elasmobranch diversity, with four of its seven (57%) species endemic, although *P. pristis* is possibly extinct in the region (Dulvy et al., 2016). No species are endemic to East Africa, The Gulf, or South Asia.

The region with the highest imperative for future research is South America. Of the 37 species endemic to the region, 32 are Data Deficient (15 spp.) or Not Evaluated (17 spp.), and only four potamotrygonid rays have been assessed in a data-sufficient category on the IUCN Red List. However, formal taxonomic descriptions have only been completed for some potamotrygonid species in recent years. Oceania, South Asia, and Southeast Asia have the highest concentrations of CR species that occur in non-marine environments. However, the occurrence of *P. pristis* and *P. zijsron* is now irregular in both South Asia (Bineesh et al., 2014) and Southeast Asia (Kyne and Simpfendorfer, 2014), and the Ganges river shark (*Glyphis gangeticus*) is rarely seen in these regions on a year-to-year basis (Li et al., 2015). Due to dense human population and conjunctly high fisheries pressure, it is likely that only small populations persist in these regions. Oceania supports the highest population densities of CR species that occur in non-marine environments (Thorburn et al., 2003; Morgan et al., 2011; White et al., 2017a). The tropical coastline of Australia has very low human population density and an extensive array of protected areas. Healthy populations of many euryhaline species that have otherwise been subject to significant range contractions throughout the Indo-Pacific indicate that it is one of the last multi-species elasmobranch conservation strongholds in the world (White and Kyne, 2010).

2.7 Future research directions

The high incidence of increased conservation concern within freshwater, euryhaline, and estuarine species is unsurprising given the historic and ongoing anthropogenic and environmental pressures on their populations. However, many of the elasmobranchs listed in the present review remain data deficient with respect to their conservation biology. This impedes the early detection of deteriorating populations and the application of effective management strategies. This can ultimately lead to abrupt local extinctions such as those observed globally for pristids (Dulvy et al., 2016).

With a trend towards a generally 'positive' public perception of elasmobranchs (Whatmough et al., 2011) there is an increased awareness and imperative to conserve and protect their populations (Simpfendorfer et al., 2011a). Future research needs to focus on key biological and human interaction aspects that will lead to better availability of information for the conservation and management of elasmobranchs in non-marine environments (Simpfendorfer et al., 2011a). Firstly, continued taxonomic resolution and description of new species (e.g. Potamotrygonidae, Dasyatidae, and *Glyphis*) is essential to a fundamental understanding about i) how many species are of conservation and management interest in non-marine environments; and, ii) how these species can be identified (Hutchings, 2017). Taxonomic resolution facilitates collection of data on the distribution and relative abundance (e.g. catch-per-unit-effort) of species, in turn informing conservation and management as it allows increases or decreases in population distribution and size to be tracked over time (Moore, 2017). Due to an absence of historical fisheries data and difficulties in documenting artisanal and subsistence fisheries catch, further information is needed on the distribution and relative abundance of many freshwater, euryhaline, and estuarine species populations (Fluet-Chouinard et al., 2018).

There are a great number of data gaps about elasmobranchs that occur in non-marine environments; data on life history (growth rate, longevity, age/length at sexual maturation, fecundity, size-at-birth, maximum size, gestation period, reproductive periodicity, and natural mortality), population structure and connectivity (i.e. population genetics), spatial ecology (long- and short-term movement patterns), and osmoregulatory physiology is needed for many species. Life history data is essential to demographic models that can be used to inform population growth, assess susceptibility to threats such as fishing mortality or environmental disasters, and population recovery potential (Cortés, 1998). This information is vital to identifying and prioritising fisheries management actions. Studies on population structure inform the spatial boundaries of their populations while spatial ecology informs their temporal distribution within and between non-marine environments, from which the application of protection and management measures can most effectively be placed (Heupel et al., 2007; Kinney and Simpfendorfer, 2009; Heupel et al., 2015). Information on the osmoregulatory physiological preferences of species throughout their life history will help to indirectly identify important environmental areas of particular non-marine systems, providing broadly applicable data for regions and river systems, or cryptic/elusive species that are logistically difficult to biologically survey. It is unrealistic that information in these fields will become readily available for all the species listed in this review, however a concerted research effort is needed on species facing higher levels of extinction risk and those assessed as Data Deficient.

There is also a need for information on the importance of non-marine elasmobranchs to human communities, the roles they play in livelihoods and food security, and the attitudes of human interactions to these species. For example, in developing nations with primarily artisanal and subsistence fisheries, non-marine environments may play an increased role in food security as they are more easily accessible than inshore coastal waters (including access during periods when offshore weather is poor) (Compagno and Cook, 1995). Furthermore, large-bodied elasmobranchs within them may be cost effective to fish, providing both a large food source and body parts for subsequent sale (e.g. fins). Conversely, in some areas of South America, potamotrygonid rays are viewed as an impediment to tourism and human safety, as they aggregate in shallow waters that otherwise have intrinsic value for swimming and fishing activities (Araújo et al., 2004). In other regions of South America, potamotrygonid rays are targeted for their high value in ornamental aquaria markets (Moreau and Coomes, 2007). Thus, key questions for the effective application of conservation and management might include: i) is there a reliance on elasmobranchs as a food or economic resource; ii) what is the economic value of elasmobranchs; iii) what other food or economic resources may be available; iv) how are elasmobranchs perceived by local communities; and, v) are there any cultural or spiritual beliefs surrounding elasmobranchs. This type of information will help identify strategies to engage local resource users in conservation management. For species with restricted distributions such as the freshwater obligates, and euryhaline or estuarine species with populations confined to particular river systems, engaging local resource users will be vital to sustained conservation and management efforts (Hueter et al., 2004). Other concerns and considerations may include the value of elasmobranchs in ‘ecotourism’ and whether they have value as a ‘non-extractive’ resource.

2.8 Conclusion

This review has refined earlier categorisations of elasmobranchs known to occur in non-marine environments, through the development of a new categorisation system. The categorisations presented here can better inform conservation and management, as species and the environments they require throughout their life history can be more easily understood. However, the conservation status of freshwater obligates, euryhaline generalist, and estuarine generalist species raises concern. Euryhaline generalist and estuarine generalist species have the highest extinction risk, presumably because movement between environments throughout their life histories raises their susceptibility to anthropogenic pressures. Meanwhile, for many freshwater obligate species there is insufficient data available to assess extinction risk, and a concerted research effort on these species is needed. As human populations continue to increase, greater pressure is being placed on elasmobranchs that require use of non-marine environments. In order to develop strategic conservation and management strategies, further information is required primarily on life history traits, population structure, spatial ecology, and human interactions for these species.

Chapter 3

Local knowledge surveys with small-scale fishers indicate challenges to sawfish conservation in southern Papua New Guinea

3.1 Introduction

Drawing on knowledge of local resource users is an effective approach to gathering information on threatened species. This approach can be particularly useful in conservation and management in remote regions lacking historical time-series data (e.g. Dulvy and Polunin, 2004). The knowledge held by local resource users can complement contemporary quantitative scientific data in numerous ways, including: i) to better understand local population trends over time, including relative abundance, and current and historical distributions (e.g. Valerio-Vargas and Espinoza, 2019); ii) infer historical population baselines from which perceived changes can be measured (e.g. Pauly, 1995; Eckert et al., 2018); iii) provide information on the timing, impact, and duration of environmental or anthropogenic disturbances that may have resulted in changes to the population over time (e.g. McDavitt, 2002); and iv) provide insights on biological characteristics of how the population interacts with the local environment (e.g. spawning seasons, migrations, or nursery areas), which may have been previously unknown, or undocumented (Ames, 2004). Furthermore, engaging with local resource users allows for an understanding of how threatened species exist within local culture, with respect to uses and values. In remote regions with limited commercial harvest activities, understanding the historical or contemporary cultural uses and value that a threatened species has, helps to inform how culturally appropriate conservation initiatives can be best developed and implemented to achieve high levels of engagement and participation from local resource users (McDavitt, 2014; Booth et al., 2019).

Sawfishes (family Pristidae) are among the most recognizable and charismatic ray species, due to their long-toothed rostrum. Historically, they were commonly distributed throughout the tropics in shallow coastal and estuarine environments, while the largetooth sawfish *Pristis pristis* was additionally common throughout tropical riverine environments (Thorson et al., 1966; Dulvy et al., 2016). Consequently, cultural beliefs, symbols, and connotations of sawfish are found within many historical and current cultures and societies within Central and South America, Africa, Asia, and northern Australia (McDavitt, 2014). High human interaction has led to widespread declines in sawfish populations globally (Dulvy et al., 2016). The green sawfish *Pristis zijsron*, largetooth sawfish *P. pristis*, and smalltooth sawfish *Pristis pectinata*, have been assessed as Critically Endangered on the IUCN Red List of Threatened Species (hereafter 'IUCN Red List'), while the dwarf sawfish *Pristis clavata* and narrow sawfish *Anoxypristis cuspidata*, are Endangered (IUCN 2020).

The imperiled conservation status of sawfishes is primarily due to incidental capture and exploitation in tropical fisheries. Fishing activities (including commercial, small-scale, and cultural) are concentrated in shallow coastal and riverine environments, particularly in developing tropical nations where sawfishes occur (Compagno and Cook, 1995; Blaber, 2009), and the toothed rostra of sawfishes increases their susceptibility to net fisheries (Dulvy et al., 2016). Degradation of coastal and riverine environments has also likely been a prominent factor in sawfish population declines, mainly through coastal development and river engineering (Hossain et al., 2015; Brame et al., 2019). Presently, northern Australia and the south-east United States are regarded as potentially the last remaining significant refuges for sawfish populations within the Indo–Pacific and Atlantic, respectively (Dulvy et al., 2016). Both of these regions have national and state legislative protection measures, and also maintain active research, monitoring, and community-based sawfish conservation efforts (Morgan et al., 2011; Brame et al., 2019). However, the rebuilding of global sawfish populations cannot rely on these refuge regions alone. There is a need to document sawfish distribution, abundance, threats, and how they interact with local culture in other nations where remnant populations may persist so that effective local conservation measures can be developed and implemented (Dulvy et al., 2016). Within the Indo-Pacific, there may be remote locations where relatively intact populations persist, as has been found with other riverine elasmobranchs (e.g. White et al., 2015). This will assist in the rebuilding of global populations and may provide alternative locations to study aspects of sawfish life history, ecology, and habitat use requirements, which will ultimately lead to more informed conservation initiatives globally.

Recently, there has been increased interest in Papua New Guinea (PNG) as a possible refuge for the four Indo–Pacific sawfish species (*A. cuspidata*, *P. clavata*, *P. pristis*, and *P. zijsron*)(White et al., 2017a; Leeney et al., 2018; White et al., 2019). Recent observations from a shark fin trader at Daru, Western Province, provided evidence that all four Indo–Pacific sawfish species still occur within southern PNG, and *A. cuspidata* and *P. pristis* were additionally observed in the bycatch of the Gulf of Papua Prawn Trawl Fishery (the only commercial fishery in southern PNG likely to catch sawfishes) (White et al., 2019). On the northern coast of PNG, Leeney et al. (2018) noted populations of *A. cuspidata* at the mouth of the Sepik and Ramu Rivers, while *P. pristis* was additionally found upstream in freshwaters of the Sepik River. Compared to northern PNG however, the southern coastline of PNG provides a higher abundance of suitable shallow habitat, with several large adjacent river basins (Fly River, Bamu/Aramia River, Turama River, Kikori River, and Purari River) draining into the Gulf of Papua. The southern coastline of PNG has very low human population density, and most of its land, rivers, and coastline remain undeveloped and largely inaccessible to commercialized activities, with communities generally living by traditional means.

While there is great potential for southern PNG to provide a refuge for Indo–Pacific sawfish species, there is still a lot of information required to assist conservation initiatives. Specifically, a greater understanding is needed on: i) distribution, abundance, and population trends of sawfishes in the region; ii) the cultural use and value of sawfishes to local people; and, iii) insights into threats sawfishes may be facing in southern PNG, with particular reference to sawfish interactions with small-scale fisheries. Gathering information on sawfishes and relevant small-scale fisheries in southern PNG however presents many logistical challenges and knowledge gaps. The remoteness and inaccessibility of southern PNG has impeded the amount of research that has been conducted, particularly on elasmobranch species (White and Ko'ou, 2018), while studies documenting small-scale fishery characteristics are restricted to the South Fly Coast (e.g. Busilacchi et al., 2014; Busilacchi et al., 2021). This lack of recent information also impedes development of conservation initiatives for threatened species such as sawfishes within PNG, as present levels of threat from small-scale fisheries are unclear, and there is no historical time-series information available to determine the extent and duration of any population declines.

The purpose of this study was to provide information on sawfishes in southern PNG including exploitation in small-scale fisheries, for use in development of fisheries management and conservation initiatives. Following recent studies that focused on local knowledge of sawfishes in other data-limited regions e.g. Brazil (Giglio et al., 2016; Feitosa et al., 2017), Costa Rica (Valerio-Vargas and Espinoza, 2019), and northern PNG (Leeney et al., 2018), this study used interviews with experienced fishers across remote communities in southern PNG to collect data on sawfish occurrences, values, and interactions with small-scale fishers to fill knowledge gaps resulting from a lack of historical baseline data.

3.2 Methods

3.2.1 Study location

This study was conducted in coastal and riverine communities in the Western and Gulf Provinces of Papua New Guinea (PNG) during 2018–2019. Within these Provinces, interviews were conducted in six broad regions; South Fly Coast, Aramia River, and Bamu River in the Western Province, and Turama River, Kikori River, and Tiamura River in the Gulf Province (Figure 3.1). The environment along the South Fly Coast is predominately marine and estuarine, with substantial outflow from the Fly River. The Oriomo and Mia Kussa Rivers also provide smaller outflow volumes and estuarine environments in their lower reaches and adjacent coastline, although their influence is significantly less than the Fly River. The Aramia River is a freshwater system flowing into the Bamu River, and is freshwater all year round, occasionally receiving saltwater inflow during spring tides in the dry season. The Bamu, Turama, and Kikori Rivers are all large high flow systems with delta areas around their respective river mouths. The environment around these deltas and adjacent coastline is estuarine, while upstream of deltas is freshwater. The Tiamura River is significantly smaller than these other rivers. Its mouth forms a large estuarine bay (Kerema Bay) with significant marine tidal influence, while its head waters provide freshwater inflow year-round.

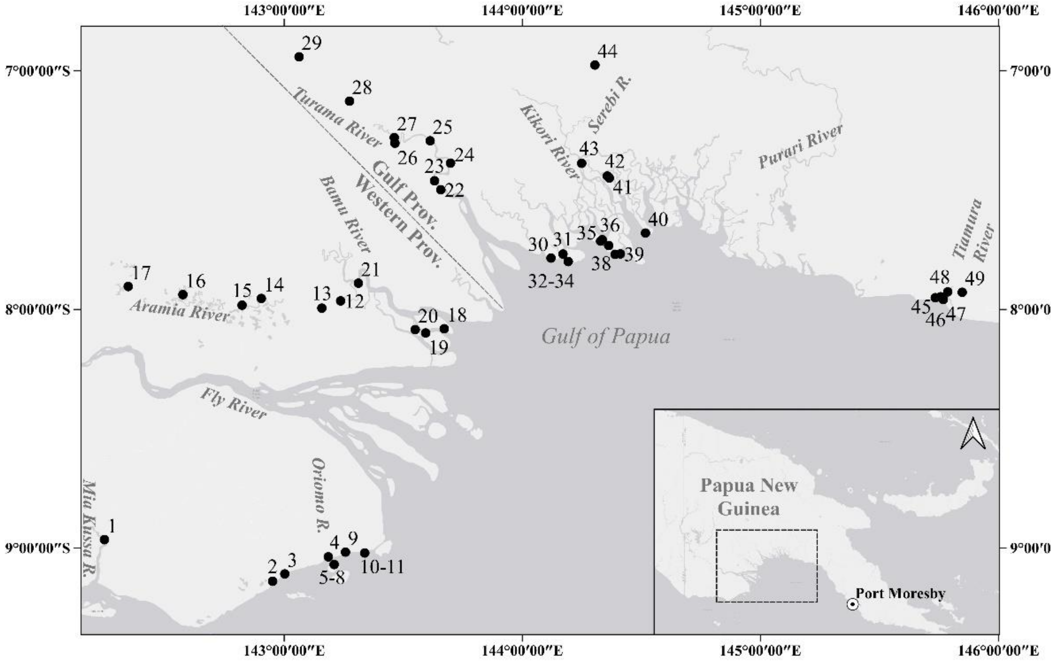


Figure 3. 1 Location of villages and fishing camps visited throughout southern Papua New Guinea. South Fly Coast: 1. Sibidiri Village, 2. Old Mawata, 3. Tureture Village, 4. Oriomo River mouth fishing camp (Kadawa Village), 5–8. Daru (capital of Western Province), 9. Kadawa Village, 10–11. Katatai Village. Aramia River: 12. Garu Village, 13. Madila Village, 14. Kewa Village, 15. Kawito Village, 16. Makapa Village, 17. Ali-Bogola Village. Bamu River: 18. Bina Village, 19. Wariho Village, 20. Sisiaimi Village, 21. Sasairi Village. Turama River: 22. Meagio Village, 23. Masusu Village, 24. Sorobo Village, 25. Sagari Village, 26. Moka 2 Village, 27. Moka 1 Village, 28. Kuri Village, 29. Haivaro Village. Kikori River: 30. Kemei Village, 31. Aiedio Village, 32–34. Goare Village, 35. Ivibirri fishing camp (Apeawa Village), 36. Kampo fishing camp (Apeawa Village), 37. Kotoiia-Bari fishing camp (Apeawa Village), 38. Veraibari Village, 39. Evamu Village, 40. Babai Village, 41. Ero Village, 42. Samoa Village, 43. Veiru Village, 44. Omo Village, ○Kikori town. Tiamura River: 45. Uaripi 1 Village, 46. Uaripi 2 Village, 47. Kerema (capital of Gulf Province), 48. Sicari fishing camp, 49. Murua Village.

3.2.2 Interview process and questionnaire

Community engagement was facilitated by local collaborators that had a history of working in the area and could act as cultural brokers and interpreters. Before arrival in any region, village Councillors or Chiefs were made aware of the research parties intent to visit and enquire about fishing activities by local project collaborators from either the Western Provincial Fisheries (South Fly Coast), Gulf Provincial Fisheries (Tiamura River), or the Piku Biodiversity Network (Aramia, Bamu, Turama, and Kikori Rivers). Where prior engagement was not always possible in particularly remote regions (e.g. Aramia, Bamu, and Turama Rivers, or upstream of the Tiamura River), discussions about the study were undertaken with village Councillors or Chiefs upon arrival.

In each region, the selection of village communities or fishing camps to visit aimed to cover a range of coastal, estuarine, and freshwater environments. Most of the regions visited were very remote, with low population densities, and highly dispersed village communities. This study aimed to conduct at least one interview per village or fishing camp visited, with two or three villages usually visited each day. Interviews could not be conducted around the mouth (coast or estuary) of the Turama River, and freshwater reaches of the Bamu, Oriomo, and Mia Kussa Rivers due to logistical issues.

Upon arrival at villages or fishing camps, identification of a suitable interviewee with prolonged fishing experience in the local area was discussed with the local Councillor, Chief, or community elders. Prospective interviewees were firstly informed about the types of questions they were going to be asked (i.e. about sawfishes and fishing activities), and that the study was being conducted through James Cook University (mediation provided by either the Piku Biodiveristy Network or Provincial Fisheries staff). It was made clear to interviewees that answers provided would be used in a study on local knowledge of sawfishes and fishing activities throughout southern PNG, and that upon completion, this study may be published and made publicly available for use by fisheries managers or conservation practitioners. Interviewees were also informed that they would not be personally identifiable as a result of participating, and that their answers would be collated with other fishers in the region, to provide a general understanding for that region. Interviewees were asked to answer questions with respect to fishing activities in the given region the interview was being conducted in, and to not take into account fishing activities of former residence elsewhere (e.g. in the South Fly Coast it was common that fishers grew up in the Fly River). However, responses about the cultural significance of sawfishes from places of former residence were included in this study. Following this explanation, all interviewees were asked if they wished to proceed with the interview. Due to literacy differences between interviewees, questions were asked verbally, and answers documented. All answers given by interviewees were reconfirmed verbally before documenting on the questionnaire.

The questionnaire used in the present study was structured into four sections, with both open and closed questions (Appendix 1). The first section was designed to ensure positive identification of sawfishes and seek information on biological aspects of sawfishes in the local environment. Interviewees were shown a picture of a sawfish (and additionally a rostrum when on hand) to firstly establish a positive identification and familiarity of sawfishes. The second section addressed characteristics of the fishery and interactions of sawfishes over time. The third section addressed social and cultural uses of sawfishes. The fourth section addressed the cultural significance of sawfishes to local people. For interviews in the Aramia, Bamu, Turama, and Kikori Rivers, an additional question was added to the survey which asked interviewees whether they would be supportive of sawfish conservation, and the reasons for their answer. This was to document information that could be applied to formulation and implementation of future conservation initiatives, which we felt was not sufficiently addressed in the initial survey trip to South Fly Coast and Tiamura River.

While this study aimed to interview one individual fisher each location, this was not always possible due to variety of reasons attributed to local culture: 1) village Councillors or Chiefs appointed a group (who fish collectively) or family of fishers for the interview; 2) equality among individuals in land and waterway ownership or fishing resources (e.g. gear, boat, engine) meant fishing activities are group or family based, and entitlement to participate in the interview was shared (and time restrictions precluded the possibility of multiple interviews being conducted); and 3) due to the extremely remote nature of many villages visited, the intrinsic factor of having visitors meant that community interest and willingness to help was exceptionally high. In the occurrence of any of these scenarios, it was deemed to be inappropriate to enforce our desire for a single interviewee. Furthermore, in most instances interviews with fishers were conducted in the presence of important village personnel (Councillors, Chiefs, elders, etc.). Where a group (>3) of interviewees contributed, their ages were not recorded as it would hinder the interpretation of any age-knowledge relationship. Where more than one interviewee contributed, consensus among interviewees in answers given was confirmed before documenting. Because the aim of the interview was to gather local knowledge on sawfishes and information on fishery characteristics from a range of environments in different regions, we did not consider that interviews conducted on small groups of collective fishers violated this aim in any instance, and thus responses from these interviews were included in analysis.

3.2.3 Data analysis

Answers received from interviewees were pooled into six regions for analysis. Only one interview (in the Aramia River) was terminated early due to an incoming tidal bore and answers from section one and two only were included in the analysis. Quantitative data were entered into Excel which was used to produce descriptive statistics. Responses to open ended questions were coded into categorical responses. Small sample sizes made statistical comparisons between regions inappropriate. Results were presented in terms of 'number of interviewees' and 'proportion of interviewees', and ranges, means, and medians were presented where appropriate. All questions in each interview were not always answered or were not applicable based on previous answers given by the interviewee. For this reason, number of interviewees (n) is presented for each aspect of the analysis.

3.3 Results

In total, 49 interviews were conducted across 42 villages or fishing camps over six regions (Table 3.1, Figure 3.1) with 36/49 conducted with a single fisher, 5/49 conducted with 2–3 fishers, and 8/49 conducted on a small group (>3 fishers). The age of interviewees ranged from 17–85 (mean 42). Most interviewees were male (92%), with only four females (8%) participating (1 in Tiamura River, 3 in Kikori River). This disparity in gender of interviewees was not reflective of gender participation in fisheries, but rather a reflection of the culture in remote communities in regions visited. For example, village Councillors or Chiefs generally recommended male fishers during the discussion process, while in some regions it is not customary that females engage with visitors, or in some instances unmarried men.

Table 3. 1 Total number of villages visited, number of interviews conducted, and mean age and age range of interviewees in each region. Ages from a group of interviewees (>3 fishers) are not included.

Region	No. villages (No. interviews)	Mean age of interviewees (range)
South Fly Coast	8 (11)	47 (23–72)
Aramia River	6 (6)	39 (27–54)
Bamu River	4 (4)	43 (25–63)
Turama River	8 (8)	35 (17–50)
Kikori River	11 (15)	37 (24–49)
Tiamura River	5 (5)	56 (39–85)

3.3.1 Identification of sawfishes

All interviewees (100%) could readily identify sawfishes from a photograph, and they were reported to be caught in all habitat types accessible from villages and fishing camps where interviews were conducted (Table 3.2). A majority of interviewees (61%) reported that only one type of sawfish was caught, which included all interviewees from villages with access to only freshwater environments. Of the 19 (39%) interviewees that reported two types being caught (none reported more than two), distinction between types was on the basis of size (9), colour (4), rostrum (2), size and colour (1), colour and shape (1), or other (2). Size distinction was always based on 'small sizes' or 'large sizes' with some language names reflecting that division (e.g. Kikori River; Table 3.2), while colour distinction between the 'two types' was either light or dark coloured, and yellow/green/orange or dark brown. Two interviewees commented that the two types caught have either narrow or wide 'saws', or teeth spaced close together or wider apart. Meanwhile, two interviewees reported "some with saw, some without" and "some have white spots". It was assumed that these were in reference to other shark-like rays (e.g. the wedgefish family Rhinidae and the giant guitarfish family Glaucostegidae) rather than sawfish with amputated rostra, as amputee sawfishes are not expected to survive (see Discussion). Furthermore, these reports came from coastal environments where these other shark-like rays occur. To avoid confusion, it was made clear to these interviewees that the remainder of the survey was only in reference to types with a 'saw' (this was repeatedly clarified during interviews).

Table 3. 2 Local names for sawfishes and types of environment sawfish were reported to be caught in across regions.

Region	Local names for sawfishes	Environment type(s) sawfish reported from
South Fly Coast	Gabara, Badiam	Offshore, coastal, estuary
Aramia River	Dibini, Tibini, Walikapi, Poke	Freshwater
Bamu River	Napora, Sawamutu, Baidamo, Suamutu	Coastal, estuary, freshwater
Turama River	Gabora, Sorowaro, Shark (no name), Shargi	Freshwater
Kikori River	Maiwo/Mai'ivo/Mivo (small), Gabora/Gabara (large)	Offshore, coastal, estuary, freshwater
Tiamura River	Love (luv-ay), Poser, Mehere	Offshore, coastal, estuary, freshwater

3.3.2 Small-scale fishery characteristics

In total, interviewees reported using seven fishing gear types across regions (Table 3.3). The largest diversity of gear types encountered came from South Fly Coast interviewees, although this is likely influenced by small sample sizes in other regions. Gillnets were the most common fishing gear with 92% of interviewees reporting use. Hook & line was the second most common, with 55% reporting use, although only 4% of interviewees reported exclusive use of hook & line. Only 4% of interviewees reported that their primary fishing gears were not gillnet or hook & line, instead they primarily use basket and drag nets (to target prawns and small fish), and spear (targeting fish in headwater pools during the dry season). While no data were explicitly collected on vessel type used by fishers, observations in the field suggest that most fishing activities are conducted using large wooden paddle-powered canoes. Meanwhile, in coastal environments fishers tend to use fibreglass 'banana boats' with outboard engines in place of wooden canoes, or wade out at low tide to set nets. Fishers that access offshore reef habitat on the South Fly Coast use fibreglass banana boats exclusively, while fishers in the Kikori and Tiamura Rivers paddle offshore occasionally when trolling baited hooks.

Table 3. 3 Gear types used by interviewees in each region and number of gillnets reported to be used by fishers. Fishing activity was categorised as targeted (fishing effort applied toward capture of particular species) or non-targeted (fishing effort applied to catch any type of fish). Number of interviewees that provided an answer in each region are shown in parenthesis (*n*). Gear types included in 'Other' were lure (South Fly Coast) and cast net (Kikori River).

Region	**Gear types and number of interviewees reporting use**						**Fishing activity**		**Range (mean) of gillnets used each day/fishing activity**
	Gillnet	Hook & line	Drag net	Basket net	Spear	Other	Targeted	Non-targeted	
South Fly Coast (*n* = 11)	10	6	2	1	1	1	11	0	2–115 (14.5)
Aramia River (*n* = 6)	6	4	0	0	0	0	1	5	1–2 (1.2)
Bamu River (*n* = 4)	4	4	0	1	1	0	1	3	1–5 (2.3)
Turama River (*n* = 8))	7	8	0	0	0	0	1	7	1–9 (3.3)
Kikori River (*n* = 15)	15	4	0	0	1	1	13	2	1–12 (3.9)
Tiamura River (*n* = 5)	3	1	0	0	1	0	5	0	2–10 (6.8)

A wide range of responses were given when interviewees were asked how many gillnets are set each day (or fishing activity) (Table 3.3). Answers ranged from 1–115 (second highest was 55), with most interviewees reporting a range, stating that it depends on how many gillnets are available at the time. However, interviewees may fish individually, or in small or large groups, depending on equity share in land and waterway or fishing resources, and many interviewees did not themselves outright own a specified number of gillnets (e.g. the interviewee that reported 115 gillnets stated that when they fish, the village has 115 gillnets to set). The questionnaire used in the present study did not specifically ask about the number of fishers each interviewee conducted fishing activities with, or how many other fishers they shared land, waterway, or fishing resources with, and so this result should not be interpreted as an estimate of the number of gillnets used per fisher in each region.

Gillnet mesh sizes ranged 1.5–9″, with the largest median mesh sizes occurring in the South Fly Coast, Aramia River, and Kikori River (Figure 3.2). Large mesh sizes were more frequent in coastal villages, and particularly around the South Fly Coast and Kikori River where fishers target barramundi *Lates calcarifer*, scaly croaker *Nibea squamosa* (locally referred to as 'stone fish'), and king threadfin salmon *Polydactylus macrochir* which are sold to commercial buyers in Daru and Kikori Town, respectively. In the Aramia River, 5/6 interviewees reported use of mesh sizes ≥ 5", although they were not explicitly targeting certain species. In the Tiamura River, target species included snappers (Lutjanidae) and mackerels (Scombridae), which are sold in local markets. In Bamu and Turama Rivers, smaller mesh sizes were reported, and interviewees generally did not report a specific target species. When target species were reported in Aramia, Bamu, and Turama Rivers, it was based on species with higher preference for eating, or species with cultural value as 'food fish', rather than those with higher economic value.

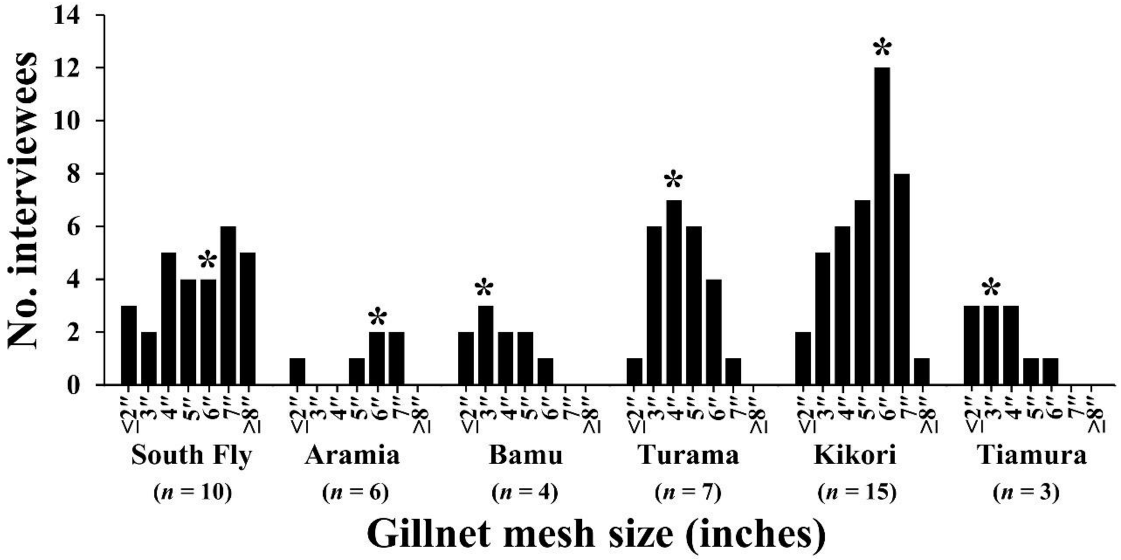


Figure 3. 2 Frequency of gillnet mesh sizes reported to be used by interviewees in each region. Asterisks show the median mesh size, within the range of mesh sizes reported in each region. Number of interviewees who provided an answer in each region are shown in parenthesis (*n*).

3.3.3 Fishery trends in sawfish catch frequency, size classes, and fate

The reported frequency of sawfish catch varied across interviewees in each region (Figure 3.3). Interviewees from the Turama River reported weekly catch frequency in villages well upriver. Within the Aramia River, sawfish were reported to be caught monthly at villages close to the confluence with the Bamu River, while upstream in the Aramia River, sawfish were reported to be caught less than yearly. One interviewee in each of the South Fly Coast and Tiamura River, reported that sawfish are caught weekly, though on a seasonal basis (April-August in South Fly Coast, April-July in Tiamura River) coinciding with 'stone fish season' (*N. squamosa*). Most interviewees (55%) reported no seasonality in sawfish catch. Of those reporting a 'sawfish season', 33% reported sawfish being more common in the dry season (generally ranging from June-December), with 13/16 of these reports coming from riverine communities (villages with access to fresh water and/or estuary only). Other reports of seasonality (12%) again highlighted that sawfish are caught when fishers target *N. squamosa* (April-July on South Fly Coast, October-March in Kikori River).

Fishing effort, measured as mean number of gillnets reported per interviewee, was compared between each categorical variable of sawfish catch frequency for all regions combined. Average fishing effort was: Weekly (*n* = 9), 8.3 gillnets; Monthly (*n* = 10), 6.2 gillnets; Every couple of months (*n* = 7), 22.0 gillnets; Couple per year (*n* = 7), 4.4 gillnets; and less than one per year (*n* = 10), 2.6 gillnets. Total average effort (*n* = 46) was 8.1 gillnets. However, some averages were skewed by two outlying results including the report of 115 gillnets from an interviewee in the South Fly Coast, and a report of 50–60 gillnets also from the South Fly Coast (Table 3.3). These outlying results were reported from two interviewees in the same village. With the removal of these data, average fishing effort for Weekly (*n* = 8) fell to 2.4 gillnets, and Every couple of months (*n* = 6) fell to 6.5 gillnets, while the total average effort (*n* = 44) fell to 4.4 gillnets.

Size classes of sawfish reported to be caught by interviewees ranged from <1 m to >4 m (Figure 3.3). All size classes were reported from the South Fly Coast, Turama River, and Kikori River, while only smaller size classes were reported in other regions. Generally, coastal villages reported higher incidence of larger sawfish being caught, while villages with access to only freshwater habitats (e.g. Aramia River) reported size classes <2 m. Only one interviewee in freshwaters of the Turama River reported sizes up to 4 m.

Across all regions, 44% of interviewees reported that they had seen large sawfish >4 m. Excluding interviews conducted in upper freshwater reaches of rivers (where large sawfish are unlikely to occur), 60% of interviewees had seen a sawfish >4 m (these data were not included in Figure 3.3, unless the interviewee had caught a sawfish >4 m themselves within the last 10 years). In the South Fly Coast, 64% of interviewees reported sawfish >4 m (two within a few months, one within 6 months, two within a year, one within 5 years, and one more than 10 years ago). The Kikori River, however, had the highest proportion (80%) of interviewees reporting having seen a sawfish >4 m (one within a month, two within a few months, four within a year, two within five years, and three more than 10 years). In the Turama

River, only one interviewee reported seeing a sawfish >4 m about one year ago. In the Aramia River, one interviewee reported seeing a sawfish >4 m in 1975. Large sawfish >4 m were not reported to have ever been seen by interviewees in the Bamu and Tiamura Rivers.

In most instances (72%), interviewees reported that sawfish are always retained when caught (Figure 3.3). The Turama River was the only region where sawfish are generally released when caught. This is due to the practising obligations of communities that identify with the Seventh Day Adventist denomination of Christianity, whereby non-scaly fish cannot be consumed, and the remoteness of the Turama River precludes the possibility of travelling to Kikori Town to sell elasmobranch catch. Of the 13 interviewees who did not always retain sawfish (categories ‘usually, ‘sometimes’, and ‘never’ in Figure 3.3), only three reported that sawfish are always untangled and released, while four reported that large sawfish are killed or ‘saw removed’ and that only small sawfish are untangled and released. The other six interviewees (five from Turama River, where retention was lowest) reported that sawfish are always either killed or ‘saw removed’ before releasing. Reasons cited were safety or to reduce damage to gillnets from sawfish thrashing their rostrum. Interviewees that reported sawfish being either usually or sometimes retained, generally reported that sawfish are secondary to other fish in terms of eating quality, and they are retained only if needed.

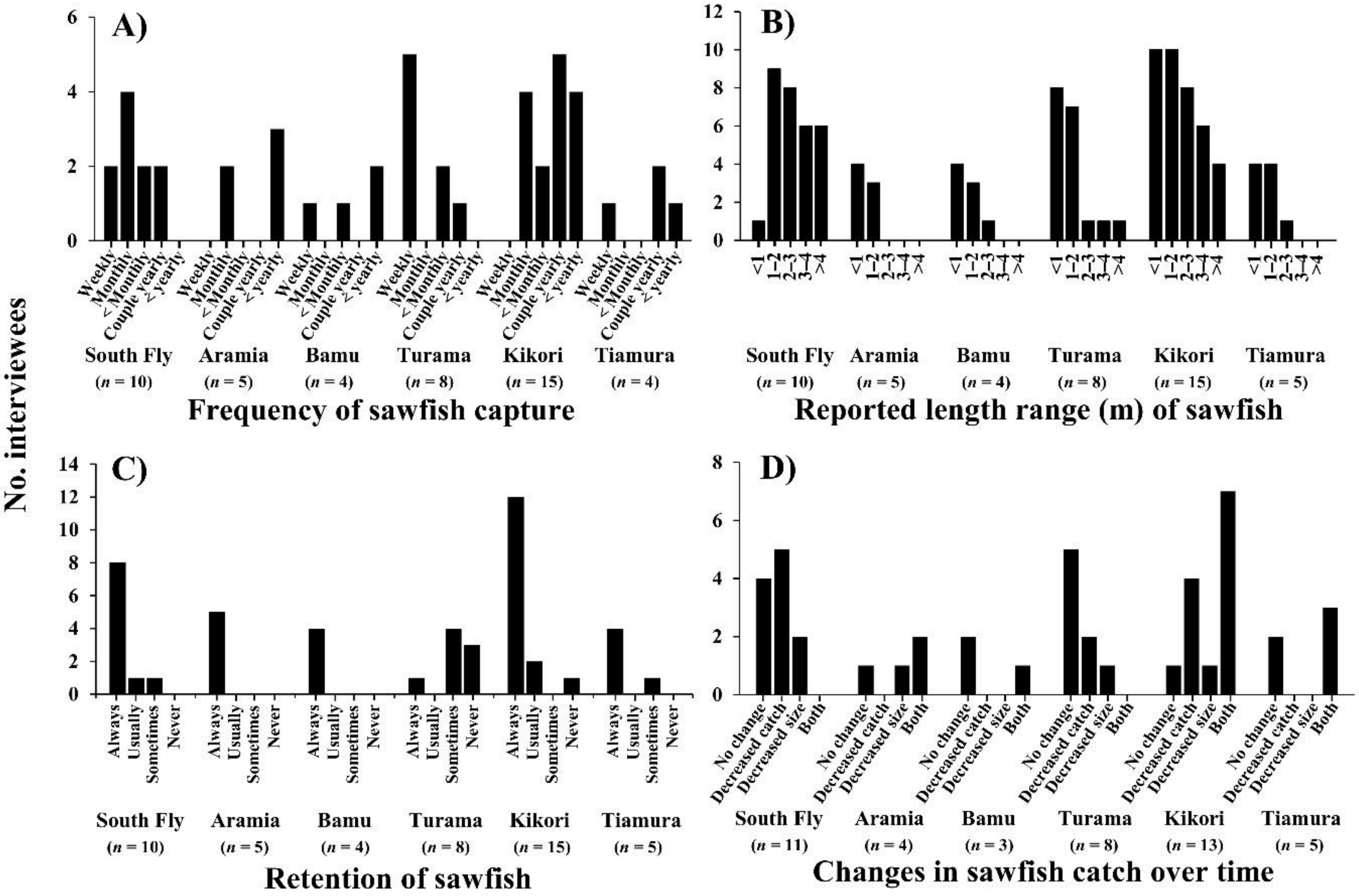


Figure 3. 3 A) Frequency of the size class (length) of sawfish reported in each region by interviewees. B) Reported frequency of sawfish catch (any size) in each region. C) Reported retention of sawfishes in each region. D) Reported changes in sawfish catch over time. Number of interviewees who provided an answer in each region for each aspect of data analysis are shown in parenthesis (*n*).

3.3.4 Trends in sawfish catch over time

Of the interviewees that provided responses about trends in sawfish catch over time (n = 44), 34% reported no noticeable change in frequency of catch or size classes caught, 25% reported decreases in catch frequency, though not in size classes caught, 11% reported decreases in size classes caught, though not catch frequency, and 30% reported decreases in both catch frequency and size classes (Figure 3.3). Only one interviewee (on the South Fly Coast) reported that sawfish are caught more commonly now, though this interviewee also reported size classes caught are smaller than caught previously. Reports of decreases in sawfish catch frequency and/or size classes were proportionately lowest in Bamu River (33%, one interviewee did not answer) and Turama River (37%), while highest (92%) in the Kikori River.

Of interviewees that provided an answer on changes in sawfish catch frequency or size classes (four interviewees did not provide an answer), 20% (9/44) reported decreases in catch frequency of other sharks also (inclusive of all other shark species). Four of these reports came from the Kikori River, while one report came from the South Fly Coast and Bamu, Turama, and Tiamura Rivers each. Two fishers in Kikori River and one on the South Fly Coast (7%) reported increases in other sharks, while all other (73%) interviewees reported no notable changes. However, this result should be interpreted carefully as fishers in freshwater or estuaries have access to fewer shark species occurring in these environments compared to coastal fishers (Chapter 2).

From the 29 interviewees that reported declines in either catch frequency or size classes of sawfish across regions, a variety of different reasons were suggested to have attributed to declines (Table 3.4). Six of these interviewees (21%) did not provide an answer as they were unsure, or reluctant to speak openly. Overall, increased fishing activity was the most commonly provided reason (34%), with seven accounts coming from the Kikori River. The second most common response were those related to changes in environment or climate (24%), three of which came from the South Fly Coast. Five (17%)

interviewees offered several reasons for observed declines, which generally encompassed a list of any commercial activities in the region (e.g. logging, Gulf of Papua Prawn Trawl Fishery, or mining operations).

Table 3. 4 Reasons that interviewees attribute declines in sawfish catch frequency or sizes classes in each region. Increased fishing activity; includes direct reports of overfishing and reports of increased fishing effort due to modern gears replacing traditional gears over time. Change in environment or climate; includes any report related to habitat degradation, such as erosion, sedimentation, increased debris and runoff, increased suspended sediments, and rising sea level. Pollution; mining operation related pollutants. Disturbance; human activities including motorised boats now used to fish and travel, tugboats from logging camps, and oil pipelines. Introduced species; presence of non-native species. Other; reasons which did not fit into any category included responses such as, the fisher used to live elsewhere, fisher now uses a smaller net or less effective gear for sawfish, or referred to sawfish behaviour such as 'they keep to themselves' or stay in deeper water. Number of interviewees that provided an answer in each region are shown in parenthesis (*n*). Some interviewees indicated multiple reasons.

Reasons for decline	**South Fly Coast (*n* = 7)**	**Aramia River (*n* = 3)**	**Bamu River (*n* = 1)**	**Turama River (*n* = 3)**	**Kikori River (*n* = 12)**	**Tiamura River (*n* = 3)**	**Total (*n* = 29)**
None provided	3			1	2		6 (21%)
Increased fishing activity	1	1			7	1	10 (34%)
Change in environment or climate	3		1		1	2	7 (24%)
Pollution	1	1	1				3 (10%)
Disturbance	1		1		2	2	6 (21%)
Introduced species		1			1		2 (7%)
Other	1			2	1		4 (14%)

3.3.5 Contemporary use of sawfish

The main direct uses of sawfish body parts were consumption of meat (92%), sale of meat (50%), sale of fin (50%), decoration in village houses (65%), weapons (15%), and cultural uses (23%) (Figure 3.4). Cultural uses included here are only those presently practised that involve a physical body part from sawfishes including use as ceremonial prop, medicine, or in rituals (for indirect and historical cultural uses see '*Historical use and cultural significance of sawfish*' below). Additionally, one interviewee on the South Fly Coast reported that rostra are occasionally sold to fin buyers, and two interviewees in Kikori River reported that they occasionally make necklaces from rostral teeth. Only one interviewee in the Turama River stated no use of sawfish.

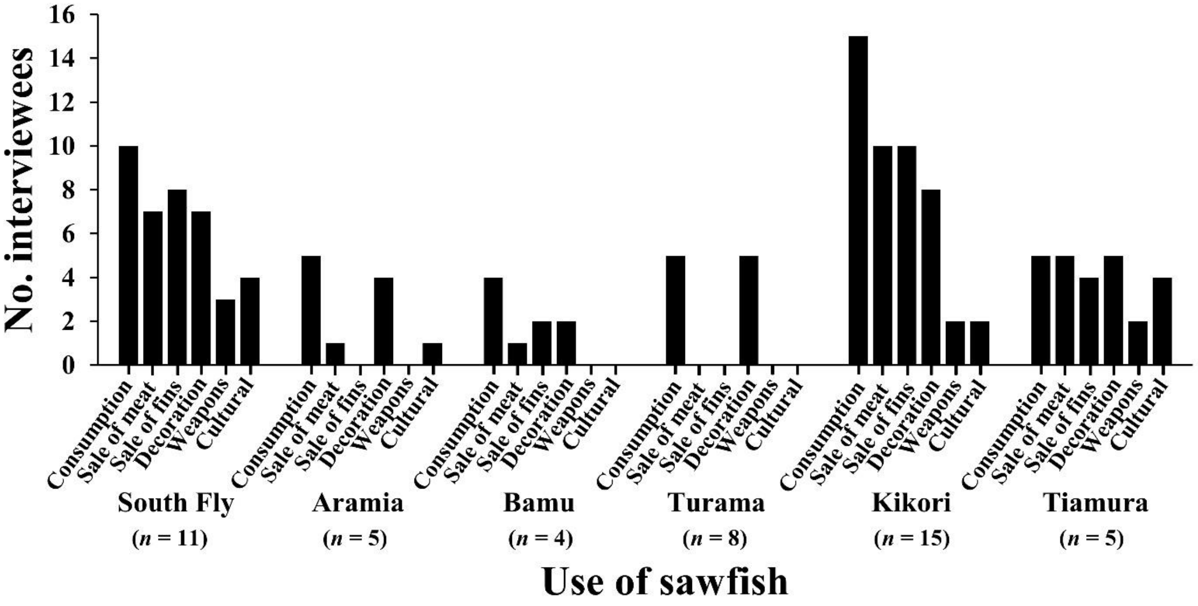


Figure 3. 4 Reported uses of sawfish by interviewees in each region. Number of interviewees who provided an answer in each region are shown in parenthesis (*n*).

Interviewees reported that prices and markets for meat and fin varied across and within regions (Table 3.5). Sawfish meat was mostly sold in local markets (non-commercial) and usually in pieces, rather than whole animals, with price depending on portion size. The only exception was in Kikori River, where the local fish plant (commercial) buys whole sharks (including sawfish and other shark-like rays) at \$3 Papua New Guinean Kina (PGK) kg^{-1} (1 PGK = ~ \$0.28 USD, 04/04/2021), with fins attached. The value of fins usually varied depending on region and reflected shark fin prices in general, rather than sawfish specifically. One interviewee in the South Fly Coast reported that fins from a single sawfish are worth ~$7 PGK, while two interviewees in the Kikori River reported $15–25 PGK per fin, and $60–300 PGK per fin set, respectively for sawfish, although it was not clear if these prices were higher than fin from other sharks of comparable size.

Table 3. 5 Prices of meat and fin and the nature of the market products are sold to in each region. Number of interviewees who provided an answer on meat and fin, respectively, in each region are also included. No interviewees in the Turama River reported sale of meat or fin. PGK, Papua New Guinean Kina (1 PGK = ~$0.28 USD, 04/04/2021).

Region	n	Price of meat (PGK) (unit)	Market	n	Price of fins PGK (unit)	Market
South Fly Coast	5	1–10 (piece)	Local	6	1–70 (kg)	Buyer
Aramia River	1	5 (piece)	Local		Not reported to be sold	
Bamu River	1	15–25 (whole)	Local	1	15–25 (kg)	Buyer, logging camp
Kikori River	12	1–15 (piece), 3 (kg), 60–70 (whole)	Local, Fish plant	8	15–20 (per fin), 60–300 (single set), 400–500 (kg), 3 (kg)	Buyer, Fish plant
Tiamura River	5	1–6 (piece)	Local	1	2 (kg)	Buyer

Overall, most interviewees stated that elasmobranch resources were not an important part of their food (77%) or economic security (77%). Interviewees in the South Fly Coast reported the highest reliance on elasmobranchs as a resource (55% reported important to both food and economic security; 18% important to food security; 9% important to economic security; 18% none). In the Kikori River, 6% of interviewees reported that elasmobranchs are important to both their food and economic security, while in the Tiamura River, 13% reported importance to both; 13% reported importance to food security only; and, 25% reported importance to economic security only. No interviewees explicitly stated that sawfish have a disproportionate price for either their meat or fins, relative to other sharks.

3.3.6 Historical use and cultural significance of sawfish

Sawfish were reported to be used either historically or culturally by 52% of interviewees (inclusive of direct cultural uses in Figure 3.4), with accounts of various stories and rituals involving sawfish either directly or indirectly being reported (Table 3.6). Most cultural stories and rituals about sawfish came from interviewees in Kikori River (which also had the largest sample size), while no historical use or cultural significance of sawfish was reported from the Turama River.

Nine interviewees (from all regions except Bamu River) reported that sawfish rostra were historically used to make weapons or tools, with only one of these reports coming from an interviewee who also reported current use of rostra in weapons from the Tiamura River. Two interviewees in the Tiamura River, and one in each of the Aramia and Kikori River, reported a connotation of sawfish being a totem animal, or representative of a clan, or group of people that identify with it. Four interviewees (three South Fly Coast, one Tiamura River) reported that sharks (including sawfish), are used for medicinal purposes involving the consumption of shark meat broth. One interviewee in the Bamu River reported that shark (including sawfish) cannot be eaten with sago (starch made from palm *Metroxylon* spp.) or cassava or it will 'make them sick', while another interviewee from Bamu River reported sawfish as a traditional food source from the river. In the Kikori River, three interviewees reported that sawfish have a tendency to make babies and young children sick, and that fishers must wash their hands after catching sawfish before touching their children.

3.3.7 Community perspective on sawfish conservation

Across the four regions (Aramia, Bamu, Turama, and Kikori Rivers) where interviewees (n = 32) were additionally asked about their perspective on sawfish conservation efforts, 88% were supportive, 9% were open to the idea, though not outright supportive, while 3% chose not to provide an answer. No interviewees were opposed to the idea of sawfish conservation effort within their region.

Table 3. 6 Cultural stories and rituals involving sawfish in each region. Number of interviewees that provided an answer in each region are shown in parenthesis (*n*). No interviewees in the Turama River reported cultural stories or rituals involving sawfish.

Region	Cultural story or ritual practice
South Fly Coast (*n* = 11)	1. Historically, large sawfish were perceived as monsters, not so much today though. Today they are considered bad luck to catch, as they may disturb other catch in the net. We generally relocate net if caught. 2. Rostral teeth were used in a gardening ritual whereby a small watermelon or pumpkins were poked with a rostral tooth around the base of the fruit to leave a small mark. This was to enrich the fruit. (From a time a few decades prior when the interviewee lived on the Fly River as a boy). 3. Shark (including sawfish) can be boiled and broth drunk when sick (reported by three separate interviewees).
Araima River (*n* = 5)	1. Men crush up sawfish rostra and perform a dance, which allows them to select any girl they like.
Bamu River (*n* = 4)	1. People will not eat sawfish (or shark in general) with sago or cassava as it would make them sick. 2. Valued as a traditional food source from the river.
Kikori River (*n* = 15)	1. The first time a young man catches and kills a sawfish there is a big celebration with dancing and a big feast. Large sawfish (locally called 'Gabora' or 'Gabara') are consumed in the longhouse†, and only men can eat these large sawfish. 2. The sawfish lives in deep parts of the river and travels upstream at night (light connotation of being 'the giant of the river'). 3. If a fisher catches a sawfish while his wife is pregnant or has a small baby, the baby will regard the sawfish as a friend and will not be able to hunt it. If the fisher catches one in his net and has children, after he touches the sawfish, he must wash his hands before he touches children, or they will get sores on their body or be sick. 4. If a man dreams of a sawfish, it is a sign giving him notice that his wife will have a child, so she will follow custom of not eating sawfish. When the baby is born, the father must catch a sawfish and wash the baby with its fat. Following this, the mother can eat sawfish again, and the child will not develop sores or become sick. 5. Historically, they only wore sawfish rostra to dance in ceremony sometimes. Pregnant women and young children were not allowed to eat sawfish or the baby when born, or as young child, would become sick. 6. Sharks and sawfish when called, used to help boats and canoes move faster and quicker through the water. If men needed to go and fight and travel quickly, they would get into one canoe and call on sharks and sawfish to help them move faster.
Tiamura River (*n* = 5)	1. Rostra are used as a prop in ceremony, where they are held when dancing.

	2. Sharks (including sawfish) are boiled with lemongrass and vegetables when sick.

† A longhouse is a large, often elaborately decorated dwelling within a village that females are not permitted to enter. Males would sleep in the longhouse while females slept in smaller family village houses with children. Longhouses were often used as places of ritualistic importance to male culture in PNG. In some regions within PNG, longhouses are still used for these traditional values.

Reasons for why interviewees gave their respective answers about sawfish conservation were grouped into four broad categories encompassing conservation for: i) future generations; ii) cultural resource or food source; iii) environment health or intrinsic value of environment; and, iv) other (Table 3.7). Responses categorized as 'other' included those that did not specifically outline a reason. Some interviewees stated that while they would support conservation, they mentioned that sawfish have very little relevance to everyday life and that they were indifferent as to why sawfish mattered. However, these same interviewees recognized increased values and uses sawfish may have to other people, hence their support, or openness to support. On the Turama River, four interviewees gave reasons that concerned the implementation of conservation effort, largely stating that it would be a collective decision to be made within the village, or among village Councillors throughout the river. While in the Kikori River, two interviewees stated that they are already doing environmental conservation in their local environment. One interviewee in each of the Araima and Turama Rivers stated that they would require a benefit (e.g. financial) to participate in sawfish conservation.

Table 3. 7 Responses on why interviewees would support or be open to supporting conservation of sawfish in their region. Number of interviewees who provided an answer in each region are shown in parenthesis (*n*).

	Aramia River (*n* = 5)	**Bamu River (*n* = 3)**	**Turama River (*n* = 8)**	**Kikori River (*n* = 15)**	**Totals (*n* = 31)**
Future generations	1	0	2	6	9 (29%)
Resource (cultural, food, economic)	2	1	1	4	8 (26%)
Ecosystem health and intrinsic value	1	0	1	8	10 (32%)
Other	2	2	4	3	11 (35%)

3.4 Discussion

3.4.1 Sawfish catch frequency and size classes

This study has provided information to suggest that sawfish are still widely encountered throughout southern PNG, building upon preliminary observations in the Western Province (White et al., 2017a) and Gulf of Papua Prawn Trawl Fishery (White et al., 2019). A wide range of size classes were reported throughout coastal regions, and while species-specific information was not sought from interviewees, these encounters may include any of the four Indo–Pacific species. In all freshwater systems surveyed, interviewees reported only smaller sawfish size classes present, which can be attributed to juvenile *P. pristis* with a reasonable degree of confidence given their ecological life history (e.g. Lear et al., 2019), and as described in Chapter 2. Thus, data obtained in the present study support suggestions of White et al. (2017a) that the South Fly Coast and delta areas of the Gulf of Papua continue to sustain sawfish populations. However, development of domestic legislative protection measures and strategic community driven conservation initiatives are needed to ensure future sustainability of populations.

Differences in sawfish catch frequency and size classes caught were apparent between regions. The highest sawfish catch frequencies came from the Turama River where most interviewees reported weekly capture, while the lowest catch frequencies were reported from the Aramia and Tiamura Rivers. Many factors may potentially influence this variation including habitat availability, site fidelity, the accessibility of habitats to fishers, the spatial extent of fishing (i.e. how far they operate from home), and fishing gear used. For example, in the Turama River two villages only a few kilometres apart reported sawfish catch frequencies of ‘weekly’ and ‘every couple of months’, respectively, which may reflect characteristics of high site fidelity which have been noted for juvenile *P. pristis* (e.g. Whitty et al., 2009; Whitty et al., 2017), *P. clavata* (Stevens et al., 2008; Thorburn et al., 2008), and *P. zijsron* (Morgan et al., 2017).

Large size classes of sawfish were less commonly reported, with interviewees in only the South Fly Coast, Kikori River, and one in the Turama River reporting sawfish of >3 m in their catches. However, it would not necessarily be expected that large sawfish would be encountered by interviewees living in upper freshwater reaches of rivers. Meanwhile, the Tiamura River is a considerably smaller system compared to other regions surveyed, and the relatively clear water bay at the river's mouth is possibly unsuitable habitat for large sawfish, or may be more favoured by *A. cuspidata* or *P. clavata* which are not known to attain sizes > 4m (Last et al., 2016). Interestingly, in some regions large sawfish were not reported even though these rivers appear to be suitable habitat. For instance, the Bamu River is a large high-flow turbid system with a significant delta at its mouth, and fishers use similar gillnets to those observed in the South Fly Coast, and Turama, and Kikori Rivers where large size classes were reported. Thus, it is unclear why large size classes were not reported here by the four experienced fishers surveyed. Furthermore, no interviewees in the Bamu River noted ever seeing a sawfish >4 m. The highest instances of interviewees reporting to have caught or seen a sawfish >4 m came from the South Fly Coast and Kikori River. The Fly River has at least historically supported a rich *P. pristis* population (White et al., 2017a), and it is likely that large sawfish encountered by South Fly Coast interviewees included *P. pristis* associated with the Fly River, possibly following its southern outflow. In addition, *P. zijsron*, which can attain sizes up to 7 m occurs along the South Fly Coast also (White et al., 2017a), although this species does not appear to associate as commonly with low salinity waters. Meanwhile, the Kikori-Purari Delta system forms an enormous expanse of estuarine mangrove habitat, and reports of large sawfish from Kikori River can likely be attributed to both ideal habitat and large portions of the delta having not been historically accessible to fishing.

3.4.2 Sawfish population trends

While the widely reported occurrence of sawfish throughout southern PNG and its rivers is a positive indication for the species' conservation potential, it was also clear that declines have occurred in all regions except possibly the Turama River, with 80% of interviewees in other regions reporting declines in either catch frequency and/or size classes. Comparatively, only 20% of interviewees reported declines in other ‘sharks’ (all species as a general grouping) which may indicate disproportionate declines in sawfish. There is a wide diversity of sharks in PNG (White et al., 2018) and differences in resilience between shark species (Cortés, 2002) may mask species-specific declines within this broader ‘shark’ grouping.

The scale and timing of sawfish declines is difficult to gauge due to a lack of historic baselines in most areas. Therefore, it is hard to distinguish whether the ‘shifting baseline syndrome’ (Pauly, 1995) is apparent with some interviewees. Quantitative evidence of declines in sawfish in southern PNG is limited to the Fly River where substantial declines have occurred since the 1970–80s, likely due to a combination of fisheries pressure and pollution associated with the Ok Tedi copper mine (Burton, 1995; Storey et al., 2009). Sawfish have been noted historically on the South Fly Coast from the Oriomo River and Daru Island within the range of the present study (Tanaka, 1991). While further westward to the Indonesian border, *P. clavata* were ‘common’ in the Morehead and Bensback Rivers during the 1970s, and *P. pristis* was also noted (White et al., 2017a). Most South Fly Coast interviewees in the present study reported either declines in catch frequency or size classes, though none reported declines in both. Most interviewees residing around Daru and east to the Fly River reported that sawfish can still be caught on offshore rocky reefs. While it was apparent that sawfish are not commonly caught in gillnets set along the beach; improved access to motorized vessels (see ‘*Shifting trends in the small-scale fishery’* below) mean that fishers now have greater access to offshore fishing grounds, including the northern Torres Strait (Busilacchi et al., 2014). The lack of sawfish declines reported on the South Fly Coast in this study could therefore reflect continued expansion of fishing effort into areas that historically were not accessible to fishers, and where sawfish may have persisted.

Surveys of the Purari Delta (eastern part of Kikori-Purari Delta) in the 1970–80s indicate that sawfish were common (Haines, 1977; Haines, 1979). During this period, Haines (1978/79) reported that while gillnets could be observed in villages, traditional gears (e.g. spears, traps, bow and arrow) were often used in their place. Therefore, significant sawfish catch may not have been occurring at this time. In the present study gillnets were the primary, and often the only fishing gear used by interviewees throughout the Kikori River Delta. Interviewees in Kikori River reported the highest sawfish declines, with more than half reporting declines in both sawfish catch frequency and size classes. Many interviewees (some as young as ~40 years old) recalled seeing 'plenty' of sawfish in the sandbanks in front of their villages during the evenings as little as 15–20 years ago. It is possible that sawfish declines in the Kikori River have been more recent than declines in other survey areas, and thus less of a 'shifting baseline syndrome' has occurred. Most interviewees in the Kikori River attributed declines to overfishing, with many remarking on the amount of nets in the water 'today'.

There is very little historical literature of sawfish in the Aramia, Bamu, Turama, and Tiamura Rivers (White et al., 2017a), therefore data from the present survey can offer insight into historical baselines. Little change in sawfish populations were reported by interviewees in the Turama River, suggesting that only minor declines (if any) have occurred in this system. Juvenile *P. pristis* are still reported to occur in freshwater pools upstream of the Tiamura River, while larger sawfish appear to have declined around the river mouth. Some interviewees suggested that the absence of large size classes is possibly due to the Gulf of Papua Prawn Trawl Fishery, which typically has the highest concentration of effort in the north-east Gulf of Papua and is known to capture *A. cuspidata* and *P. pristis* incidentally (White et al., 2019). Within the Aramia and Bamu River basin, sawfish (almost certainly *P. pristis*) were reported to be more common downstream in the Aramia River at its junction with the Bamu River, compared to the floodplain environment upstream. Interviewees in this upstream environment reported that sawfish were once common, although now they are seldom caught once per year. However, this may reflect population declines in the Fly River Basin (Storey et al., 2009), as interviewees reported wet season connectivity with the Fly River basin (through both Fly and Strickland River floodplains), and that sawfish migrate into the Aramia River floodplain from these systems.

3.4.3 Uses of sawfish by small-scale fishing communities

The main reason for retaining sawfish catch across regions was consumption (92%) followed by sale of meat (50%) or fin (50%). While 65% of interviewees reported use of sawfish rostra for decoration, this was a secondary use, with no interviewees reporting sawfish capture for this purpose alone. Similarly, use of rostra or rostral teeth in weapons was never explicitly mentioned as a reason for retaining sawfish. The higher instance of consumption compared to sale of sawfish products was due to three main reasons: i) interviewees had limited access to markets to sell products (i.e. Aramaia, Bamu, and Turama Rivers); ii) interviewees reported a tendency to consume elasmobranchs and sell teleost fish, as fish meat is considered easier to sell and more valuable; and, iii) elasmobranchs are not frequently caught limiting marketability (mainly freshwater environments). These reasons also contributed to the high number of interviewees reporting that elasmobranchs were not important to their food security, and that they are consumed secondarily to fish. Interviewees who sold meat or fin from elasmobranchs and did not consider it important to their economic security, usually stated similar reasons and that opportunistic sale complimented their primary income. Secondary uses of incidentally captured sawfish have also been noted in South America for rostra (McDavitt and Charvet-Almeida, 2004), and likely represents the opportunistic use of resources by local fishers in developing nations.

PNG is a signatory to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In coastal regions from South Fly Coast to Kikori River, interviewees mentioned buyers travelling from Indonesia to purchase shark fin (‘shark fin’ refers to any species, inclusive of sawfish) and swim bladder. Illegal trade routes stemming from Merauke, Indonesia, into the South Fly Coast were noted by Busilacchi et al. (2021), and the present study indicates that this network extends east to at least Kikori River Delta. PNG-based buyers (presumably licensed) travelling from Port Moresby were also mentioned by interviewees from Kikori River to Tiamura River. Additionally, sale of shark fin to licensed buyers in Daru and Kikori Town was reported by interviewees in the South Fly Coast and Kikori River, respectively. The issue for PNG's national fisheries and conservation authorities is that Indonesian-based buyers purchasing sawfish fin (within 'shark fin') from PNG's small-scale fishers contravenes the CITES Appendix I listing of sawfishes. Furthermore, the subsequent market chains for trade of shark fin by licensed PNG-based buyers appears to result in export to three central nodes in Asia (Hong Kong, Singapore, and Kuala Lumpur, Busilacchi et al., 2021). Therefore, PNG has a responsibility to the international community to enforce CITES trade restricted species within its export markets, and this study indicates a need for greater enforcement capacity.

From the few interviewees that felt comfortable discussing sale of shark fin, it was mentioned that sale to PNG-based buyers (those from Port Moresby, Daru, and Kikori Town) fetch significantly lower prices compared to non-licensed buyers. Interviewees who gave a larger range in prices they may expect for shark fin were likely those who sold to non-licensed buyers as their responses did not reflect fixed rates for shark fin, such as those offered at Kikori Fish Plant (\$3 PGK kg^{-1} of whole animal weight). Prices of shark fin reported were generally significantly less than prices given by Leeney et al. (2018) of \$100–350 PGK kg^{-1} in northern PNG, and interviewees did not mention any 'grades of fin quality', or variability in price for particular species. This suggests an overall less structured shark fin market in PNG's south, probably due to high market infiltration of non-licensed buyers. Unfortunately, the questionnaire used did not specifically address attitudes or incentives driving an interviewees participation in either legal or illegal shark fin markets, but this would have required specialised survey techniques that are beyond the scope of the present study. On the South Fly Coast, Busilacchi et al. (2021) found that engagement with illegal markets (including sale of shark fin) was driven mainly by: i) a need to improve living standard; ii) they are the only markets available; and, iii) non-licenced buyers provide additional goods (e.g. flour, rice, and batteries). It is unclear if these drivers are also present in regions other than the South Fly Coast, and this remains an important area for future research. For example, fishers in Kikori River consistently indicated that much higher shark fin prices were offered by non-licensed buyers compared to Kikori Fish Plant, while Busilacchi et al. (2021) found that higher prices were offered by licensed PNG-based buyers on the South Fly Coast. This is likely due to a lack of commercial competition in the Kikori River (currently monopolised by the Kikori Fish Plant), whereas multiple licensed buyers exist in Daru, and they may compete for supply from local fishers on the South Fly Coast. Further information on social and economic aspects of the shark fin trade in the wider Gulf of Papua would complement information provided by Busilacchi et al. (2021) for the South Fly Coast, and ultimately be useful to inform more strategic management approaches within PNG's shark fin trade markets. A more transparent shark fin trade in PNG would assist in enforcement of CITES restricted species may and help to disincentivise retention and sale of sawfish parts, ultimately helping to facilitate conservation of sawfishes in PNG.

3.4.4 Cultural significance of sawfishes

Sawfish specifically, were generally not prominent within culture across regions visited in the present study, with the exception of the Kikori River. Many cultural stories, particularly medicinal or food source related, referenced sharks in general and were inclusive of sawfishes rather than specific to sawfishes. There was no mention of sawfish art for example, which differs from Sepik River communities who possibly share more cultural connections specifically with sawfish (McDavitt, 2014; White et al., 2017a). Regardless, this study suggests that sawfish do have importance to at least some communities in all regions except Turama River, and this should be considered and integrated in the formulation of both community-based and legislative conservation initiatives of sawfish in southern PNG.

Aspects of the interview approach may have limited the sharing of cultural information. It is likely that intimate aspects of culture were not shared by interviewees in some cases due to the short nature of many of the village visits. Surveys in the Turama and Aramia Rivers appeared to be a very novel experience for communities, and for this reason, it is likely that the interviewees in these regions shared a reluctance to divulge aspects of their culture. This contrasted with the Kikori River where communities have a longstanding relationship with the Piku Biodiversity Network, and regular contact with researchers. Sawfish appeared to have the highest cultural value in the Kikori River, but these limiting factors mean that interpretations of the cultural significance of sawfish to communities from this study should be considered with caution, and may only reflect a superficial account of cultural values and connections.

3.4.5 Shifting trends in the small-scale fishery

Gillnets were the primary fishing gear used by interviewees across all regions surveyed. Only one interviewee in the headwaters of the Tiamura River reported a traditional gear (spear) as their main fishing method. All other interviewees reported that they now use either gillnet (92%), hook and line (4%), or basket and drag nets (2%) predominantly, or a combination of these gears. A shift to ‘westernised’ fishing techniques has previously been noted in PNG’s better studied Island Provinces and northern coast (Quinn, 2011; Leeney et al., 2018) and is largely attributed to the time-consuming nature of constructing traditional gears, when nylon-based nets are now relatively cheap, effective, and easily repairable or replaceable. Within our study regions, gillnets were noted to be readily available in general stores, and these nets were routinely observed set along rivers or within delta areas in all regions visited.

Throughout southern PNG, fishing effort is becoming increasingly sophisticated and focused on high value products (mainly swim bladder also known as fish maw, from *L. calcarifer* and *N. squamosa*, and to a lesser extent shark fin), while management or monitoring of fisheries remains scarce to non-existent. Large mesh-size gillnets were most common along the South Fly Coast and delta environments of Kikori River. In both of these regions commercial fish buyers are present (Daru and Kikori Town, respectively) and fishers reportedly lease high quality gillnets (and even fiberglass boats and outboard engines) from these buyers under the arrangement that high value fish and fish products are sold back to the leaser. This practice has historically occurred in the Kikori-Purari Delta through commercial fish buyers, defined as ‘village level commercial fishing’, as opposed to ‘subsistence fishing’ where catch is only consumed or sold in local markets (Haines and Stevens, 1983). In the South Fly Coast, village level commercial fishing falls under the Western Provinces Barramundi Management Plan (NFA, 2003). Between village level commercial fisheries in the South Fly Coast and Kikori River, there is no management of allowable fishing effort and there is no management of non-target species (mainly elasmobranchs), which are either consumed, sold locally at Daru or Kikori Town market, respectively, or are traded with non-licensed buyers (shark fin only). Management initiatives around the Kikori Fish Plant (within Gulf Province) remain less clear than for commercial fish buyers in Daru, and it is not presently understood if there are particular target species that Kikori Fish Plant is licensed to buy from local fishers (although a clear preference for *L. calcarifer*, *N. squamosa* and *P. macrochir* was noted) or if any restrictions are in place on total allowable catch. Presently, Kikori Fish Plant purchases sawfish from small-scale fishers at \$3 PGK kg^{-1} (with fins attached). This is concerning as any economic incentive to retain sawfishes would likely undermine future conservation efforts.

3.4.6 Considerations for the conservation of sawfish

Presently, small-scale fishers throughout southern PNG sell sawfish parts (i.e. fin) to domestic and international buyers. Given their CITES Appendix I listing, greater enforcement from PNG to cease international trade (either directly to Indonesian-based buyers, or in subsequent market chains for licensed PNG-based buyers) will result in less economic opportunity for small-scale fishers. While it is hard to determine what the effects of this will be for small-scale fisher communities, most interviewees in the present study stated they have little economic reliance on the sale of elasmobranchs (including fin). The exception was South Fly Coast where many interviewees stated that elasmobranchs were important to their economic security, as also noted in previous studies (e.g. Busilacchi et al., 2014; Busilacchi et al., 2021). Given the low catch rate of sawfish, coupled with an absence of responses indicating that sawfish fins have a disproportionately higher value relative to other elasmobranchs, it is unlikely that eradication of sawfish trade in PNG would have a substantial long-term economic effect on small-scale fishers. National fisheries and conservation authorities in PNG need to consider the nation's role as a CITES signatory and seek to ensure that efforts are made to cease international trade of sawfish.

At the community level, engagement and awareness will still be needed to manifest any conservation actions reflective of legislation or greater international trade enforcement from national authorities. Congruently, receptiveness by interviewees to supporting the conservation for sawfish was overwhelmingly positive. Although, responses as to why interviewees were receptive, and the reasons why they valued sawfish, revealed the complexity of considerations needed in both the formulation and implementation of any conservation initiative. Broadly speaking, the local perspective of sawfish differs to that of the wider 'global conservation community'. Sawfish were mainly perceived by interviewees as a traditional food source, rather than an animal of intrinsic biodiversity value, as perceived by global conservationists. These differences in global and local values towards sawfish can result in poor community engagement and participation in conservation initiatives that are formulated from a global conservationist perspective (e.g. Foale and Manele, 2004). A further consideration is that interviewees in some communities expressed the view that any conservation initiative toward sawfish would be a decision to be made within the village, or among local village Councillors, or that conservation was already being practised locally. This suggests that a lack of receptiveness to 'outside' conservation initiatives may be encountered in some areas throughout southern PNG. Any prospective conservation initiatives must consider the complex 'customary management' framework within PNG's small-scale fisheries, which is governed by traditional land and waterway ownership rights held by family groups, or clans and tribes (Cinner and Aswani, 2007). Working with Traditional Owners in the development of conservation initiatives will be important to achieving engagement and participation from the broader community.

Development of effective community engagement for sawfish conservation initiatives can draw upon experiences of the threatened pig-nose turtle (*Carettochelys insculpta*) in the Kikori River. *Carettochelys insculpta* conservation initiatives recognise that while complete elimination of harvest is unlikely, a more 'sustainable fishery' type approach can be taken so that communities target specific life stages while managing the volume and areas harvested (Eisemberg et al., 2011; Eisemberg et al., 2015). The perception of sawfish being primarily valued as a food source aligns closely with local perceptions of *C. insculpta* and formulation of sawfish conservation initiatives should follow a similar fishery approach, although there is a subtle difference to consider. Within local perceptions of these food sources, *C. insculpta* is valued as a traditionally important species for consumption and trade, and is actively targeted by locals through cultural harvest activities on a seasonal basis (e.g. harvest of nesting females and eggs in the dry season) (Eisemberg et al., 2011). Sawfish differ in this regard as they do not appear to be actively targeted, but rather are incidentally caught while fishers target more favoured or economically valued teleost species. This is reflected by the high proportion of interviewees stating that sawfish are not important to their food or economic security, and that many interviewees prefer to consume and sell more palatable teleost species when concurrently caught with sawfish. Conversely, a high proportion of interviewees also cited the value of sawfish as a food item or as a resource for future generations when questioned as to why they were supportive toward sawfish conservation. While it appears sawfish are more often consumed opportunistically rather than relied upon, they still have value as a traditional, albeit irregular food source, to those communities that do consume them. However, the prominent issue for sawfish was the tendency for interviewees to kill or amputate rostra from entangled sawfish, regardless of any intended or required use (e.g. Turama River fishers who do not consume sawfish but kill to untangle them). While sawfish consumption and trade may be low, fisheries-imposed mortality of captured individuals is high. Therefore, while it is unlikely that complete elimination of sawfish consumption throughout southern PNG could be achieved, conservation initiatives aiming to minimize retention for non-essential consumption and trade, coupled with awareness and education for better sawfish release practices, may have potential.

The issue of killing or amputating rostra from sawfish was mentioned by interviewees to be primarily for preservation of fishing gear and fisher safety. Available evidence of sawfish with amputated rostra suggests they have an impeded ability to forage, and that it likely results in eventual death (Morgan et al., 2016). Release guides for sawfish in gillnets are widely available, although they are generally orientated to western fisheries with high technical capacity and may recommend inflicting damage to the gillnet on the premise that repair tools and spare mono-filament line is readily available (e.g. NOAA safe release guide https://www.fisheries.noaa.gov/resource/educational-materials/endangered-sawfish-handling-release-and-reporting-procedures). For small-scale fishers in southern PNG, a gillnet may represent a significant investment, or a leased asset requiring payments to local commercial fish buyers. Therefore, it is unlikely that fishers would, or should be expected to, damage their fishing gear for the safe release of an individual sawfish. Furthermore, resource materials to repair gillnets are seldom available in fishing camps. However, this mainly applies to capture of large sizes >150 cm, as juvenile sawfish can generally be restrained by hand and untangled from nets with appropriate technique (e.g. QLD DAF safe release guide https://www.daf.qld.gov.au/__data/assets/pdf_file/0005/49109/Sawfish-Guide-Final-Nov-2010.pdf).

There is potential to engage with freshwater communities about better sawfish release practices in particular, as only small size classes were reported from these environments. Development of a sawfish safe release guide appropriate to local fishing methods and gear in PNG would likely be more favourably received than the presently available guides intended for more affluent high capacity commercial fisheries in other nations. The safe release of larger sawfish sizes from gillnets in coastal regions is more challenging, and concerns minimizing gear damage as well as injury to the fisher(s). Engaging with local fishers to find feasible solutions to encourage live and unharmed release of sawfish should be considered in future work as this will maximise local participation. Education and awareness materials outlining sawfish status and importance to some local cultures may help increase broader community engagement and participation in sawfish conservation, and these materials could effectively be distributed through local schools and markets where people from different communities regularly transit.

3.5 Conclusion

While southern PNG sustains extant sawfish populations, a considerable amount of work is needed to secure the conservation of sawfishes. Future actions should consider a combination of legislative fisheries management that includes threatened non-target species and greater enforcement of international trade obligations (i.e. Appendix I CITES listing), coupled with community-driven conservation initiatives that minimize unnecessary fisheries mortality. The present survey has indicated that a shift from traditional fishing gears to gillnets over recent decades has likely resulted in declines of sawfish throughout southern PNG. Historical collapses of sawfish due to net-based fishing activities in other nations (e.g. Giglio et al., 2016), indicate that the present unregulated use of gillnets in small-scale fisheries, coupled with the current practice of killing or amputating rostra from entangled animals, is the most immediate threat to PNG's sawfish.

This study has indicated that conservation initiatives for sawfish will need to carefully consider their use by local fishers. Further research and community engagement should focus on social aspects of cultural appropriateness of various conservation initiatives (e.g. development of safe release guides and de-incentivising sale of sawfish products in local and commercial markets) that could achieve high levels of engagement and participation across a range of communities. Additionally, further research on small-scale fisheries in southern PNG that could help further inform conservation include: i) quantifying elasmobranch catch in village level commercial fishing operations and their uses and values as a resource; ii) sustainability assessment of species that support high value fish products (primarily swim bladder, but also shark fin) currently driving small-scale fishing effort in southern PNG; iii) more detailed study on the livelihoods of small-scale fishers throughout southern PNG to complement existing information on the South Fly Coast (e.g. Busilacchi et al., 2021), and their reliance on fisheries with respect to alternative livelihood options; iv) building a greater understanding of the traditional fisheries management structure through mapping traditionally owned land and waterway boundaries held by different clan and tribe groups; and, v) improved capacity building for local, provincial, and national government and non-government institutions and organisations to assist in monitoring and enforcement. Collectively, this information will help guide more strategic and culturally appropriate conservation effort for sawfishes.

Chapter 4

Papua New Guinea: a potential refuge for threatened Indo–Pacific river sharks and sawfishes

4.1 Introduction

Across the Indo–Pacific there is mounting concern about conservation status of elasmobranchs (sharks and rays) (White and Kyne, 2010). The major threats of fishing pressure and habitat degradation are generally concentrated in riverine and inshore environments (Compagno and Cook, 1995). Consequently, elasmobranchs that require access to shallow coastal or riverine environments during their life history have been most affected (Chapter 2; Dulvy et al., 2014). Elasmobranchs generally have slow population growth rates resulting in high vulnerability to anthropogenic pressures, and protracted population recovery times (Cortés, 2000). Conservation of elasmobranch species within riverine and inshore environments of the Indo–Pacific is extremely challenging. Most tropical nations are considered ‘developing’ and are characterized by having high human population density, low economic stability, and often high reliance on aquatic resources (Cheung and Sumaila, 2008). Elasmobranchs have become important to the livelihoods of an increasing amount of people for food security (e.g. Vieira et al., 2017) or sale to Asian markets (Blaber et al., 2009). Furthermore, artisanal and subsistence fisheries (hereafter ‘small-scale fisheries’) dominate developing Indo–Pacific nations. Data on these small-scale fisheries are often lacking due to limited capacity and resources for assessment and monitoring (e.g. catch composition, catch trends, biological characteristics, human livelihood dependence) (Ban et al., 2009; White and Kyne, 2010). These factors create challenging social and cultural considerations for developing sustainable elasmobranch fishing practices in Indo–Pacific nations (White and Kyne, 2010; Booth et al., 2019).

The three Indo–Pacific river shark (genus *Glyphis*) and four sawfish (family Pristidae) species epitomize the extinction risk of elasmobranchs in this region. The Ganges River shark *Glyphis gangeticus*, northern river shark *Glyphis garricki*, green saw fish *Pristis zijsron*, and the largetooth sawfish *Pristis pristis*, are listed as Critically Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (hereafter 'IUCN Red List'), while the speartooth shark *Glyphis glyphis*, dwarf sawfish *Pristis clavata*, and narrow sawfish *Anoxypristis cuspidata*, are listed as Endangered (IUCN 2021). A large factor in the high extinction risk for river sharks and sawfishes are their life history strategies which compound their exposure to anthropogenic pressures (i.e. fisheries and habitat degradation) in both non-marine (freshwater and estuarine environments) and marine environments (Chapter 2).

It is well documented that all sawfish species have experienced dramatic global declines and local extinctions within their historic Indo–Pacific distributions (Dulvy et al., 2016; Yan et al., 2021). In contrast, taxonomic issues and a lack of historic records preclude a clear understanding of the historical distribution of river shark species (Li et al., 2015). Northern Australia is presently the only nation where viable populations of *G. garricki* (Feutry et al., 2020), *G. glyphis* (Feutry et al., 2017), and four Indo–Pacific sawfish species (e.g. Peverell, 2005; Morgan et al., 2011) are known to occur. Elsewhere in the Indo–Pacific, distributions of river shark and sawfish species are generally fragmented (e.g. Elhassan, 2018), and reported encounters are infrequent (White et al., 2015; Jabado et al., 2018). However, many Indo–Pacific regions are poorly studied, and there is a need for further investigation into the status of river sharks and sawfishes in these areas. This information would facilitate the implementation of conservation actions at appropriate local and regional scales, helping to alleviate extinction risk of these species.

One nation that has recently emerged as a potential refuge for Indo–Pacific river shark and sawfish species is Papua New Guinea (PNG). A brief survey in PNG's Western Province during 2014 resulted in the scientific rediscovery of both *G. garricki* and *G. glyphis* outside of Australia (White et al., 2015). All four Indo–Pacific sawfish species were also observed in this survey (White et al., 2017a), while *A. cuspidata* and *P. pristis* were also later observed in the Gulf of Papua Prawn Trawl Fishery (White et al., 2019). Historically, sawfishes have been observed widely throughout PNG (White et al., 2017a) and these recent observations indicate the contemporary presence of all species. Surveys exploring local knowledge of sawfishes in PNG's north (Leeney et al., 2018) and south (Chapter 3) coasts further substantiate their contemporary presence in small-scale fisheries, although both studies reported declining catch frequency by local fishers. This indicates that conservation initiatives may be required in PNG to prevent similar trends of regional extinction as seen in other Indo–Pacific nations (Dulvy et al., 2016).

Further information is required to assess the viability and conservation potential of river shark and sawfish populations in PNG. While aforementioned studies have provided some preliminary information, conservation assessments and planning are impeded by a lack of data on: 1) contemporary species-specific distributions; and 2) catch frequency and exploitation level by small-scale fishers. There are presently no protection measures in place for river shark or sawfish species in PNG. This raises concern as small-scale fisheries are prominent throughout PNG's coastal and riverine environments (Chapter 3; Leeney et al., 2018), and the level of threat they pose is presently not well understood for most regions where river sharks and sawfishes likely occur (White et al., 2015; White et al., 2017a).

This study surveyed small-scale fishing villages throughout riverine and coastal communities in the Western, Gulf, and East Sepik Provinces, to observe elasmobranch catch within small-scale fisheries. Information gathered aims to: 1) assess the present level of threat posed by small-scale fishers; 2) provide information to inform the development of conservation initiatives for river sharks and sawfishes in PNG; and, 3) ultimately determine whether PNG has potential to provide a long-term refuge for these species within an Indo–Pacific context.

4.2 Methods

Surveys of elasmobranch catches were conducted in riverine and coastal areas on the mainland of PNG from 2017–2020. Survey locations were selected based upon historical and contemporary records of river sharks and sawfishes (White et al., 2015; White et al., 2017a) (Figure 4.1). Working closely with the National Fisheries Authority, Provincial Fisheries Authorities, University of Papua New Guinea, and the Piku Biodiversity Network, surveys consisted of visiting village communities and fishing camps in coastal, estuarine, and freshwater environments (Table 4.1). Surveys coincided with the onset of the dry season when most fishing activity occurs (~September to March), due to safer fishing conditions afforded by calmer whether. Fishers in regions surveyed primarily use gillnets of varied mesh sizes to target croakers (Sciaenidae), barramundi (*Lates calcarifer*), and elasmobranchs (see Chapter 3; Leeney et al., 2018). With consent from village leaders, local fishermen were invited to present any elasmobranch catch, sawfish rostra, or shark fin. Two or three villages or fishing camps were typically visited each day. In some instances, a camp was set up in villages to observe catch over a period of up to 5 days.

4.2.1 Data collection

For each whole animal encountered, stretched total length (TL) was recorded for all sharks and shark-like-rays (i.e. guitarfishes, sawfishes, and wedgefishes) and disc width (DW) was recorded for other rays. Maturity was determined by inspection of clasper calcification in males, and uteri and ovaries (presence and size of ova) in females (e.g. White et al., 2001). In most instances it was not possible to dissect specimens to determine maturity status from inspection of internal organs as catch often had to be transported to market, was on sale at market, or was quickly portioned and consumed. For small specimens, the presence of an umbilical scar (indicating recent birth) was also noted. For all specimens, gear type used in their capture was recorded and mesh size (inches) for gillnets used was noted when possible (Appendix 2; Tables A2. 7, A2. 8). When possible, tissue samples were taken from specimens for species verification using genetic analysis.

Table 4. 1 Dates, locations, and in-country partners that assisted on each survey trip.

Field trip dates	**Location**	**In-country facilitating organisation**
11–28 Sep 2017	Sepik River	National Fisheries Authority; University of Papua New Guinea
23 Nov–10 Dec 2017	South Fly Coast	Western Provincial Fisheries; University of Papua New Guinea
13–18 Dec 2017	Kerema Coast	Gulf Provincial Fisheries; University of Papua New Guinea
14–22 May 2018	South Fly Coast	Western Provincial Fisheries
23–28 May 2018	Kerema Coast	Gulf Provincial Fisheries
19 Oct–9 Dec 2018	Turama, Aramia, and Bamu Rivers	Piku Biodiversity Network
1 Oct–6 Nov 2019	Kikori River	Piku Biodiversity Network

When dried fins were encountered (sharks and shark-like-rays), the first dorsal fin (D1) from each individual present was identified and photographed. Measurements taken for D1 included, length, height, and anterior margin length (Appleyard et al., 2018). Data collected from sawfish rostra included: photographs, rostral teeth counts (left/right), total rostrum length, and standard rostrum length (these rostrum length measurements followed those described in Whitty et al., 2014). It was also noted when possible what gear type was used, and an approximate date (usually given as month/year) of capture.

In addition to our surveys, cameras and basic data sheets were left with self-nominated fishers at various locations so they could enumerate shark and ray landings (hereafter referred to as 'enumerators') (Table 4.2). These enumerators were asked to take photographs and record date of capture, TL (sharks and shark-like-rays), DW (other rays), sex, fishing gear used, and any other information that may be of interest (e.g. presence of embryos, litter size) for sharks and rays captured during their fishing activities. It was carefully communicated to enumerators to record catch during their routine fishing operations and not to target any specific species (i.e. river sharks or sawfishes).

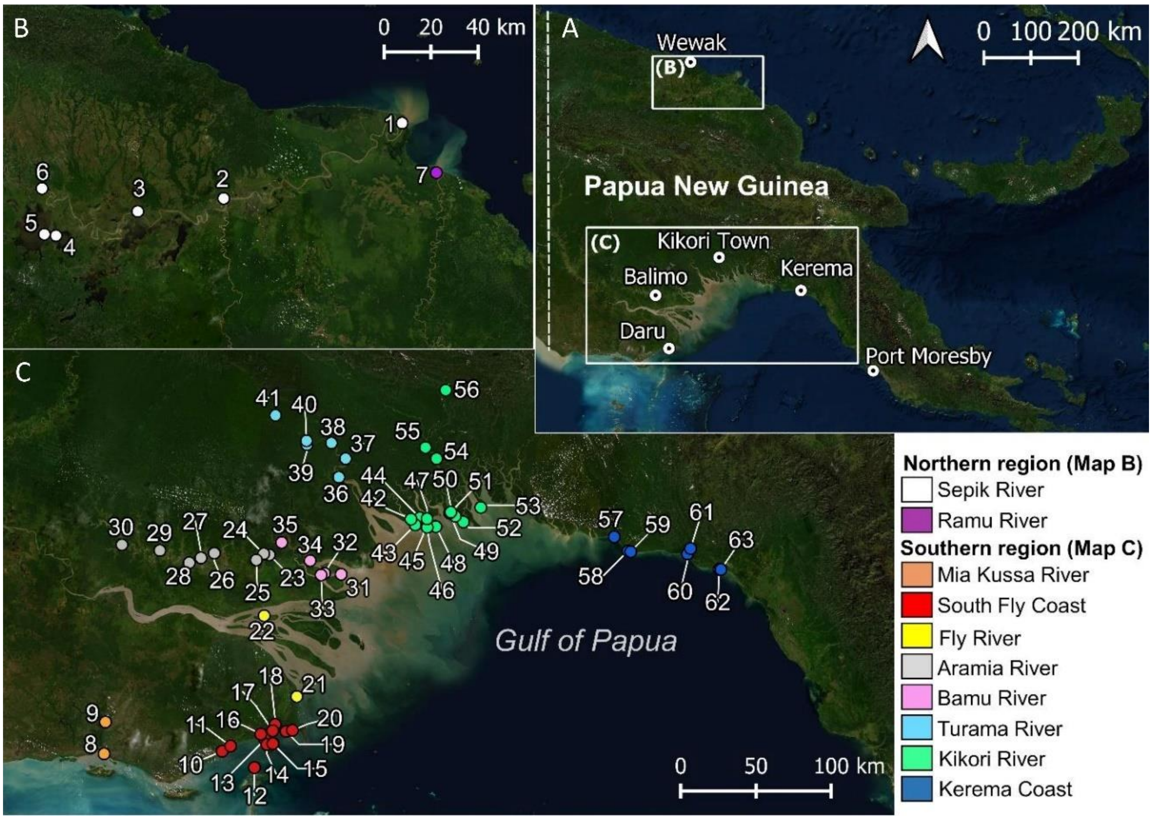


Figure 4. 1 Locations where elasmobranchs (including fins and sawfish rostra) were encountered during surveys. (A) Papua New Guinea mainland, showing major trading centres for regions surveyed; (B) northern region surveyed; and, (C) southern region surveyed. Village names corresponding to each location in (B) and (C) are provided in Appendix 2 (Table A2. 1).

4.2.2 Data analysis

For specimens where tissue could not be taken for genetic species identification (ID) (mainly enumerator observations and sawfish rostra), species were identified using photographs taken at the time of observation (see Appendix 2, '*Species identification*').

Table 4. 2 Location of enumerators and the time period when they collected data on elasmobranch landings.

Province	Region	Village [Figure 4.1 map reference]	Period of enumeration
Northern region			
East Sepik	Sepik River	Kopar Village [1]	Oct-Nov 2017
Southern region			
Western	Mia Kussa River	Buzi Village [8]	March-Apr 2018
Western	Mia Kussa River	Sibidiri Village [9]	Dec 2017-Apr 2018
Western	South Fly Coast	Katatai Village [19]	July-Dec 2017
Western	Fly River	Nemadabu fishing camp [22]	Jan-May 2018
Gulf	Kikori River	Goare Village [46]	Dec 2018, Oct 2019 – Jan 2020
Gulf	Kerema Coast	Marieke Village [57]	Mar 2018

Location data for all species encountered were pooled into two regions, 'northern' and 'southern' (Figure 4.1). Due to low sample sizes of maturity observations, maturity was assigned where appropriate using length-at-maturity estimations given by White et al. (2017b). Length measurements taken of sawfish rostra and dried fin (all sharks and shark-like-rays) were used to estimate TL from available relationships (Appendix 2; Tables A2. 2, A2. 3, A2. 4).

4.3 Results

4.3.1 Species composition

A total of 783 elasmobranchs were observed during surveys and by enumerators across locations visited (Figure 4.1). Observations included 552 (70.5%) whole animals, 117 sawfish rostra (15.0%), 101 dried fins (each from a separate individual) (12.9%), 12 heads (1.5%), and one ray tail (0.1%).

In the northern region, 176 individuals were observed comprising the families Carcharhinidae (57.4%), Sphyrnidae (25.5%), Pristidae (14.8%), Glaucostegidae (1.1%), Aetobatidae (0.6%), and Rhinidae (0.6%) (Appendix 2; Table A2. 7). In the southern region, 607 individuals were observed comprising the families Carcharhinidae (56.7%), Pristidae (20.3%), Sphyrnidae (11.2%), Dasyatidae (7.4%), Rhinidae (1.6%), Glaucostegidae (1.5%), Hemiscylliidae (0.5%), Aetobatidae (0.3%), Hemigaleidae (0.3%), and Orectolobidae (0.2%). Most observations in the northern (67.6%) and southern (83.4%) regions were immature size classes (Appendix 2; Table A2. 8).

Threatened species comprised a large proportion of the observed catch. In the northern and southern regions, 44.3% (eight species) and 70.7% (16 species) of observations, respectively, were from species assessed as threatened with extinction on the IUCN Red List (Critically Endangered, Endangered, or Vulnerable) (Figure 4.2). In the northern region, *Anoxypristis cuspidata* (7.4%) and *P. pristis* (7.4%) accounted for 14.8% of observations, while no river sharks were recorded. In the southern region, *Glyphis garricki* (23.1%), *G. glyphis* (6.3%), and two *Glyphis* sp. (0.3%) accounted for 29.7% of observations, with *G. garricki* being the most encountered species overall (*n* = 140). Additionally, all four Indo–Pacific sawfishes were observed in the southern region, where *A. cuspidata* (8.6%), *Pristis clavata* (1.5%), *Pristis pristis* (9.9%), *Pristis zijsron* (0.2%), and one Pristidae sp. (0.2%) accounted for 20.5% of observations. Collectively, river sharks and sawfishes accounted for over half of observations (50.2%) in the southern region. However, it should be noted that sawfish rostra were more likely to be observed as they have a bias for being kept longer than shark fin or meat, as they are mostly used for decoration rather than sale when retained (Chapter 3). Likewise, shark fin is sold in batches, and species that are finned were more likely to be observed than those retained only for meat (e.g. small sharks and rays that are quickly consumed or sold whole). Therefore, present observations (excluding enumerator data) should be interpreted carefully for use in relative catch rate inferences between species.

Enumerators caught a total of 409 elasmobranchs, comprising 52.2% of the total 783 observations (Figure 4.3). Most enumerator observations came from Katatai Village (Figure 4.1, location 19), with 128 records encompassing 26 different species. Enumerators in delta regions of the Fly and Kikori Rivers (Figure 4.1, locations 22 and 46, respectively) recorded very high proportions of river sharks (84.9% and 62.1%, respectively). Sawfishes were recorded in low numbers at all enumerator locations except the Fly River, with the highest catch abundance (10.6%) occurring in the Mia Kussa River (Figure 4.1, location 9). The enumerator at Marieke Village (Figure 4.1, location 57) only recorded one specimen. The enumerator at Sibidiri Village (Figure 4.1, location 8) recorded only eight specimens due to a change in fishing gear for seasonal targeting of mud crab.

4.3.2 Sawfish and river shark distribution and size

In the northern region, *A. cuspidata* (n = 13) was observed from the mouth of both the Sepik and Ramu Rivers (Figure 4.4). Size classes ranged from 100.0–300.0 cm TL at the Sepik River (all whole specimens), while two mature sized specimens, 231.4 and 276.5 cm TL, were observed at the Ramu River mouth from dried rostra caught three months prior. *Pristis pristis* (n = 13) were observed from the mouth of the Sepik River, upstream to Korogu Village and Chambri Lake (Figure 4.1, locations 4–6). Size classes ranged from 270.4–486.9 cm TL at the river mouth, while all specimens upstream were <90 cm TL. All observations were made from dried rostra except one smoked whole specimen measuring 49 cm (distorted body length from smoking). All sawfish records from examined rostra were reported to have been caught within the last two years at the time of surveys (2017).

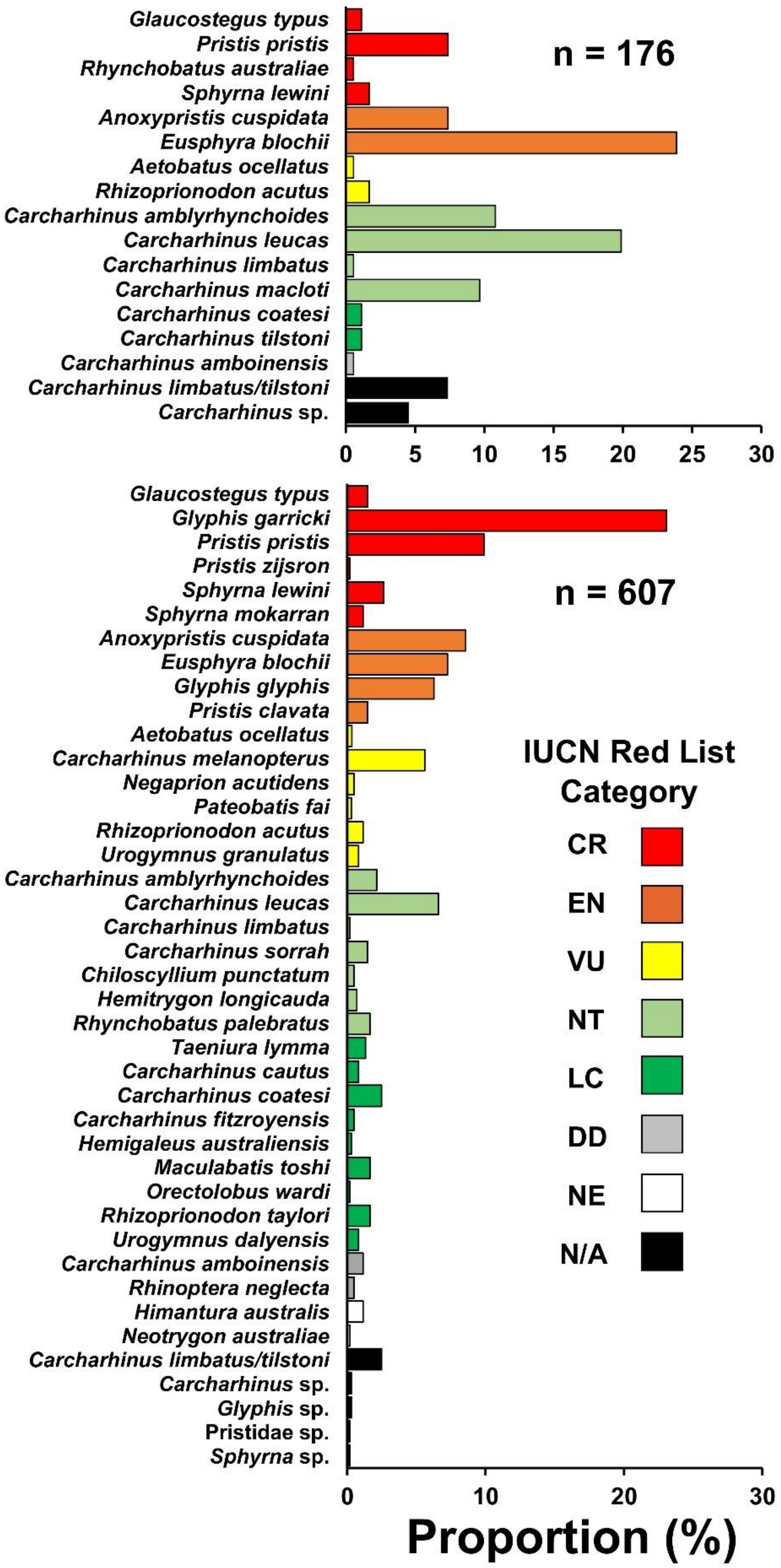


Figure 4. 2 Species compositions encountered from small-scale fisheries in the northern region (top) and southern region (bottom) of Papua New Guinea. Species are categorised into their current IUCN Red List category (IUCN 2021). CR; Critically Endangered, EN; Endangered, VU; Vulnerable, NT; Near Threatened, LC; Least Concern, DD; Data Deficient, NE; Not Evaluated, N/A Not applicable.

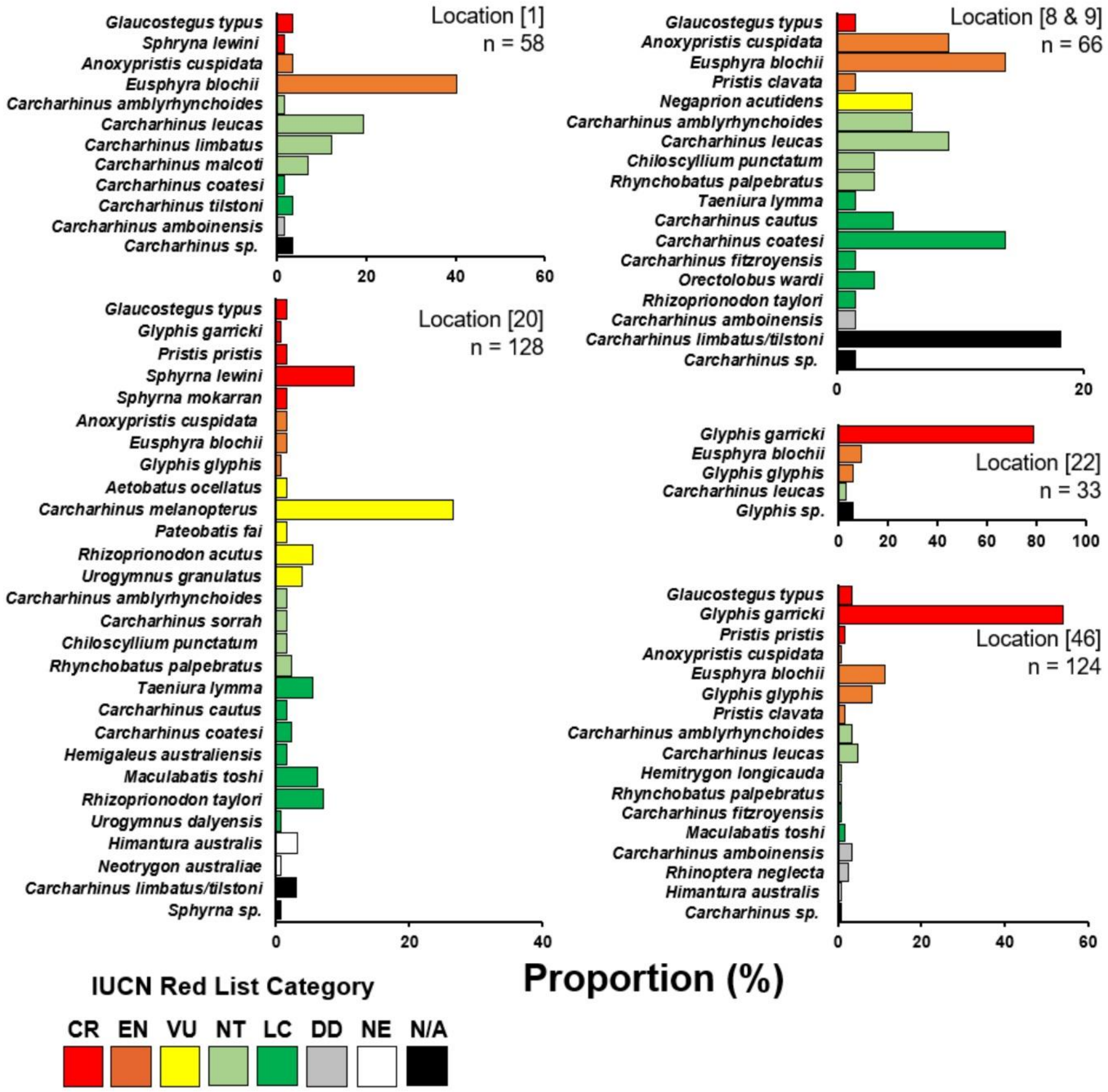


Figure 4. 3 Species composition of enumerator recorded catch. (A) Kopar Village, Sepik River; (B) Sibidiri and Buzi Village combined, Mia Kussa River; (C) Katatai Village, South Fly Coast; (D) Nemadabu fishing camp, Fly River; and, (E) Goare Village, Kikori River. Location numbers from Figure 4.1 are provided in square parentheses with number of specimens (n) observed by each enumerator. Species are categorised into their current IUCN Red List category (IUCN 2021). CR; Critically Endangered, EN; Endangered, VU; Vulnerable, NT; Near Threatened, LC; Least Concern, DD; Data Deficient, NE; Not Evaluated, N/A Not applicable.

In the southern region, *A. cuspidata* (n = 52) was the most commonly encountered sawfish, with observations from Mia Kussa River to the Kerema Coast (Figure 4.4). Most specimens (82.7%)

observed from dried rostra (n = 46) were estimated to be mature (228.8–309.4 cm TL). Of the whole specimens observed, the enumerator at the Mia Kussa River mouth caught five immature specimens (55.0–134.0 cm TL), while the enumerator in the Kikori River Delta caught one 101.0 cm TL specimen. The next most commonly encountered sawfish was *P. pristis* (n = 60), which was observed from the South Fly Coast to the Kerema Coast (Figure 4.4). Observations were made from rostra (n = 54), fin (n = 3), and whole specimens (n = 3). Of the 32 rostra observed where a capture date (usually month/year) could be provided, 30 were reported to have been caught since 2016. All fins with capture date information had been caught within the month of observation. Specimens observed upstream (n = 30) from river delta environments ranged from 72.9–207.1 cm TL, although sizes were generally small with only six specimens >100 cm TL (three in each of the Aramia and Turama Rivers). Specimens observed in river deltas and coastal environments (n=30) ranged from 99.0–561.8 cm TL, although only four of these specimens were <200 cm TL (all in the Kikori River Delta). Other sawfish species were les commonly encountered (Figure 4.4). *Pristis clavata* (n = 9) was observed from the Mia Kussa River and Kikori River Delta. All were immature (103.0–248.4 cm TL). Two specimens were caught in the Kikori River Delta (203.0 and 248.4 cm TL), and one was caught at the Mia Kussa River mouth (203.9 cm TL). Other observations came from dried fin (n = 3) and rostra (n = 3) reported to be from recent catch during each of the 2018 and 2019 survey trips. Only one *P. zijsron* was observed from a historic rostrum on the South Fly Coast (352 cm TL).

Glyphis garricki (n = 140) was encountered from Mia Kussa River to Kikori River Delta (Figure 4.4), while *G. glyphis* was encountered from the South Fly Coast to Kikori River Delta. Specimens encountered of both species were all immature ranging from 49.0–117.0 cm TL for *G. garricki*, and 46.4–122.0 cm TL for *G. glyphis*. *Glyphis garricki* specimens encountered included 102 (72.9%) whole specimens and 38 (27.1%) from dried fin. *Glyphis glyphis* specimens encountered included 26 (68.4%) whole specimens, six (15.8%) dried fin, and six (15.8%) from heads/carcasses.

4.3.3 Small-scale fishing characteristics

Gillnets were the most used gear by small-scale fishers in both northern and southern regions accounting for 709 (90.5%) of total catch observations, and was the only gear used in capture of elasmobranchs in the northern region (176; 100%). In the southern region, hook and line additionally

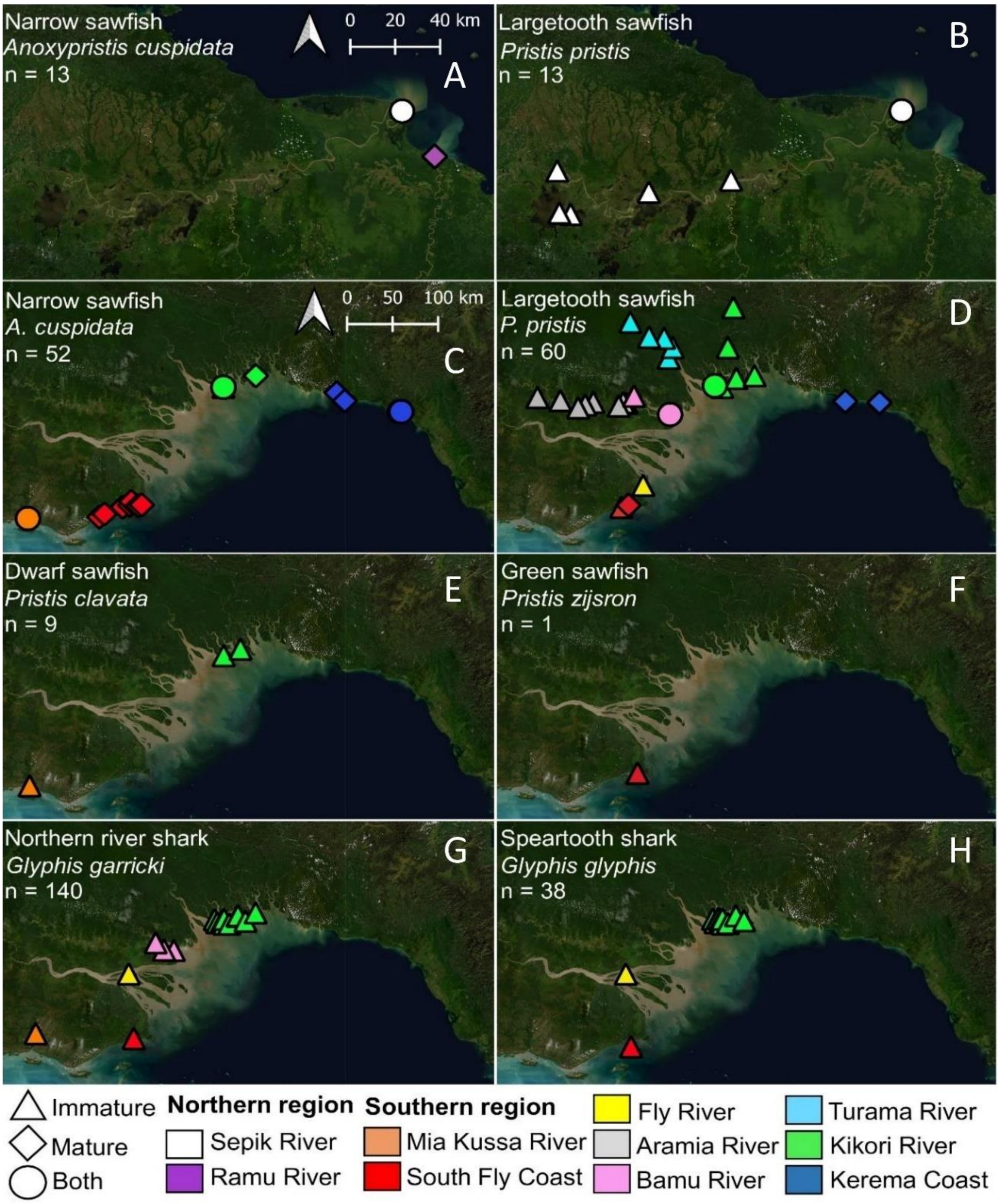


Figure 4. 4 Locations where sawfish (A–F) and river shark (G–H) species were observed during surveys of northern (A–B) and southern Papua New Guinea (C–H). Estimated maturity of each specimen observed is indicated, and abundance (n) for each species is given.

accounted for 23 (2.9%) of total catch observations, while poison root was reported to be used in capture of five (0.6%) mangrove whipray *Urogymnus granulatus*. No information on gear type was available for 46 (5.8%) specimens. It was not always possible to record gillnet mesh size for each specimen as multiple nets of a range of mesh sizes were usually checked by fishers each fishing expedition before catch was recorded back on shore. Furthermore, many sawfish rostra and fin records were from previous catch, and fishers could not recall mesh size used. Of the 233 specimens that mesh size could be recorded for (32.9% of total gillnet catch), mesh sizes ranged from 2–8 inches (″) with a median of 6″ (Figure 4.5). For sawfishes, 22 specimens (18.5% of sawfish gillnet catch) had mesh size recorded ranging from 3″ and 5–7″, with a median of 6″, and 130 *Glyphis* spp. (73.4% of river shark gillnet catch) had mesh size reported ranging from 4–6″ and 8″, with a median of 6″ (Figure 4.5).

Across all regions, gillnet fishing activity was usually oriented around the tides, with nets often remaining in the water 24 hours a day, only being checked and re-set if needed on low tides. On spring tide cycles fishermen generally did not fish due to increased chance of floating debris damaging nets, and a general consensus that fishing was not as productive. In freshwater environments, nets were observed soaking both night and day, although there was less tendency for fishers to leave nets soaking 24 hours a day. In freshwater environments, fishing activity was mainly subsistence in nature, likely due to a lack of market access to sell excess catch (excluding the Kikori River where fishers sell catch at Kikori Town market). Gillnets were most commonly set from the bank stretching out into the channel, or perpendicular to coast, where they were secured by tying to large sharpened sticks or bamboo that were stuck into the substrate. This generally restricted fishing activity to shallow water where the high tide mark did not exceed depths of ~5m.

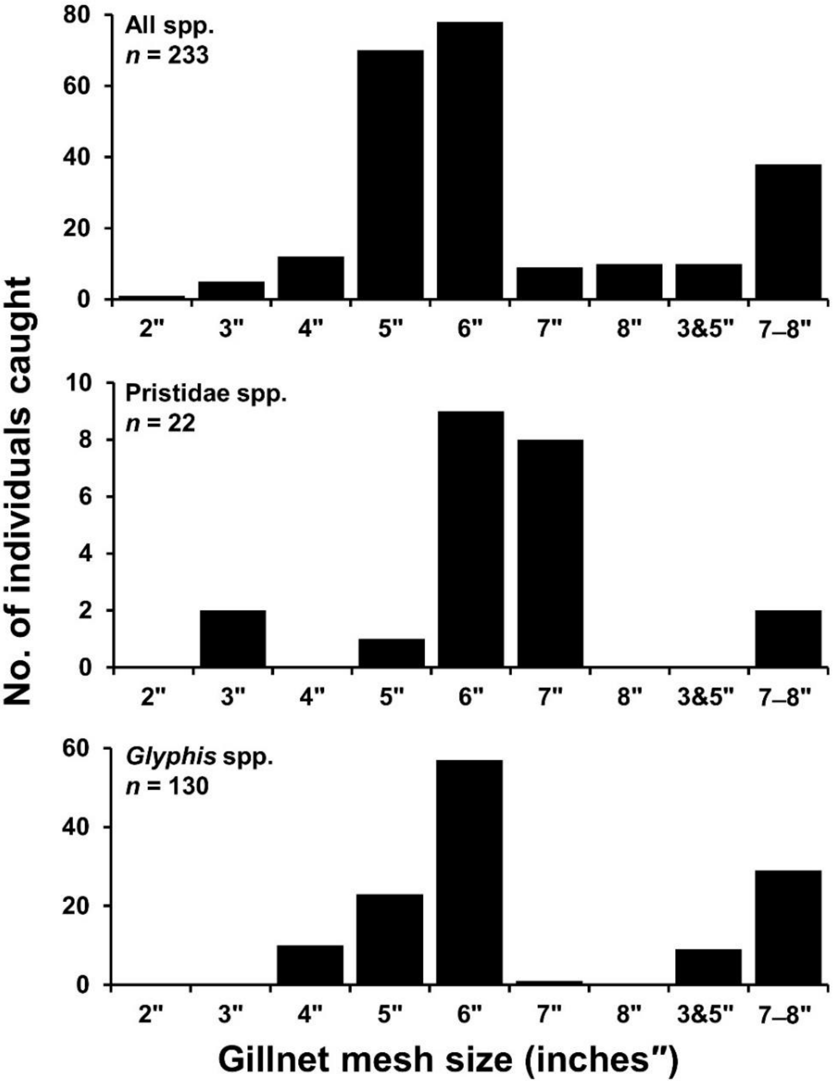


Figure 4. 5 Number of specimens caught where records of gillnet mesh size (inches) was reported in small-scale fisheries of Papua New Guinea. All species (Top), Pristidae spp. (Middle), *Glyphis* spp. (Bottom). 3&5″ refers to mesh sizes overlaid in a single net, 7–8″ were records reported from either 7″ or 8″ nets though not discernible per specimen caught.

4.4 Discussion

4.4.1 Species diversity

Thirty-eight elasmobranch species (22 sharks, 16 rays) were observed in PNG's small-scale fisheries. This represents 29.2% of known PNG elasmobranch diversity (130 species; White et al. 2017b) which is a similar level to the commercial Gulf of Papua prawn trawl (31% of elasmobranch diversity; White et al. 2019) and higher than the former shark long-line fishery (13.8% of elasmobranch diversity; White et al. 2020). The highest species diversity was observed in PNG's southwest (South Fly Coast and Mia Kussa River), encompassing 81.6% of species observed in this study. This diversity is likely due to fishers in this region accessing a range of estuarine, inshore, and reef habitats. In the Gulf of Papua, outflow from several major river systems results in high turbidity and lowered salinity in much of the inshore region (e.g. sediment plume evident in Figure 4.1). Consequently, catch was dominated by river sharks, bull sharks *Carcharhinus leucas*, and sawfishes, which all have increased tolerance for such conditions (Chapter 2). Lower species diversity observed in the northern region was likely due to: 1) more limited spatial and temporal scale of surveys; 2) lack of estuary habitat in the Sepik and Ramu Rivers; and, 3) narrow continental shelf along the Bismarck coastline limiting inshore habitat availability (Coates, 1987).

Considering most of the fishing activity observed in this study was in riverine and inshore environments, it is unsurprising that catch mainly comprised immature size classes. Shallow coastal environments are generally used as nurseries by inshore marine elasmobranchs (Heupel et al., 2007), with some species preferring river outflow areas (e.g. Heupel et al., 2019). Meanwhile, estuarine or freshwater environments are preferentially used as nurseries by euryhaline and estuarine generalist elasmobranchs (Chapter 2).

4.4.2 Population status of river sharks

It is difficult to quantify the extent of any population trends over time for river sharks in regions surveyed. The best available data are from observations by Haines (1979) in the Purari and Kikori Rivers, where river sharks (reported as *Carcharhinus gangeticus* or *Carcharhinus glyphis*) were reported to be rare. Present enumerator data in Kikori River indicates that both species are commonly caught relative to other elasmobranchs. It is difficult to make interpretations about population trends in river sharks as the validity of species identifications by (Haines, 1979) cannot be certain due to poorly resolved taxonomy at the time (Compagno and Cook, 1995), and it is not possible to examine differences in gillnet fishing methods used between historic and present studies. However, the large number of smaller sized individuals of both species observed in this study is a clear indicator that breeding adults are present.

The estuarine delta systems of rivers throughout the Gulf of Papua appear to be important nursery habitat for both river shark species. Despite extensive surveys in upstream freshwater environments during this study, neither species occurred far from the estuary. Similar habitat use patterns have been observed for *G. glyphis* (Dwyer et al., 2020) and *G. garricki* (Pillans et al., 2009) in northern Australia, suggesting that neither species penetrates far into freshwater reaches of rivers like other euryhaline species do (e.g. *C. leucas*, Dwyer et al. 2020). Meanwhile, the absence of larger size classes is likely because fishers in the Gulf of Papua remain within rivers and delta environments. Mature sized *G. garricki* and *G. glyphis* (some reportedly with near-term pups) were observed offshore (~3 km) on the South Fly Coast (Figure 4.1, location 19) in October 2014 by White et al. (2015). Congruently, neonates (with open umbilical scars) of both species were observed in October during this study. The absence of river sharks in the northern region can likely be attributed to the lack of estuarine environment in the Sepik River and limited coastal shelf habitat along the Bismarck coastline (Coates, 1987).

4.4.3 Population status of sawfishes

Declines in sawfish catch have recently been reported in the northern (Leeney et al., 2018) and southern (Chapter 3) regions surveyed. Present enumerator data suggest a small number of interactions with *A. cuspidata* (excluding northern PNG), *P. clavata*, and *P. pristis*, and rostra from recently caught animals (e.g. <1 month) were not commonly encountered in surveys. Collectively, this indicates that while sawfish populations persist, efforts to prevent further declines and rebuild populations are required.

In southern PNG, juvenile *P. pristis* were observed in freshwater reaches of the Aramia, Bamu, Turama, and Kikori Rivers. Small sawfish in upstream freshwater environments were additionally reported by locals from each of the Mia Kussa and Fly Rivers in Western Province, and Purari, Vailala, and Tiamura Rivers in Gulf Province. There are numerous historic reports of *P. pristis* throughout rivers of southern PNG (White et al., 2017a) and this study indicates they still occur in the rivers presently surveyed. Furthermore, *P. pristis* is typically philopatric to natal river systems (Feutry et al., 2015; Phillips et al., 2017), and their presence in multiple rivers may indicate the existence of several populations within southern PNG. However, aside from the Turama River, *P. pristis* did not appear common. Declines in sawfish catch frequency and in sizes caught were recently reported by fishers throughout southern PNG in freshwater reaches of the same rivers as the present study (Chapter 3). While comparable historical data of *P. pristis* in southern PNG is limited, fisheries surveys by Haines (1979) indicate that *P. pristis* was commonly caught in comparison to other elasmobranchs in the Kikori River during the 1970s. Present observations and enumerator data in the Kikori River, however, suggest that while *P. pristis* is persisting, they are not caught commonly relative to other elasmobranchs. Elsewhere in southern PNG, declines of *P. pristis* have been noted in the Fly River (Storey et al., 2009). Collectively, declines can be inferred for *P. pristis* throughout southern PNG, although given populations are persisting, declines appear less severe than in other Indo–Pacific regions, excluding northern Australia (Yan et al., 2021).

In northern PNG, *P. pristis* was reported to be very common in the Sepik River during surveys in the 1930s, while abundance appears to have reduced by the 1980s (Coates, 1987). Most rostra observed in present surveys were reportedly caught one or two years prior to our arrival indicating *P. pristis* are not presently common, as supported by Leeney et al. (2018). *Pristis pristis* has historically been observed upstream to Ambunti Village (White et al., 2017a) and it is possible this species occurs much further upstream and in floodplain areas not accessible in present surveys.

For the other sawfish species, comparable historic data mainly include anecdotal observations (White et al., 2017a). On the South Fly Coast, *P. clavata* were reported to be 'common' ~100 km east of the Mia Kussa River at the mouth of the Bensbach and Morehead Rivers in the early 1970s (White et al., 2017a). In the present study, *P. clavata* was caught just once over the respective enumeration periods in the Mia Kussa and Kikori Rivers. While it is difficult to infer any population trend, the present enumerator observations and lack of dried rostra in fishing communities indicate this species is not commonly caught within the small-scale fishery observed.

Anoxypristis cuspidata was the most commonly encountered sawfish species in coastal and riverine delta environments. Most observations came from the Mia Kussa River mouth and Kerema Coast. Both of these regions receive significantly less river outflow than locations surveyed in the north and western Gulf of Papua, and fishing pressure was also noted to be lighter. It is unclear if the higher presence of *A. cuspidata* around the Mia Kussa River and Kerema Coast is a function of the environmental preferences (salinity and turbidity) of this species, or lower local fishing pressure. *Anoxypristis cuspidata* occurs around river and creek outflows in northern Australia suggesting tolerance to estuarine conditions (e.g. Thorburn et al. 2003), however rivers within the Gulf of Papua have considerably higher outflow volumes. On the Kerema Coast, most observations of *A. cuspidata* were rostra from mature sizes in coastal villages. Village leaders cited concerns about men using sawfish rostra to fight (Appendix 2; Figure A2. 1) suggesting a bias for fishers to retain larger rostra. Meanwhile, only juveniles were observed at the Mia Kussa River mouth indicating it is a nursery area. In northern PNG, a single specimen of *A. cuspidata* was collected near the mouth of the Ramu River in 1965, although no other data is available to compare present observations. Nine specimens were caught in just five days of observation at Kopar Village, Sepik River mouth, with two more specimens during November 2017. *Anoxypristis cuspidata* likely occurs in along the coastline of the adjacent Murik lakes region to the west, and in Broken Water Bay and around the Ramu River to the east, due to very similar environmental conditions.

It is unclear if *P. zijsron* persists in PNG. It is hard to determine if the single specimen observed had migrated from Australia to PNG, as Green et al. (2018) suggest a similar movement was made by a male *A. cuspidata*. Australia to PNG migrations would be most expected on the South Fly Coast due to its closer proximity and homogeneity of adjoining habitat. Historically, *P. zisjron* has only been recorded in the southeast Gulf of Papua, while a single Sepik River record is uncertain (White et al., 2017a). White et al. (2017a) observed *P. zijsron* fins at Daru (Western Province) however, due to the presence of the Torres Strait Trade Treaty (see Busilacchi et al., 2014), it is possible that these fins originated in Australian waters.

4.4.4 Conservation considerations and challenges

Threats to populations of sawfishes in PNG have previously been outlined (Chapter 2; White et al., 2017a; Leeney et al., 2018; White et al., 2019). Key threats identified include: 1) widespread gillnet use by small-scale fishers; 2) tendency of fishers to kill sawfishes or amputate their rostra to untangle animals from nets; 3) absence of bycatch reduction devices in the Gulf of Papua prawn trawl; 4) commercial and non-commercial markets for sawfish products including meat, fin, and rostra (Appendix 2; Figures A2. 2, A2. 3); 5) lack of enforcement and monitoring of PNG's international shark fin trade; 6) environmental degradation from mining and logging activities (e.g. Storey et al., 2009); and, 7) possible ecological implications resulting from introduced fish species. While many of these threats also apply to river sharks, conservation concern for these two species may not be as high. Only juvenile size classes of river sharks appear to be caught in substantial numbers in PNG's small-scale fisheries. Most long-lived carcharhinids can withstand relatively high fisheries mortality in instances where fishing pressure is exclusive to young age classes (e.g. Smart et al., 2020). However, essential life history information (age and growth, reproductive parameters etc.) is lacking for these river shark species to make an informed assessment. We caution risk of population declines in the near future if present levels of fisheries mortality are sustained. Conversely for sawfishes, a range of size classes including breeding adults appear to be caught. This suggests that current fishing mortality in PNG's small-scale fishery may carry higher risks to sawfish populations compared to river sharks.

Only juvenile *P. pristis* occur in PNG's upstream freshwater environments. Very few fishers in these communities sell fin (limited access to shark fin traders) and consumption or sale of meat at local markets is opportunistic when other fish are not caught, or markets can be accessed (Chapter 3; Leeney et al., 2018). The largest issue appears to be the tendency for fishers to kill or remove rostra from *P. pristis* entangled in gillnets, irrespective of fishers using the animal for consumption or trade (Chapter 3). Therefore, conservation initiatives focused on minimising non-essential use, coupled with better release practices have potential to be successful for *P. pristis* in freshwater environments.

4.5 Threat posed by the swim bladder fishery

Fishers in all coastal and lower riverine environments observed in this study primarily target teleost swim bladder (mainly from barramundi *Lates calcarifer* and scale croaker *Nibea squamosa*) (see Chapter 3). Elasmobranchs (including river sharks and sawfishes) are incidentally caught in this fishery. Dried swim bladder (also called 'fish maw') is used mainly as a food or medicine in Asia, and value can be as high as \$23,433 USD kg^{-1} in Asian markets with croakers (Sciaenidae) generally having the highest value (Sadovy de Mitcheson et al., 2019). In PNG, dried swim bladder from large individuals of *L. calcarifer* and *N. squamosa* (a sciaenid) are worth 500–1400 Papua New Guinean Kina (PGK) kg^{-1} (1 PGK = ~\$0.28 USD, 04/04/2021) through licensed buyers in Gulf Province (Appendix 2; Table A2. 9; Ibana 2020), while in both the Western and Gulf Provinces, fishers reported value up to 10,000 PGK kg^{1} from non-licensed buyers (mainly for large *N. squamosa*, this figure was verified several times with fishers throughout 2019–2020). Comparative to the value of shark fin (inclusive of sawfish), ~1–75 PGK kg^{-1} in southern PNG (Chapter 3; Busilacchi et al., 2021) or 100–350 PGK kg^{-1} in northern PNG (Leeney et al., 2018), swim bladder has a significantly higher economic incentive for local fishers.

Swim bladder values in the Gulf of Papua appear to be considerably higher than Busilacchi et al. (2021) report for legal (131 PGK kg^{-1}) and illegal (152 PGK kg^{-1}) markets on the South Fly Coast. The differences in value are likely due to the species of origin and weight of swim bladder. For example, in the Gulf Province, Ibana (2020) indicates that swim bladders (<0.2 kg) are worth 50–300 PGK kg^{-1} from smaller *L. calcarifer*, *N. squamosa*, or varied sizes of less-valued species such as catfishes (Siluriformes) and king threadfin salmon *Polydactylus macrochir*. The Gulf of Papua has extensive riverine habitat availability for *L. calcarifer* and *N. squamosa*, and due to less historical fishing effort compared to South Fly Coast (White et al., 2017a), it is likely that a greater availability of larger individuals are present. It is also possible that alternative market chains operate out of Gulf Province (and possibly extend to the eastern South Fly Coast) where the extremely high value of *N. squamosa* swim bladder in illegal markets was reported. Busilacchi et al. (2021) indicated that end user market prices for swim bladder were 18 times higher than value local South Fly Coast fishers receive. This indicates that: 1) *N. squamosa* is highly valued by end users, and/or 2) the market chain operating out of the Gulf Province may have more direct links to Asia and does not appear to be subject to the same incremental price increases along its market chain (i.e. an increase of 18 times for *N. squamosa* based on Gulf Province illegal market value would equal ~$50,400 USD kg^{-1} in end user markets). It remains unclear why swim bladder buyers would offer such high value to local fishers, assuming they are aware of the comparatively lower value of alternative markets. The apparent presence multiple of local markets does however complicate management of this fishery in southern PNG. Meanwhile, further information is needed on the swim bladder trade in northern PNG, including value and market chains comparative to shark fin.

For river sharks and sawfishes, the concern is that due to their overlapping habitat use with *L. calcarifer* and *N. squamosa* (lower riverine and inshore areas), they have increased vulnerability to incidental capture in the swim bladder fishery (e.g. spatial fishing effort indicated by Eisemberg et al., 2015). River sharks and sawfishes unsurprisingly were more commonly caught by large gillnet mesh sizes (5–

8 inches), which are mainly used by fishers targeting swim bladder in river mouth and coastal-estuarine environments (see Chapter 3 for further details on small-scale fishery characteristics). Meanwhile, small mesh sizes were observed to mainly be used by fishers in sheltered waters that are protected from tidal currents to target small fish for subsistence purposes. All reports of fishers using gillnets with 7- and 8-inch mesh came from the Fly River, and eastern South Fly Coast. In the Western Province, fishers are permitted to use a maximum mesh size of 6 inches to target *L. calcarifer* under the Barramundi Management Plan (NFA, 2003). Since the implementation of this management plan, *N. squamosa* appears to have emerged as an additional target species of local fishers, and larger mesh sizes appear to be used to target this species. This may comprimise the effectiveness of 6-inch mesh size gear restriction under the Barramundi Management plan, as *N. squamosa* has overlapping habitat use in coastal-estuarine environments. Furthermore, we caution that future increases in fishing effort targeting high value swim bladder are likely throughout southern PNG, and this could have severe conservation consequences for river sharks and sawfishes. The disproportionate local economic value of swim bladder has had negative impacts for incidentally captured species in many regions throughout the globe (Sadovy de Mitcheson et al., 2019). Most notably in Mexico, vaquita (*Phocoena sinus*) faces imminent extinction resulting from illegal targeting of totoaba (*Totoaba macdonaldi*) for swim bladder (Rojas-Bracho et al., 2006).

Fishers targeting swim bladder (mainly lower riverine and coastal communities) generally retained all incidental elasmobranch catch, further complicating river shark and sawfish conservation approaches. While some consumption of meat occurs (Chapter 3), remote communities with limited market access retain surplus elasmobranch catch for fin only, with carcasses being discarded (Appendix 2; Figure A2. 3). Because fishers lack access to refrigeration, excess catch either needs to be quickly transported to market or smoked. In remote communities however, the use of fuel to travel to markets precludes its economic viability, and readily available fresh fish means smoked elasmobranch products are less marketable. Dried products such as swim bladder and shark fin are therefore more practical for local fishers (Vieira et al., 2017), notwithstanding their higher economic value than meat. Easily accessible legal and illegal trade markets for dried swim bladder and shark fin likely increase incentives for local fishers to engage in fisheries as a livelihood (Chapter 3; Busilacchi et al., 2021) as other livelihood options such as agriculture are not practical in PNG's river delta environments (Allen et al., 2005). Ultimately, management is required to ensure future sustainability of PNG's inshore teleost and elasmobranch fishery resources, although the complex social and cultural characteristics of the swim bladder fishery, including its high value, present numerous challenges (Chapter 3; Busilacchi et al., 2021;).

A concerted effort to examine characteristics of the swim bladder fishery and incidentally caught threatened elasmobranch species is needed by PNG's National Fisheries Authority (NFA) and Conservation and Environment Protection Authority (CEPA), respectively. Furthermore, until there is a spatially broader understanding of market and trade routes, and livelihood aspects to compliment information on the South Fly Coast (Busilacchi et al., 2021), conservation of threatened incidentally caught species will be challenging as their value to local fishers is not well understood. The present lack of information about fisher livelihoods risks poor engagement, participation, and compliance with conservation initiatives. Better availability of information on the swim bladder fishery would also help inform enforcement efforts for illegal shark fin trade (including contravention of the Convention on the International Trade of Endangered Species of Flora and Fauna Appendix I listing of sawfishes; Chapter 3), as the value of shark fin appears to be supplementary to the swim bladder trade in PNG's legal and illegal markets.

4.6 PNG's status as a refuge

Populations of river sharks and sawfishes are persisting in PNG primarily due to low historic human population density, which has resulted in lower exposure to intense pressures experienced by these species elsewhere in the Indo–Pacific. PNG appears to be only the second nation with viable populations of both river sharks and sawfishes in the Indo–Pacific, along with Australia (e.g. Morgan et al., 2011). However, population pressures in PNG appear to be increasing with increases in human population. This threatens PNG's role as a refuge for remnant populations of these species into the future. The main pressures facing PNG's river sharks and sawfishes include: lack of nationally legislated species-specific protections; lack of riverine and inshore fishery management; widespread use of fishing gears that species are highly susceptible to; the economic value of river sharks and sawfishes to local fishers; and, ongoing environmental impacts from mining and logging. Despite these pressures, PNG also has many positive conservation attributes for these species: limited coastal and riverine development; free-flowing unobstructed rivers; generally low human population density (southern PNG only) relative to other Indo-Pacific nations; customary ownership of land and waterways with general awareness and interest in environmental protection and management by local people; and, presence of adult and juvenile size classes observed in this study that currently appear to be at considerably higher population densities relative to other global regions, excluding Australia (e.g. Li et al., 2015; Yan et al., 2021). Collectively, these positive attributes are unique to PNG. Therefore, great potential exists for PNG to play a significant role in global conservation for river sharks and sawfishes as a refuge nation into the future.

Moving forward, conservation and fisheries management actions need to focus on alleviating current population pressures, and safe-guarding PNG's positive attributes where possible. There is also a need for further surveys in regions not covered in the present study where river sharks and sawfishes may also be persisting (e.g. White et al., 2017a). Understanding the extent of population distributions and specific local threats, which may differ to those identified in the present study, will assist in overall population management and development of both national and locally appropriate conservation initiatives for these species. Considerations to sawfish conservation have previously been discussed in detail (including efforts at both government and community level, Chapter 3; Leeney et al., 2018), and we identify that incidental capture in the swim bladder fishery is the primary, and most immediate threat to both river shark and sawfish populations in PNG. Due to the larger expanse of river delta and coastal-estuarine habitat (where target swim bladder species occur), southern PNG has the highest imperative for inshore fishery management initiatives to be developed. Improved management of the swim bladder fishery would help manage incidentally caught elasmobranchs and be a major step forward in securing PNG as a long-term refuge for threatened river shark and sawfish species.

Chapter 5

Diadromous life history movements of threatened non-marine elasmobranchs revealed through elemental analysis of vertebrae

5.1 Introduction

Riverine environments (freshwater and estuaries) are critical to the life histories of non-marine elasmobranch species (sharks and rays) (Chapter 2). Riverine environments are spatially restricted and strongly influenced by seasonal changes in temperature and rainfall, while lower riverine environments are additionally influenced by saltwater intrusion from tides. This creates ecological and physiological challenges for species that use them (Compagno, 2002; Ballantyne and Robinson, 2010). Consequently, there are only 10 euryhaline, and 19 estuarine generalist species that each display diadromous riverine habitat use patterns during their life histories (non-marine species categories and environmental salinity ranges of freshwater ≤ 5ppt; estuarine >5 ppt and ≤ 30 ppt, and; marine > 30 ppt, following Chapter 2). Globally, humans have had drastic impacts on riverine environments through a prolonged history of resource extraction (including fisheries), waste disposal, and environmental modification, leading to widespread declines of biodiversity and deteriorating populations (e.g. He et al., 2019; Tickner et al., 2020; Harper et al., 2021). Presently, 50% and 65% of euryhaline and estuarine generalist species, respectively, are listed in threatened categories (Critically Endangered, Endangered, or Vulnerable) on the International Union for the Conservation of Nature Red List of Threated Species (here after IUCN Red List) (Chapter 2). However, many of these species remain poorly studied, and there is a need to gain a greater understanding on their life history and habitat use to inform temporal vulnerabilities to riverine pressures for use in future conservation planning.

Elemental analysis of chondrichthyan (sharks, rays, and chimaeras) hard parts (mainly vertebrae or dorsal spines) is a technique with applications to life history, and habitat use and movement (McMillan et al., 2017). Chondrichthyan vertebrae are composed of calcified cartilage (hydroxyapatite) within an extracellular matrix of proteins (proteoglycan and collagen) (Dean and Summers, 2006). These materials accrete concentrically in a distal orientation from the vertebrae's focus as the animal grows, and once deposited they are metabolically inert with no remodelling or reabsorption (Clement, 1992). Accretion is heterogenous over time, and it is generally accepted that differences in environmental factors such as temperature cause a 'banding pattern' within accretions (Cailliet and Goldman, 2004). The seasonal accretion of 'band pairs' with differing density properties is the basis of ageing chondrichthyan vertebrae (Cailliet and Goldman, 2004). Although a widely used and valuable tool, recent studies have questioned the validity of this ageing technique as being broadly applicable in vertebrae across all chondrichthyan species (see James, 2020; James and Natanson, 2020) or in large size classes (Harry, 2018). However, several studies have successfully validated or verified annual band pair depositions for size classes approaching and close to sexual maturity when somatic growth rates are highest (e.g. Simpfendorfer et al., 2002; Hall et al., 2012). While some discrepancies persist around temporal periodicity of band pair depositions in vertebrae or across taxonomic groups, the concentric manner of accretion and inert properties of accreted material is not challenged. Therefore, examining the elemental composition of vertebrae have potential to be biologically informative, as vertebrae effectively preserve a continuous record of the animals' life history (McMillan et al., 2017).

Elemental analyses of vertebrae for habitat use investigation focus on 'environmental trace elements' (e.g., Ba, Cu, Li, Sr) (McMillan et al., 2017). Generally speaking, the relative concentration of particular elements within vertebrae can be used to infer their concentration in the local environment that the animal was inhabiting at the time of accretion (see McMillan et al., 2017, for discussion around this assumption). These elements enter the blood primarily through diffusion across gills, or through diet, although diet as a source of trace elements in vertebrae requires further investigation. These elements are accreted in vertebrae mainly through direct substitution with Ca in calcium phosphate hydroxyapatite [$Ca_{10}(PO_4)_6(OH)_2$] or may less commonly be 'trapped' within the protein matrix (e.g., Zn is only incorporated in this way) (McMillan et al., 2017). Therefore, the relative concentration of particular trace elements to Ca can be used to infer information about the type of environment the animal was using at a particular time of accretion along the growth axis of the vertebrae. The most common application of elemental analysis of vertebrae to elasmobranchs has been to investigate stock structure (McMillan et al., 2017). For example, in instances where populations are segregated at a particular life stage only (e.g. multiple unconnected nursery areas) elemental analysis can allow insights into the relative contribution of certain nursery habitats to the overall mixed population at latter life history stages (e.g. Feitosa et al., 2020). Meanwhile, use of elemental analysis to discern life history movements of diadromous species has only been sparsely applied to elasmobranchs (e.g. Otake et al., 2005; Tillett et al., 2011; Scharer et al., 2012), despite wide application to teleost fishes (Elsdon et al., 2008). For example, Sr:Ca, Ba:Ca, and Sr:Ba ratios along the otolith growth axis of barramundi *Lates calcarifer* (McCulloch et al., 2005) and vertebral growth axis of bull sharks *Carcharhinus leucas* (Tillett et al., 2011) have provided insights into freshwater, estuarine, and marine habitat use patterns throughout their life histories. In such studies, Ba typically has higher concentrations for life history phases associated with freshwater, while Sr typically has higher concentrations for life history phases associated with marine environments (Elsdon et al., 2008; McMillan et al., 2017). This informs management requirements of these species such as identifying key nursery river systems, importance of preserving migratory routes within these systems, and indicates temporal vulnerability to riverine or marine population pressures with respect to their life histories.

In the Indo–Pacific, river sharks (*Glyphis* spp.) and sawfishes (Pristidae) underline the imperilled conservation state of non-marine elasmobranchs, with viable populations now largely restricted to regions of low human population density (e.g. Chapter 4; Morgan et al., 2011). Presently, our limited understanding of river shark and sawfish biology may be impeding their effective conservation management (Li et al., 2015; Dulvy et al., 2016). However, drastic declines in their historical range coupled with reduced populations (e.g. Yan et al., 2021), mean that obtaining new information on their biology for use in conservation management is challenging (e.g. Kyne et al., 2021b). Species protections often preclude the possibility of lethal sampling (e.g. Heupel and Simpfendorfer, 2010), and declines in abundance make conventional tagging approaches time consuming and costly to achieve an effective sample size. Furthermore, sampling efforts are hampered by a lack of knowledge about broadscale habitat use patterns creating difficulties in locating animals in data poor size classes (e.g., adults). However, an increased understanding of habitat use throughout the life history of river sharks and sawfishes is needed to provide better management advice for conservation efforts.

This study used elemental analysis of vertebrae to explore diadromous environmental use patterns of two river sharks (the northern river shark *Glyphis garricki* and the speartooth shark *Glyphis glyphis*) and two species of sawfishes (largetooth sawfish *Pristis pristis* and narrow sawfish *Anoxypristis cuspidata*). Neonate and juveniles of both river shark species are known to occur in large tropical rivers of northern Australia (Pillans et al., 2009; Lyon et al., 2017; Dwyer et al., 2020) and Papua New Guinea (Chapter 4). However, it is unclear how long they remain in riverine environments, and whether these species have segregated or communal nurseries in rivers they co-occur in. Moreover, information is lacking on habitat use patterns of subadult and adult size classes, and it is unclear if they persist around riverine environments primarily, as records from marine environments lacking river outflow influence are very limited (Pillans et al., 2009). Habitat use patterns of *P. pristis* are better understood (e.g. Morgan et al., 2011), although it remains unclear if pupping occurs directly in low salinity estuarine and freshwater nursery environments, or in inshore marine environments, requiring juveniles to migrate upstream through the estuary where they may be exposed to greater pressures (e.g. predation). Habitat use of *A. cuspidata* is presumed to be largely estuarine and inshore on the basis of capture locations (e.g. Thorburn et al., 2003; White et al., 2017), although limited information is available on long-term habitat use patterns within estuarine and marine environments during their life history.

The aim of this study was to explore riverine environmental habitat use patterns for these river shark and sawfish species through elemental analysis of vertebrae. A number of additional species were also included in the analysis to allow elemental signatures to be interpreted relative to other species with better known environmental use patterns. The bull shark *Carcharhinus leucas* was included as a well-studied euryhaline generalist species that is known to use riverine environments including freshwater for its first few years of life, before moving to marine environments (e.g. Simpfendorfer et al., 2005; Heupel and Simpfendorfer, 2011). While several stenohaline-marine inshore and offshore species were included to provide a reference for marine environment elemental signatures. The overall purpose of this study was to provide information about the temporal vulnerabilities to riverine pressures for these river shark and sawfish species to aid future conservation planning.

5.2 Methods

5.2.1 Sample collection

Vertebrae samples of *G. garricki*, *G. glyphis*, *C. leucas*, *A. cuspidata*, *P. pristis*, and bottlenose wedgefish (*Rhynchobatus australiae*) were collected opportunistically during small-scale fishery observations in Papua New Guinea (PNG) in 2017–2020 (Chapter 4). River shark samples from the South Fly Coast were opportunistically collected in 2014, also from observation of small-scale fisheries (White et al., 2015). Silky shark (*Carcharhinus falciformis*) and grey reef shark (*Carcharhinus amblyrhynchos*) samples were obtained from commercial long-line vessels in 2014 by observers from the National Fisheries Authority (NFA) of PNG (Smart et al., 2016a; Grant et al., 2018). Samples of Australian blackspot shark (*Carcharhinus coatesi*) were obtained from the Gulf of Papua Prawn Trawl Fishery by observers from the NFA in 2014–2015 (Baje et al., 2019). Vertebrae samples of *P. pristis* in Australia were opportunistically collected from deceased animals found in evaporated floodplain waterholes of the Daly River by members of Charles Darwin University (CDU) in collaboration with the Malak Malak Ranger Group under NT Fisheries Special Permit S17/3252, and Charles Darwin University Animal Ethics Committee A11041. An additional *P. pristis* was an unexpected mortality of another project on the Adelaide River and was donated to CDU. Australian *G. glyphis* samples from the Adelaide River were collected during target surveys with approval by the Charles Darwin University Animal Ethics Committee (Approval No. A11041 and A19008) and undertaken through Northern Territory *Fisheries Act* Special Permits S17/3364 and S17/3467. One *G. glyphis* from the West Alligator River was an unexpected mortality of historic fishery surveys and was opportunistically located in a storage freezer at CDU (Figure 5.1). All specimens had total length and sex recorded at the time of observation. All samples from Australia and some samples from PNG additionally had maturity status assessed following the method prescribed by White et al. (2001). Due to the nature of small-scale fishery observations in PNG, it was not always possible to perform dissections to assess maturity status in females (see Chapter 4). Measurements of salinity were taken at the time of collection for all Australian *G. glyphis* and one *P. pristis* sample, while salinity measurements were not able to be taken for other Australian *P. pristis* or any PNG samples (Appendix 3, Table A3. 1). Approximately 10 thoracic vertebrae were removed from each animal. Residual tissue was removed, and vertebrae were stored frozen until preparation for ageing at James Cook University or CDU.

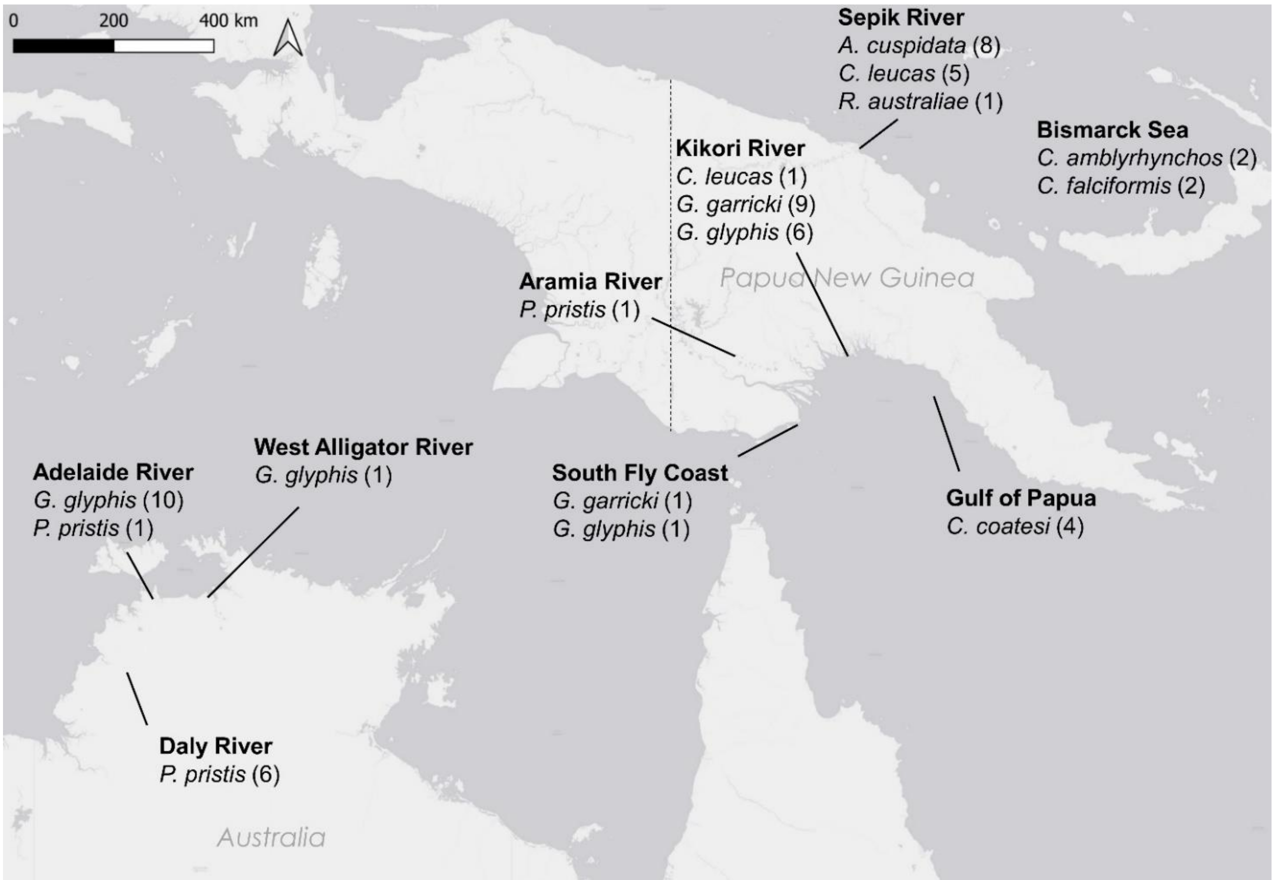


Figure 5. 1 Location and sample size of vertebrae samples for each species used in elemental analysis.

5.2.2 Sample preparation

Protocols for preparing vertebrae for ageing and elemental analysis followed Cailliet et al. (2006). Vertebrae were thawed, and remaining tissue including neural and haemal arches were removed using a scalpel. Vertebrae were then carefully divided into individual centra, using a scalpel. Samples of *C. amblyrhynchos*, *C. falciformis*, and *C. coatesi* from PNG, and *G. glyphis* and *P. pristis* from

Australia, were soaked in a 4-5 % sodium hypochlorite solution for 5–30 minutes, depending on the size of centra, to remove excess tissue. Samples of *G. garricki*, *G. glyphis*, *A. cuspidata*, *P. pristis*, *C. leucas*, and *R. australiae* from PNG were not soaked in sodium hypochlorite as an *a priori* precaution for elemental analysis. It should be noted that there is little evidence that brief exposure to sodium hypochlorite (or 'bleaching' generally) effects the internal elemental composition of vertebrae for elements analysed in this study (Mohan et al., 2017). All samples were rinsed with milliQ water, strained, and placed in a drying oven at 60 °C for 24 hrs.

One centrum from each individual was randomly selected for sectioning. Centra were mounted onto a low speed circular saw (Beuhler, Illinois, USA) and a section of approximately 400–600 µm was cut on a sagittal axis using two diamond-tip wafering blades that passed through a water bath filled with millQ water to lubricate blades. Between sectioning of each individual centrum, the saw apparatus including blades and water bath were cleaned in an ultrasonic bath with milliQ water to prevent cross sample contamination. Vertebral sections were mounted onto glass slides using Crystal Bond resin (SPI supplies, Pennsylvania, USA). Vertebral sections were then rinsed again in an ultra-sonic cleaner using milliQ water and placed into a drying oven at 60°C for ~1 hr. Samples were then stored in a sealed slide box until ageing and elemental analysis.

5.2.3 Age estimation

Mounted vertebral sections were examined through a dissecting microscope using transmitted light. Ages were estimated by counting the number of translucent and opaque bands (collectively called 'band pairs') in the corpus calcareum. The birthmark was identified by a clear acute angle change on the inner margin of the corpus calcareum, that often coincided with a thin translucent band. These features indicate the shift from pre-natal growth to post-natal growth (Cailliet and Goldman, 2004). Each proceeding band pair was considered to represent a year of growth (Figure 5.2). Only *C. leucas* has had annual band pair depositions verified (Hoarau et al., 2021), although most carcharhinids generally appear to deposit growth bands annually, at least in younger age classes (e.g. Hall et al., 2012; Chin et al., 2013; Harry et al., 2013). No age validation studies have been conducted for pristid or rhinid species included in this study, although annual band pair deposition has been validated for age 0–3 smalltooth sawfish *Pristis pectinata* through analysis of seasonal salinity trends and Sr:Ca (Scharer et al., 2012). In this study, each band pair for all species was assumed to equal 1 year of growth.

An age estimate for each individual was achieved by having two 'readers' independently estimate ages without knowledge of the individuals' total length. Reader 1 (present author, MIG) conducted two reads to allow measurements of ageing bias and precision within reader, while reader 2 (Sushmita Mukherji; SM) conducted one read to allow measurements of ageing bias and precision between readers. Age bias analysis was only conducted on PNG river shark specimens as other samples had already been aged in previous studies, or had low sample sizes that precluded statistical age bias analysis. Some systematic bias was evident in estimated ages within and between readers, although average percent agreement ±1 year was high (Appendix 3, Figure A3. 1). Any issues with differing age estimates between readers were overcome by conducting consensus reads (between MIG and SM). Difficulties were encountered in estimating ages for *A. cuspidata* due to extreme variability in banding pattern and large inconsistencies between suspected band pairs present and specimen length. Consensus reads involving a third reader (Colin Simpfendorfer; CS) were conducted, although no age estimates could be agreed so *A. cuspidata* samples were not aged. Band pair counts from specimens aged in previous studies (*C. amblyrhynchos* Smart et al. 2017; *C. coatesi* Baje et al. 2019; *C. falciformis* Grant et al. (2018), and Australian *G. glyphis* Kyne unpubl data) were re-identified for analysis by MIG and SM. Due to low sample sizes and size-class bias (i.e. lack of adults), no fitting of growth curves to length-at-age data were conducted in this study as resulting growth parameter estimates would be prone to inaccuracies (Smart et al., 2016a; Smart and Grammer, 2021).

5.2.4 Laser ablation using LA-ICP-MS

Elemental analysis of vertebrae was conducted at the Advanced Analytical Centre of James Cook University (Townsville campus), using a Teledyne Analyte G2 193nm ArF Excimer laser ablation system connected to a Thermo iCAP-RQ. The ablation cell HelEx II was connected to the iCAP-RQ via Tygon tubing and a 3-way mixing bulb (volume ~5 cm^3). This system provides both a very stable time-resolved signal and rapid signal washout.

All instrument tuning was performed on NIST 610 glass standard using a 5 Hz repetition rate, 65 µm beam aperture, and 3 J/cm2 energy density. Under these conditions, the ablation rate for NIST 610 was about 0.1 µm per laser pulse. Tuning was achieved by iteratively adjusting the He carrier gas, Ar sampling gas, RF Power, extraction lens and other lenses voltage to achieve $^{238}U/^{232}Th$ ratio of ~1, (ThO/Th < 1 % typically 0.5 %) for NIST610. For sample analysis, the total measurement time was set at 60 seconds. The first 30 seconds was for gas blank measurement (Laser firing but with the shutter closed after 20 seconds), with the shutter opened to allow sample ablation for the final 30 seconds. NIST610 standard was used as the calibration standard and NIST612 was analysed as a secondary standard for quality control purpose. Standard bracketing was used throughout the study to correct for remaining elemental fractionation and mass bias.

Li, Mg, P, Mn, Co, Cu, Zn, As, Sr, Ba, and Pb were measured in all vertebrae samples and concentrations were normalised to Ca. Samples were ablated along a transect line, at 165 µm intervals within the corpus calcareum, starting at the vertebrae focus and ending at the distal edge (Figure 5.2). All data was processed using Iolite software and extracted in parts per million (ppm). To remove potential surface contaminants on vertebral sections, material ablated in the first second of each spot was removed from the data.

Elemental analysis data outputs were generated by Iolite software and organised in Microsoft Excel. All data corresponding to each ablation spot were allocated to either the pre-natal zone or an annual band pair (i.e., age) along the growth axis for each specimen. This was achieved by photographing each ablated vertebral section using a camera attached to a dissecting microscope and overlaying markers on band pairs digitally (Figure 5.2). This additionally allowed the position of ablation spots to be checked and erroneous ablations overlapping residual tissue to be removed.

5.2.5 Statistical analysis

Multivariate principal component analysis (PCA) was used to investigate broad environmental habitat use patterns between each species across life stages through simultaneously plotting all element concentrations (ppm). PCA's were used to identify differences in trace element abundance across all species in age class 0 (hereafter age 0+), and prenatal growth (as a proxy of pregnant female habitat use). PCA's were only conducted on these two life history phases as all samples could be included, while available sample size would decrease substantially with comparisons of age classes greater than 0+. Separate PCA's were also conducted on samples from each species in northern PNG, southern PNG, and Australia respectively, to allow for better resolution of environmental partitioning within regions between species. This also helped to alleviate issues with different regions likely having different geological characteristics and subsequently different environmental element concentrations. PCA analysis were conducted in the R environment (RStudio Team, 2020) using Factoextra (Kassambara and Mundt, 2020) and FactoMineR (Le et al., 2008) packages, following Kassambara (2017). Due to limitations of sample size, no comparisons between sexes were considered for this study.

5.2.6 Salinity-at-age

Element ratios (Ba:Ca, Li:Ca, Sr:Ca and Sr:Ba) were used to infer the ambient salinity environment at age. Generally, both Sr and Li ions occur in higher densities in marine water (>30 ppt), while Ba occurs at higher densities in freshwater (<5 ppt), hence these elements are commonly used for such interpretations (Kerr and Campana, 2014; McMillan et al., 2017). To investigate changes in these elemental ratios, mean values (± standard deviation) for the prenatal zone and each available age class, for each species, were calculated. Due to ageing difficulties in *A. cuspidata*, only mean elemental ratios were calculated for the pre-natal growth zone, while elemental ratios for each subsequent ablation spot along the post-natal growth axis were presented individually.

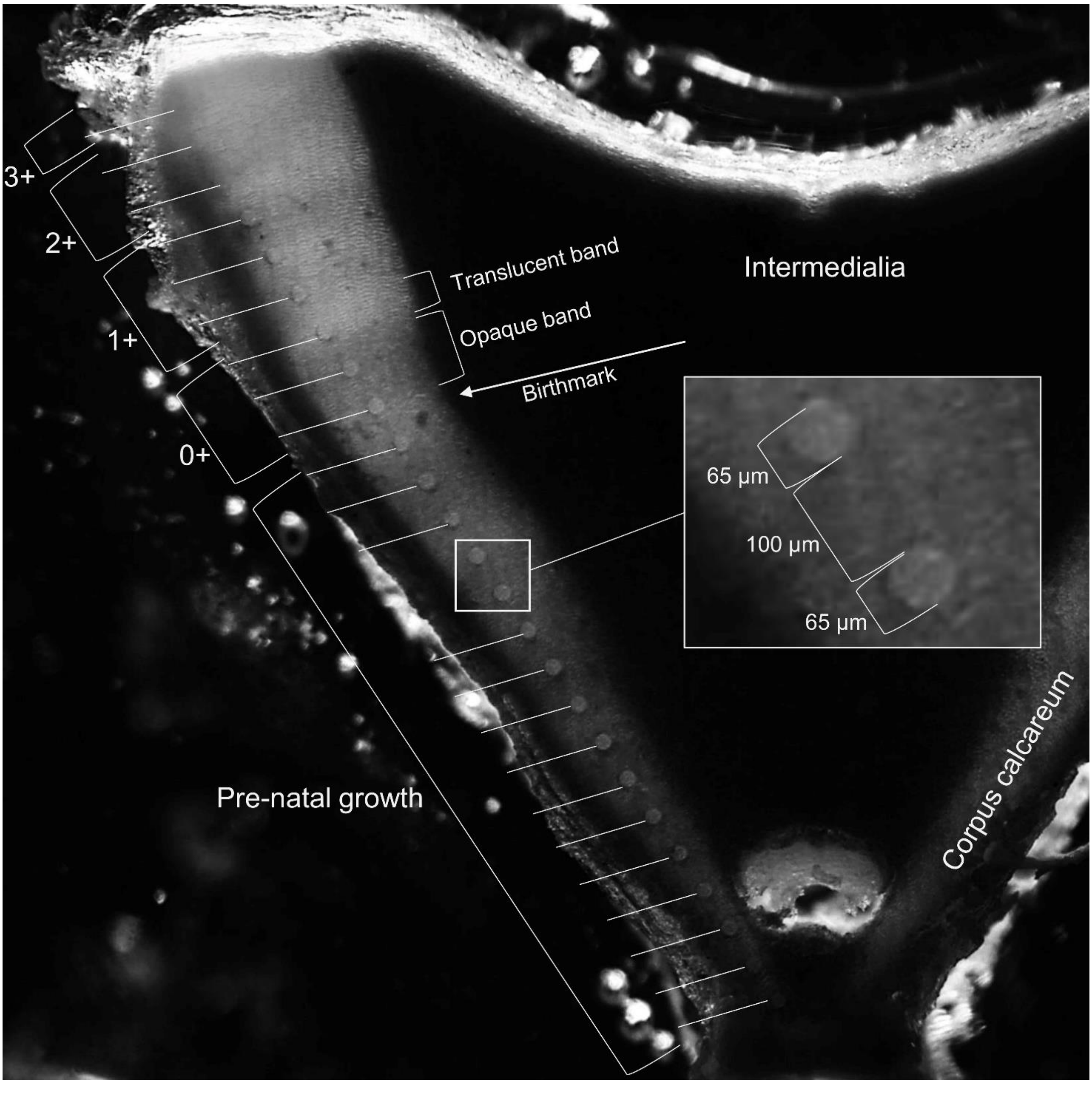


Figure 5. 2 Ablated vertebral section of an immature *Glyphis garricki* (79.2 cm TL) from Papua New Guinea estimated to be 3 years old. Brackets indicate the age class each ablation spot was allocated to, and the location of the birthmark, and first opaque and translucent band pair (collectively approximating one year of growth) are indicated.

5.3 Results

5.3.1 Age estimates

The size of individuals, along with their estimated ages, indicated that most were juveniles and subadults (Table 5.1). Only 1 specimen of each *A. cuspidata* (228.8 cm male), *G. glyphis* (228.0 cm male, 22 years), and *R. australiae* (231.4 cm female, 18 years) were mature. The mature *R. australiae* specimen had large yolked ova (~2–3 cm diameter) although the uterus was not enlarged and flaccid, indicating that pupping had not recently occurred. Estimated ages for *G. glyphis* made available for this study (Kyne, unpubl. data) provide new information on length-at-age, with ages ranging from 0–22 years. All *G. glyphis* with estimated ages of ≤ 11 years were immature (Kyne, unpubl. data), although a lack of size and age classes between 11 and 22 years in this study preclude any further interpretations about size and age at maturity.

Table 5. 1 Length range and estimated ages for each species, from each sample location (indicated in Figure 5.1). n, sample size; TL, total length; NA, not applicable (see 5.2 Methods). Further information on each individuals size, age, and catch location characteristics is provided in Appendix 3 (Tables A3. 1–A3. 2).

Region	Species (n)	Length range (cm TL)	Estimated age classes present (years+)
Australia			
Adelaide River	*G. glyphis* (10)	59.8–189.0	0, 1, 4, 6, 8, 10, 11
	P. pristis (1)	106.0	0
Daly River	*P. pristis* (6)	102.0–121.0	0, 1
West Alligator River	*G. glyphis* (1)	85.0	2
Papua New Guinea			
Aramia River	*P. pristis* (1)	90.0	0
Bismarck Sea	*C. amblyrhynchos* (2)	143.0–144.0	9, 11
	C. falciformis (2)	130.8–147.6	7, 9
Gulf of Papua	*C. coatesi* (4)	73.0–77.0	9, 10, 11
Kikori River	*C. leucas* (1)		2
	G. garricki (9)	74.0–93.4	2, 3, 4, 5
	G. glyphis (6)	59.3–122.0	0, 1, 2, 4
Sepik River	*A. cuspidata* (8)	103.4–222.8	NA
	C. leucas (5)	76.0–157.7	0, 5, 11
	R. australiae (1)	231.4	18
South Fly Coast	*G. garricki* (1)	133.0	6
	G. glyphis (1)	228.0	22

5.3.2 Elemental signatures

5.3.2.1 All species

Differences between species (all regions combined) were observed across elemental signatures in the age 0+ and pre-natal regions of vertebrae, respectively (Figure 5.3). In the age 0+ PCA, species known to use lower salinity environments in juvenile age classes (*P. pristis* and *Glyphis* spp.) were clustered toward the left mainly driven by Ba, and to a lesser extent Pb and Co. Species known to use higher salinity environments (*Carcharhinus* spp. apart from *C. leucas*, and *R. australiae*) were clustered toward the right, mainly driven by Li and Sr. *Anoxypristis cuspidata* was grouped with these marine species. Cu appeared to have high concentrations in the *R. australiae* individual, although it showed very little association to either Ba or Sr as indicated by the almost perpendicular direction of Cu (Figure 5.3). *Carcharhinus leucas* had the widest distribution of all species, overlapping species known to use freshwater (*P. pristis*), estuarine (river sharks), and marine (other species) environments as nurseries. The pre-natal PCA showed the same broad left-right species distribution pattern as the age 0+ PCA, although species were more closely clustered in the pre-natal PCA (Figure 5.3). The species distribution in the pre-natal PCA also indicated differences in ambient salinity environment, with Ba, Zn, and Sr having the highest influence. Between age 0+ and pre-natal PCAs, a notable difference in influence of species groupings were observed between Li (high in age 0+, moderate in pre-natal) and Zn (low in age 0+, high in pre-natal), while little difference was observed in other elements.

5.3.2.2 Northern PNG

In northern PNG, the age 0+ PCA indicated a lack of influence from Ba for *A. cuspidata*, indicating use of a ‘high’ salinity nursery area for this species. Neither *A. cuspidata* or *R. australiae* overlapped with *C. amblyrhynchos* or *C. falciformis*, although *A. cuspidata* displayed some overlap with *C. leucas* (Figure 5.4). This can be interpreted to suggest inshore marine environment use by *R. australiae* and *A. cuspidata*, with *A. cuspidata* additionally using environments overlapping with some juvenile *C. leucas* individuals. The elemental signature of *R. australiae* indicates a different habitat to *A. cuspidata* and *C. leucas*, through higher concentrations of Cu, Pb, and Li. Meanwhile, the small concentration ellipses produced for *C. amblyrhynchos* and *C. falciformis* on the PCA reflect the more stable water chemistry of offshore marine environments compared to inshore and riverine environments used by other species analysed. The large concentration of ellipses produced for *C. leucas* likely reflects some individuals using inshore marine habitats (such as those overlapping with *A. cuspidata*), and others using low salinity environments within the Sepik River indicated by high Ba concentrations.

The pre-natal PCA indicated similar broad habitat use patterns that largely corresponded to age 0+ (Figure 5.4). The most notable difference was a much larger concentration ellipse on the PCA for *A. cuspidata*, driven mainly by Co and Cu. A larger concentration ellipse was also apparent for *C. leucas*, however Ba and Pb were the main varying elements. Little difference between *C. amblyrhynchos* and *C. falciformis* was observed, again likely reflecting the relative elemental homogeneity of offshore marine environments. Overall, Sr and Li had a substantially smaller effect on the pre-natal PCA compared to the age 0+, with only *C. leucas* additionally showing use of lower salinity environments.

5.3.2.3 Southern PNG

In the age 0+ PCA, there was a clear separation of euryhaline species from *C. coatesi*. This was due to higher Ba in the euryhaline species, while *C. coatesi* had higher Li, As, Sr, and Zn (Figure 5.5). The three data points for *P. pristis* were separated from other euryhaline species due to higher Ba, Pb, and Cu. Juvenile *G. garricki* individuals from the Kikori River and South Fly Coast had overlapping elemental compositions, while juvenile *G. glyphis* from these same respective regions were more separated, mainly due to higher concentration of Cu and Pb from the South Fly Coast. Sample size was however limited to one individual of *G. garricki* and *G. glyphis* from the South Fly Coast. Within the Kikori River, these river shark species were generally clustered around the same area on the PCA. However, *G. garricki* had a more vertically orientated concentration ellipse due to Ba, indicating some additional use of lower salinity environments, while *G. glyphis* had a more horizontal concentration ellipse due to Li, As, Zn, and Sr, indicating some additional use of higher salinity environments. The *C. leucas* individual from the Kikori River displayed an elongated concentration ellipse along the axis of Cu, Pb and Co, although most data points clustered tightly among the river shark individuals from the Kikori River.

The same general pattern was observed in the pre-natal PCA, with *C. coatesi* being separated from other euryhaline species due to higher Sr, As, and Li, while lacking Ba (Figure 5.5). However, there was slightly more overlap between *C. coatesi* and euryhaline species compared to the age 0+ PCA. Pb had the highest influence in the pre-natal PCA over ambient environmental salinity indicators (Ba, Sr, and Li), suggesting similar environmental use with respect to salinity across this life stage among species. *Pristis pristis* only marginally overlapped with other euryhaline species, with higher Ba concentrations suggesting a closer association to lower salinity habitats. *Glyphis garricki* from the Kikori River and the South Fly Coast showed high overlap, with concentration ellipses having similar shape and orientation on the PCA. The concentration ellipse of both river sharks and the *C. leucas* individual broadly overlapped, suggesting a generally similar habitat use between these species at this life stage.

5.3.2.4 Northern Australia

In both age 0+ and pre-natal PCAs, *G. glyphis* was distinctly separated from *P. pristis* (Figure 5.6). *Glyphis glyphis* from the Adelaide and West Alligator Rivers had higher Li and Sr concentrations suggesting use of higher salinity environments compared to *P. pristis* (which had higher Ba) at each life stage analysed. The concentration ellipse of age 0+ *G. glyphis* in the Adelaide River was orientated broadly along the Ba, and, Li and Sr axis, while the single individual analysed from the West Alligator River showed tight clustering. In the pre-natal PCA, the concentration ellipse of *G. glyphis* from both rivers were almost perpendicular to the Ba, and Li and Sr axis, suggesting use of a more stable environment with respect to salinity (Figure 5.6).

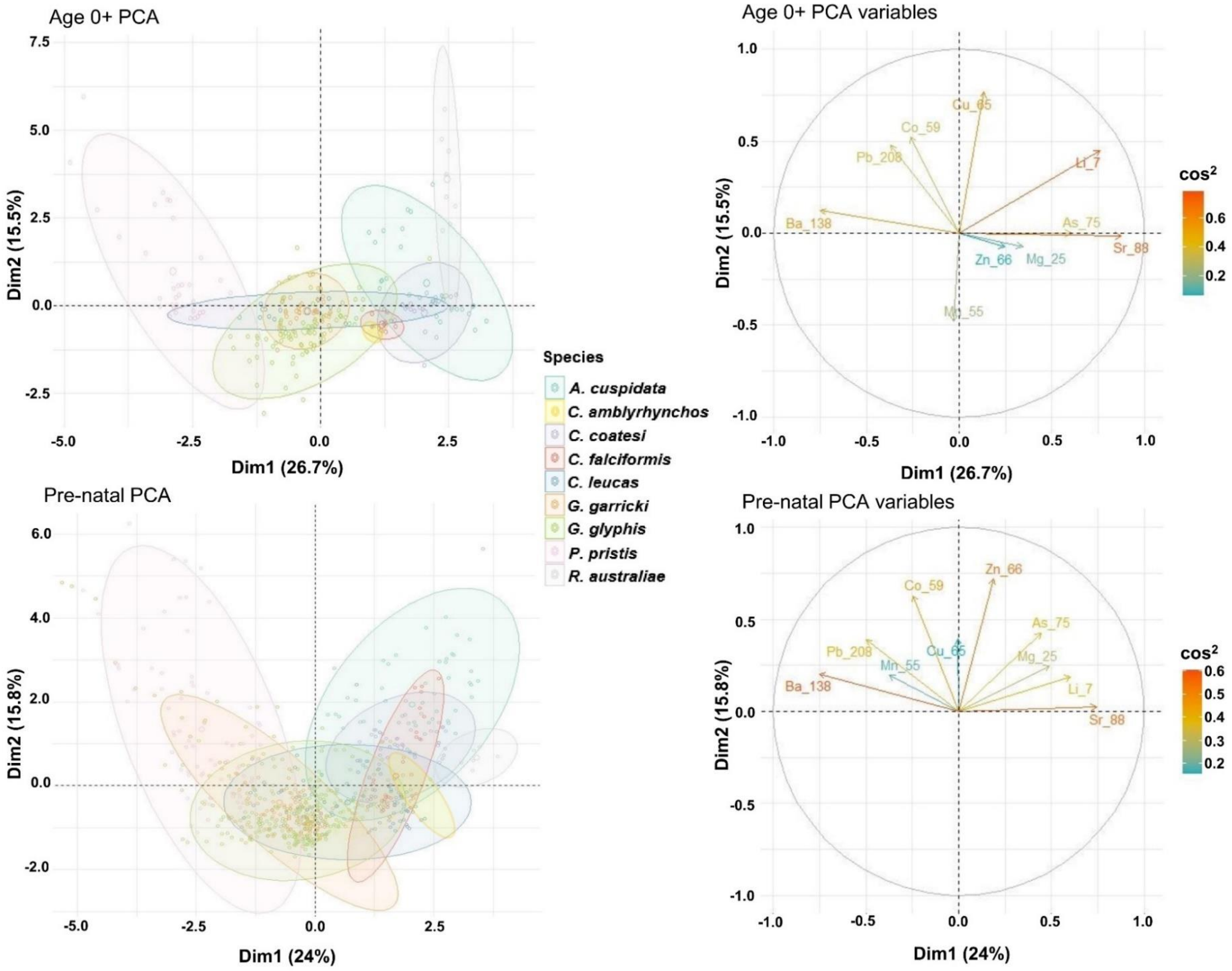


Figure 5. 3 Left; Principal component analysis of LA-ICP-MS results in the age 0+ and pre-natal vertebrae zone for each species (all regions combined). Right; Contributing variables to each principal dimension. Cos^2 values closer to one indicate larger contributions.

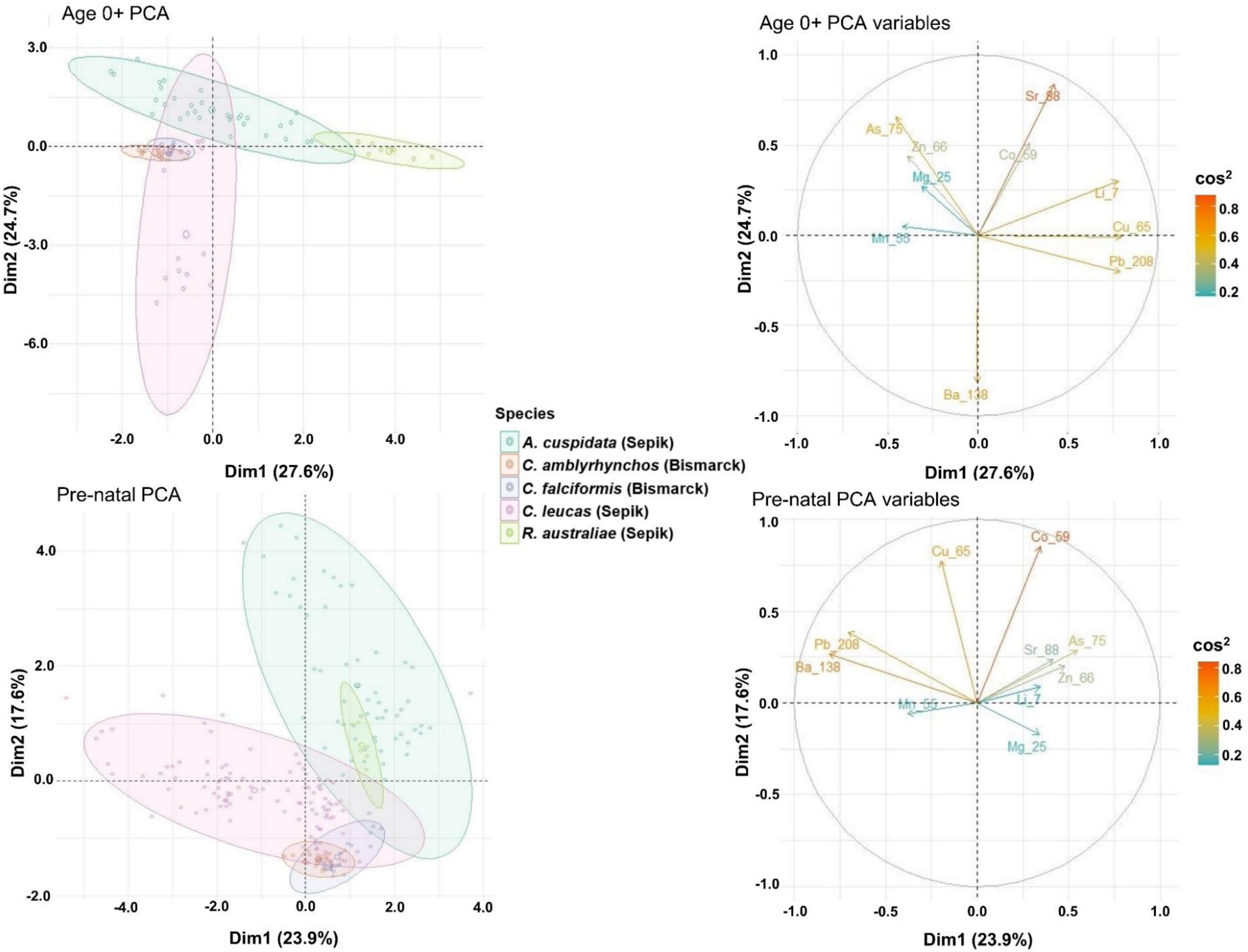


Figure 5. 4 Left; Principal component analysis of LA-ICP-MS results in the age 0+ and pre-natal vertebrae zone for each species from northern Papua New Guinea. Right; Contributing variables to each Principal dimension. Cos^2 values closer to one indicate larger contributions.

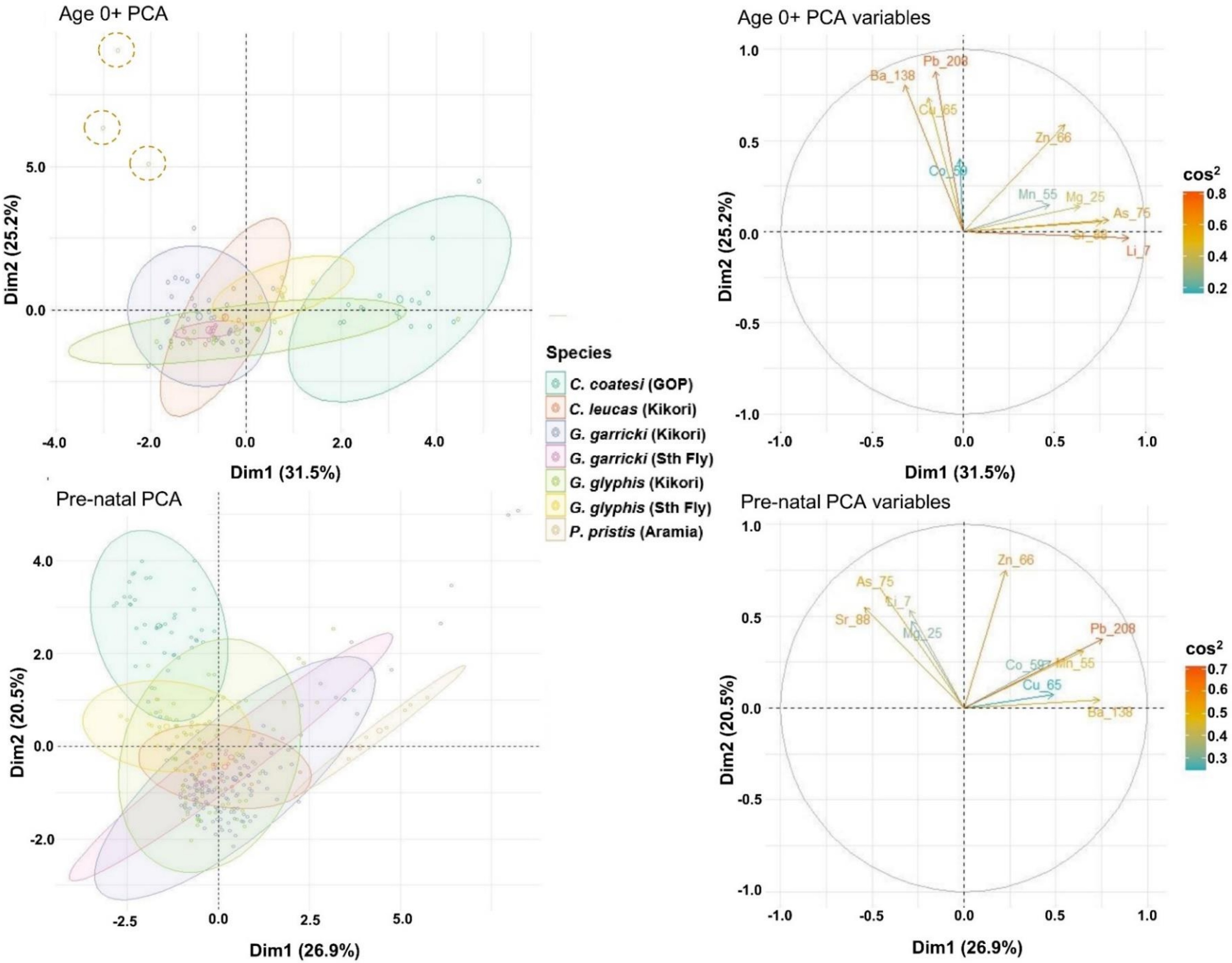


Figure 5. 5 Left; Principal component analysis of LA-ICP-MS results in the age 0+ and pre-natal vertebrae zone for each species from southern Papua New Guinea. Right; Contributing variables to each Principal dimension. Cos^2 values closer to one indicate larger contributions. A lack of data points precluded plotting of a concentration ellipses for Pristis pristis in the Aramia River.

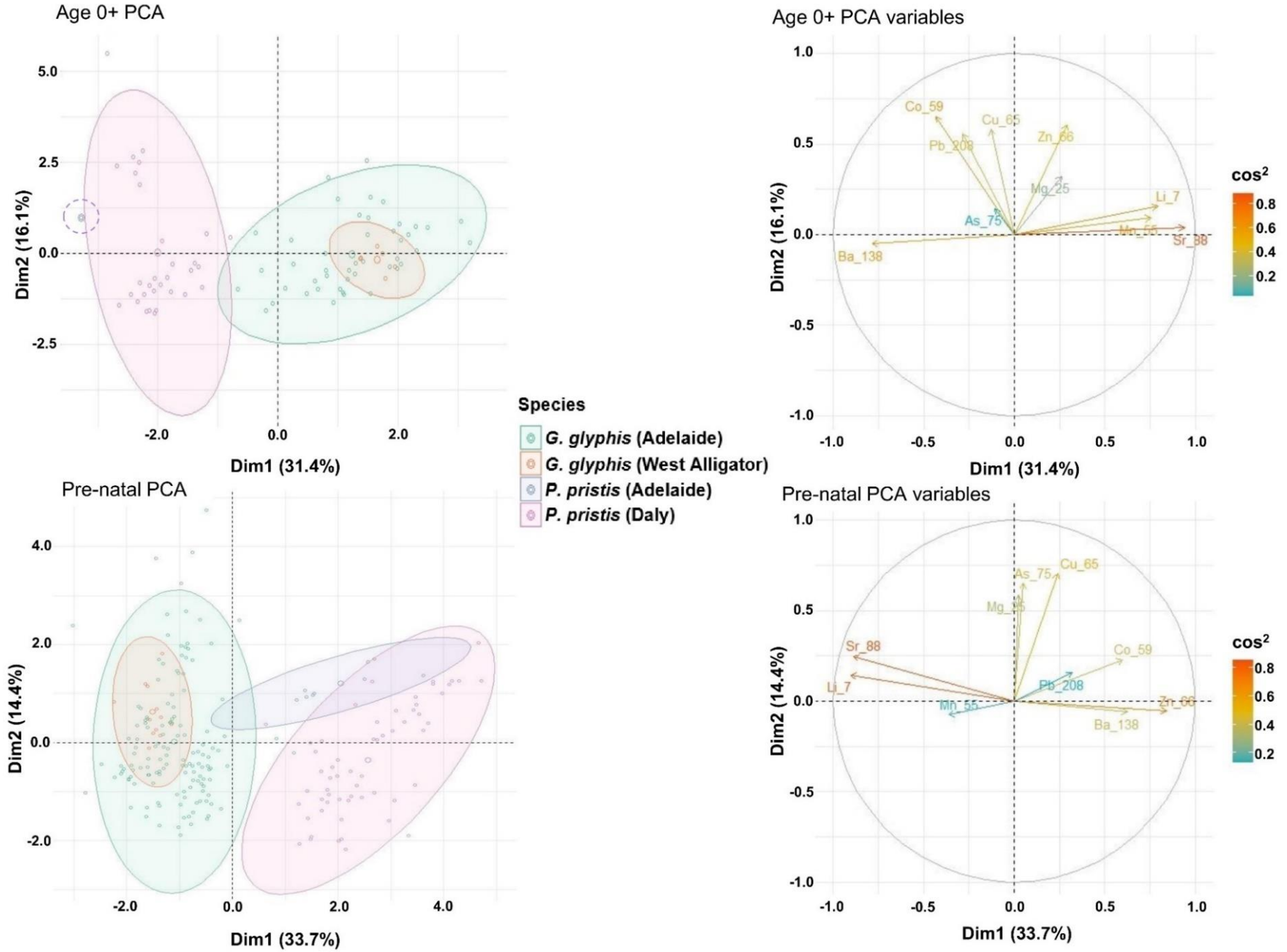


Figure 5. 6 Left; Principal component analysis of LA-ICP-MS results in the age 0+ and pre-natal vertebrae zone for each species from Australia. Right; Contributing variables to each Principal dimension. Cos^2 values closer to one indicate larger contributions. A lack of data points precluded plotting of a concentration ellipses for *Pristis pristis* in the Adelaide River

5.3.3 Environmental salinity-at-age

Elemental ratios used as ‘ambient environmental salinity indicators’ along the growth transect generally showed corresponding patterns among species. In each region, species with higher Ba:Ca ratios almost always had lower Li:Ca, Sr:Ca, and Sr:Ba ratios compared to other species. Any changes in mean ratio values along the growth transect were generally observed to occur at corresponding ages for each element ratio.

In northern PNG, lower Ba:Ca, and higher Sr:Ca and Sr:Ba supported use of lower salinity environments for *C. leucas* across immature age classes in comparison to other species (Figure 5.7). In particular, Ba:Ca and Sr:Ca showed inversely corresponding patterns. While Li:Ca also supported use of lower salinity environments, differences between *C. leucas*, and *C. amblyrhynchos* and *C. falciformis* were less pronounced, while *R. australiae* had much higher values compared to these carcharhinids in all age classes. For *C. leucas*, there was also a clear shift in element ratio between pre-natal and natal growth, with the pre-natal values being similar to the other marine species. *Carcharhinus amblyrhynchos* and *C. falciformis* generally had similar and stable elemental ratios, though differences were observed for Sr:Ba. A large range in Sr:Ba values were observed for *C. falciformis*, varying from ~1000 ppm to ~2000 ppm during pre-natal to age class 3+, before decreasing to ~1200 ppm in the 8+ age class.

The ablation transects of *A. cuspidata* showed some variation in values for element ratios with the exception of Sr:Ca, which was relatively uniform across individuals (Figure 5.8). Ba:Ca values generally ranged from $1.0•10^{-5}$–$2.0•10^{-5}$ ppm, which were similar to values of *R. australiae*. Two individuals of 147.0 cm TL and 103.4 cm TL had large Ba:Ca values approaching $4.0•10^{-05}$ ppm toward the distal edge of their respective vertebrae, which were close to the lower values observed in juvenile age classes of *C. leucas*. Sr:Ba values across individuals ranged considerably, indicating that some individuals were using higher salinity environments (values of 450–700 ppm are comparable to *R. australiae* and *C. amblyrhynchos*, Figure 5.7) while others were using lower salinity environments, although these lower values were slightly higher than those obtained for *C. leucas*. The only notable shift in element ratios between pre-natal and post-natal growth observed for *A. cuspidata* was Li:Ca being consistently lower in the pre-natal life stage compared to post-natal growth.

In southern PNG, *C. coatesi* was clearly separated from the euryhaline species, through low Ba:Ca ratios, and high Li:Ca, Sr:Ca, and Sr:Ba ratios (Figure 5.9). Within the euryhaline species (all other species), *P. pristis* was separated from the river sharks and *C. leucas* through higher Ba:Ca and lower Li:Ca and Sr:Ba ratios. This indicates use of lower salinity environments by *P. pristis* in pre-natal and age 0+ life stages. Although, no differences were observed for Sr:Ca between *P. pristis* and other euryhaline species. In each corresponding age class, the *G. glyphis* individual from the South Fly Coast had a higher Ba:Ca ratio compared to conspecifics and other euryhaline species from the Kikori River. However Li:Ca and Sr:Ca ratios were higher than those observed for the same species in the Kikori River, giving contrasting results of lower and higher environmental salinity habitat use, respectively. A notable shift in all element ratios excluding Sr:Ca was observed at age 8+ in the South Fly Coast *G. glyphis* individual, indicating a distinct change in environment at this age class. This change corresponded to pre-natal values for Ba:Ca and Sr:Ba, though not Li:Ca, while Sr:Ca was relatively uniform throughout this individuals' life. No 'return' to juvenile habitat was observed in subsequent age classes. All river shark and *C. leucas* individuals from the Kikori River had very similar element ratios across pre-natal and natal growth, indicating no major differences in use of differing environmental salinity habitats. The exception was high pre-natal Li:Ca values in *G. glyphis*, although no corresponding pattern of low Ba:Ca was observed, while only a moderate, though corresponding decrease in Sr:Ba was observed.

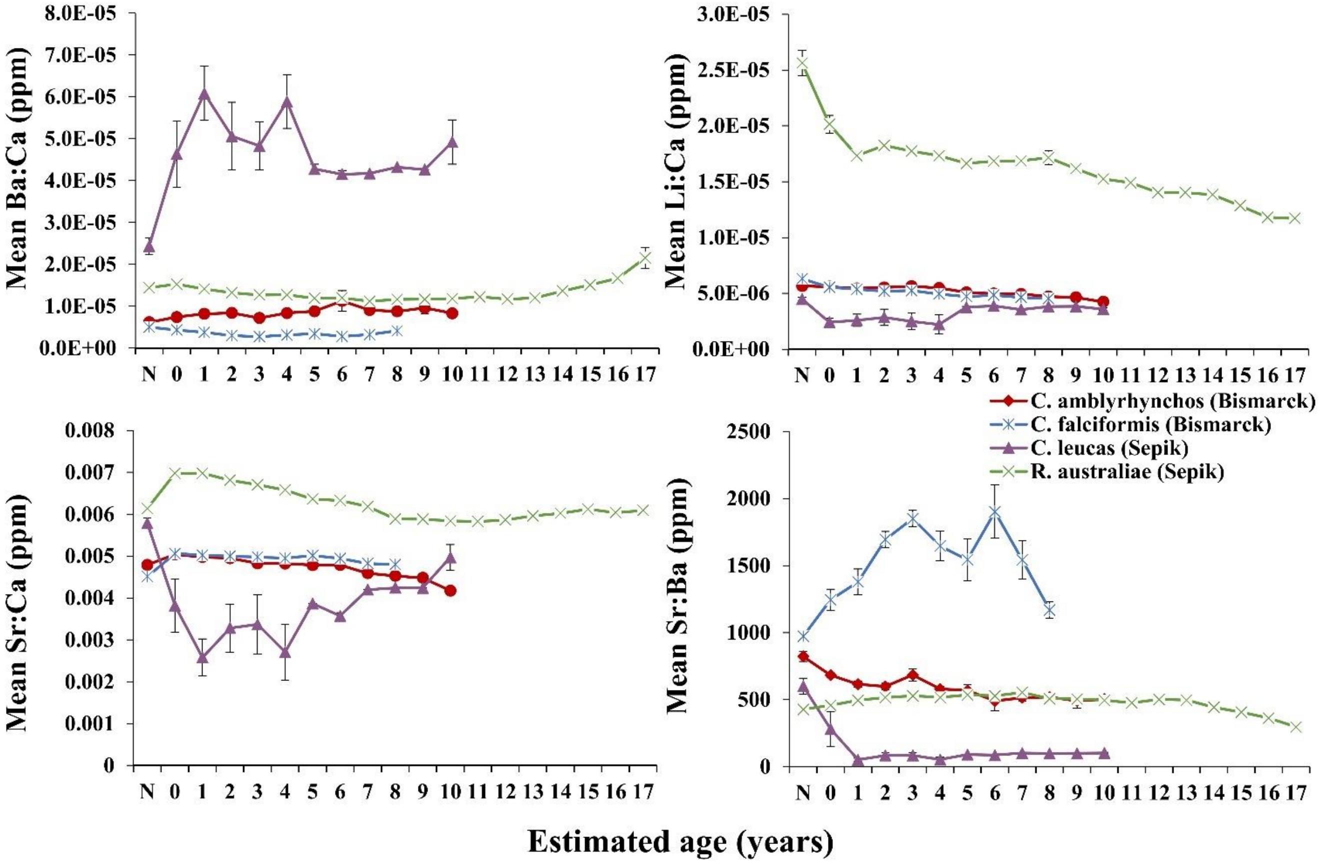


Figure 5. 7 Mean element ratio values in each age class for 'environmental salinity' indicating elements in species from northern Papua New Guinea. N, pre-natal vertebrae zone.

In northern Australia, all element ratios indicated that *P. pristis* individuals were occurring at lower environmental salinities than *G. glyphis* (Figure 5.10). While only *G. glyphis* individuals from the Adelaide River had age classes greater than 1+, element ratios did not change substantially across age classes analysed. A large decrease in Sr:Ba was observed for the individual from the West Alligator River between pre- and post-natal growth, although only small corresponding changes were observed for Ba:Ca and Li:Ca, while there was a small increase in Sr:Ca. For *P. pristis*, element ratios suggested movement to lower salinity habitats following birth, except for Li:Ca. Pre-natal values of *P. pristis* in the Adelaide River suggest use of an environmental salinity similar, or slightly lower in salinity than observed for *G. glyphis* also from the Adelaide River.

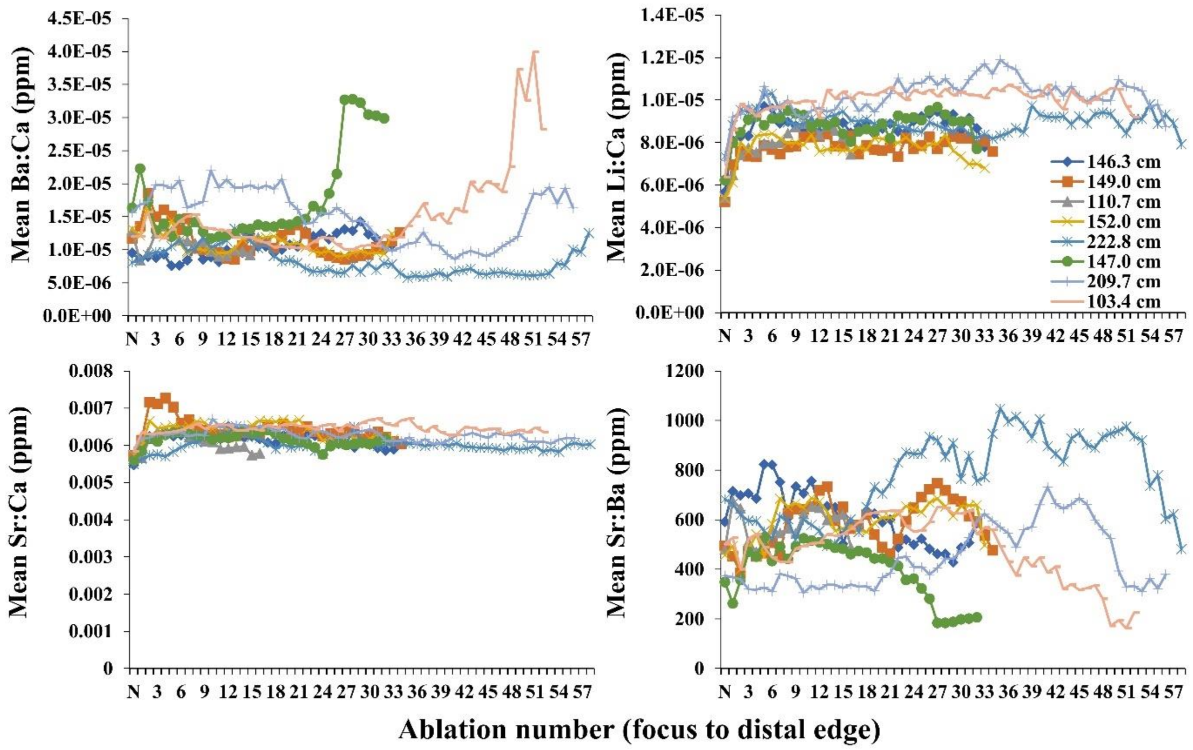


Figure 5. 8 Element ratio values for 'environmental salinity' indicating elements in *Anoxypristis cuspidata* from northern Papua New Guinea. Due to difficulties in identifying the band pairs proceeding the birthmark, mean pre-natal values (N) are plotted, followed by elemental ratio values in each successive ablation spot toward the distal edge. Total lengths of each individual are indicated.

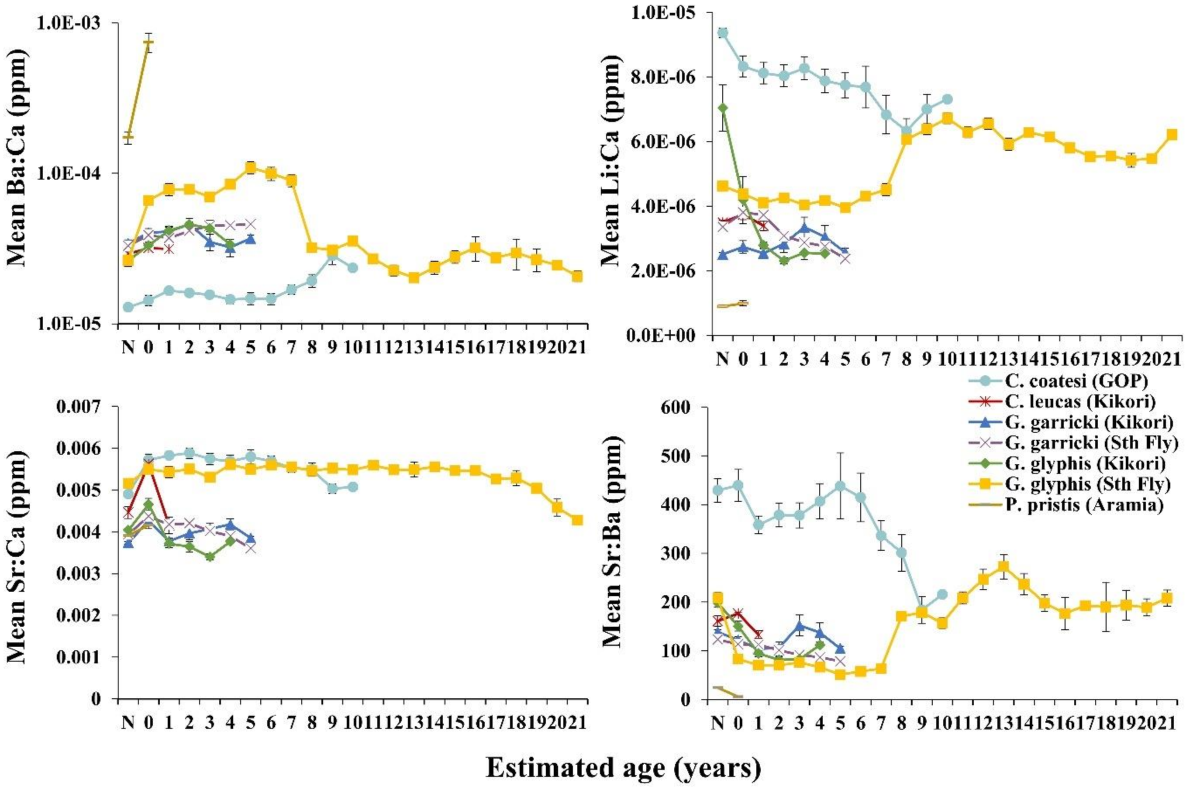


Figure 5. 9 Mean element ratio values in each age class for 'environmental salinity' indicating elements in species from southern Papua New Guinea. N, pre-natal vertebrae zone.

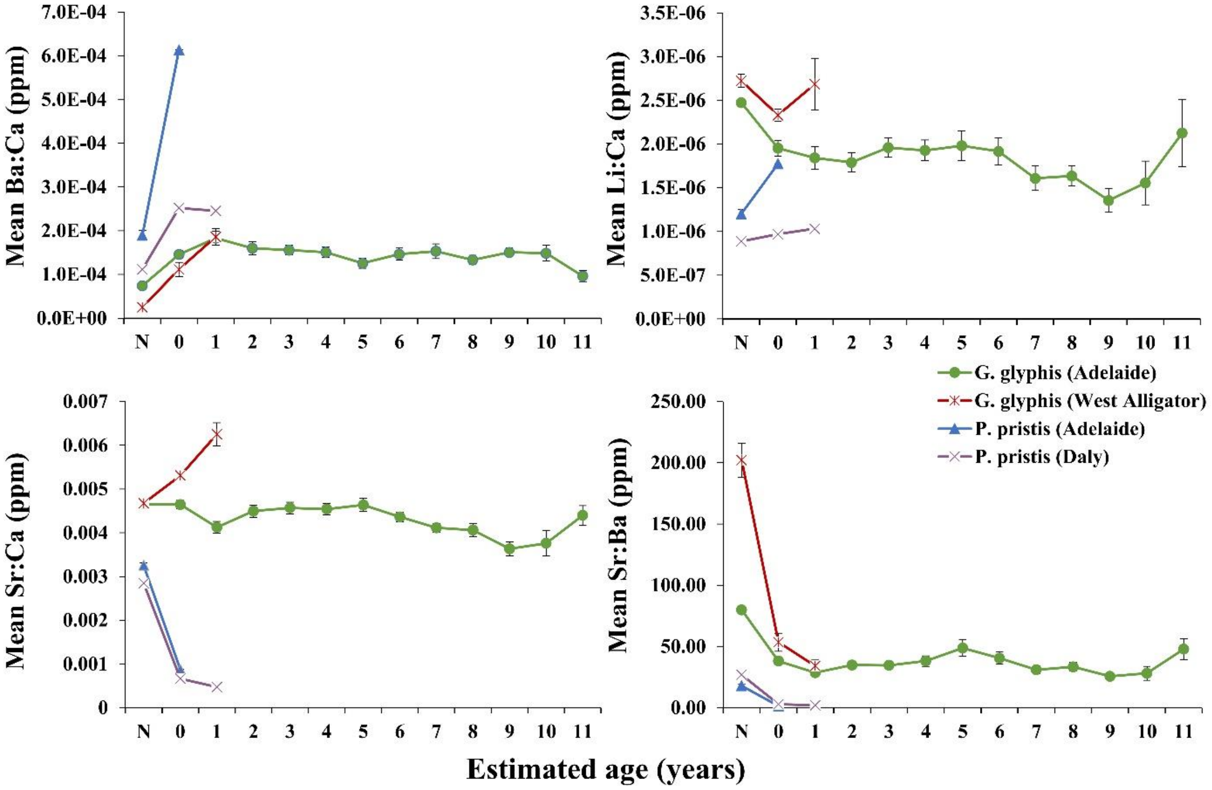


Figure 5. 10 Mean element ratio values in each age class for 'environmental salinity' indicating elements in species from Australia. N, pre-natal vertebrae zone.

Between pre- and post-natal growth for *P. pristis*, Sr:Ba values were higher in the pre-natal growth zone for individuals in each of the three locations (Figure 5.11). A sharp decrease in Sr:Ba values was observed between the last two pre-natal ablation points for all individuals in each location. Only two individuals, one in each of the Daly and Aramia Rivers, continued to show a decrease in Sr:Ba following birth in the post-natal zone. Sr:Ba values were stable in the post-natal zone indicating use of a freshwater environment with no marine influence. Differences in the number of ablation points in the pre-natal zone were due to differences in the size of vertebral centra between individuals.

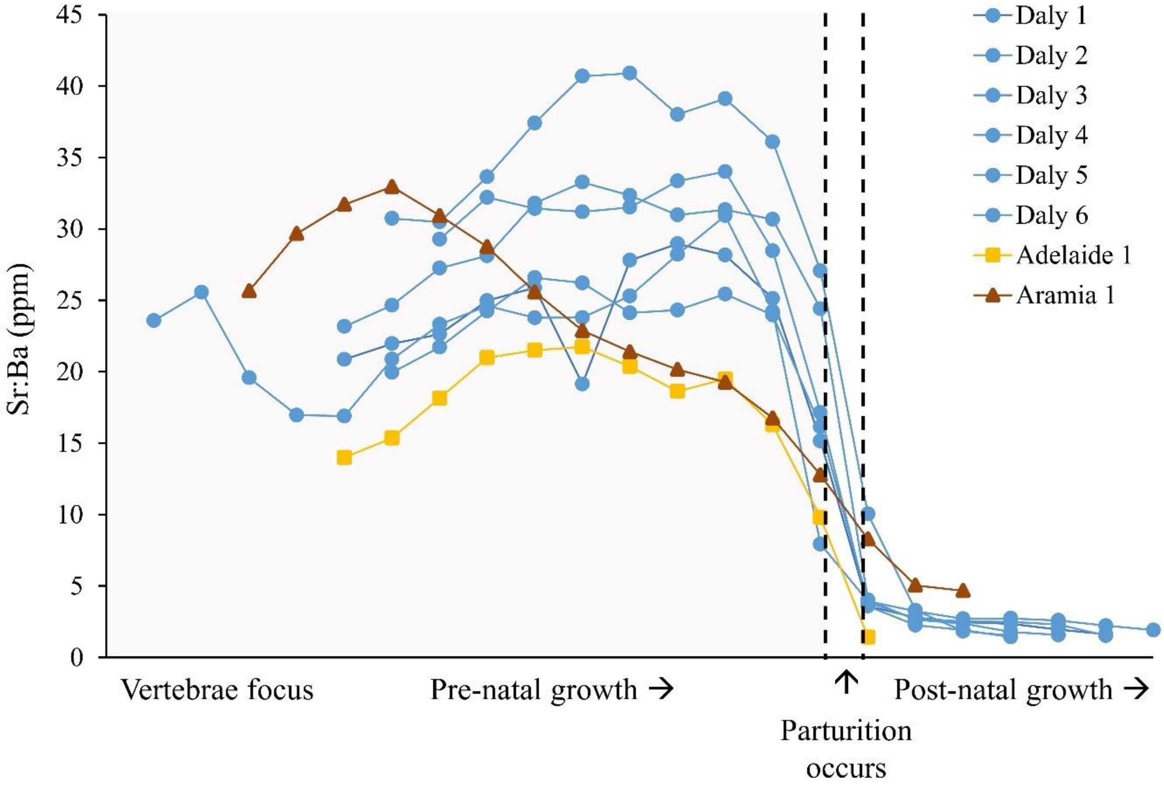


Figure 5. 11 Sr:Ba values for *Pristis pristis* individuals in the Daly and Adelaide Rivers in Australia, and Aramia River in Papua New Guinea. For each individual, Sr:Ba values are plotted from the focus to the distal edge of the vertebrae. The black dotted lines represent the period in between the last ablation spot falling in the pre-natal zone, and the first ablation spot falling in the post-natal zone along the growth direction transect.

5.4. Discussion

The elemental signatures across species corresponded well to the type of environment (freshwater, estuarine, or marine) that each species is known or suspected to use in juvenile age classes. Of the nine species analysed there were clear groupings of species into those that use: freshwater (*P. pristis*); estuarine environments encroaching on freshwater (*G. garricki* and *G. glyphis*); inshore marine environments (*A. cuspidata*, *C. coatesi*, and *R. australiae* – with *A. cuspidata* possibly encroaching into estuarine environments); and offshore marine environments (*C. amblyrhynchos* and *C. falciformis*). Meanwhile *C. leucas* had an elemental signature that indicated different individuals were using environments ranging from upper estuary encroaching on, or even into freshwater, through to inshore marine. In the pre-natal vertebrae zone, there were four groups that were apparent: estuarine encroaching on freshwater (*P. pristis*); estuarine encroaching into marine (*G. garricki*, and *G. glyphis*); marine (*A. cuspidata*, *C. amblyrhynchos*, *C. coatesi*, *C. falciformis*, and *R. australiae*); and a combination of marine and estuarine (*C. leucas*). PCAs indicated a broader distribution of elements for species in freshwater, estuarine, and inshore marine environments, compared to *C. amblyrhynchos* and *C. falciformis* samples that were obtained offshore in the Bismarck Sea. These groupings indicate that each environment type has differing elemental signatures that have influenced the elemental composition of vertebrae analysed. Barium was the main indicator of freshwater environments (evidenced by high levels in juvenile *P. pristis*), while Sr and secondarily Li were the main indicators of marine environments (indicated by high levels in a range of marine species analysed). Furthermore, PCAs consistently showed a strong inverse relationship between Ba, and Sr and Li concentrations. These results assert that relationships known to exist between environmental elements used as 'salinity' indicators (i.e. Ba, freshwater; Li and Sr, marine) and their relative concentration in diadromous fish otoliths (e.g. Gillanders, 2005; Walther and Thorrold, 2006), are reflected in the vertebrae of multiple elasmobranch species.

With investigations into diadromous movements of elasmobranchs using elemental analysis techniques being very limited (e.g. Otake et al., 2005; Tillett et al., 2011; Scharer et al., 2012; Feitosa et al., 2021), this study also demonstrates that a frame of reference is needed to make inferences about elemental concentrations in vertebrae and environment. In the present study, investigations into the use of non-marine environments were achieved by testing elemental ratios of multiple species with known association with freshwater (juvenile *P. pristis*) and marine (e.g. *C. coatesi*) environments, and comparing to species with less understood environmental use patterns. Alternative approaches could analyse elemental composition of water across a salinity spectrum of local environments, or incorporate time series measurements of local physical water parameters over the corresponding temporal period of animal growth (e.g. use of temporal salinity data in Scharer et al., 2012). However, physiological processes leading to element incorporation in elasmobranch vertebrae requires further research, as do relative elemental concentrations between vertebrae and the ambient environment (Pistevos et al., 2019). Furthermore, elemental analysis of vertebrae from historic collections may create logistical difficulties in collection of water samples or relevant data on temporal physical environmental parameters. Until further information is available on these factors, comparisons of species from different environments provide a suitable basis for inferring environmental use patterns for less understood species. An implicit assumption in the present study is that physiological processes leading to incorporation of environmental elements into vertebrae are reasonably consistent across species and family groups. The 'all species' PCA also assumed that environmental element concentrations are relatively similar among river basins, and between Australia and PNG. This is unlikely to be true due to differing geological characteristics across the sample locations (e.g. Martin and Meybeck, 1979) and therefore, subsequent data analysis was presented in three broad regions (northern PNG, southern PNG, and northern Australia), where large differences in environmental element concentrations due to geological characteristics would likely be less pronounced. Fittingly, the two main principal components were consistently higher in the regional PCAs compared to the 'all species' PCA, although it is not possible to determine whether this was due to finer spatial resolution, or differences in the number of species being concurrently analysed.

While this study generally found congruence between salinity indicating elements, in some instances Sr:Ca remained stable despite fluctuations in Ba:Ca, Li:Ca, and Sr:Ba along the growth axis. For example, there was a lack of a freshwater signal from Sr:Ca for *P. pristis* in the Aramia River, a lack of variation from Sr:Ca for *A. cuspidata* despite fluctuations in Ba:Ca and Sr:Ba at the Sepik River, and Sr:Ca also failed to show the movement into a more marine environment in the adult *G. glyphis* from the South Fly Coast. To our knowledge, no other studies investigating diadromous movements of elasmobranchs through elemental analysis have presented data on changes in each of Ba:Ca, Li:Ca, Sr:Ca, and Sr:Ba. All studies have presented data for only one (Sr:Ca, Otake et al. 2015; Peverell 2009; Scharer et al. 2012. Sr:Ba, Tillet et al. 2011) or two (Ba:Ca and Sr:Ca, Feitosa et al. 2021), making comparisons of our present observations within literature difficult. Data presented by Feitosa et al. (2021) for the longnose stingray (*Hypanus guttatus*) did show one individual (from an n = 3) exhibiting fluctuations of Ba:Ca, with limited congruent fluctuation in Sr:Ca. Similarly Hegg et al. (2021) through experimental analysis of rostral teeth found a lack of fluctuations in Sr:Ca, despite fluctuations in Ba:Ca and Sr:Ba (although there is presently no substantial evidence that rostral teeth can be used for ageing purposes). In the teleost literature, the relationship between ambient salinity and Sr:Ca is generally positive, although there are studies that show a negative, or no apparent relationship (see Gillanders, 2005, for futher discussion on Sr:Ca relationships; Elsdon et al., 2008). A plausible explanation for the lack of fluctuation in Sr:Ca, despite fluctuation in other salinity indicating elements, may be differing geological characteristics between sample source river basins. For example, the Aramia River *P. pristis* and South Fly Coast *G. glyphis* individuals were collected from habitats highly influenced by the Fly River Basin. It is possible that the Fly River Basin has ambient freshwater Sr concentrations that are more similar to marine environments. Ambient marine Sr concentrations are relatively stable globally, while freshwater Sr concentrations can vary substantially across temporal and spatial scales (Elsdon et al., 2008). The lack of Sr:Ca fluctuation for the Sepik River *A. cuspidata* is more complex, as congruent fluctuations between Sr:Ca and other salinity indicating elements were observed for *C. leucas* samples also from the Sepik River. The discrepancy in *A. cuspidata* Sr:Ca ratios may be attributed to their predominant use of very shallow inshore marine environments (See *4.2 Sawfish life history environmental habitat use patterns*), that may be influenced by direct terrigenous rainfall runoff from the shoreline, rather than outflow from the Sepik River. Collectively, this again highlights our present lack of understanding about factors influencing incorporation of different elements, and their relative concentration, into vertebrae. It is suggested that consideration of other salinity indicating elements (i.e. Ba and Li) in addition to Sr:Ca are used in future investigations of diadromous movements of elasmobranchs until influencing factors are better understood. Given the consistently inverse relationship between Sr and Ba across the various species and sample locations in the present study, it appears that Sr:Ba ratios provide the most reliable insights into diadromous life history movements of elasmobranchs.

5.4.1 River shark life history environmental habitat use patterns

Elemental signatures indicated that immature individuals of both river shark species used predominately estuarine environments. No overlap with freshwater or marine species occurred for either river shark species. The 'salinity at age' analysis indicated that *G. garricki* in PNG remain within low salinity environments for at least five years, while *G. glyphis* appeared to remain within low salinity environments for eight years in southern PNG, and for at least 11 years in the Adelaide River. However, it is worth noting that adults from the Adelaide River were not available in this study to compare their environmental element signatures. During this period of prolonged lower salinity environment use, there was little fluctuation in salinity indicating elements. This is consistent with movement studies, where *G. glyphis* demonstrated long-term movements to remain within particular salinity ranges in response to seasonal rainfall (Lyon et al., 2017; Dwyer et al., 2020). Furthermore, short term movements of *G. glyphis* (Pillans et al., 2009; Dwyer et al., 2020) appear to be tidally assisted over small spatial ranges (~12-14 km), which may also be linked to environmental preferences. The salinity-at-age analysis of *C. leucas* from the Sepik River, did not show a pronounced movement into a more marine influenced environment like the adult *G. glyphis* in southern PNG did at age 8+. However, the Li:Ca and Sr:Ca ratios indicated that by four years old, this *C. leucas* individual was likely using environments with increased marine influence at least intermittently. A similar pattern of gradual shifting to marine environments by age 2–4 *C. leucas* has also been observed in northern Australia (Thorburn and Rowland, 2008; Tillett et al., 2011). Like river sharks, juvenile *C. leucas* also show long-term seasonally driven movements within their juvenile environments, and a restricted short-term spatial use pattern of up to ~14 km within estuaries during their first couple of years (Heupel et al., 2010). Collectively this indicates that juveniles of river sharks and *C. leucas* are similar in that they both use a small spatial scale within their juvenile riverine environments, although river sharks appear to have a much more prolonged occupation of these environments. Furthermore, *C. leucas* appears to have a greater ability to use a wider range of environments, including freshwater to marine, in juvenile age classes (e.g. catch locations in Thorburn et al., 2003), while river sharks appear to strictly require estuarine environments from juvenile to at least subadult age classes (Chapter 4; Pillans et al., 2009; Lyon et al., 2017; Dwyer et al., 2020). The broader diversity of juvenile *C. leucas* environment use suggests a greater portfolio effect (Yates et al., 2012) in recruitment to the adult population compared to river sharks.

There is limited information available on interspecific differences in riverine habitat use between *G. garricki* and *G. glyphis*. The salinity-at-age analysis suggest a general overlap in the Kikori River. Differences between each species on the South Fly Coast indicated that some differing habitat use may have been occurring (likely within the lower Fly River), with Ba:Ca, Sr:Ca, and Li:Ca indicating that *G. glyphis* used a marginally more marine influenced habitat, while Sr:Ba suggested a very similar habitat use. In northern Australia, *G. garricki* juveniles have been observed in salinities ranging 2–36 ppt (Thorburn and Morgan, 2004; Pillans et al., 2009), and *G. glyphis* have been observed in salinities ranging 0.4–28 ppt (Pillans et al., 2009; Dwyer et al., 2020). Although, there are issues with extrapolating environmental preferences from single salinity measurements in tidally influenced estuarine systems. Regardless, it appears that juvenile river sharks are able to tolerate salinities ranging from freshwater (<5 ppt) to marine (≥30 ppt), and the present study indicates they preferentially use salinities within the estuarine range (≥5 – <30 ppt), except in King Sound where most observations of *G. garricki* (Morgan et al., 2011) are in marine salinities (>30 ppt) (these environmental salinity categorisations follow Chapter 2). This indicates that differing local factors (e.g. environmental availability, interspecific competition, and predation risk) influence juvenile habitat use patterns across different river systems. However, unlike *C. leucas*, there are presently no records of river sharks beyond the tidal influence in upstream freshwater environments. Dwyer et al. (2020) recently found interspecific habitat segregation between juvenile *G. glyphis* (lower estuary, mean salinity 19.22 ppt) and *C. leucas* (upper estuary, mean salinity 1.99 ppt) in a communal estuary in the Wenlock River, northern Australia. Habitat segregation between river sharks and *C. leucas* also appears to occur in southern PNG rivers, as catch in lower estuarine delta environments is dominated by river sharks with only a few *C. leucas* being concurrently caught, despite being observed further upstream (Chapter 4). It would be expected that *G. garricki* and *G. glyphis* would segregate at either a spatial or trophic level in communal areas, and the combination of methods used by Dwyer et al. (2020) would likely be effective in capturing any differences.

This study also indicated differences in adult habitat use between river sharks and *C. leucas*, through analysis of pre-natal vertebrae zones. Individuals of both river shark species had pre-natal elemental signatures that partially overlapped *C. coatesi* and *A. cuspidata* (both presumably using inshore marine environments), although the higher concentration of Ba in the river sharks suggests greater overlap with estuarine environments. Meanwhile, the pre-natal elemental signature of *C. leucas* indicated substantial overlap with both river sharks, but also substantial overlap with *A. cuspidata*, *C. coatesi*, *C. amblyrhynchos*, and *C. falciformis*. Adult *C. leucas* are observed in a range of riverine, inshore, and offshore environments (e.g. White et al., 2020; Espinoza et al., 2021), and this diversity of adult environment use is reflected in the broad pre-natal elemental signature across individuals. While these pre-natal elemental signatures are inherently restricted to pregnant females only, it is interesting that the complete spectrum of environments known to be used by adult *C. leucas* was observed. Assuming that the complete spectrum of environments used by adult female river sharks are also represented, these results suggest that adult female river sharks have a more restricted environmental range (estuarine encroaching on marine), compared to adult female *C. leucas*. Furthermore, the environment shift observed in the adult male *G. glyphis* from southern PNG appeared to also indicate use of lower estuarine environments rather than marine. From the *G. glyphis* samples in northern Australia, the pre-natal zone had low Sr:Ba values (~75 ppm) in the Adelaide River, which were lower compared to the individual from West Alligator River (~200 ppm in the pre-natal growth phase). While it is difficult to put these values in context to those that would be expected in the inshore marine environments of the Van Diemen Gulf, the pre-natal values in the West Alligator River are similar to the highest river shark Sr:Ba values observed in southern PNG. The present indication from these results is that adult river sharks are primarily using lower estuaries and river outflow influenced inshore environments, and not venturing into non-river influenced inshore or offshore environments for prolonged periods like *C. leucas*. However, recent genetic population structure studies on *G. garricki* (Devloo-Delva et al. *In*

Press) and *G. glyphis* (Kyne et al., 2021a) indicate that some dispersal does occur for both species between river systems that would require transit through marine environments. Moreover, there is a single observation of an adult *G. garricki* in the Wessel Islands, Northern Territory, further substantiating that use of marine environments, for at least transiting between riverine environments, does occur (Pillans et al., 2009).

Historically, there has been an acute lack of knowledge about environmental preferences of adult river sharks. For example, the first published observations of adult *G. glyphis* were only recently made (White et al., 2015). Records of river sharks in commercial fisheries are limited in northern Australia (e.g. Field et al., 2013), and this has been attributed to high likelihood of mis-identification with *C. leucas* by fisheries observers, or assumptions that adult river sharks occur outside the spatial range of northern Australian net and line fisheries. Within the Northern Territory and Western Australia, commercial fisheries are not permitted to operate within rivers. The results of the present study indicate that adult river sharks are primarily using estuarine environments, which occur within the closed waters of rivers in northern Australia for most of the year outside of wet season. Therefore, the lack of river shark captures of any size class is likely because juveniles are using upper estuarine environments, while larger size classes are primarily using lower estuarine environments, outside the spatial range of commercial fisheries in Northern Territory and Western Australia. Meanwhile, commercial fisheries in Queensland are permitted to operate within estuarine zones of rivers, and this makes river sharks far more susceptible to capture. Only *G. glyphis* occurs in Queensland. Their Gulf of Carpentaria range is limited to Port Musgrave (Ducie and Wenlock Rivers, Dwyer et al., 2020), and Weipa region (Embly and Hey Rivers, Peverell et al., 2006), while their east Queensland range is limited to Princess Charlotte Bay (Bizant and Normanby Rivers, Peverell et al., 2006). There are several other large, and seemingly suitable river systems in Queensland that river sharks have not been recorded from (e.g., Mitchell, Gilbert, Staaten Rivers), and targeted survey effort in estuarine environments may be required to inform species ranges. The apparent environmental restriction of river sharks to estuaries also suggests that populations would be inherently small. Small river shark population sizes are supported for *G. garricki* on the basis of close-kin mark-recapture methods (Bravington et al., 2019), and furthermore, all river sharks species are presently listed as threatened with extinction on the IUCN Red List on the basis small mature population sizes (Kyne et al., 2021c; Kyne et al., 2021d; Rigby et al., 2021). This places increased necessity on protection for river shark populations, as they appear to be susceptible to rapid depletion from fisheries owing to their reliance on spatially restricted estuarine environments.

In southern PNG, most small-scale fishing occurs within lower riverine environments or in upstream freshwater, and *Glyphis* up to ~ 120 cm TL are caught (Chapter 4). Due to much higher rainfall in PNG compared to northern Australia, the upper estuary where juveniles are caught, generally occurs around the river mouth. Hence the lack of larger *Glyphis* spp. size classes is likely because the lower estuary occurs offshore (e.g. see sediment plume in Chapter 4, Figure 4.1). The only region of PNG where fishers access offshore environments is along the South Fly Coast, which congruently is where the observations of adult *G. glyphis* were made (White et al., 2015). Offshore environments on the South Fly Coast receive substantial outflow from the Fly River, which tends to run west toward the Indonesian boarder. Considering current spatial fishing characteristics in southern PNG, juvenile age classes are susceptible to the intensive estuarine based swim bladder fishery presently operating in southern PNG, while adults are additionally susceptible along the more marine influenced South Fly Coast (Chapter 3; Chapter 4). There are presently no observations of river sharks within the catch of the Gulf of Papua Prawn Trawl Fishery, which is the only commercial fishery operating in PNG that would be likely to catch river sharks (White et al., 2015; White et al., 2019).

5.4.2 Sawfish life history environmental habitat use patterns

It is well established that juvenile *P. pristis* utilise freshwater environments within Australia and PNG (e.g. Chapter 4; Thorburn et al., 2007; Feutry et al., 2015; White et al., 2017a; Whitty et al., 2017; Lear et al., 2019; Kyne et al., 2021b), and results from the elemental analysis reflected this pattern. The Ba:Ca and Sr:Ba ratios indicated that juveniles were using environments with substantially higher

Ba concentrations than all other species except for some overlap with *C. leucas*. While samples of *P. pristis* and *C. leucas* from the same river system were not available, Sr:Ba values for *P. pristis* in all rivers were comparable to values for *C. leucas* in the Sepik River, although Ba:Ca was substantially higher in *P. pristis*. It is known that juvenile *C. leucas* penetrate into overlapping freshwater environments (Thorburn et al., 2003; Thorburn and Rowland, 2008), and are predators of *P. pristis* (Thorburn et al., 2014; Morgan et al., 2017). Further elemental investigation on freshwater associated *C. leucas* and *P. pristis* within the same river could provide insights into the temporal habitat overlap between these species, to further understand the temporal predation risk that *C. leucas* presents to juvenile *P. pristis* (see Chapter 6).

Elemental ratios for the pre-natal zone of *P. pristis* suggest limited overlap with adult *C. leucas* and river sharks. Pre-natal values for Ba:Ca, Sr:Ca, and Sr:Ba indicate that pregnant *P. pristis* are primarily using upper estuaries and encroaching into freshwater in Australia, with similar values to juvenile *G. glyphis* (e.g. Figure 5.9). This was consistent across individuals from the Adelaide and Daly Rivers. Peverell (2009) found a similar pattern for *P. pristis* in Queensland, Australia, where Sr:Ca ratios during pre-natal growth were slightly higher than juvenile Sr:Ca values (which indicated freshwater), though substantially lower than adult Sr:Ca values (which indicated marine). The congruent results from multiple salinity indicating elements in the present study supports these preliminary observations by Peverell (2009). Meanwhile, the *P. pristis* individual from the Aramia River in PNG indicated use of a primarily freshwater environment in the pre-natal zone, with no overlap in Ba:Ca, Li:Ca, and Sr:Ba ratios occurring with juvenile river sharks from the Kikori River or South Fly Coast. Prolonged use of freshwater environments throughout the life history of *P. pristis* has only been observed in the West Atlantic, in Lake Nicaragua and adjoining San Juan River (Thorson, 1976; Thorson, 1982). Local fishers in the Aramia River report that *P. pristis* enters the Aramia from the Fly or Strickland Rivers during wet season when these three rivers are connected by an expansive flood plain (Chapter 3). It is therefore possible that elemental values for the Aramia River individual reflect pre-natal growth in freshwater of the Fly River, and post-natal growth in the Aramia River. These data and considerations suggest that *P. pristis* could plausibly be using freshwater environments in the Fly River Basin for prolonged periods.

The present results suggest that *P. pristis* are pupping in freshwater, or at least at the upper most freshwater margin of the estuary (which may coincide with the tidal interface). Sr:Ba values in the last ablation spot in the pre-natal growth zone showed a clear decrease in all individuals. A further decrease of similar magnitude was observed in the first post-natal growth ablation spot, where subsequent post-natal growth values remained constant with no marine influence evident. Given that pupping occurs during the wet season, it is still unclear how far *P. pristis* may penetrate into rivers to give birth. For example, Peverell (2005) observed two near-term *P. pristis* at the mouth of the Leichardt and Mitchell Rivers, respectively, both during periods of high freshwater flow close to the end of the Australian wet season. In King Sound, Western Australia, pupping is presumed to occur at the mouth of the Fitzroy River, with upstream migration being highly dependent on freshwater flow (Thorburn et al., 2007; Lear et al., 2019). However, the Fitzroy River receives less wet season rainfall than river systems in the Northern Territory, and PNG, and large tidal fluctuations (~12 m) may increase risk of stranding if large females penetrated too far into the estuary. Larger river systems may allow *P. pristis* to penetrate further into the freshwater reaches of the river to give birth, as depth and other spatial factors are unlikely to be as constraining (e.g., the Fly River in PNG is still several kilometres wide well into year-round freshwater reaches). While the present study indicates that pupping occurs in freshwater, there are two possibilities regarding the location of pupping; 1) parturition may occur around the river mouth or tidal interface, and be triggered by large rainfall events when downstream estuarine environments become fresh, or 2) pregnant individuals may migrate upstream into freshwater environments to give birth. The former is most likely in spatially constrained systems such as the Fitzroy River, while the latter is additionally possible in large systems such as the Fly River.

The finding that pregnant female *P. pristis* occur primarily in upper estuarine environments provides valuable information for their conservation management. It demonstrates the substantial impact that riverine fisheries could potentially have on *P. pristis* populations if pregnant females are concentrated within estuarine reaches of rivers. As afore mentioned, commercial fisheries cannot operate within riverine environments of Northern Territory and Western Australia. The present finding suggests that this spatial restriction of fisheries provides a high degree of protection for pregnant females, and efforts should be made to preserve this spatial restriction of fisheries effort into the future. *P. pristis* populations in Queensland are considered to be more depleted than these other two jurisdictions (DoE, 2015). Commercial fishing activity is permitted in riverine environments in Queensland, and additionally many Queensland rivers have been subject to intense agricultural practices including extraction for irrigation, and construction of barriers to water flow. Furthermore, legislation protecting Queensland rivers has been weakened alongside an agenda of development in the catchment of these systems (Chin et al., 2012). The identification of river systems in Queensland with persisting *P. pristis* populations, and restriction of commercial fishing in those systems, would be a substantial step forward to the protection of populations. Along with this, preservation of free-flowing rivers with uninhibited estuarine-freshwater connectivity would have positive outcomes (Lear et al., 2019), as well as having benefits for inshore fisheries production (Halliday et al., 2012; Leahy and Robins, 2021). The present interest in damming major drainages within northern Australia (e.g. Petheram et al., 2017; Petheram et al., 2018) would reduce the present range of *P. pristis* considerably, through effectively eliminating vital *P. pristis* nursery habitats.

For *A. cuspidata*, the elemental analysis indicated use of a predominately inshore marine environment. At the individual level there was substantial variation in Sr:Ba ratios. Two individuals appeared to utilise an environment with increased freshwater influence for a prolonged period (indicated by multiple adjacent ablation spots with high and low Ba:Ca and Sr:Ba values, respectively), although most individuals had element signatures fluctuating around values more indicative of marine environments, similar to *C. amblyrhynchos* and *R. australiae*. In particular, the only adult *A. cuspidata* individual analysed in this study appeared to be using a marine environment with limited freshwater influence in its latter life history stages (possibly further offshore than other *A. cuspidata* individuals analysed). Based on fisheries interactions in northern Australia, juvenile *A. cuspidata* are known to use shallow inshore environments as juveniles, while adults are more commonly captured further offshore (Peverell, 2005; Field et al., 2013). In east Queensland, Australia, *A. cuspidata* juveniles occupy extremely shallow nearshore habitats (Adkins et al., 2016), which is likely a predator avoidance behaviour. Coastal regions of the East Sepik Province receive substantial rainfall, and the fluctuations in Sr:Ba may indicate that juvenile *A. cuspidata* remain in nearshore habitats during periods of high rainfall, tolerating increased freshwater input rather than moving to higher salinities further from shore. Such behaviour of tolerating periods of increased freshwater influence would likely be to maintain the predator avoidance strategy afforded by near shore shallow water and contrasts other inshore species such as pigeye sharks (*Carcharhinus amboinensis*) which temporarily move away from areas of decreased salinity during rainfall periods (Knip et al., 2011).

Despite *A. cuspidata* being the most commonly caught sawfish species in northern Australian fisheries, there is a lack of research on this species' ecology. Across Australia there is very limited evidence that *A. cuspidata* penetrates into estuaries within rivers (e.g. lack of riverine records in study areas of Thorburn et al., 2003; Peverell, 2005; Morgan et al., 2011; Field et al., 2013). Furthermore, in recent fisheries surveys in southern PNG, *A. cuspidata* were more frequently observed in coastal areas of decreased river outflow influence, and only one individual was observed to be concurrently caught with river sharks within an actual riverine environment (Chapter 4). All *A. cuspidata* specimens used in the present study were obtained from a fishery operating mainly within, and closely adjacent, to the mouth of the Sepik River (Chapter 4). However, the salinity indicating elements suggest that these individuals were generally not using the low salinity environment at the river mouth. The Sepik River is an unusual system that lacks an estuarine zone, with water being practically fresh at the mouth (Coates, 1987). Only two individuals in this study appeared to inhabit the mouth of the Sepik River for a prolonged period. These two individuals suggest that *A. cuspidata* does have an increased physiological tolerance to lower salinities, as per its inclusion as an estuarine generalist in Chapter 2. Although, it seems that this species does not occur within the closed waters of riverine environments regularly during its life history. Conservation management of *A. cuspidata* therefore mainly concerns inshore and offshore fisheries (Peverell, 2005; Field et al., 2013; White et al., 2019).

5.5 Conclusion

The use of elemental analysis of vertebrae in this study has provided further support for the application of this technique to elasmobranchs for 1) discerning broad habitat use patterns across a range of species; and 2) identifying temporal habitat use patterns in diadromous species. The congruence in concentrations of environmental salinity indicating elements when compared to species with well understood temporal diadromous habitat use patterns (e.g., *C. leucas* and *P. pristis*), also support the inertness of vertebral band pair depositions throughout an individual's life history. This study also indicates that Ba, Sr, and Li, are effective indicators of freshwater and marine environments and hence useful indicators for diadromous movements of elasmobranch species. Further research on the underlying physiological processes that lead to environmental element incorporation in vertebrae, and relative concentrations of elements between the ambient environment and vertebrae would assist in future applications of elemental analysis for elasmobranchs. Until such information is available, it is suggested that future studies consider analysis of multiple species to aid data interpretation, or incorporate measurements of physical or chemical water parameters over a broad range of differing salinity environments.

Chapter 6

Population viability analysis of largetooth sawfish *Pristis pristis* informs future management and research priorities in northern Australia

6.1 Introduction

Anthropogenic pressures on freshwater and marine environments have become increasingly severe over the last century due to the rapidly growing human population. Many species in these environments have been adversely affected, primarily by overfishing and habitat degradation/modification (Dulvy et al., 2014; Su et al., 2021). Long-lived species are at greatest risk as they generally share 'slow' life history traits including slow growth rates, late attainment of maturity, and protracted breeding cycles (Kindsvater et al., 2016). These traits result in low population productivity, increased susceptibility to negative anthropogenic pressures, and low potential for severely depleted populations to recover (Cortés, 2000). Consequently, many long-lived species in freshwater and marine environments are threatened with extinction, and management action is required to prevent further population declines and to rebuild populations (Dulvy et al., 2017; He et al., 2019).

In the development of population management for threatened long-lived species, various factors need to be considered. Firstly, management options targeting different life history stages need to be assessed as these may exhibit varied responses to anthropogenic pressures (e.g. from differences in ecology and spatial scales) (Crouse et al., 1987). Secondly, environmental (e.g. upwellings, monsoon, drought) and ecosystem (e.g. predator and prey abundances, inter- and intraspecific competition) processes may require consideration as variable phenomena can influence demographic aspects such as age or stage specific survivorship and reproductive output (Carr et al., 2003; Skern-Mauritzen et al., 2016). Lastly, implementation of management initiatives can be complicated where species distributions cover multiple jurisdictions (Heupel et al., 2015), resources or requisite information for conservation are limited (Wilson et al., 2006; Walsh et al., 2015), or they overlap with urban or economically important areas (Miller and Hobbs, 2002), or cultural livelihoods (Poe et al., 2014). Consideration of these factors is important as management initiatives are often overlooked or undermined where they have limited capacity or flexibility to be integrated into existing political and economic regimes, or cultural livelihoods (Simpfendorfer et al., 2011a; Booth et al., 2019).

Population Viability Analysis (PVA) has been a popular tool used by conservation biologists across a wide range of taxa (e.g. turtles, whales, and birds) to quantify extinction risk and evaluate the effectiveness of various approaches to population management (Morrison et al., 2016). PVA incorporates species-specific demographic information with environmental and or anthropogenic variables to estimate changes in population size over time (Coulson et al., 2001). PVA is also commonly used to examine the effect of different life history parameter estimates on population projections (e.g. Carlson and Simpfendorfer, 2015). Exploring the effect of different life history parameter estimates on demographic attributes is particularly important where there are knowledge gaps or regional ambiguity in intraspecific life history parameter estimates (Grant et al., 2019). Collectively, this can make PVA a powerful tool in the identification of future research priorities for data poor species in both a biological and social sciences setting.

Sawfishes (Pristidae) are among the most threatened marine vertebrates (Dulvy et al., 2016; Yan et al., 2021). Three species are listed as Critically Endangered (green sawfish *Pristis zijsron*, largetooth sawfish *Pristis pristis*, and smalltooth sawfish *Pristis pectinata*) and two species Endangered (dwarf sawfish *Pristis clavata* and narrow sawfish *Anoxypristis cuspidata*) on the IUCN Red List of Threatened Species (hereafter 'IUCN Red List', IUCN, 2021). Population declines have primarily occurred due to targeted (Thorson, 1976) and incidental fisheries exploitation (e.g. White et al., 2017a; Brame et al., 2019), while habitat degradation and modification are also contributing factors (Dulvy et al., 2016; Lear et al., 2019). Sawfishes are particularly susceptible to these anthropogenic pressures as their distribution throughout tropical freshwater (*P. pristis* only), estuarine, and inshore marine environments overlaps with environments of increased human exploitation (Chapter 2; Compagno and Cook, 1995).

Furthermore, sawfishes have ‘slow’ life history traits, which lowers their resilience to population disturbances, and protracts the time needed for populations to recover (Simpfendorfer, 2000; Moreno Iturria, 2012; Carlson and Simpfendorfer, 2015).

Pristis pristis has a unique life history compared to its congeners. Juveniles occur in upper freshwater reaches of rivers and opportunistically access seasonal floodplains for the first few years of life (Thorburn et al., 2007). Meanwhile, subadults and adults primarily occur in estuarine and marine environments (excluding Lake Nicaragua where there is limited movement to marine areas) (Thorburn et al., 2007; Peverell, 2009). Furthermore, genetic studies suggest females are philopatric to natal river systems (Phillips et al., 2011; Feutry et al., 2015). The requirement of *P. pristis* to access freshwater, estuarine, and marine environments during its life history exposes it to both marine and non-marine environmental and anthropogenic pressures (Chapter 2). Marine pressures include fisheries and habitat degradation. In non-marine environments, pressures include inland fisheries, aquaculture, and habitat degradation resulting from river engineering (e.g. dams, weirs, and canals), water extraction and waste disposal (Compagno and Cook, 1995; Lear et al., 2019). Due to their compounding exposure to these marine and non-marine pressures, *P. pristis* has experienced significant population declines throughout all its subpopulations globally (Kyne et al 2013).

Northern Australia has long been regarded as the most important, and possibly last significant remnant population of *P. pristis* globally (e.g. Morgan et al., 2011b; Dulvy et al., 2016). In Australia, *P. pristis* is protected from retention by commercial and recreational fishers under the national *Environment Protection and Biodiversity Conservation* (EPBC) Act 1999 (listed as Vulnerable in 2006), and state legislation in Western Australia (Wildlife Conservation Act 1950; Fish Resources Management Act 1994), Northern Territory (Parks and Wildlife Conservation Act 2000; Fisheries Act 1988), and Queensland (Fisheries Act 1994). As a requirement of its Vulnerable listing under the EPBC Act, *P. pristis* is included in the *Sawfish and River Sharks Multi-species Recovery Plan* (DoE, 2015), which provides a framework to improve present understanding of population status and identify anthropogenic activities that may hinder species recovery. Despite an array of legislative protection, it is suspected that *P. pristis* populations are still declining throughout much of northern Australia (e.g. Wueringer, 2017) and that further management is required to assist the rebuilding of the population.

The population viability of *P. pristis* has never been examined in Australia. This is due to data limitations and knowledge gaps including: 1) limited and confounded life history information resulting from low sample sizes and regional ambiguities; 2) a lack of data on the effects of negative environmental and anthropogenic pressures, particularly the extent of interactions with the commercial fisheries sector (Field et al., 2008); and 3) limited ability to estimate total population size or relative population trajectory. Unfortunately, missing information on important life history characteristics (age and growth, litter size, etc.) is unlikely to be obtained in the near-term, not only due to their rarity, but also because legislative protection in Australia and other regions where *P. pristis* still occur precludes the possibility of lethal sampling (Kyne et al., 2021). However, new information has recently become available on: 1) reproductive biology (Kyne et al., 2021); 2) the relationship between wet season rainfall and juvenile recruitment and survival in riverine nursery habitat (Lear et al., 2019; Lear et al., 2020); and 3) risk that predation by crocodiles (which have largely recovered following their protection in 1971; Fukuda et al., 2011) may pose to survival of juvenile *P. pristis* in nursery habitats (Morgan et al., 2017). Collectively, this new information allows for more informed demographic models to be developed for *P. pristis* in Australia. While some of the data has accuracy issues (e.g. log book reporting in commercial fisheries), is location specific (e.g. juvenile recruitment rates), or is broad or anecdotal in nature (e.g. effect of crocodile predation), there is a need to use the best available information to inform management approaches and outline future research priorities to ensure population recovery and long-term security of the *P. pristis* population in Australia.

The primary purpose of this research was to assess whether present threats to *P. pristis* are suppressing population recovery, and whether further management efforts are required to help rebuild populations. Using PVA, this study developed a model that allows analysis of i) various combinations of ambiguous life history parameters and their effect on population trajectories and resilience; ii) various levels of pressure from current anthropogenic and environmental pressures; iii) probability of extinction over a projected three generation time period; and iv) effectiveness of different population management approaches for the rebuilding of *P. pristis* populations. Secondarily, this allowed us to also outline future research priorities that will facilitate better management actions through reducing uncertainty in data inputs to population models. Due to a lack of information, population sizes estimated in this study are not intended to serve as true estimates of population size. Rather, they are intended to serve as a hypothetical representation of the depleted *P. pristis* population in Australia. This is to allow a basis for examination of management actions that are likely to be effective in facilitating population recovery.

6.2 Methods

6.2.1 Overview of demographic model

All analysis was performed in the commercial software package RAMAS *Metapopulation*. A stage-structured Lefkovitch (1965) matrix model (A) was used to determine the population size at time $t + 1$ (N_{t+1}), from N_t as follows:

$$N_{t+1} = AN_t$$

RAMAS *Metapopulation* calculates λ as the dominant eigenvalue from matrix elements. The finite rate of population growth (λ) can be related to the intrinsic rate of population growth (r) produced by life tables via the relationship (Simpfendorfer, 2004):

$$\lambda = e^r$$

Population growth is stable when $\lambda = 1$, decreasing when $\lambda < 1$ and increasing when $\lambda > 1$.

The matrix model used in the present analysis was single sex (female) with a post breeding census, following other elasmobranch demographic studies (e.g. Mollet and Cailliet, 2002; Smart et al., 2017)

6.2.1.1 Calculation of matrix elements

Available life history information was used to calculate matrix elements using Microsoft Excel (Table 6.1). The matrix had three elements; i) fertility at stage *i* (f_i) formed the top row of the matrix, ii) probability an individual at time *t* would survive and remain in stage *i* at time *t* + 1 (P_i), formed the diagonal of the matrix, and iii) probability an individual would survive in stage *i* at time *t* though move to stage *i* + 1 at time *t* + 1 (G_i), formed the sub-diagonal of the matrix (Figure 6.1). Calculation of matrix elements followed Crouse et al. (1987) and Cortés (1999) where, f_i is equal to the sum of births from the proportion of individuals that survived to time *t* + 1 though remained in stage *i* (i.e. P_i) and the proportion of individuals that survived to time *t* + 1 and moved to stage *i* + 1 (i.e. G_i):

$$f_i = (b_i P_i) + (b_{i+1} G_i)$$

and b_i is equal to the number of female pups per litter at stage *i*.

To calculate P_i and G_i, age-specific survivorship (S_a) and stage-specific survivorship (S_i) were calculated as:

$$S_a = e^{-Ma}$$

Where M_a is the age-specific mortality estimate. Because there are no direct estimates of natural mortality available for *P. pristis*, M_a was calculated using the indirect mortality estimator of Peterson and Wroblewski (1984) (Table 6.1). For this relationship, dry weight was estimated as one fifth of wet weight following Cortés (2002), using the length-weight relationship estimated by Simpfendorfer (2000) (Table.1). For stages 0–7, S_a was equal to S_i. For stages 8–14, the highest S_a value from all the age classes comprising stage *i* was made to equal S_i. This was to represent increased relative survival under circumstances of a severely depleted population exhibiting a density-dependent response.

Using the values of S_i, G_i and P_i were calculated as follows:

$$G_i = \frac{S_i^{dj}(1 - S_i)}{1 - S_i^{dj}}$$

and

$$P_i = \left(\frac{1 - S_i^{dj-1}}{1 - S_i^{dj}}\right) S_i$$

Where *dj* is equal to the number of age classes in stage *i*.

To incorporate stochasticity into survival matrix elements, a standard deviation of 10% was applied to *Gi* and *Pi* using the *Standard Deviation Matrix* function in RAMAS *Metapopulation*.

Table 6. 1 Life history information for *Pristis pristis* used to calculate matrix elements for population viability analysis. VBGF, Von Bertalanffy growth function; L_0, size-at-birth; k, growth completion rate; L_∞, asymptotic size; TL, total length; W_a, weight-at-age; M_a, mortality-at-age.

Life history parameter	**Value**	**Source**
VBGF parameters:		
L_0	74.4 cm TL	Peverell (2009)
k	0.08 year^{-1}	
L_∞	638 cm TL	
Longevity	36 years	Kyne et al (2021)
Generation time	12 years	Kyne et al (2013)
Age at maturity	8 years	Peverell (2009)
Litter size (LS)	7.3 pups (mean) $LS = 11.951 + (0.0542TL)$	Thorson (1976) Kyne et al (2021)
Reproductive periodicity	Annual Biennial	Peverell (2009) Thorson (1976)
Weight-at-age relationship	$W_a = 0.00004TL^{2.56}$	Simpfendorfer (2000)
Mortality-at-age	$M_a = 1.92{W_a}^{-0.25}$	Peterson and Wrobleski (1984)

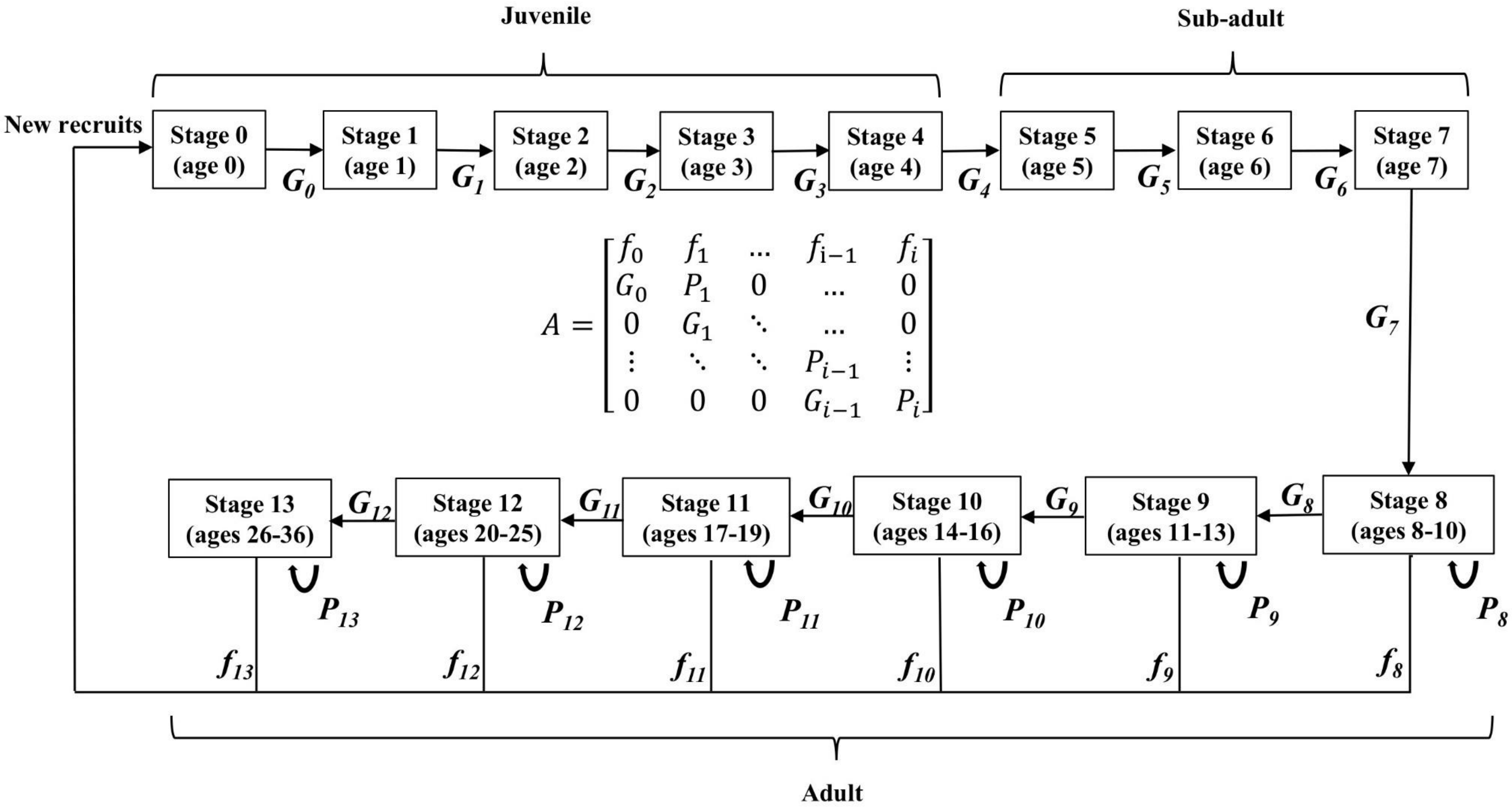


Figure 6. 1 Life cycle graph showing stage structured Lefkovitch (1965) matrix model used in population viability analysis of *Pristis pristis*. Boxes indicate the ages comprising stage *i*, G_i and P_i indicate transition probabilities between stages at each time step (P_i is the probability of remining in a stage and G_i is the probability of moving to the next stage) and f_i indicates reproductive contribution at stage *i*.

6.2.1.2 Development of 'base case' natality parameters

Due to high ambiguity in litter size and reproductive periodicity for *P. pristis*, four different combinations of possible natality parameters were used to calculate four estimations of matrix element *f*. This was done to capture a range of possible population growth (λ) estimates resulting from uncertainty in the reproductive biology of *P. pristis*.

Firstly, for litter size, results from the two available studies were considered: 1) the mean litter size estimate of 7.3 given by Thorson (1976) for *P. pristis* in Lake Nicaragua, and 2) the maternal size – litter size relationship given by Kyne et al. (2021b) which captured the known upper litter size range of *P. pristis* (20 pups). To incorporate the Thorson (1976) mean litter size into the model, b_i was equal to half of 7.3 (considering a 1:1 female to male sext ratio). To incorporate the Kyne et al. (2021b) relationship, b_i was equal to half of the mean age-specific fecundity of Stage *i*.

Secondly for reproductive periodicity, results from the two available studies were considered. 1) Thorson (1976) noted that about 50% of mature females observed were pregnant in any given year (based on the Western Atlantic sub-population). From this, Thorson (1976) deduced a biennial reproductive cycle. 2) Peverell (2009) noted large oocytes in a pregnant female in northern Australia, suggestive of an annual reproductive cycle. To incorporate biennial reproduction into the model, b_i was halved, so that while all mature females produced a litter annually, the net births at time $t + 1$ was equal to the number of births that would occur if individuals produced a whole litter every second year. Annual reproduction was implicit in the model, so no changes to the fertility matrix element were necessary.

The resulting four natality 'base case' combinations were 1) Annual reproduction and maternal size – litter size relationship (hereafter, annual maternal relationship; AMR), 2) Annual reproduction and mean litter size (hereafter annual litter size; ALS), 3) Biennial reproduction and maternal size – litter size relationship (hereafter, biennial maternal relationship; BMR), and 4) Biennial reproduction and mean litter size (hereafter biennial litter size BLS) (Table 6.2). For each reproductive base case, the standard deviation of 40% given by Kyne et al. (2021b) for litter size was applied to the matrix fertility element *f* using the *Standard Deviation Matrix* function in RAMAS *Metapopulation*. Other life history parameters (e.g. VBGF parameters, longevity, age-at-maturity) and survival elements *G* and *P* were held constant between base cases. This ensured that the sensitivity of population growth (λ) estimates resulting from these four reproductive parameter combinations could be captured.

6.2.1.3 Other matrix outputs

Additionally, RAMAS *Metapopulation* calculates the stable stage distribution (*w*) and reproductive values (*v*) as the right and left eigenvectors of the matrix, respectively. These were produced from the matrix of each natality base case (Appendix 4 '*Other matrix outputs*').

Table 6. 2 The four base case natality parameter combinations and their resulting population growth estimate used in population viability analysis of *Pristis pristis*. TL, total length; AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

Reproductive base cases	**Reproductive periodicity**	**Litter size (LS)**	$\boldsymbol{\lambda}$	**Finite rate of population growth (r year^{-1})**
1. AMR	Annual	$LS = 11.951 + (0.0542TL)$	1.1384	13.1%
2. ALS	Annual	3.65	1.1009	9.5%
3. BMR	Biennial	$LS = 11.951 + (0.0542TL)$	1.0826	7.7%
4. BLS	Biennial	3.65	1.0459	4.9%

6.2.1.4 Elasticity

RAMAS *Metapopulation* produces elasticities corresponding to each stage-specific matrix element. Elasticities inform the effect of proportional changes in matrix elements (fertility *f* or survival *P* and *G*) on λ when other matrix elements are held constant. In this way, elasticities can identify the life history phases (e.g. juvenile, subadult, and adult survival) for which changes to matrix elements will most effect λ (de Kroon et al., 1986). Elasticities of matrix elements are calculated in RAMAS *Metapopulation* as:

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

where a_{ij} is the matrix element corresponding to row i and column j, v_i is the value of row i in the reproductive value vector v, w_j is the value of column j in the stable stage distribution vector w, and $\langle w, v\rangle$ is the scalar product of vectors w and v. The sum of all matrix element elasticities equals 1. Elasticities for survival in each life history phase (juvenile, subadult, and adult) and fertility, were calculated by summating the relevant stage specific values (Table 6.3). Elasticity ratios were also calculated for each life history phase survival elasticities, and fertility. Elasticity ratios are used to identify the potential effects of exploitation on the population's compensation between survival and fertility (Cortés, 2002). For example, a compensation ratio for a given life history phase equal to 3.5 indicates that a 10% decrease in survival of that life history phase would require a 35% increase in fertility to maintain the original λ (Heppell et al., 1999; Cortés, 2002). Therefore, this provides a useful management insight as it can help to indicate the life history phases where survival has the greatest effects on population growth (λ).

Table 6. 3 Matrix element elasticities for *Pristis pristis* in each life history phase for each natality base case. AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

Reproductive base cases	**Elasticities**				**Elasticity ratios**		
	Fertility	**Juvenile survival**	**Subadult survival**	**Adult survival**	**Juvenile**	**Subadult**	**Adult**
AMR	0.076	0.378	0.227	0.320	4.999	3.000	4.231
ALS	0.077	0.384	0.231	0.308	4.991	2.996	4.003
BMR	0.069	0.347	0.208	0.375	5.000	2.999	5.408
BLS	0.070	0.350	0.210	0.370	4.993	2.997	5.275

6.2.1.5 Jurisdictional management boundaries

The Australian metapopulation of *P. pristis* was divided into three jurisdictions, reflecting state fisheries management boundaries: Queensland Gulf of Carpentaria, Northern Territory, and Western Australia (Figure 6.2). Eastern Australia was not included in the analysis due to a paucity of region-specific commercial fisheries catch and effort data, and uncertainty in extant range (Wueringer, 2017). Eastern Australia has had a higher historic fisheries impact, and it is unclear if viable *P. pristis* populations remain along this coast. Phillips et al. (2017) indicate from historic samples that eastern Australian *P. pristis* are likely discrete when compared to other fisheries jurisdictions being considered in this study. Eighty Mile Beach was used as southern extent of the Western Australian range following observation data from Morgan et al. (2011b), and noting the single observation of this species from Cape Naturaliste was likely a vagrant (Chidlow, 2007).

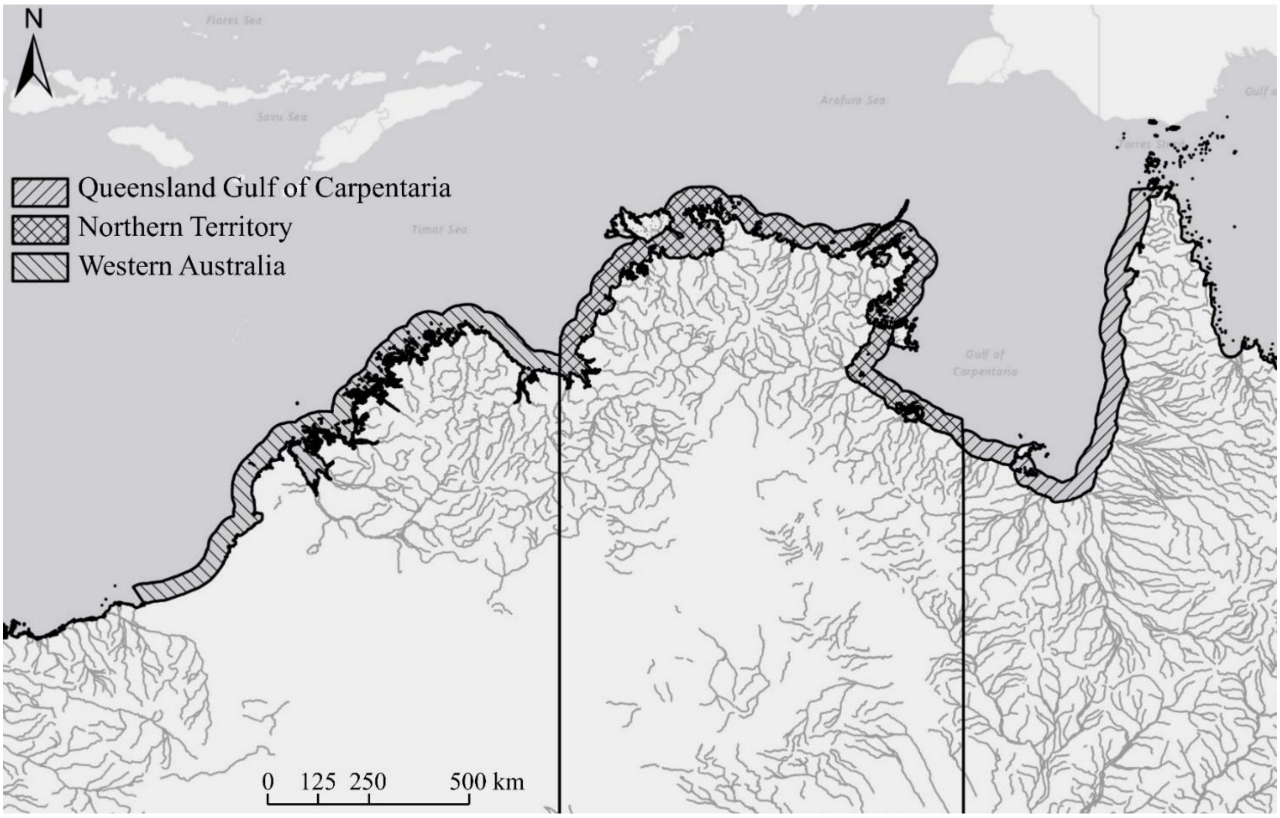


Figure 6. 2 Distribution of *Pristis pristis* in each state used in calculation of population size. The subadult and Adult portion of the population were assumed to occur up to 25 nautical miles from the coast (indicated by grey shaded area) following data from Peverell (2009). The Queensland Gulf of Carpentaria distribution extended from the western tip of Cape York Peninsula. The Western Australia distribution extended to the southern point of 80 mile beach (Morgan et al., 2011b).

6.2.1.6 Estimation of initial population size

No data are available on total population size for any pristid species in northern Australia, and it was not possible to calculate relative population size from available fisheries catch and effort data. In order to estimate initial population size, encounter data from Wiley and Simpfendorfer (2010) for the congener *P. pectinata* was used. Wiley and Simpfendorfer (2010) estimated a population density of 0.001–0.05 *P. pectinata* km^{-2} in areas that were not considered 'critical habitat' (critical habitat was defined as areas where all size classes were encountered and this likely included nursery areas). The majority of size classes encountered outside the critical habitat areas were subadult and adult size classes, therefore this density estimation excludes nursery areas. This population density data is the best available for pristids, and so the median of this population density (0.025 *P. pristis* per km^{-2}) was used in calculations to estimate female *P. pristis* subadult and adult population size. In doing this, the following is acknowledged: 1) it is unknown if *P. pristis* across northern Australia has undergone population density depletion comparable to *P. pectinata* or if the respective habitats of these species can support similar population densities; and 2) it is unknown whether subadults and adults of *P. pristis* disperse from their nursery habitat (freshwater) to occupy coastal waters at comparable densities to *P. pectinata* dispersal from 'critical habitat' areas defined by Wiley and Simpfendorfer (2010). For these reasons, two sensitivity tests for differences in initial population size were conducted (see '*Population Viability Analysis*').

To estimate coastal habitat size in which the abundance density estimation could be applied, catch data from the Gulf of Carpentaria Inshore Fin Fish Fishery (GOCIFFF) was considered. Peverell (2009) indicated that *P. pristis* is most commonly caught within 7 nautical miles from shore, and only rarely in the portion of the fishery that operates 7–25 nautical miles (NM) from shore. Therefore, this study considered that the marine habitat of subadult and adult *P. pristis* extends to 25 NM (approximately 46.3 km) from shore. The possibility that *P. pristis* may occasionally occur further out to sea than this estimate is acknowledged, however there is no available data to support this. Furthermore, it is likely that only a very small portion of the population may occur further from shore than 25 NM, and that the portion of the population captured by the 25 NM habitat extent is sufficient for the purpose of this study.

Table 6. 4 Initial population size estimated from stable stage distribution for each natality base case for *Pristis pristis*. Initial population sizes estimated are a post-breeding census (i.e. annual mortalities have not yet been applied). AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

Region	Area (km^2)	Subadult and adult population size	Initial population size
Queensland Gulf of Carpentaria	54136	1353	1. AMR = 7500 2. ALS = 6155 3. BMR = 5580 4. BLS = 4530
Northern Territory	110057	2751	1. AMR = 15237 2. ALS = 12510 3. BMR = 11355 4. BLS = 9210
Western Australia	84628	2116	1. AMR = 11717 2. ALS = 9623 3. BMR = 8730 4. BLS = 7083

For each of the three fisheries management jurisdictions (Queensland Gulf of Carpentaria, Northern Territory, and Western Australia), the area (km^2) from the shore (inclusive of bays, inlets, and river mouths) to 25 nautical miles offshore was calculated using ARC GIS. The area of each jurisdiction was multiplied by 0.025 to estimate female *P. pristis* subadult and adult population size. It is assumed this estimation was exclusive of juveniles, as they occupy upper freshwater reaches of rivers until approximately five years of age (Thorburn et al., 2007). The size of the juvenile population in each jurisdiction was determined by iteratively producing a stable stage distribution with a subadult and adult population size equal to that calculated from the density calculation. This was done for each of the natality base case combinations, resulting in four population size estimates for each jurisdiction due to different stable stage distribution models for each natality schedule (Table 6.4). It is thought that dispersal of female *P. pristis* across northern Australia is very low due their strong philopatric relationship to natal rivers (Phillips et al., 2011; Feutry et al., 2015). Therefore, no consideration for dispersal between jurisdictions within this study was included, as it would likely be negligible over the 66 year time period modelled (see '*Population Viability Analysis*').

6.2.2 Anthropogenic and environmental factors considered in PVA

6.2.2.1 Commercial fisheries mortality

Varied amounts of data were provided for each commercial fishery that interacts with sawfishes across jurisdictions. In the Queensland Gulf of Carpentaria, effort (days) were provided by Queensland Fisheries for the Gulf of Carpentaria Inshore Fin Fish Fishery (GOCIFFF, 2000–2017) and Queensland Demersal Fish Trawl Fishery (QDFTF, 2004–2015). In the Northern Territory, effort (days, 2002–2016) were provided by Northern Territory Fisheries (NT Fisheries) for the Northern Territory Barramundi Fishery (NTBF) and Northern Territory Offshore Net and Line Fishery (NTONLF). Effort (days) and *P. pristis* catch information were provided for the Northern Territory Demersal Fish Trawl Fishery (NTDFTF). In Western Australia, sawfish interaction data from logbooks (2004–2018) were provided by Western Australian Fisheries (WA Fisheries) for the Kimberley Gillnet and Barramundi Fishery (KGBF), Pilbara Fish Trawl (PFT), and Western Australia prawn trawl fisheries collectively (WAPTF), although effort data were not provided. For the Northern Prawn Fishery (NPF) which spans all jurisdictions, effort data (days fished 2006–2017) and daily catch rate were provided by the Australian Fisheries Management Authority (AFMA) and Northern Prawn Fishery Industry (NPFI).

Data from these fisheries were used to estimate an average annual *P. pristis* catch that could be used for PVA (Table 6.5–6.6). In most instances data provided were not sufficient, so CPUE from literature or information provided by alternative fisheries jurisdictions were used in calculations. This included GOCIFFF and NTBF (Peverell, 2005), QDTFT and NTDFTF (data provided by NT Fisheries), and NTONLF (Field et al., 2008) (Appendix 4 '*Commercial fisheries calculations*'). Due to the varied time periods of effort data available for each fishery, only data from 2006–2016 was considered, except QDFTF (2006–2015).

Commercial fisheries operate only in marine waters in Northern Territory and Western Australia so commercial fishing mortality in these jurisdictions was only applied to subadult and adult age classes. In the Queensland Gulf of Carpentaria, the GOCIFFF is additionally permitted to operate in estuaries, and juveniles as well as adults are reported in catch (Peverell, 2005). Therefore, fishing pressure from the GOCIFFF was applied to all age classes while fishing pressure from other Queensland Gulf of Carpentaria commercial fisheries was only applied to subadult and adult age classes. A baseline of 50% post release survival for *P. pristis* captured in all commercial fisheries was assumed. This was based on observation of 'alive or dead' condition for other sawfish species encountered in the NTBF, *A. cuspidata* (49% alive), *P. clavata* (55% alive), and *P. zijsron* (45%) (Field et al., 2008). Due to instances of under reporting of sawfish catch in commercial fisheries (e.g. Field et al., 2008), raw estimates of annual *P. pristis* catch calculated from available data were considered a 'low' estimate. Estimates of annual catch were additionally doubled and tripled to produce a 'moderate' and 'extreme' estimate. For the GOCIFFF and NTBF, the low, moderate, and extreme estimates corresponded to the three methods of CPUE application to their respective effort data (Appendix 4 '*Commercial fishery calculations*'). This provided a range of fishing pressures for use in PVA (see '*Population viability analysis*).

To apply commercial fishing mortality in RAMAS *Metapopulation*, the number of *P. pristis* estimated to be caught in each jurisdiction was applied as a proportion of the number of individuals exposed, calculated from each natality base cases' initial population size estimate, using the *Harvest* function.

Table 6. 5 Low, moderate, and extreme commercial fishing pressure applied to the Queensland Gulf of Carpentaria (QGOC) jurisdiction. Average annual female catch of QGOC commercial fisheries was applied to subadult and adult stages only, and included the Queensland Demersal Fish Trawl Fishery and Northern Prawn Fishery. Average annual female catch of the Gulf of Carpentaria Inshore Fin Fish Fishery (GOCIFFF) was applied to all stages.

	QGOC commercial fisheries (stages 5–13)			**GOCIFFF (stages 0–13)**		
Year	**Low**	**Moderate**	**Extreme**	**Low**	**Moderate**	**Extreme**
2006	19	37	56	271	938	1875
2007	16	32	48	269	928	1856
2008	21	42	64	284	982	1964
2009	21	42	64	253	875	1751
2010	20	39	59	233	806	1612
2011	18	35	53	229	791	1581
2012	13	26	39	235	811	1622
2013	13	26	40	226	779	1559
2014	14	27	41	200	691	1382
2015	15	30	45	212	732	1464
2016*	13	26	40	208	720	1440
Average	17	34	51	238	823	1646
Female	**8**	**17**	**25**	**119**	**412**	**823**

*Due to an absence of data for Queensland Demersal Fish Trawl Fishery (QDFTF), only years 2006-2015 were used to calculate average annual *P. pristis* catch for Queensland GOC fisheries excluding Gulf of Carpentaria Inshore Fin Fish Fishery (GOCIFFF) which was calculated separately.

Table 6. 6 Low, moderate, and extreme commercial fishing pressure applied to the Northern Territory (NT) and Western Australia (WA) jurisdictions calculated from commercial fisheries data.

	NT commercial fisheries (stages 5–13)			**WA commercial fisheries (stages 5–13)**		
Year	**Low**	**Moderate**	**Extreme**	**Low**	**Moderate**	**Extreme**
2006	71	202	373	1	2	3
2007	62	180	336	1	2	3
2008	69	188	340	1	2	3
2009	68	179	319	1	2	3
2010	67	180	325	1	2	3
2011	71	187	335	1	2	3
2012	80	203	354	1	2	3
2013	76	185	317	1	2	3
2014	73	175	297	1	2	3
2015	72	175	298	1	2	3
2016	81	200	345	1	2	3
Average	72	187	331	1	2	3
Female	**36**	**93**	**165**	**1**	**1**	**2**

6.2.2.2 Other fisheries

Aside from commercial fisheries, there is very little information on other fisheries sectors (recreational, Illegal Unreported and Unregulated (IUU), and cultural harvest) that may contribute to mortality of *P. pristis*. Morgan et al. (2011b) for example note the presence of an unsubstantiated take of sawfish in various fishery sectors of Western Australia (possibly due to harvest of rostra for curios). *Pristis pristis* is also included in the recent reconstructed catch analysis by Braccini et al. (2021), which accounted for aspects of IUU fishing. Indigenous communities are known to fish using a variety of methods and gears (Henry and Lyle, 2003) including discarded commercial nets (Peverell, 2009). Most Indigenous fishing effort is likely to be localized in easily accessible areas, i.e. close inshore, riverine and floodplain environments. Sawfishes are reported to be caught by Indigenous fishers although data quantifying catch is presently limited. In the absence of available data quantifying these three fisheries, a fishing pressure of $F = 0.01$ yr^{-1} was applied in each jurisdiction to represent 'other fisheries' using the *Harvest* function in RAMAS *Metapopulation*.

6.2.2.3 Low wet season rainfall

Available evidence suggests that juvenile *P. pristis* recruitment into nursery (freshwater) habitat is dependent on periods of high rainfall, when connectivity from the estuary to upper freshwater habitat is increased (Lear et al., 2019). Furthermore, higher rainfall years are likely to yield greater juvenile survival through increased volume and connectivity of habitat, more stable environmental conditions (e.g. water temperature and dissolved oxygen), and greater food availability (Gleiss et al., 2017; Whitty et al., 2017; Lear et al., 2020). This relationship has also been demonstrated for euryhaline fish species such as barramundi (*Lates calcarifer*) in Northern Australia (Staunton-Smith et al., 2004).

To incorporate the effects of low wet season rainfall, the probability of October-April (approximate wet season) rainfall being less than the average wet season rainfall was calculated. Historical data were examined from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/cdo/about/cdo-rainfall-feature.shtml) at Vanrook Station (1922–2019) for the Gulf of Carpentaria, Darwin International Airport (1901–2019) for Northern Territory, and Gogo Station (1909–2019) for Western Australia. The probability of a given year having a low wet season rainfall was calculated for each jurisdiction (Gulf of Carpentaria = 0.55, Northern Territory = 0.56, Western Australia = 0.57, Appendix 4 '*Rainfall data*') and incorporated into the model using the *Catastrophe* function in RAMAS *Metapopulation*. Low wet season rainfall years were estimated to result in 50% additional mortality for young-of-the-year (through prevention of recruitment to nursery habitat and increased effects of intra- and interspecific competition), and an additional 10% mortality for other juvenile age classes (age classes 1–4), which are reliant on ecological functions of freshwater environments and would also be subject to intra- and interspecific competition (Lear et al., 2020). The variation of flow regimes across northern Australian rivers is acknowledged, and these low wet season mortality schedules are based on a conservative interpretation of *P. pristis* recruitment into the Fitzroy River which is a comparatively dry system (Lear et al., 2019).

6.2.2.4 Crocodile predation

Following Australia's protection of crocodiles in 1971, crocodile populations (estuarine crocodile *Crocodylus porosus*, and freshwater crocodile *Crocodylus johnsoni*) are considered to have recovered to carrying capacity (Lindner, 2004; Fukuda et al., 2011). Recent evidence suggests that crocodiles may pose a higher than previously thought predation risk to juvenile *P. pristis* (Morgan et al., 2017). Morgan et al. (2017) provide preliminary evidence to support concern that the disparity in the respective high densities of crocodiles and low densities of *P. pristis* may be resulting in a higher net rate of juvenile *P. pristis* predation by crocodiles relative to the predation rate that would occur at virgin biomass levels of each species. Furthermore, due to stable abundances of other crocodilian prey items (e.g. *L. calcarifer* fisheries are effectively managed across northern Australia), and presence of introduced non-native species (e.g. water buffalo *Bubalus bubalis* and pigs *Sus* spp.), it is unlikely that depletions in *P. pristis* populations will produce a 'prey-density-dependent' response in crocodile populations. In order to examine the potential impact of increased predation pressure from crocodiles on juvenile *P. pristis*, this study explored the effect of increasing juvenile (stages 0–4) mortality by 20% using the *Harvest* function in RAMAS *Metapopulation*.

6.2.2.5 Juvenile floodplain management

In recent years, conservation efforts in the Northern Territory and Western Australia have collaborated with local Indigenous communities and ranger groups to relocate juvenile *P. pristis* found in evaporating floodplains and tributaries. These relocations typically happen after high rainfall wet seasons, when overbank flooding occurs and animals are stranded in slowly evaporating floodplain pools after flood waters recede. In order to investigate the effectiveness of saving juveniles in this manner, the probability of a given wet season rainfall exceeding 125% of the average rainfall for each jurisdiction was firstly calculated from the same historic rainfall data sets as '*Low wet season rainfall*' (resulting probabilities were GOC = 0.2, NT = 0.27, WA = 0.14) (Appendix 4, Table A4. 4). It was considered that 5% of each juvenile age class (stages 0–4) could be 'saved' in these high rainfall years.

Inversely using the *Catastrophe* function in RAMAS *Metapopulation*, the occurrence of a high wet season rainfall resulted in stage abundances being multiplied by 1.05, mimicking a 're-introduction' of these individuals into the population.

6.2.3 Population Viability Analysis

RAMAS *Metapopulation* allows for 'Scenarios' to be introduced to the model, so that their effects on N_{t+1} can be examined. In this study, 12 Scenarios were applied to each jurisdiction, for each of the four natality base case combinations (i.e. AMR, ALS, BMR, BLS). These 12 Scenarios aimed to capture present or future threats (Scenarios 1–5), different management options to those threats (Scenarios 6–10), and the effect of alternative initial population sizes (Scenarios 11–12) (Table 6.7). Scenarios 1–3 explored the effect of the low, moderate, and extreme commercial fisheries mortality estimates, respectively (see '*Commercial fishing*'). The moderate level of commercial fishing was used in all subsequent scenarios. Scenario 4 increased the probability of a low wet season rainfall occurring by 25% to simulate possible effects of increased drought frequency in accordance with climate change (in all other scenarios the probability was held constant at average levels see '*Low wet season rainfall*'). Scenario 5 explored the effect of increased crocodile mortality on juvenile age classes. Scenario 6 increased post release survival in commercial fisheries to 95% (from the base level of 50%). Scenario 7 explored the effectiveness of relocating juveniles in evaporating floodplains (see '*Juvenile floodplain management*'). Scenario 8 and 9 removed inshore gillnet fisheries (GOCIFFF, NTBF, and KGBF) and trawl fisheries (NPF, QDFTF, and NTDFT), respectively. Scenario 10 explored whether the effects of crocodile mortality (i.e. Scenario 5) could be compensated by increasing post release survival in commercial fisheries to 95% (i.e. Scenario 6) and relocating juveniles in evaporating floodplains (i.e. Scenario 7). Finally, Scenario 11 and 12 explored the effect of alternative initial population sizes using subadult and adult female population densities of half (0.0125 female *P. pristis* km^{-1}) and double (0.05 female *P. pristis* km^{-1}) the density used to calculate the initial population sizes applied in other scenarios. Calculation of corresponding juvenile population size followed the same approach of using stable stage distribution models (see '*Estimating initial population size*'). These alternative population sizes were applied to the same pressures used in Scenario 2. Other fisheries mortality (see '*Other fishing'*) was held constant at $F = 0.01$ year^{-1} across all scenarios.

Population projections of the 12 scenarios, in each of the three jurisdictions, for each of the four natality base cases (144 models in total), were simulated 1,000 times for a duration of 66 years (three generation times; Kyne et al., 2021) in RAMAS *Metapopulation*. A Beverton and Holt 'Contest' model was used to incorporate density-dependence into population projections (see Carlson and Simpfendorfer 2015 for further details). To estimate carrying capacity, it was assumed a net 80% depletion in population abundance of *P. pristis* has occurred in each jurisdiction. While this assumption is arbitrary, it was chosen as a basis to test the effectiveness of various population management approaches for the rebuilding of populations in each jurisdiction. Therefore, carrying capacity in each region was calculated by dividing each natality base cases' initial population size by 0.2 with a coefficient of variation (CV) of 10% applied.

6.2.3.1 Extinction probability

Probability of terminal extinction was calculated for each time step (t+1) during model simulations in RAMAS *Metapopulation*. A Kolmogorov-Smirnov test was incorporated to produce 95% confidence intervals (CI). These CI values were calculated as a function of replicates (1000 in this study), which determines the CI distribution width (in this study CI was always ±2.8% for the 1000 replicates used). This study used a model duration of three generation lengths for *P. pristis* to meet Criterion 5 *Quantitative Analysis* for listing under the EPBC Act (1999) (Appendix 4, Table A4. 5). Models for each jurisdiction were produced separately and summated for the metapopulation. This allowed extinction probability to be calculated in each jurisdiction as well as for the metapopulation.

Table 6. 7 Summary of scenarios used in *Pristis pristis* population viability analysis. Variables adjusted for each scenario are shown in bold. *F* Commercial fisheries pressure, QGOC Queensland Gulf of Carpentaria, NT Northern Territory, WA Western Australia, GOCIFFF Gulf of Carpentaria Inshore Fin Fish Fishery, NTBF Northern Territory Barramundi Fishery, KGBF Kimberley Gillnet and Barramundi Fishery, NPF Northern Prawn Trawl, QDFTF Queensland Demersal Fish Trawl Fishery, NTDFTF Northern Territory Demersal Fish Trawl Fishery.

Scenario	Initial population size (subadult and adult) (*P. pristis* km^{-1})	Commercial fishing pressure	Other fishing (year^{-1})	Probability of low wet-season rainfall	Crocodile mortality (year^{-1})	Post- release survival	Probability of increased juvenile survival (5%)	Commercial fisheries excluded
1. Low commercial *F*	0.025	**Low estimate**	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	50%	0	None
2. Moderate commercial *F*	0.025	**Moderate estimate**	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	50%	0	None
3. Heavy commercial *F*	0.025	**Extreme estimate**	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	50%	0	None
4. Increased drought frequency	0.025	Moderate estimate	0.01	**QGOC = 0.69** **NT = 0.70** **WA = 0.71**	0	50%	0	None
5. Additional crocodile mortality	0.025	Moderate estimate	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	**0.2**	50%	0	None
6. 95% post-release survival	0.025	Moderate estimate	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	**95%**	0	None
7. Juvenile floodplain management	0.025	Moderate estimate	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	50%	**QGOC = 0.20** **NT = 0.27** **WA = 0.14**	None
8. No inshore gillnet *F*	0.025	Moderate estimate	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	50%	0	**GOCIFFF NTBF KGBF**
9. No trawl *F*	0.025	Moderate estimate	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	50%	0	**NPF QDFTF NTDFTF**
10. Additional crocodile mortality & Scenario 6 and 7	0.025	Moderate estimate	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	**0.2**	**95%**	**QGOC = 0.20** **NT = 0.27** **WA = 0.14**	None
11. Smaller initial *N*	**0.0125**	Moderate estimate	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	50%	0	None
12. Larger initial *N*	**0.05**	Moderate estimate	0.01	QGOC = 0.55 NT = 0.56 WA = 0.57	0	50%	0	None

6.3 Results

6.3.1 Population growth estimates

Different combinations of natality parameters (litter size and reproductive periodicity) resulted in different estimates for population growth (λ) where only the indirect natural mortality estimate of Peterson and Wroblewski (1984) was considered (Table 6.2). The highest rate of population growth ($\lambda = 1.14$) occurred for AMR and the lowest rate of population growth ($\lambda = 1.05$) occurred for BLS. Stable stage distributions for each natality showed that more fecund base cases had a higher proportion of the population in juvenile age classes (Appendix 4, Figure A4. 1). Therefore, population size estimated using the stable stage distribution for each natality resulted in different estimates reflecting reproductive output, with increased estimates of natality (and subsequently population growth) giving larger population size estimates (Table 6.4). Higher reproductive output was also captured by reproductive values in each natality base case (Appendix 4, Figure A4. 2).

Matrix element elasticities produced for each natality base case showed little variance, likely because natural mortality, longevity, and age-at-reproduction were held constant. The lowest values occurred for fertility (0.069–0.077). The largest values occurred for juvenile survival in AMR (0.378) and ALS (0.384), while the largest values occurred in adult survival for BMR (0.375) and BLS (0.370). These differences in life history phase survival elasticities were also reflected in elasticity ratios between natality base cases. Juvenile (4.991–5.000) and subadult (2.996–3.000) elasticity ratios showed very little variance across natality base cases.

6.3.2 Scenarios

Scenarios 1–3 testing varied rates of commercial fishing each resulted in considerable differences across natality base cases in the Queensland Gulf of Carpentaria and Northern Territory (Figure 6.3–6.4). Western Australia only had marginal differences across these three scenarios (Figure

6.5). Scenario 1 '*Low commercial F*' resulted in population increases in all jurisdictions and natality base cases except for BLS which showed substantial declines (>50%) in all jurisdictions. Scenario 2 '*Moderate commercial F*' resulted in slightly smaller population increases in the Northern Territory for AMR, ALS, and BMR, although only the AMR natality had a population increase in Queensland Gulf of Carpentaria. Scenario 3 '*Extreme commercial F*' resulted in population declines for all natalities in the Queensland Gulf of Carpentaria (with -100% for BLS). Declines were less severe in the Northern Territory with only the biennial natality base cases (BMR and BLS) resulting in population declines. Scenario 4 '*Increased drought frequency*' produced more negative results than Scenario 2 '*Moderate commercial F*' in Queensland Gulf of Carpentaria and Northern Territory. A greater negative effect was observed when compared to Scenario 3 '*Extreme commercial F*' in Northern Territory (except AMR) and Western Australia, though not Queensland Gulf of Carpentaria (Figure 6.3–6.5). For Scenario 5 '*Additional crocodile mortality*' substantial declines were observed for AMR across the Queensland Gulf of Carpentaria (-92.3%), Northern Territory (-73.7%), and Western Australia (-55.0%), with all other natality base cases resulting in even larger declines (Figure 6.3–6.5). Complete population depletion (-100%) was observed in the Queensland Gulf of Carpentaria (BMR and BLS) and Northern Territory (BLS).

Five management approaches were tested in Scenarios 6–10 (Figure 6.3–6.5). Scenario 6 '*95% post-release survival*' produced the most optimistic population changes in the Queensland Gulf of Carpentaria and Northern Territory, with population growth over 200% in both jurisdictions for AMR. Substantial declines (>-50%) were still observed for BLS across all jurisdictions. Scenario 7 '*juvenile floodplain monitoring*' produced the most optimistic population changes in Western Australia, although in general positive effects of Scenario 7 were only slightly better than Scenario 2 '*Moderate commercial F*' across all jurisdictions. Scenarios 8 '*No inshore gillnet F*' and 9 '*No trawl F*' both had positive effects when compared to Scenario 2 '*Moderate commercial F*' in the Queensland Gulf of Carpentaria and Northern Territory. In both of these jurisdictions removal of gillnet fishing in Scenario 8 resulted in more positive effect than removal of trawl fishing in Scenario 9. In Western Australia, Scenarios 8 and 9 had little effect and the more positive effect of Scenario 8 was due to stochasticity of other sources of mortality within the model, as only trawl fisheries are reported to catch *P. pristis* from data used in this study. Scenario 10 '*Additional crocodile mortality & Scenario 6 and 7*' resulted in population declines greater than -50% for all natality base cases in each jurisdiction except AMR in Western Australia (-47.6%). For biennial natality base cases (BMR and BLS), a decline of -100% occurred in the Queensland Gulf of Carpentaria, while all other jurisdictions had declines greater than -90%.

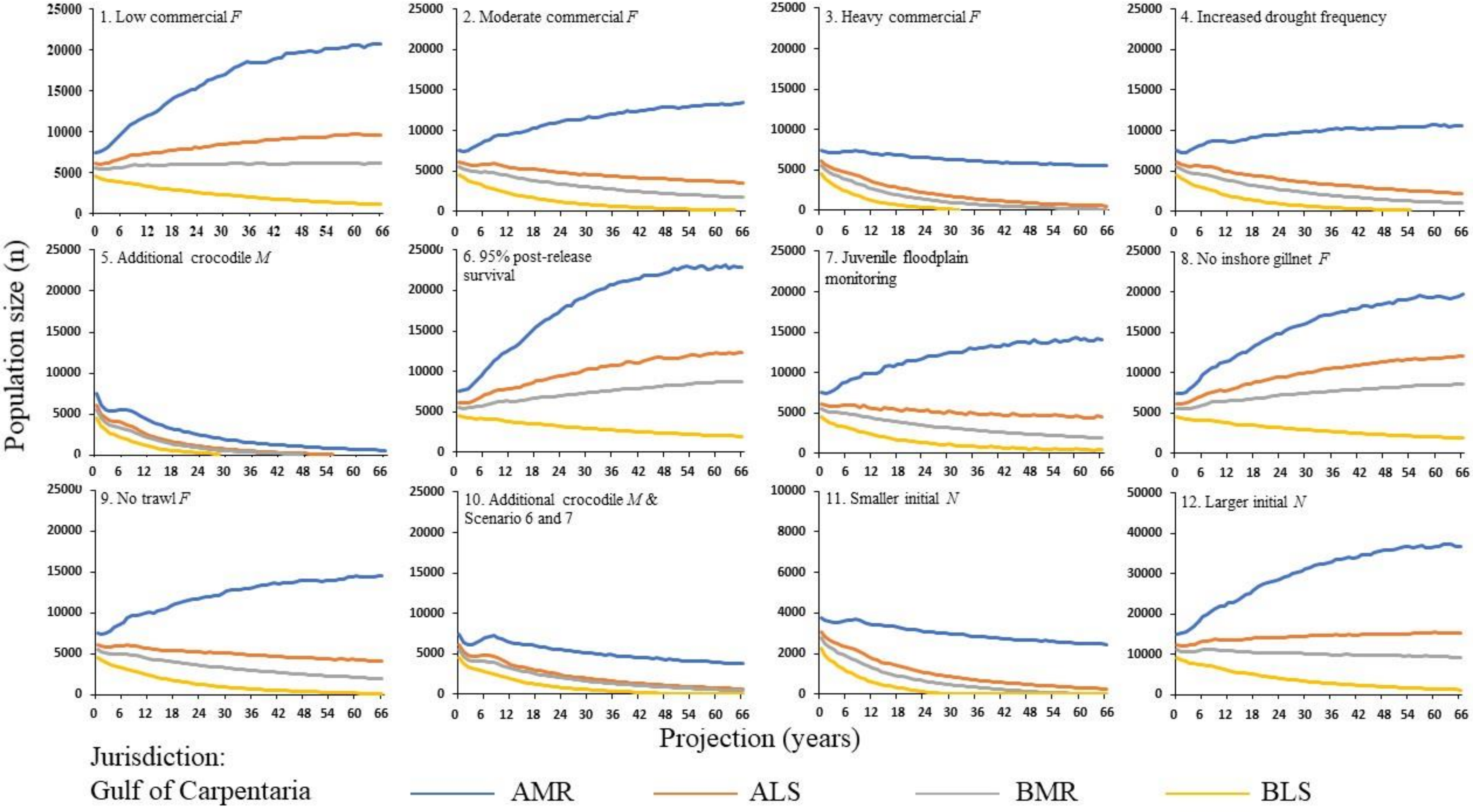


Figure 6. 3 Mean population projections for scenarios 1–12 for each natality base case in the Queensland Gulf of Carpentaria. Standard deviation values for each time step can be found in Supplementary Material. AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

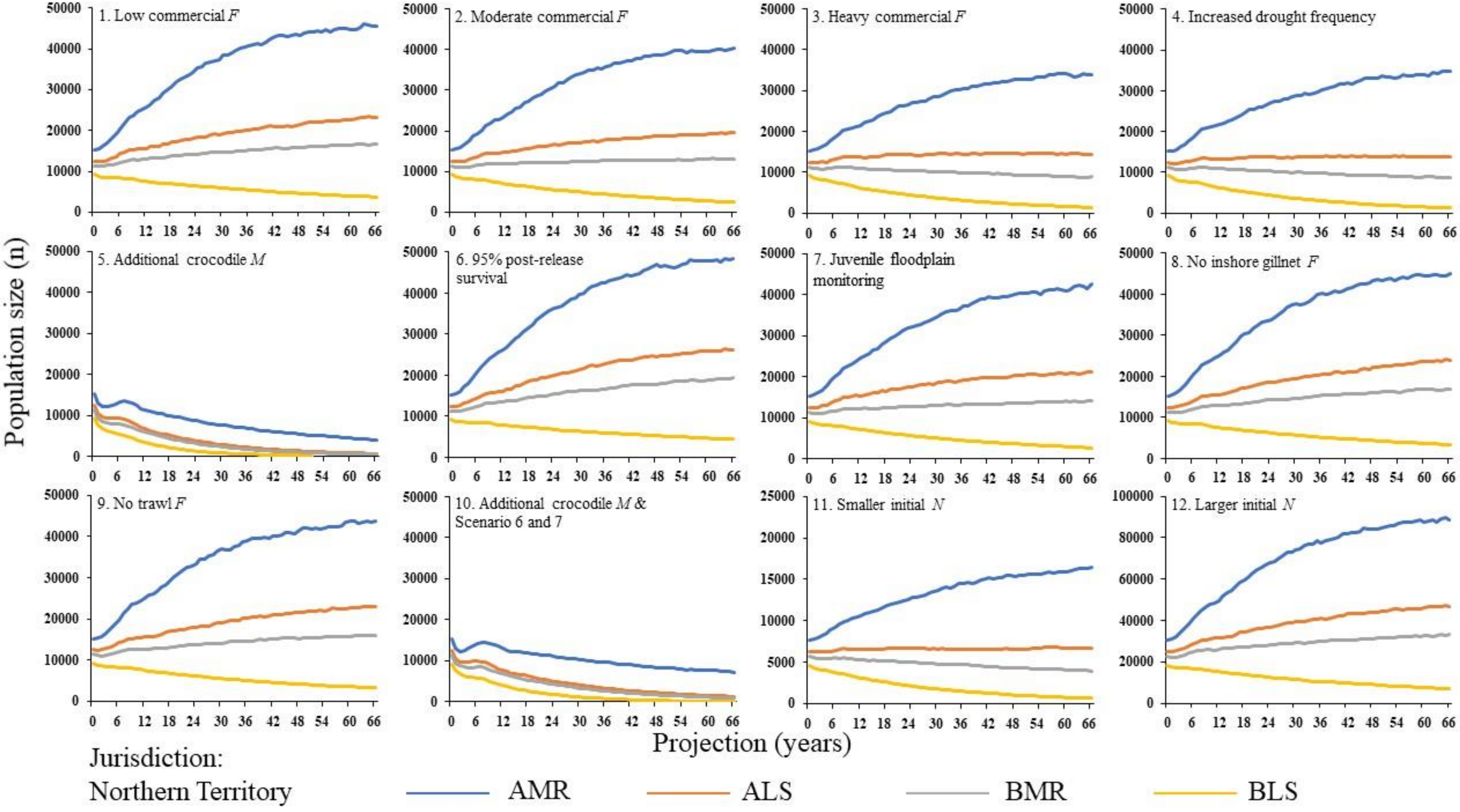


Figure 6. 4 Mean population projections for scenarios 1–12 for each natality base case in the Northern Territory. Standard deviation values for each time step can be found in Supplementary Material. AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

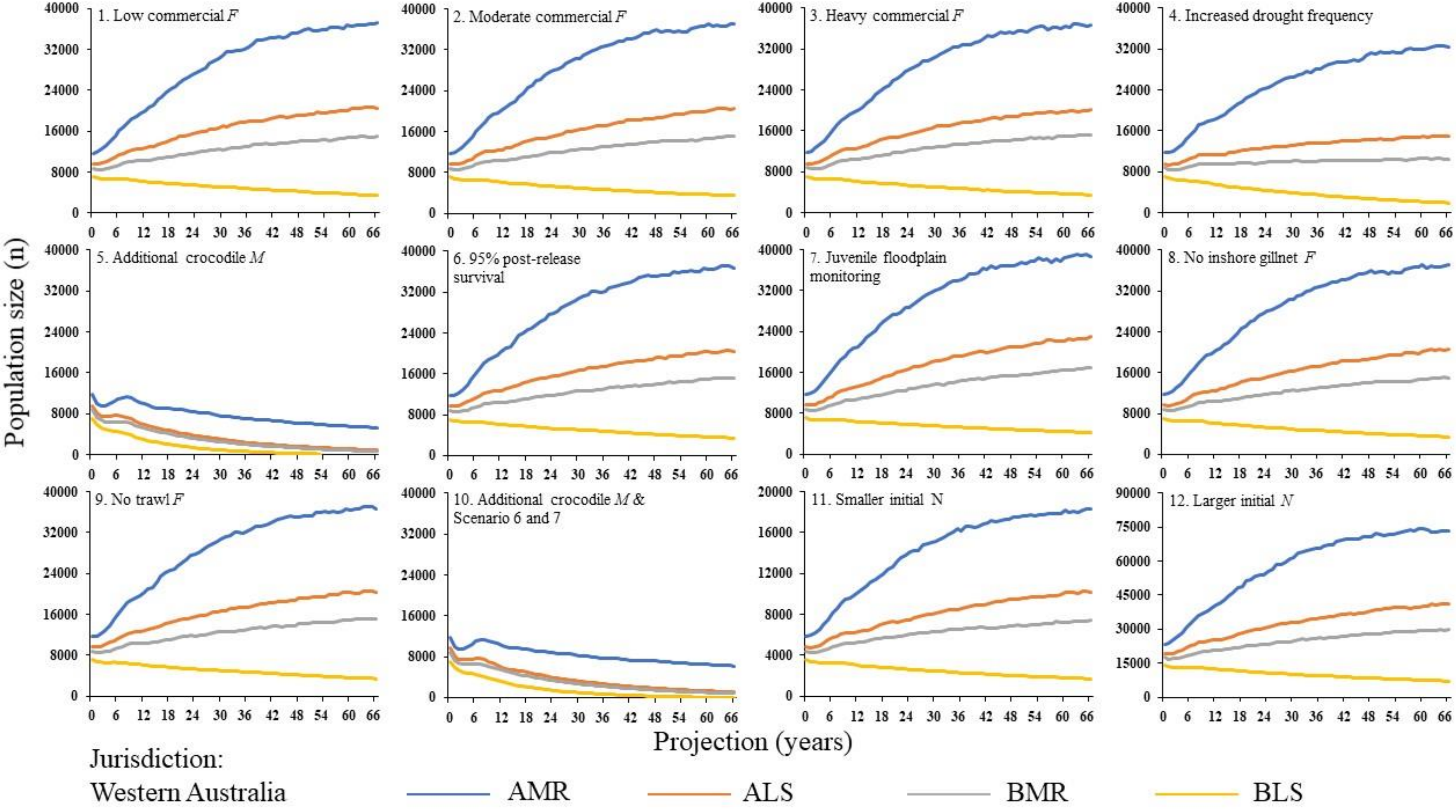


Figure 6. 5 Mean population projections for scenarios 1–12 for each natality base case in the Western Australia. Standard deviation values for each time step can be found in Supplementary Material. AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

Scenario 11 ‘*Smaller initial N*’ resulted in lower population growth or more severe declines in corresponding natalities and jurisdictions compared to Scenario 2 ‘*moderate commercial F*’, Similarly, Scenario 12 ‘*Larger initial N*’ resulted in higher population growth or less severe declines when compared to Scenario 2. In Scenario 11, substantial declines occurred in Queensland Gulf of Carpentaria (exceeding -90% for ALS, BMR, and BLS) while large declines were also observed in Northern Territory for BMR (-30.8%), and BLS (-86.8%) (Figure 6.3–6.4). In Scenario 12, population increased in all jurisdictions for natality base cases AMR, ALS, and BMR (excluding Queensland Gulf of Carpentaria) (Figure 6.3–6.5). Large declines occurred for BLS in Queensland Gulf of Carpentaria (-87.4%), Northern Territory (-61.9%), and Western Australia (-49.3%).

Population increases were generally observed across scenarios for the metapopulation (Figure 6.6). However, BLS resulted in declines exceeding -50% for all scenarios excluding Scenario 12 ‘*Larger initial N*’ in Western Australia. For other natality base cases, substantial declines (exceeding -99%) were also observed in Scenario 5 ‘*Additional crocodile mortality*’ and Scenario 10 ‘*Additional crocodile mortality & Scenario 6 and 7*’ in other natality base cases.

6.3.3 Extinction probability

Across all scenarios and natality base cases in the metapopulation, terminal extinction of *P. pristis* only occurred three times (Table 6.8). Two of these were in Scenario 5 ‘*Additional crocodile mortality*’ with 0.4% and 95.1% extinction probability for BMR and BLS, respectively. There was also a 73.5% extinction probability for BLS in Scenario 10 ‘*Additional crocodile mortality & Scenario 6 and 7*’. Under the EPBC Criteria 5, this equates to two instances of meeting the threshold for Critically Endangered (BLS in Scenario 5 and 10). Other metapopulation extinction probabilities fell below the 10% threshold for Vulnerable.

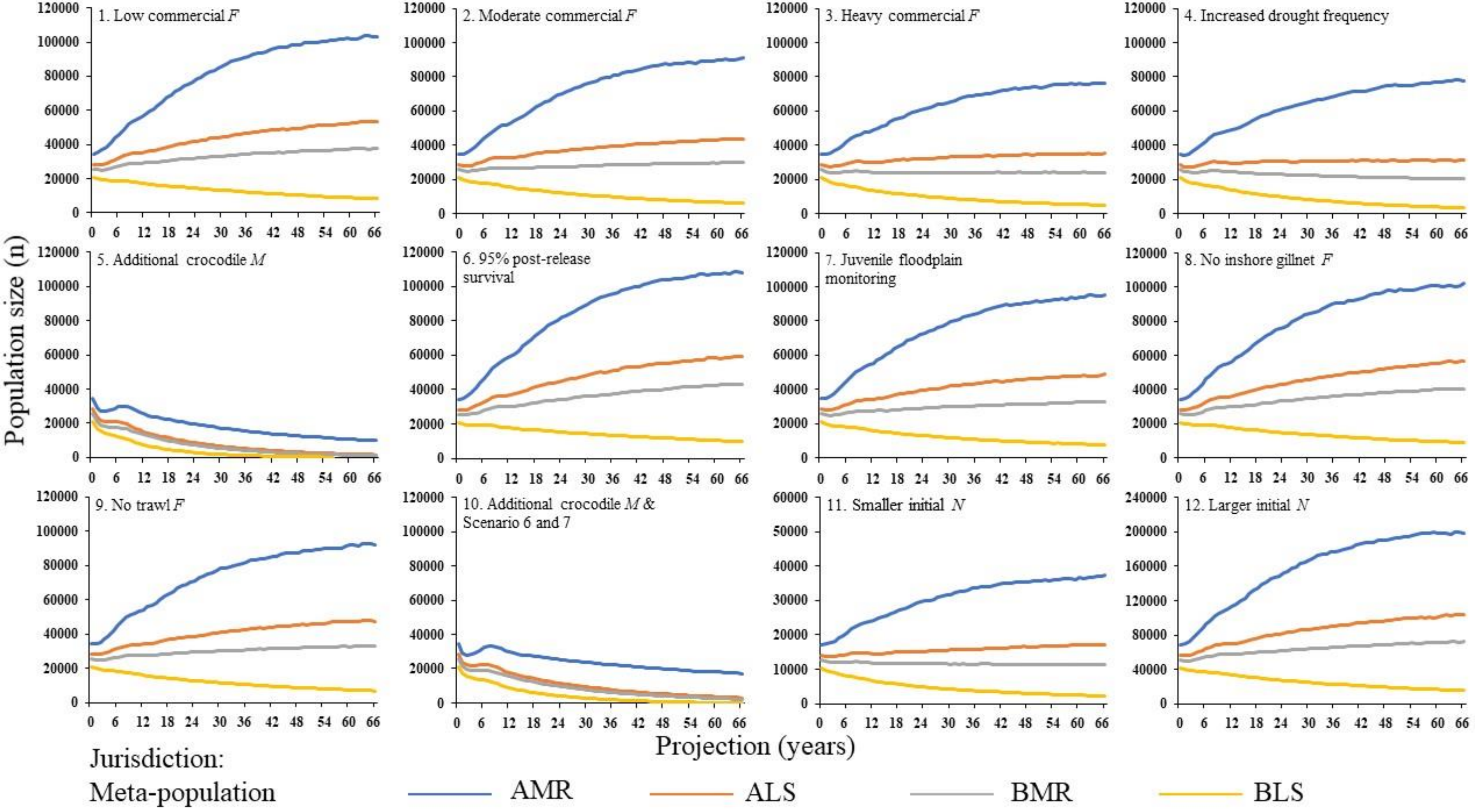


Figure 6. 6 Mean population projections for scenarios 1–12 for each natality base case for the Metapopulation. Standard deviation values for each time step can be found in Supplementary Material. AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

Table 6. 8 Extinction probabilities for each scenario across jurisdictions and natality bases cases. Scenarios or base cases with no extinction risk (i.e. probability = 0) are excluded and those with extinction probability that would result in listing on the Environmental Protection and Biodiversity Conservation (EPBC) Act (1999) are shown in bold along with their threat listing. VU Vulnerable, EN Endangered, CR Critically Endangered, AMR Annual maternal size-litter size relationship, ALS Annual mean litter size, BMR Biennial maternal size-litter size relationship, BLS Biennial mean litter size.

	Probability (%) of extinction within three generation times												
	Queensland Gulf of Carpentaria				**Northern Territory**			**Western Australia**			**Meta-population**	
Scenario	AMR	ALS	BMR	BLS	ALS	BMR	BLS	ALS	BMR	BLS	BMR	BLS
1. Low commercial *F*				0.1								
2. Moderate commercial *F*				**65.0 (CR)**								
3. Heavy commercial *F*		2.9	**61.1 (CR)**	**100 (CR)**			0.1					
4. Increased drought frequency			0.1	**90.4 (CR)**			0.1					
5. Additional crocodile mortality	3.2	**92.8 (CR)**	**99.3 (CR)**	**100 (CR)**	2.0	8.7	**98.8 (CR)**	1.3	5.0	**96.3 (CR)**	0.4	**95.1 (CR)**
7. Juvenile floodplain management				**60.0 (CR)**								
9. No trawl *F*				**60.2 (CR)**								
10. Additional crocodile mortality & Scenario 6 and 7		6.5	**16.5 (VU)**	**86.6 (CR)**	0.2	0.6	**90.7 (CR)**	0.2	2.4	**93.4 (CR)**		**73.5 (CR)**
11. Smaller initial *N*		**27.1 (EN)**	**92.7 (CR)**	**100 (CR)**			2.1			0.1		

Probability of extinction within each jurisdiction was varied (Table 6.8). In the Queensland Gulf of Carpentaria, there was a chance of extinction occurring for one or more of the natality base cases in nine out of 12 scenarios. Extinction probability was highest in Scenario 5 '*Additional crocodile mortality*' with high risk in ALS (92.8%), BMR (99.3%), and BLS (100%). High extinction probability, or certainty, was also observed in Scenario 11 '*Smaller initial population size*', Scenario 10 '*Additional crocodile mortality & Scenario 6 and 7*'and Scenario 3 '*Extreme commercial F'*. In Northern Territory and Western Australia, chance of extinction was only apparent for Scenario's 5 '*Additional crocodile mortality*' and 10 '*Additional crocodile mortality & Scenario 6 and 7*'. However, the extinction probabilities were only low (≤ 5.0%) for AMR (Northern Territory only), ALS, and BMR. Meanwhile, BLS had an extinction probability higher than 90% for these two scenarios in both Northern Territory and Western Australia.

6.4 Discussion

6.4.1 Demographic attributes of P. pristis

New life history information on *P. pristis* provided by Kyne et al. (2021b) allowed four estimates of population growth to be considered in this study, ranging from λ = 1.05–1.14 year^{-1}. Compared to estimates of intrinsic rate of increase (r) in previous studies (here converted to λ), e.g. λ = 0.99–1.13 year^{-1} (life tables, Simpfendorfer, 2000) and λ = 0.97–1.25 year^{-1} (life tables and Leslie matrix, Moreno Iturria, 2012), values in this study fall within the previously known range for *P. pristis*. However, estimates of λ in the upper and lower ranges of these studies resulted from experimental deviations in life history traits (e.g. age-at-maturity, longevity, and reproductive periodicity). Simpfendorfer (2000) surmised that a λ = 1.05–1.07 year^{-1} was likely the most reasonable estimate for the Western Atlantic sub-population of *P. pristis*. This range was based on a biennial reproductive periodicity and the mean litter size estimate used in this study, both provided by Thorson (1976) for the Western Atlantic sub-population. Compared to λ values estimated in this study for biennial natality base cases (λ = 1.05–1.08 year^{-1}), similar values were obtained. However, the evidence for annual reproductive periodicity comes from Australia (Peverell, 2009). This leads to speculation that rates of population increase produced from the annual natality base cases (λ = 1.10–1.14 year^{-1}) may be more representative of the Indo–West Pacific sub-population (which includes Australia).

Annual reproduction is only supported by a single 5.8 m female with both near term embryos and large (~8 cm diameter) developing ova (Peverell, 2009). Meanwhile, biennial reproduction is supported by multiple observations of pregnant and non-pregnant females (in an approximate 1:1 ratio) within the same year in the Western Atlantic (see Kyne et al., 2021). It remains unclear if the co-occurrence of embryos and large ova observed by Peverell (2009) indicate annual reproduction (i.e. ova ready to be fertilised soon after birth of gestating litter) or biennial reproduction (i.e. increased maternal input in young by larger parents). Large egg size is a common trait of freshwater fish, as freshwater environments are generally less stable and lower in resource availability compared to inshore marine environments (Closs et al., 2013). Therefore, the large developing ova observed by Peverell (2009) may not actually indicate annual reproduction, as this interpretation was based on reproductive biology characteristic patterns of marine elasmobranchs. In this study, reproductive periodicity had a large influence on λ and subsequently, resilience and population recovery times. Therefore, better information on the reproductive biology of *P. pristis* should be a high priority for future research. The use of ultrasound techniques has potential to provide this information in a harmless manner (e.g. Anderson et al., 2018) compliant with national protection in Australia. This would also lead to better information on litter size and would strengthen data availability to inform the weak, though sample size restricted, maternal size-litter size relationship indicated by Kyne et al. (2021).

Under the natural mortality schedule used, the majority of reproductive contributions came from stage 9 (or first three years of maturity). This was evidenced by higher reproductive value in stages 10–14 for BMR when compared to corresponding stages for ALS, despite BMR having a lower λ than ALS (Appendix 4, Figure A4. 2). Age-at-first-capture models for long-lived sharks have demonstrated that populations can be harvested at very high levels from age-at-maturity + two or three years, if younger age classes are not exposed to additional mortality (e.g. Smart et al., 2017; Grant et al., 2019). This is due to the very small proportion of the population that survives into age classes approaching longevity. Within elasmobranchs, young adults proportionately make the largest reproductive contribution, as unlike many teleost fish, fecundity does not increase by orders of magnitude with maternal size (Cortés, 2002). Anthropogenic factors affecting sawfishes in northern Australia are more pronounced in marine environments (i.e. commercial fishing). Therefore, management actions focusing on protection of juveniles, subadults (those recruiting to the breeding population), and young adults to ensure individuals reproduce at least once are likely to produce positive population recovery responses.

Elasticities for all natality base cases indicate that proportionately juvenile survival (which usually includes subadults also for comparisons to literature) has a higher influence on λ than adult survival or fertility for *P. pristis*. Higher juvenile survival elasticities are typical of elasmobranchs throughout a range of life strategies (Cortés, 2000). Elasticities indicated that minimising mortality in the adult portion of the population is more important for BMR and BLS, than AMR or ALS. This is unsurprising as biennial reproduction as a life strategy generally relies on a protracted reproductive longevity, as observed in long-lived deep water elasmobranch species (Rigby and Simpfendorfer, 2015). Given the unique catadromous life strategy of *P. pristis* among chondrichthyans, it is interesting that elasticities did not differ to general trends observed for other steno-marine species with similar age-at-maturity (e.g. Cortés, 2002). However, like all indirect mortality estimators used in elasmobranch demography studies, the Peterson and Wroblewski (1984) method is designed for application to marine environments, which are typically more stable. It is likely that *P. pristis* have different juvenile mortality schedules in their freshwater nursery environment, compared to species with nurseries in inshore marine waters. Lear et al. (2019) for example suggest a ‘boom and bust’ type cycle to *P. pristis* recruitment and survival in the Fitzroy River which is influenced by environmental regimes, whereas species with marine nurseries would typically have more stable recruitment and survival, when density-dependent responses are not considered (Gedamke et al., 2007). Therefore, it is unclear how suitable marine-based indirect mortality estimators are for catadromous species like *P. pristis*. In the present model, the ‘low rainfall wet season’ mortality additionally considered represents the variability in year-to-year natural mortality for *P. pristis* in freshwater environments. Multiple mortality estimators were not tested in this study as these have been explored in previous work (Simpfendorfer, 2000; Moreno Iturria, 2012). The purpose of this study was rather to explore the ambiguity in reproductive parameters and effects of other anthropogenic mortality sources on population growth. In producing four estimates of λ which captured the range of λ produced in earlier studies, our use of the Peterson and Wroblewski (1984) method to focus on other demographic influences was justified.

Population sizes estimated for *P. pristis* in this study were intended to represent an 80% depletion level. This allowed for PVA to explore management approaches to optimise population recovery from depleted levels. It cannot be certain that *P. pristis* is depleted by 80% in all jurisdictions considered in this study, nor is it known if population sizes used here are representative of 80% depletion abundance. The *P. pectinata* population density data used to estimate initial population sizes of *P. pristis* in this study comes from a population that is suspected to have been depleted by 95–99% of virgin biomass levels (NMFS, 2009) and includes both sexes. However, *P. pectinata* has experienced considerable range contraction, and it should not necessarily be expected that population density in remaining refuges is depleted by 95–99%. Rather, this depletion estimate is a net depletion over the historic range of *P. pectinata*, and therefore includes areas of local extinction. Regardless, the use of *P. pectinata* population density data to calculate population size is not ideal, though it does represent population density of a depleted pristid population which is what this study aimed to investigate.

6.4.2 Threats and management of P. pristis *in marine environments*

The largest impact on subadult and adult *P. pristis* in northern Australia is commercial fishing (e.g., Kyne et al., 2021). The greatest adverse population affects from commercial fishing were observed for the Queensland Gulf of Carpentaria where commercial fishing effort, and particularly inshore gillnet effort, is highest. Commercial fishing scenarios had negligible effects in Western Australia due to minor commercial fishing activity in the Kimberley Region. Based on the commercial fisheries data available in Northern Territory and Queensland Gulf of Carpentaria, it is likely that Scenario 1 '*Low commercial F*' represents the minimum expected exploitation level. Although poorly quantified, it is strongly suspected that reported catch of sawfishes in commercial log books is an under-representation of true catch levels (Field et al., 2008). This is due to poor observer coverage since concerted elasmobranch bycatch studies were conducted throughout the early to mid-2000s (Peverell, 2005; Salini et al., 2007; Field et al., 2008) and poor taxonomic resolution of catches that are reported. Therefore, exploitation levels in Scenario 2 '*Moderate commercial F*' or Scenario 3 '*Extreme commercial F*' may be closer to actual catch rates for *P. pristis*. These higher levels of exploitation are concerning for the Queensland Gulf of Carpentaria and Northern Territory if ALS, BMR, or BLS are most representative of *P. pristis* natality. Higher *P. pristis* depletions in these jurisdictions are most likely to have occurred due to historical fishing effort, and this data indicates that declines may be ongoing if population sizes are close to those estimated here. Sensitivity tests of population size showed that the threat posed by commercial fishing varies, with smaller population sizes resulting in substantial declines across all natality base cases in the Queensland Gulf of Carpentaria and biennial base cases in the Northern Territory. Collectively, the results of these population size sensitivity tests place emphasis on attempting to estimate population sizes in the Northern Territory and Queensland Gulf of Carpentaria to inform better estimates of the extinction risk that commercial fisheries pose. Recent advancements in population size estimation through genetic techniques of threatened shark species (e.g. Hillary et al., 2018) may be possible for *P. pristis*, although large sample sizes required would be challenging to achieve.

Management scenario 6 '*95% post release survival*' demonstrates that with better sawfish handling and release practices in commercial fisheries, *P. pristis* populations have potential to recover amongst ongoing commercial fishery operations. Furthermore, Scenarios 8 '*No inshore gillnet F*' and 9 '*No trawl F*' indicate that virtually eliminating mortality in either fishery type would also allow *P. pristis* populations to rebuild from depleted states. However, the post release survival rate of *P. pristis* is a contentious topic. Our use of 50% post release survival was based on the condition (alive or dead) of other sawfish species observed by Field et al. (2008) (See *Methods*). It is unclear however if post release survival rates approaching 95% are achievable, as fishery characteristics such as soak or trawl times need to be considered, and it cannot be expected that 95% of sawfish would be alive upon gear retrieval to 'survive post release'. Another factor is that commercial fishers in some instances amputate the rostrum from live sawfish to release them from gear. Anecdotal conversation with fishers suggest that this practice stems from concerns for fisher safety, and from time and logistical constraints where rostra are severely tangled during laborious gear retrieval in tide-access dependent areas. Morgan et al. (2016) suggests that amputating the rostrum leads to reduced foraging capacity, predation defence, and likely eventual death. Complete rostrum removal also occurs in the recreational fishing sector, where rostra are retained as curios (Morgan et al., 2011b), and this may have drastically more severe consequences for survival than partial amputation. While studying the survival of amputee, or partial amputee sawfish is extremely opportunistic (e.g. Morgan et al., 2016), continued investigation into potential improvements of available 'sawfish safe release guides' for fishery specific gears and situations should continue to be made in order to minimise instances of rostrum amputations and increase post-release survival. Ultimately however, reduction of sawfish interactions with commercial fisheries is going to produce the best outcomes for sawfish populations. Continued research on the spatial use patterns of sawfish or bycatch mitigation techniques (e.g. Stevens et al., 2008) could help inform approaches to minimising negative sawfish interactions.

6.4.3 Threats and management of P. pristis in freshwater environments

The inclusion of additional 'low wet season rainfall' mortality on juvenile *P. pristis* was the main reason that BLS produced population declines across scenarios. The BLS natality parameters are based on the Lake Nicaragua population, which is suspected to complete its life cycle within non-marine environments of Lake Nicaragua and adjoining San Juan River (Thorson, 1976). The Lake Nicaragua population also appeared to have a smaller maximum size (~429 cm TL). Therefore, it is possible that the BLS natality schedule is an adaption of a genetically distinct *P. pristis* sub-population to Lake Nicaragua and is not necessarily representative of the wider *P. pristis* distribution where the life cycle is catadromous. Evidence of this can be deducted from this study and time-series recruitment data provided by Lear et al. (2019). In the Fitzroy River, *P. pristis* juvenile recruitment only appeared to be high (2 years) or moderate (1 year) in three years over a 17 year study period from 2002–2018. This represents ‘good’ recruitment in 17.6% of years. If a biennial natality schedule is considered, an individual female in effect has an 8.8% chance of pupping in a ‘good’ recruitment year. In the present study, used a probability of ‘good’ recruitment occurring on 43% of years, although large population declines were still observed across scenarios for BLS. Because negligible commercial fishing was considered in Western Australia, the main additional mortality source was other fishing ($F = 0.01$ year^{-1}) and low wet season rainfall.

There are two likely explanations for the population declines observed for BLS. 1) life history data was incorrect. The most likely sources of data that would have a large influence on λ are overestimated natural mortality, or underestimation of longevity (and specifically reproductive longevity). However, the λ value of 1.05 year^{-1} is similar to other elasmobranchs with small litter sizes and biennial reproductive periodicity e.g. oceanic whitetip shark *Carcharhinus longimanus* λ = 1.05 year^{-1} and the bigeye thresher *Alopias superciliosus* λ = 1.02 year^{-1} (Smart et al., 2020), and is therefore not unusually low for this natality schedule. Meanwhile, longevity estimates of elasmobranchs are prone to underestimation (Harry, 2018). Recent observations of unfished snapper (Lutjanidae) in Western Australia indicate that tropical fishes may reach much older ages than previously thought (Taylor et al., 2021). There is a need to develop alternatives to vertebral analysis for longevity estimation in elasmobranchs. 2) BLS is simply an underestimate of natality for *P. pristis*. The Fitzroy River is probably the most protected *P. pristis* population globally (Morgan et al., 2011b). Hence, it would be expected that population growth would be increasing in the Western Australia jurisdiction under a scenario of 80% depletion as modelled in this study, considering that effects of low wet season rainfall were more generous than Lear et al. (2019) indicate. While data in the present study are not accurate enough to confidently discount BLS, it appears likely that other natality schedules (including BMR) are more representative of *P. pristis* natality assuming other life history information used is reasonably accurate (e.g. longevity, age-at-maturity, age and growth parameters etc). Alternatively, if future research indicates that BLS is the most representative natality of *P. pristis* in the Indo–West Pacific sub-population as observed in the Western Atlantic sub-population, then other life history parameters need to be scrutinised further.

Scenario 4 ‘*Increased drought frequency*’ had a reasonably negative influence on population growth. In the Queensland Gulf of Carpentaria, affects were not as severe as Scenario 3 ‘*Extreme commercial F*’ while in the Northern Territory affects between these scenarios were similar. Excluding Western Australia, with ongoing presence of commercial fisheries in Queensland Gulf of Carpentaria and Northern Territory, increased drought frequency appears to pose a significant risk to *P. pristis* populations if AMR is an overestimate of natality. This indicates that other preventable mortality sources (e.g. commercial fishing) will need to be addressed in the near future as climate change becomes more prevalent. For Western Australia, a drying climate may pose the most significant risk of factors presently considered to *P. pristis* excluding crocodiles (See *Crocodiles*). It remains unclear to what extent *P. pristis* breeds in rivers aside from the Fitzroy River in Western Australia, as observations outside this system are limited (Thorburn et al., 2003; West et al., 2021).

Very marginal population increases were observed for scenario 7 ‘*Juvenile floodplain management*’. The ‘saving’ rate used in this study was far higher than the number of individuals presently relocated in situations of drying floodplains. For example, in the Northern territory, considering 5% of the BMR initial juvenile population size, 430 juveniles would need to be relocated annually. Furthermore, these ‘relocated’ individuals were considered to have 100% survival until the next time step. The marginal population increases suggest this practice may not have a population level effect or would need to occur on a much larger scale to have an effect. However, the value of juvenile *P. pristis* relocations extends to factors external to demographic mathematics. Firstly, need for *P. pristis* relocations are typically identified by Indigenous ranger groups, who usually also carry out the relocations. These actions may help Indigenous communities enhance and maintain community connection and custodianship of traditional lands, and can also generate media attention that increases community awareness of *P. pristis* conservation. Secondly, the activity may have a localised benefit to increase survivorship in a specific river when the activity occurs (e.g. relocation of 100 pups in the Daly River may have a substantial population effect in that system). The next research step is to investigate the post-translocation survivorship of sawfish to understand their movement to subsequent life stages and contribution to the population.

6.4.4 Crocodiles

Crocodile predation of *P. pristis* appears to potentially pose a significant and recently emergent threat to the rebuilding of populations, as initially suggested by Morgan et al. (2017). The level of gross mortality imposed on juvenile *P. pristis* in scenario 5 '*Additional crocodile mortality*' was quite severe, with the natural mortality estimator, low wet season rainfall, and crocodile mortality all considered together. However, each of these factors is based on independent evidence, so they were applied discretely. For example, the natural mortality estimator largely serves 'good' recruitment years (or in this case, 'non-drought' years when freshwater environments are more stable), as the Peterson and Wroblewski (1984) indirect estimator is intended for relatively stable marine environments. An argument could be made that crocodile mortality is captured in the natural mortality estimator. Although the feeling of various independent research groups (in Northern Territory and Western Australia) is that the low *P. pristis* density (prey) and high crocodile density (predator) is unnaturally balanced. It is important to note that other common prey items of crocodiles (e.g. *L. calcarifer*) are not significantly depleted like *P. pristis*, and introduced prey items (e.g. water buffalo e.g. *B. bubalis*, feral pigs *Sus* spp.) are readily available and commonly consumed in freshwater habitats (e.g. Fordham et al., 2006; Adame et al., 2018). Therefore, it is not expected that depleted *P. pristis* populations would produce a density-dependent response in crocodiles, as might occur in a virgin environment. This predator-prey density disparity has therefore possibly created an ethological trap (Spencer et al., 2016) for *P. pristis*, that is preventing population recovery and driving extinction risk as hypothesized by Morgan et al. (2017) and supported here.

Carcharhinus leucas is also a natural predator of juvenile *P. pristis* (Thorburn and Rowland, 2008). This species is unlikely to be depleted far from carrying capacity in the jurisdictions presently considered (Espinoza and Sparks, 2019). In a situation where *P. pristis* is depleted in a given river system, even low to moderate rates of predation from *C. leucas* and crocodiles will result in suppression of the population, and in extreme cases continued population declines as recruitment to the breeding population is in turn reduced. The later has been captured in the results of Scenario 5 in this study based on an additional mortality of $M = 0.2$. Only crocodile mortality was considered in Scenario 5 as, 1) *C. leucas* would likely not benefit from introduced terrestrial species to the extent of crocodiles (Adame et al., 2018), and thereby may not have 'unnaturally' high population levels; and 2) it remains unclear if juvenile *C. leucas* predation always results in mortality (Morgan et al., 2017). Therefore, it is less likely an 'unnatural' balance exists between *P. pristis* and *C. leucas*, and *C. leucas* predation is likely captured in the Peterson and Wroblewski (1984) mortality estimator. It is only in the Fitzroy River that *C. leucas* may pose a disproportionately high predation risk. The Camballin Barrage appears to be a significant barrier to the upstream migration of juvenile *P. pristis* (Morgan et al., 2011a), and Thorburn et al. (2014) indicate that *P. pristis* are the most energetically important prey source of *C. leucas* below the Camballin Barrage. Elsewhere in northern Australia, it is likely that crocodiles pose a greater risk to *P. pristis* in rivers with intermittent flow, as crocodiles can move between pools and billabongs to exploit trapped prey resources, including *P. pristis*. While observation of successful predation attempts by crocodiles on elasmobranchs are rare (Lucifora et al., 2020), observation of failed predation attempts (e.g. Morgan et al., 2017) does not mean an individual would survive subsequent attempts over a dry season. Large *C. porosus* are known to penetrate well into freshwater reaches of the Adelaide River in the Northern Territory, including floodplain and billabong environments where *P. pristis* nurseries are located (Letnic, 2008). It is known there are differences in crocodile density throughout northern Australian rivers (Fukuda et al., 2011; Corey et al., 2018), and the 'over-predation risk' of crocodiles likely varies in each system (e.g. Hanson et al., 2015).

The exploration of crocodile mortality on juvenile *P. pristis* in this study represents a complicated conservation situation. Scenario 10 '*Additional crocodile mortality & scenario 6 and 7*' (i.e., 95% post-release survival and juvenile floodplain management) indicated that in combining these management strategies, *P. pristis* populations would still decline substantially under the crocodile mortality rate used. This raises three points to consider; Firstly, further information on crocodile predation of *P. pristis* is needed (and possibly with some urgency) to verify the severity of this threat. This can most easily be achieved through time series recruitment studies of *P. pristis* similar to Lear et al. (2019) that additionally consider crocodile density and diet (e.g. through isotope analysis or genetic analysis of stomach contents). Furthermore, research is needed on further systems to the Fitzroy River, as risk of crocodile predation may vary between rivers (e.g. highest densities are reported from Kakadu Nation Park, Northern Territory, Fukuda et al., 2011). However, a consideration of crocodile diet studies is that individual predation rates may be very low, owing to low *P. pristis* population density in comparison to other prey items such as *L. calcarifer*. Therefore, it is unsurprising that *P. pristis* are not detected in existing crocodile diet studies (e.g. Adame et al., 2018). Secondly, there is need to consider ways to reduce crocodile mortality rates. Removal of existing migration barriers (e.g. Camballin Barrage) and restrictions on construction of new barriers would limit the predator-prey concentration effect they produce (Thorburn et al., 2014). Management actions that facilitate the swift migration of juvenile *P. pristis* to shallow upstream environments would aid in lowering predation rates.

The third and most obvious option, which also provides socio-economic benefits, would be to encourage further Indigenous led commercial harvest of crocodiles under a ‘population control program’. It is acknowledged that this is a polarising topic, and one that has raised discussions previously primarily concerning human safety (e.g. Ross, 1989; Britton and Campbell, 2014; Burgin and Hardiman, 2016) but also protection of livestock (McHale et al., 2013). Crocodiles support tourism in regional areas (e.g. Kakadu National Park), and these eco-tourism ventures can have broader benefits for general environmental conservation (Macdonald et al., 2017). Furthermore, crocodiles may be viewed as beneficial to control of northern Australia’s introduced species through high predation rates (Adame et al., 2018). Although there may be other alternatives. Indigenous people can gain economic benefits from harvest of introduced species such as *B. bulbalis* (Collier et al., 2011) and ‘hunting’ tourism ventures exist (e.g. Roper River, Northern Territory). Some Indigenous communities also benefit from harvest of crocodile eggs and juveniles (e.g. Corey et al., 2018). There is likely scope for each of these activities to be scaled up to the benefit of local and Indigenous livelihoods, as well as broader ecological and environmental benefits. Ultimately, this study does not suggest large-scale crocodile removal, but identification of river systems important to rebuilding *P. pristis* populations regionally (e.g. Fitzroy, Daly, Adelaide, Wenlock Rivers), as well as other locally threatened species (e.g. freshwater turtle *Elseya lavarackorum* and pig-nosed turtle *Carettochelys insculpta*) may allow conversations to develop about carefully considered localised crocodile population control to develop multi-species refugia. It may be possible to achieve a balance between high crocodile density in important areas for tourism (e.g. Kakadu National Park) and lower density in ecologically important areas that otherwise do not have a strong eco-tourism establishment around crocodiles. This is obviously an incredibly complex consideration for governing bodies and Traditional Owners, however, further conversation on the issue of recovered crocodile populations in northern Australia is encouraged in the context of broader native biodiversity conservation.

6.4.5 Extinction Risk of P. pristis

Extinction risk varied between scenarios and natality schedules for the metapopulation. Terminal extinction of the metapopulation only occurred in a few instances due to 0% extinction probability in the Northern Territory and Western Australian jurisdictions in most scenarios. However, large population declines in the metapopulation were still common for the ALS, BMR, and BLS natalities. Probability of extinction in the metapopulation was highest when the BLS natality schedule was considered in the presence of additional crocodile mortality. In this instance, *P. pristis* has an extinction probability of >73% within three generation lengths. Therefore, a conservative interpretation of this study under Criteria 5 of the EPBC Act (1999) would likely lead to a Critically Endangered (probability of extinction ≥50%) listing for *P. pristis* until further information is available on their reproductive biology and threat posed by recovered crocodile populations. Hence, reproductive biology and crocodile predation have a high imperative for future research. Due to significant historic declines of sawfishes in eastern Queensland (Wueringer, 2017), it is assumed that *P. pristis* remains heavily depleted, and that inclusion of this jurisdiction in the present study would not have led to more optimistic outcomes for the Australian metapopulation.

Extinction risk within each region varied widely and was heavily influenced by natality and population size. High extinction risk across scenarios and natality base cases in the Queensland Gulf of Carpentaria was driven by high commercial fisheries pressure. In particular, the GOCIFFF has considerable effort compared to inshore gillnet fisheries in the Northern Territory or Western Australia and appears to have significantly more interactions with *P. pristis* than any other fishery. The GOCIFFF is also the only commercial fishery permitted to operate in estuaries (Peverell, 2005) and this is the likely reason for high *P. pristis* interactions. This study has indicated that management is required for the GOCIFFF to reduce *P. pristis* interactions and increase post release survival. Failure to address the current risks posed by the GOCIFFF risks local extinction. While *P. pristis* likely benefits from the seasonal closure of this fishery (October-January) to protect breeding *L. calcarifer* stocks, it remains unclear if this closure period aligns completely or partially with *P. pristis* pupping. Furthermore, a review of the necessity of commercial fishing within estuarine waters in the Queensland Gulf of Carpentaria is required. Alternatively, consideration of spatial fishing closures in at least a few river systems that are important to *P. pristis* (e.g. Wenlock, Mitchell, Gilbert, Norman Rivers) would likely have positive population outcomes.

While extinction risk in the Northern Territory and Western Australia was low (excluding BLS in Scenario 5 & 10), this study has identified research priorities in these jurisdictions. In the Northern Territory, continued actions to reduce *P. pristis* interactions or increase post release survival in commercial fisheries should continue to be perused. The largest risk in Northern Territory may however be crocodile predation. If the predator-prey disparity is in effect anywhere in northern Australia, it is most likely within the Northern Territory. In Western Australia, the greatest management priority exists for freshwater nurseries and maintenance of free-flowing rivers (e.g. Camballin Barrage). The interests around damming and irrigation in Western Australia (Fitzroy River), but also Northern Territory ('Darwin catchment' which includes the Adelaide, Finniss, Mary, and Wildman Rivers) and Queensland Gulf of Carpentaria (Mitchell River) (see Petheram et al., 2017), would have dire consequences for *P. pristis* in each of these jurisdictions. Damming of the Fitzroy River would remove what is currently the most significant *P. pristis* population in Western Australia. Damming of the

‘Darwin catchment’ would lead to loss of multiple nursery environments for *P. pristis* and have large impacts on populations that occur in the Beagle Gulf and Van Diemen Gulf. These areas of Northern Territory, along with the Fitzroy River in Western Australia, are the most important refuge areas for *P. pristis* globally. Damming of the Mitchell River would be a significant loss of habitat for *P. pristis* and likely have a large impact on the Queensland Gulf of Carpentaria populations, which based on this study has the highest likelihood of local extinction. Also relevant to all jurisdictions is the potential for increased surface and ground water abstraction (e.g. for agricultural irrigation, Petheram et al., 2017) to decrease the quality of freshwater habitat across northern Australian rivers. Lear et al. (2020) showed that survivorship and body condition of *P. pristis* juveniles is adversely affected during low rainfall years, and this would be exacerbated by water abstraction practices which can result in ‘drought-like’ conditions for freshwater environments (Finn et al., 2009).

6.5 Conclusion

Sawfishes are among the worlds most threatened elasmobranchs, and Australia has been regarded as the only refuge for all four Indo–Pacific species (Morgan et al., 2011b; Dulvy et al., 2016; Yan et al., 2021). Although *P. pristis* has the widest distribution of the sawfishes, it is possibly the most vulnerable to population declines from anthropogenic factors due to its unique catadromous life strategy. Results from this study raise questions about the broad identification of northern Australia as a long-term refuge for *P. pristis*, and rather indicate that Western Australia, and possibly Northern Territory are the only part of northern Australia where *P. pristis* are not heavily depleted. This was evidenced by generally positive population growth across scenarios in these jurisdictions, indicating that populations are unlikely to be at levels near 80% depletion as modeled in the present study. If populations were at ~80% depletion levels, the present threats modeled would be expected to produce plateauing population growth, or declines. This is obviously contingent on accuracy of data for each threat used in this study. It is acknowledged that better data is needed on aspects of *P. pristis* biology, and threats this species faces in northern Australia, and it is hoped this study will lead to concerted future research of *P. pristis* in a six main aspects including: 1) reproductive biology; 2) natural mortality in freshwater nursery environments; 3) more accurate records of sawfish interactions with fisheries; 4) mitigation of interactions in commercial fisheries and better methods for increasing post release survival; 5) environmental factors influencing recruitment in freshwater environments in systems additional to the Fitzroy River; and 6) predator-prey relationship of crocodiles and *P. pristis*. The significant contribution that researchers in the Fitzroy River have contributed to our understanding of *P. pristis* in Australia is acknowledged. Although moving forward, it will be important to facilitate data collection from other river systems with varied flow regimes across Northern Australia as a basis for future comparisons with the relatively ‘dry’ Fitzroy River. This will ensure continued building of knowledge for management and conservation purposes and ultimately, help rebuild *P. pristis* populations in Australia and inform suitable approaches in other global regions.

Chapter 7

General discussion

There is global concern around the increasing loss of biodiversity driven by direct (e.g., fishing) and indirect (e.g., climate change) human pressures. In marine environments, chondrichthyan (sharks, rays, and chimaeras) populations are under immense pressure primarily from fisheries, but also habitat degradation for some species (Dulvy et al. 2021). Presently 32.6% of chondrichthyans are listed as threatened with extinction based on the Categories and Criteria of the International Union for the Conservation of Nature Red List of Threatened Species (hereafter 'IUCN Red List') (Dulvy et al. 2021). With substantial ongoing global catch and trade of chondrichthyans (Okes and Sant 2019), there are numerous broad challenges to their conservation. These include: 1) mitigating incidental capture in fisheries (Dulvy et al. 2021); 2) reducing targeted catches to sustainable levels (Simpfendorfer and Dulvy 2017); and 3) restricting trade of products to those with sustainable sources (e.g. in agreement with international policy guidelines such as the Convention for International Trade of Endangered Species of Flora and Fauna; CITES) and improving adherence of signatory nations to international conservation commitments (e.g. Convention on Migratory Species, Lawson and Fordham 2018). Additionally, to enable better conservation implementation there is a need for: i) improved species-specific data feedback in existing and emerging market chains (e.g. Dent and Clarke 2015); ii) overcoming negative perceptions of 'sharks' owing to human-shark conflicts (Carlson et al. 2019; Simpfendorfer et al. 2021); and iii) improved understanding of the role chondrichthyans have to the livelihoods of people in developing nations with high reliance's on marine resources, and how effective conservation measures can be developed in such contexts (e.g. Booth et al. 2018; Booth et al. 2021c).

The conservation of non-marine elasmobranchs (sharks and rays) is further challenged by a lack of information on pressures in riverine environments (Chapter 2; Compagno and Cook 1995). A bias to marine species research and conservation attention has also been observed within teleost literature (Darwall et al. 2011; He et al. 2021). This creates difficulties in properly assessing risks to non-marine elasmobranchs in riverine environments, as our understanding of conservation is based on species in marine environments where fishing is the primary, and often only pressure to populations (Dulvy et al. 2021). Therefore, this dissertation has aimed to review the conservation status of non-marine elasmobranchs and explore research methods that will assist in informing future conservation efforts.

The primary purpose of the categorisations of non-marine elasmobranchs presented in Chapter 2 was to improve our understanding of which species use non-marine environments in their life cycle. This foundational aspect is vital to future conservation planning, as having clear distinctions between species that rely on non-marine environments during their life cycles will identify which species are most susceptible to riverine environmental pressures. Furthermore, the categorisations presented in Chapter 2 provide significant improvements on the previous categorisations proposed by Thorson et al. (1983), Compagno and Cook (1995), and Martin (2005). Unlike these, species categorisation is now based on the life history of the species being considered, rather than physiological capacity (Thorson et al. 1983) or occurrence and ecological movements (Compagno and Cook 1995; Martin 2005). The improved ability to now consider the life cycle of species associating with non-marine environments provides an more realistic context for conservation, as susceptibility to threats across freshwater, estuarine, and marine environments can now be appraised across different life history stages. It is well understood that elasmobranch populations have differing capacities to tolerate additional human impacts across different life stages (Simpfendorfer 1999; Smart et al. 2020). For example, for many species (including the species examined in this work), the juveniles have the greatest capacity to sustain fishing pressure, while subadult and young adult individuals make the greatest reproductive contribution and are therefore more important to population dynamics (e.g. Grant et al. 2019; Smart et al. 2020). Being able to distinguish which life stages are occurring in non-marine environments will therefore assist in future conservation planning and priortisation. Furthermore, the inclusion of salinity thresholds for each category also allows for better differentiation between species associating with estuarine environments, as the greatest source of confusion in previous categorisations was an inability to categorize species that occur in both marine and estuarine (generally referred to as ‘brackish’ in previous literature) environments. Through providing inclusion criteria for each non-marine elasmobranch category, it is hoped that the species falling in each category will be more open to amendment as new species-specific information becomes available.

The review of extinction risk across non-marine elasmobranch categories in Chapter 2 also raises conservation concern for these species. Half (50%) of euryhaline generalists, and almost two-thirds (65%) of estuarine generalist species are listed as threatened on the IUCN Red List (those assessed as Critically Endangered, Endangered, or Vulnerable). Compared to the overall proportion of threatened chondrichthyans (32.6 %, Dulvy et al. 2021), euryhaline and estuarine generalist elasmobranchs are facing extinction at up to twice the rate of all chondrichthyan species considered together. A similarly dire conservation outlook was recently highlighted for oceanic elasmobranchs by Pacoureau et al. (2021). The identification of shared conservation concern among species within broad ecological groups has value to overall chondrichthyan conservation planning, as it can act to prioritise and refine future conservation resource and effort allocation. A further strength is that it provides an opportunity to address uniform pressures across particular ecological groups (e.g., high seas fishing effort for oceanic elasmobranchs; Pacoureau et al., 2021), which if addressed may result in positive outcomes for a number of species (Simpfendorfer et al. 2011a).

Several pressures may have attributed to historic and ongoing population declines of euryhaline and estuarine generalist elasmobranchs. For some species, the conservation requirement is probably not as simple as solely reducing fisheries mortality, as is generally the requirement for marine species (e.g. Dulvy et al. 2021; Finucci et al. 2020; Kyne et al. 2020; Pacoureau et al. 2021). For example, across the global tropics, most major river basins have barriers to water flow (Figure 7.1). While the effects of these barriers to non-marine elasmobranchs are presently unquantified, there are very few instances of species occurring beyond dam infrastructure (e.g. Bennett's stingray *Hemitrygon bennetti* in the Pearl River, China, Rigby et al. 2020). However, there are several instances of species only occurring below dam infrastructure such as the giant freshwater whipray *Urogymnus polylepis* in the Citarum River, Indonesia (Grant et al. 2021c), and the white-edge whipray *Fluvitrygon signifier* in the Perak River,

Figure 7. 1 A map of the world dam infrastructure complied by Grill et al. (2019). Different colour dots correspond to the different databases used to construct the map (see http://globaldamwatch.org/).

Peninsular Malaysia (Grant et al. 2021e). Therefore, it is reasonable to assume that the widespread construction of barriers to water flow over the past century has had significant impacts on the movement of non-marine elasmobranchs into upstream freshwater environments and connectivity between habitats. Additionally, through decreasing freshwater outflow, it is also likely that barriers to water flow have had a significant influence on the deterioration, and extent of available estuarine habitat downstream (e.g. deterioration of the Indus River Delta, Memon 2005). Even small barriers can have significant conservation implications. As revealed in Chapter 6, the construction of a single weir may be causing additionally mortality of *P. pristis*, which may have significant impact in the species' conservation outlook and local extinction risk. Furthermore, other factors that have undoubtably also deteriorated habitat quality and affected non-marine elasmobranchs include land clearing within river catchments for agriculture and development (Gardner et al. 2018), mineral resource extraction (Maus et al. 2020), and general pollution arising from human uses of rivers and river catchments inclusive of excess nutrient runoff from agriculture and sewage (Fedele et al. 2021; Tuholske et al. 2021). While these factors are less conspicuous than barriers to water flow, the combination of these pressures is severe across tropical rivers where non-marine elasmobranchs occur (Compagno and Cook 1995). Furthermore, the increasing severity of climate change impacts are forecast to be pronounced in riverine environments, and changing climate regimes are likely to exacerbate the effects of present riverine pressures, leading to further reduced quality of habitat (Lennox et al. 2019). Indeed, non-marine elasmobranchs are assessed as those being at highest risk from climate change (Chin et al., 2010). Riverine pressures are likely to vary between river basins and nations and there is a need for a better understanding of how different riverine pressures effect non-marine elasmobranchs so that locally appropriate conservation initiatives can be developed.

The other concerning outcome from the non-marine elasmobranch extinction risk review in Chapter 2 was the high proportion of freshwater obligate species that are Data Deficient (DD) or are Not Evaluated (NE) on the IUCN Red List. Almost all DD and NE species in this group are neotropical stingrays (Potamotrygonidae) and further efforts are needed to assess the conservation status for most of these species. However, the high incidence of NE among the potamotrygonids can partly be attributed to the recent description of some species. Presently, the lack of information on population status risks population declines going undetected and impedes the identification and development of conservation initiatives for species that may be under population pressure. While freshwater obligate species are also subject to riverine pressures listed above, a further concern for potamotrygonid rays is that they are only found in South America and furthermore, some are endemic to a single river basin or tributary (e.g. Last et al. 2016). These small ranges inherently carry higher vulnerabilities to extinction (Purvis et al. 2000). This means that protecting the quality of habitat in large systems such as the Amazon and Orinoco River Basins is important to the conservation of multiple species. There are presently large concerns around deforestation and its flow on hydrological effects within South America (Staal et al. 2020; Swann et al. 2015), while broad interest in construction of hydropower reservoirs and dams (Zarfl et al. 2015) additionally threatens freshwater environments.

Many obligate freshwater rays are harvested for both consumptive purposes and the ornamental trade. The threat of harvest for international ornamental markets has been noted for several potamotrygonid species (Araújo et al. 2004) and eight species are listed on Appendix III of the Convention of International Trade in Endangered Species of Flora and Fauna (CITES) in Colombia, while all potamotrygonid species are CITES listed (Appendix III) in Brazil. These listings require exporters to demonstrate that specimens were legally obtained. Despite recent attempts, no potamotrygonid species are currently listed on Appendix II of CITES (which would require exporters to demonstrate that specimens were not collected in a manner that may be detrimental to wild populations (e.g. through evidence of sustainable harvest), although demand in the United States, Europe, and Asia is likely placing increased pressure on populations as supply to international markets is primarily through wild harvest (Araújo et al. 2004; Moreau and Coomes 2007; Rosa et al. 2010). No substantial information is presently available on harvest of dasyatid freshwater rays for ornamental purposes, although ornamental harvest is known to occur, at least in Indonesia (Grant et al. 2021d; Grant et al. 2021e). During field surveys in Thailand in the 1990s, Compagno and Cook (2005) observed a government funded aquaculture operation that aimed to supplement wild harvest of freshwater rays due to deteriorating populations (which were likely also affected by fisheries). While this operation appeared to have failed and subsequently ceased in the late 1990s, the observations of Compagno and Cook (1995) provide an ominous indication of the conservation state of obligate freshwater rays in Thailand at the time.

A major challenge to the conservation of many non-marine elasmobranch species is that they occur in remote regions of developing nations. In developing nations, threatened species are logistically difficult and costly to survey, and they are not always a priority to local communities and governments due to more locally pressing issues. This creates challenges to collecting information to assess local populations and inform conservation initiatives. For example, inland fisheries are generally characterized as being small-scale (inclusive of artisanal, cultural, and subsistence fisheries), and often harness multiple gear types, spanning various net, hook, trap, spear, and electro-fishing methods (Ainsworth et al. 2021). Inland fisheries in developing nations generally lack data collection mechanisms (e.g. Soe et al. 2020) and unless there is concerted research effort ongoing at the time, catch quantities are generally not recorded, limiting our ability to understand long-term population trends, and local value and trade demand. Furthermore, available catch in small-scale fishery market hubs is quickly sold, and transported elsewhere or consumed, due to a lack of storage capacity along the market chain (i.e., refrigeration or availability of ice) (Fluet-Chouinard et al. 2018). This can also limit time for observation even when research effort is present (e.g. Haque et al. 2021). This situation is very different from marine elasmobranch fisheries, where data collection from commercial fisheries often allows for time series catch and effort data to be considered for population trend and trade assessments (e.g. Okes and Sant 2019; Pacoureau et al. 2021).

The methods applied in Chapter 3 and 4 aimed to provide information on the population status of threatened non-marine elasmobranchs in extremely remote and data-poor regions of Papua New Guinea (PNG). At the beginning of these surveys, it was understood that all four Indo-Pacific sawfish (Pristidae) species were likely to be present in PNG (White et al. 2017a), while contemporary records of river sharks (*Glyphis* spp) were known from a single village in PNG's southwest (White et al. 2015). In Chapter 3 and 4, the combination of interviewing local fishers across numerous locations to harness knowledge (Chapter 3, which additionally helped to direct research effort in Chapter 4), examining dried fin and rostra, visiting local fish markets, and living in communities to observe fishing activity, provided significant amounts of new information on elasmobranchs and fishing characteristics in PNG. The collaboration and genuine engagement with local institutions (e.g., Provincial Fisheries Administrations and the Piku Biodiversity Network) allowed for increased receptiveness from local community leaders and ensured research activities were conducted with cultural and ethical consideration. Ultimately this led to better research outcomes, demonstrated through the successful data collection through enumerators in Chapter 4. Enumeration by small-scale fishers allowed for the development of temporary data collection from remote fisheries, providing an opportunity to gather information on the relative fishery interaction rates of non-marine elasmobranchs. Furthermore, the inclusion of local institutions in the field surveys of Chapters 3 and 4 provided opportunities for them to conduct field research and build capacity, knowledge, and relationships with local communities. Their inclusion in publication outputs arising from Chapters 3 and 4 (Grant et al. 2021f; Grant et al. 2021g) acted to build further trust in the authenticity of the research collaboration. When working internationally, there are many short- and long-term benefits to engaging local institutions (Chin et al. 2019), and the field surveys conducted during Chapter 3 and 4 have underlined these strengths.

The application of local ecological knowledge surveys in Chapter 3 was successful in providing information on sawfishes relating to: 1) distribution; 2) present threats; 3) recent population trends; 4) uses and values to local resource users; and 5) interest in conservation by local resource users. The finding that small-scale fishers in PNG primarily value sawfish as a traditional food source, rather than species of innate biodiversity value, aligns with fisher values to sawfish in other developing nations (e.g. Haque et al. 2020; Valerio-Vargas and Espinoza 2019). Chapter 3 indicates a ‘sustainable fishery’ type approach to sawfish conservation management will likely be needed in PNG, as harvest for traditional and cultural purposes precludes the ethical appropriateness of outright bans on catch and retention. Making this distinction is an important step in development of local conservation initiatives for sawfishes in developing nations, as ethically inappropriate conservation approaches can have negative social and economic outcomes for small-scale fishers (Booth et al. 2021b). Negative community responses to inappropriate conservation initiatives risks development of non-compliance and 'black' markets, that ultimately further implicate population monitoring initiatives through erosion of trust with local fishing communities and consequently, an inability to gauge actual levels of fisheries harvest (Aceves-Bueno et al. 2021). Collectively, the present use of local ecological knowledge surveys has further contributed evidence that social science methods can have immense value to informing ethically and culturally appropriate conservation initiatives for non-marine elasmobranchs in developing nations.

Chapter 4 built on the local ecological knowledge surveys, and provided new information on species distributions and fishery interactions. The high incidence of threatened species observations in Chapter 4 indicate that non-marine elasmobranch populations in PNG have not been depleted to levels seen in other tropical nations (e.g. Arunrugstichai et al. 2018; Blaber et al. 2009; Booth et al. 2021a; Haque et al. 2021). For example, species observations were dominated by river sharks, sawfishes, and hammerheads (Sphyrnidae), with giant guitarfish (*Glaucostegus typus*) and two species of wedgefish (Rhinidae) also being observed in small numbers. There is global concern for each of these groups of species (e.g. Kyne et al. 2020; Li et al. 2015; Yan et al. 2021), and PNG now has the opportunity to play a significant role in securing their populations into the future. However, it is clear from population trends in other nations that species in each of these groups are highly vulnerable to fisheries pressure. Resources and capacity are severely limited within fisheries and conservation governing bodies in PNG, and there are very few non-government organizations (NGOs) actively working within marine and aquatic resource management and conservation. Riverine and coastal fisheries in PNG presently lack any effective management, and there are no legislative species protections in place for any elasmobranch species. Furthermore, the consistent observations of CITES listed species in the fin trade (which is known to extend to international markets through both legal and illegal export market chains, Busilacchi et al. 2021) raises concerns about PNG's adherence to its obligations as a signatory of CITES. The primary reason for the persistence of populations of threatened elasmobranchs in PNG is almost certainly attributable to the nation's historically low human population density and unsuitable landscape for development and agriculture. As human populations continue to grow into the future, it will be critical for PNG to put actions in place that safeguard the vulnerable elasmobranch species that are currently caught by small-scale fishers. Moreover, most fishing effort observed in PNG during field work related to Chapters 3 and 4, was concentrated in freshwater and estuarine environments. This suggests that non-marine elasmobranchs that are primarily using those environments are most susceptible to unsustainable catch levels. PNG has an opportunity to provide a long-term refuge for multiple threatened non-marine elasmobranchs (i.e., river sharks and sawfishes), and efforts are urgently needed to manage riverine fisheries harvest, and also to engage government bodies (National Fisheries Authority and the Conservation and Environmental Authority) to take steps that would ensure their populations and habitats are protected into the future.

A common trait of non-marine elasmobranchs generally, is a lack of information about their long-term habitat use patterns (Chapter 2). This is particularly relevant to the conservation of euryhaline and estuarine generalist species, as it is unclear how long most of these species use non-marine environments for in their life cycle. For species that occur in regions where riverine pressures may be greater than coastal-marine (which is possibly the case in southern PNG), this lack of information impedes the development of effective conservation initiatives for their populations. Conventional approaches to understanding habitat use and movement of marine elasmobranchs usually use acoustic telemetry approaches (Matley et al. 2021). However, the setting of acoustic receiver arrays in tropical rivers subject to flooding or with large tidal flow estuaries (that additionally are subject to large fluctuations in salinity and conductivity of water) is costly and requires high technical capacity, limiting its applicability in many developing regions. Furthermore, many non-marine elasmobranch populations are heavily depleted, and there is a paucity of information available on where reliable populations occur that would allow a suitable number of animals to be tagged with transmitters.

The use of elemental analysis of vertebrae described in Chapter 5 overcomes this constraint and provided valuable information on long-term habitat use patterns for river sharks and two species of sawfishes. Furthermore, Chapter 5 revealed that a range of elemental ratios (e.g. Ba:Ca, Li:Ca, Sr:Ca, and Sr:Ba) used to investigate diadromous movements in teleost otoliths (Elsdon et al. 2008), are also applicable to elasmobranch vertebrae (see *7.1 Future directions*). The primary finding of Chapter 5 was the protracted use of estuarine environments by river sharks. River sharks have historically been considered exceptionally rare species (Li et al. 2015; Peverell et al. 2006), and it is only in recent years that a better understanding of their environmental preferences have been made within Australia (e.g. Kyne et al. 2021a) and PNG (Chapter 4). Outside of Australia and PNG, the Ganges River shark (*Glyphis gangeticus*) has a fragmented distribution in Pakistan, India, and Sabah, Malaysia (Li et al. 2015). *Glyphis gangeticus* is presently the only chondrichthyan species listed as Critically Endangered on the IUCN Red List on the basis of both population size reduction and small mature population size (< 250) (Rigby et al. 2021). It is likely that *G. gangeticus* was once widespread throughout large tropical rivers of the Indo-West Pacific, and assuming this species also has protracted use of estuarine environments, its reliance on estuaries in densely populated nations has likely contributed to its severe population declines. For example, Myanmar supports one of the world's largest inland fisheries (Baran et al. 2018; Soe et al. 2020), and *G. gangeticus* has not been observed in the Ayeyarwady River Delta since 1896 (Li et al. 2015). Chapter 5 indicates that protection of estuaries from fisheries pressure within the remaining range of *G. gangeticus* would be an important step toward preventing the extinction of this species. Furthermore, there is an undescribed species of river shark from western and southern Borneo (Adrim and Fahmi 2009; Li et al. 2015). Information provided in Chapter 5 indicates that targeted surveys within the estuaries of Bornean rivers would be most effective in an attempt to locate this undescribed species and provide a formal taxonomic description. There is immense conservation concern for this undescribed species, as for example, it is unclear if *G. gangeticus* are persisting in parts of Borneo (Manjaji-Matsumoto et al. 2016), likely owing to riverine and inshore fisheries pressure. There is a need to describe this species in the near future so that its conservation status can be assessed, and it can be included in legislative protections within Indonesia and Malaysia where necessary.

This dissertation has indicated that the conservation of non-marine elasmobranchs requires consideration of additional threats to those considered in marine environments. Using a Population Viability Analysis (PVA), Chapter 6 produced a population model that incorporated both riverine and marine pressures for a euryhaline generalist, the largetooth sawfish *Pristis pristis* in Australia. While it was found that marine pressures were having the greatest negative effects on the Australian population (i.e., commercial fisheries), this model demonstrated the severe impact that additional riverine environmental pressures can have on population dynamics. For example, the inclusion of additional crocodile (*Crocodylus porosus* and *C. johnsoni*) mortality demonstrated that a source of significant mortality in juvenile age classes (i.e., when *P. pristis* uses riverine environments) can lead to population crashes in a euryhaline species, even in the absence of marine pressures. This is significant, as even if marine based conservation initiatives are achieved, species that additionally use riverine environments are still liable to significant population decline if riverine pressures are not also addressed. Chapter 6 has therefore underlined the complexity of conservation approaches for euryhaline generalist species, as conservation effort needs to focus on both riverine and marine pressures to ensure positive population outcomes.

While the PVA was effective in providing distinctions between riverine and marine pressures, the lack of jurisdictional and species-specific data available to populate the model was evident. Australia is regarded as a 'stronghold' for *P. pristis* (Dulvy et al. 2016; Yan et al. 2021), and this species has been listed as protected since 2006 (listed as Vulnerable on the *Environment Protection and Biodiversity Conservation Act 1999*), was included in the *Sawfish and River Shark Multispecies Recovery Plan* (DoE, 2015), and was recently listed in the *100 Priority Species Threatened Species Strategy* (DoE, 2021). Despite prolonged conservation concern for *P. pristis* in Australia, there was a lack of reliable information on fisheries interactions, and almost no quantitative data available on riverine pressures. Greater efforts are needed by state and national governments to improve availability and reliability of information for use in population modelling, and the present PVA indicates that better data on fisheries interactions, improved information on natality and juvenile recruitment and survival, and investigation on crocodile mortality, are needed.

7.1 Future directions

Considering the present global concern around deteriorating riverine environments (Harper et al. 2021; Tickner et al. 2020), Chapter 6 indicates that human pressures in riverine environments need more attention for euryhaline and estuarine generalist species than they currently receive. Meanwhile, conservation actions for obligate freshwater species require complete consideration of riverine pressures. The issue, however, is that our understanding of how riverine pressures effect non-marine elasmobranchs is very poor. While major pressures noted in broader freshwater biodiversity literature include: fisheries (He et al. 2019); ornamental harvest (Reid et al. 2013); invasive species (Vilizzi et al. 2019); pollution (Tuholske et al. 2021); barriers to water flow (Grill et al. 2019); vegetation and land repurposing (Gardner et al. 2018); climate change (Lennox et al. 2019); mining related resource extraction (Maus et al. 2020); and general human reliance's of riverine systems (Fedele et al. 2021); these types of studies are scarce for non-marine elasmobranchs. Furthermore, in many instances these pressures are concurrently occurring (Tickner et al. 2020). With non-marine elasmobranchs generally facing high levels of extinction currently, a concerted effort to research and conserve their populations is likely needed with some urgency.

For many species, there is still fundamental research to be conducted on their taxonomy and distribution. Further to the afore-mentioned undescribed *Glyphis* sp. in Borneo, there are possibly two undescribed *Fluvitrygon* sp. in Sumatra, Indonesia (Iqbal et al. 2018b), and it is known there are further descriptions to be made of potamotrygonid spp. in South America (Loboda et al. 2021). It is important that these species are described in the near future, as taxonomic resolution facilitates data collection on distribution and population trend, allows species population status to be assessed, and for conservation management actions to be developed and implemented where necessary. Furthermore, recent social media and fish market-based research has revealed significant range 'expansions' for many non-marine elasmobranch species in Indonesia in recent years (Iqbal et al. 2020; Iqbal et al. 2019a; Iqbal et al. 2017; Iqbal et al. 2018a; Iqbal and Yustian 2016; Iqbal et al. 2019b; Iqbal et al. 2018b; Windusari et al. 2019) indicating the lack of primary information on species distributions. For cryptic species, or those that occur in remote regions that are difficult to survey, there is great value in engaging local fishers through social media platforms in order to improve our understanding of contemporary geographic range (McDavitt and Kyne 2020). It is likely that social media, coupled with field surveys, can help improve our overall understanding of non-marine elasmobranch distributions into the future, and thereby provide a spatial context to conservation requirements.

The methods used in Chapter 3 and 4 would be effective in providing baseline information on the population status of non-marine elasmobranchs in many regions. Concerted field surveys are required for many species, particularly those with small ranges. For example, the Chindwin cowtail ray (*Makararaja chindwinensis*) has only two recorded observations in the Chindwin River, Myanmar (Grant et al. 2021a). Myanmar supports one of the world's largest inland fisheries (Baran et al. 2018; Soe et al. 2020), and there is immense concern for the status of this species. Local ecological knowledge surveys would likely provide useful information for *M. chindwinensis* and assist in understanding historical baselines and present abundances. Throughout developing regions where non-marine elasmobranchs occur, engaging local institutions in survey efforts will also be important to facilitate greater time-series data availability into the future. In regions such as the Mekong River, fish fauna and market survey effort is often present (e.g. Patricio et al. 2019), and efforts are needed to raise awareness within active research groups about the importance of collecting information on local non-marine elasmobranchs. Fishery catch and effort information is vital to inform population trends and accurately assess extinction risk or population recovery. In recent IUCN Red List assessments for Indo-Pacific freshwater obligate rays (e.g. Grant et al. 2021b; Grant et al. 2021d), many species lacked any new information on population trend over the last decade. This limits accuracy of population assessments and risks severe deterioration in populations going unnoticed. While concern around riverine pressures other than fisheries have been raised in the present dissertation, examination of fisheries landings provides the best measure of population trend in the absence of concerted abundance surveys. Given fisheries are prominent in all regions where non-marine elasmobranchs occur, research on local fisheries will provide needed information on population trends and facilitate research on other local factors that may be influencing population trends.

In the assessment of a species vulnerability to human pressures, it important to understand life history and demographic characteristics. For example, the basis of elasmobranch fisheries management is identifying harvest levels that are sustainable based on mortality and natality schedules (i.e., productivity) of the species being exposed to fishing (Cortés 2000). Meanwhile, the most commonly applicable IUCN Red List criterion for elasmobranchs is assessing population size reduction over a period of three generation lengths (i.e., Criteria A) (Dulvy et al. 2021). Information on age and growth, and sexual maturity forms the basis of calculating generation length for IUCN applications, while litter size is additionally essential for calculations of population growth and productivity to inform sustainable fishing limits. Presently, there is a severe lack of information on these vital life history parameters for almost all non-marine elasmobranchs. Age and growth information from the bull shark *Carcharhinus leucas* (e.g. Hoarau et al. 2021; Natanson et al. 2014) and *P. pristis* (Peverell 2009; Simpfendorfer 2000) indicate these euryhaline species are slow growing and long lived, while the present age estimates of *G. glyphis* in Chapter 5 indicate river sharks also share these traits. For non-marine ray species, there is almost no age and growth information available (e.g. Charvet et al. 2018; Otake et al. 2005), limiting our ability to understand their vulnerability to population decline and assess their conservation status. Therefore, gathering information on life history characteristics of non-marine elasmobranchs is one of the highest research priorities for these species.

Obtaining samples for age-and-growth, and reproductive assessment presents challenges, as examination of deceased specimens is presently required (Heupel and Simpfendorfer 2010). Most non-marine elasmobranchs are threatened, and owing to their spatially constrained environments, population sizes are likely to be small. Using methods similar to Chapter 4, observation of riverine fisheries is likely to present opportunistic sample collection. Collecting specimens from fisheries (where animals are otherwise being consumed or sold) would be preferable to adding additional mortality from lethal research sampling to the already depleted populations of most non-marine elasmobranch species. Furthermore, due to recent advancements in age and growth modelling (Smart and Grammer 2021), sample sizes for vertebral ageing analysis do not need to be large where information is available on size-at-birth and maximum size. It is however important to obtain samples across the size spectrum of a given species to reduce uncertainty in age and growth estimates (Smart et al. 2016a; Smart and Grammer 2021). An alternative non-lethal approach that would likely be effective for movement restricted obligate freshwater rays, is age-and-growth via mark-recapture. Growth analysis through mark-recapture has been effectively applied to threatened sturgeon (Hamel et al. 2014), and is commonly applied to sea turtles (e.g. Casale et al. 2009). Mark-recapture studies can additionally provide information on mortality and would be useful to understand spatial habitat use patterns (i.e., through comparisons of individuals catch locations). A limitation is that effective mark-recapture studies require knowledge of where reliable populations occur, and tagging of some neonate specimens would be necessary for age-and-growth applications. Combining mark-recapture with opportunistic sample collection from fisheries would provide opportunity to compare growth estimates with vertebral ageing, and would collectively provide useful information to understanding population dynamics. The application of elemental analysis used in Chapter 5 on opportunistically collected vertebrae samples would also provide useful habitat requirement information across the life histories of euryhaline and estuarine generalist species. Furthermore, there may be opportunities to use elemental analysis on historic vertebrae samples, or museum specimens.

A greater availability of life history data for different non-marine elasmobranch species will facilitate increased opportunity to apply population models such as PVA to guide conservation and research priorities. Furthermore, recent developments in analytical genetic techniques now allow for increased ability to estimate population size through close-kin mark-recapture methods (Bradford et al. 2018; Bravington et al. 2019; Hillary et al. 2018). It is likely that close-kin mark-recapture methods would be highly suitable to non-marine elasmobranchs owing to their inherently small population ranges, although collection of enough samples is presently the largest challenge to their application. Obtaining estimates of population size, when coupled with life history data, would allow a range of demographic modeling approaches to be used on non-marine elasmobranchs (Grant et al. 2019; Smart et al. 2017), and this would greatly increase our understanding of their productivity and propensity to tolerate fisheries mortality and other riverine pressures.

Overall, the present conservation status of non-marine elasmobranchs, coupled with the paucity of species-specific information raises great concern for their future. Considering the widespread declines of riverine environments globally and declining trends for these species, the future outlook of non-marine elasmobranchs appears dire. A concerted effort to raise awareness of non-marine elasmobranchs is needed, and commitment from national governing bodies will be critical to securing the survival of populations for the future. The present dissertation and associated research outputs have highlighted the global status and key pressures facing non-marine elasmobranchs that need urgent attention, and also demonstrated some of the key research gaps and methodological approaches that would provide the critical information needed to inform conservation and management. It is hoped that this thesis will help provide the impetus and guidance to direct additional efforts and resources to stabilise declines and rebuild populations of these species, and ultimately, to safeguard their existence for future generations.

References

Aceves–Bueno, E., Read, A. J., & Cisneros–Mata, M. A. (2021). Illegal fisheries, environmental crime, and the conservation of marine resources. *Conservation Biology, 35*(4), 1120–1129.

Adame, M. F., Jardine, T. D., Fry, B., Valdez, D., Lindner, G., Nadji, J., & Bunn, S. E. (2018). Estuarine crocodiles in a tropical coastal floodplain obtain nutrition from terrestrial prey. *PLoS One, 13*(6), e0197159.

Adkins, M. E., Simpfendorfer, C. A., & Tobin, A. J. (2016). Large tropical fishes and their use of the nearshore littoral, intertidal and subtidal habitat mosaic. *Marine and Freshwater Research, 67*(10), 1534–1545.

Adrim, M., & Fahmi. (2009). The first record of a shark of the genus *Glyphis* in Indonesia. *The Raffles Bulletin of Zoology, 57*, 113–118.

Ainsworth, R., Cowx, I. G., & Funge–Smith, S. J. (2021). *A review of major river basins and large lakes relevant to inland fisheries. FAO Fisheries and Aquaculture Circular No. 1170. Rome, FAO.*

Allen, B., Bourke, R. M., & Gibson, J. (2005). Poor rural places in Papua New Guinea. *Asia Pacific Viewpoint, 46*(2), 201–217.

Almeida, M. P., Viana, A. D., Barthem, R. B., & Charvet–Almeida, P. (2009). Factors affecting the distribution and abundance of freshwater stingrays (Chondrichthyes: Potamotrygonidae) at Marajó Island, mouth of the Amazon River. *Pan–American Journal of Aquatic Sciences, 4*(1), 1–11

Ames, E. (2004). Atlantic Cod Stock Structure in the Gulf of Maine. *Fisheries, 29*, 10–28.

Anderson, B., Belcher, C., Slack, J., & Gelsleichter, J. (2018). Evaluation of the use of portable ultrasonography to determine pregnancy status and fecundity in bonnethead shark *Sphyrna tiburo*. *Journal of Fish Biology, 93*(6), 1163–1170.

Appleyard, S., White, W., Vieira, S., & Sabub, B. (2018). Artisanal shark fishing in Milne Bay Province, Papua New Guinea: biomass estimation from genetically identified shark and ray fins. *Scientific Reports, 8*(1), 1–12.

Araújo, M., Charvet–Almeida, P., Almeida, M. P., & Pereira, H. (2004). Freshwater stingrays (Potamotrygonidae): status, conservation and management challenges. *Information document AC*, *20*, pp 1–6. Retrieved from http://www.cites.org/common/cttee/animals/20/E20–inf–08.pdf

Arunrugstichai, S., True, J. D., & White, W. T. (2018). Catch composition and aspects of the biology of sharks caught by Thai commercial fisheries in the Andaman Sea. *Journal of Fish Biology, 92*(5), 1487–1504.

Baje, L., Smart, J. J., Grant, M. I., Chin, A., White, W. T., & Simpfendorfer, C. A. (2019). Age, growth and maturity of the Australian blackspot shark (*Carcharhinus coatesi*) in the Gulf of Papua. *Pacific Conservation Biology, 25*(4), 403–412.

Ballantyne, J. S., & Robinson, J. (2010). Freshwater elasmobranchs: a review of their physiology and biochemistry. *Journal of Comparative Physiology B, 180*(4), 475–493.

Ban, N. C., Hansen, G. J. A., Jones, M., & Vincent, A. C. J. (2009). Systematic marine conservation planning in data–poor regions: Socioeconomic data is essential. *Marine Policy, 33*(5), 794–800.

Baran, E., Ko, W. K., Wah, Z. Z., Nwe, K. M., Ghataure, G., & Soe, K. M. (2018). Fisheries in the Ayeyarwady Basin. Ayeyarwady State of the Basin Assessment (SOBA) Report 4.1. National Water Resources Committee (NWRC), Myanmar.

Barrios–Garrido, H., Bolivar, J., Benavides, L., Viloria, J., Dugarte, F., & Wildermann, N. (2017). Evaluation of the artisanal longline fishery and its effect on the longnose stingray (*Dasyatis guttata*) in Zapara Island, Gulf of Venezuela. *Latin American Journal of Aquatic Research, 45*(2), 302–310.

Bass, A. J., D'Aubrey, J. D. D., & Kistnasamy. (1973). *Sharks of the east coast of southern Africa. I. The genus Carcharhinus (Carcharhinidae)*. Report number 33, Oceanographic Research Institute, Durban, South Africa.

Bierwagen, S. L., Heupel, M. R., Chin, A., & Simpfendorfer, C. A. (2018). Trophodynamics as a tool for understanding coral reef ecosystems. *Frontiers in Marine Science, 5*(24), 1–13.

Bineesh, K. K., Moore, A. B. M., & Kyne, P. M. (2014). Indo–West Pacific. *Chapter 7*. In L. R. Harrison & N. K. Dulvy (Eds.), *Sawfish: A Global Conservation Category* (pp. 62). Vancouver, Canada: IUCN Species Survival Commission's Shark Specialist Group.

Blaber, S. J. M. (2009). Relationships between tropical coastal habitats and (offshore) fisheries. In I. Nagelkerken (Ed.), *Ecological Connectivity among Tropical Coastal Ecosystems* (pp. 533–564). Dordrecht: Springer Netherlands.

Blaber, S. J. M., Dichmont, C. M., White, W., Buckworth, R., Sadiyah, L., Iskandar, B., . . . Fahmi. (2009). Elasmobranchs in southern Indonesian fisheries: the fisheries, the status of the stocks and management options. *Reviews in Fish Biology and Fisheries, 19*(3), 367–391.

Booth, H., Chaya, F., Ng, S., Tan, V., Rao, M., Teepol, B., . . . Gumal, M. (2021a). Elasmobranch fishing and trade in Sarawak, Malaysia, with implications for management. *Aquatic Conservation: Marine and Freshwater Ecosystems, 31*(11), 3056–3071.

Booth, H., Mardhiah, U., Siregar, H., Hunter, J., Giyanto, Putra, M. I. H., . . . Yulianto, I. (2021b). An integrated approach to tackling wildlife crime: Impact and lessons learned from the world's largest targeted manta ray fishery. *Conservation Science and Practice, 3*(2), e314.

Booth, H., Muttaqin, E., Simeon, B., Ichsan, M., Siregar, U., Yulianto, I., & Kassem, K. (2018). Shark and ray conservation and management in Indonesia: Status and strategic priorities 2018–2023. *Wildlife Conservation Society: Bogar, Indonesia*.

Booth, H., Squires, D., & Milner–Gulland, E. J. (2019). The neglected complexities of shark fisheries, and priorities for holistic risk–based management. *Ocean & Coastal Management, 182*(1), 104994.

Booth, H., Squires, D., Yulianto, I., Simeon, B., Muhsin, Adrianto, L., & Milner–Gulland, E. J. (2021c). Estimating economic losses to small–scale fishers from shark conservation: A hedonic price analysis. *Conservation Science and Practice, 3*(9), e494.

Braccini, M., Kangas, M., Jaiteh, V., & Newman, S. (2021). Quantifying the unreported and unaccounted domestic and foreign commercial catch of sharks and rays in Western Australia. *Ambio, 50*(7), 1337-1350.

Bradford, R. W., Thomson, R., Bravington, M. V., Foote, D., Gunasekera, R., Bruce, B. D., . . . Feutry, P. (2018). A close–kin mark–recapture estimate the population size and trend of east coast grey nurse shark. Report to the National Environmental Science Program, Marine Biodiversity Hub. CSIRO Oceans & Atmosphere, Hobart, Tasmania.

Brame, A. B., Wiley, T. R., Carlson, J. K., Fordham, S. V., Grubbs, R. D., Osborne, J., . . . Poulakis, G. R. (2019). Biology, ecology, and status of the smalltooth sawfish *Pristis pectinata* in the USA. *Endangered Species Research, 39*, 9–23.

Bravington, M. V., Feutry, P., Pillans, R. D., Hillary, R. M., Johnson, G. J., Saunders, T., . . . Kyne, P. M. (2019). Close–Kin Mark–Recapture population size estimate of Glyphis garricki in the Northern Territory. Report to the National Environmental Science Program, Marine Biodiversity Hub. CSIRO Oceans & Atmosphere, Hobart.

Britton, A., & Campbell, A. (2014). Open season on crocodiles is not the solution to attacks on people. *The Conversation, 21*.

Brown, K. T., Seeto, J., Lal, M. M., & Miller, C. E. (2016). Discovery of an important aggregation area for endangered scalloped hammerhead sharks, *Sphyrna lewini*, in the Rewa River estuary, Fiji Islands. *Pacific Conservation Biology, 22*(3), 242–248.

Burgin, S., & Hardiman, N. (2016). Crocodiles and grey nomads: a deadly combination? *Current Issues in Tourism, 19*(1), 60–63.

Burton, J. (1995). Middle Fly and north Morehead area study. Ok–Fly social monitoring project report No. 10. Pacific Social Mapping, Canberra.

Busilacchi, S., Butler, J. R. A., Skewws, T., Posu, J., Shimada, T., Rochester, W., & Milton, D. (2014). *Characterization of the traditional fisheries in the Torres Strait Treaty communities, Papua New Guinea. AFMA Torres Strait Research Project. Report number 2013/0802.*

Busilacchi, S., Butler, J. R. A., van Putten, I., Cosijn, M., Posu, J., Fitriana, R., & Slamet, A. (2021). Why does illegal wildlife trade persist in spite of legal alternatives in transboundary regions? *Human Dimensions of Wildlife*, 1–18.

Cailliet, G. M., & Goldman, K. J. (2004). Age determination and validation in chondrichthyan fishes. In J. Carrier, J. Musick, & M. Heithaus (Eds.), *Biology of Sharks and Their Relatives* (pp. 399–447). Boca Raton, Florida CRC Press.

Cailliet, G. M., Smith, W. D., Mollet, H. F., & Goldman, K. J. (2006). Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes, 77*(3–4), 211–228.

Carlson, J. K., Heupel, M. R., Young, C. N., Cramp, J. E., & Simpfendorfer, C. A. (2019). Are we ready for elasmobranch conservation success? *Environmental Conservation*, 1–3.

Carlson, J. K., & Simpfendorfer, C. A. (2015). Recovery potential of smalltooth sawfish, *Pristis pectinata*, in the United States determined using population viability models. *Aquatic Conservation: Marine and Freshwater Ecosystems, 25*(2), 187–200.

Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R., & Largier, J. L. (2003). Comparing marine and terrestrial ecosystems: Implications for the design of coastal marine reserves. *Ecological Applications, 13*(1), 90–107.

Casale, P., Mazaris, A. D., Freggi, D., Vallini, C., & Argano, R. (2009). Growth rates and age at adult size of loggerhead sea turtles (Caretta caretta) in the Mediterranean Sea, estimated through capture–mark–recapture records. *Scientia Marina, 73*(3), 589–595.

Castellanos–Galindo, G. A., Herrón, P., Navia, A. F., & Booth, H. (2021). Shark conservation and blanket bans in the eastern Pacific Ocean. *Conservation Science and Practice, 3*(7), e428.

Castello, H. P. (1975). Hunting for freshwater stingrays. *Tropical Fish Hobbyist, 23*, 19–34.

Castro, J. I. (1993). The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. In L. S. Demski & J. P. Wourms (Eds.), *The reproduction and development of sharks, skates, rays and ratfishes* (pp. 37–48). Dordrecht: Springer Netherlands.

Charvet–Almeida, P., Araújo, M., & Almeida, M. P. d. (2005). Reproductive aspects of freshwater stingrays (Chondrichthyes: Potamotrygonidae) in the Brazilian Amazon Basin. *Journal of Northwest Atlantic Fishery Science, 35*, 165–171.

Charvet, P., Santana, F., De Lima, K., & Lessa, R. (2018). Age and growth of the endemic Xingu River stingray *Potamotrygon leopoldi* validated using fluorescent dyes. *Journal of Fish Biology, 92*(6), 1985–1999.

Cheung, W. W., & Sumaila, U. R. (2008). Trade–offs between conservation and socio–economic objectives in managing a tropical marine ecosystem. *Ecological economics, 66*(1), 193–210.

Chidlow, J. A. (2007). First record of the freshwater sawfish, *Pristis microdon*, from southwestern Australian waters. *Records of the Western Australian Museum, 23*(3), 307–308.

Chin, A., Baje, L., Donaldson, T., Gerhardt, K., Jabado, R. W., Kyne, P. M., . . . Wen, C. (2019). The scientist abroad: Maximising research impact and effectiveness when working as a visiting scientist. *Biological Conservation, 238*, 108231.

Chin, A., Kyne, P. M., Walker, T. I., & McAULEY, R. (2010). An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Global Change Biology, 16*(7), 1936–1953.

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

Cinner, J. E., & Aswani, S. (2007). Integrating customary management into marine conservation. *Biological Conservation, 140*(3), 201–216.

Clement, J. (1992). Re–examination of the fine structure of endoskeletal mineralization in chondrichthyans: Implications for growth, ageing and calcium homeostasis. *Marine and Freshwater Research, 43*(1), 157–181.

Cliff, G., & Dudley, S. (1991). Sharks caught in the protective gill nets off Natal, South Africa. 5. The Java shark *Carcharhinus amboinensis* (Müller & Henle). *South African Journal of Marine Science, 11*(1), 443–453.

Closs, G. P., Hicks, A. S., & Jellyman, P. G. (2013). Life histories of closely related amphidromous and non–migratory fish species: a trade–off between egg size and fecundity. *Freshwater Biology, 58*(6), 1162–1177.

Coates, D. (1987). Consideration of fish introductions into the Sepik river, Papua New Guinea. *Aquaculture Research, 18*(3), 231–241.

Collen, B., Whitton, F., Dyer, E. E., Baillie, J. E., Cumberlidge, N., Darwall, W. R., . . . Böhm, M. (2014). Global patterns of freshwater species diversity, threat and endemism. *Global ecology and Biogeography, 23*(1), 40–51.

Collier, N., Austin, B. J., Bradshaw, C. J., & McMahon, C. R. (2011). Turning pests into profits: introduced buffalo provide multiple benefits to indigenous people of northern Australia. *Human Ecology, 39*(2), 155–164.

Collins, A. B., Heupel, M. R., & Simpfendorfer, C. A. (2008). Spatial distribution and long–term movement patterns of cownose rays *Rhinoptera bonasus* within an estuarine river. *Estuaries and Coasts, 31*(6), 1174–1183.

Colonello, J. H., Lucifora, L. O., & Massa, A. M. (2006). Reproduction of the angular angel shark (*Squatina guggenheim*): geographic differences, reproductive cycle, and sexual dimorphism. *Ices Journal of Marine Science, 64*(1), 131–140.

Compagno, L. (2002). Freshwater and estuarine elasmobranch surveys in the Indo–Pacific region: threats, distribution and speciation. In S. Fowler, T. Reed, & F. Dipper (Eds.), *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July, 1997* (pp. 168–180). Oxford, UK: Information Press.

Compagno, L., & Cook, S. (1995). The exploitation and conservation of freshwater elasmobranchs: status of taxa and prospects for the future. *Journal of Aquariculture and Aquatic Sciences, 7*, 62–91.

Compagno, L., & Cook, S. F. (2005). Giant freshwater stingray or whipray *Himantura chaophraya* Monkolprasit & Roberts, 1990. In S. L. Fowler, R. D. Cavanagh, M. Camhi, G. H. Burgess, G. M. Cailliet, S. V. Fordham, C. A. Simpfendorfer, & J. A. Musick (Eds.), *Sharks, Rays and Chimaeras: The Status of the Chondrichthyan Fishes.* IUCN, Gland, Switzerland and Cambridge, UK.: IUCN/SSC Shark Specialist Group.

Compagno, L. J., & Roberts, T. R. (1984). Dasyatidae. In J. Daget, J. Gosse, & D. Thys van den Audenaerde (Eds.), *Check–list of the freshwater fishes of Africa, Cloffa* (pp. 4–5). Bruxelles, Belgium Institut Royal des Sciences Naturelles de Belgique.

Corey, B., Webb, G., Manolis, S. C., Fordham, A., Austin, B., Fukuda, Y., . . . Saalfeld, K. (2018). Commercial harvests of saltwater crocodile *Crocodylus porosus* eggs by Indigenous people in northern Australia: lessons for long–term viability and management. *Oryx, 52*(4), 697–708.

Cortés, E. (1998). Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research, 39*(2), 199–208.

Cortés, E. (1999). *A stochastic stage–based population model of the sandbar shark in the western North Atlantic.* Paper presented at the American Fisheries Society Symposium.

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

Cortés, E. (2002). Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. *Conservation Biology, 16*(4), 1048–1062.

Coulson, T., Mace, G. M., Hudson, E., & Possingham, H. (2001). The use and abuse of population viability analysis. *Trends in Ecology & Evolution, 16*(5), 219–221.

Crouse, D. T., Crowder, L. B., & Caswell, H. (1987). A stage–based population model for loggerhead sea turtles and implications for conservation. *Ecology, 68*(5), 1412–1423.

da Silva, N. J., Ferreira, K. R. C., Pinto, R. N. L., & Aird, S. D. (2015). A severe accident caused by an ocellate river stingray (*Potamotrygon motoro*) in central Brazil: how well do we really understand stingray venom chemistry, envenomation, and therapeutics? *Toxins, 7*(6), 2272–2288.

Darwall, W. R. T., Holland, R. A., Smith, K. G., Allen, D., Brooks, E. G. E., Katarya, V., . . . Vié, J.–C. (2011). Implications of bias in conservation research and investment for freshwater species. *Conservation Letters, 4*(6), 474–482.

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

de Bruyn, P. J. N., Hofmeyr, G. J. G., & de Villiers, M. S. (2006). First record of a vagrant Commerson's dolphin, *Cephalorhynchus commersonii*, at the southern African continental shelf. *African Zoology, 41*(1), 131–133.

de Kroon, H., Plaisier, A., van Groenendael, J., & Caswell, H. (1986). Elasticity: The Relative Contribution of Demographic Parameters to Population Growth Rate. *Ecology, 67*(5), 1427–1431.

Dean, M. N., & Summers, A. P. (2006). Mineralized cartilage in the skeleton of chondrichthyan fishes. *Zoology, 109*(2), 164–168.

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

DoE. (2015). Sawfish and river sharks multispecies recovery plan. Department of the Environment, Canberra.

Dudgeon, D. (2019). Multiple threats imperil freshwater biodiversity in the Anthropocene. *Current Biology, 29*(19), R960–R967.

Duffy, C. A. J., Forrester, N. D., Gibson, T. K., & Hathaway, S. (2017). Occurrence of the whitetip reef shark *Triaenodon obesus* at the Kermadec Islands, Southwest Pacific Ocean. *New Zealand Journal of Zoology, 44*(4), 354–360.

Dulvy, N., & Polunin, N. (2004). Using informal knowledge to infer human-induced rarity of a conspicuous reef fish. *Animal Conservation, 7*(4), 365–374.

Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J. V., Cortés, E., Domingo, A., . . . Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems, 18*(5), 459–482.

Dulvy, N. K., Davidson, L. N. K., Kyne, P. M., Simpfendorfer, C. A., Harrison, L. R., Carlson, J. K., & Fordham, S. V. (2016). Ghosts of the coast: global extinction risk and conservation of sawfishes. *Aquatic Conservation: Marine and Freshwater Ecosystems, 26*(1), 134–153.

Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., . . . White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *Elife, 3*, e00590.

Dulvy, N. K., Freckleton, R. P., & Polunin, N. V. C. (2004). Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters, 7*(5), 410–416.

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., . . . Simpfendorfer, C. A. (2021). Overfishing drives over one–third of all sharks and rays toward a global extinction crisis. *Current Biology, 31(21)*(4773–4787.E8).

Dulvy, N. K., Simpfendorfer, C. A., Davidson, L. N., Fordham, S. V., Bräutigam, A., Sant, G., & Welch, D. J. (2017). Challenges and priorities in shark and ray conservation. *Current Biology, 27*(11), R565–R572.

Dwyer, R. G., Campbell, H. A., Cramp, R. L., Burke, C. L., Micheli–Campbell, M. A., Pillans, R. D., . . . Franklin, C. E. (2020). Niche partitioning between river shark species is driven by seasonal fluctuations in environmental salinity. *Functional Ecology, 34*(10), 2170–2185.

Ebert, D., Fowler, S., & Compagno, L. (2013). *Sharks of the world*. Plymouth: Wild Nature Press.

Eckert, L. E., Ban, N. C., Frid, A., & McGreer, M. (2018). Diving back in time: Extending historical baselines for yelloweye rockfish with Indigenous knowledge. *Aquatic Conservation: Marine and Freshwater Ecosystems, 28*(1), 158–166.

Eisemberg, C., Rose, M., Yaru, B., & Georges, A. (2011). Demonstrating decline of an iconic species under sustained indigenous harvest – The pig–nosed turtle (*Carettochelys insculpta*) in Papua New Guinea. *Biological Conservation, 144*(9), 2282–2288.

Eisemberg, C. C., Amepou, Y., Rose, M., Yaru, B., & Georges, A. (2015). Defining priority areas through social and biological data for the pig–nosed turtle (*Carettochelys insculpta*) conservation program in the Kikori Region, Papua New Guinea. *Journal for Nature Conservation, 28*, 19–25.

Elhassan, I. S. (2018). Occurrence of the green sawfish *Pristis zijsron* in the Sudanese Red Sea with observations on reproduction. *Endangered Species Research, 36*, 41–47.

Elliott, M., Whitfield, A. K., Potter, I. C., Blaber, S. J., Cyrus, D. P., Nordlie, F. G., & Harrison, T. D. (2007). The guild approach to categorizing estuarine fish assemblages: a global review. *Fish and Fisheries, 8*(3), 241–268.

Elsdon, T. S., Wells, B. K., Campana, S. E., Gillanders, B. M., Jones, C. M., Limburg, K. E., . . . Walther, B. D. (2008). Otolith chemistry to describe movements and life–history parameters of fishes: hypotheses, assumptions, limitations and inferences. *Oceanography and marine biology: an annual review, 46*(1), 297–330.

Espinoza, M., Lédée, E. J. I., Smoothey, A. F., Heupel, M. R., Peddemors, V. M., Tobin, A. J., & Simpfendorfer, C. A. (2021). Intra–specific variation in movement and habitat connectivity of a mobile predator revealed by acoustic telemetry and network analyses. *Marine Biology, 168*(6), 80.

Espinoza, M., & Sparks, J. S. (2019). Bull shark, *Carcharhinus leacus*, Report Card Assessment. FRDC, published 1 March 2019. https://www.fish.gov.au/docs/SharkReport/FRDC_Carcharhinus_leucas.pdf

Faria, V. V., McDavitt, M. T., Charvet, P., Wiley, T. R., Simpfendorfer, C. A., & Naylor, G. J. P. (2013). Species delineation and global population structure of Critically Endangered sawfishes (Pristidae). *Zoological Journal of the Linnean Society, 167*(1), 136–164.

Fedele, G., Donatti, C. I., Bornacelly, I., & Hole, D. G. (2021). Nature–dependent people: Mapping human direct use of nature for basic needs across the tropics. *Global Environmental Change*, 102368.

Feitosa, L. M., Dressler, V., & Lessa, R. P. (2020). Habitat use patterns and identification of essential habitat for an endangered coastal shark with vertebrae microchemistry: The case study of *Carcharhinus porosus*. *Frontiers in Marine Science, 7*(125).

Feitosa, L. M., Martins, A. P. B., Giarrizzo, T., Macedo, W., Monteiro, I. L., Gemaque, R., . . . Sampaio, I. (2018). DNA–based identification reveals illegal trade of threatened shark species in a global elasmobranch conservation hotspot. *Scientific Reports, 8*(1), 3347.

Feitosa, L. M., Queiroz, A. P. N., Labonne, M., Dressler, V. L., & Lessa, R. P. (2021). Habitat use and nursery evaluation for the longnose stingray *Hypanus guttatus* (Bloch & Schneider, 1801) using vertebral microchemistry. *Journal of Fish Biology, 99*(5), 1538–1549.

Feitosa, M. L., Barbosa Martins, A. P., & Silva Nunes, J. L. (2017). Sawfish (Pristidae) records along the Eastern Amazon coast. *Endangered Species Research, 34*, 229–234.

Feutry, P., Berry, O., Kyne, P. M., Pillans, R. D., Hillary, R. M., Grewe, P. M., . . . Bravington, M. (2017). Inferring contemporary and historical genetic connectivity from juveniles. *Molecular Ecology, 26*(2), 444–456.

Feutry, P., Devloo–Delva, F., Tran Lu Y, A., Mona, S., Gunasekera, R. M., Johnson, G., . . . Kyne, P. M. (2020). One panel to rule them all: DArTcap genotyping for population structure, historical demography, and kinship analyses, and its application to a threatened shark. *Molecular Ecology Resources, 20*(6), 1470–1485.

Feutry, P., Kyne, P. M., Pillans, R. D., Chen, X., Marthick, J. R., Morgan, D. L., & Grewe, P. M. (2015). Whole mitogenome sequencing refines population structure of the Critically Endangered sawfish *Pristis pristis*. *Marine Ecology Progress Series, 533*, 237–244.

Field, I. C., Charters, R., Buckworth, R. C., Meekan, M. G., & Bradshaw, C. (2008). Distribution and abundance of *Glyphis* and sawfishes in northern Australia and their potential interactions with commercial fisheries.

Field, I. C., Tillett, B. J., Charters, R., Johnson, G. J., Buckworth, R. C., Meekan, M. G., & Bradshaw, C. J. A. (2013). Distribution, relative abundance and risks from fisheries to threatened *Glyphis* sharks and sawfishes in northern Australia. *Endangered Species Research, 21*(2), 171–180.

Finn, M., Boulton, A., & Chessman, B. (2009). Ecological responses to artificial drought in two Australian rivers with differing water extraction. *Fundamental and Applied Limnology / Archiv für Hydrobiologie, 175*(3), 231–248.

Finucci, B., Cheok, J., Ebert, D., Herman, K., Kyne, P., & Dulvy, N. (2020). Ghosts of the deep – Biodiversity, fisheries, and extinction risk of ghost sharks. *Fish and Fisheries, 22*, 1–22.

Fluet–Chouinard, E., Funge–Smith, S., & McIntyre, P. B. (2018). Global hidden harvest of freshwater fish revealed by household surveys. *Proceedings of the National Academy of Sciences, 115*(29), 7623.

Foale, S., & Manele, B. (2004). Social and political barriers to the use of Marine Protected Areas for conservation and fishery management in Melanesia. *Asia Pacific Viewpoint, 45*(3), 373–386.

Fordham, D., Georges, A., Corey, B., & Brook, B. W. (2006). Feral pig predation threatens the indigenous harvest and local persistence of snake–necked turtles in northern Australia. *Biological Conservation, 133*(3), 379–388.

Fricke, R., Eschmeyer, W. N., & Van der Laan, R. (2021). Eschmeyer's catalog of fishes: genera, species, references. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 12/11/2021.

Frisk, M. G., Miller, T. J., & Fogarty, M. J. (2001). Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences, 58*(5), 969–981.

Fukuda, Y., Webb, G., Manolis, C., Delaney, R., Letnic, M., Lindner, G., & Whitehead, P. (2011). Recovery of saltwater crocodiles following unregulated hunting in tidal rivers of the Northern Territory, Australia. *The Journal of Wildlife Management, 75*(6), 1253–1266.

Gardner, R., Finlayson, M., Davidson, N., Damm, A., Fennessy, S., Darwall, W., . . . Okuno, E. (2018). Global wetland outlook: State of the world's wetlands and their services to people. Gland, Switzerland: Ramsar Convention Secretariat.

Gedamke, T., Hoenig, J. M., Musick, J. A., DuPaul, W. D., & Gruber, S. H. (2007). Using demographic models to determine intrinsic rate of increase and sustainable fishing for elasmobranchs: pitfalls, advances, and applications. *North American Journal of Fisheries Management, 27*(2), 605–618.

Gerst, J. W., & Thorson, T. B. (1977). Effects of saline acclimation on plasma electrolytes, urea excretion, and hepatic urea biosynthesis in a freshwater stingray, *Potamotrygon* sp. Garman, 1877. *Comparative Biochemistry and Physiology Part A: Physiology, 56*(1), 87–93.

Giglio, V. J., Luiz, O. J., Reis, M. S., & Gerhardinger, L. C. (2016). Memories of sawfish fisheries in a southwestern Atlantic estuary. *SPC Traditional Marine Resource Management and Knowledge Information Bulletin, 36*, 28–32.

Gillanders, B. (2005). Otolith chemistry to determine movements of diadromous and freshwater fish. *Aquatic Living Resources, 18*(3), 291–300.

Gleiss, A. C., Morgan, D. L., Whitty, J. M., Keleher, J. J., Fossette, S., & Hays, G. C. (2017). Are vertical migrations driven by circadian behaviour? Decoupling of activity and depth use in a large riverine elasmobranch, the freshwater sawfish (*Pristis pristis*). *Hydrobiologia, 787*(1), 181–191.

Grant, M. I., Rigby, C., Mizrahi, M., & Sayer, C. (2021a). *Makararaja chindwinensis*. The IUCN Red List of Threatened Species 2021: e.T161698A124530183. https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T161698A124530183.en.

Grant, M. I., Rigby, C., & Sayer, C. (2021b). *Hemitrygon laosensis*. The IUCN Red List of Threatened Species 2021: e.T39407A124411226. https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T39407A124411226.en. Accessed on 13 December 2021.

Grant, M. I., Rigby, C. L., Bin Ali, A., Fahmi, Haque, A. B., Hasan, V., & Sayer, C. (2021c). *Urogymnus polylepis*. The IUCN Red List of Threatened Species 2021: e.T195320A104294071. https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T195320A104294071.en.

Grant, M. I., Rigby, C. L., Bin Ali, A., Fahmi, Hasan, V., & Sayer, C. (2021d). *Fluvitrygon oxyrhynchus*. The IUCN Red List of Threatened Species 2021: e.T44185A2993563. https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T44185A2993563.en. Downloaded on 08 December 2021.

Grant, M. I., Rigby, C. L., Bin Ali, A., Fahmi, Hasan, V., & Sayer, C. (2021e). *Fluvitrygon signifer*. The IUCN Red List of Threatened Species 2021: e.T39411A2924238. https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T39411A2924238.en. Downloaded on 08 December 2021.

Grant, M. I., Smart, J. J., Rigby, C. L., White, W. T., Chin, A., Baje, L., & Simpfendorfer, C. A. (2019). Intraspecific demography of the silky shark (*Carcharhinus falciformis*): implications for fisheries management. *Ices Journal of Marine Science, 77*(1), 241–255.

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

Grant, M. I., White, W. T., Amepou, Y., Appleyard, S. A., Baje, L., Devloo–Delva, F., . . . Chin, A. (2021f). Papua New Guinea: A potential refuge for threatened Indo–Pacific river sharks and sawfishes. *Frontiers in Conservation Science, 2*(48).

Grant, M. I., White, W. T., Amepou, Y., Baje, L., Diedrich, A., Ibana, D., . . . Chin, A. (2021g). Local knowledge surveys with small–scale fishers indicate challenges to sawfish conservation in southern Papua New Guinea. *Aquatic Conservation: Marine and Freshwater Ecosystems, 31*(10), 2883–2900.

Green, M. E., Anastasi, B. R., Hobbs, J.–P. A., Feldheim, K., McAuley, R., Peverell, S., . . . White, W. T. (2018). Mixed–marker approach suggests maternal philopatry and sex–biased behaviours of narrow sawfish *Anoxypristis cuspidata*. *Endangered Species Research, 37*, 45–54.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., . . . Zarfl, C. (2019). Mapping the world's free–flowing rivers. *Nature, 569*(7755), 215–221.

Haines, A. K. (1977). Fish and fisheries of the Purari River and delta. In: Purari River (Wabo) Hydroelectric Scheme Environmental Studies, Vol 1. Office of Environment and Conservation and the Department of Minerals and Energy, Konedobu.

Haines, A. K. (1978/79). The subsistence fishery of the Purari delta. *Science in New Guinea, 6*, 80–95.

Haines, A. K. (1979). An ecological survey of the Lower Purari River System, Papua New Guinea. In: Purari River (Wabo) Hydroelectric Scheme Environmental Studies, Vol. 6. Office of Environment and Conservation, Waigani and Department of Minerals and Energy, Konedobu.

Haines, A. K., & Stevens, R. N. (1983). Subsistence and commercial fisheries. In T. Petr (Ed.), *The Purari — tropical environment of a high rainfall river basin* (pp. 385–408). Dordrecht: Springer Netherlands.

Hall, N., G, Bartron, C., White, W., T, Dharmadi, & Potter, I., C. (2012). Biology of the silky shark *Carcharhinus falciformis* (Carcharhinidae) in the eastern Indian Ocean, including an approach to estimating age when timing of parturition is not well defined. *Journal of Fish Biology, 80*(5), 1320–1341.

Halliday, I. A., Saunders, T., Sellin, M. J., Allsop, Q., Robins, J. B., McLennan, M. F., & Kurnoth, P. (2012). Flow impacts on estuarine finfish fisheries of the Gulf of Carpentaria. FRDC Project No. 2007/002, Department of Agriculture, Fisheries and Forestry. Brisbane, Australia.

Hamel, M. J., Koch, J. D., Steffensen, K. D., Pegg, M. A., Hammen, J. J., & Rugg, M. L. (2014). Using mark–recapture information to validate and assess age and growth of long–lived fish species. *Canadian Journal of Fisheries and Aquatic Sciences, 71*(4), 559–566.

Hanson, J. O., Salisbury, S. W., Campbell, H. A., Dwyer, R. G., Jardine, T. D., & Franklin, C. E. (2015). Feeding across the food web: The interaction between diet, movement and body size in estuarine crocodiles (*Crocodylus porosus*). *Austral Ecology, 40*(3), 275–286.

Haque, A., & Das, S. (2019). New records of the Critically Endangered Ganges shark *Glyphis gangeticus* in Bangladeshi waters: urgent monitoring needed. *Endangered Species Research*.

Haque, A. B., Cavanagh, R. D., & Seddon, N. (2021). Evaluating artisanal fishing of globally threatened sharks and rays in the Bay of Bengal, Bangladesh. *PLoS One, 16*(9), e0256146.

Haque, A. B., Leeney, R. H., & Biswas, A. R. (2020). Publish, then perish? Five years on, sawfishes are still at risk in Bangladesh. *Aquatic Conservation: Marine and Freshwater Ecosystems, 30*(12), 2370–2383.

Harasti, D., Lee, K., Bruce, B., Gallen, C., & Bradford, R. (2017). Juvenile white sharks *Carcharodon carcharias* use estuarine environments in south–eastern Australia. *Marine Biology, 164*(3), 58.

Harper, M., Mejbel, H. S., Longert, D., Abell, R., Beard, T. D., Bennett, J. R., . . . Cooke, S. J. (2021). Twenty–five essential research questions to inform the protection and restoration of freshwater biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems, 31*(9), 2632–2653.

Harry, A. V. (2018). Evidence for systemic age underestimation in shark and ray ageing studies. *Fish and Fisheries, 19*(2), 185–200.

Harry, A. V., Tobin, A. J., & Simpfendorfer, C. A. (2013). Age, growth and reproductive biology of the spot–tail shark, *Carcharhinus sorrah*, and the Australian blacktip shark, *C. tilstoni*, from the Great Barrier Reef World Heritage Area, north–eastern Australia. *Marine and Freshwater Research, 64*(4), 277.

He, F., Jähnig, S. C., Wetzig, A., & Langhans, S. D. (2021). More exposure opportunities for promoting freshwater conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems, 31*(12), 3626–3635.

He, F., Zarfl, C., Bremerich, V., David, J. N. W., Hogan, Z., Kalinkat, G., . . . Jähnig, S. C. (2019). The global decline of freshwater megafauna. *Global Change Biology, 25*(11), 3883–3892.

Hegg, J. C., Graves, B., & Fisher, C. M. (2021). Sawfish, read in tooth and saw: Rostral teeth as endogenous chemical records of movement and life–history in a critically endangered species. *Aquatic Conservation: Marine and Freshwater Ecosystems, 31*(9), 2334–2347.

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution, 23*(4), 202–210.

Henry, G. W., & Lyle, J. M. (2003). National recreational and indigenous fishing survey. Australian Government Department of Agriculture, Fisheries and Forestry. FRDC Project No. 99/158. Retrieved from www.affa.gov.au/recfishsurvey

Heppell, S. S., Crowder, L. B., & Menzel, T. R. (1999). Life table analysis of long–lived marine species with implications for conservation and management. In J. Musick (Ed.), *Life in the Slow Lane: Ecology and Conservation of Long–Lived Marine Animals* (pp. 137–148). Bethesda, MD: American Fisheries Society.

Heupel, M., & Simpfendorfer, C. (2010). Science or slaughter: need for lethal sampling of sharks. *Conservation Biology, 24*(5), 1212–1218.

Heupel, M. R., Carlson, J., & Simpfendorfer, C. (2007). Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series, 337*, 287–297.

Heupel, M. R., Knip, D. M., Simpfendorfer, C. A., & Dulvy, N. K. (2014). Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series, 495*, 291–298.

Heupel, M. R., Munroe, S. E. M., Lédée, E. J. I., Chin, A., & Simpfendorfer, C. A. (2019). Interspecific interactions, movement patterns and habitat use in a diverse coastal shark assemblage. *Marine Biology, 166*(6), 68.

Heupel, M. R., & Simpfendorfer, C. A. (2008). Movement and distribution of young bull sharks *Carcharhinus leucas* in a variable estuarine environment. *Aquatic Biology, 1*, 277–289.

Heupel, M. R., & Simpfendorfer, C. A. (2011). Estuarine nursery areas provide a low–mortality environment for young bull sharks *Carcharhinus leucas*. *Marine Ecology Progress Series, 433*, 237–244.

Heupel, M. R., Simpfendorfer, C. A., Collins, A. B., & Tyminski, J. P. (2006). Residency and movement patterns of bonnethead sharks, *Sphyrna tiburo*, in a large Florida estuary. *Environmental Biology of Fishes, 76*(1), 47–67.

Heupel, M. R., Simpfendorfer, C. A., Espinoza, M., Smoothey, A. F., Tobin, A., & Peddemors, V. (2015). Conservation challenges of sharks with continental scale migrations. *Frontiers in Marine Science, 2*, 12.

Heupel, M. R., Yeiser, B. G., Collins, A. B., Ortega, L., & Simpfendorfer, C. A. (2010). Long–term presence and movement patterns of juvenile bull sharks, *Carcharhinus leucas*, in an estuarine river system. *Marine and Freshwater Research, 61*(1), 1–10.

Hillary, R. M., Bravington, M. V., Patterson, T. A., Grewe, P., Bradford, R., Feutry, P., . . . Bruce, B. D. (2018). Genetic relatedness reveals total population size of white sharks in eastern Australia and New Zealand. *Scientific Reports, 8*(1).

Hoarau, F., Darnaude, A., Poirout, T., Jannel, L.–A., Labonne, M., & Jaquemet, S. (2021). Age and growth of the bull shark (*Carcharhinus leucas*) around Reunion Island, South West Indian Ocean. *Journal of Fish Biology, 99*(3), 1087–1099.

Hossain, M. A., Thompson, B. S., ChowdHury, G. W., Mohsanin, S., Fahad, Z. H., Koldewey, H. J., & Islam, M. A. (2015). Sawfish exploitation and status in Bangladesh. *Aquatic Conservation: Marine and Freshwater Ecosystems, 25*(6), 781–799.

Hueter, R., Heupel, M., Heist, E., & Keeney, D. (2004). Evidence of philopatry in sharks and implications for the management of shark fisheries. *Journal of Northwest Atlantic Fishery Science, 35*(7), 1–10.

Hutchings, P. (2017). An advocate for taxonomic research in Australia. *Pacific Conservation Biology, 25*(1), 34–36.

Ibana, D. (2020). Fish maw report. Report prepared for the Gulf Provincial Administration, Fisheries and Marine Resource Division, Kerema, Papua New Guinea.

Ip, Y. K., Tam, W. L., Wong, W. P., & Chew, S. F. (2005). Marine (*Taeniura lymma*) and freshwater (*Himantura signifer*) elasmobranchs synthesize urea for osmotic water retention. *Physiological and Biochemical Zoology, 78*(4), 610–619.

Iqbal, M., Setiawan, A., Windusari, Y., Yustian, I., & Zulkifli, H. (2020). Updating status of the distributional records of giant freshwater stingray *Urogymnus polylepis* (Bleeker, 1852) in Indonesia. *AIP Conference Proceedings, 2260*(1), 020004.

Iqbal, M., Setiawan, A., & Yustian, I. (2019a). First inland record of bull shark *Carcharhinus leucas* (Carcharhiniformes: Carcharhinidae) in Indonesian Borneo. *Ecologica Montenegrina, 24*, 52–57.

Iqbal, M., Setiawan, D., & Ajiman, A. (2017). Presence of *Fluvitrygon oxyrhynchus* in Sumatra, Indonesia (Chondrichthyes: Dasyatidae). *Ichthyological Exploration of Freshwaters, 28*, 83–85.

Iqbal, M., Setiawan, D., & Ajiman, A. (2018a). New data on the distribution of the endangered white–edge freshwater whipray *Fluvitrygon signifer* (Chondrichthyes: Dasyatidae). *Ichthyological Exploration of Freshwaters, 28*(2), 171–176.

Iqbal, M., & Yustian, I. (2016). Occurrence of the giant freshwater stingray Urogymnus polylepis in Sumatra, Indonesia (Chondrichthyes: Dasyatidae). *Ichthyological Exploration of Freshwaters, 27*, 333–336.

Iqbal, M., Yustian, I., Setiawan, A., Nurnawati, E., & Zulkifli, H. (2019b). Filling a gap on the blank distribution of the giant freshwater stingray *Urogymnus polylepsis*: first records in Malay Peninsula (Chondrichthyes: Dasyatidae). *Ichthyological Exploration of Freshwaters, 29*(4), 371–374.

Iqbal, M., Zulkifli, H., & Yustian, I. (2018b). The valid Species and Distribution of Stingrays (Myliobatiformes: Dasyatidae) in South Sumatran waters, Indonesia. *BIOVALENTIA: Biological Research Journal, 4*.

Jabado, R. W., Kyne, P. M., Nazareth, E., & Sutaria, D. N. (2018). A rare contemporary record of the Critically Endangered Ganges shark *Glyphis gangeticus*. *Journal of Fish Biology, 92*(5), 1663–1669.

Jaiteh, V. F., Loneragan, N. R., & Warren, C. (2017). The end of shark finning? Impacts of declining catches and fin demand on coastal community livelihoods. *Marine Policy, 82*, 224–233.

James, K. C. (2020). Vertebral growth and band–pair deposition in sexually mature little skates *Leucoraja erinacea*: is adult band–pair deposition annual? *Journal of Fish Biology, 96*(1), 4–13.

James, K. C., & Natanson, L. J. (2020). Positional and ontogenetic variation in vertebral centra morphology in five batoid species. *Marine and Freshwater Research*, *72*, 887–898.

Kassambara, A. (2017). *Practical guide to principal component methods in R: PCA, M (CA), FAMD, MFA, HCPC, factoextra* (Vol. 2): STHDA, 2017.

Kassambara, A., & Mundt, F. (2020). factoextra: Extract and visualize the results of multivariate data analyses. R package version 1.0.7. https://CRAN.R–project.org/package=factoextra.

Kerr, L. A., & Campana, S. E. (2014). Chemical composition of fish hard parts as a natural marker of fish stocks. In S. Cadrin, L. Kerr, & S. Mariani (Eds.), *Stock Identification Methods* (Second ed., pp. 205–234). San Diego Academic Press.

Kindsvater, H. K., Mangel, M., Reynolds, J. D., & Dulvy, N. K. (2016). Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and evolution, 6*(7), 2125–2138.

Kinney, M. J., Hussey, N. E., Fisk, A. T., Tobin, A. J., & Simpfendorfer, C. A. (2011). Communal or competitive? Stable isotope analysis provides evidence of resource partitioning within a communal shark nursery. *Marine Ecology Progress Series, 439*, 263–276.

Kinney, M. J., & Simpfendorfer, C. A. (2009). Reassessing the value of nursery areas to shark conservation and management. *Conservation Letters, 2*(2), 53–60.

Kirchhoff, K. N., Hauffe, T., Stelbrink, B., Albrecht, C., & Wilke, T. (2017). Evolutionary bottlenecks in brackish water habitats drive the colonization of fresh water by stingrays. *Journal of Evolutionary Biology, 30*(8), 1576–1591.

Knip, D. M., Heupel, M. R., Simpfendorfer, C. A., Tobin, A. J., & Moloney, J. (2011a). Ontogenetic shifts in movement and habitat use of juvenile pigeye sharks *Carcharhinus amboinensis* in a tropical nearshore region. *Marine Ecology Progress Series, 425*, 233–246.

Knip, D. M., Heupel, M. R., Simpfendorfer, C. A., Tobin, A. J., & Moloney, J. (2011b). Wet–season effects on the distribution of juvenile pigeye sharks, *Carcharhinus amboinensis*, in tropical nearshore waters. *Marine and Freshwater Research, 62*(6), 658–667.

Kyne, P. M., Davies, C.–L., Devloo–Delva, F., Johnson, G. J., Amepou, Y., Grant, M. I., . . . Feutry, P. (2021a). Molecular analysis of newly–discovered geographic range of the threatened river shark *Glyphis glyphis* reveals distinct populations. Report to the National Environmental Science Program, Marine Biodiversity Hub. Charles Darwin University and CSIRO.

Kyne, P. M., & Feutry, P. (2017). Recreational fishing impacts on threatened river sharks: A potential conservation issue. *Ecological Management & Restoration, 18*, 209–213.

Kyne, P. M., Jabado, R. W., Rigby, C. L., Dharmadi, Gore, M. A., Pollock, C. M., . . . Dulvy, N. K. (2020). The thin edge of the wedge: Extremely high extinction risk in wedgefishes and giant guitarfishes. *Aquatic Conservation: Marine and Freshwater Ecosystems, 30*(7), 1337–1361.

Kyne, P. M., Oetinger, M., Grant, M. I., & Feutry, P. (2021b). Life history of the Critically Endangered largetooth sawfish: a compilation of data for population assessment and demographic modelling. *Endangered Species Research, 44*, 79–88.

Kyne, P. M., Rigby, C. L., Cheok, J., Darwall, W. R. T., Grant, M. I., & Simpfendorfer, C. A. (2021c). *Glyphis garricki*. The IUCN Red List of Threatened Species 2021: e.T42712A68624151. https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T42712A68624151.en. Downloaded on 05 November 2021.

Kyne, P. M., Rigby, C. L., Darwall, W. R. T., Grant, M. I., & Simpfendorfer, C. A. (2021d). *Glyphis glyphis*. The IUCN Red List of Threatened Species 2021: e.T39379A68624306. https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T39379A68624306.en. Downloaded on 05 November 2021.

Kyne, P. M., & Simpfendorfer, C. A. (2014). Indo–West Pacific. Chapter 7. In L. R. Harrison & N. K. Dulvy (Eds.), *Sawfish: A Global Conservation Category* (pp. 64). Vancouver, Canada: IUCN Species Survival Commission's Shark Specialist Group.

Last, P. (2002). Freshwater and estuarine elasmobranchs of Australia. In S. Fowler, T. Reed, & F. Dipper (Eds.), *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July, 1997* (pp. 185–193). Oxford, UK: Information Press.

Last, P., Naylor, G., Séret, B., White, W., Stehmann, M., & de Carvalho, M. (2016a). *Rays of the World*. Australia: CSIRO Publishing.

Last, P. R., Naylor, G., & Manjaji–Matsumoto, B. M. (2016b). A revised classification of the family Dasyatidae (Chondrichthyes: Myliobatiformes) based on new morphological and molecular insights. *Zootaxa, 4139*(3), 345–368.

Last, P. R., White, W. T., & Kyne, P. M. (2016c). *Urogymnus acanthobothrium* sp. nov., a new euryhaline whipray (Myliobatiformes: Dasyatidae) from Australia and Papua New Guinea. *Zootaxa, 4147*(2), 162.

Lawson, J. M., & Fordham, S. V. (2018). Sharks Ahead: Realizing the Potential of the Convention on Migratory Species to Conserve Elasmobranchs. Shark Advocates International, The Ocean Foundation, Washington, DC, USA. 76 pp.

Le, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software, 25*(1), 1–18.

Leahy, S. M., & Robins, J. B. (2021). River flows affect the growth of a tropical finfish in the wet–dry rivers of northern Australia, with implications for water resource development. *Hydrobiologia, 848*(18), 4311–4333.

Lear, K. O., Gleiss, A. C., Whitty, J. M., Fazeldean, T., Albert, J. R., Green, N., . . . Morgan, D. L. (2019). Recruitment of a critically endangered sawfish into a riverine nursery depends on natural flow regimes. *Scientific Reports, 9*(1), 17071.

Lear, K. O., Morgan, D. L., Whitty, J. M., Beatty, S. J., & Gleiss, A. C. (2020). Wet season flood magnitude drives resilience to dry season drought of a euryhaline elasmobranch in a dry–land river. *Science of The Total Environment, 750*, 142234.

Leeney, R. H., Mana, R. R., & Dulvy, N. K. (2018). Fishers ecological knowledge of sawfishes in the Sepik and Ramu rivers, northern Papua New Guinea. *Endangered Species Research, 36*, 15–26.

Lees, A. C., & Gilroy, J. J. (2014). Vagrancy fails to predict colonization of oceanic islands. *Global ecology and Biogeography, 23*(4), 405–413.

Lennox, R. J., Crook, D. A., Moyle, P. B., Struthers, D. P., & Cooke, S. J. (2019). Toward a better understanding of freshwater fish responses to an increasingly drought–stricken world. *Reviews in Fish Biology and Fisheries, 29*, 71–92.

Letnic, M. (2008). A comparison of saltwater crocodile (*Crocodylus porosus*) populations in freshwater–floodplain and tidal river habitats of the Adelaide River catchment, Northern Territory, Australia. *Applied Herpetology, 5*(3), 243–252.

Li, C., Corrigan, S., Yang, L., Straube, N., Harris, M., Hofreiter, M., . . . Naylor, G. J. P. (2015). DNA capture reveals transoceanic gene flow in endangered river sharks. *Proceedings of the National Academy of Sciences, 112*(43), 13302–13307.

Lindner, G. (2004). *Crocodile management—Kakadu National Park.* Paper presented at the Crocodiles. Proceedings of the 17th Working Meeting of the IUCN–SSC Crocodile Specialist Group. The International Union for Conservation of Nature and Natural Resources (IUCN), Gland, Switzerland.

Loboda, T., Lasso, C., Rosa, R., & Carvalho, M. (2021). Two new species of freshwater stingrays of the genus *Paratrygon* (Chondrichthyes: Potamotrygonidae) from the Orinoco basin, with comments on the taxonomy of *Paratrygon aiereba*. *Neotropical Ichthyology, 19*.

Lozano, I. E., Llamazares Vegh, S., Gómez, M. I., Piazza, Y. G., Salva, J. L., & Fuentes, C. M. (2019). Episodic recruitment of young *Prochilodus lineatus* (Valenciennes, 1836) (Characiformes: Prochilodontidae) during high discharge in a floodplain lake of the River Paraná, Argentina. *Fisheries Management and Ecology, 26*(3), 260–268.

Lucifora, L., Bellagamba, P., Vega, L., Bo, M., Alvarenga, P., & Diaz de Astarloa, J. (2020). Significance of stingrays (Chondrichthyes: Myliobatiformes) as prey of crocodilians (Reptilia: Crocodylia) in non–marine environments. *Ichthyological Exploration of Freshwaters*.

Lucifora, L. O., Balboni, L., Scarabotti, P. A., Alonso, F. A., Sabadin, D. E., Solari, A., . . . Díaz de Astarloa, J. M. (2017). Decline or stability of obligate freshwater elasmobranchs following high fishing pressure. *Biological Conservation, 210*, 293–298.

Lucifora, L. O., Barbini, S. A., Vegh, S. L., Scarabotti, P. A., Vargas, F., Solari, A., . . . Díaz de Astarloa, J. M. (2016). Geographic distribution of the short–tailed river stingray (*Potamotrygon brachyura*): assessing habitat loss and fishing as threats to the world's largest obligate freshwater elasmobranch. *Marine and Freshwater Research, 67*(10), 1463–1478.

Lucifora, L. O., Carvalho, M. R., Kyne, P. M., & White, W. T. (2015). Freshwater sharks and rays. *Current Biology, 25*(20), 971–973.

Lyon, B. J., Dwyer, R., Pillans, R. D., Campbell, H., & Franklin, C. (2017). Distribution, seasonal movements and habitat utilisation of an endangered shark, *Glyphis glyphis* from northern Australia. *Marine Ecology Progress Series, 573*, 203–213.

Macdonald, C., Gallagher, A. J., Barnett, A., Brunnschweiler, J., Shiffman, D. S., & Hammerschlag, N. (2017). Conservation potential of apex predator tourism. *Biological Conservation, 215*, 132–141.

Macneil, A., Chapman, D., Heupel, M., Simpfendorfer, C., Heithaus, M., Meekan, M., . . . Gorham, T. (2020). Global status and conservation potential of reef sharks. *Nature, 583*, 801–806.

Manjaji–Matsumoto, B. M., Kyne, P. M., Yee, J. C., & Dickson, A. F. (2016). Tagging and monitoring of coastal marine and freshwater elasmobranch population in Sabah. WWF Malaysia Project Report (Shark Protection – Marine Programme; Project Number MA010311–000–GENF/ UMS Project Code GL00138). 50 pp.

Manjaji–Matsumoto, B. M., & Last, P. R. (2006). *Himantura lobistoma*, a new whipray (Rajiformes: Dasyatidae) from Borneo, with comments on the status of *Dasyatis microphthalmus*. *Ichthyological Research, 53*(3), 290–297.

Márquez–Farías, J. F. (2007). Reproductive biology of shovelnose guitarfish *Rhinobatos productus* from the eastern Gulf of California México. *Marine Biology, 151*(4), 1445–1454.

Martin, A. R. (2005). Conservation of freshwater and euryhaline elasmobranchs: a review. *Journal of the Marine Biological Association of the United Kingdom, 85*(5), 1049–1073.

Martin, J.–M., & Meybeck, M. (1979). Elemental mass–balance of material carried by major world rivers. *Marine Chemistry, 7*(3), 173–206.

Martins, A., Heupel, M., Chin, A., & Simpfendorfer, C. (2018). Batoid nurseries: definition, use and importance. *Marine Ecology Progress Series, 595*, 253–267.

Matley, J. K., Klinard, N. V., Barbosa Martins, A. P., Aarestrup, K., Aspillaga, E., Cooke, S. J., . . . Fisk, A. T. (2021). Global trends in aquatic animal tracking with acoustic telemetry. *Trends in Ecology & Evolution, 37*(1), 79–94.

Maus, V., Giljum, S., Gutschlhofer, J., da Silva, D. M., Probst, M., Gass, S. L. B., . . . McCallum, I. (2020). A global–scale data set of mining areas. *Scientific Data, 7*(1), 289.

McCulloch, M., Cappo, M., Aumend, J., & Müller, W. (2005). Tracing the life history of individual barramundi using laser ablation MC–ICP–MS Sr–isotopic and Sr/Ba ratios in otoliths. *Marine and Freshwater Research, 56*(5), 637–644.

McDavitt, M. (2002). Lake Nicaragua revisited: conversations with a former sawfish fisherman. *Shark News, 14*(5).

McDavitt, M., & Charvet–Almeida, P. (2004). Quantifying trade in sawfish rostra: two examples. *Shark News, 16*, 10–11.

McDavitt, M. T. (2014). The cultural value of sawfishes. *Chapter 4*. In L. R. Harrison & N. K. Dulvy (Eds.), *Sawfish: A global conservation stategy* (pp. 30–31). Vancouver, Canada: IUCN Species Survival Commissions's Shark Speacialist Group.

McDavitt, M. T., & Kyne, P. M. (2020). Social media posts reveal the geographic range of the Critically Endangered clown wedgefish, *Rhynchobatus cooki*. *Journal of Fish Biology, 97*(6), 1846–1851.

McHale, J., Parke, E., Tapper, D., & McKechnie, S. (2013). There are calls tonight for a cull of crocodiles in the east Kimberley with claims they are attacking and eating many cattle on pastoral properties. ABC1 Perth. Retrieved from https://search.informit.org/doi/abs/10.3316/tvnews.tsm201310150148

McLusky, D. S. (1993). Marine and estuarine gradients — An overview. *Netherland Journal of Aquatic Ecology, 27*(2), 489–493.

McMillan, M. N., Izzo, C., Wade, B., & Gillanders, B. M. (2017). Elements and elasmobranchs: hypotheses, assumptions and limitations of elemental analysis. *Journal of Fish Biology, 90*(2), 559–594.

Memon, A. A. (2005). Devastation of the Indus river delta. In *Impacts of global climate change. Conference proceedings of the World Water and Environmental Resources Congress, May 15–19, 2005, Anchorage, Alaska, United States* (pp. 1–12).

Miller, J. R., & Hobbs, R. J. (2002). Conservation where people live and work. *Conservation Biology, 16*(2), 330–337.

Mills, C. A., & Mann, R. H. K. (1985). Environmentally–induced fluctuations in year–class strength and their implications for management. *Journal of Fish Biology, 27*, 209–226.

Mohan, J. A., TinHan, T. C., Miller, N. R., & David Wells, R. J. (2017). Effects of sample cleaning and storage on the elemental composition of shark vertebrae. *Rapid Communications in Mass Spectrometry, 31*(24), 2073–2080.

Mollet, H. F., & Cailliet, G. M. (2002). Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage–based matrix models. *Marine and Freshwater Research, 53*(2), 503–515.

Moore, A. B. M. (2017). Are guitarfishes the next sawfishes? Extinction risk and an urgent call for conservation action. *Endangered Species Research, 34*, 75–88.

Moreau, M. A., & Coomes, O. T. (2007). Aquarium fish exploitation in western Amazonia: conservation issues in Peru. *Environmental Conservation, 34*(1), 12–22.

Moreno Iturria, D. A. (2012). *Demography of the family Pristidae as an aid to conservation and management.* Bachelor of Marine Science (Honours) dissertation. James Cook University, Townsville, Queensland, Australia.

Morgan, D. L., Beatty, S. J., Allen, M. G., Gleiss, A. C., Keleher, J., & Whitty, J. M. (2011). Addressing knowledge gaps and questions from the Fitzroy River (Kimberley region, Western Australia) fishway review. Report prepared for the Department of Water, Government of Western Australia pp 57.

Morgan, D. L., Ebner, B. C., Allen, M. G., Gleiss, A. C., Beatty, S. J., & Whitty, J. M. (2017). Habitat use and site fidelity of neonate and juvenile green sawfish in a nursery area in Western Australia. *Endangered Species Research, 34*, 235–249.

Morgan, D. L., Somaweera, R., Gleiss, A. C., Beatty, S. J., & Whitty, J. M. (2017). An upstream migration fought with danger: freshwater sawfish fending off sharks and crocodiles. *Ecology, 98*(5), 1465–1467.

Morgan, D. L., Whitty, J. M., Phillips, N. M., Thorburn, D. C., Chaplin, J. A., & McAuley, R. (2011). North–western Australia as a hotspot for endangered elasmobranchs with particular reference to sawfishes and the northern river shark. *Journal of the Royal Society of Western Australia, 2*, 345–358.

Morgan, D. L., Wueringer, B. E., Allen, M. G., Ebner, B. C., Whitty, J. M., Gleiss, A. C., & Beatty, S. J. (2016). What is the fate of amputee sawfish? Essays, Fisheries Magazine, American Fisheries Society. Retrieved from: https://fisheries.org/2016/02/what–is–the–fate–of–amputee–sawfish/.

Morrison, C., Wardle, C., & Castley, J. G. (2016). Repeatability and reproducibility of population viability analysis (PVA) and the implications for threatened species management. *Frontiers in Ecology and Evolution, 4*, 98.

Muktha, M., Akhilesh, K. V., Sukumaran, S., & Kizhakudan, S. (2019). A new report confirming the presence of bennett's stingray, *Hemitrygon Bennettii* (Elasmobranchii: Myliobatiformes: Dasyatidae), from the Western Bay of Bengal. *Acta Ichthyologica Et Piscatoria, 49*, 101–108.

Musick, J. A. (1999). *Ecology and conservation of long–lived marine animals. In J. Musick (Ed.), Life in the Slow Lane: Ecology and Conservation of Long–Lived Marine Animals (pp. 1–19). Bethesda, MD: American Fisheries Society Symposium.* Paper presented at the American fisheries society symposium.

Natanson, L. J., Adams, D. H., Winton, M. V., & Maurer, J. R. (2014). Age and growth of the bull shark in the western north Atlantic Ocean. *Transactions of the American Fisheries Society, 143*(3), 732–743.

NFA. (2003). Barramundi Management Plan. National Fisheries Authority, Port Moresby, Papua New Guinea, pp 1–9. .

Ng, H. H., Tan, H. H., Yeo, D. C., & Ng, P. K. (2010). Stingers in a strange land: South American freshwater stingrays (Potamotrygonidae) in Singapore. *Biological invasions, 12*(8), 2385–2388.

Ng, P. K., Chou, L., & Lam, T. (1993). The status and impact of introduced freshwater animals in Singapore. *Biological Conservation, 64*(1), 19–24.

NMFS. (2009). Recovery plan for smalltooth sawfish (*pristis pectinata*). Prepared by the smalltooth sawfish recovery team for the National Marine Fisheries Service, Silver Spring, Maryland.

Norton, D. A. (1998). *Revisiting rarity: a botanical perspective on the meanings of rarity and the classification of New Zealand's uncommon plants.* Paper presented at the Ecosystems, entomology & plants: proceedings of a symposium held at Lincoln University to mark the retirement of Bryony Macmillan, John Dugdale, Peter Wardle and Brian Molloy, 1 September 1995.

Okes, N., & Sant, G. (2019). *An overview of major shark traders, catchers and species. WWF TRAFFIC, Cambridge, UK.*

Ostrovski, R., Martins, G., Brito, M., Jean, Valentin, L., & Vianna, M. (2021). The media paradox: influence on human shark perceptions and potential conservation impacts. *Ethnobiology and Conservation, 10*, 12.

Otake, T., Ishii, T., & Tanaka, S. (2005). Otolith strontium: calcium ratios in a freshwater stingray, *Himantura signifer* (Compagno and Roberts, 1982), from the Chao Phraya River, Thailand. *Coastal Marine Science, 29*, 147–153.

Pacoureau, N., Rigby, C. L., Kyne, P. M., Sherley, R. B., Winker, H., Carlson, J. K., . . . Dulvy, N. K. (2021). Half a century of global decline in oceanic sharks and rays. *Nature, 589*(7843), 567–571.

Patricio, H. C., Zipper, S. A., Peterson, M. L., Ainsley, S. M., Loury, E. K., Ounboundisane, S., & Demko, D. B. (2019). Fish catch and community composition in a data–poor Mekong River subcatchment characterised through participatory surveys of harvest from an artisanal fishery. *Marine and Freshwater Research, 70*(2), 153–168.

Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution, 10*(10), 430.

Peterson, I., & Wroblewski, J. (1984). Mortality rate of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences, 41*(7), 1117–1120.

Petheram, C., Rogers, L., Read, A., Gallant, J., Moon, A., Yang, A., . . . Barber, M. (2017). Assessment of surface water storage options in the Fitzroy, Darwin and Mitchell catchments. A technical report to the Australian Government from the CSIRO Northern Australia Water Resource Assessment, part of the National Water Infrastructure Development Fund: Water Resource Assessments. CSIRO, Australia.

Petheram, C., Watson, I., Bruce, C., & Chilcott, C. e. (2018). Water resource assessment for the Mitchell catchment. A report to the Australian Government from the CSIRO Northern Australia Water Resource Assessment, part of the National Water Infrastructure Development Fund: Water Resource Assessments. CSIRO, Australia.

Peverell, S., McPherson, G., Garrett, R., & Gribble, N. (2006). New records of the river shark *Glyphis* (Carcharhinidae) reported from Cape York Peninsula, northern Australia. *Zootaxa, 1233*(1), 53–68.

Peverell, S. C. (2005). Distribution of sawfishes (Pristidae) in the Queensland Gulf of Carpentaria, Australia, with notes on sawfish ecology. *Environmental Biology of Fishes, 73*(4), 391–402.

Peverell, S. C. (2009). *Sawfish (Pristidae) of the Gulf of Carpentaria, Queensland, Australia.* Masters of Science dissertation, James Cook University, Townsville, Queensland, Australia.

Phillips, N. M., Chaplin, J. A., Morgan, D. L., & Peverell, S. C. (2011). Population genetic structure and genetic diversity of three critically endangered *Pristis* sawfishes in Australian waters. *Marine Biology, 158*(4), 903–915.

Phillips, N. M., Chaplin, J. A., Peverell, S. C., & Morgan, D. L. (2017). Contrasting population structures of three Pristis sawfishes with different patterns of habitat use. *Marine and Freshwater Research, 68*(3), 452–460.

Piermarini, P., & Evans, D. (1998). Osmoregulation of the Atlantic Stingray (*Dasyatis sabina*) from the Freshwater Lake Jesup of the St. Johns River, Florida. *Physiological Zoology, 71*(5), 553–560.

Pillans, R. D., & Franklin, C. E. (2004). Plasma osmolyte concentrations and rectal gland mass of bull sharks *Carcharhinus leucas*, captured along a salinity gradient. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 138*(3), 363–371.

Pillans, R. D., Good, J. P., Anderson, W. G., Hazon, N., & Franklin, C. E. (2005). Freshwater to seawater acclimation of juvenile bull sharks (*Carcharhinus leucas*): plasma osmolytes and Na+/K+–ATPase activity in gill, rectal gland, kidney and intestine. *Journal of Comparative Physiology B, 175*(1), 37–44.

Pillans, R. D., Stevens, J. D., Kyne, P. M., & Salini, J. (2009). Observations on the distribution, biology, short–term movements and habitat requirements of river sharks *Glyphis* spp. in northern Australia. *Endangered Species Research, 10*, 321–332.

Pinto, R., & Marques, J. C. (2015). Ecosystem Services in Estuarine Systems: Implications for Management. In L. Chicharo, F. Müller, & N. Fohrer (Eds.), *Ecosystem Services and River Basin Ecohydrology* (pp. 319–341). Dordrecht: Springer Netherlands.

Pistevos, J. C. A., Reis–Santos, P., Izzo, C., & Gillanders, B. M. (2019). Element composition of shark vertebrae shows promise as a natural tag. *Marine and Freshwater Research, 70*(12), 1722–1733.

Poe, M. R., Norman, K. C., & Levin, P. S. (2014). Cultural dimensions of socioecological systems: Key connections and guiding principles for conservation in coastal environments. *Conservation Letters, 7*(3), 166–175.

Polovina, J. J., Abecassis, M., Howell, E. A., & Woodworth, P. (2009). Increases in the relative abundance of mid–trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996–2006. *Fishery Bulletin, 107*(4), 523–531.

Potter, I. C., Tweedley, J. R., Elliott, M., & Whitfield, A. K. (2015). The ways in which fish use estuaries: a refinement and expansion of the guild approach. *Fish and Fisheries, 16*(2), 230–239.

Poulakis, G. R., Stevens, P. W., Timmers, A. A., Wiley, T. R., & Simpfendorfer, C. A. (2011). Abiotic affinities and spatiotemporal distribution of the endangered smalltooth sawfish, *Pristis pectinata*, in a south–western Florida nursery. *Marine and Freshwater Research, 62*(10), 1165–1177.

Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the royal society of London. Series B: Biological Sciences, 267*(1456), 1947–1952.

Quinn, J. (2011). Traditional methods of fishing (Southwest Pacific). *The role of food, agriculture, forestry and fisheries in human nutrition, 2*, 140–161.

Ramsden, S., Cotton, C. F., & Curran, M. C. (2017). Using acoustic telemetry to assess patterns in the seasonal residency of the Atlantic stingray *Dasyatis sabina*. *Environmental Biology of Fishes, 100*(2), 89–98.

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., . . . Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews, 94*(3), 849–873.

Reid, G. M., Contreras, M. T., & Csatádi, K. (2013). Global challenges in freshwater-fish conservation related to public aquariums and the aquarium industry. *International Zoo Yearbook, 47*(1), 6–45.

Rigby, C., & Simpfendorfer, C. A. (2015). Patterns in life history traits of deep–water chondrichthyans. *Deep Sea Research Part II: Topical Studies in Oceanography, 115*, 30–40.

Rigby, C. L., Bin Ali, A., Chen, X., Derrick, D. H., Dharmadi, Ebert, D. A., . . . Zhang, J. (2020). *Hemitrygon bennetti*. The IUCN Red List of Threatened Species 2020: e.T161533A104115348. https://dx.doi.org/10.2305/IUCN.UK.2020–3.RLTS.T161533A104115348.en. Downloaded on 08 December 2021.

Rigby, C. L., Derick, D., Dulvy, N. K., Grant, M. I., & Jabado, R. W. (2021). *Glyphis gangeticus.* The IUCN Red List of Threatened Species 2021: e.T169473392A124398647. https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T169473392A124398647.en. Downloaded on 05 November 2021.

Rojas–Bracho, L., Reeves, R. R., & Jaramillo–Legorreta, A. (2006). Conservation of the vaquita *Phocoena sinus*. *Mammal Review, 36*(3), 179–216.

Rosa, R. S., Charvet–Almeida, P., & Quijada, C. C. D. (2010). Biology of the South American potamotrygonid stingrays. In J. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Sharks and their relatives II: biodiversity, adaptive physiology, and conservation* (pp. 241–285). Boca Raton: CRC Press.

Ross, G. F. (1989). Some Crocodile Dundee after effects in northern Australia. *Psychological Reports, 65*(3), 991–994.

RStudio Team. (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.

Sadovy de Mitcheson, Y., To, A. W.–l., Wong, N. W., Kwan, H. Y., & Bud, W. S. (2019). Emerging from the murk: threats, challenges and opportunities for the global swim bladder trade. *Reviews in Fish Biology and Fisheries, 29*(4), 809–835.

Salini, J., McAuley, R., Blaber, S., Buckworth, R., Chidlow, J., Gribble, N., . . . Stevens, J. (2007). Northern Australian sharks and rays: the sustainability of target and bycatch species, phase 2. FRDC report Project No 2002/064, 166.

Salini, J. P., Blaber, S. J. M., & Brewer, D. T. (1990). Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. *Marine Biology, 105*(3), 363–374.

Scharer, R. M., Patterson III, W. F., Carlson, J. K., & Poulakis, G. R. (2012). Age and growth of endangered smalltooth sawfish (*Pristis pectinata*) verified with LA–ICP–MS analysis of vertebrae. *PLoS One, 7*(10), e47850.

Schwartz, F. J. (1995). Elasmobranchs frequenting fresh and low saline waters of North Carolina during 1971–1991. *Journal of Aquariculture and Aquatic Sciences, 7*, 45–51.

Séret, B. (1990). Dasyatidae In C. Lévêque, D. Paugy, & G. G. Teugels (Eds.), *Faune des poissons d'eaux douces et saumâtres de l'Afrique de l'Ouest– The fresh and brackish water fishes of West Africa: Tome 1. Coll. Faune Tropicale n28* (pp. 62–75). Paris, France: ORSTOM.

Sills, J., Harrison, I., Abell, R., Darwall, W., Thieme, M. L., Tickner, D., & Timboe, I. (2018). The freshwater biodiversity crisis. *Science, 362*(6421), 1369–1369.

Simpfendorfer, C. (2004). Demographic models: Life tables, matrix models and rebound potential. In J. A. Musick & R. Bonfil (Eds.), *Elasmobranch Fisheries Management Techniques* (pp. 187 – 204). Singapore: APEC Secretariat.

Simpfendorfer, C. A. (1999). Demographic analysis of the dusky shark fishery in southwestern Australia. In J. Musick (Ed.), *Life in the Slow Lane: Ecology and Conservation of Long–Lived Marine Animals* (pp. 149–160). Bethesda, MD: American Fisheries Society Symposium.

Simpfendorfer, C. A. (2000). Predicting population recovery rates for endangered western Atlantic sawfishes using demographic analysis. *Environmental Biology of Fishes, 58*(4), 371–377.

Simpfendorfer, C. A., & Dulvy, N. K. (2017). Bright spots of sustainable shark fishing. *Current Biology, 27*(3), R97–R98.

Simpfendorfer, C. A., Freitas, G. G., Wiley, T. R., & Heupel, M. R. (2005). Distribution and habitat partitioning of immature bull sharks (*Carcharhinus leucas*) in a southwest Florida Estuary. *Estuaries, 28*(1), 78–85.

Simpfendorfer, C. A., Heupel, M. R., & Kendal, D. (2021). Complex human–shark conflicts confound conservation action. *Frontiers in Conservation Science, 2*(35).

Simpfendorfer, C. A., Heupel, M. R., White, W. T., & Dulvy, N. K. (2011a). The importance of research and public opinion to conservation management of sharks and rays: a synthesis. *Marine and Freshwater Research, 62*(6), 518–527.

Simpfendorfer, C. A., & Kyne, P. M. (2009). Limited potential to recover from overfishing raises concerns for deep–sea sharks, rays and chimaeras. *Environmental Conservation, 36*(02), 97–103.

Simpfendorfer, C. A., McAuley, R. B., Chidlow, J., & Unsworth, P. (2002). Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. *Marine and Freshwater Research, 53*(2), 567–573.

Simpfendorfer, C. A., & Milward, N. E. (1993). Utilisation of a tropical bay as a nursery area by sharks of the families Carcharhinidae and Sphyrnidae. *Environmental Biology of Fishes, 37*(4), 337–345.

Simpfendorfer, C. A., Yeiser, B. G., Wiley, T. R., Poulakis, G. R., Stevens, P. W., & Heupel, M. R. (2011b). Environmental influences on the spatial ecology of juvenile smalltooth sawfish (*Pristis pectinata*): results from acoustic monitoring. *PLoS One, 6*(2), e16918.

Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C., & Kjesbu, O. S. (2016). Ecosystem processes are rarely included in tactical fisheries management. *Fish and Fisheries, 17*(1), 165–175.

Smart, J. J., Chin, A., Baje, L., Green, M. E., Appleyard, S. A., Tobin, A. J., . . . White, W. T. (2016a). Effects of including misidentified sharks in life history analyses: A case study on the grey reef shark *Carcharhinus amblyrhynchos* from Papua New Guinea. *PLoS One, 11*(4), e0153116.

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

Smart, J. J., Chin, A., Tobin, A. J., White, W. T., Kumasi, B., & Simpfendorfer, C. A. (2017). Stochastic demographic analyses of the silvertip shark (*Carcharhinus albimarginatus*) and the common blacktip shark (*Carcharhinus limbatus*) from the Indo–Pacific. *Fisheries Research, 191*, 95–107.

Smart, J. J., & Grammer, G. L. (2021). Modernising fish and shark growth curves with Bayesian length–at–age models. *PLoS One, 16*(2), e0246734.

Smart, J. J., White, W. T., Baje, L., Chin, A., D'Alberto, B. M., Grant, M. I., . . . Simpfendorfer, C. A. (2020). Can multi–species shark longline fisheries be managed sustainably using size limits? Theoretically, yes. Realistically, No. *Journal of Applied Ecology. 10.1111/1365–2664.13659, 57*(9), 1847–1860.

Smith, V. H. (2003). Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environmental Science and Pollution Research, 10*(2), 126–139.

Soe, K., Baran, E., Grantham, R., Tezzo, X., & Johnstone, G. (2020). Myanmar inland fisheries and aquaculture: a decade in review, monograph no. 209, Australian Centre for International Agricultural Research, Canberra, & WorldFish, Yangon, 93 pp.

Spencer, R.–J., Van Dyke, J. U., & Thompson, M. B. (2016). The ethological trap: functional and numerical responses of highly efficient invasive predators driving prey extinctions. *Ecological Applications, 26*(7), 1969–1983.

Staal, A., Flores, B. M., Aguiar, A. P. D., Bosmans, J. H. C., Fetzer, I., & Tuinenburg, O. A. (2020). Feedback between drought and deforestation in the Amazon. *Environmental Research Letters, 15*(4), 044024.

Staunton–Smith, J., Robins, J. B., Mayer, D. G., Sellin, M. J., & Halliday, I. A. (2004). Does the quantity and timing of fresh water flowing into a dry tropical estuary affect year–class strength of barramundi (*Lates calcarifer*)? *Marine and Freshwater Research, 55*(8), 787–797.

Stevens, J., Bonfil, R., Dulvy, N. K., & Walker, P. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *Ices Journal of Marine Science, 57*(3), 476–494.

Stevens, J., McAuley, R., Simpfendorfer, C., & Pillans, R. (2008). Spatial distribution and habitat utilisation of sawfish (*Pristis* spp) in relation to fishing in northern Australia. *A report to Department of the Environment, Water, Heritage and the Arts, 31*.

Stevens, J., & McLoughlin, K. (1991). Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. *Marine and Freshwater Research, 42*(2), 151–199.

Storey, A. W., Yarrao, M., Tenakanai, C., Figa, B., & Lynas, J. (2009). Use of changes in fish assemblages in the Fly River system, Papua New Guinea, to assess effects of the Ok Tedi copper mine. *Developments in Earth and Environmental Sciences, 9*, 427–462.

Su, G., Logez, M., Xu, J., Tao, S., Villéger, S., & Brosse, S. (2021). Human impacts on global freshwater fish biodiversity. *Science, 371*(6531), 835–838.

Swann, A. L. S., Longo, M., Knox, R. G., Lee, E., & Moorcroft, P. R. (2015). Future deforestation in the Amazon and consequences for South American climate. *Agricultural and Forest Meteorology, 214–215*, 12–24.

Tam, W. L., Wong, W. P., Loong, A. M., Hiong, K. C., Chew, S. F., Ballantyne, J. S., & Ip, Y. K. (2003). The osmotic response of the Asian freshwater stingray (*Himantura signifer*) to increased salinity: a comparison with marine (*Taeniura lymma*) and Amazonian freshwater (*Potamotrygon motoro*) stingrays. *Journal of Experimental Biology, 206*(17), 2931–2940.

Tanaka, S. (1991). Age estimation of freshwater sawfish and sharks in northern Australia and Papau New Guinea. *University Museum, University of Tokyo Nature and Culture, 3*, 71–82.

Taniuchi, T. (2002). Outline of field surveys for freshwater elasmobranchs conducted by a Japanese research team. In S. Fowler, T. Reed, & F. Dipper (Eds.), *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July, 1997* (pp. 181–184). Oxford, UK: Information Press.

Taylor, B. M., Wakefield, C. B., Newman, S. J., Chinkin, M., & Meekan, M. G. (2021). Unprecedented longevity of unharvested shallow–water snappers in the Indian Ocean. *Coral Reefs, 40*(1), 15–19.

Thorburn, D., Gill, H., & Morgan, D. (2014). Predator and prey interactions of fishes of a tropical Western Australia river revealed by dietary and stable isotope analyses. *Journal of the Royal Society of Western Australia, 97*, 363–387.

Thorburn, D., Peverell, S., Stevens, J., Last, P., & Rowland, A. (2003). Status of freshwater and estuarine elasmobranchs in northern Australia. *Final Report to Natural Heritage Trust*.

Thorburn, D. C., & Morgan, D. L. (2004). The northern river shark *Glyphis* sp. C (Carcharhinidae) discovered in Western Australia. *Zootaxa, 685*, 1–8.

Thorburn, D. C., Morgan, D. L., Rowland, A. J., & Gill, H. S. (2007). Freshwater sawfish *Pristis microdon* Latham, 1794 (Chondrichthyes: Pristidae) in the Kimberley region of western Australia. *Zootaxa, 1471*(2), 27–41.

Thorburn, D. C., Morgan, D. L., Rowland, A. J., Gill, H. S., & Paling, E. (2008). Life history notes of the critically endangered dwarf sawfish, *Pristis clavata*, Garman 1906 from the Kimberley region of Western Australia. *Environmental Biology of Fishes, 83*(2), 139–145.

Thorburn, D. C., & Rowland, A. J. (2008). Juvenile bull sharks' *Carcharhinus leucas* (Valenciennes, 1839) in northern Australian rivers. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory, 24*, 79–86.

Thorson, T., Brooks, D., & Mayes, M. (1983). The evolution of freshwater adaptation in stingrays. *National Geographic Society Research Reports, 15*, 663–694.

Thorson, T. B. (1971). Movement of bull sharks, *Carcharhinus leucas*, between Caribbean Sea and Lake Nicaragua demonstrated by tagging. *Copeia, 1971*(2), 336–338.

Thorson, T. B. (1976). Observations on the reproduction of the sawfish, *Pristis perotteti*, in lake Nicaragua, with recommendations for its conservation. *Investigations of the Ichthyofauna of Nicaraguan lakes, 53*, 641 – 650.

Thorson, T. B. (1982). Life history implications of a tagging study of the largetooth sawfish, *Pristis perotteti*, in the Lake Nicaragua–Río San Juan system. *Environmental Biology of Fishes, 7*(3), 207–228.

Thorson, T. B. (1983). Observations on the morphology, ecology, and life history of the euryhaline stingray, *Dasyatis guttata* (Bloch and Schneider) 1801. *Acta Biologica Venezuelica, 11*(4), 92–125.

Thorson, T. B. (1987). Human impacts on shark populations. *Sharks: an inquiry into biology, behavior, fisheries and use*, 31–37.

Thorson, T. B., Cowan, C. M., & Watson, D. E. (1966). Sharks and sawfish in the Lake Izabal–Rio Dulce System, Guatemala. *Copeia, 1966*(3), 620–622.

Thorson, T. B., Cowan, C. M., & Watson, D. E. (1973). Body fluid solutes of juveniles and adults of the euryhaline bull shark *Carcharhinus leucas* from freshwater and saline environments. *Physiological Zoology, 46*(1), 29–42.

Thorson, T. B., Wotton, R. M., & Georgi, T. A. (1978). Rectal gland of freshwater stingrays, *Potamotrygon* spp.(Chondrichthyes: Potamotrygonidae). *The Biological Bulletin, 154*(3), 508–516.

Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., . . . Young, L. (2020). Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *BioScience, 70*(4), 330–342.

Tillett, B. J., Meekan, M. G., Parry, D., Munksgaard, N., Field, I. C., Thorburn, D., & Bradshaw, C. J. (2011). Decoding fingerprints: elemental composition of vertebrae correlates to age–related habitat use in two morphologically similar sharks. *Marine Ecology Progress Series, 434*, 133–142.

Treloar, M. A., Barrett, N. S., & Edgar, G. J. (2017). Biology and ecology of *Zearaja maugeana*, an Endangered skate restricted to two south–western Tasmanian estuaries. *Marine and Freshwater Research, 68*(5), 821–830.

Tuholske, C., Halpern, B. S., Blasco, G., Villasenor, J. C., Frazier, M., & Caylor, K. (2021). Mapping global inputs and impacts from of human sewage in coastal ecosystems. *PLoS One, 16*(11), e0258898.

Valerio–Vargas, J. A., & Espinoza, M. (2019). A beacon of hope: distribution and current status of the largetooth sawfish in Costa Rica. *Endangered Species Research, 40*, 231–242.

Vieira, S., Kinch, J., White, W., & Yaman, L. (2017). Artisanal shark fishing in the Louisiade Archipelago, Papua New Guinea: Socio–economic characteristics and management options. *Ocean & Coastal Management, 137*, 43–56.

Vilizzi, L., Copp, G. H., Adamovich, B., Almeida, D., Chan, J., Davison, P. I., . . . Zeng, Y. (2019). A global review and meta–analysis of applications of the freshwater Fish Invasiveness Screening Kit. *Reviews in Fish Biology and Fisheries, 29*(3), 529–568.

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., . . . Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature, 467*(7315), 555–561.

Walsh, J. C., Dicks, L. V., & Sutherland, W. J. (2015). The effect of scientific evidence on conservation practitioners' management decisions. *Conservation Biology, 29*(1), 88–98.

Walther, B. D., & Thorrold, S. R. (2006). Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. *Marine Ecology Progress Series, 311*, 125–130.

West, K., Travers, M. J., Stat, M., Harvey, E. S., Richards, Z. T., DiBattista, J. D., . . . Bunce, M. (2021). Large–scale eDNA metabarcoding survey reveals marine biogeographic break and transitions over tropical north–western Australia. *Diversity and Distributions, 27*(10), 1942–1957.

Whatmough, S., Van Putten, I., & Chin, A. (2011). From hunters to nature observers: a record of 53 years of diver attitudes towards sharks and rays and marine protected areas. *Marine and Freshwater Research, 62*(6), 755–763.

White, W., Baje, L., Simpfendorfer, C., Appleyard, S., Chin, A., Sabub, B., . . . Naylor, G. (2019). Elasmobranch bycatch in the demersal prawn trawl fishery in the Gulf of Papua, Papua New Guinea. *Scientific Reports, 9*(1), 1–16.

White, W. T., Appleyard, S. A., Kyne, P. M., & Mana, R. R. (2017a). Sawfishes in Papua New Guinea: a preliminary investigation into their status and level of exploitation. *Endangered Species Research, 32*, 277–291.

White, W. T., Appleyard, S. A., Sabub, B., Kyne, P. M., Harris, M., Lis, R., . . . Naylor, G. J. (2015). Rediscovery of the threatened river sharks, *Glyphis garricki* and *G. glyphis*, in Papua New Guinea. *PLoS One, 10*(10), e0140075.

White, W. T., Baje, L., Appleyard, S. A., Chin, A., Smart, J. J., & Simpfendorfer, C. A. (2020). Shark longline fishery of Papua New Guinea: size and species composition and spatial variation of the catches. *Marine and Freshwater Research, 71*(6), 627–640.

White, W. T., Baje, L., Sabub, B., Appleyard, S. A., Pogonoski, J. J., & Mana, R. R. (2017b). *Sharks and rays of Papua New Guinea*. Canberra: ACIAR Monograph No. 189. Australian Centre for International Agricultural Research.

White, W. T., & Ko'ou, A. (2018). An annotated checklist of the chondrichthyans of Papua New Guinea. *Zootaxa, 4411*(1), 1–82.

White, W. T., & Kyne, P. M. (2010). The status of chondrichthyan conservation in the Indo–Australasian region. *The Journal of Fish Biology, 76*(9), 2090–2117.

White, W. T., Platell, M. E., & Potter, I. C. (2001). Relationship between reproductive biology and age composition and growth in *Urolophus lobatus* (Batoidea: Urolophidae). *Marine Biology, 138*(1), 135–147.

Whitty, J. M., Keleher, J., Ebner, B. C., Gleiss, A. C., Simpfendorfer, C. A., & Morgan, D. L. (2017). Habitat use of a Critically Endangered elasmobranch, the largetooth sawfish *Pristis pristis*, in an intermittently flowing riverine nursery. *Endangered Species Research, 34*, 211–227.

Whitty, J. M., Morgan, D. L., Peverell, S. C., Thorburn, D. C., & Beatty, S. J. (2009). Ontogenetic depth partitioning by juvenile freshwater sawfish (*Pristis microdon*: Pristidae) in a riverine environment. *Marine and Freshwater Research, 60*(4), 306–316.

Whitty, J. M., Morgan, D. L., Thorburn, D. C., Fazeldean, T., & Peverell, S. C. (2008). Tracking the movements of freshwater sawfish (*Pristis microdon*) and northern river sharks (*Glyphis sp. C*) in the Fitzroy River. In J. M. Whitty, N. M. Phillips, D. L. Morgan, J. A. Chaplin, D. C. Thorburn, & S. C. Peverell (Eds.), *Habitat associations of Freshwater Sawfish (Pristis* *microdon) and Northern River Shark (Glyphis sp. C): including genetic analysis of P. microdon across northern Australia.* (pp. 8–46). Centre for Fish & Fisheries Research (Murdoch University) report to the Department of the Environment, Water, Heritage and the Arts, Australian Government.

Whitty, J. M., Phillips, N. M., Thorburn, D. C., Simpfendorfer, C. A., Field, I., Peverell, S. C., & Morgan, D. L. (2014). Utility of rostra in the identification of Australian sawfishes (Chondrichthyes: Pristidae). *Aquatic Conservation: Marine and Freshwater Ecosystems, 24*(6), 791–804.

Wiley, T. R., & Simpfendorfer, C. A. (2007). The ecology of elasmobranchs occurring in the Everglades National Park, Florida: implications for conservation and management. *Bulletin of Marine Science, 80*(1), 171–189.

Wiley, T. R., & Simpfendorfer, C. A. (2010). Using public encounter data to direct recovery efforts for the endangered smalltooth sawfish *Pristis pectinata*. *Endangered Species Research, 12*(3), 179–191.

Wilson, K. A., McBride, M. F., Bode, M., & Possingham, H. P. (2006). Prioritizing global conservation efforts. *Nature, 440*(7082), 337–340.

Windusari, Y., Iqbal, M., Hanum, L., Zulkifli, H., & Yustian, I. (2019). Contemporary distribution records of the giant freshwater stingray *Urogymnus polylepis* in Borneo (Chondrichthyes: Dasyatidae). *Ichthyological Exploration of Freshwaters, 2019*, 1–6.

Wong, S. Z. H., Ching, B., Chng, Y. R., Wong, W. P., Chew, S. F., & Ip, Y. K. (2013). Ascorbic acid biosynthesis and brackish water acclimation in the euryhaline freshwater white–rimmed stingray, *Himantura signifer*. *PLoS One, 8*(6), e66691.

Wueringer, B. E. (2017). Sawfish captures in the Queensland Shark Control Program, 1962 to 2016. *Endangered Species Research, 34*, 293–300.

WWF. (2018). Living Planet Report: Aiming Higher. Grooten, M. and Almond, R.E.A. (Eds). WWF, Gland, Switzerland.

Xiong, W., Sui, X., Liang, S.–H., & Chen, Y. (2015). Non–native freshwater fish species in China. *Reviews in Fish Biology and Fisheries, 25*(4), 651–687.

Yan, H. F., Kyne, P. M., Jabado, R. W., Leeney, R. H., Davidson, L. N. K., Derrick, D. H., . . . Dulvy, N. K. (2021). Overfishing and habitat loss drive range contraction of iconic marine fishes to near extinction. *Science Advances, 7*(7), eabb6026.

Yates, P. M., Heupel, M. R., Tobin, A. J., & Simpfendorfer, C. A. (2012). Diversity in young shark habitats provides the potential for portfolio effects. *Marine Ecology Progress Series, 458*, 269–281.

Yeiser, B. G., Heupel, M. R., & Simpfendorfer, C. A. (2008). Occurrence, home range and movement patterns of juvenile bull (*Carcharhinus leucas*) and lemon (*Negaprion brevirostris*) sharks within a Florida estuary. *Marine and Freshwater Research, 59*(6), 489–501.

Yokota, L., & Lessa, R. P. (2007). Reproductive biology of three ray species: *Gymnura micrura* (Bloch & Schneider, 1801), *Dasyatis guttata* (Bloch & Schneider, 1801) and *Dasyatis marianae* Gomes, Rosa & Gadig, 2000, caught by artisanal fisheries in Northeastern Brazil. *Cahiers de Biologie Marine, 48*(3), 249.

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences, 77*(1), 161–170.

Zhang, J., Yamaguchi, A., Zhou, Q., & Zhang, C. (2010). Rare occurrences of *Dasyatis bennettii* (Chondrichthyes: Dasyatidae) in freshwaters of Southern China. *Journal of Applied Ichthyology, 26*(6), 939–941.

Appendix 1

(Corresponding to Chapter 3)

Sawfish questionnaire

Age of interviewee:
Province and river/coast of village:
Name of village (optional):

Part I – Sawfish biology

1. Have you ever seen this animal before? (show picture of sawfish)

Yes/No

(If no, terminate interview)

2. What do you call this animal?

3. Are sawfish ever caught in your village?

Yes/No

(If no, go to Part II)

4. Are different types of sawfish caught?

Yes/No

If yes, how are they separated?

5. Where do you mostly catch sawfish? (can pick more than one)

Off the coast/ close in shore / in the river (salt) / in the river (fresh)

6. Is there a particular habitat you catch them in?
(note these key words - Sandy/Rocky/Muddy/Plant debris & mangrove/Reef/Seagrass)

7. Have you noticed if you catch sawfish more often in dirty or clear water?

8. Are there particular times of year where you catch sawfish? i.e. Dry season or wet season? Any particular months?

Part II – Fisheries

9. What is the main target species you fish for?

10. What types of fishing gear do you use? (list)

… (if applicable) what mesh/hook size?

11. How many gill nets (or hooks) are set each day/night?

12. How regularly are sawfish caught? (choose one)

Weekly/monthly/every couple of months/a couple per year/less than one per year

13. Do you retain sawfish?

Never/sometimes/usually/always

14. Do you retain or not retain certain sizes?

15. (on the type of fishing gear they use) Roughly, what sizes of sawfish are usually caught?

<1m | 1-2m | 2-3 m | 3-4 m | > 4m

16. Are different sizes caught in different areas (i.e. reef, inshore, mangroves, freshwater)?

17. If you catch a sawfish in a gillnet, how do you untangle the animal? Are there differences per size?

18. Have you noticed any decreases in sawfish catch over time?

19. Have you noticed any decreases in the size of sawfish caught over time?

20. (if they reported that sawfish > 4m are caught) when was the last time a sawfish greater than 4m was caught?

Less than a; week/month/few months/6 months/ year/5 years/>10 years

21. (if decrease in number or size are reported) why do you think these (size and/or number) decreases have occurred?

22. Have you also observed decreases in size/number of other sharks too?

<u>Part III – Social and economics</u>

23. Which of the following describe the use of sawfish?

Consumption/sale of meat/sale of fins/sale of rostra/liver oil/other

Other:

24. Are the saw or teeth ever used to make tools/weapons or ornaments? Historically, have they been?

25. (If any part of the animal is sold) what is the value?

26. Do you sell the (animal part) to a buyer or directly in a market? (ask for each sale product)

27. Is the sale of shark/ray products an important part of the villages economy?

Yes/No

28. Is the capture of shark/rays an important part of the villages food security?

Yes/No

29. Would you support any conservation measures and/or species protection for sawfishes if they were proposed for Papua New Guinea? Why or why not?

***This question was only included for communities in the Aramia, Bamu, Turama, and Kikori Rivers**.

Part IV – cultural beliefs

30. Do you have any cultural beliefs involving sawfish?

(i.e. do they indicate season/ have religious connotations or spiritual significance?)

Appendix 2

(Corresponding to Chapter 4)

Additional Methods

Table A2. 1 Survey locations displayed in Figure 1.

Map B	Sepik River	1. Kopar Village, 2. Angoram, 3. Timbunke Village, 4. Aibom Village, 5. Idingai Village, 6. Korogu Village
	Ramu River	7. Marangis
Map C	Mia Kussa River	8. Buzi Village, 9. Sibidiri Village
	South Fly Coast	10. Old Mawatta Village, 11. Tureture Village, 12. Warrior Reef, 13. Daru Market, 14. Daru Passage, 15. Bristow Island, 16. Oriomo River Mouth, 17. Kadawa Village, 18. Upiari Village, 19. Katatia Village, 20. Gaziro fishing camp (Katatai Village)
	Fly River	21. Sui Village, 22. Nemadabu fishing camp (Wariobodoro Village)
	Aramia River	23. Garu Village, 24. Saiwase Village, 25. Madila Village, 26. Kewa Village, 27. Kawito Village, 28. Tebini Village, 29. Makapa Village, 30. Ali (Bogola Village)
	Bamu River	31. Bina Village, 32. Oropai Village, 33. Sisiaimi Village, 34. Sogere Village, 35. Sasairi Village
	Turama River	36. Meagio Village, 37. Masusu Village, 38. Saragi Village, 39. Moka 2 Village, 40. Moka 1 Village, 41. Kuri logging station
	Kikori River	42. Begere fishing camp (Kemei Village), 43. Kemei Village, 44. Pioi fishing camp (Mubagowo Village), 45. Aiedio Village, 46. Goare Village, 47. Bomobari fishing camp (Goare Village), 48. Omarti Creek (Goare Village), 49. Evamu Village, 50. Babi Village, 51. Kotoioia fishing camp (Apeawa Village), 52. Iribibari (Babeio Village), 53. Veraibari Village, 54. Babeio Village, 55. Kikori market, 56. Omo Village (Sirebi tributary)
	Kerema Coast	57. Marieke Village, 58. Vailala 1 Village (Vailala River Mouth), 59. Vailala 2 Village (Vailala River Mouth), 60. Kerema Town, 61. Siroui fishing camp (Kerema Village), 62. Karama Village, 63. Pukari Village

Species identification

Due to inaccuracies that can arise in species identification (ID) from photographs (Smart et al. 2016a; Tillett et al. 2012; White et al. 2020), species ID's were assigned to all photographs by two assessors independently (MIG and WTW). Species ID's agreed for 395/458 (86.2%) specimens. Where ID's differed (63 specimens), a consensus ID was conducted with both assessors. If an agreement to species level could not be made, specimens were identified to lowest taxonomic level possible (genera or family). River sharks were generally difficult to ID due to poor quality photographs taken by some enumerators (poor lateral resolution) and discrete differentiating morphological features. For this reason, a third assessor (PMK) assisted with consensus ID's. In total, only three river sharks could not be identified to species level from consensus ID's from whole specimens. Species ID from 99 specimens from the Sepik River were also identified from photographs (WW) although these specimens contributed to a report prepared for the Australian Centre for International Agricultural Research (FIS-2012-102) and these ID's are not included in the above numbers.

In some instances, specimens observed were already finned and portioned for sale, or enumerators recorded a species or common name though did not take a photograph. These species were recorded at genus or family level where available data were not sufficient to make a higher-level ID. Due to the high degree in morphological similarity between the common blacktip shark *Carcharhinus limbatus* and Australian blacktip shark *Carcharhinus tilstoni*, these species were identified as *C. limbatus/tilstoni* in instances where tissue was not available for genetic ID.

Genetic ID's based on COI barcodes

As per Appleyard et al. (2018) where required for genetic ID, genomic DNA was extracted from muscle or fin tissue using a Promega Wizard® Genomic DNA Purification kit (Promega Corporation, USA) at the CSIRO Marine Laboratories in Hobart, Tasmania, Australia. DNA was precipitated in water, diluted to 10 ng/μl and stored at 4°C for working applications. Archival DNA is stored at -80°C at the Marine Laboratories.

Barcoding of the mitochondrial DNA cytochrome oxidase subunit 1 (COI) gene using the Fish-BCL-5′TCAACYAATCAYAAAGATATYGGCAC-3′ and Fish-BCH-5′ACTTCYGGGTGRCCRAARAATCA-3′ primers (Baldwin et al. 2009) and the Big Dye Terminator v3.1 cycle sequencing ready reaction kit (Thermofisher, USA) with cycle sequenced products run on an ABI 3130XL DNA Autosequencer (Applied Biosystems™, USA) at the Marine Laboratories (as per protocols outlined in Appleyard et al. 2018). Forward and reverse sequences were trimmed; *denovo* assembled; sequences were checked by eye; and then converted into consensus sequences (using Geneious R8.1.4; Biomatters Ltd, New Zealand). Consensus sequences were compared using the BarCode of Life Database (http://www.boldsystems.org/) BOLD IDS tool, where species identification was based on a percentage of sequence identity with homology of ≥98%.

For specimens suspected to be *Glyphis* spp., a 463 bp region in the cytochrome B (cytB) gene was selected for optimal inter- and intra-specific variation. Newly designed primers were used to amplify this region: Ggar14277_For-5’ATTCCTACCTGGACTTTAACCAAGAC-3’ and Car14731_ rev-5’CCGACGAAGGCTGTTGCTAT-3’. PCR and dual-direction Sanger sequencing were performed at the Australian Genome Research Facility in Brisbane, Queensland using the Big Dye Terminator kit and the products run on an ABI 3730XL DNA Analyzer. Resulting paired-end sequences were analysed in Geneious R11.1.5. Primer sequences were removed, and low-quality bases were removed at a 0.05 error probability from both 5’ and 3’ ends. Forwards and reversed reads were paired and merged. The resulting sequences were blasted (Megablast) against the GenBank nr/nt database. All sequences had an identity ≥99% to species level.

In total, 256 specimens (94 ‘other species’ and 142 *Glyphis* spp.) were identified from these respective genetic approaches.

Sawfish rostra

Length measurements for sawfish rostra were used to estimate total length (TL) using available relationships from the literature (Table A2). Total length was estimated for all species using standard rostrum length (SRL)–TL relationships presented in Whitty et al. (2014). Due to possible bias in SRL–TL relationships in Whitty et al. (2014) source data (e.g. largely based on immature specimens), measurements of total rostrum length (TRL) were additionally converted to TL using the TRL–TL relationship available in Morgan et al. (2011) for largetooth sawfish *Pristis pristis*, Thorburn et al. (2008) for dwarf sawfish *P. clavata*, and Morgan et al. (2011) for green sawfish *P. zijsron*. No TRL–TL relationship is currently available for narrow sawfish *Anoxypristis cuspidata*, so TL was estimated using the proportion ratio given by Whitty et al. (2014), which was equal to the ratio also calculated from measurements made in this study (Table A3).

Where only one of either SRL or TRL was measured, SRL/TRL ratios in Whitty et al. (2014) were used to estimate the other. This was to allow estimations of TL from both SRL and TRL relationships. Final estimations of TL from rostra were the average of these SRL and TRL relationships. In a few instances, only body length could be measured for *A. cuspidata* as their rostrums had been cut and discarded at sea prior to observation. In order to estimate TL, the body length/TRL ratio available in Whitty et al. (2014) was used.

Table A2. 2 Published relationships for rostra and total length (TL) used to estimate TL from total rostrum length (TRL) and standard rostrum length (SRL) for sawfish species.

Species	Relationship	r^2	Source
Anoxypristis cuspidata	Figure 3 p 796	0.81	Whitty et al. (2014)
	TRL = 0.26TL	N/A	Whitty et al. (2014); This study
Pristis clavata	$SRL = 0.5033TL^{0.8643}$	0.98	Whitty et al. (2014)
	$TRL = 0.6142TL^{0.8475}$	Not presented	Thorburn et al. (2008)
Pristis pristis	$SRL = 0.5592TL^{0.8749}$	0.99	Whitty et al. (2014)
	TRL = 3.7768+(0.209TL)	0.98	Morgan et al. (2011)
Pristis zijsron	$SRL = 0.0733TL^{1.1683}$	0.96	Whitty et al. (2014)
	TRL = 0.2825TL-3.7389	Not presented	Morgan et al. (2011); Faria (2007)

Table A2. 3 Rostral morphometric data collected from sawfish species in Papua New Guinea. Difference between left and right rostral tooth counts is presented as absolute values. SE, standard error; SRL, standard rostrum length; TRL, total rostrum length.

		Rostral Teeth				**Rostral proportions**		
Species	**Statistic**	**Left**	**Right**	**Total**	**Left–Right difference**	**SRL/TRL**	**SRL/TL**	**TRL/TL**
Anoxypristis cuspidata	*n*	48	48	48	48	7	3	13
	Range	19–27	18–26	37–51	0–3	0.72–0.78	0.21–0.27	0.20–0.36
	Mean ±SE	21.9 ±0.26	22.0 ±0.25	43.9 ±0.48	1.1 ±0.12	0.75 ±0.01	0.23 ±0.02	0.26 ±0.01
Pristis clavata	*n*	6	6	6	6	2	2	2
	Range	21–25	21–25	42–48	0–3	0.95–0.96	0.18	0.19
	Mean ±SE	22.3 ±0.56	23.0 ±0.58	45.3 ±0.88	1.3 ±0.49	0.95 ±0.00	0.18 ±0.00	0.19 ±0.00
Pristis pristis	*n*	55	55	55	55	27	1	1
	Range	16–23	16–23	32–45	0–2	0.90–0.96	0.23	0.25
	Mean ±SE	19.7 ±0.21	19.9±0.25	39.6 ±0.45	0.5 ±0.09	0.94 ±0.00		
Pristis zijsron	*n*	1	1	1	1			
	Range	27	26	53	1			

Dried fin

Data used in total length (TL) estimation from dried fin is shown in Table A4. Proportionate ratios for use in TL estimation were produced for *Glyphis garricki* (Table A5) and *Glyphis glyphis* (Table A6) from measurements taken during this study.

Table A2. **4** First dorsal height (D1H) and dorsal caudal margin (DCM) to total length (TL) conversion ratios used to estimate TL from dried fin encountered during surveys.

Species	**1st dorsal fin dimension – total length (TL) relationship**	**Source**
Carcharhinus amboinensis	TL = D1H/0.109	Garrick (1982); W. White (unpubl. data)
Carcharhinus coatesi	TL = D1H/0.098	W. White (unpubl. data)
Carcharhinus fitzroyensis	TL = D1H/0.089	Garrick (1982); W. White (unpubl. data)
Carcharhinus leucas	TL = D1H/0.102	Garrick (1982)
Carcharhinus limbatus	TL = D1H/0.125	Garrick (1982)
Carcharhinus sorrah	TL = (D1H/0.106)+1.523	Garrick (1982); W. White (unpubl. data)
Eusphyra blochii	TL = D1H/0.150	W. White (unpubl. data)
Sphryna mokarran	TL = D1H/0.166	Gilbert (1967)
Rhynchobatus palpebratus	TL = (D1H/0.109)+0.516	Based on *Rhynchobatus australiae*, W. White (unpubl. data)
Anoxypristis cuspidata	TL = D1H/0.08	White et al. (2017)
Pristis clavata	TL = D1H/0.06 TL = DCM/0.14	White et al. (2017)
Pristis pristis	TL = D1H/0.07	White et al. (2017)
Glyphis garricki	TL = D1H/9.38	Compagno et al. (2008); This study
Glyphis glyphis	TL = D1H/8.41	Compagno et al. (2008); This study

Table A2. 5 First dorsal fin dimensions to total length (TL; in mm) ratios for *Glyphis garricki*. Ratios provided for first dorsal length (D1L), height (D1H), anterior length (D1A), and second dorsal height (D2H).

Country & sample size	Statistic	D1L/TL	D1H/TL	D1A/TL	D2H/TL	D2H/D1H
Australia*	**Mean**	**17.40**	**10.17**	**14.27**	**6.30**	**62.00**
n = 8	Standard Error	0.25	0.22	0.18	0.15	1.30
TL range 670–1418	Minimum	16.70	9.40	13.90	5.80	57.55
	Maximum	18.70	10.80	15.20	6.90	67.01
Papua New Guinea	**Mean**	**15.98**	**8.83**	**12.54**	**5.20**	**59.34**
n = 10 **	Standard Error	0.29	0.36	0.31	0.16	1.72
TL range 655–1050	Minimum	14.57	7.20	11.53	4.32	48.25
	Maximum	17.39	10.86	13.98	6.23	68.33
Combined	**Mean**	**16.57**	**9.38**	**13.25**	**5.65**	**60.43**
n = 18	Standard Error	0.26	0.28	0.29	0.18	1.16
TL range 655–1418	Minimum	14.57	7.20	11.53	4.32	48.25
	Maximum	18.70	10.86	15.20	6.90	68.33

*Data sourced from Compagno et al. (2008)

** Additionally, a male *G. garricki* individual of 1050 mm TL had a pectoral fin length/TL ratio of 0.176, pectoral fin anterior length/TL ratio of 0.211, and a dorsal caudal margin/TL ratio of 0.252

Table A2. 6 First dorsal fin dimensions to total length (TL; in mm) ratios for *Glyphis glyphis*. Ratios provided for first dorsal length (D1L), height (D1H), anterior length (D1A), and second dorsal height (D2H).

Country & sample size	Statistic	D1L/TL	D1H/TL	D1A/TL	D2H/TL	D2H/D1H
Australia*	**Mean**	**18.09**	**8.88**	**13.82**	**6.28**	**71.14**
n = 9	Standard Error	0.34	0.33	0.30	0.17	2.09
TL range 590–1447	Minimum	16.20	6.80	12.30	5.50	66.27
	Maximum	19.60	10.30	15.00	7.00	85.29
Papua New Guinea	**Mean**	**16.40**	**8.00**	**11.76**	**5.18**	**64.80**
n = 10**	Standard Error	0.32	0.22	0.20	0.14	1.40
TL range 593–715	Minimum	14.37	7.18	10.94	4.65	60.34
	Maximum	17.48	9.58	12.68	5.92	72.73
Combined	**Mean**	**17.20**	**8.41**	**12.74**	**5.73**	**67.97**
n = 19	Standard Error	0.30	0.21	0.30	0.17	1.44
TL range 590–1447	Minimum	14.37	6.80	10.94	4.65	60.34
	Maximum	19.60	10.30	15.00	7.00	85.29

*Data sourced from Compagno et al. (2008)

**Additionally, two male *G. glyphis* individuals of 710 and 700 mm TL had a pectoral fin length/TL ratio of 0.131 (SE ±0.005) and a pectoral fin anterior length/TL ratio of 0.160 (SE ±0.002).

Additional Results and Discussion

Table A2. 7 Abundance (*n*), proportion of total abundance (%), size range (DW, disc width; TL, total length), sex ratio (F, female; M, male; ?, unknown), size-at-maturity from White et al. (2017b), *n* mature for each sex, gear type used in capture, location of capture (Figure 1 map reference) and IUCN Red List of Threatened Species category (IUCN 2021) for all specimens observed in small-scale fisheries on the north coast of Papua New Guinea. CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient. Aetobatidae size is in disc width (DW), all others are in total length (TL).

Species	*n* (% of catch)	Size range (cm DW/TL)	Sex ratio (F:M:?)	Size-at-maturity (cm DW/TL)	*n* mature	Gear type (*n*)	Locality (Figure 1)	IUCN Red List category
Aetobatidae	**1 (0.6)**							
Aetobatus ocellatus	1 (0.6)	44.3	F: 1	F: 155 M: 115		Gillnet (1)	1	VU
Carcharhinidae	**101 (57.4)**							
Carcharhinus amblyrhynchoides	19 (10.8)	75.3–160.9	F: 7 M: 12	F & M: 112.5	F: 3 M: 7	Gillnet (19)	1	NT
Carcharhinus amboinensis	1 (0.6)	117.0	F: 1	F: 210.5 M: 202.5		Gillnet (1)	1	DD
Carcharhinus coatesi	2 (1.1)	71.7–123*	F: 1 M: 1	F & M: 70	F: 1 M: 1	Gillnet (2)	1	LC
Carcharhinus leucas	35 (19.9)	71.0–157.7	F: 17 M: 18	F: 230 M: 220		Gillnet (35)	1	NT
Carcharhinus limbatus	1 (0.6)	135.0	F: 1	F: 172.5 M: 185		Gillnet (1)	1	NT
Carcharhinus limbatus/tilstoni	13 (7.4)	73.4–168.0	F: 10 M: 3			Gillnet (13)	1	
Carcharhinus macloti	17 (9.7)	65.4–82.6	F: 5 M: 12	F: 79.5 M: 71.5	F: 0 M: 11	Gillnet (17)	1	NT
Carcharhinus tilstoni	2 (1.1)	118.0–145.0	F: 2	F: 110 M: 107.5	F: 2	Gillnet (2)	1	LC
Carcharhinus sp.	8 (4.5)					Gillnet (8)	1	
Rhizoprionodon acutus	3 (1.7)	67.6–74.5	F: 1 M: 2	F: 47 M: 42		Gillnet (3)	1	VU
Glaucostegidae	**2 (1.1)**							
Glaucostegus typus	2 (1.1)	73.0–76.0	F: 1 M: 1	F: & M: 165		Gillnet (2)	1	CR
Pristidae	**26 (14.8)**							

Anoxypristis cuspidata	13 (7.4)	100.0–300.0	F: 7 M: 4 ?: 2	F: 225 M: 200	F: 1 M: 1 ?: 2	Gillnet (13)	1, 7	EN
Pristis pristis	13 (7.4)	49.0–484.9	?: 13	F & M: 290	?: 5	Gillnet (13)	1–6	CR
Rhinidae	**1 (0.6)**							
Rhynchobatus australiae	1 (0.6)	231.4	F: 1	F: ? M: 120	F: 1	Gillnet (1)		CR
Sphyrnidae	**45 (25.6)**							
Eusphyra blochii	42 (23.9)	64.4–155.0	F: 15 M: 27	F: 115.5 M: 105.5	F: 9 M: 13	Gillnet (42)	1	EN
Sphryna lewini	3 (1.7)	53.5–73.5	F: 2 M: 1	F: 210 M: 160		Gillnet (3)	1	CR

Table A2. 8 Abundance (*n*), proportion of total abundance (%), size range (DW, disc width; TL, total length), sex ratio (F, female; M, male; ?, unknown), size-at-maturity from White et al. (2017b), *n* mature for each sex, gear type used in capture, location of capture (Figure 1 map reference) and IUCN Red List of Threatened Species category (IUCN 2021) for all specimens observed in small-scale fisheries on the south coast of Papua New Guinea. CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; NE, Not Evaluated. Aetobatidae and Dasyatidae sizes are in disc width (DW), all others are in total length (TL).

Species	*n* (% of catch)	Size range (cm DW/TL cm)	Sex ratio (F:M:?)	Size-at-maturity (cm DW/TL)	*n* mature	Gear type	Locality	IUCN Red List category
Aetobatidae	**2 (0.3)**							
Aetobatus ocellatus	2 (0.3)	70.0–89.0	F: 1 M: 1	F: 155 M: 115		Gillnets (2)	12, 15	VU
Carcharhinidae	**344 (56.7)**							
Carcharhinus amblyrhynchoides	13 (2.1)	55.0–125.0	F: 2 M: 4 ?: 7	F & M: 112.5	F: 1	Gillnet (13)	8, 13, 17, 19, 46	NT
Carcharhinus amboinensis	7 (1.2)	56.9–120.2	F: 1 M: 2 ?: 4	F: 210.5 M: 202.5		Gillnet (7)	8, 21, 46, 49	DD
Carcharhinus cautus	5 (0.8)	64.0–118.0	M: 2 ?: 3	F: 85 M: 80	M: 2 ?: 2	Gillnet (5)	8, 12, 19	LC
Carcharhinus coatesi	15 (2.5)	32.0–78.0	F: 2 M: 2 ?: 11	F: & M: 70	?: 2	Gillnet (6) Hook & line (9)	8–9, 13, 16, 19	LC
Carcharhinus fitzroyensis	3 (0.5)	71.0–96.5	F: 1 ?: 2	F: 90 M: 80	?: 1	Gillnet (3)	8, 46	LC
Carcharhinus leucas	40 (6.6)	49.0–130.0	F: 12 M: 7 ?: 21	F: 230 M: 220		Gillnet (40)	9, 13, 16, 20, 22, 31, 33–34, 36, 39, 43–47, 49, 52, 61	NT
Carcharhinus limbatus	1 (0.2)	94.4	?: 1	F: 172.5 M: 185		Unspecified (1)	62	NT
Carcharhinus limbatus/tilstoni	15 (2.5)	57.0–91.0	F: 2 ?: 13			Gillnet (15)	8–9, 17, 19	
Carcharhinus melanopterus	34 (5.6)	62.0–127.0	F: 13 M: 18 ?: 3	F: 113 M: 98	M: 2	Gillnet (34)	12–13, 15, 17	VU
Carcharhinus sorrah	9 (1.5)	61.9–100.0	F: 2 M: 2 ?: 5	F & M: 92.5	F: 1 M: 1 ?: 1	Gillnet (8) Unspecified (1)	8, 17, 19, 57	NT

Carcharhinus sp.	2 (0.3)	59.0–60.0	M: 1 ?: 1			Gillnet (2)	8, 46	
Glyphis garricki	140 (23.1)	49.0–117.0	F: 56 M: 40 ?: 44	F: 177 M: 140		Gillnet (139) Unspecified (1)	9, 17, 22, 31–32, 34, 42–43, 45–50, 52–53	CR
Glyphis glyphis	38 (6.3)	46.4–122.0	F: 11 M: 16 ?: 11	F: 250 M: 228		Gillnet (38)	15, 22, 42–49, 52	EN
Glyphis sp.	2 (0.3)	88.5–97.0	F: 2			Gillnet (2)	22	
Negaprion acutidens	3 (0.5)	70.0–113.0	M: 1 ?: 2	F & M: 220		Gillnet (3)	8–9	VU
Rhizoprionodon acutus	7 (1.2)	56.5–65.0	F: 3 M: 2 ?: 2	F: 75.5 M: 70		Gillnet (7)	12–13, 19	VU
Rhizoprionodon taylori	10 (1.6)	45.0–95.0	F: 6 M: 3 ?: 1	F: 48.5 M: 41	F: 6 M: 3	Gillnet (9) Hook & line (1)	8, 13, 19	LC
Dasyatidae	**45 (7.4)**							
Himantura australis	7 (1.2)	32.0–47.0	F: 4 M: 2 ?: 1	F: Unkown M: ~112		Gillnet (7)	13, 19 , 46	NE
Hemitrygon longicauda	4 (0.7)	36.0	M: 1	F & M: Unknown		Gillnet (1) Unspecified (3)	13, 46	NT
Maculabatis toshi	10 (1.6)	45.0–68.0	F: 5 M: 5	F: Unknown M: 50	M: 2	Gillnet (9) Unspecified (1)	12–14, 19, 46	LC
Neotrygon australiae	1 (0.2)	23.0	F: 1	M: 31		Gillnet (1)	15	NE
Pateobatis fai	2 (0.3)	58.0–67.0	F: 1 M: 1	F: Unknown M: 112		Gillnet (2)	12, 19	VU
Rhinoptera neglecta	3 (0.5)	30.0–134.2	F: 1 M: 1 ?: 1	F: Unknown M: 115		Gillnet (3)	46	DD
Taeniura lymma	8 (1.3)	20.0–27.0	F: 6 ?: 3	F: Unknown M: 20		Gillnet (7) Unspecified (1)	8, 12–13, 15, 19	LC
Urogymnus dalyensis	5 (0.8)	77.0–100.0	F: 2 M: 2 ?: 1	F: Unknown M: 90		Gillnet (1) Hook & Line (4)	19, 35, 46	LC

Urogymnus granulatus	5 (0.8)	31.0–36.0	F: 5	F: Unknown M: 60		Poison root (5)	15	VU
Glaucostegidae	**9 (1.5)**							
Glaucostegus typus	9 (1.5)	50.5–186.0	F: 4 M: 2 ?: 3	F & M: 165	F: 1 M: 1	Gillnet (9)	8, 15, 19, 46, 52	CR
Hemigaleidae	**2 (0.3)**							
Hemigaleus australiensis	2 (0.3)	79.0–87.0	F: 2	F: 65 M: 60	F: 2	Gillnet (2)	19	LC
Hemiscylliidae	**3 (0.5)**							
Chiloscyllium punctatum	3 (0.5)	54,0–83.0	F: 1 M: 2	F: 84 M: 65.5	M: 2	Gillnet (2) Hook & line (1)	9, 13, 19	NT
Orectolobidae	**1 (0.2)**							
Orectolobus wardi	1 (0.2)	52.2	F: 1	F: Unknown M: 45		Hook & Line (1)	9	LC
Pristidae	**123 (20.3)**							
Anoxypristis cuspidata	52 (8.6)	55.0–309.4	F: 1 ?: 51	F: 225 M: 200	?: 43	Gillnet (49) Unspecified (3)	8, 10–11, 16–20, 46, 53, 57–59, 62–63	EN
Pristis clavata	9 (1.5)	103.0–248.4	?: 9	F: Unknown M: 260		Gillnet (9)	8, 46, 51	EN
Pristis pristis	60 (9.9)	72.9–561.8	F: 1 M: 2 ?: 57	F & M: 290	?: 8	Gillnet (34) Hook & Line (7) Unspecified (19)	16–17, 19, 21, 23–30, 35–38, 40–41, 43, 45–46, 50, 53–54, 56, 59–60	CR
Pristis zijsron	1 (0.2)	352.0		F & M: 430		Gillnet (1)	19	CR
Pristidae sp.	1 (0.2)	210.0	?: 1			Unspecified (1)	46	
Rhinidae	**10 (1.6)**							
Rhynchobatus palpebratus	10 (1.6)	60.0–166.0	F: 1 M: 6 ?: 3	F: Unknown M: 103	M: 1	Gillnet (10)	8, 12, 14, 17, 19, 46	NT
Sphyrnidae	**68 (11.2)**							

Eusphyra blochii	44 (7.2)	40.0–188.0	F: 3 M: 18 ?: 23	F: 115.5 M: 105.5	F: 1 M: 3 ?: 14	Gillnet (29) Unspecified (15)	8–9, 14, 17, 22, 46, 57, 62–63	EN
Sphyrna lewini	16 (2.6)	51.8–91.0	F: 2 M: 2 ?: 14	F: 210 M: 160		Gillnet (16)	13, 19	CR
Sphyrna mokarran	7 (1.2)	94.1–255.4	F: 1 M: 4 ?: 2	F: 255 M: 247	?: 1	Gillnet (7)	9, 11–12, 19	CR
Sphyrna sp.	1 (0.2)	108.0	M: 1			Gillnet (1)	19	

Figure A2. 1 Sawfish rostra from the South Fly Coast that have been modified for use as weapons. Left; *Anoxypristis cuspidata* (ventral). Top right; *A. cuspidata* (dorsal). Middle right; *Pristis pristis* (ventral). Bottom right; *P. pristis* (dorsal).

Figure A2. 3 Sawfish (Pristidae) rostra for sale at a market in Port Moresby, National Capital District Province, Papua New Guinea. Left image: Rostra on the top of image were $200 PGK (Papua New Guinean Kina, = 0.28 USD, 04/04/2021) each and are identified as largetooth sawfish *Pristis pristis*. Rostra on bottom of image were $100 PGK each and are identified as narrow sawfish *Anoxypristis cuspidata*. Right image: Rostra were $500 PGK each and are identified as *P. pristis*. All rostra reportedly came from Western Province (no further location information available). Observed by YA on 18 July 2020.

Figure A2. 3 Top image: Discarded catch from swim bladder fishers in the Kikori River Delta. Elasmobranch bycatch include a narrow sawfish *Anoxypristis cuspidata*, an eyebrow wedgefish *Rhynchobatus palpebratus* and several *Carcharhinus* spp. A large barramundi *Lates calcarifer*, estimated to be over 1m in length is also discarded with only its swim bladder harvested, despite a value of $40–60 PGK at the nearby Kikori Fish Plant (comparatively, elasmobranch is valued at $3 PGK kg^{-1}, with fin attached at this facility). Bottom Image: Elasmobranch catch from fishers at the Sepik River mouth. In this instance, winghead sharks *Eusphyra blochii* constituted most of the elasmobranch catch. All individuals were finned, and carcasses discarded. Shark fin in an important economic resource for the community at the mouth of the Sepik River (Leeney et al. 2018). The value of swim bladder and its role in local economies comparatively is not understood, although fishers in coastal regions around the Sepik and Ramu Rivers do target croakers (Sciaenidae) for swim bladder.

Table A2. 9 Estimated commercial prices for swim bladder for the four key species being traded in Gulf Province. Estimates made by Gulf Provincial Fisheries (Ibana 2020). PGK, Papua New Guinean Kina (1 PGK = ~$0.28 USD, 04/04/2021)

Grade	Dried weight range per grade (g)	Maximum estimated price for key species (PGK)			
		Catfish (Siluriformes)	King Threadfin (*Polydactylus macrochir)*	Barramundi (*Lates calcarifer*)	Jewel Fish (*Nibea squamosa*)
A	200–1000	300	300	500	1400
B	70–199	150	150	300	750
C	0–69	50	50	50	300

Literature Cited

Appleyard, S., White, W., Vieira, S., Sabub, B. 2018. Artisanal shark fishing in Milne Bay Province, Papua New Guinea: biomass estimation from genetically identified shark and ray fins. Scientific Reports. 8: 1–12.

Baldwin, C., Mounts, J., Smith, D., Weigt, L. 2009. Genetic identification and color descriptions of early life-history stages of Belizean Phaeoptyx and Astrapogon (Teleostei: Apogonidae) with comments on identification of adult Phaeoptyx. Zootaxa. 26: 1–22.

Compagno, L.J.V., White, W.T., Last, P.R. 2008. *Glyphis garricki* sp. nov., a new species of river shark (Carcharhiniformes: Carcharhinidae) from northern Australia and Papua New Guinea, with a redescription of *Glyphis glyphis* (Müller & Henle, 1839). CSIRO Marine and Atmospheric Research Paper. 22: 203–226

Faria, V.V. 2007. Taxonomic review, phylogeny, and geographical population structure of the sawfishes (Chondrichthyes, Pristiforms). PhD Thesis, Iowa State University, Ames, Iowa.

Garrick, J.A.F. 1982. Sharks of the genus *Carcharhinus*. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) Circular. 445: 1–194

Gilbert, C.R. 1967. A revision of the hammerhead sharks (family Sphyrnidae). Proceedings of the United States National Museum. 199: 1–88.

Ibana, D. 2020. Fish Maw Report. Report prepared for the Gulf Provincial Administration, Fisheries and Marine Resource Division.

IUCN. 2021. The IUCN Red List of Threatened Species. Version 2021-1. https://www.iucnredlist.org.

Leeney, R.H., Mana, R.R., Dulvy, N.K. 2018. Fishers ecological knowledge of sawfishes in the Sepik and Ramu rivers, northern Papua New Guinea. Endangered Species Research. 36: 15–26.

Morgan, D.L., Whitty, J.M., Phillips, N.M., Thorburn, D.C., Chaplin, J.A., McAuley, R. 2011. North-western Australia as a hotspot for endangered elasmobranchs with particular reference to sawfishes and the northern river shark. Journal of the Royal Society of Western Australia. 2: 345–358.

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

Thorburn, D.C., Morgan, D.L., Rowland, A.J., Gill, H.S., Paling, E. 2008. Life history notes of the critically endangered dwarf sawfish, *Pristis clavata*, Garman 1906 from the Kimberley region of Western Australia. Environmental Biology of Fishes. 83: 139–145.

Tillett, B.J., Field, I.C., Bradshaw, C.J.A., Johnson, G., Buckworth, R.C., Meekan, M.G., Ovenden, J.R. 2012. Accuracy of species identification by fisheries observers in a north Australian shark fishery. Fisheries Research. 127–128: 109–115.

White, W.T., Appleyard, S.A., Kyne, P.M., Mana, R.R. 2017a. Sawfishes in Papua New Guinea: a preliminary investigation into their status and level of exploitation. Endangered Species Research. 32: 277–291.

White, W.T., Baje, L., Sabub, B., Appleyard, S.A., Pogonoski, J.J., Mana, R.R. 2017b. Sharks and rays of Papua New Guinea. ACIAR Monograph No. 189. Australian Centre for International Agricultural Research, Canberra.

White, W.T., Baje, L., Appleyard, S.A., Chin, A., Smart, J.J., Simpfendorfer, C.A. 2020. Shark longline fishery of Papua New Guinea: size and species composition and spatial variation of the catches. Marine and Freshwater Research. 71: 627–640.

Whitty, J.M., Phillips, N.M., Thorburn, D.C., Simpfendorfer, C.A., Field, I., Peverell, S.C., Morgan, D.L. 2014. Utility of rostra in the identification of Australian sawfishes (Chondrichthyes: Pristidae). Aquatic Conservation: Marine and Freshwater Ecosystems. 24: 791–804.

Appendix 3

(Corresponding to Chapter 5)

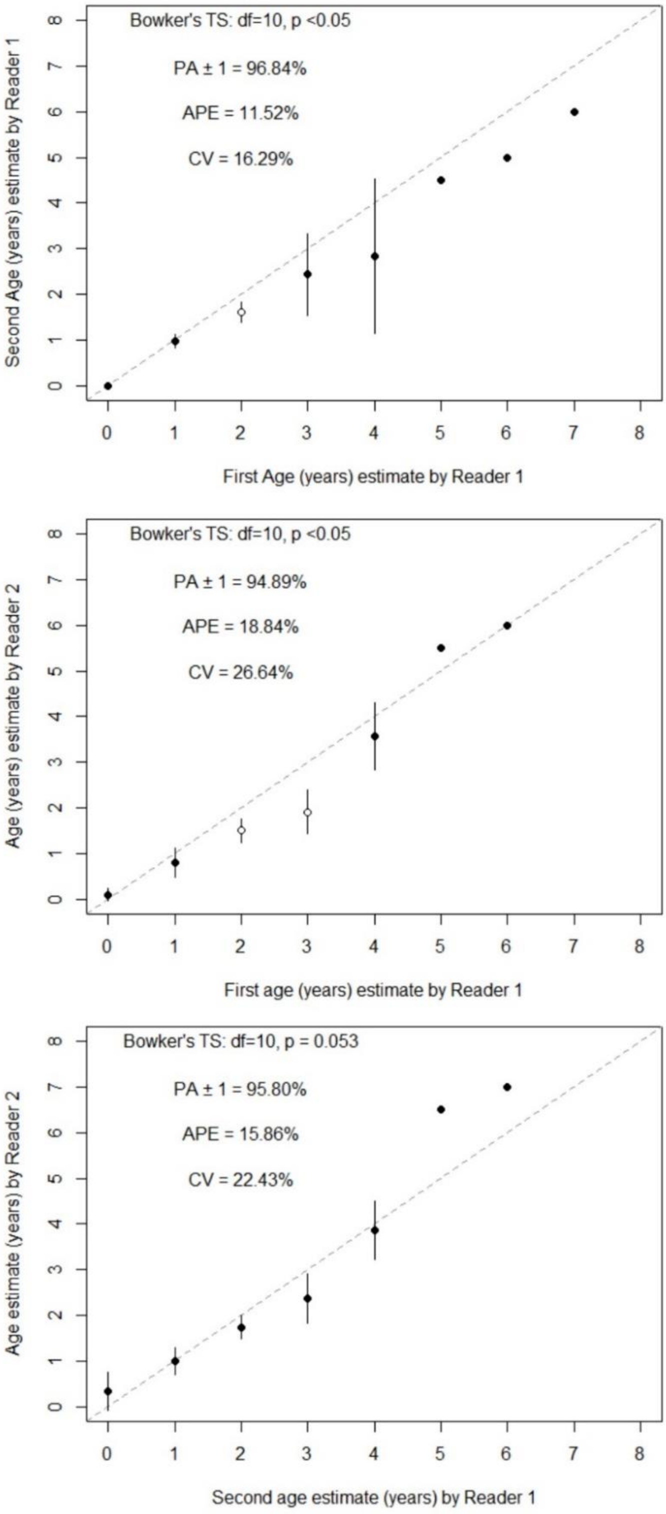


Figure A3. 1 Age bias plots for Glyphis species displaying values for Bowkers test of symmetry (Bowkers TS), percent agreement (PA) ± 1 year, average percent error (APE), and Changs coefficient of variation (CV).

Table A3. 1 Sex, length, location, age, and salinity at capture data for samples from northern Australia

Species	Sex	Total length (cm)	Location	Latitude	Longitude	Salinity (ppt)	Estimated age
Glyphis glyphis	F	144.5	Adelaide River	-12.50701	131.39429	19.06	6
Glyphis glyphis	M	101.5	Adelaide River	-12.50701	131.39429	19.06	4
Glyphis glyphis	F	127.0	Adelaide River	-12.50701	131.39415	17.21	6
Glyphis glyphis	F	80.1	Adelaide River	-12.50701	131.39415	17.21	1
Glyphis glyphis	M	139.5	Adelaide River	-12.47871	131.37001	15.37	5
Glyphis glyphis	M	153.2	Adelaide River	-12.50696	131.39406	12.12	8
Glyphis glyphis	F	189.0	Adelaide River	-12.67560	131.33289	5.05	10
Glyphis glyphis	F	181.5	Adelaide River	-12.69685	131.29323	4.15	11
Glyphis glyphis	F	161.0	Adelaide River	-12.68193	131.33482	6.29	8
Glyphis glyphis	F	59.8	Adelaide River	-12.75479	131.28258	4.04	0
Glyphis glyphis	F	85.0	West Alligator River				2
Pristis pristis			Daly River	-13.61082	130.60127	0.20	1
Pristis pristis	M	121.0	Daly River	-13.60379	130.59518		0
Pristis pristis	M	106.0	Adelaide River	-13.19995	131.15763		0
Pristis pristis	M	113.5	Daly River	-13.60335	130.59222		0
Pristis pristis	F	108.0	Daly River	-13.60335	130.59222		0

Pristis pristis	F	111.1	Daly River	-13.60335	130.59222	0

Table A3. 2 Sex, length, location, and estimated age for samples from Papua New Guinea

Species	Sex	Total length (cm)	Location	Latitude	Longitude	Estimated age
Anoxypristis cuspidata	F	146.3	Sepik River	-3.845697222	144.5275583	
Anoxypristis cuspidata	M	149.0	Sepik River	-3.845697222	144.5275583	
Anoxypristis cuspidata	M	119.6	Sepik River	-3.845697222	144.5275583	
Anoxypristis cuspidata	F	152.0	Sepik River	-3.845697222	144.5275583	
Anoxypristis cuspidata	M	222.8	Sepik River	-3.845697222	144.5275583	
Anoxypristis cuspidata	M	147.0	Sepik River	-3.845697222	144.5275583	
Anoxypristis cuspidata	F	209.7	Sepik River	-3.845697222	144.5275583	
Anoxypristis cuspidata	F	103.4	Sepik River	-3.845697222	144.5275583	
Carcharhinus amblyrhynchos	M	143.0	Bismark Sea			11
Carcharhinus amblyrhynchos	M	144.0	Bismark Sea			9
Carcharhinus coatesi	M	77.0	Gulf of Papua			10
Carcharhinus coatesi	M	73.0	Gulf of Papua			10
Carcharhinus coatesi	M	68.0	Gulf of Papua			9
Carcharhinus coatesi	M	76.0	Gulf of Papua			11
Carcharhinus falciformis	F	130.8	Bismark Sea			7
Carcharhinus falciformis	F	147.6	Bismark Sea			9
Carcharhinus leucas			Kikori River	-7.79908889	144.193011	2
Carcharhinus leucas	M	157.7	Sepik River	-3.845697222	144.5275583	11
Carcharhinus leucas	F	116.1	Sepik River	-3.845697222	144.5275583	5
Carcharhinus leucas	F	80.8	Sepik River	-3.845697222	144.5275583	0
Carcharhinus leucas	F	78.0	Sepik River	-3.845697222	144.5275583	0
Carcharhinus leucas	F	76.0	Sepik River	-3.845697222	144.5275583	0
Glyphis garricki	M	93.0	Kikori River	-7.79908889	144.193011	4

Glyphis garricki	F	80.0	Kikori River	-7.79908889	144.193011	2
Glyphis garricki		113.0	South Fly Coast	-9.020763889	143.3384306	6
Glyphis garricki	F	86.0	Kikori River	-7.79908889	144.193011	3
Glyphis garricki	M	74.0	Kikori River	-7.79908889	144.193011	2
Glyphis garricki	F	91.0	Kikori River	-7.79908889	144.193011	3
Glyphis garricki	M	87.5	Kikori River	-7.79908889	144.193011	4
Glyphis garricki	M	79.2	Kikori River	-7.79908889	144.193011	3
Glyphis garricki	F	78.0	Kikori River	-7.79908889	144.193011	4
Glyphis garricki	M	93.4	Kikori River	-7.79908889	144.193011	5
Glyphis glyphis	F	119.5	Kikori River	-7.79908889	144.193011	4
Glyphis glyphis	F	122.0	Kikori River	-7.79908889	144.193011	4
Glyphis glyphis	M	70.0	Kikori River	-7.79908889	144.193011	1
Glyphis glyphis	M	59.3	Kikori River	-7.79908889	144.193011	0
Glyphis glyphis	F	71.5	Kikori River	-7.79908889	144.193011	0
Glyphis glyphis	M	77.5	Kikori River	-7.79908889	144.193011	2
Glyphis glyphis	M	228.0	South Fly Coast	-9.020763889	143.3384306	22
Pristis pristis	F	90.0	Aramia River	-7.903702778	142.3449056	0
Rynchobatus australiae	F	231.4	Sepik River	-3.845697222	144.5275583	18

Appendix 4

(Corresponding to Chapter 6)

Additional Methods

Other matrix outputs

The stable stage distribution (*w*) and reproductive values (*v*) are estimated as the right and left eigenvectors, respectively. Stable stage distribution describes the proportion of population (N) in each stage. Stable stage distributions are sensitive to different natality schedules, therefore each natality base case used in this study had different stable stage distributions (Figure A1; Table A1). The stage specific reproductive value gives the number of offspring that an individual while in S_i will produce, including all of its descendants, relative to the reproductive value of S_1 (Figure A2). Therefore, the reproductive value of S_1 is always 1.

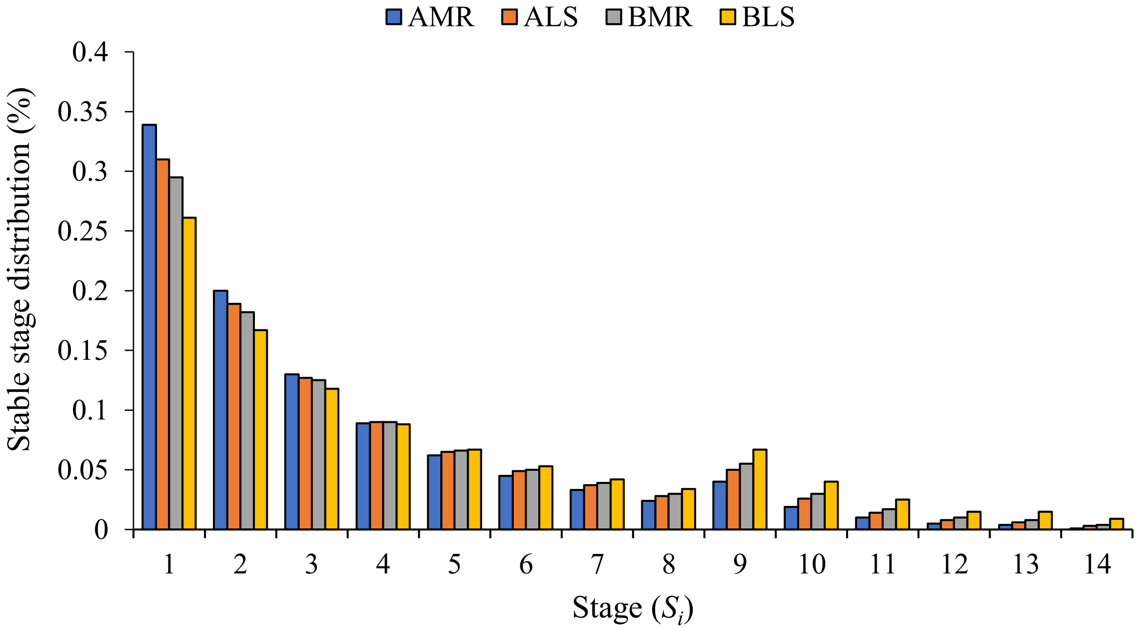
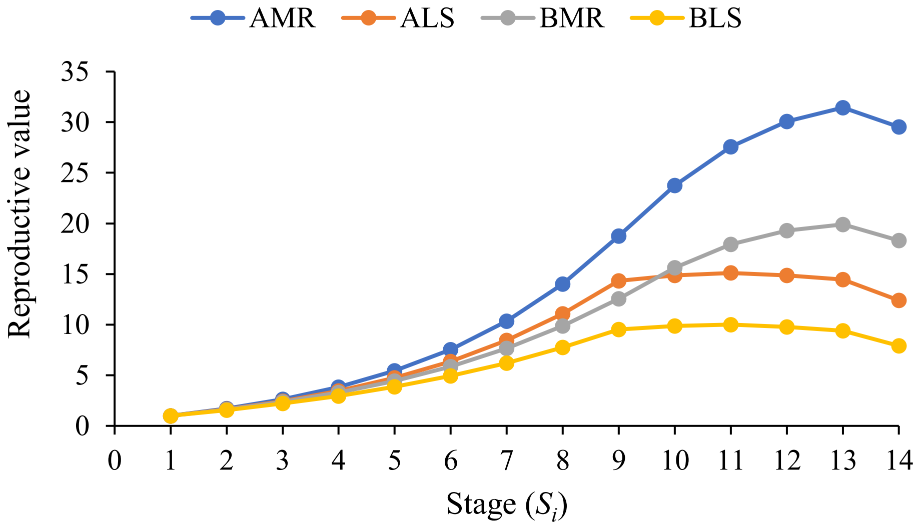


Figure A4. 1 Stable stage distribution for each natality base case. AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

Table A4. 1 Proportion of population in each life history phase for each natality base case. AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.

Life history phase	AMR	ALS	BMR	BLS
Juvenile	0.82	0.781	0.758	0.701
Subadult	0.102	0.114	0.119	0.129
Adult	0.079	0.107	0.124	0.171

Figure A4. 2 Stage specific reproductive values for each natality base case. AMR, annual maternal size-litter size relationship; ALS, annual mean litter size; BMR, biennial maternal size-litter size relationship; BLS, biennial mean litter size.



Commercial fisheries calculations

In order to estimate annual *P. pristis* catch in the Gulf of Carpentaria Inshore Fin Fish Fishery (GOCIFFF) from effort data provided, measurements of catch-per-unit-effort (CPUE) from research observer data were used. Peverell (2005) provides CPUE (500 m net day^{-1}) for *P. pristis* at a spatial resolution of 30 minute grid cells. This data was collected in 2000–2002 and represented 15.9% of days fished during that time. Both the effort and CPUE data collected by Peverell (2005) were presented as ranges for each 30 minute grid cell. The issue with this data was that *P. pristis* was not captured in all grid cells, which was likely due to limitations of observer coverage, although could also have been due to differences in environmental suitability for *P. pristis* between grid cells. This means that any application of provided effort in these grid cells with no *P. pristis* catch always results in a value of zero, To overcome this, we assumed a CPUE equal to the midpoint of the range given by (Peverell, 2005). We then calculated a daily catch rate using three different methods: 1) the average of midpoint CPUE values for all grid cells including those with no *P. pristis* interactions, 2) the average of midpoint CPUE values for grid cells with *P. pristis* interactions only (7/28 grid cells), and 3) the average of highpoint CPUE values for grid cells with *P. pristis* interactions only. This resulted in a low, moderate, and extreme daily catch rate for *P. pristis*, respectively. These daily catch rates were then applied to the annual effort data provided for the GOCIFFF for 2006–2016 (Table A2). We then used the average annual *P. pristis* catch for each daily catch rate estimate in the GOCIFFF for use in PVA. Because no CPUE data is available for *P. pristis* in the Northern Territory Barramundi Fishery (NTBF) (e.g. this species was not observed by Field et al., 2008), we also applied these three daily catch rate estimates to the annual effort data for the NTBF (2006-2016) to produce three estimates of annual *P. pristis* catch in the NTBF for PVA (Table A2).

Table A4. 2 Effort (days) and estimated *Pristis pristis* catch for the Gulf of Carpentaria Fin Fish Fishery and Northern Territory Barramundi Fishery. Estimates were obtained using three interpretations of catch-per-unit effort given by Peverell (2005).

	Gulf of Carpentaria Inshore Fin Fish Fishery				**Northern Territory Barramundi Fishery**			
Year	**Effort (days)**	**Low (0.0108)**	**Moderate (0.0349)**	**Extreme (0.0757)**	**Effort (days)**	**Low (0.0108)**	**Moderate (0.0349)**	**Extreme (0.0757)**
2006	24672	271	938	1875	3704	71	202	373
2007	24419	269	928	1856	3499	62	180	336
2008	25837	284	982	1964	3073	69	188	340
2009	23036	253	875	1751	2672	68	179	319
2010	21216	233	806	1612	2885	67	180	325
2011	20808	229	791	1581	2855	71	187	335
2012	21345	235	811	1622	2647	80	203	354
2013	20507	226	779	1559	2090	76	185	317
2014	18189	200	691	1382	1848	73	175	297
2015	19265	212	732	1464	1873	72	175	298
2016	18945	208	720	1440	2390	81	200	345

For the Northern Territory Demersal Fish Trawl Fishery (NTDTF) the daily catch rate (0.02 *P. pristis* day^{-1}) provided by NT fisheries from scientific observers was applied to annual effort data and averaged to produce an annual catch estimate for PVA (Table A3). Because no data were available to estimate daily *P. pristis* catch in the Queensland Demersal Fish Trawl Fishery (QDFTF), the daily catch rate from the NTDFTF was used to produce an annual catch estimate for use PVA for this fishery also (Table A3).

For the Northern Territory Offshore Net and Line Fishery (NTONLF), the daily catch rate (0.002 *P. pristis* day^{-1}) provided by Field et al. (2008) was applied to annual effort data provided. Annual catch estimates were then averaged to produce an annual catch estimate for the NTONLF for PVA (Table A3).

For Western Australian fisheries, no *P. pristis* were reported in annual logbook data provided. However, most catch was reported as unspecified sawfish species. To estimate the sawfish species composition for these unspecified sawfish records, research data for gillnet (*P. pristis* 0.7% of sawfish catch) and trawl fishing methods (*P. pristis* 0.7% of sawfish catch) provided by Western Australian Fisheries was used. Due to the small amount of annual reported sawfish catch in each fishery, the average annual catch of *P. pristis* in each fishery was zero (Table A3).

For the NPF, a daily catch rate for *P. pristis* (0.02 *P. pristis* day^{-1}) and unidentified sawfish (0.2 day^{-1}) was provided. The sawfish species composition of identified sawfish catch in the NPF was applied to the unidentified sawfish daily rate, where 1% of attributed to *P. pristis* (Table A3). Because the NPF operates across the Gulf of Carpentaria, Northern Territory, and into the Kimberley region of Western Australian waters, estimated *P. pristis* catch was divided proportionately, equal to the average division of effort in each jurisdiction, using effort data from 2016–2018 (Gulf of Carpentaria; 33%, Northern Territory; 64% Western Australia; 3%, Laird, 2019).

Due to the offshore habitat extent considered for *P. pristis* in this study (25 nautical miles offshore), the spatial boundaries of some commercial fisheries fell outside the 25NM habitat extent. Therefore, it was assumed that any reported *P. pristis* catch was taken within the portion of the fishery operating with 25NM of the coast (e.g. NTOTLF and NPF).

Table A4. 3 Effort (days) and estimated *Pristis pristis* catch for fisheries operating along Northern Australia that report sawfish interactions excluding the Gulf of Carpentaria Fin Fish Fishery and Northern Territory Barramundi Fishery which are given in Table A2. *Pristis pristis* catch was rounded to whole animals, except for Western Australian fisheries to demonstrate that while catch was estimated, it did not equate to a whole animal in any year.

	Northern Territory Offshore Net & Line Fishery		Northern Territory Demersal Fish Trawl Fishery		Queensland Demersal Fish Trawl Fishery		Northern Prawn Trawl Fishery		Kimberley Gillnet and Barramundi Fishery		Western Australia Prawn Trawl Fisheries	
Year	**Effort (days)**	***P. pristis* catch (No.)**	**Effort (days)**	***P. pristis* catch (No.)**	**Effort (days)**	***P. pristis* catch (No.)**	**Effort (days)**	***P. pristis* catch (No.)**	**Effort (days)**	***P. pristis* catch (No.)**	**Effort (days)**	***P. pristis* catch (No.)**
2006	729	2	281	6	729	2	281	6		0		0
2007	780	2	297	6	780	2	297	6		0.49		0.03
2008	941	3	344	7	941	3	344	7		0.03		0.08
2009	820	2	505	11	820	2	505	11		0.22		0.05
2010	808	2	321	7	808	2	321	7		0		0.06
2011	891	3	562	12	891	3	562	12		0		0.17
2012	717	2	1122	24	717	2	1122	24		0		0.05
2013	502	1	1212	26	502	1	1212	26		0.01		0.11
2014	643	2	1125	24	643	2	1125	24		0.15		0
2015	437	1	1145	24	437	1	1145	24		0		0.14
2016	607	2	1264	27	607	2	1264	27				0.17

Rainfall data

Table A4. 4 Information used in calculation of a) below average rainfall and b) above 125% average rainfall, for each fishery jurisdiction. Historical data were examined from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/cdo/about/cdo-rainfall-feature.shtml) at Vanrook Station (1922–2019) for the Queensland Gulf of Carpentaria, Darwin airport (1901–2019) for Northern Territory, and Gogo Station (1909–2019) for Western Australia.

	Queensland Gulf of Carpentaria	**Northern Territory**	**Western Australia**
Years with data	87	118	102
Average rainfall	946	1635	456
Below average rainfall calculation			
No. years below average	48	66	58
Proportion	0.55	0.56	0.57
125% average rainfall calculation			
125% average rainfall	1183	2044	571
No. years above 125% average	17	17	28
Proportion	0.2	0.14	0.27

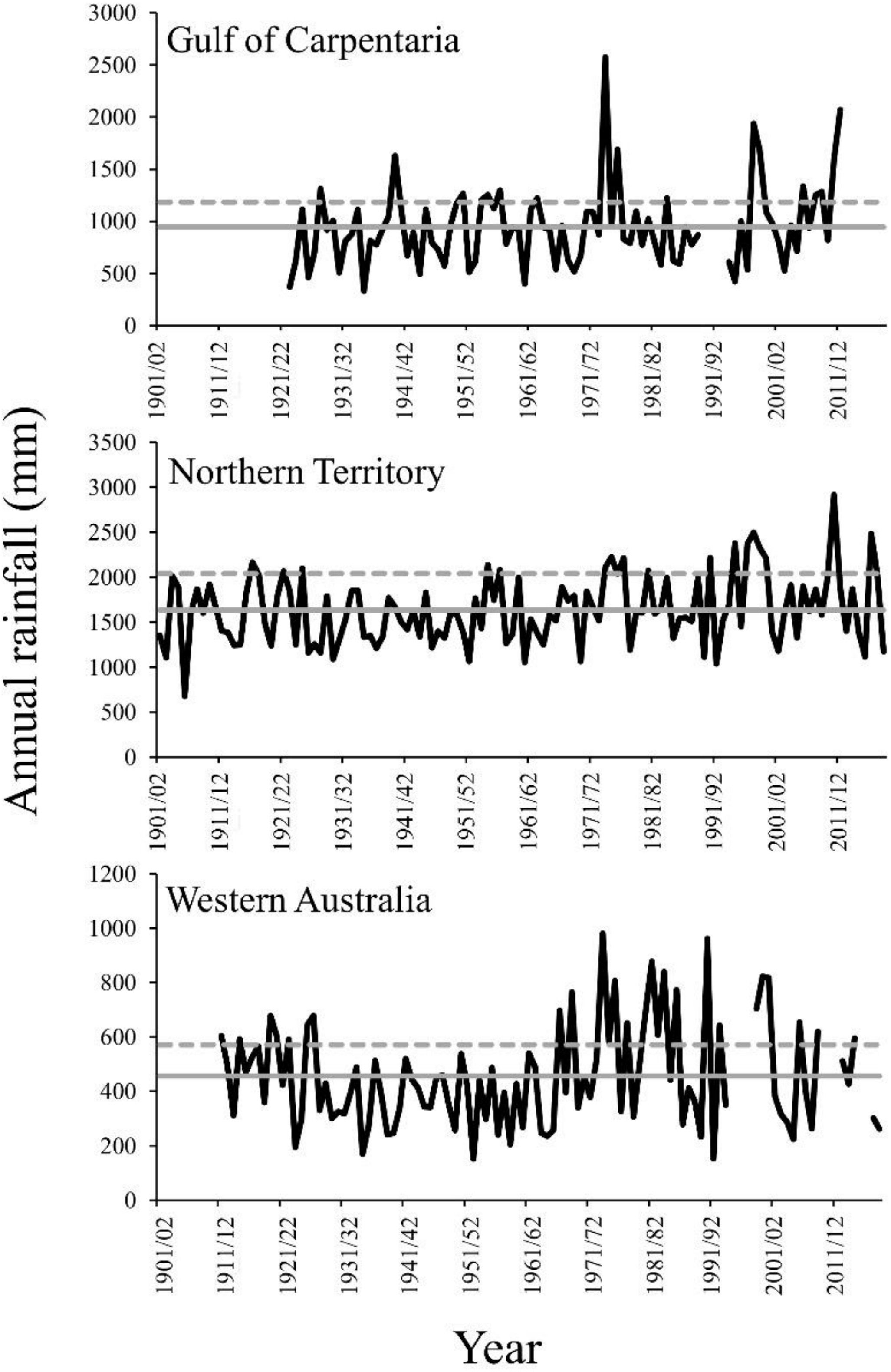


Figure A4. 3 Rainfall data used in calculation of a) below average rainfall (solid grey line) and b) above 125% average rainfall (dashed grey line), for each fishery jurisdiction. Historical data were examined from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/cdo/about/cdo-rainfall-feature.shtml) at Vanrook Station (1922–2019) for the Queensland Gulf of Carpentaria, Darwin airport (1901–2019) for Northern Territory, and Gogo Station (1909–2019) for Western Australia

Table A4. 5 Environmental Protection and Biodiversity Conservation Act (1999) Criterion 5. Quantitative Analysis

	EPBC Criterion 5. Quantitative Analysis		
Category:	Critically Endangered	Endangered	Vulnerable
Timeframe:	Immediate future	Near future	Medium-term future
Indicating the probability of extinction in the wild to be:	≥ 50% in 10 years or 3 generations, whichever is longer (100 years max.)	≥ 20% in 20 years or 5 generations, whichever is longer (100 years max.)	≥ 10% in 100 years

Additional Results

Table A4. 6 Final population change (%) for each scenario across jurisdictions and natality base cases. AMR Annual maternal size-litter size relationship, ALS Annual mean litter size, BMR Biennial maternal size-litter size relationship, BLS Biennial mean litter size. Population declines are in bold

	Final population change percentage (±95% confidence intervals)															
	Queensland Gulf of Carpentaria				**Northern Territory**				**Western Australia**				**Metapopulation**			
Scenario	AMR	ALS	BMR	BLS	AMR	ALS	BMR	BLS	AMR	ALS	BMR	BLS	AMR	ALS	BMR	BLS
1. Low commercial *F*	176.1 (±5.1)	56.5 (±3.7)	9.5 (±3.0)	**-75.8** **(±0.8)**	198.0 (±5.7)	86.2 (±4.5)	47.5 (±3.7)	**-59.8** **(±1.5)**	216.9 (±6.2)	113.0 (±4.6)	71.2 (±4.3)	**-51.6** **(±1.7)**	199.6 (±5.8)	88.8 (±4.4)	47.3 (±3.7)	**-60.5** **(±1.4)**
2. Moderate commercial *F*	79.4 (±4.1)	**-42.8** **(±1.7)**	**-69.3** **(±1.0)**	**-98.1** **(±0.2)**	165.3 (±5.4)	55.6 (±3.7)	15.6 (±3.2)	**-73.2** **(±1.0)**	217.3 (±6.2)	114.1 (±4.7)	72.3 (±4.3)	**-51.2** **(±1.7)**	164.3 (±5.4)	54.1 (±3.6)	16.4 (±3.1)	**-71.1** **(±1.1)**
3. Heavy commercial *F*	**-25.5** **(±2.0)**	**-90.9** **(±0.3)**	**-97.9** **(±0.2)**	**-100.0** **(±0.0)**	123.1 (±4.5)	15.7 (±3.0)	**-21.8** **(±2.5)**	**-84.8** **(±0.6)**	212.7 (±5.9)	108.8 (±4.7)	74.0 (±4.1)	**-51.0** **(±1.8)**	121.2 (±4.4)	24.2 (±3.0)	**-5.7** **(±2.5)**	**-76.6** **(±0.9)**
4. Increased drought frequency	40.6 (±3.3)	**-64.5** **(±1.2)**	**-82.1** **(±0.6)**	**-99.6** **(±0.1)**	128.1 (±4.7)	11.6 (±3.1)	**-23.8** **(±2.3)**	**-85.8** **(±0.5)**	175.7 (±5.6)	56.0 (±3.7)	20.5 (±3.4)	**-73.0** **(±1.1)**	125.2 (±4.7)	10.1 (±2.9)	**-21.4** **(±2.3)**	**-84.4** **(±0.6)**
5. Additional crocodile mortality	**-92.3** **(±0.3)**	**-99.7** **(±0.0)**	**-100** **(±0.0)**	**-100** **(±0.0)**	**-73.7** **(±0.8)**	**-95.0** **(±0.2)**	**-96.1** **(±0.1)**	**-100** **(±0.0)**	**-55.0** **(±1.3)**	**-91.0** **(±0.3)**	**-92.7** **(±0.3)**	**-99.9** **(±0.0)**	**-71.4** **(±0.9)**	**-94.7** **(±0.2)**	**-95.8** **(±0.2)**	**-100** **(±0.0)**
6. 95% post-release survival	204.4 (±5.6)	100.8 (±4.6)	56.7 (±3.9)	**-56.6** **(±1.5)**	217.2 (±6.4)	109.8 (±4.6)	69.8 (±4.1)	**-52.3** **(±1.6)**	213.2 (±5.7)	110.9 (±4.6)	72.6 (±4.0)	**-51.6** **(±1.7)**	213.0 (±5.9)	108.2 (±4.6)	67.9 (±4.0)	**-53.0** **(±1.6)**
7. Juvenile floodplain management	87.2 (±3.7)	**-26.5** **(±2.0)**	**-65.7** **(±1.1)**	**-89.6** **(±0.2)**	179.1 (±5.6)	70.53 (±3.9)	24.5 (±3.3)	**-70.8** **(±1.1)**	230.8 (±6.2)	138.7 (±5.2)	92.7 (±4.5)	**-39.0** **(±2.1)**	176.7 (±5.4)	72.6 (±3.9)	28.1 (±3.2)	**-64.1** **(±1.2)**
8. No inshore gillnet *F*	164.3 (±5.2)	95.2 (±4.4)	54.4 (±4.0)	**-58.4** **(±1.5)**	195.0 (±5.7)	91.9 (±4.2)	48.5 (±3.7)	**-62.6** **(±1.4)**	217.3 (±6.2)	114.1 (±4.7)	72.3 (±4.3)	**-51.2** **(±1.7)**	195.9 (±5.8)	100.2 (±4.4)	57.9 (±4.0)	**-57.8** **(±1.5)**
9. No trawl *F*	93.1 (±4.1)	**-32.7** **(±2.0)**	**-65.4** **(±1.2)**	**-97.7** **(±0.2)**	187.2 (±5.4)	83.0 (±4.2)	40.9 (±3.6)	**-64.7** **(±1.3)**	213.2 (±5.7)	110.9 (±4.6)	72.6 (±4.0)	**-51.6** **(±1.7)**	175.6 (±5.2)	67.3 (±3.9)	28.6 (±3.2)	**-67.4** **(±1.2)**
10. Additional crocodile mortality & Scenario 6 and 7	**-49.6** **(±1.4)**	**-89.4** **(±0.4)**	**-91.8** **(±0.4)**	**-100** **(±0.0)**	**-52.2** **(±1.4)**	**-89.6** **(±0.4)**	**-91.8** **(±0.3)**	**-99.7** **(±0.1)**	**-47.6** **(±1.6)**	**-89.1** **(±0.4)**	**-91.0** **(±0.3)**	**-99.8** **(±0.1)**	**-50.1** **(±1.5)**	**-89.4** **(±0.4)**	**-91.5** **(±0.3)**	**-99.8** **(±0.0)**

11. Smaller initial *N*	**-34.6** **(±1.8)**	**-91.6** **(±0.4)**	**-99.4** **(±0.1)**	**-100.0** **(±0.0)**	116.4 **(±4.5)**	7.0 **(±3.1)**	**-30.8** **(±2.2)**	**-86.8** **(±0.5)**	213.2 **(±5.8)**	110.8 **(±4.6)**	69.8 **(±4.2)**	**-52.5** **(±1.6)**	116.4 **(±4.4)**	20.8 **(±3.0)**	**-11.5** **(±2.4)**	**-78.0** **(±1.2)**
12. Larger initial *N*	145.1 **(±4.8)**	24.3 **(±3.2)**	**-16.8** **(±2.5)**	**-87.4** **(±0.5)**	190.4 **(±5.6)**	86.6 **(±4.3)**	45.6 **(±3.7)**	**-61.9** **(±1.5)**	212.2 **(±6.0)**	114.4 **(±4.6)**	72.7 **(±4.3)**	**-49.3** **(±1.8)**	188.0 **(±5.6)**	82.5 **(±4.2)**	41.2 **(±3.6)**	**-63.2** **(±1.4)**