Title
Untangling Bycatch: An Interdisciplinary Approach to Measure and Mitigate Shark and Ray Capture in Industrial Tuna Fisheries

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UNTANGLING BYCATCH: AN INTERDISCIPLINARY APPROACH TO MEASURE AND MITIGATE SHARK AND RAY CAPTURE IN INDUSTRIAL TUNA FISHERIES

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ECOLOGY & EVOLUTIONARY BIOLOGY

By

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September 2022

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ABSTRACT

UNTANGLING BYCATCH: AN INTERDISCIPLINARY APPROACH TO MEASURE AND MITIGATE SHARK AND RAY CAPTURE IN INDUSTRIAL TUNA FISHERIES

Melissa R. Cronin

Industrial fisheries threaten oceanic sharks and rays. Effective management and conservation responses require solutions that incorporate biological, ecological, and policy considerations. In this dissertation, I use an interdisciplinary approach to measure and mitigate fisheries impacts for data-poor but highly threatened pelagic elasmobranchs. First, I describe the quantity, composition, and potential impact of industrial tuna fishing on 22 elasmobranch species using catch data reported by global tuna fisheries and a catch estimation approach. I show that publicly accessible catch rates indicate that these fisheries report ~2.9 million individual sharks and rays per year, but that estimated catches are as much as five times higher. Importantly, these impacts are understudied: only 20% (15 of 76) of the examined populations had been formally assessed and of these, roughly 30% are overexploited. Given these findings, in the second chapter I focus on one particularly vulnerable group: manta and devil rays (collectively, Mobulids). I analyzed the genetic population structure of three species in the eastern Pacific Ocean and found weak but statistically significant population genetic structure among all four species. These findings suggest that Mobulids exhibit metapopulation structure and local selection occurring regionally in the eastern Pacific, and support the identification of unique regional units for conservation and fisheries management. Finally, and as a way forward, I assess the policy response of five large tuna Regional Fisheries Management bodies responsible for managing and mitigating to elasmobranch bycatch. Using a mitigation hierarchy framework, I show that current policies are not adequate to sufficiently reduce oceanic shark and ray bycatch, and make management, data, and transparency recommendations that are likely to reduce the impacts of bycatch on threatened sharks and rays.

DEDICATION

This dissertation is dedicated to my family:

my dad, for teaching me to ask questions

my mom, for teaching me to create

and my brother, for teaching me to laugh.

And, to the Mobulids.

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The land on which I completed my PhD is the unceded territory of the Awaswas-speaking Uypi Tribe. The Amah Mutsun Tribal Band, comprised of the descendants of indigenous people taken to missions Santa Cruz and San Juan Bautista during Spanish colonization of the Central Coast, is today working hard to restore traditional stewardship practices on these lands and heal from historical trauma.

They say “it takes a village”; in my case, I think it took a small metropolis. First and foremost, I want to express my deepest gratitude to Don Croll and Bernie Tershy for their constant intellectual support, conservation expertise, career guidance, and, shockingly, for the open-faced s-sandwiches. I am also grateful to Jennifer Jacquet, who I consider my conservation moral compass, and who has always pushed me to make my work matter. I am deeply grateful to Marm Kilpatrick, Katy Seto, and Giacomo Bernardi, all of whom lent extreme patience and generosity with their time and knowledge, and from whom I learned mountains. I also would like to thank Jordan Watson, Nerea Lezama-Ochoa, Kelly Zilliacus, Mark Carr, and Remy Gatins, all of whom were a constant source of academic and emotional help and encouragement. Finally, I am forever grateful to Erika Zavaleta, who gave me guidance, tools, inspiration and confidence to build something powerful.

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INTRODUCTION

The scale and intensity of fishing on marine ecosystems has accelerated dramatically over the past century. Though humans have hunted marine species for more than 40,000 years, postwar technology and inexpensive fossil fuels allowed for the rapid expansion of fishing effort after 1950 (Bell et al. 2016). This expansion has been led by large-scale industrial fisheries, which now operate in more than half of the world's ocean area (Kroodsma et al. 2018). These fisheries are mainly comprised of international fleets targeting large epipelagic fishes like tuna and swordfish on the high seas (FAO 2020). Tuna, valued at more than $40 billion annually, account for nearly 20% of the economic value of wild marine fisheries (Merrie et al. 2014; FAO 2020). The global catch of major commercial tuna species (albacore, bigeye, bluefin, skipjack, and yellowfin) has increased by tenfold over the last five decades (Merrie et al. 2014).

The global industrial tuna fishery has exerted substantial impacts on marine ecosystems, including overfishing, fishing-induced demographic and genetic changes within heavily exploited populations, and population decline and collapse of non-target or "bycatch" species (Ortuño Crespo et al. 2017; Wallace et al., 2010; Anderson et al., 2011; Lewison et al., 2014; Dulvy et al., 2008; Oliver et al., 2015). As a result, fishery management tools like catch limits and spatiotemporal closures have been developed to reduce industrial overfishing and its associated impacts

(Worm et al. 2005; Aranda et al. 2012; Leadbitter et al. 2014). In some cases (particularly for well-resourced fisheries flagged to wealthy countries), these tools have led to improvements in the status of previously depleted tuna populations (IUCN 2021; ISSF 2021). These successes are greatly facilitated by the r-selected life history characteristics of tuna and related teleost fish species, including high fecundity, fast growth, and early maturation and reproduction—which make these species relatively resilient to recover from fishing (Juan-Jorda et al. 2012).

However, many other species like mammals, sea turtles, seabirds, and sharks are captured in these same fisheries in large numbers (Hall and Roman 2013; Clarke et al. 2014). In contrast to tunas, these species exhibit K-selected life history strategies, and therefore more vulnerable intense fishing pressure (Lewison et al 2014). Of these megafauna groups, sharks and rays (elasmobranchs) make up the majority (~97%) of the volume of bycatch reported by industrial tuna fisheries (WCPFC 2021). One of the most evolutionarily distinct and functionally diverse vertebrate groups, elasmobranchs have particularly slow growth, late maturation, low fecundity, and long generation times (Dulvy et al. 2008, 2017; Pardo et al. 2016; Stein et al. 2018; Pimiento et al. 2020). For this reason, traditional fishery management tools used to address overfishing for fast-growing teleost species may not work for elasmobranchs (Myers and Worm, 2005; Dulvy et al. 2014). As a result of this and other anthropogenic threats, one third of elasmobranchs are globally threatened with extinction (Dulvy et al. 2021).

Of elasmobranchs, large pelagic species account for an estimated 52% of identified catch worldwide (Worm et al, 2013). These species are highly migratory, often traveling from coastal waters to the high seas and back (Quieroz et al, 2019). Though population declines have been observed in both coastal and pelagic elasmobranchs, oceanic species are more likely to encounter multiple and potentially compounding pressures threats across their large ranges (Lascelles et al. 2014; Harrison et al. 2018). As a result, their global abundance is estimated to have declined by 71% over the last half-century (Pacoureau et al. 2021).

Bycatch: An understudied threat

Fisheries impacts have been identified as the primary driver of elasmobranch population declines, both from target and bycatch fisheries (Pacoureau et al. 2021). The term ‘bycatch’ generally refers to the incidental catch of non-target species or individuals that are discarded back into the ocean alive or dead, often for regulatory reasons or because it lacks economic value (Hall 1996). Global fisheries incidentally capture and discard an estimated 9.1 million tonnes annually, representing roughly 11% of global catch (Gilman et al 2020). For elasmobranchs, though few global estimates exist, some studies suggest that 50% of the global elasmobranch catch is bycatch (Bonfil et al. 1995; Oliver et al. 2015). For some pelagic elasmobranch species, bycatch is a main source of mortality, triggering local or global population declines across their range (Baum et al 2003; Feretti et al. 2010; Young and Carlson 2020). Even for individuals for which bycatch does not cause mortality, sub-lethal effects of capture may combine with other threats to exert negative impacts on fitness (Wilson et al, 2014). Beyond conservation implications, bycatch generates costs, hinders profitability for fishers (Boyce 1996), causes animal suffering, and may invite public criticism of fishing practices (Hall 1996, Kaiser and Edwards-Jones 2006). Despite this, most conservation and public attention related to shark conservation focuses on shark finning and unsustainable fishing, while bycatch remains relatively under-scrutinized (Shiffman 2020).

Pelagic elasmobranch bycatch in industrial fisheries is a thorny problem for fisheries managers and conservationists. Due to the inaccessible and remote nature of most industrial fishing operations and the sometimes blurry boundaries between target catch and bycatch, accurate estimates of the scale and impact of bycatch are difficult to obtain (Hall et al. 2000). Further, roughly two thirds of these fisheries lack adequate observer coverage, which is necessary to accurately estimate bycatch (Gilman et al. 2014). Due to these data limitations, much research on fisheries bycatch is descriptive rather than quantitative, limiting the applicability of bycatch research for fisheries management. Compounding this problem, baseline information about the abundance and population structure remains largely unknown for many pelagic elasmobranch species, making effective management challenging.

Informing conservation solutions

Nevertheless, in recent decades regional and global efforts have sought to address the problem of elasmobranch bycatch. The 1982 Law of the Sea Convention and the 1995 Fish Stocks Agreement, both of which obliged States to consider the effects of fishing on bycatch species, prompted the development an array of policy and management solutions. Some of these interventions include gear modifications to prevent bycatch or release individuals after catch, spatiotemporal protection, and alternative handling methods to reduce mortality. However, no research has examined whether and which methods are currently being used by these fisheries, and their efficacy for reducing pelagic elasmobranch bycatch.

To address these gaps, my dissertation uses an interdisciplinary approach to describe the scale and potential impact of pelagic elasmobranch bycatch in tuna fisheries, and to illuminate policy and management solutions that could reduce its effects. In **Chapter 1,** I present a broad synthesis of publicly available shark and ray catch data in four oceans, and use a systematic review to reconstruct bycatch for 22 pelagic elasmobranch species. I show that these fisheries report ~2.9 million individuals per year, but estimate that true catch may be as much as 16 million individuals, roughly five times higher than reported data suggests. Despite the large scale of this catch, only 20% (15 of 76) of eligible elasmobranchs populations have been assessed, and at least 30% of the assessed elasmobranch catch is from overexploited populations. Given these findings, in the **Chapter 2** I use a fractional genomics approach to assess genetic population structure for three species of manta and devil rays (collectively, Mobulids), a group that is particularly vulnerable to bycatch in industrial tuna fisheries. I show that Mobulid species show evidence of gene flow between populations but local, geographically-mediated selection is occurring even within the same region—factors which suggest that Mobulid genetic diversity is important and should be considered in conservation efforts. Finally, in **Chapter 3** I assess the policy response of the four large tuna Regional Fisheries Management bodies responsible for managing and mitigating pelagic elasmobranch bycatch. This study demonstrates that current policies are not adequate to avoid or sufficiently minimize bycatch for pelagic elasmobranchs. As a way forward, I make recommendations for management, data, and transparency gaps that could be filled to achieve more precautionary management in industrial tuna fisheries. Overall, this work draws together quantitative, molecular, and policy analysis methods to present a holistic approach to measuring and mitigating an important conservation threat to pelagic elasmobranchs.

CHAPTER 1

How many sharks and rays are caught in industrial tuna fisheries? A global review to inform conservation and management

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Abstract

Several species of sharks and rays are experiencing severe population declines, yet clarity about where to focus management and conservation actions is lacking. Industrial tuna fisheries target or incidentally catch (i.e., “bycatch”) vulnerable shark and ray (i.e., elasmobranch) species in significant numbers, with potentially long-lasting impacts. However, due to often limited data collection, the contribution of these fisheries to elasmobranch mortality is often incomplete, regionally-focused, and poorly understood. Here, we used quantitative and qualitative approaches to quantify pelagic elasmobranch catch in four tuna Regional Fisheries Management Organizations (tRFMOs) and describe the scale and impact of industrial tuna fisheries on 13 threatened oceanic shark species and 9 Mobulid ray species. We compiled publicly reported catch data and estimated that tRFMO-managed purse seine and longline fisheries reported an annual mean of 2.9 million individual pelagic elasmobranchs over the last decade (2007–2017), corresponding to roughly one elasmobranch reported for every tonne of tuna caught. Additionally, given underreporting of elasmobranchs in some fisheries, we used a literature review approach to extract catch rates to estimate that the true average total catch may be as high as 16 million individuals (range: 724,557–36,092,653 individuals) per year. Based on existing stock assessments, we estimate that at least 30% of reported catch came from overexploited populations, though only 20% (15 of 76) of the examined populations had been formally assessed. These results present a broad understanding

of global and regional catches, and should guide improved data collection and access, research, and conservation efforts for increasingly vulnerable oceanic elasmobranchs.

1. Introduction

One third of shark, ray, and closely related species (i.e., elasmobranchs) are threatened with extinction, and the global abundance of pelagic sharks and rays has been estimated to have declined by 71% since 1970 (Dulvy et al. 2021; Pacoureau et al. 2021). Because most pelagic elasmobranchs are higher trophic level predators, this decline can perturb pelagic ecosystems through cascading effects of the reduction of top-down predation pressure over large spatial and temporal scales (Stevens et al. 2000; Ferretti et al. 2010; Heupel et al. 2014). Economically, this decline may contribute to loss to some coastal communities where elasmobranch fisheries support food security and livelihoods (Simpfendorfer and Dulvy, 2017) as well as loss of elasmobranch-related ecotourism (Dent & Clarke 2015; Healy et al. 2020). Beyond their economic value, elasmobranchs are important to many indigenous cultures around the world, and their loss may compromise the prominence of socially important resources and symbols (Leeney & Poncelet 2015).

Multiple anthropogenic stressors have led to population declines of pelagic elasmobranchs, including targeted harvest for meat, fins, gills, and other body parts;

bycatch (here defined as the portion of the catch that is unintentionally captured and discarded alive or dead (Davies et al. 2009; Hall 1996; Kelleher, 2005)); climate change (Osgood et al., 2021); habitat loss, and possibly pollution (Clarke et al. 2006; Germanov et al. 2018). However, fishing impacts—both targeted and bycatch—are the primary drivers of pelagic elasmobranch declines (Dulvy et al. 2021; Pacoureau et al. 2021). Because of their vulnerability, which is exacerbated by life history traits including low fecundity, delayed maturation, slow growth rates, and long life spans, shark and rays are less resilient to exploitation (Stevens et al. 2000; Dulvy et al. 2008, 2014).

Among pelagic elasmobranchs, there has been particular conservation concern for a subset of 13 pelagic shark and 10 Mobulid ray species (Table 1). These species were recently listed (except the blue shark - *Prionace glauca*) under Appendix II of the Convention on International Trade in Endangered Species (CITES), which restricts international trade (Lawson et al., 2017). Additionally, all except blue shark were listed on the Convention for Migratory Species (CMS), which helps set conservation priorities and policy guidance for species whose ranges straddle international boundaries. These listings have brought more international attention to understanding the primary threats to pelagic elasmobranchs (Vincent et al. 2013; Cardeñosa et al. 2018). As a result, recent conservation efforts from non-governmental organizations have focused on marketing campaigns to reduce consumer demand for shark meat and fins or banning their trade in some regions, although these appear to have had limited success (Clarke et al. 2007; Ferretti et al.

2020). Nonetheless, while listings on biodiversity treaties like CITES and CMS can be useful to attract conservation attention and regulate trade of these species, many species listed on both agreements continue to face immediate threats (Lawson & Fordham, 2018; Fowler et al. 2021).

Globally, the capture of pelagic elasmobranchs is greatest for longline, gillnet, and purse seine gears, which are the main methods used to target tuna and other high-value tuna-like species by industrial fisheries (Oliver et al. 2015; Croll et al. 2016). Elasmobranchs are considered bycatch in many of these fisheries, though some fisheries using longlines target (e.g. blue shark, *Prionace glauca*) or opportunistically retain some elasmobranch species (e.g. shortfin mako, *Isurus oxyrinchus)* (Clarke et al. 2014; Booth et al. 2019). Because tuna vessels using these gears, particularly longline, overlap in space and time with pelagic elasmobranch habitat (Queiroz et al. 2019; Murua et al., 2021), these elasmobranch species can comprise as much as 12% to 25% of the total catch in some tuna longline fisheries, even when they are not targeted (Gilman 2011; Coulter et al. 2020). However, low observer coverage, poor catch reporting practices and retention bans for some species, coupled with lack of incentives to carefully manage non-target species in many fisheries, has made it difficult to assess the scale and impact of tuna fishery interactions with elasmobranchs (Barker & Schluessel, 2005; Molina & Cooke, 2012; Mucientes et al., 2022), though it is considered an important threat (Oliver et al. 2015; Jorgensen et al., 2022). Moreover, although some fisheries release incidentally caught elasmobranchs alive, post-release mortality studies in tuna longline and purse seine fisheries have shown that survival varies widely between species, gears, and handling and release methods (Gilman et al., 2008; Hall & Roman 2013; Hutchinson et al., 2015; Musyl and Gilman, 2018; Hutchinson et al., 2021).

Pelagic fisheries that target tuna and tuna-like species fall broadly under the management of five oceanic tuna Regional Fishery Management Organizations (tRFMOs), each of which facilitates data collection, research, conservation, and fishery management in its respective Convention Area. In recent years, there has been increasing recognition (including within their own convention texts, e.g. the Antigua Convention in the Eastern Pacific Ocean) that tRFMOs should maintain or restore populations of non-target species at biologically sustainable levels (Clarke et al. 2012; de Bruyn et al. 2012). In response, all tRFMOs have adopted management measures for pelagic elasmobranchs (Cullis-Suzuki & Pauly, 2010; Clarke et al. 2013; Tolotti et al. 2015; Juan-Jorda et al. 2017; Simpfendorfer & Dulvy, 2017). However, with the exceptions of blue shark and shortfin mako in the Atlantic Ocean, there are no limits imposed on their catch (though landing and retention bans exist for several species) (Juan-Jordá et al. 2017; Sims & Quieroz, 2016; ICCAT 2019). While there is growing concern about the impact of coastal artisanal fisheries that are largely unregulated and extremely data-poor (Martinez et al., 2015, IATTC 2020, Oliveros-Ramos et al, 2020, Lennert-Cody et al. 2022), there are relatively better elasmobranch data for industrial tuna fisheries to develop effective management measures for industrial tuna fisheries. As a result, there is both a critical need for improved management and conservation of pelagic elasmobranchs within industrial tuna fisheries (Jorgensen et al., 2022).

While the unsustainable impacts of tuna fisheries on pelagic elasmobranchs was identified as a management issue more than a decade ago (Clarke et al. 2006; Gilman et al. 2008), recently observed shark population declines warrant finer-scale investigation to determine which fisheries may be contributing to these trends (Dulvy et al. 2021; Pacoureau et al. 2021). A lack of reliable fine-scale data has stymied global analyses of the scale of elasmobranch catch in fisheries in general, and tuna fisheries in particular (Heidrich et al. 2022). However, recent developments in data accessibility, including the publication of public domain datasets of comparable reported species catches, offer an opportunity to describe and assess pelagic elasmobranch catch in multiple oceans in a standardized way (Le Manach et al 2016; Williams et al. 2016; Taconet et al. 2017; Coulter et al. 2020). Further, all five tRFMOs have recently undertaken efforts to assess the impact of tuna fishing on the population status of sharks and rays (Clarke et al. 2013; Dent & Clarke 2015; Griffiths et al. 2019), including stock assessments (e.g., Kleiber et al. 2009; Rice 2013, 2017; Heidrich et al. 2022) and ecological risk assessments (e.g., Murua et al. 2012, 2018; Cortes et al. 2010; Arrizabalaga et al. 2011; Griffiths et al. 2017, 2022 IATTC 2022).

In this study, we used multiple approaches to aggregate and synthesize knowledge on the reported catch to tRFMOs and estimate potential capture of 13 shark species and 9 Mobulid ray species. Specifically, we aimed to examine: 1) the quantity and composition of reported elasmobranch catch to tRFMOs, 2) the quantity and composition of estimated catch, and 3) the proportion of pelagic elasmobranch catch that is i) formally assessed and considered overexploited by a stock assessment, and ii) considered threatened according to the IUCN Red List. This synthesis uses several data sources to understand the potential impacts of tuna fisheries on elasmobranchs as well as providing guidance for future elasmobranch conservation and management more broadly.

2. Materials and Methods

Publicly available elasmobranch catch data that is reported to tRFMOs by its Members and Cooperating non-members (data summarized from vessel logbooks and/or observer programs) was downloaded from tRFMO websites (Table S1). These data were used to describe patterns in reported catches by species, gear type, and ocean, and to describe the proportion of the catch that is publicly reported to compare to estimated total elasmobranch catch. Second, and in supplement to reported data, potential catch was estimated by combining derived catch-per-unit-effort (CPUE) from the literature with publicly available tRFMO fishing effort data in each ocean. Finally, to evaluate the potential sustainability of these catches, published stock assessments and IUCN Red List designations were used for each stock and species, respectively.

These reported data are referred to as “catch”, but it is important to note that this catch consists mostly of incidental catch (i.e., bycatch) as well as, in certain occasions, targeted catch. Because differences in observer coverage and data reporting between gears and oceans likely present biases in the quality of the data over time, these data were constrained to the past ten years where data was available from all tRFMOs. We focused our analysis on four major tRFMOs (Inter-American Tropical Tuna Commission (IATTC), International Commission for the Conservation of Atlantic Tunas (ICCAT), Indian Ocean Tuna Commission (IOTC), and Western and Central Pacific Fisheries Commission (WCPFC)) that manage tropical tuna fisheries (Table S1). The Commission for the Conservation of Southern Bluefin Tuna was excluded from this analysis, as it is a unique special commission for fisheries targeting only one temperate tuna species, which overlaps with the convention areas of the other tRFMOs.

2.1 Characterizing reported catch

Three main sources of publicly available data from tRFMO websites were used: 1) elasmobranch catch; 2) tuna catch, and 3) fishing effort. Data sources for each tRFMO are described in Table S1. For the elasmobranch catch data (1), public datasets, which were sourced from observer data (IATTC, WCPFC) and logbook data (IOTC, ICCAT) were downloaded from each tRFMO website. Because data from artisanal fisheries are either scant, unreliable, or not representative of entire fleets, data were constrained to include catches from industrial purse seine and longline vessels only. However, we acknowledge that pelagic elasmobranch catch from smaller vessels being a likely source of substantial mortality, particularly in the Indian Ocean (Murua et al. 2018), eastern Pacific Ocean (Martinez-Oritz et al. 2015), and elsewhere. Where available in the industrial fisheries data, information on gear type, vessel flag, and geographic location of capture was included. Data for species representing the genera *Alopias, Isurus, Mobula,* and the family *Sphyrnidae* were generally available only as species aggregations at the genus or family level in most data sources, likely because of difficulty in accurately identifying individual species. Therefore, species within each taxonomic aggregations were analyzed together (Table 1).

Because two tRFMOs (IOTC and ICCAT) report elasmobranch catch data in tonnes and two (IATTC and WCPFC) report in individuals, data was harmonized using a hierarchical process. First, where available, average sizes were computed from observer-collected length data for each species and gear (using only data for 2007–2017) (e.g., mean length for silky sharks caught in purse seine gear in the Atlantic Ocean). This data was available upon request from IATTC and publicly available from IOTC and ICCAT for most species and gears. Second, where these data were not available within these three tRFMOs, mean length was computed from the available length estimates for that species and gear in other tRFMOs. Third, if no region- and gear-specific data were available from any tRFMO data or documents, we reviewed the scientific literature for length measurements and conversion parameters that can be used for each species and gear as a next best estimate. For WCPFC, length data was not available; thus mean lengths were calculated by averaging data available for species from other oceans. Because sex distribution of the catch was generally not available, we did not differentiate by sex. (Curran and Bigelow (2016).

These data were used to calculate weight using the equation $W = a * L^b$, where L is length, parameter a is the intercept of the line and parameter b is the slope of the line. For data that were grouped by genus or family (e.g., *Alopias, Sphyrnidae, Isurus,* and *Mobula*), gear-specific species weights were first calculated, then averaged to produce a mean genus or family weight. To produce ratios of the number of pelagic elasmobranchs to tuna catch, tuna catch data was downloaded for longline and purse seine gears from each tRFMO website. The following tuna and tuna-like species were included: skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), bluefin tuna (*T. thynnus*), albacore (*T. alalunga*), bigeye tuna (*T. obesus*), swordfish (Xiphias gladius) and marlin (genus *Makaira*). To produce reported catch ratios for the last decade, tuna catch was divided by the average annual reported elasmobranch catch (Data S1) using

$$R_{g,r} = \frac{\sum_{T=2017}^{2007} L_{g,r}}{C_{g,r}}$$

where g is gear type, r is ocean region, L is elasmobranch catch (individuals and tonnes), and C is tuna catch (tonnes). These ratios were compared across different gear types and oceans using Kruskal-Wallis tests.

2.2 Estimating catch using catch rates

Given the likelihood that the reported data underestimates total catch (Babcock & Pikitch 2011; Forget et al. 2021), we used a systematic literature review approach following methods described by (Pullin & Stewart 2006) to derive catch rates (catch/effort) that can be used to estimate potential total elasmobranch catch. Peer-reviewed literature and tRFMO reports were reviewed to collate a sample of case studies on elasmobranch interactions with tuna fisheries (Data S5). In addition, all papers that were cited by two key review papers on elasmobranchs and tuna fisheries were reviewed (Gilman et al. 2008; Pacoureau et al. 2021). The following inclusion criteria were used: 1) the study contained information on the capture of elasmobranchs within a longline or purse seine fishery that predominantly targets one or more large migratory predatory fish species, including: tuna, swordfish, billfish, or marlin; 2) the study provided quantitative data on the catch, discard, or retention in individuals of at least one of the 23 species included in this study, as well as a comparable metric of fishing effort (e.g., number of hooks or net sets) for the study period. Because fishing strategies evolve, only papers published after 1990 were included. Samples were omitted in cases where catch was pooled for multiple species simultaneously. Papers for which CPUE was not available or could not be calculated (e.g., effort was reported in incomparable units such as number of longline sets or fishing trips, Data S4), or where CPUE was standardized or projected, were also excluded. This literature search yielded 224 references, of which 145 were excluded as they did not meet our inclusion criteria, leaving 83 sources.

Data recorded for each sample included fishery (defined as a collection of fishers targeting one or more large migratory predatory fish species with one type of gear), target species, tRFMO convention area, vessel flag, gear type, and elasmobranch species for each sample. Pooled CPUE rates for multiple species were excluded. Nominal CPUE was recorded at the species level, except for *Sphyrnidae, Alopias, Mobulidae* and *Isurus*, which were analyzed at the genus level. If CPUE was not available but catch and effort were available for concordant time periods and gear, nominal CPUE was calculated by dividing catch by effort.

Data were found to be non-normal using a Shapiro-Wilk test ($p<0.005$), thus data were log-transformed data prior to analysis. We added one-tenth of the lowest non-zero CPUE estimate to the four CPUE rates that were zero to enable log transformation. We used generalized linear models to determine whether differences existed among literature derived CPUE rates (response variable) for each gear type, ocean region and species (independent variables) (Kruskal-Wallis tests). We then used Wilcoxon tests to examine differences further using multiple comparisons for those groups with significant difference. Given these model results we used region-specific catch rates in our analyses (Fig. S1).

Mean CPUE rates ($\underline{q}$) were derived from these nominal CPUE rates (expressed in the equation below as catch (*L*) divided by effort (*E (L)*) from the literature for each gear (*g*), ocean region (*r*), and taxa (*s*) divided by the number of samples (*N*) collected from the literature for a given *g, r,* and *s*. Mean, standard deviation, and upper and lower 95% confidence intervals of CPUE values were calculated. For species without data for a given gear and ocean, a mean q was estimated from data from all oceans where data were available.

$$\underline{q}_{g,s,r} = \frac{\sum_{g,r,s} \frac{L_{g,r,s}}{E(L)\ g,r}}{N}$$

2.3 Estimating potential total catch

Using the derived catch rates, annual gear-, region-, and species-specific elasmobranch catch estimates ($\underline{L}_{g,s,r}$) were calculated, where T is the number of years over which the data were averaged (in our case, 10), and E is the total effort by gear-, region- and time collated from tRFMOs.

$$\underline{L}_{g,s,r} = \frac{\sum_{t=1}^{T} \underline{q}_{g,s,r} * E_{g,r,t}}{T}$$

Annual upper and lower bound estimates were calculated from upper and lower 95% confidence intervals (CI) of the catch rates for each species, gear, and region (mean ± 1.96 * standard error). Each of the mean q, lower q (lower CI bound), and upper q (upper CI bound) were multiplied by annual reported effort to produce catch estimates for the 10-year period in the equation above for each gear type and species.

These were then averaged for the 10-year period and compared to tRFMO-reported catch data for the study period.

2.4 Evaluating sustainability of catches

We sought to review the status of elasmobranch populations included in this study through the framework of fishery stock assessments, which can determine stock status, including whether a stock is overexploited, meaning that it is either overfished (the biomass is below a reference biomass value) or subject to overfishing (the fishing mortality is above a reference fishing mortality), or both (Begg et al. 1999). Stock assessment documents published on tRFMO websites and in the scientific literature were collected. Except for some mobulid rays and the pelagic thresher, all species in this study are globally distributed (Table 1); thus, for each tRFMO, we considered only species that is within the tRFMO's remit as eligible for stock assessment for each tRFMO. We assumed a total of 76 possible populations or 'stocks' eligible for assessment based on distribution within tRFMO Convention Areas (Table S3). In cases where a population had more than one assessment, the most recent assessment was used. In a case where a population was split into two or more stocks in one ocean based on genetic structure, we included both designations but, for simplicity, considered them a dual designation for that population in that ocean. If the assessment did not result in a conclusive status determination, it was characterized the result as "undetermined". If an assessment was conducted for a migratory species in more than one tRFMO (e.g., if an assessment was intended to assess trends in more than one convention area across the population's range—for example, a Pacific-wide assessment for silky shark), this assessment was considered applicable to that species in all tRFMOs within the geographic scope of the study.

In addition to stock assessments, IUCN Red List designations were included as a subjective indicator of conservation status, as is common for pelagic elasmobranchs (Dulvy et al. 2014b, 2021, IUCN 2022). Red List designations were matched with reported catch to examine the proportion of catch that falls within each category. Where two species within a genus that are reported together in the catch data had different IUCN designations (e.g. Mobulids, two of which are considered Vulnerable, and seven of which are considered Endangered), the more conservative listing for that genus was used, following the precautionary approach (e.g., Endangered for Mobulids).

3. Results

3.1 Characterizing reported catch

For the analysis period of 2007–2017, the total global catch of pelagic elasmobranchs calculated from data reported by tRMFOs was 31,291,355 individuals (1,219,037 tonnes), with an annual average catch of 2,905,322 (sd = 287,749) individuals (110,822 tonnes; sd = 10,648). Catches were dominated by longline gear, representing 97.9% of total catch (n= 2,818,162), while purse seine gear represented

2.1% (n= 610,117) (Fig 1A). The longline and purse seine catches were each dominated by blue shark (80.9%) and silky shark (77.5%), respectively. Across all gear types and species, ICCAT reported the largest proportion of the combined total catch of elasmobranchs (64%), followed by IOTC (30.2%), IATTC (4%), and WCPFC (1.5%). However, within purse seine gear alone, reported catch was mainly from WCPFC (45.4%), IATTC (29.5%), and ICCAT (24.6%), while and IOTC reported near-zero purse seine elasmobranch catch (Fig 1B). Some species included in this study were missing from publicly reported data, including: Mobulids in WCPFC and IATTC, and whale sharks in IATTC.

To contextualize these data relative to target species catch, data for tuna and tuna-like species was used to calculate ratios of elasmobranch catch to target catch based on reported public data. For the most recent decade with available data (2007–2017), average annual target catch for the species we included in this study across all tRFMOs combined was 2,940,656 tonnes per year (± 184,052.6 tonnes, Fig. S2). Over these same years for both gear types combined, the average reported elasmobranch to target catch ratio was 0.987 individuals per tuna and tuna-like species tonne (sd ± 0.080). The mean catch ratio for the most recent decade with data (2007–2017) was significantly greater for longline gear (3.96 ± 0.55 individuals per tonne) than for purse seine gear (0.023 ± 0.014 individuals per tonne) (Kruskal-Wallis test, $P<0.001$).

3.2 Estimating catch rates from literature

A total of 295 species-specific CPUE estimates were extracted and averaged for each species in each convention area, for both longline and purse seine gears (Fig. S3). More CPUE data were available for longline gear (n=195) than for purse seine gear (n=100). The mean number of samples (CPUE values) per species was 47.3; however, some species were better represented than others, in particular hammerhead (n=50), thresher (n=49), and mako sharks (n=49) had more estimates than less frequently caught species, such as whale shark (n=3) and porbeagle (n=18). For longline data, GLMs detected significant differences ($p<0.05$) in catch rates between one or more ocean regions for half of the taxonomic groups (n=4). For purse seine gear, differences were detected for one species, oceanic whitetip (Fig. S1).

CPUE rates used to derive catch rates (q) varied across more than five orders of magnitude across gear and species (Table 2). Grouping oceans, overall combined mean q for longline gear was 0.44 (± 1.16) individuals per thousand hooks and 0.340 (± 1.22, Fig S2) individuals per set for purse seine gear. Across all species, the greatest q was in longline fishing gear was for blue sharks (3.43 ± 6.02). For purse seine gear, the highest q was for silky shark in WCPFC (4.86 ± 6.581 individuals per set).

3.3 Estimating total catch

Annual catch estimates were calculated by multiplying CPUE rates by annual effort for each ocean region and fishing gear and averaged for the last decade (2007–2017). Overall, mean annual estimated elasmobranch catch numbers of 16,206,635 individuals (range: 724,557—36,092,653 individuals) or 1,227,599 tonnes (range: 101,627—2,727,688 tonnes) were roughly 5.6 times higher than mean annual reported catch (N=2,905,322 individuals) for the same period (Fig 2A). As with reported data, longline gear made up the majority (86.1%) of estimated catch compared to purse seine gear (13.9%) (Fig 2A). For all species, mean estimated catch was much greater than reported catch (Fig 2C).

3.4 Evaluating sustainability of elasmobranch catch

To compare reported catch with stock size as a metric of the threat of fishing for pelagic elasmobranchs, existing stock assessments for pelagic elasmobranch populations conducted by tRFMOs were collected. A total of 19 stock assessments that determine stock status were identified, which represented ~20% (n=15) of the 76 eligible elasmobranch populations across all four tRFMOs (Table 3). However, these assessed populations accounted for the majority (89%) of total reported catch in individuals (Fig 4A).

Of the 19 stock assessments examined, 11 assessments (58%) indicated that a stock was considered overexploited (overfished and/or experiencing overfishing)

(Table 3). These overexploited stocks represented 30% of the reported annual elasmobranch catch by weight, (n=711,470 individuals, Figure 4A). Stocks considered unexploited (e.g., not overfished and no overfishing) represented 59% of the catch (n=1,399,932). Reported catch from stocks whose status is unknown (including those species assessed without a conclusive designation and those not yet assessed) represented 11% of the reported catch (n=259,908).

Reported catch of individuals (Fig. 1) were matched with global IUCN Red List designations. We found that 23.9% of the reported catch was designated "threatened", including 1.7% considered Critically Endangered (n=42,772), 10.9% considered Endangered (n=273,073), and 11.3% considered Vulnerable (n=284,844). The remaining 76.1% of pelagic elasmobranch catch is considered 'Near Threatened' by the IUCN Red List (n = 1,909,676, Fig 4B).

4. Discussion

We present the first comprehensive global synthesis of publicly available data for pelagic shark and ray catch in both industrial purse seine and longline tuna fisheries, which represent 78% of the tuna captured globally (FAO 2020). We paired our analysis of reported catch data with estimated catch data based on catch rates collected from scientific literature and tuna RFMO fishing effort information. We found that although tuna fisheries reported 2.9 million pelagic elasmobranchs captured annually in recent years, catch rates coefficients derived from the literature suggest that the real volume of catch is likely to be substantially higher for nearly all species (except mako in longline gear, potentially due to its status as a commercial species), and potentially more than five times higher overall. Further, our finding that only 20% of eligible populations are currently assessed (representing 89% of total catch in weight) —and that 30% of reported catch is from an overexploited population—suggests that both significant knowledge gaps and conservation concerns exist. Overall, this work points to the potential impact of tuna fishing on pelagic elasmobranchs as well as the large variability in CPUE patterns across species and regions. Importantly, there are substantial differences in the data sources we used (observer data versus logbook data, Table S1), as well as the accuracy of length-weight conversion parameters and available CPUE data, which may have led to large differences in both reported and estimated elasmobranch bycatch. This underscores the need for precautionary management until data collection and reporting, as well as the derived stock assessments, can be improved.

4.1 Patterns in elasmobranch catch

Both reported and estimated elasmobranch bycatch rates are highly influenced by gear type. Reported elasmobranch catch, catch-to-target catch ratios, and catch rates are significantly greater for longline compared to purse seine gear. Indeed, longline gear is responsible for 93.5% of total reported elasmobranch catch, but yields

<23% of tuna production in any ocean (Clarke et al, 2014). This suggests that purse seine fishing may be a relatively less impactful fishing mode on pelagic elasmobranchs. However, it is important to note that this analysis does not account for the impact of potential passive fishing (also called “ghost fishing”); for example from the use FADs in purse seine fishing, which can entangle and kill elasmobranchs—though many tRFMOs now require non-entangling FADs (Moreno et al. 2018) (Filmalter et al. 2013). However, it is noted that since 2013 tRFMOs have adopted lower risk entanglement FAD designs in recent years to minimize ghost fishing mortality (IATTC 2019; IOTC 2019; ICCAT 2021; WCPFC 2021). Further, low observer coverage in the Indian and Atlantic Oceans, where elasmobranch catch in purse seine gear was relatively low—and where purse seine observer coverage is 5%— suggests that missing data may also be driving this pattern (IATTC 2019; IOTC 2019; ICCAT 2021, Table S2). In addition, set type (e.g., whether a vessel deploys a purse seine directly on a tuna school, on a FAD, or on associated dolphins) can substantially impact catch rate and therefore impact on bycatch species (Hall et al., 2013). Future research on elasmobranch catch should seek to improve and incorporate purse seine catch data, particularly data disaggregated by set type. Additionally, better coverage of unobserved fleet fragments-regions as well as the incorporation of indirect mortality caused by fishing gears could help improve estimates of their impact.

Further, the greater reported catch attributed to longline gear may be attributed to greater distributional overlap of longline fisheries and elasmobranch habitat: 60%

of the world's 7,500 tuna longline vessels are not large vessels (<24 meters in length) (Clarke et al., 2014), and thus likely fishing in coastal areas of high productivity where interaction rates with elasmobranchs are likely be greater. These results point to the critical need to assess coastal artisanal fisheries using longline and gillnet gears, among others, which are largely unobserved and in many contribute to significantly high catch of vulnerable elasmobranch species (Martinez-Oritz et al. 2015, Murua et al. 2018, Di Lorenzo et al. 2022, Lennert-Cody et al, 2022). The magnitude of elasmobranch catch in these small-scale fisheries, which were excluded from this study, is a major important gap that future research should investigate (Oliveros-Ramos et al. 2020; Lennert-Cody et al. 2022).

Beyond differences in gear type, we identified taxonomic patterns in reported catch that provide insight into variable fishing impacts for different species. In longline gear, for example, blue sharks comprise 83.5% of reported catch. This can be attributed to two main drivers: first, while elasmobranchs are generally not primary target species of industrial tuna fleets, in some cases, tuna fishing vessels may directly or opportunistically target sharks, particularly blue, mako and porbeagle sharks (Hall & Roman 2013; Clarke et al. 2014; Juan-Jordá et al. 2017). Blue sharks are the target of fisheries in both the Indian and Atlantic Oceans, and stock assessments in each of these oceans have concluded that northern blue shark population in the Atlantic Ocean is overexploited while the southern populations of the Atlantic and Indian Oceans are not overfished (Table 3). One remedy tRFMOs could pursue to address overexploited populations that are both bycatch and target catch is to include those elasmobranchs which are targeted as ‘principal species’ in their Conventions (rather than only as non-target species). This would signal that they should be managed with the seriousness of target tuna and billfish. Some tRFMOs are already moving in this direction; for example, IATTC’s Antigua Convention mandates mitigation for impacted non-tuna species. Similarly, ICCAT manages mako, blue, and porbeagle sharks as target species because they are targeted by several member fleets (ICCAT 2021) and has recently adopted new convention text establishing its responsibility for pelagic elasmobranchs (ICCAT 2019). Beyond evaluating management status of these species, well-enforced and science-based management and conservation plans, improved data collection, and full traceability of shark fin and meat products are all key steps to improving the status of impacted elasmobranch populations (Dulvy et al. 2017; Simpfendorfer & Dulvy, 2017).

Reported catch for other species we examined were several orders of magnitude lower than those of blue and silky sharks. Catches of hammerhead, oceanic whitetip, porbeagle, and whale sharks was low in comparison to other species. However, low relative catch cannot be conflated with low impact: it is possible that these species are infrequently caught because they are rare, poorly identified and/or not considered important for data collection, or already impacted, and may be even more vulnerable than species with high bycatch rates. Still, given the wide variability in bycatch rates we identified across species in this study, corresponding management and conservation responses from tRFMOs should not be uniform for all species (Booth et al. 2019). For instance, species with high catch rates may be good candidates for total allowable bycatch limits, tools which are used to regulate management for target tunas and have recently been implemented for blue and mako sharks in ICCAT (Pons et al. 2018; ICCAT 2019b) or dynamic ocean management, an adaptative management framework that has drawn some attention in some tRFMOs (e.g. IATTC, SAC-10-INF-D). Conversely, capture for those species with relatively low but potentially impactful catch rates may benefit more from targeted precautionary measures, like pre-capture bycatch avoidance and/or post-capture life and safe release mitigation best practices (de Bruyn et al. 2013), at least until better data is available about the impact of tuna fishing on their population status. Risk-based vulnerability assessments such as the recently developed EASI-Fish approach (Griffiths et al. 2019) or traditional productivity-susceptibility analyses can help prioritize species for these types of management (Hobday et al. 2011; Griffiths et al. 2019; Gilman et al. 2021).

There are also some important taxonomic gaps in data collection. While Mobulid species represent nine of the 22 pelagic elasmobranch species examined by this study (Table 1), only two tRFMOs (ICCAT and IOTC) include Mobulids in their publicly reported data. This is incongruous with current policy agendas in tRFMOs, all of which except ICCAT have adopted Mobulid management measures in recent years, including retention bans (Fordham et al. 2022). However, this lack of data can probably by attributed to the retention bans themselves, which may reduce the likelihood that an animal is counted as it may be quickly released (though this still may result in a mortality event) (Tolotti et al. 2015). Still, the scarcity of public data on Mobulid bycatch is alarming, given the fact that all Mobulid species are experiencing population declines globally, and that ecological risk assessments show that they are among the most vulnerable elasmobranch species to the impacts of tuna purse seine fisheries (Ward-Paige et al. 2013; Duffy et al. 2019; Griffiths et al. 2019, 2021). Improved observer coverage, data collection, and inclusion in public domain data for Mobulids and other non-shark pelagic elasmobranchs is a necessary first step toward meaningful conservation efforts.

4.2 Estimated elasmobranch catch

We estimated the potential magnitude of pelagic elasmobranch bycatch in tRFMOs at a mean of ~16 million individuals annually. However, these estimates contain very high uncertainty in catch estimates—including confidence intervals that overlap with reported catch—mainly driven by fluctuations in CPUE data extracted from the literature that inform our estimates. A major challenge associated with producing global estimates of elasmobranch catch from literature-derived data is the difficulty in identifying "representative" catch rates, given discrepancies in fleet and vessel behavior and seasonality, environmental conditions, fishing locations, and fishing modes that can drastically impact catch rates (Bi et al. 2021; Wang et al. 2021; Roberson & Wilcox 2022). Though we attempted to address these inconsistencies by using region- and species-specific catch rates, it is clear that our estimates are most powerful for highlighting relative differences as well as the poor quality of data available to assess the impact of tuna fisheries on pelagic elasmobranchs, pointing to the need for improved data collection and reporting.

Still, despite this high uncertainty, our estimate of elasmobranch catch in tuna fisheries is not incongruous with previous estimates of global elasmobranch fisheries bycatch in all fisheries. Worm et al. (2013) estimated total global shark mortality at 1.4 million tonnes, although Clarke et al. (2006) estimated the shark catch for the fin trade alone at 1.7 million tonnes in 2000. Biery et al (2012) reconstructed shark catch for 2000–2009 at 0.57 million tonnes ± 0.11 million tonnes per year. Our estimate of 1.2 million tonnes lies below all these, just under Worm et al.'s estimate, three-quarters of Clarke et al.'s estimate, and 2.1 times Biery et al.'s estimate. These discrepancies can be attributed to different data sources and methods used by each analysis (e.g., Clarke et al. used import/export data, while Worm et al. and Biery et al. used data from the FAO), and to the fact that these estimates incorporate non-tuna and artisanal fisheries. Nonetheless, our findings suggest that tuna fisheries account for a substantial portion of the world's estimated pelagic elasmobranch catch, and that actual catch is probably much greater than what is reported by tRFMOs. Perhaps most importantly, the potential underreporting identified in this study points to the need for better observer coverage, data collection and reporting, and stricter enforcement of national reporting policies to tRFMOs.

Our study also suggests that existing research may not be adequate to fully describe the threat to elasmobranchs posed by tuna fishing. For example, while we found that 30% of elasmobranch catch by weight is from overexploited populations, only one in five eligible populations have been assessed (although they represent 80% of the catch in total weight). This could be due to the greater incentive to assess and manage commercially important species. However, it is possible that this proportion may be different from that of unassessed species. Stock assessments are generally conducted for populations of economically important species (e.g. blue, mako, and porbeagle sharks) and/or having high catch rates (e.g., blue and silky sharks) and thus likely have higher quantity and/or quality catch and CPUE data. An investigation of the status of data-poor, unassessed species is urgently needed as well as the development of improved methods for data poor species.

4.3 Data constraints and improving data quality

The use of publicly reported catch data dictates several caveats for interpretation, including likely biases in catch data toward higher catch reported for species that are easily identified and more abundant and more catch reported in regions and gears with better observer coverage, in addition to general underreporting of non-tuna species across all oceans (Clarke et al. 2013; Hall & Roman 2013). Additionally, the length-weight parameters used to convert catch data is a potential source of bias, as fine-scale length frequency data was not available for every species in each gear and region, and using a mean value risks eliding the important size variability among individuals caught. Though we attempted to address biases in catch data with congruent data from a systematic literature review, catch rates from the scientific literature are also hindered by taxonomic biases that are compounded by discrepancies in catch rates between fisheries, regions, fishing practices, environment and even in the data collection methods and term used (e.g. bycatch) (Gilman, 2011). Literature-derived catch rates are also unlikely to be truly representative, as they reflect small and better-studied sectors of the fishery, do not incorporate differential impact on different life stages, are generally too broad to lead to fine-scale reliable catch estimates. Further, it is likely that spatial, temporal, and annual variation in past and current population status and dynamics, environmental and ecological conditions as well as variation in post-capture mortality rates can significantly impact CPUE, species survival rates, and correspondingly, total mortality for a given unit of effort (Lewison et al. 2009; Hutchinson et al. 2015; Escalle et al. 2016). In fact, we entirely exclude post-release mortality rates from this study—though mortality can in some cases for some species be very low, particularly for fisheries and vessels that have implemented best handling and release practices. These factors are largely excluded from this study, and thus the data we present are a coarse representation of estimated catch, and not necessarily mortality. However, we suggest that the publication of a dataset of comparable public domain data as well as catch rates is useful for future research assessing the impact and threat of fisheries to elasmobranchs.

4.4 Management implications

The data limitations described here should not deter the action and research to understand and mitigate the impacts of industrial tuna fishing on pelagic elasmobranchs; rather, they should motivate urgent improvement of data collection and submission resolution in tuna RFMOs for sharks and deeper investigation of the scope and impact of fishing on these and other non-target species.

The recent commitment by IATTC and ICCAT to include sharks under their remits could be followed by other tRFMOs, potentially affording greater attention and resources for their management and conservation. In past cases, tRFMOs and tuna fishing nations have been proactive in addressing sustainability issues for non-target species (Hall 1996; Jenkins 2007); however, they need to strengthen their efforts to help reverse elasmobranchs populations' declining trends and ensure their sustainability in the long term. To address the gaps and concerns identified by this study, we suggest the following immediate actions that tRFMOs and CPCs can take:

- Improve data collection and reporting so that elasmobranch catch and stock status can be adequately quantified and assessed in all tuna fisheries, which could be done through increasing human and/or electronic observer coverage (particularly in longline fisheries and small-scale/artisanal fisheries),
- Improve the small-scale fisheries data collection and assess the impact of those fisheries unmonitored fisheries on pelagic elasmobranch populations,

- Increase the number of shark stock assessed and use emerging data-poor methods (e.g. EASI-Fish) to evaluate elasmobranch populations' vulnerability on a regular basis; this will allow for the implementation of precautionary management until stock assessments exist,
- For overexploited and data-deficient populations, consider conservation and management measures, such as 1) limits on catches; 2) static or dynamic spatiotemporal management measures for important habitats and fishing inefficiency areas, and 3) the development of gear tools and safe handling and release best practices to reduce pre- and post-release mortality (e.g., deterrents, release devices, etc.),
- Quantify, assess, and address indirect impacts like ghost fishing and the differential effects of conservation and management measures on different species, and
- Improve enforcement procedures as well as monitoring, surveillance and control systems.

Policies and mitigation measures for elasmobranchs at the tRFMO level have the potential to influence fishing over enormous ocean areas and reduce the impact of fishing by multiple fleets at once. Given the low likelihood that tuna fishing pressure on elasmobranchs will abate significantly in the immediate future (though see White & Costello 2014), tRFMOs remain uniquely positioned to implement these measures in their convention areas all over the world. This study underscores the need for tuna fisheries, tuna fishing nations, and tRFMO policymakers to take immediate and meaningful action to conserve threatened pelagic elasmobranchs.

Table 1.1 Pelagic elasmobranch species included in this study. All species except *P. glauca* are listed on CITES Appendix II and are reported in tRFMO capture records. Reporting level indicates the taxonomic level at which most data was available and analyzed.

Reporting level	**Species**	**Common name**	**IUCN Red List Designation**	**Distribution**
Alopias Thresher	*Alopias pelagicus*	Pelagic thresher	Endangered	Indian, Pacific
	Alopias superciliosus	Bigeye thresher	Vulnerable	Global
	Alopias vulpinus	Common thresher	Vulnerable	Global
Carcharhinus falciformis Silky shark	*Carcharhinus falciformis*	Silky shark	Vulnerable	Global
Carcharhinus longimanus Oceanic whitetip	*Carcharhinus longimanus*	Oceanic whitetip shark	Critically endangered	Global
Isurus Mako	*Isurus oxyrinchus*	Shortfin mako	Endangered	Global
	Isurus paucus	Longfin mako	Endangered	Global
Lamna nasus Porbeagle	*Lamna nasus*	Porbeagle	Vulnerable	Global
Mobulidae Mobulid	*Mobula alfredi*	Reef manta ray	Vulnerable	Indian, Western Pacific
	Mobula birostris	Oceanic manta ray	Vulnerable	Global
	Mobula eregoodootenkee	Longhorned pygmy devil ray	Endangered	Indian, Western Pacific
	Mobula hypostoma	Atlantic devil ray	Endangered	Atlantic
	Mobula kuhlii	Shorfin devil ray	Endangered	Indian, Western Pacific
	Mobula mobular	Spinetail devil ray	Endangered	Global

	Mobula munkiana	Munk’s devil ray	Vulnerable	Eastern Pacific
	Mobula tarapacana	Sicklefin devil ray	Endangered	Global
	Mobula thurstoni	Bentfin devil ray	Endangered	Global
Prionace glauca Blue shark	*Prionace glauca*	Blue shark	Near threatened	Global
Rhincodon typus Whale shark	*Rhincodon typus*	Whale shark	Endangered	Global
Sphyrna Hammerhead	*Sphyrna lewini*	Scalloped hammerhead	Critically endangered	Global
	Sphyrna mokarran	Great hammerhead	Critically endangered	Global
	Sphyrna zygaena	Smooth hammerhead	Vulnerable	Global

Table 1.2. Catch rate coefficients for pelagic elasmobranchs derived from a review of the scientific literature. Where ocean-region specific rates were not available for a given species and gear type (n≤1), a global mean for that species and gear was used.

Gear	**Species or Group**	**tRFMO**	**n**	***q***	**sd**	**Lower 95% C.I. *q***	**Upper 95% C.I. *q***
LL	Blue shark	wcpfc	9	3.434	6.019	0	7.367
LL	Blue shark	iccat	19	1.092	1.777	0.293	1.891
LL	Blue shark	iotc	2	0.001	0.001	0	0.001
LL	Blue shark	iattc	7	0.255	0.553	0	0.665
LL	Hammerhead	wcpfc	4	0.002	0.001	`	0.003
LL	Hammerhead	iccat	10	0.006	0.011	0	0.012
LL	Hammerhead	iotc	5	0.001	0.001	0	0.001
LL	Hammerhead	iattc	10	0.457	1.169	0	1.181
LL	Mako	wcpfc	10	0.042	0.041	0.017	0.067
LL	Mako	iccat	19	0.161	0.346	0.006	0.317
LL	Mako	iotc	3	0.001	0.001	0	0.001
LL	Mako	iattc	6	0.001	0.001	0	0.002

LL	Mobulid	wcpfc	1	0.001	0.001	0	0.002
LL	Mobulid	iccat	1	0.001	0.001	0	0.002
LL	Mobulid	iotc	0	0.001	0.001	0	0.002
LL	Mobulid	iattc	4	0	0	0	0
LL	Oceanic whitetip	wcpfc	7	0.207	0.333	0	0.454
LL	Oceanic whitetip	iccat	5	0.019	0.04	0	0.054
LL	Oceanic whitetip	iotc	2	0.001	0.001	0	0.001
LL	Oceanic whitetip	iattc	2	0.016	0.022	0	0.046
LL	Porbeagle	wcpfc	3	0.787	0.935	0	1.844
LL	Porbeagle	iccat	5	0.017	0.023	0	0.037
LL	Porbeagle	iotc	0	0.233	0.492	0	0.482
LL	Porbeagle	iattc	7	0.15	0.269	0	0.35
LL	Silky	wcpfc	5	0.482	0.578	0	0.988
LL	Silky	iccat	4	0.001	0.001	0	0.002
LL	Silky	iotc	2	0.006	0.008	0	0.018
LL	Silky	iattc	1	0.203	0.427	0	0.444
LL	Thresher	wcpfc	18	0.257	0.677	0	0.57
LL	Thresher	iccat	10	0.051	0.082	0	0.102
LL	Thresher	iotc	5	0.012	0.016	0	0.026
LL	Thresher	iattc	9	0.138	0.305	0	0.337
LL	Whale shark	wcpfc	0	0	0	0	0
LL	Whale shark	iccat	0	0	0	0	0
LL	Whale shark	iotc	0	0	0	0	0
LL	Whale shark	iattc	0	0	0	0	0
PS	Blue shark	wcpfc	1	0.009	0.015	0	0.021
PS	Blue shark	iccat	3	0.013	0.019	0	0.034
PS	Blue shark	iotc	1	0.009	0.015	0	0.021
PS	Blue shark	iattc	0	0.009	0.015	0	0.021
PS	Hammerhead	wcpfc	0	0.051	0.075	0.019	0.083
PS	Hammerhead	iccat	15	0.037	0.047	0.013	0.06
PS	Hammerhead	iotc	3	0.014	0.01	0.003	0.025
PS	Hammerhead	iattc	3	0.162	0.134	0.01	0.314
PS	Mako	wcpfc	0	0.051	0.124	0	0.124
PS	Mako	iccat	8	0.06	0.147	0	0.162
PS	Mako	iotc	2	0.018	0.022	0	0.048
PS	Mako	iattc	1	0.051	0.124	0	0.124
PS	Mobulid	wcpfc	1	0.019	0.026	0.008	0.03

PS	Mobulid	iccat	13	0.012	0.012	0.005	0.018
PS	Mobulid	iotc	0	0.019	0.026	0.008	0.03
PS	Mobulid	iattc	8	0.032	0.038	0.006	0.059
PS	Oceanic whitetip	wcpfc	1	0.202	0.382	0	0.418
PS	Oceanic whitetip	iccat	5	0.013	0.008	0.006	0.019
PS	Oceanic whitetip	iotc	1	0.202	0.382	0	0.418
PS	Oceanic whitetip	iattc	5	0.396	0.541	0	0.87
PS	Porbeagle	wcpfc	0	0	0	0	0
PS	Porbeagle	iccat	2	0	0	0	0
PS	Porbeagle	iotc	1	0	0	0	0
PS	Porbeagle	iattc	0	0	0	0	0
PS	Silky	wcpfc	2	4.863	6.581	0	13.983
PS	Silky	iccat	5	0.42	0.428	0.045	0.796
PS	Silky	iotc	3	3.085	2.46	0.301	5.868
PS	Silky	iattc	6	1.4	1.542	0.166	2.633
PS	Thresher	wcpfc	0	0.002	0.003	0	0.004
PS	Thresher	iccat	4	0.001	0.001	0	0.002
PS	Thresher	iotc	2	0	0	0	0
PS	Thresher	iattc	1	0.002	0.003	0	0.004
PS	Whale shark	wcpfc	1	0.003	0.003	0	0.006
PS	Whale shark	iccat	1	0.003	0.003	0	0.006
PS	Whale shark	iotc	0	0.003	0.003	0	0.006
PS	Whale shark	iattc	1	0.003	0.003	0	0.006

Table 1.3. Relevant stock assessments for pelagic elasmobranchs captured by longline and purse seine tuna fisheries. Stock assessments that did not determine stock status are included in this table.

RFMO	Common name	Population (if indicated)	Year Assessed	Conc-lusive?	Over-exploited?	Stock status	Reference	Link
IATTC	Blue shark	northern	2017	X		not overfished	ISC 2017	http://isc.fra.go.jp/pdf/ISC17/ISC17_Annex13-Stock_Assessment_and_Future_Projections_of_Blue_Shark.pdf
IATTC	Silky	Pacific-wide	2015			undetermined	Aires-da-Silva et al, 2015	https://www.iattc.org/GetAttachment/9b8da34e-791e-4345-beba-fd6586511886/SAC-06-08b%20-%20Updated%20indicators%20for%20silky%20sharks
ICCAT	Blue shark	southern	2015			undetermined	ICCAT 2015	https://www.iccat.int/Documents/SCRS/DetRep/BSH_SA_ENG.PDF
ICCAT	Blue shark	northern	2015	X	X	overfishing	ICCAT 2015	https://www.iccat.int/Documents/SCRS/DetRep/BSH_SA_ENG.PDF
IATTC	Porbeagle	southern hemisphere	2017	X		not overfished	Hoyle et al. 2017	https://www.wcpfc.int/doc/sc13-sa-wp-12/southern-hemisphere-porbeagle-shark-assessment-placeholder
ICCAT	Porbeagle	northwest	2020	X	X	overfished	ICCAT 2020	https://www.iccat.int/Documents/Meetings/Docs/2020/REPORTS/2020_POR_SA_ENG.pdf
ICCAT	Porbeagle	northern and southern	2020			undetermined	ICCAT 2020	https://www.iccat.int/Documents/Meetings/Docs/2020/REPORTS/2020_POR_SA_ENG.pdf
ICCAT	Porbeagle	northeast	2009	X	X	overfished, overfishing	ICCAT 2009	https://www.iccat.int/Documents/Meetings/Docs/2009_POR_ASSESS_ENG.pdf
ICCAT	Porbeagle	southwest	2009	X	X	overfished, overfishing	ICCAT 2009	https://www.iccat.int/Documents/Meetings/Docs/2009_POR_ASSESS_ENG.pdf
ICCAT	Shortfin mako	northern	2019	X	X	overfished, overfishing	ICCAT 2019	https://www.iccat.int/Documents/SCRS/DetRep/SMA_SA_ENG.pdf
ICCAT	Shortfin mako	southern	2017	X	X	overfishing	ICCAT 2017	https://www.iccat.int/documents/meetings/docs/2017_sma_ass_rep_eng.pdf
IOTC	Porbeagle	southern hemisphere	2017	X		not overfished	Hoyle et al. 2017	https://www.wcpfc.int/doc/sc13-sa-wp-12/southern-hemisphere-porbeagle-shark-assessment-placeholder
IOTC	Shortfin mako		2018	X	X	overfishing occurrin	Brunel et al., 2018	http://www.iotc.org/documents/WPEB/14/37

						g, not overfished		
IOTC	Silky		2018	X	X	overfishing, not overfished	Urbina et al, 2018	https://www.iotc.org/documents/preliminary-stock-assessment-silky-shark-indian-ocean-using-data-limited-approach
IOTC	Blue shark		2018	X		Not overfished, no overfishing	IOTC, 2021	https://iotc.org/documents/SC/24/RE
WCPFC	Whale shark		2018	X		not overfished	WCPFC 2018	https://www.wcpfc.int/doc/19/whale-shark-2018
WCPFC	Blue shark	northern	2017	X		not overfished	WCPFC 2017	https://www.wcpfc.int/doc/15/north-pacific-blue-shark
WCPFC	Blue shark	southern	2017	X		overfishing unlikely	WCPFC 2017	https://www.wcpfc.int/doc/15/north-pacific-blue-shark
WCPFC	Oceanic whitetip		2019	X	X	overfished, overfishing	WCPFC 2019	https://www.wcpfc.int/file/361982/download?token=SeN4NxdL
WCPFC	Shortfin mako	northern	2017	X		not overfished, no overfishing	WCPFC 2019	https://www.wcpfc.int/file/361986/download?token=taiLMq8p
WCPFC	Silky		2018	X	X	overfishing, not overfished	WCPFC 2019	https://www.wcpfc.int/file/361983/download?token=g1tpvUEc
WCPFC	Porbeagle	southern hemisphere	2017	X		not overfished	Hoyle et al. 2017	https://www.wcpfc.int/doc/sc13-sa-wp-12/southern-hemisphere-porbeagle-shark-assessment-placeholder
WCPFC	Bigeye thresher		2016			undetermined	Fu et al 2016	https://www.wcpfc.int/doc/sc13-sa-wp-11/bigeye-thresher-shark-assessment

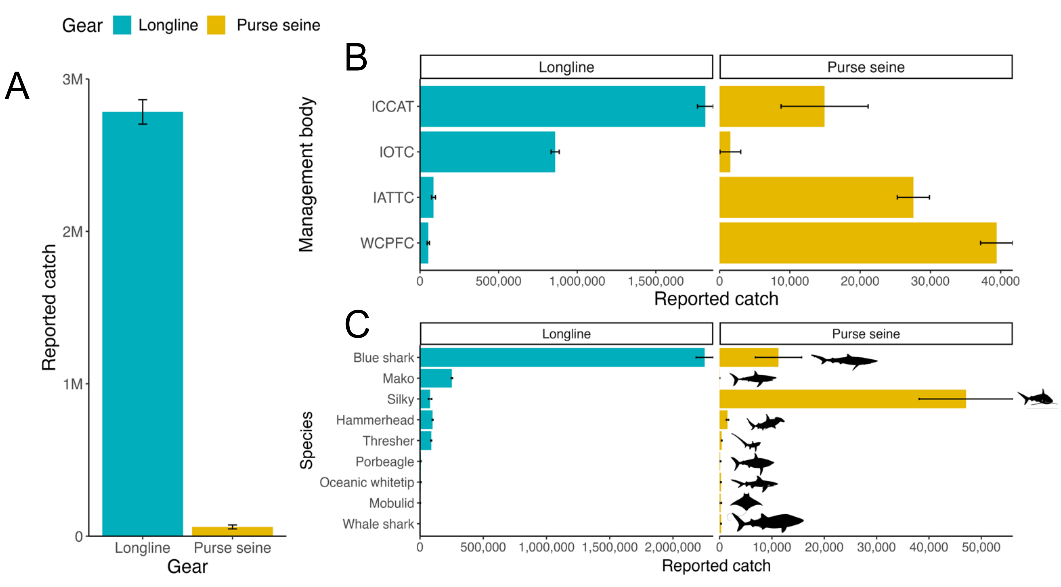

Figure 1.1 Global annual mean reported catch (individuals) of elasmobranchs in tuna fisheries (2007-2017) by (A) gear type, (B) tRFMO, and (C) species or genus. Error bars represent one standard error from the mean. Note different axes.

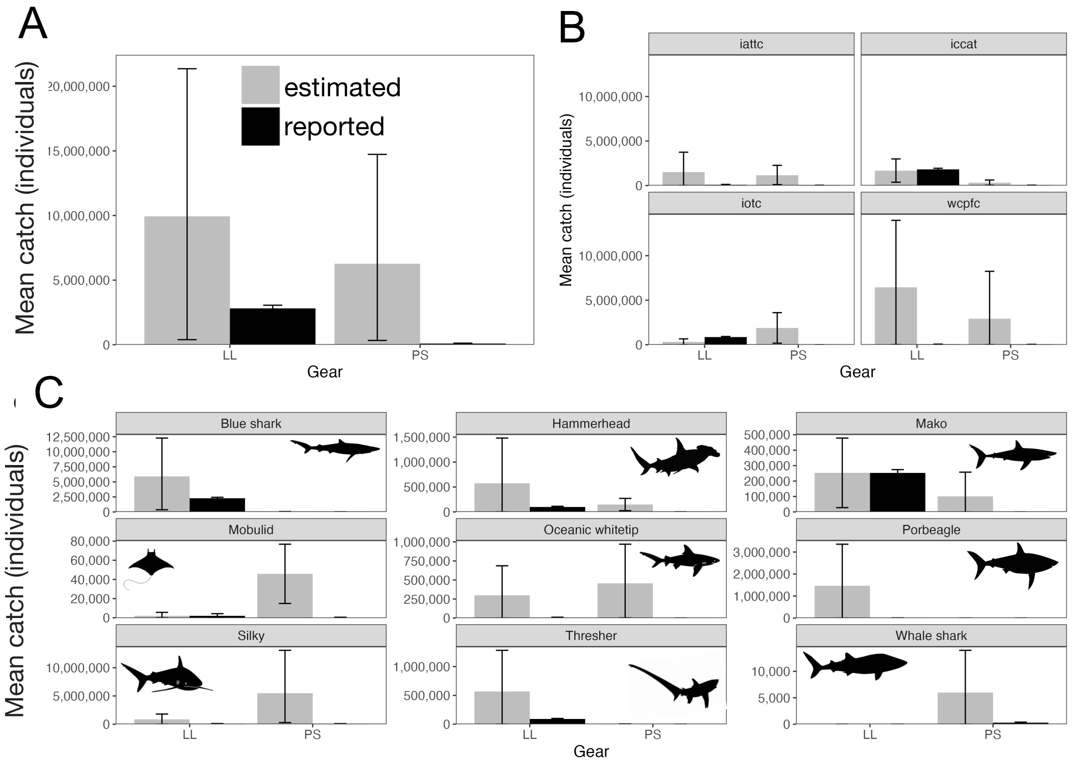

Figure 1.2. Annual average reported and estimated catch of pelagic elasmobranchs (individuals) captured by A) longline and purse seine gears and B) grouped by species (2007–2017). For reported data (black bars), error bars represent 95% CIs. For estimated data (gray bars), error bars represent projected catches using the upper and lower 95% confidence intervals for catch rate coefficient and averaged across years.

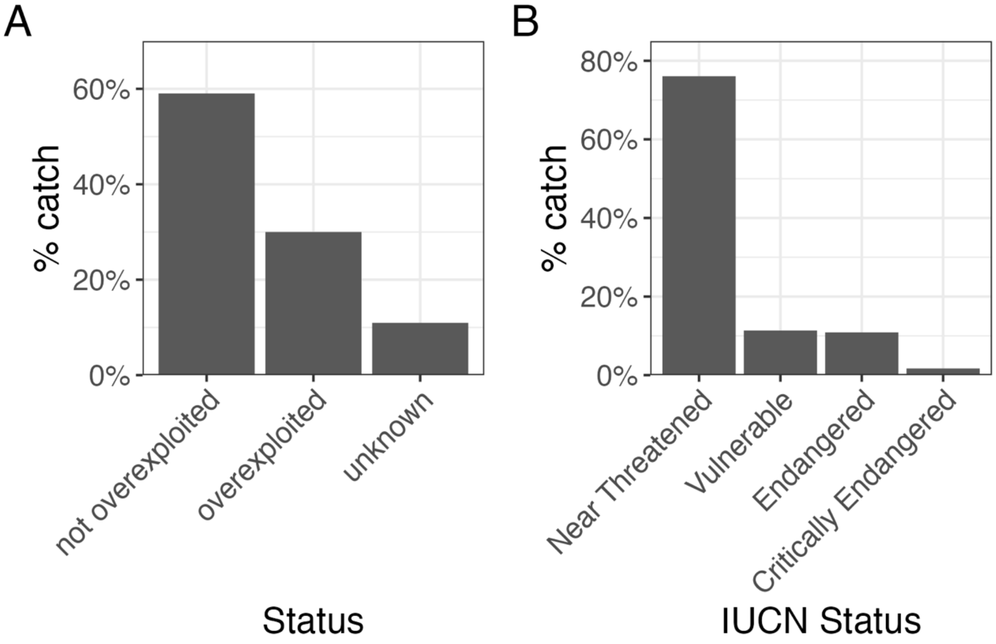

Fig. 1.3 A) Stock assessment stock status and B) IUCN evaluation as a proportion of reported annual elasmobranch catch in tRFMOs (2007–2017).

CHAPTER 2

Mobile mobulid metapopulations: Genetic population structure and conservation implications for three Mobulid species in the Eastern Pacific Ocean

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Abstract

Manta and devil rays (Family Mobulidae) are a charismatic but understudied group of nine widely-ranging, filter-feeding elasmobranch species. Mobulids are impacted by multiple anthropogenic threats, and population declines have been observed in many regions. However, lack of clarity about both population sizes and genetic population structure for these species prevents the implementation of informed and targeted conservation and management interventions. We use genome sequencing to describe patterns of population genetic structure and diversity for three of the five mobulid species occurring in the eastern Pacific Ocean. We used sequences from individuals within four regions in tropical and subtropical Pacific Ocean, using samples from the Indian Ocean as outgroups for comparison for globally distributed species. We used Restriction-Site Associated Sequencing (RADseq) to generate 25,195 single-nucleotide polymorphisms (SNPs) from 110 individuals and Bayesian clustering to analyze neutral loci and loci under potential selection (outlier loci). Results show that all species examined exhibit weak but statistically significant population structure among sites (F_{ST} = 0.001 – 0.036), but neutral loci analyses suggest gene flow exists among populations. Using outlier loci, we show geographically mediated local selection occurs between Indian Ocean and eastern Pacific Ocean populations in two species (*Mobula birostris* and *M. thurstoni*), as well as within Eastern Pacific Ocean regions for all species. We found evidence for high levels of inbreeding in two species (*M. thurstoni* and *M. munkiana*), potentially due to low population sizes and genetic bottlenecks. This study provides critical information to inform conservation and management for threatened mobulids and suggests that manta and devil rays should be managed regionally rather than globally to preserve genetic diversity and healthy populations.

Introduction

Biodiversity is increasingly imperiled by the expansion of anthropogenic activities (Ceballos et al. 2020). In the ocean, fisheries are a primary driver of biodiversity loss, with negative consequences for ecosystem function and related ecosystem services like food security and resilience to disturbance (Cardinale et al. 2012). In many marine taxa, this loss is reflected not only in the loss of species but in the loss of intraspecific genetic diversity (Gandra et al. 2021). The loss of genetic diversity is often a cause for concern, as numerous studies have established a positive relationship between genetic diversity and a population's adaptive capacity, stability under stressful environmental conditions, and the preservation of ecosystem function and services (Hughes et al. 2008; Bolnick et al. 2011; Prunier et al. 2019).

Due to the large and diffuse nature of ocean ecosystems, many species, particularly highly migratory pelagic fishes, are assumed to have very high levels of connectivity and gene flow (i.e. panmictic populations) (Rosenblatt & Waples 1986;

Palumbi 1992; Cowen et al. 2000). Theoretically, because pelagic organisms do not face physical barriers to their movements, there is high gene flow between distant locations, and therefore may be more resilient to intense fishing pressure (Waples 1998; Hellberg 2009). However, multiple studies on a variety of pelagic fish species have suggested that at least some marine species exhibit population structure, often driven by spatial or temporal factors that restrict gene flow (Reiss et al. 2009; Iacchei et al. 2013; Thia et al. 2021). Among pelagic fishes, oceanic sharks and rays (i.e., elasmobranchs) are highly vulnerable to anthropogenic impacts, for which baseline genetic data on population structure and gene flow is often lacking (Dudgeon et al. 2012). Due to their uniquely slow growth, low fecundity, and mortality in target and bycatch fisheries, the abundance of pelagic elasmobranch has been estimated to decline by 71% over the past half-century (Dulvy et al. 2021; Pacoureau et al. 2021).

Knowledge of genetic population structure in elasmobranchs is crucial for developing conservation and management strategies for vulnerable species and populations as it can identify evolutionarily significant units that are potentially important to maintaining genetic diversity and population health (Moritz 1994; Reiss et al. 2009). Further, population genetic studies can be used to estimate effective population size (N_e), which is useful for highly pelagic marine species that are difficult to study with traditional ecological methods (Ovenden 1990; Beheregaray 2008; Ovenden et al. 2016). Unfortunately, many elasmobranchs lack necessary reference population genetic information with which to understand fishing impacts and potential management strategies (Beheregaray, 2008; Waples et al. 2008). Data suggest that elasmobranchs exhibit a wide spectrum of population structure, from global or regional panmixia (e.g. blue shark, *Prionace glauca*; whale shark, *Rhincodon typus;* Portuguese dogfish, *Centroscymnus coelolepis*), to populations with weak but relevant genetic structure among oceans (e.g., shortfin mako shark *Isurus oxyrinchus;* bonnethead shark, *Sphyrna tiburo*), to highly structured populations with low gene flow (e.g., white shark, *Carcharodon carcharia*; zebra shark, *Stegostoma fasciatum*; spot-tail shark, *Carcharhinus sorrah*) (Pardini et al. 2001; Schrey & Heist 2003; Castro et al. 2007; Dudgeon et al. 2009; Ovenden et al. 2009; Blower et al. 2012; Veríssimo et al. 2012, 2017; Escatel-Luna et al. 2015).

Among elasmobranchs, manta and devil rays (Mobulidae) are a charismatic but understudied group of nine widely-ranging, filter-feeding batoid species found circumglobally in tropical and subtropical waters (Couturier et al. 2012). Mobulids have low reproductive rates (as few as one pup every two to seven years) and extremely low population growth rates; life history traits that make them highly vulnerable to overexploitation (Marshall & Bennett 2010; Couturier et al. 2012; Deakos 2012; Pardo et al. 2016; Stevens 2016). A primary threat to mobulids is targeted and incidental capture ("bycatch") in fisheries, with the highest catch rates reported from industrial vessels using gillnets (Fernando & Stewart 2021) and purse seines, and to a lesser extent longlines (Hall & Roman 2013; Croll et al. 2016). Artisanal fisheries likely capture mobulids in substantial numbers, though data collection and reporting for mobulids in these fisheries is often poor or nonexistent (Fernando & Stewart 2021; Haque et al. 2021). Target fisheries for mobulids are driven mainly by demand for meat and the trade in gill plates; the latter marketed as traditional medicine in Asia (Croll et al. 2016; O'Malley et al. 2017). As a result of these threats, all 9 of the recognized mobulid species are listed as Endangered on the IUCN Red List (7 Endangered and two Vulnerable) (IUCN 2022). Five of these 9 mobulid species occur in the Eastern Pacific (Notarbartolo di Sciara 1988).

Over the past few decades, advances in genomic methods helped to clarify mobulid phylogeny (Kashiwagi et al. 2012; Poortvliet et al. 2015; Hosegood et al. 2018) and estimate when mobulids diverged from closely related taxa (Rhinoptera), ~30 million years ago (Poortvliet et al. 2015). However, few studies have investigated the degree of genetic differentiation within and among mobulid populations, especially for the smaller more understudied devil rays (Lawson et al. 2017). Given known anthropogenic impacts and reported population declines for all Mobulids (Ward-Paige et al. 2013; Stewart et al. 2018), there is growing interest in the identification of unique populations and estimation of population sizes inform effective fisheries management (Stewart et al., 2018), particularly in the Eastern Pacific (Griffiths & Lezama-Ochoa et al, 2021).

To address these research needs, we build on early studies of mobulid genetics by using fractional genomic tools to investigate population genetics for three eastern Pacific mobulid species (Table 1). We use restriction site-associated DNA sequencing (RADseq) to generate single nucleotide polymorphisms (SNPs) from genotyped individuals belonging to *Mobula birostris, M. munkiana,* and *M. thurstoni,* captured through their ranges in the Pacific as well as an Indian Ocean outgroup. Using these data, we ask: 1) do mobulids show evidence of population structure or panmixia? and 2) what are effective population sizes for mobulids? Answering these questions and their implications will help fill critical knowledge gaps necessary to effectively target management and conservation action for mobulids.

Methods

Sample collection

Tissue samples were collected in the Indian and Pacific Oceans from three mobulid species: *M. birostris, M. munkiana,* and *M. thurstoni* (Table 2). Dedicated sampling was conducted in one country (Nicaragua) and combined these with opportunistic sampling from existing research collections. Original samples collected for this study were approved by UCSC IACUC #CROLD1802. Tail and muscle tissue samples were collected by trained technicians in Nicaragua under the coordination of the Inter-American Tropical Tuna Commission (CITES permit #14116) (Table 2). Opportunistic samples were also obtained from collections used by Poortvliet et al. (2015) and Stewart et al. (2017) that were collected in Mexico, Ecuador, and Peru. Samples from the Indian Ocean and Southeast Asia were originally collected by Blue Resources Trust and the Large Marine Vertebrates Research Institute Philippines and previously stored at University of California, San Diego, Scripps Institute of Oceanography. All samples were stored in ethanol or silica desiccant and refrigerated to await processing. Opportunistic samples were all collected and imported to the U.S. prior to listing on Appendix II of CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) (2013 for *M. birostris* and 2016 for *M. munkiana* and *M. thurstoni*), thus no CITES permit was obtained for these samples. Sample sites were grouped regionally for analysis into two ocean basins: Indian Ocean (Sri Lanka and India) and eastern Pacific Ocean (Mexico, Nicaragua, Ecuador, Peru). Within the eastern Pacific Ocean sites, samples were grouped into three regions for analysis: north (Baja California peninsula and Revillagigedo Islands), central (Nicaragua), and south (Ecuador and Peru).

DNA extraction and RAD library preparation

DNA was extracted using Qiagen DNAeasy Blood & Tissue Kits following kit protocol for high-quality DNA. We used Restriction Site Associated DNA Sequencing (RAD-Seq), a fractional genome sequencing method that subsamples the genome at homologous locations. We prepared six libraries of 96 samples each with restriction enzyme SbfI (Miller et al. 2007; Baird et al. 2008; Longo & Bernardi 2015). Extracted genomic DNA was standardized to 100ng per sample. We physically sheared libraries on a BioRuptor NGS sonicator for four 30s cycles at 4°C. Ampure XP beads (Agencourt) were used for size selection and purification. The final PCR amplification step was carried out in 15µl reaction volumes with 8, 10, and 12 amplification cycles, and the best PCR was chosen. After library creation, each library containing 96 individually barcoded samples was sequenced in two lanes of 100bp single-end reads on an Illumina HiSeq 4000 at the Vincent J. Coates Genomic Sequencing Lab at University of California, Berkeley.

Data analysis for single nucleotide polymorphisms

Sequences were filtered and single nucleotide polymorphism (SNP) discovery and genotyping was conducted using the software program STACKS v 2.62 (Davey et al. 2011; Catchen et al. 2013; Narum et al. 2013). We sorted, filtered, and demultiplexed reads using the '*process_radtags'* script with individual barcodes that were ligated during the RADseq library preparation (Catchen et al. 2013; Rochette et al. 2019). All sequenced fragments were trimmed from the 3′ end to a length of 92 bp. We filtered out reads that did not match to the 6-bp barcode and 8-bp SbfI restriction site. Individuals with degraded DNA and/or poor sequence coverage, including all samples from Bohol Sea in the Philippines, were excluded from analyses. Data from each individual were grouped *de novo* into loci and polymorphic nucleotide sites were identified, and then matched against a catalogue of alleles produced for individuals from each species with >8x coverage. For samples from individuals that were unidentified, a phylogenetic tree using the program PAUP v 4.0a169 with a catalog of three individuals with high coverage from each species was produced. We used this tree and a separate STRUCTURE plot containing all individuals to assign correct species identification. We ran multiple iterations of the '*populations'* script within STACKS using the command -write_single_snp to generate output files. We only included loci that were present in 75% of the individuals (-r 0.75) per population. We used a first '*populations'* script to identify individuals with more than 50% missing data and removed those from the analysis using VCFTOOLS v 0.1.16, and adjusted the parameters to minimize the proportion of missing data (Table 3). We generated *genepop* files for use in the software GENODIVE v 3.03 (Meirmans, 2020).

Population structure

Neutral and outlier loci were evaluated using Bayesian clustering analyses with the software STRUCTURE v 2.3.4 (Pritchard et al. 2000; Falush et al. 2003, 2007; Hubisz et al. 2009). Ten replicates were run for each genetic cluster (K) up to n+2, where n is the number sample sites for a given species, each with a burn-in of 10,000 iterations, 100,000 Markov Chain Monte Carlo reps with no admixture and no priori location assumptions. We identified the most likely number of clusters according to the DeltaK statistic, which was calculated using the Evanno method (Evanno et al. 2005) and the application STRUCTURE Harvester. The R package *Pophelper* v 2.3.1 (Francis, 2017) was used to summarize and plot results from replicate STRUCTURE runs. We also performed a principal components analysis (PCA) and a discriminant analysis of principal components (DAPC), a multivariate method to describe clusters of genetically related individuals, using the R package *adegenet* v2.1.4 (Jombart & Bateman 2008; Jombart et al. 2010). Twenty principal components (PCs) and two discriminant analyses (DAs) were retained for each DAPC analysis.

Outlier analysis

In addition to examining neutral loci, we evaluated outlier loci, which are loci that are extremely divergent from the rest of the genome (Luikart et al. 2003). These loci are considered to potentially be undergoing selection, possibly leading to local adaptation if associated to environmental drivers (Ahrens et al. 2018). In this study, loci under selection were categorized by identifying outliers with *phist* values (produced by STACKS) greater than three standard deviations from the mean for each species (Weir 1996; Bernardi et al. 2016). Outlier loci were used to run separate STRUCTURE analyses using the same parameters and replicates described above. We also conducted PCA and DAPC analyses using only these loci.

Genomic statistics

We calculated genomic statistics for populations with at least four individuals per site. Number of alleles, nucleotide diversity, observed and expected heterozygosity were obtained using GENODIVE v 3.03 (Meirmans 2020). We used 10,000 permutations to calculate pairwise Wright's fixation index (F_{ST}), which measures genetic variation among geographically separated populations (Wright 1965), G'_{ST} (Nei et al. 1975), and global F_{ST} using an analysis of molecular variance (AMOVA). We extracted nucleotide diversity and number of alleles from the STACKS output. We grouped individuals of the same species to estimate effective population size for each species (N_e).

Kinship

We evaluated relatedness within species using kinship coefficients (Loiselle et al. 1995) for each pair of individuals using GENODIVE v 3.03 (Meirmans 2020). We binned relatedness into the following bins using GENODIVE v 3.03: nearly identical ($0.57 > k > 0.375$), full-sib ($0.374 > k > 0.1875$), half-sib ($0.1874 > k > 0.09375$) and quarter-sib ($0.09374 > k > 0.047$) following Crane et al. (2018). The dataset was screened for duplicate sampling by assessing any nearly identical individuals; if a duplicate was identified, it was removed and only one individual was retained for downstream analysis.

Effective population size

Effective population size (N_e) is defined as the size of an 'ideal' population that would have the same rate of genetic change as the given population (Wright 1931). Though N_e does not always reflect census sizes because it only reflects individuals that are reproducing and passing their genes to the next generation, it is widely used in conservation as an indicator of genetic diversity, drift, and inbreeding (Waples & Do 2010). We used two methods to calculate N_e. First, we used N_eEstimator v. 2.1 (Do et al., 2014), which uses the single-time-point linkage disequilibrium method to estimate N_e for each species (Waples & Do 2010). We report jackknifed 95% confidence intervals using a critical value of 0.05. We also estimated N_e by using the value of Tajima's π (Pi) obtained from STACKS and the equation $\pi = 4 N_e \mu$, where μ is mutation rate (Watterson 1975; Tajima 1983). We used two mutation rate values that have been estimated for fishes (10^{-8} and 10^{-9}) (Brumfield et al. 2003; Crane et al. 2018).

Results

A total of 25,195 sequenced loci were retained from 110 individuals belonging to three mobulid species after removing individuals with low coverage (Fig. 1, Table 3). We evaluated genomic statistics, population structure and gene flow among sample sites using both neutral loci (Table 4) and outlier loci (Table 5), genetic diversity within species (Table 6) and populations (Table 7), and estimated effective population size for each species (Table 7). Across all species, population structure analyses using neutral loci indicated high gene flow among populations and a lack of or very weak population structure (Table 4, Fig 2A, 3A, 4A). However, for all species, outlier analyses showed clear partition between different geographic sites (Fig 2B, 3B, 4B).

Mobula birostris exhibited the highest genetic diversity, based on observed and expected heterozygosity and nucleotide diversity ($H_o = 0.63$, $H_E = 0.66$, $\Phi = 0.00064$), while *M. munkiana* had the lowest genetic diversity ($H_o = 0.037$, $H_E = 0.043$, $\Phi = 0.00038$). *Mobula.thurstoni* fell in between these ($H_o = 0.48$, $H_E = 0.072$, $\Phi = 0.00054$, Table 7). Inbreeding was highest for *M. thurstoni* ($F_{is} = 0.333$), followed by *M. munkiana* ($F_{is} = 0.149$), and lowest for *M. birostris* ($F_{is} = 0.046$, Table 7). Beyond comparisons between species, we compared populations within each of these species below.

Mobula birostris

We analyzed sequences from 36 *M. birostris* individuals from three sampling sites after removing individuals with low coverage (Table 2). We identified 8,359 polymorphic loci among these individuals (Table 3). Overall, we found evidence for the presence of local selection that is geographically partitioned, despite gene flow, occurring between the Indian Ocean and Eastern Pacific Ocean, as well as between the northern (Mexico) and southern Eastern Pacific Ocean (Peru). Indication of weak but statistically significant population differentiation was found when examining neutral loci, and outlier loci further suggest geographically mediated partitioning. Among *M. birostris*, genetic diversity was similar across populations, but highest in Peru ($H_o = 0.124$ $H_E = 0.118$, $\Phi = 0.00062$), followed by Mexico ($H_o = 0.121$, $H_E = 0.117$, $\Phi = 0.00062$) and the Indian Ocean ($H_o = 0.113$, $H_E = 0.114$, $\Phi = 0.0006$).

Population structure

Global F_{ST} among all populations of *M. birostris* indicated weak but significant genetic differentiation (AMOVA $F_{ST} = 0.006$; $p<0.001$). The STRUCTURE analysis using neutral loci indicated that the most likely number of clusters was K=2, yet, the STRUCTURE plot revealed no visible population structure patterns (Figure 2A). However, both the PCA and DAPC analysis revealed some clustering among populations (Figure 2C, 2D).

The outlier analysis identified 187 outlier loci under selection. The STRUCTURE analysis for outlier loci suggested that K=3 was the most likely number of clusters, and the STRUCTURE plot indicated distinct genetic differences between individuals from each of the three sites (Fig. 2B).

For neutral loci, pairwise population differentiation F_{ST} ranged between 0.001 and 0.007 (Table 4), and appeared to indicate low but statistically significant population structure between the Indian Ocean and Mexico ($F_{ST} = 0.007$, $p<0.005$), and the Indian Ocean and Peru ($F_{ST} = 0.007$, $p<0.005$), though not between Mexico and Peru. For outlier loci, pairwise population differentiation F_{ST} was significant for all regional pairs, and ranged from 0.101 to 0.172 (Table 5).

Effective population size

The effective population size, N_e, across all populations was 393.4 – infinite as calculated by N_eEstimator. The mutation rate calculation indicated an effective population size of 500 – 5,000 individuals (Table 8).

Kinship

No highly related individuals were identified among individuals sampled.

Mobula munkiana

We analyzed sequences from 36 *M. munkiana* individuals from eight sampling sites after removing individuals with low coverage (Table 2). We identified

7,990 polymorphic loci among these individuals (Table 3). Overall, we found evidence for gene flow and local selection that is geographically partitioned. Analyses using neutral loci suggest gene flow occurs between populations, yet outlier loci data suggest local selection is occurring for each of the northern (Mexico), central (Nicaragua), and southern populations (Peru). Individuals from Nicaragua had the genetic diversity ($H_o = 0.141$, $H_E = 0.144$, $\Phi = 0.00055$; Table 7), followed by Peru ($H_o = 0.139$, $H_E = 0.123$, $\Phi = 0.00048$) and Mexico ($H_o = 0.132$, $H_E = 0.123$, $\Phi = 0.00047$).

Population structure

Global F_{ST} among all populations indicated significant genetic differentiation (AMOVA F-value = 0.003; $p<0.01$). The STRUCTURE analysis using neutral loci indicated that the most likely number of clusters was K = 2. The STRUCTURE plot did not reveal any clear genetic differentiation related to sampling location for neutral loci (Fig. 4A). Visually, no clustering was indicated by the PCA, but the DAPC analysis showed each population clustering distinctly, with some overlap (Fig 3C, 3D). We identified 325 outlier loci under selection; the STRUCTURE plot (K=3) revealed three distinct clusters that were grouped by sample location for these loci (Fig. 3B).

For neutral loci, pairwise population differentiation F_{ST} ranged between -0.002 and 0.005. Weak but significant differentiation was identified between Nicaragua and Mexico ($F_{ST}= 0.005$, $p<0.005$); significant differentiation was not found between other paired sites using neutral loci (Table 4). For outlier loci, all pairwise F_{ST} values were significant, and ranged from 0.116 to 0.23 (Table 5).

Kinship

Two pairs of half-sibs were identified among the individuals from Mexico (k=0.144 and k= 0.188).

Effective population size

N_eEstimator indicated that effective population size across all populations was 59.5 - infinite individuals. The mutation rate calculation indicated an effective population size of 250 - 2,500 individuals (Table 8).

M. thurstoni

We analyzed sequences from 38 *M. thurstoni* individuals from five sampling sites after removing individuals with low coverage (Table 2). We identified 8,810 polymorphic loci among these individuals (Table 3). Overall, we found evidence for gene flow among populations when examining neutral loci, but outlier loci indicate geographically driven selection between the Indian Ocean, Mexico, Nicaragua, and Ecuador. The Ecuador population also exhibited the highest nucleotide diversity, expected heterozygosity, and observed heterozygosity data ($H_o = 0.126$, $H_s = 0.13$, $\Phi = 0.00091$; Table 6).

Population structure

Global F_{ST} among all populations indicated weak but significant genetic differentiation (AMOVA F-value: 0.018; $p<0.0001$). The STRUCTURE analysis for neutral loci indicated that the most likely number of clusters was K=2, and the STRUCTURE plot (n=8,810) did not indicate any spatial relationship to population structure (Figure 4A). However, individuals from Ecuador (particularly one single individual) clustered separately from the other populations in the DAPC analysis, and also demonstrated greater genetic diversity than other populations in the PCA analysis (Figure 4C, 4D).

We identified 198 outlier loci under selection. The STRUCTURE analysis using only outlier loci indicated that the most likely number of clusters was K=4, and the plot showed clear differentiation among the four sample regions (Figure 4B). The Nicaragua and Mexico populations appeared visually somewhat more mixed than others when examining outlier loci. There was strong data partitioning between these two northern sites (Nicaragua and Mexico) and the Ecuador population, which is supported by the results of the DAPC analysis (Figure 5D). There was also strong partitioning between the Indian Ocean and the rest of the populations using outlier loci (Fig 5B).

For neutral loci, pairwise population differentiation F_{ST} ranged between 0.001 and 0.036 (Table 4). Weak but significant differentiation was identified between the Indian Ocean and Nicaragua (F_{ST}= 0.033, $p<0.05$) and between the Indian Ocean and Ecuador (F_{ST}= 0.032, $p<0.05$), but not between paired eastern Pacific sites. For outlier loci, all pairwise comparisons were significant (p<0.001), and F_{ST} values ranged from 0.029 to 0.245 (Table 4).

Effective population size

N_eEstimator indicated that effective population size across all populations was 149.6 - infinite individuals. The mutation rate calculation indicated an effective population size of 500 – 5,000 individuals, which was the same as for *M. birostris* (Table 7).

Kinship

We identified one pair of highly related individuals, categorized as quarter-sibs (k=0.092) among individuals sampled from India.

Discussion

We present the first population genomic assessment to examine and compare population structure for multiple mobulid species, and the first investigation of population genetic structure for *M. munkiana* and *M. thurstoni*. Overall, our results suggest that for the species we examined; M. birostris, *M. thurstoni* and *M. munkiana;* gene flow exists among these populations despite very weak but statistically significant structure in some cases, particularly between the Indian and Eastern Pacific sites. Additionally, we found that geographically mediated local selection occurs between and within ocean basins. We found low genetic diversity, low effective population size, and high inbreeding in *M. munkiana* and *M. thurstoni*, potentially pointing to depleted population sizes and/or possible genetic bottlenecks, though further study is required to verify the mechanism producing these results. These findings suggest that preserving and increasing genetic diversity is important to maintain the stability of mobulid species in the future, and can help delineate management and conservation units for these increasingly threatened species.

Geographically mediated local selection

Consistently, we found that the mobulid populations we examined exhibited only weak or no discernable structure when examining neutral loci, but outlier analyses using markers under selection revealed data partitioning and therefore geographically mediated selection. This pattern is consistent with that of metapopulations, in which local populations that are undergoing selection are simultaneously interacting with other populations through gene flow and migration (Hanski 1998). Notably, some of the genetic differences we observe are congruent with well-recognized biogeographic barriers. For example, we find that for *M. birostris* and *M. thurstoni*, fixation index values in the Indian Ocean were significantly different from those in the Eastern Pacific Ocean in most cases, and that some F_{ST} values were relatively high (e.g., neutral loci $F_{ST} = 0.036$ between India and Nicaragua for *M. thurstoni*) compared to those observed elsewhere in this study. These findings mirror others for elasmobranch populations that show that large oceanic expanses can pose a barrier to gene flow (Duncan et al. 2006; Keeney & Heist 2006; Schultz et al. 2008; Portnoy et al. 2010).

Still, while this study shows that local selection is occurring, we also find evidence of connectivity across populations, indicated by the absence of population structure for all species when examining neutral loci (rather than only those loci under selection). This finding is supported by other studies showing that even highly residential mobulids make occasional long-distance movements, potentially contributing to genetic mixing we show here (Stewart et al. 2016; Armstrong et al. 2019; Andrzejaczek et al. 2021). However, the unique evolutionary history of mobulids—namely, their slow mutation rate, long generation time, recent divergence from their closest ancestor (~30 mya), and relatively residential behavior could help explain this pattern (Poortvliet et al. 2015). It is possible that (as our outlier loci data suggest) mobulids exhibit strong geographically mediated selection and resultant population structure, but that their slow evolution obscures what would otherwise be a robust signal of population structure.

Overall, our findings contribute to a growing body of research suggesting that weak genetic differentiation exists within mobulid species. For example, for reef manta rays (*M. alfredi*), genetic population structure was identified between sites in the Indian and Pacific Oceans ($F_{ST} = 0.110–0.288$; (Hosegood et al. 2018)), between cleaning sites within New Caledonia ($F_{ST} = 0.01$; (Lassauce et al. 2022)), and between Mozambique and Western Australia ($F_{ST} = 0.377$; (Venables et al. 2020)). For oceanic manta ray (*M. birostris*), genetic partitioning was observed between Sri

Lanka, offshore Mexico, and nearshore Mexico (Stewart et al. 2017), as well as among the western Pacific, eastern Pacific, and Gulf of Mexico (Clarke 2002). Still, using only neutral loci Hosegood et al. (2018) found evidence for global genetic panmixia in *M. birostris*, which aligns with our analyses. This suggests that the patterns of concurrent gene flow and local selection we observe may be consistent more generally for mobulids, and that exploration of outlier loci should be pursued in future studies of mobulid genetics to investigate population structure. Overall, our findings build on these, suggesting that mobulids form metapopulations, connected regionally and globally by some degree of gene flow while simultaneously experiencing local selection. Thus, further research should seek to quantify the level of gene flow (e.g., number of individual migrants per generation) necessary to produce these results.

This study is the first to show that like the larger manta species (*M. birostris* and *M. alfredi*), the smaller devil ray species *M. thurstoni* and *M. munkiana* also exhibit local selection. Interestingly, *M. munkiana* (the smallest species we examined and one of the smallest devil ray species) stands out for its relatively low effective population sizes in comparison to other species (though the confidence intervals for these estimates are overlapping); both methods we used to estimate effective population size produced the lowest values for *M. munkiana*. The mutation rate method produced a minimum estimate that was half that of the other species, and the NeEstimator method produced minimum estimates that were roughly ~1/6 and ~1/3 smaller than those of *M. birostris* and *M. thurstoni,* respectively. This is surprising, as

M. munkiana is often observed in large aggregations, sometimes forming schools a few tens of meters in diameter, and is thought to be far more abundant than the other, larger species (Notarbartolo-di-Sciara 1988). There are multiple possible explanations for this, including the relatively small range of this species and size-related transportation constraints on long-distance movements (maximum disc width 130 cm, Table 1). It is also possible that these low estimates result from greater inbreeding, which is supported by the high inbreeding rate and low genetic diversity we found for *M. munkiana* overall (F_{is} =0.149, $H_o = 0.037$, $H_E = 0.043$, $\Phi = 0.00038$, Table 6). Taken together, these results could support historic population depletion in this species, potentially leading to a smaller genetic pool and possible genetic bottleneck. Importantly, *M. munkiana* is listed as Vulnerable by the IUCN Red List (IUCN 2022). Unfortunately, the tendency of this species to form large aggregations may lead to a false interpretation of its population abundance and status. Our genomic results suggest that *M. munkiana* could be at risk of inbreeding depression if impacted by further population declines.

In addition to *M. munkiana*, N_e estimates produced using the mutation rate method were also extremely low for other species examined. There are multiple reasons why effective population size may be low, including low genetic diversity due to bottlenecks or inbreeding, sperm competition, non-viable offspring, or depleted population sizes that lead to reduced diversity within a population (Nei et al. 1975; Frankham 2008). Other research that has identified similarly low N_e values for some elasmobranchs, has suggested that their particularly slow growth rates, long gestation periods, and few offspring, combined with recent depletion, may be driving these low estimates (Blower et al. 2012; Pazmiño et al. 2017; Reid-Anderson et al. 2019). While an investigation of the drivers of low effective population size is beyond the scope of this study, it may be a cause for concern given described population declines for all mobulid species (Ward-Paige et al. 2013). Continuing population declines could expose mobulid populations to detrimental impacts, including the potential for deleterious allele fixation and loss of genetic adaptive capacity. These findings point to the urgent need to conduct stock assessments for mobulids in the eastern Pacific Ocean, which could draw both traditional and emerging methods, such as genomic tools like close-kin-mark-recapture, a method that has been successfully used to estimate population size and inform conservation efforts for other threatened elasmobranch species (Hillary et al. 2018; Trenkel et al. 2022).

Conservation and management implications

Our results have important implications for mobulid conservation and management. Though we show that there is connectivity among mobulid populations regionally, we also demonstrate selection exists, and is acting at a regional and local level, even within the Eastern Pacific Ocean. Given this local selection, low genetic diversity, and relatively high inbreeding at least for *M. munkiana* and *M. thurstoni*, effective management should aim to maintain what genetic diversity exists among mobulids. Therefore, we make the following suggestions for potentially relevant management units considering these results:

- ***M. birostris*** could be grouped into one major oceanic unit in the Eastern Pacific Ocean. Within the Eastern Pacific Ocean, regional units could be grouped by northern (e.g., Mexico) and southern units (e.g., Peru). Future sampling efforts should focus on Central America to investigate further differentiation in the central region between these sites.

- ***M. munkiana*** could be grouped into northern (e.g., Mexico), central (e.g., Nicaragua), and southern regional units (e.g., Peru) within its range in the eastern Pacific Ocean.

- ***M. thurstoni*** could be grouped into one major oceanic unit in the Eastern Pacific Ocean. Within the Eastern Pacific Ocean, regional units could be grouped by northern (e.g., Mexico), central (e.g., Nicaragua), and southern units (e.g. Ecuador).

These proposed management units are based only on the limited sampling sites in this study, and do not encompass the full ranges of these species. Further research should attempt to expand the geographic scope of knowledge about mobulid population structure with greater geographic and taxonomic coverage, as well as finer-scale comparisons, given the fact that we find differences even among relatively close sites in the eastern Pacific Ocean. Importantly, genetic structure studies of other Mobulid species in the eastern Pacifc should also be undertaken. Still, we suggest that the incorporation of population genetic information into delineating biologically relevant conservation and management units can help inform more effective conservation for threatened mobulids.

Beyond the designation of management units, given the low effective population sizes and genetic diversity we find, research efforts should prioritize filling in information gaps crucial for conservation and management, including biological and ecological parameters as well as categorizing the relative impacts of anthropogenic threats to mobulids (Stewart et al. 2018). Considering substantial incidental catches of mobulids in artisanal and industrial fisheries in the eastern Pacific Ocean (Lezama-Ochoa et al. 2020; Griffiths & Lezama-Ochoa 2021), further research should seek to design and test bycatch avoidance and reduction tools, combined with best handling and release practices to reduce fishery-associated mortality (Cronin et al. 2022). Further, our results suggest that fisheries that target mobulids in the eastern Pacific (e.g., in Peru, Nicaragua, and Guatemala) (Alfaro-Cordova et al. 2017) should be investigated, given their potential contribution to high levels of inbreeding and low genetic diversity we identify. Overall, these results elevate and emphasize urgent calls for effective conservation and management for threatened mobulids.

Acknowledgements

The authors are grateful to the Inter-American Tropical Tuna Commission, which facilitated sample collection and coordinated CITES permits in Guatemala and Nicaragua. We would also like to thank the undergraduate research assistants who aided with DNA extraction: Jeannie Johnson, Christina Langford, Jennifer Waldo, Lauren Puffer, and Isabella Ossiander. MRC was funded by a National Science Foundation Graduate Research Fellowship. Funding for sample collection and analysis was provided by the Save Our Seas Foundation, the Monterey Bay Aquarium, and the Seymour Marine Discovery Center.

Table 2.1. Mobulid species examined in this study.

Species	Common name	Species Code	Maximum size (disc width)	IUCN Red List Status	Distribution
Mobula birostris	Oceanic Manta Ray	RMB	700 cm	Endangered	Global
Mobula munkiana	Munk's Pygmy Devil Ray	RMU	130 cm	Vulnerable	Eastern Pacific
Mobula thurstoni	Bentfin Devil Ray	RMO	183 cm	Endangered	Global

Table 2.2. Sampling locations for Mobulids included in this study.

Region	Location of sample	Species	Population ID	Year Collected
Indian Ocean	India	*M. birostris*	RMB_IND	2010-2013
		M. thurstoni	RMO_IND	
	Sri Lanka	*M. birostris*	RMB_SRI	2010 - 2013
North America	Isla El Pardito, Mexico	*M. munkiana*	RMU_ELP	2014
		M. thurstoni	RMO_ELP	2014
	Islas Revillagigedo, Mexico	*M. birostris*	RMB_REV	2013-2015
Central America	Nicaragua	*M. munkiana* *M. thurstoni*	RMU_NIC RMO_NIC	2020
South America	Ecuador	*M. thurstoni*	RMO_ECU	2009
	Peru	*M. birostris*	RMB_PER	2012-2013
		M. munkiana	RMU_PER	

Table 2.3. Number of individuals, SNPs and missing data for each species included in this study. These measures reflect the data after low-coverage individuals were removed.

Species	N	N SNPs	Missing data	Parameters	Mean coverage	sd
M. birostris	36	8,395	15.8%	0.75, -p3	13.9x	11x
M. munkiana	36	7,990	14.2%	0.75, -p3	12.4x	8.0x
M. thurstoni	38	8,810	32.8%	0.75, -p3	10.4x	3.8x

Table 2.4. Pairwise FST values (above the diagonal) and Nei's G'_$_{ST}$ (below the diagonal) between neutral loci for populations of Mobulid species: *M. birostris,* based on 8,395 RADseq loci; *M. munkiana,* based on 9,159 loci; and *M. thurstoni,* based on 8,810 outlier loci. Bold values indicate significant differences: * < 0.05; ** < 0.005.

M. birostris			
	Indian Ocean	Peru	Mexico
Indian Ocean		**0.007****	**0.007****
Peru	**0.007****		0.001
Mexico	**0.007****	0.001	

M. munkiana			
	Mexico	Nicaragua	Peru
Mexico		0.005	0.003
Nicaragua	**0.005***		-0.002
Peru	0.003	0	

M. thurstoni				
	Indian Ocean	Mexico	Nicaragua	Ecuador
Indian Ocean	-	0.034	**0.033****	**0.032****
Mexico			0.001	0.005
Nicaragua	**0.036***	0.001		0.004
Ecuador	**0.033***	0.005	0.004	

Table 2.5. Pairwise FST values (above the diagonal) and Nei's G'_{ST} (below the diagonal) between outlier loci for populations of Mobulid species: *M. birostris,* based on 187 RADseq outlier loci; *M. munkiana,* based on 325 outlier loci; and *M. thurstoni,* based on 198 outlier loci. Bold values indicate significant differences: * < 0.05; ** < 0.005.

M. birostris			
	Indian Ocean	Mexico	Peru
Indian Ocean		**0.102****	**0.106****
Mexico	**0.101****		**0.172****
Peru	**0.101****	**0.168****	

M. munkiana			
	Mexico	Nicaragua	Peru
Mexico		**0.206****	**0.23****
Nicaragua	**0.161****		**0.172****
Peru	**0.173****	**0.132****	

M. thurstoni				
	Mexico	Indian Ocean	Ecuador	Nicaragua
Mexico		**0.201****	**0.044****	**0.029****
Indian Ocean	**0.177****		**0.225****	**0.28****
Ecuador	**0.039****	**0.188****		**0.128****
Nicaragua	**0.029***	**0.245****	**0.12****	

Table 2.6. Genomic statistics for Mobulids included in this study**,** grouped as species. *N:* number of individuals; *Na:* Number of alleles; H_O*:* observed heterozygosity: H_E*:* expected heterozygosity; *Pi:* nucleotide diversity; F_{IS}*:* inbreeding coefficient.

Species	***N***	***N (STACKS)***	N_a	H_o	H_E	***Pi (STACKS)***	F_{is}
M. birostris	36	31.490	1.359	0.063	0.066	0.00064	0.046
M. munkiana	36	24.706	2.0	0.037	0.043	0.00038	0.149
M. thurstoni	38	17.771	1.347	0.048	0.072	0.00054	0.333

Table 2.7. Genomic statistics for Mobulids included in this study, grouped by population within each species. *N:* number of individuals; *Na:* Number of alleles; H_O*:* observed heterozygosity: H_E*:* expected heterozygosity; *Pi:* nucleotide diversity; F_{IS}*:* inbreeding coefficient.

Location	***N (STACKS)***	N_a	H_o	H_E	***Pi (STACKS)***	F_{is}
M. birostris						
Indian Ocean	10.5	1.567	0.113	0.114	0.0006	0.00007
Peru	8.85	1.532	0.124	0.118	0.00062	-0.00003
Mexico	11.08	1.598	0.121	0.117	0.00062	0.00002
M. munkiana						
Mexico	9.91827	1.514	0.132	0.123	0.00047	-0.074
Nicaragua	9.9482	1.685	0.141	0.144	0.00055	0.027
Peru	6.82573	1.408	0.139	0.123	0.00048	-0.126
M. thurstoni						
Indian Ocean	6.50721	1.32	0.103	0.098	0.00066	-0.05
Mexico	8.49051	1.503	0.099	0.119	0.0008	0.167
Nicaragua	9.72869	1.548	0.101	0.119	0.0008	0.154
Ecuador	7.36257	1.568	0.13	0.136	0.00092	0.046

Table 2.8. Effective population sizes (Ne) for three species of Mobulids calculated using the linkage disequilibrium method in Ne Estimator and using the mutation rate method.

Species	**SNPs used**	***Ne* Estimator** (Linkage disequilibrium method)	**Pi** (nucleotide diversity)	**Mutation rate method** $(10^{-8} - 10^{-9})$
M. birostris	1,881	393.4 - infinite	0.00002	500 - 5,000
M. munkiana	12,557	59.5 - infinite	0.00001	250 - 2,500
M. thurstoni	4,969	149.6 - infinite	0.00002	500 - 5,000

Fig. 2.1. Genetic samples of Mobulid rays collected for this study**.** Size of each point is scaled to the number of samples collected from that site. Points are jittered (2,2) to distinguish between adjacent sites.

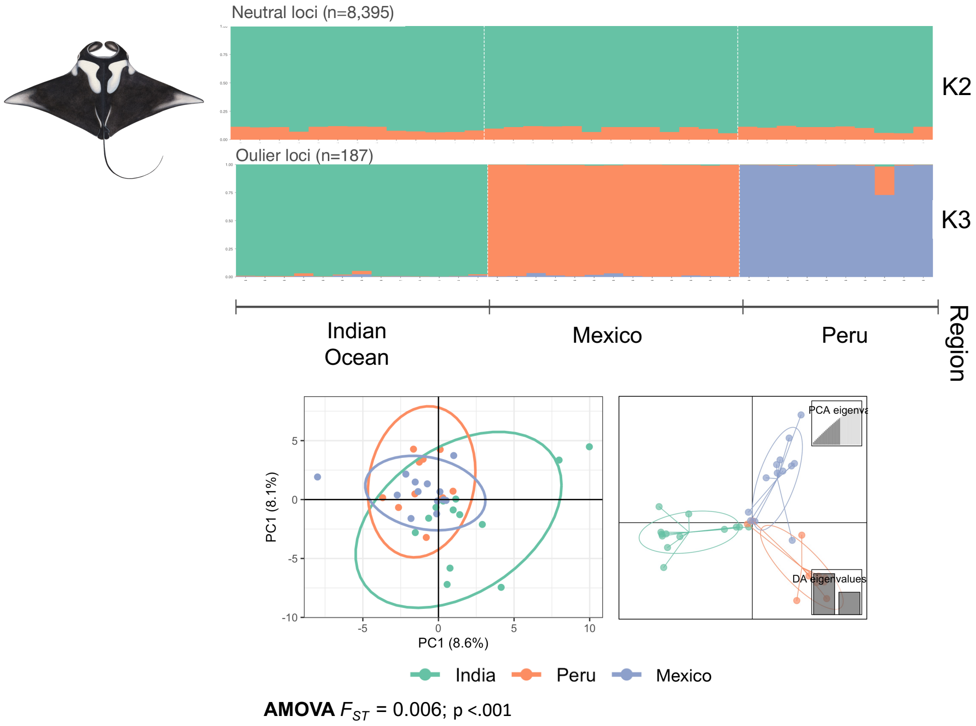


Fig 2.2. Genetic population structure for 36 M. birostris individuals: A) STRUCTURE plot (K=2) generated from neutral loci (n=8,359 SNPs); B) STRUCTURE plot (K=3) generated from outlier loci (phist>mean + 3 sd, n= 187); C) Principal Components Analysis for neutral loci (20 principal components retained), and D) DAPC plot for neutral loci.

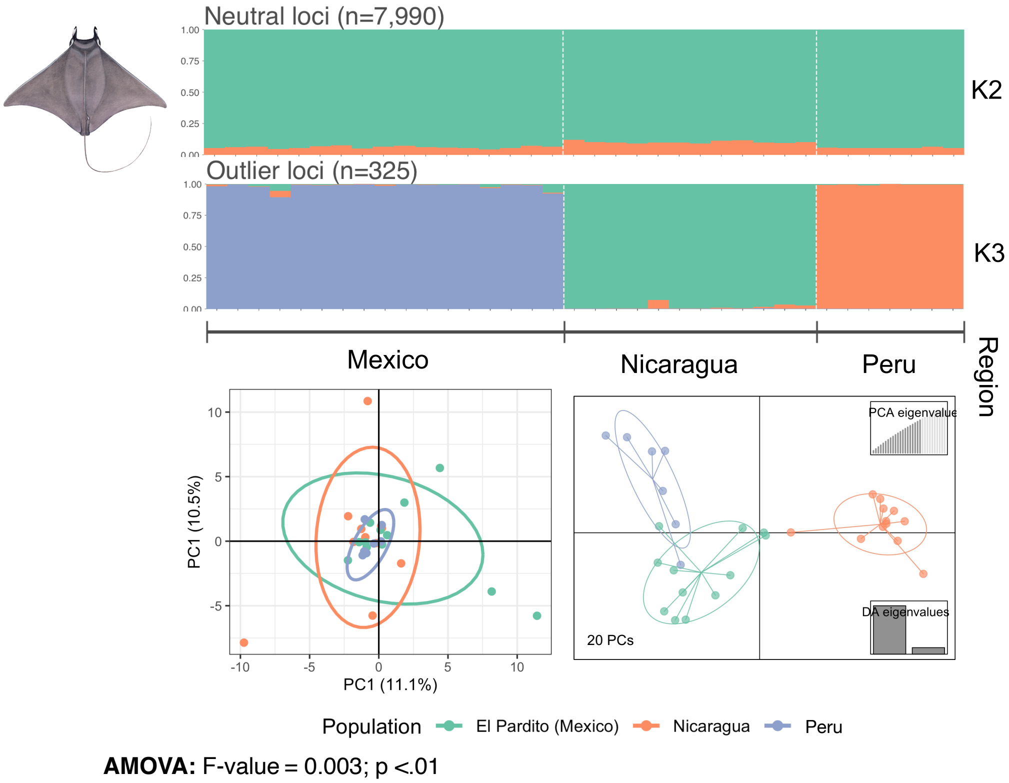
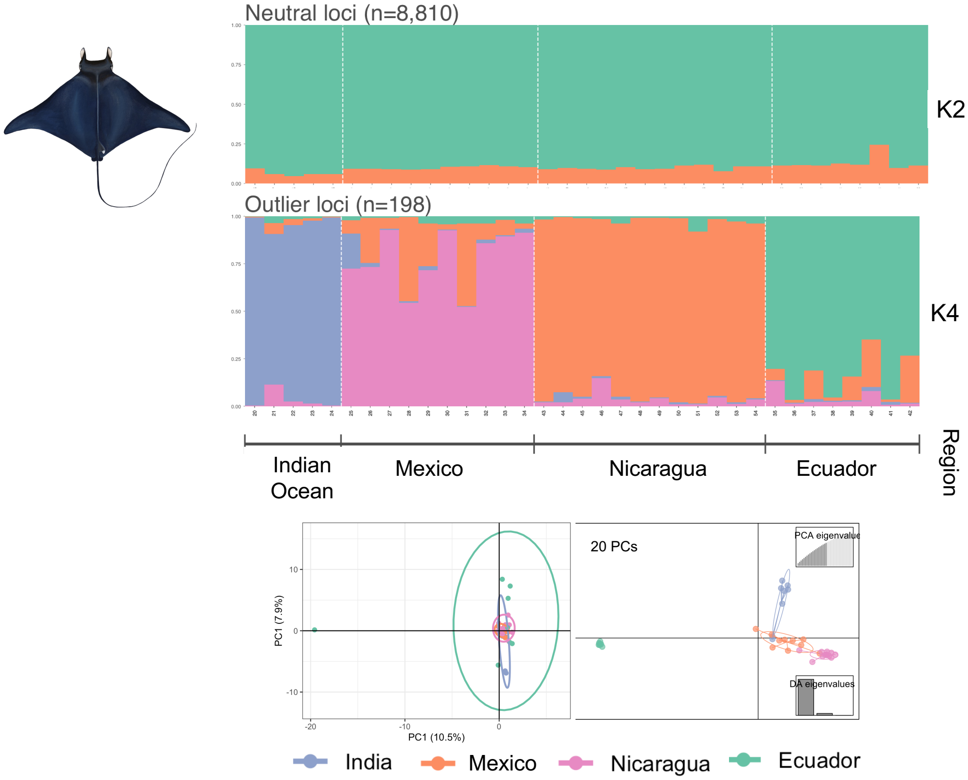


Fig 2.3. Genetic population structure for 36 M. munkiana individuals: A) STRUCTURE plot (K=2) generated from neutral loci (n=7,990 SNPs); B) STRUCTURE plot (K=3) generated from outlier loci (phist>mean + 3 sd, n= 325); C) Principal Components Analysis for neutral loci (20 principal components retained), and D) DAPC plot for neutral loci.



AMOVA F_{ST} = 0.018; p <.001

Fig 2.4. Genetic population structure for 38 M. thurstoni individuals: A) STRUCTURE plot (K=2) generated from neutral loci (n=8,810 SNPs); B) STRUCTURE plot (K=4) generated from outlier loci (phist>mean + 3 sd, n= 198); C) Principal Components Analysis for neutral loci (20 principal components retained), and D) DAPC plot for neutral loci.

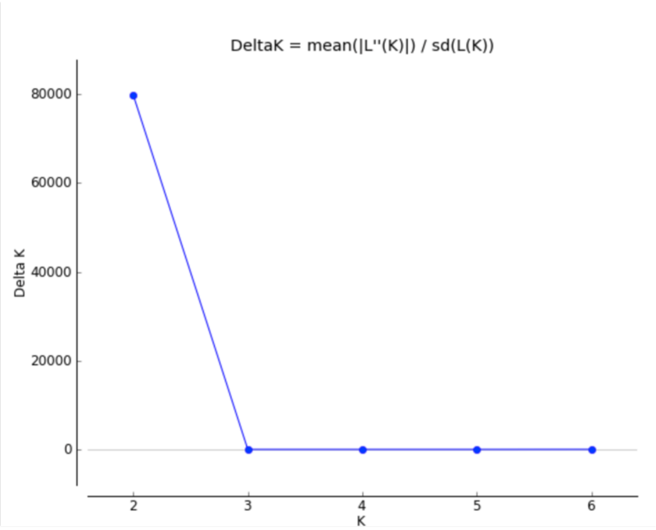


Fig S2.1. DeltaK output from STRUCTURE harvester for neutral loci for M. birostris.

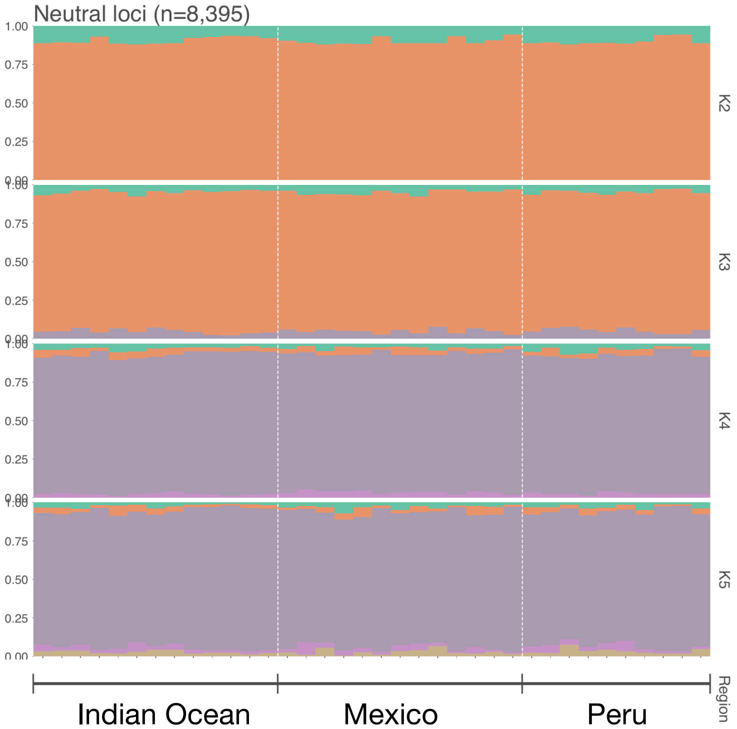


Fig S2.2. STRUCTURE results for K=2-5 for neutral loci (n=8,395) analyzed for *M. birostris*.

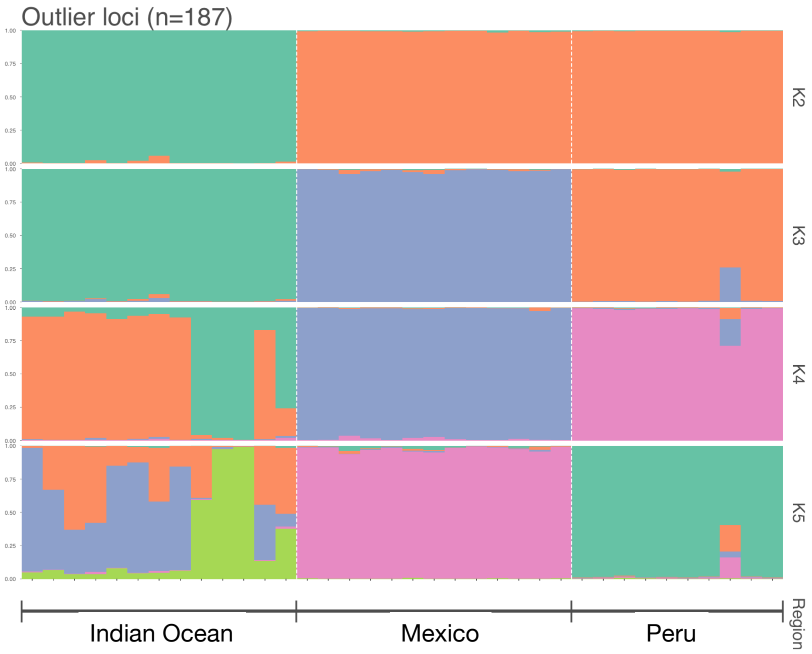


Fig S3.3. STRUCTURE results for K=2-5 for outlier loci (n=464) analyzed for M. birostris.

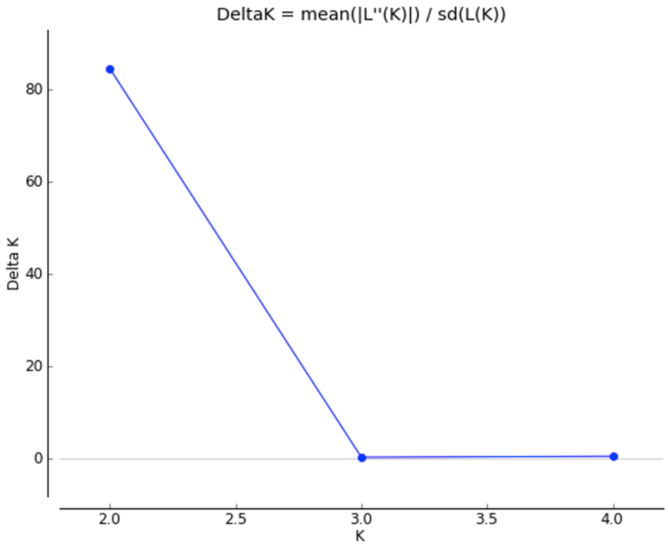


Fig S2.4. DeltaK output from STRUCTURE harvester for neutral loci for *M. munkiana*.

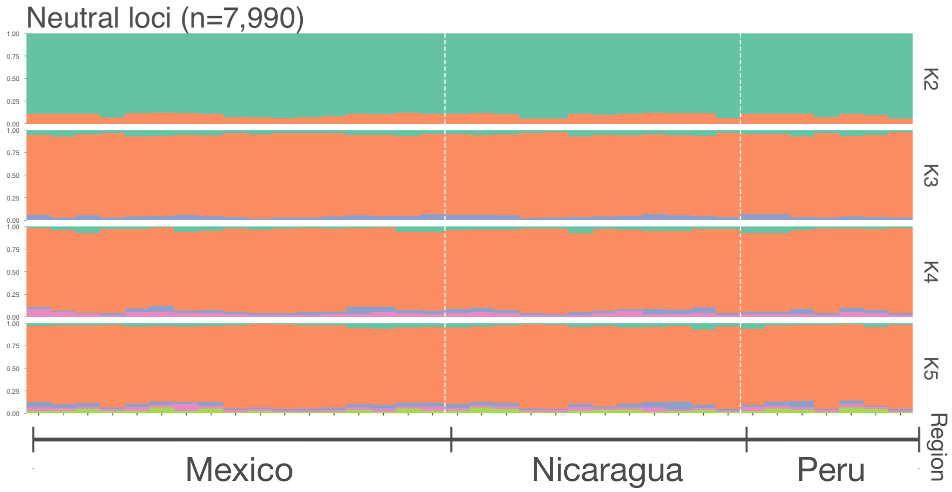


Fig S2.5. STRUCTURE results for K=2-5 neutral loci (n=7,990) analyzed for *M. munkiana*.

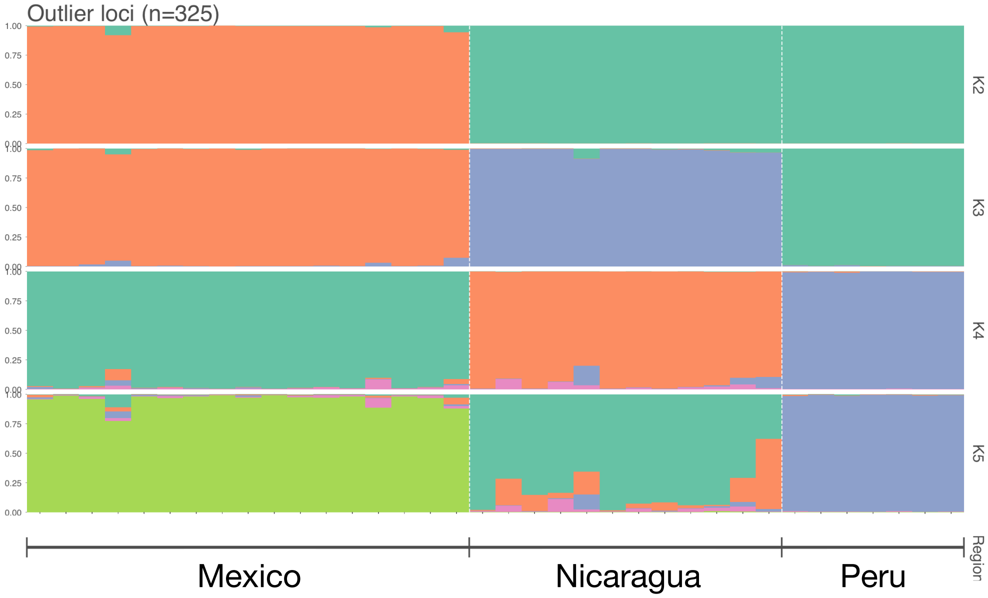


Fig S2.6. STRUCTURE results for K=2-5 outlier loci (n=325) analyzed for *M. munkiana*.

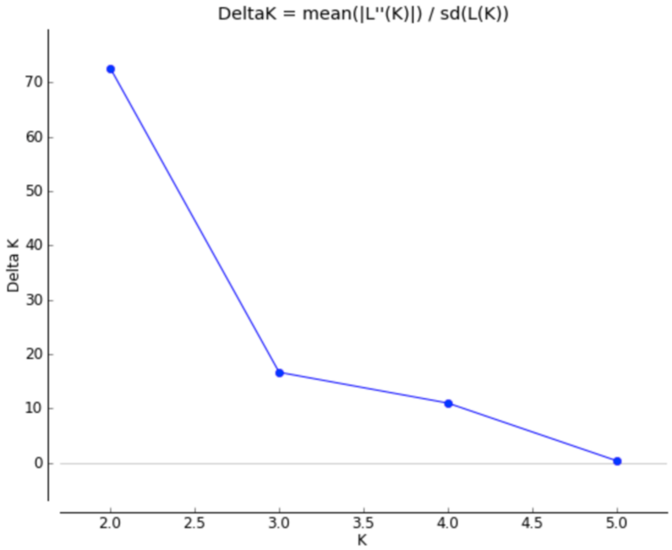


Fig S2.7. DeltaK output from STRUCTURE harvester for neutral loci for M. thurstoni.

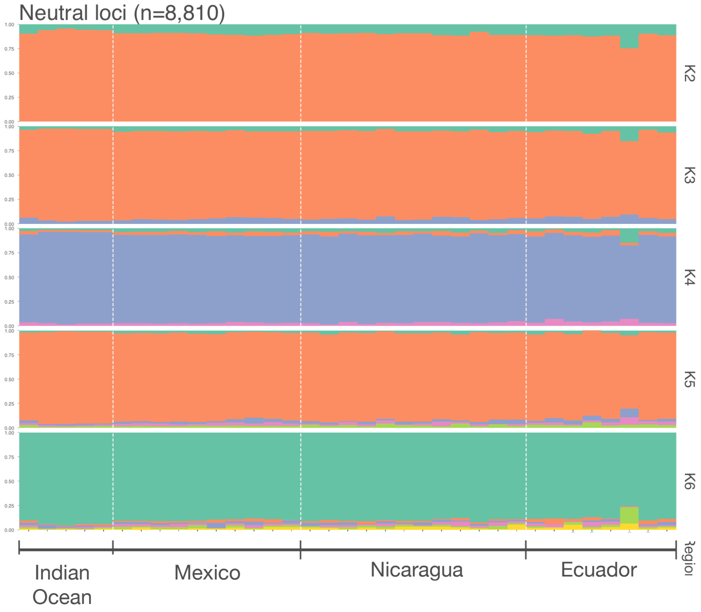


Fig S2.8. STRUCTURE results for K=2-6 for neutral loci (n=8,810) analyzed for M. thurstoni.

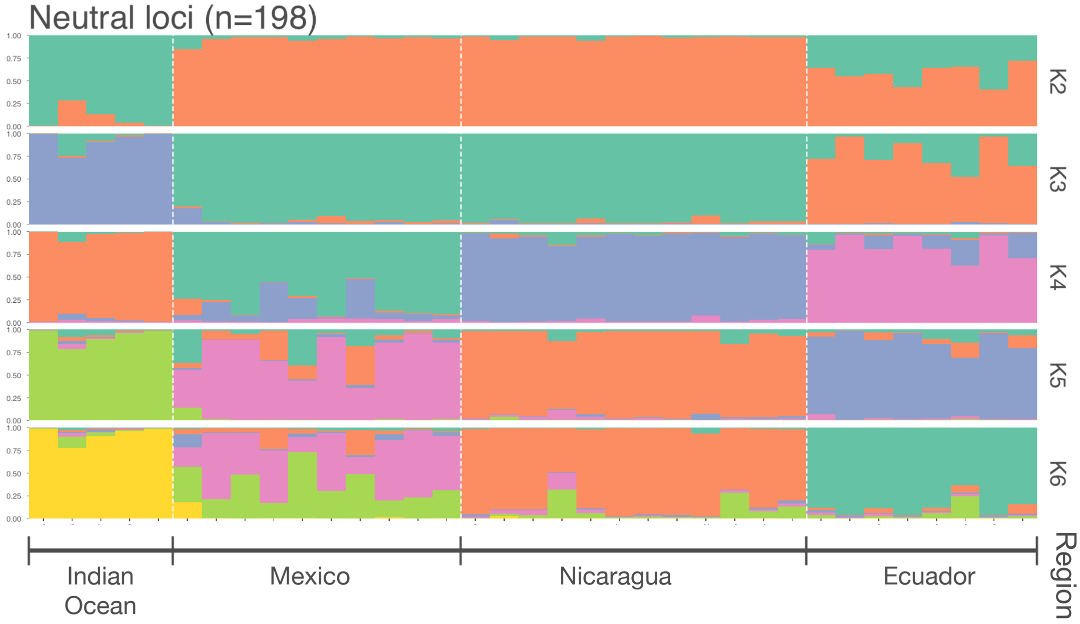


Fig S2. 9. STRUCTURE results for K=2-6 for outlier loci (n=198) analyzed for *M. thurstoni.*

CHAPTER 3

Policy without teeth: Policy and transparency gaps for oceanic shark and rays in high seas tuna fisheries

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Abstract

The incidental capture by marine fisheries as bycatch poses a global threat to pelagic sharks and rays. In large, industrialized fisheries that often operate in areas beyond national jurisdiction, at least 23 threatened species of pelagic elasmobranchs are caught as bycatch, representing the majority of megafauna bycatch in tuna fisheries. Here, we investigate 1) the efficacy of the current policies of the five tuna-related Regional Fisheries Management Organizations (tRFMOs) in mitigating elasmobranch bycatch, 2) data needed to better assess the amount and impact of elasmobranch bycatch, and 3) the research necessary for the adoption of new policies. We found that tRFMOs have adopted 34 active policies that address pelagic elasmobranch bycatch. However, most policies (~76%, n=26) are unlikely to avoid or minimize elasmobranch bycatch. Instead, most policies focus on mitigating post-capture mortality via remediation and requiring or encouraging research and data collection. Despite the emphasis on research mandates, we find that the existence of research was not related to policy adoption, suggesting that lack of research has not historically prohibited policymaking. Overall, we suggest that current research and data transparency, though perhaps not necessary for policy adoption, are not sufficient to adequately evaluate the population-level impacts of bycatch on many elasmobranch species in tRFMO-managed fisheries. Given these results, we recommend a precautionary approach that involves reforms in tRFMO voting processes to facilitate the adoption of effective policies such as binding requirements

for elasmobranch catch limits, bycatch avoidance, pre- and post-capture handling and release modifications, and protection of areas important to threatened pelagic elasmobranchs.

Introduction

Many oceanic sharks and rays have globally declining populations (Dulvy et al., 2021; Pacoureau et al., 2021). Due to their vulnerable life histories, pelagic sharks, rays, and skates (together referred to as pelagic elasmobranchs) are generally at greater extinction risk than other marine vertebrates (Dulvy et al., 2008, 2014). Globally, pelagic elasmobranch populations are estimated to have declined by more than 70% over the past half century (Pacoureau et al., 2021). The impact of these declines is ecologically and socioeconomically significant: many elasmobranch species are apex predators that play important roles in marine food webs, as well as for and coastal ecotourism sectors and livelihoods (Baum et al., 2003; Gallagher & Hammerschlag, 2011; Grubbs et al., 2016).

These declines have been attributed mainly to accelerating overexploitation by fisheries (Davidson et al., 2016; Pacoureau et al., 2021). While some elasmobranchs are targeted for their meat or fins, fisheries bycatch, or unintentional capture in fishing gear, may make up as much as 50% of the total global elasmobranch catch (Bonfil, 1994). Industrial fishing fleets targeting large epipelagic fishes like tuna and swordfish are a primary source of capture of large numbers of pelagic elasmobranchs

(Clarke et al., 2014; E. Gilman et al., 2008, 2014; Molina & Cooke, 2012). Publicly available data for bycatch species in these fisheries is sparse, but some suggest that pelagic shark and rays make up the majority of their megafauna bycatch (Clarke et al., 2014; Hall & Roman, 2013a). For example, in the Western and Central Pacific Fisheries Commission (WCPFC), which publishes reported bycatch data from tuna fisheries collected by fisheries observers, elasmobranchs make up 97.6% of reported megafauna bycatch in terms of individuals (Fig 1; (WCPFC, 2022). While comparable data are not readily available for other regions, available evidence suggests that elasmobranch catch is similarly high in other tuna fisheries (Clarke et al., 2013; Hall & Roman, 2013b; Queiroz et al., 2019). Further, it is likely that pelagic elasmobranch bycatch is even higher than reported data for these fisheries due to poor compliance, low observer coverage, and poor enforcement of reporting requirements (Babcock & Pikitch, 2011; Forget et al., 2021; Miyake et al., 2004; Oliver et al., 2015).

These fisheries mainly operate on the high seas (i.e., the ocean area beyond national jurisdiction), and have expanded their geographic range and capacity over the past half century (Swartz et al., 2010). Established by international agreement under the United Nations Convention on the Law of the Sea, these fisheries are broadly managed by five tuna Regional Fisheries Management Organizations (tRFMOs, Table S1, Fig. S1). tRFMOs are comprised of Contracting Parties and Cooperating Members (CCMs), or nations and territories with an interest in fishing migratory species in an ocean region. These regulatory bodies set policy by formally adopting Resolutions, Recommendations or Conservation and Management Measures (CMMs), which are agreements that detail binding and non-binding responsibilities for members (Table S3). These can be broad policies for all elasmobranchs, as well as more tailored policies specifically for each or a subset of the 22 species (13 shark species and 9 rays) that are most frequently captured (Table 1) (Tolotti et al., 2015). In the context of pelagic elasmobranch conservation, these measures apply to the majority of vessels fishing the high seas (and many in coastal waters as well), and thus exert considerable and critical influence over the sustainability of regional elasmobranch populations (Gilman et al., 2011).

RFMOs were originally tasked with the management of a handful of tuna and tuna-like species at the ocean basin scale. However, over the last several decades all but one tRFMO have included non-target or ecologically related species in their convention texts (e.g., convention agreements, Table S1) (Juan-Jordá et al., 2017; Pons et al., 2018). All five tRFMOs have passed recent CMMs specifically focused on elasmobranchs. Despite these efforts, tRFMOs have still failed to demonstrate significant bycatch reduction for most taxa in spite of several decades of fishery management (Cullis-Suzuki & Pauly, 2010; Gilman et al., 2011). This has led to calls for more meaningful action to mitigate their impacts on non-target species (Juan-Jordá et al., 2017; Techera & Klein, 2011).

There are multiple reasons cited for tRFMOs' failure to reduce bycatch, including: low rates of data collection and reporting, lack of biological and fishery knowledge necessary to design effective policies (Gilman & Kingma, 2013; Koehler, 2013), insufficient capacity to develop policy, and poor enforcement and compliance of existing measures. The lack of adequate scientific knowledge, often in the form of stock or population assessments, is a particular challenge for pelagic elasmobranchs. Many species are data-poor and lack the basic population-level demographic and life history data necessary to conduct a stock assessment (Clarke et al., 2013). Further, the absence of a stock assessment is often used as argument by tRFMO delegates to prevent to the adoption of bycatch reduction policies for pelagic elasmobranchs (IOTC, 2014; Mandelik et al., 2005).

However, it is unclear whether and what scientific knowledge is required for the successful adoption and implementation of bycatch mitigation policy. It is likewise unclear if regulatory policies currently in place are effective in mitigating bycatch of pelagic elasmobranchs in tuna fisheries. In this study, we examine 1) the efficacy of the current policies of the five tuna-related Regional Fisheries Management Organizations (tRFMOs) in reducing or mitigating elasmobranch bycatch, 2) data needed to better assess the amount and impact of bycatch on impacted elasmobranch species, and 3) the research necessary for the adoption of new policies. Answering these questions can help understand the efficacy of current tRFMO elasmobranch bycatch mitigation policy and identify the research necessary to develop and adopt effective elasmobranch bycatch reduction policy in the future.

One way to assess the effectiveness of regulatory policies for conservation goals is by using a mitigation hierarchy, a risk-based biodiversity conservation approach initially developed to mitigate terrestrial biodiversity loss (Mandelik et al., 2005). This approach has been adapted for marine megafauna (Arlidge et al., 2020; Milner-Gulland et al., 2018) and recently applied to elasmobranch bycatch (Booth et al., 2019). The mitigation hierarchy includes five measures important in identifying and mitigating the impacts of bycatch: *Avoid* the likelihood of capture, *Minimize* the likelihood of capture, *Remediate* capture by reducing the likelihood of post-capture mortality, *Compensate* to pay monetarily for damage done to the population, and *Research* the impact of bycatch (Fig. 2) (Milner-Gulland et al., 2018).This framework is structured as a hierarchy of management options according to the relative likelihood of reducing bycatch mortality, with *Avoid* approaches having the greatest likelihood and *Research* having the lowest likelihood to reduce immediate bycatch mortality (Booth et al., 2019).

Despite its broad utility, the bycatch mitigation hierarchy has not been applied to pelagic elasmobranch bycatch in tRFMOs. We use it here to classify current tRFMO pelagic elasmobranch bycatch policies and their efficacy in reducing or mitigating bycatch. Specifically, we identify the tRFMO policies that are currently in place for addressing pelagic elasmobranch bycatch, classify those policies according to the mitigation framework approaches to understand their likely relative efficacy; and ascertain whether the availability of scientific information is a necessary precursor to policy adoption. Finally, we use a scoring rubric to identify major gaps in data collection and availability, that, if addressed, would enable more informed and effective management and conservation for pelagic elasmobranchs. Overall, we aim to understand whether tRFMO pelagic elasmobranch bycatch mitigation policies are adequate to meet the stated aims of elasmobranch conservation.

Methods

Pelagic elasmobranch species

We focus on a subset of 22 threatened pelagic elasmobranchs (Table 1) that have been the center of recent conservation concern. All are listed under the Convention on International Trade in Endangered Species (CITES) Appendix II, and the Convention for Migratory Species Appendix II (Cardeñosa et al., 2018; Vincent et al., 2014), with the exception of blue shark (*Prionace glauca*), which is listed on CMS but not CITES. In addition, all these species are the focus of data collection and policy efforts in tRFMOs. We omitted elasmobranch species that have been listed on CITES, but which are not currently the focus of data collection or policy in any tRFMO because their catch is low or largely undocumented.

Policy analysis

We compiled a comprehensive database of all bycatch policies adopted by four tRFMOs that apply to threatened pelagic elasmobranchs and bycatch. This included policies (Conservation and Management Measures, Resolutions, Recommendations, and Amendments) dating from 1976-2021 that were formally proposed, agreed upon, and adopted and contained the keywords “bycatch,” “bycatch" or "incidental catch," and also contained the words "elasmobranch," "shark," or "ray" within the body text. We gathered policies from public tRFMO websites (IATTC: https://www.iattc.org/ResolutionsActiveENG.htm, IOTC: https://iotc.org/cmms, WCPFC: https://www.wcpfc.int/system/files/booklets/31/CMM%20and%20Resolutions.pdf, ICCAT: https://www.iccat.int/en/RecRes.asp). Because CCSBT is a special commission that follows the bycatch policies established by other tRFMOs when fishing in their convention areas (RESOLUTION 18/02 ON MANAGEMENT MEASURES FOR THE CONSERVATION OF BLUE SHARK CAUGHT IN ASSOCIATION WITH IOTC FISHERIES, 2018), we excluded it from all policy analyses to avoid double-counting duplicate policies. We also screened out six policies that were no longer active because they were replaced by newer amendments, but also noted the first year that the policy was adopted in its earliest version.

This screening yielded 35 active policies applicable to pelagic elasmobranch bycatch (Data S1). We coded each of these policies based on 1) species (if mentioned), 2) gear type, 3) date of adoption, and 4) whether the policy was binding. We determined whether each policy was considered 'binding' or 'not binding' (this determination is dependent on the legal language used by each tRFMO; for example, ICCAT considers 'Recommendations' binding, and 'Resolutions' non-binding, while the opposite is true for IOTC, Table S2).

Mitigation hierarchy

We used the bycatch mitigation hierarchy to categorize policy contents along a spectrum of mitigation approaches. A single policy document may contain multiple approaches within the bycatch mitigation hierarchy; therefore, within each policy we coded for the presence or absence of each of the five approaches (Fig. 1): Avoid, Minimize, Remediate, Compensate, and Research. Presence of an approach was defined as a clearly stated and specific requirement to be carried out by state or non-state parties regarding bycatch using that approach (Table 2). Within each of the five approaches, we also noted the specific requirement directed by the policy (e.g., landing ban, bycatch limit, etc.; Table S3).

Gaps and research requirements for single-species policy

Finally, we examined a subset of single-species/genus policies to understand the impact of scientific information on policy decisions for species considered of conservation concern. Commonly, tRFMO policy focuses narrowly on a single species (e.g. retention ban for silky shark) or genus (e.g., handling modifications for Mobulid rays); for simplicity we refer to these as “single-species” policies though they may pertain to a genus. For each the species within each tRFMO, we recorded whether that species was the subject of one or more single-species policy. For those with single-species policy, we noted which of the following non-research policy instruments applied in each tRFMO, each of which represents one of the mitigation approaches: 1) landing, retention, and transshipment ban (Remediate), 2) bycatch/catch limit (Minimize), and 3) spatial management (Avoid). These instruments were chosen as they were the most frequently appearing requirements within single-species policies based on a preliminary reading of the policies. With the exception of some Mobulid rays and the pelagic thresher shark, all species in this study are globally distributed; thus for each tRFMO, we considered all species included in Table 1 that have overlapping distributions with the Convention Area as potentially eligible for a single-species policy for each tRFMO (Table S3). In a case where a “single-species” policy was established for a genus, we considered that policy to apply to each member of the genus that is distributed in that tRFMO’s Convention Area.

To understand the effect of research knowledge on the likelihood of policy adoption, we matched our single-species policy data with published stock assessments from the RAM Legacy Stock Assessment database (http://ramlegacy.org/) and tRFMO websites for the species included in this study (Data S2). In the context of elasmobranchs and tRFMOs, stock assessments are quantitative studies that may be conducted either internally or externally, and are based on catch time series, demographic data, and life history parameters. These assessments fit statistical population dynamics models to produce time series estimates of biomass, fishing mortality and uncertainty, and compare these to biological reference points for one or more species (Begg et al., 1999; Hilborn & Walters, 1992). Normally a stock assessment will result in one or more of the following stock status designations: 1) overfishing is occurring (fishing mortality exceeds a certain threshold, e.g., mortality rate that is some fraction of F_{MSY}), 2) the population is in an overfished state (stock biomass falls below a certain threshold, e.g., below spawning stock biomass threshold), 3) the population is not overfished 4) the population is not currently being overfished, 5) some combination of the above (e.g., the population is not overfished but is currently being overfished), or 6) that the uncertainty is too high to make a determination (Ricard et al., 2012). As above, for each tRFMO we considered only species that have overlapping distributions with the Convention Area as eligible for assessment (Table S3). In cases where a population is considered to be two or more populations in one Convention Area based on genetic structure, we included both stock status determinations for that eligible population in that region (e.g., “overfished/overfishing occurring"). If an assessment was conducted for a population’s distribution across more than one commission’s Convention Area, we considered this assessment as applicable to that population in all tRFMOs within the scope of the study. If the assessment did not result in a clear population status determination, we characterized the result as “undetermined.”

We examined whether the existence of a stock assessment was associated with the likelihood of adoption of single-species policy instruments. To do this, we matched single-species policies with corresponding stock assessments in the same ocean region to ask whether a species was more likely to have a single-species policy if it was assessed. We used a Chi-Squared test to test for independence of the existence of a stock assessment and the adoption of single-species policies.

Data gap analysis

We used information available on tRFMO websites to evaluate data collection, availability, and transparency related to elasmobranchs and identify areas for improvement. We scored each tRFMO against a rubric of seven categories (Table S4). These categories included: 1) public availability of elasmobranch bycatch data, 2) public availability of spatial data for elasmobranch capture, 3) availability of fishing effort data, 4) inclusion of elasmobranchs in convention text (Table S1), 5) mandated observer coverage for purse seine vessels, 6) mandated observer coverage for longline vessels, and 7) proportion of captured elasmobranch species with stock assessments. Categories 1-4 were scored from 0-2 based on the predefined rubric criteria (Table S4). For the longline observer coverage category (#5), following Babcock et al. (2011) and used a threshold of 50% observer coverage, which is considered necessary to estimate rare bycatch events, and scored longline observer coverage as a proportion of this 50% threshold. For purse seine observer coverage (#6), because there are mandates for 100% observer coverage, we used 100% as the observer coverage threshold. For this analysis, unlike the policy analysis, we included CCSBT as it could be scored independently of the other bodies. We note that CCSBT does not have significant purse seine vessel activity so we excluded this category and it was not factored into its final score. For the final category (#7), which was concerned with the proportion of elasmobranch species assessed by stock assessments, we used the same criteria for inclusion as described above in the stock assessments section, and divided the number of assessed species by the number of eligible species for each tRFMO. Categories #5-7, which were scaled as a proportion of 2 to match the weighting of the other categories. Because some rubric categories are not independent of one another and because tRFMO contexts vary substantially from ocean to ocean, we did not produce an overall total score but instead present these as separate sub-categories for each tRFMO.

Results

Mitigation hierarchy

Of the five approaches of the bycatch mitigation hierarchy, *Research* was the most prevalent mitigation approach, and was included in all 34 active policies (Fig 3). Examples of common *Research* approaches were requirements to conduct a stock assessment for a particular species, gather life history or biological data, or increase observer coverage. This was followed by *Remediate* approaches which appeared in 23 policies. Frequently appearing *Remediate* policies included requirements to modify gear to reduce the likelihood of mortality, such as prohibiting the use of wire leaders (otherwise known as “shark lines”), finning regulations (e.g. rules regarding fin-to-carcass ratios) and prohibitions of harmful handling practices (e.g., prohibition on gaffing animals). *Minimize* approaches appeared less frequently, in just 9 policies, and included gear modifications to reduce the likelihood of capture, including alterations to bait type and the design of fish aggregation devices (FADs) so that they are less likely to entangle non-target species. Finally, just one of the 34 policies included *Avoid* approaches, and none included *Compensate* approaches (Fig. 3A).

The only policy containing an *Avoid* approach was adopted by IATTC, and was concerned with avoiding pupping areas for silky shark (Resolution C-21-06).

Pelagic elasmobranch bycatch policies were first adopted in 1995, but have been increasing in number, particularly since 2010 (Fig. 3B). The first policies to use *Minimize* and *Avoid* approaches were adopted in 2012 and 2016, respectively; tRFMO policies implemented prior to 2012 used *Remediate* and *Research* approaches exclusively.

When examining the strength of policy response, we found that non-binding policies for pelagic elasmobranchs were relatively uncommon; ICCAT was the only commissions to adopt non-binding policy for elasmobranchs, representing just 2 of all policies examined.

Research gaps

Given that we found a focus on research mandates in tRFMO policy, we next asked whether these research mandates in fact led to improved scientific knowledge, specifically in the form of stock assessments. Of those species with overlapping distributions with the five tRFMO Convention Areas, stock assessments have been conducted for ~19% (n=18) of the 96 eligible populations. The remaining ~81% (n=78) of eligible pelagic elasmobranch populations were unassessed. Of those 18 populations with stock assessments, ~39% (n=7) were determined to be “overfished” or “overfishing occurring,” ~39% (n=7) were determined to be “not overfished,” and ~11% (n= 2) were determined to be “overfishing unlikely.” Two populations had dual designations, both of which were coincidentally “not overfished/undetermined.” The remaining two populations (~11%) had stock assessments conducted, but the results of those assessments were inconclusive.

Policy gaps

We examined current gaps in single-species policy for pelagic elasmobranchs. The species with the most single-species policies were for blue (n=4) and mako (n=4) sharks (though all mako shark policies were in a single tRFMO, ICCAT), followed by mobulids (n=3) and oceanic whitetip (n=3), silky (n=3), and thresher (n=2) shark. Thresher and whale sharks each had two policies, and hammerhead and porbeagle sharks had one policy each (Fig. S3). Single-species policies were not more likely to be adopted in the year immediately after a major biodiversity treaty listing (e.g., CITES or CMS, Fig. S3).

Of the 77 eligible populations (this total excludes CCSBT, which follows the policy of other tRFMOs), just over half (51%, n=39) had single-species policy measures. All but two of these measures were landing, retention, and transshipment bans (orange cells, Table 3). The other half of populations (n=38) had no single-species policy measures at all (red cells, Table 3). Two species had catch limit measure (shortfin mako and blue shark, both in ICCAT), and one species had a spatial management measure (silky shark in IATTC) (Table 3).

We then combined these single-species policies with our stock assessment data to ask whether there was a corresponding policy response to scientific information (e.g., a stock assessment) for 77 eligible populations (again, this total excludes CCSBT populations as CCSBT follows the single-species policies of other tRFMOs and therefore could not be included). Of the 18 populations with stock assessments, ~39% (n=7) had single-species policies. Of the 59 unassessed but eligible populations, ~56% (n=33) had single-species policies. A Chi-Square test of independence detected no significant association between these the existence of a stock assessment and the adoption of a single-species policy for a given population; in other words, an unassessed species was just as likely to have a single-species policy adopted as an assessed species (Fig S4, x^2 (1, N=76) = 0.6367, P = 0.42).

Data collection and transparency gaps

We investigated the state of scientific data collection and transparency in each tRFMO regarding pelagic elasmobranchs (Fig 3). No tRFMO achieved the highest score in all categories, and the only high score achieved in the rubric categories were for purse seine observer coverage and the inclusion of elasmobranchs in convention text.

Discussion

The goal of this study was to assess the effectiveness of elasmobranch bycatch mitigation policy and identify data collection and transparency gaps in tuna management organizations. Given global pelagic elasmobranch declines, we identify three major concerns for threatened pelagic elasmobranch bycatch in tRFMO fisheries: 1) the majority of tRFMO policies concerning threatened pelagic elasmobranchs are focused on research (appearing in 100% of policies) and remediation (appearing in ~68% of policies), while few policies are directed at mitigation by avoiding, minimizing, or compensating for bycatch, 2) major data collection and transparency gaps in all five tRFMOs prevent rigorous external science for these species, and 3) these policy and transparency deficits are concerning given our finding that few stock assessments are available for pelagic elasmobranch populations (18 of 96 eligible populations), and 7 of the 18 assessed populations are overfished. We suggest that these shortcomings can be attributed to systemic challenges of conservation and fishery policymaking at the tRFMO level, including the inherent difficulty of managing transboundary resources, the differential costs and incentives of bycatch mitigation approaches, obstructive consensus-based decision-making processes in tRFMOs, and lack of institutional commitment to the conservation of non-target species.

Improving data availability and assessments

The scarcity of stock assessments for pelagic elasmobranchs is notable, given the fact that 100% of the policies we examined contain requirements for research, including stock assessments. This points to the significant challenges in assessing data-poor species lacking long time series catch data (Barker & Schluessel, 2005; Carvalho et al., 2018; Clarke et al., 2006). Yet surprisingly, we found that the existence of a stock assessment was not associated with a corresponding policy response; in fact, more unassessed populations have bycatch mitigation measures than populations *with* stock assessments. It is important to note that this finding does not suggest that an unassessed species is somehow more likely to be the subject of future policy adoption— rather, it more likely indicates that policy adoption is the result of complex political and legal processes that may or may not draw on stock assessments. Perhaps more importantly, this suggests that a stock assessment is not necessarily a prerequisite of mitigation policy, further implying that precautionary decision-making for elasmobranchs in tRFMOs is possible in the absence of high-quality data. This result is supported by previous study by Galland et al, (2018), which reported that policymakers at two tRFMOs, ICCAT and WCPFC, followed the advice of their scientists in making fishery management decisions only 39% and 17% of the time, respectively. These findings are important in the context of threatened bycatch species, as they indicate that policymaking is not only possible in data-poor scenarios, but regularly occurs. They also lends momentum to recent urgent calls for tRFMOs to better implement precautionary approaches to fisheries management for non-target species (de Bruyn et al., 2013; Hewison, 1996; Restrepo et al., 2017). Still, these findings do not suggest that better data on elasmobranch bycatch isn’t useful or necessary; on the contrary, well-targeted and effective policy requires grounding in good science, as well as clear communication of that science to policymakers (Beddington et al., 2007; Caddy, 1999; Galland et al., 2018)

Nevertheless, for decades tRFMO managers and fishing flag state delegates have cited a lack of adequate data as a major hindrance for effective management and policy for pelagic elasmobranchs in tuna fisheries (Barker & Schluessel, 2005; Tolotti et al., 2015). Our finding that no tRFMO achieved a high score for data collection and transparency supports this, and points to areas that each tRFMO could focus on to improve the quality and availability of data received from countries. For instance, one potential remedy to increase data reporting is for tRFMOs to adopt and enforce measures that require countries to submit high-quality, publicly available data as a prerequisite to access to the fishery. ICCAT has implemented a version of this in the form of "shark check sheets" that assess country compliance with regulations and are a requirement for participation in the fishery (Recommendation 18-06). In addition, increasing observer coverage in these fisheries is a crucial component to producing better data, particularly in longline fisheries where observer coverage in most cases is insufficient to adequately estimate rare bycatch events (Babcock & Pikitch, 2011). Prioritizing international and in-country funding to address the data gaps identified in Fig. 4, coupled with the use of recently emerging stock assessment methods for data-poor species, could help provide a fuller understanding of the status of these populations and their ability to withstand current levels of bycatch (Andrade, 2015; Clarke et al., 2018).

Moving beyond calls for more research

In contrast to the many *Research* approaches we identified among these policies, we found that policies that target the avoidance of capture were extremely rare, appearing in only one of the 34 policies we reviewed. This is potentially concerning, as avoidance is widely considered the most effective bycatch mitigation approach for threatened pelagic elasmobranchs, particularly given that in tuna longline, purse seine, and gillnet fisheries, a large portion of incidentally caught sharks die during or shortly after release (Booth et al., 2019; E. L. Gilman, 2011; Hutchinson et al., 2015; Poisson et al., 2014). Further, the single *Avoid* approach we reviewed was implemented by IATTC and directs counties to require vessels “to not fish in silky shark pupping area” —however, the policy neglects to define the geographic location of silky shark pupping areas (Resolution C-21-06). This renders it unlikely to meaningfully avoid silky shark bycatch as currently written. To address the lack of avoidance approaches, tRFMOs could begin by adopting policies that include: static or dynamic spatiotemporal management in well-defined and biologically relevant bycatch hotspots; depth avoidance; and total allowable bycatch limits for all high-risk species. These approaches are already widely used in the context of tRFMOs for target fishes and other bycatch species (Grande, Ruiz, et al., 2019; IATTC, 2020; ICCAT, 2019), and have shown promising results for reducing bycatch mortality for pelagic sharks without significantly reducing target fish catch (Hazen et al., 2018; Kerwath et al., 2013; Maxwell et al., 2015; Watson et al., 2009).

Beyond avoiding important areas, research has established that one of the methods most likely to reduce the impact of bycatch on pelagic elasmobranchs is to increase post-capture survival, including using modified handling and release devices and practices (Grande, Murua, et al., 2019; Murua et al., 2021). While several of these methods and technologies are being tested in some tuna fisheries, they have not been widely adopted and their efficacy at reducing bycatch mortality remains largely uninvestigated (Tolotti et al, 2015). Further work should seek to identify and scale up effective technologies so that they can be adopted across tuna fleets. Finally, reductions in fishing effort, particularly for gears with relatively high bycatch rates, can reduce interaction rates with pelagic elasmobranchs (Watson & Bigelow, 2014).

In addition to gaps in policy approaches, we identified taxonomic gaps in the representation of elasmobranch species within policies. In particular, nearly all policies we examined focused on sharks; we found no tRFMO policies for ray species other than Mobulids (Fig. S3). Mobulid policies have been recently adopted (since 2015), likely as a result of increasing global attention to their conservation [58]. However, the need for bycatch mitigation policies for other ray and skate species should be examined, as there is growing evidence that other rays and skates exhibit similarly vulnerable life histories (Dulvy et al., 2000; Dulvy & Reynolds, 2002) and are likely threatened by bycatch in tuna fisheries (Arrizabalaga et al., 2011; Báez et al., 2016).

This study examined policies adopted at the tRFMO level, and did not investigate enforcement, monitoring, or compliance with fishing and bycatch regulations. Because tRFMOs are large multinational regulatory bodies composed of many CCMs, further work should investigate compliance and enforcement rates for bycatch policy at the flag state, company, and vessel levels. This would require the availability of tRFMO compliance reports, many of which are currently not publicly available. Similarly, limited access to research-grade, disaggregated datasets for bycatch species also prevents independent assessments of the efficacy of policy implementation on bycatch rates. Further work should seek to quantify the impact of a given policy approach on achieving bycatch reduction targets, as has been done for other technical bycatch interventions (Huang et al., 2016; Walsh et al., 2009; Watson et al., 2005).

Aligning incentives

Alongside the development and adoption of these mitigation strategies, it is important to consider their differential economic incentives and costs, which may help explain the patterns observed here (Squires & Garcia, 2018). Incentives for bycatch mitigation may include bycatch reduction awards, taxes or levies, individual transferrable quotas, retention requirements, or penalties paired with total allowable catch quotas (Pascoe et al., 2010). Each of the mitigation approaches examined in this study comes with its own set of costs and potential incentives. For example, avoidance and minimization approaches like time-area closures and restrictions on fishing effort can be costly if they lead to foregone catch and consequentially negative socioeconomic impacts for fishers (Komoroske & Lewison, 2015; Pascoe et al., 2010). Additionally, they can risk inducing cross-taxa conflicts with other target or non-target species, as has occurred in the past with other bycatch mitigation interventions (Gilman et al., 2019). These factors may help explain why they are currently underutilized in the policies we examined. As a way forward, a growing body of research is concerned with identifying static or dynamic inefficiency areas where non-target catch is high and target catch is low, which can avoid or reduce bycatch without risking economic loss from foregone catch (Hazen et al., 2018; O'Keefe et al., 2021). Further analyses of tRFMO policy should seek to identify avoidance policies that can confer benefits to multiple taxonomic groups while minimizing harm to fishery yield.

In contrast, remediation approaches like gear changes and handling and release modifications are often considered more cost-effective, and may be "lower hanging fruit" mitigation approaches (though they still may require training and specific onboard equipment), which may explain why they are more frequently required in tRFMO policy. Fortunately, for some species, changes in handling and release such as those required by tRFMO policy can substantially improve likelihood of survival, and recent advances in innovative technology appear promising (Forget et al., 2021; Hutchinson et al., 2015; Swimmer et al., 2020; Zollett & Swimmer, 2019). However, significant knowledge gaps exist about the potential for these technologies to fully resolve bycatch problems alone, and these technologies are not always transferrable from one fishery context to another (Gilman et al., 2019; Poisson et al., 2022). The successful application of effective remediation technology will require better understanding of the utility and limits of these methods for elasmobranchs, particularly for species with high post-release mortality rates. These can be paired with tRFMO policies requiring their adoption as well as economic and social incentives like sustainability certifications or awards that reward the adoption of best practices.

Though requirements for research were found in every policy we examined, their economic implications vary widely depending on the type and rigor of research, data collection, and personnel required to complete it. On the other hand, we did not identify a single tRFMO policy using a compensatory approach for elasmobranchs, despite the fact that this has been suggested as a relatively cost-effective and socio-politically feasible conservation strategy, especially for species with low survival (Booth et al., 2019; Pascoe et al., 2010; Wilcox & Donlan, 2007). However, substantial challenges associated with this approach exist, including concerns about the difficulty of fully compensating the direct and indirect impacts of bycatch and the complexity of matching compensation to the scale of impact (Finkelstein et al., 2008). Further, to our knowledge, the compensatory mitigation approach has not yet been applied for sharks in any fishery context (Booth et al., 2019). Additional research could investigate whether it could be effectively adapted to the tuna fishery setting despite these challenges.

Finally, scrutiny of the potentially unequal distributional impacts of mitigation policies among country members and contracting parties is crucial, as mitigation measures are likely to have downstream effects of seafood supply chains and therefore on human communities. Further, it is important to consider that societal values and social norms also influence the acceptability of bycatch and bycatch regulations—and in some cases may be as or more powerful incentives than economic ones. Overall, developing appropriate social and economic incentives that complement the mitigation approaches identified in this study should be considered as accompaniment to any existing or proposed mitigation policy. Still,

Implications for tRFMO governance

Given the importance of sharks and rays to the maintenance of many marine ecosystems and thus to oceanic ecosystem services, the shortcomings in tRFMO bycatch policy identified here present significant opportunities for improvement. Meaningful reform of bycatch policy in tRFMO-managed fisheries would involve binding research mandates that fill data gaps needed to assess the current status of pelagic elasmobranch populations, as well as the adoption of more bycatch avoidance and minimization measures. The current mode of decision-making in tRFMOs, which relies heavily on consensus among country members, will make the development and implementation of such policies challenging (Pons et al., 2018). This consensus-based framework has been identified as an impediment to management progress in other related areas, including adaptive management in response to climate change (Pentz et al., 2018), ecosystem-based fishery management (Juan-Jordá et al., 2017), and equitable tuna stock allocation (Seto et al., 2021). The tRFMOs could more readily utilize their established voting procedures instead of defaulting to consensus-based decision-making, as well as so-called “circuit-breaker” safeguard processes, e.g., providing a neutral mediator to reconcile differences between opposing countries or a review panel to assess decisions (Lodge et al., 2007). As fishing activities continue to drive accelerating population declines, these policy and transparency modifications can help achieve conservation goals across enormous geographic scales for threatened pelagic elasmobranchs.

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Table 3.1. Pelagic elasmobranch species included in this study. All species except *P. glauca* were recently listed on CITES Appendix II, and all species are reported in tRFMO capture records.

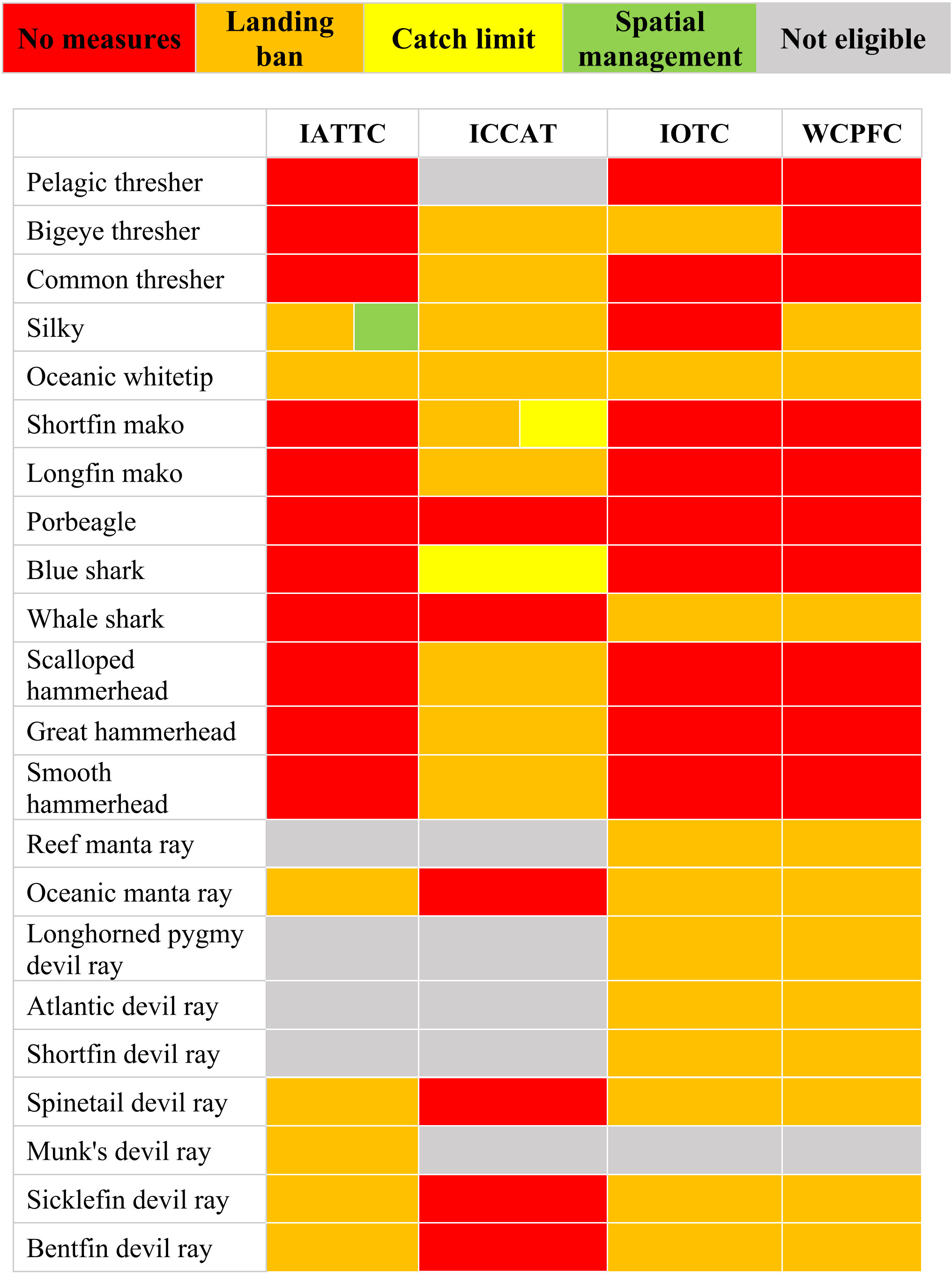
Species	**Common name**	**IUCN Red List Designation**	**Distribution**	**CITES Appendix**
Sphyrna zygaena	Smooth hammerhead	VU	Global	II
Sphyrna mokarran	Great hammerhead	CR	Global	II
Sphyrna lewini	Scalloped hammerhead	CR	Global	II
Rhincodon typus	Whale shark	EN	Global	II
Prionace glauca	Blue shark	NT	Global	-
Mobula thurstoni	Bentfin devil ray	EN	Global	II
Mobula tarapacana	Sicklefin devil ray	EN	Global	II
Mobula rochebrunei	Lesser Guinean devil ray	VU	E. Pacific	II
Mobula mobular	Spinetail devil ray	EN	Global	II
Mobula kuhlii	Shorfin devil ray	EN	Indian, W. Pacific	II
Mobula hypostoma	Atlantic devil ray	EN	Atlantic	II
Mobula munkiana	Munk’s devil ray	VU	E. Pacific	II
Mobula eregoodootenkee	Longhorned pygmy devil ray	EN	Indian, W. Pacific	II
Mobula birostris	Oceanic manta ray	VU	Global	II
Mobula alfredi	Reef manta ray	VU	Indian, W. Pacific	II
Lamna nasus	Porbeagle	VU	Global	II
Isurus oxyrinchus	Shortfin mako shark	EN	Global	II
Isurus paucus	Longfin mako shark	EN	Global	II
Carcharhinus longimanus	Oceanic whitetip shark	CR	Global	II
Carcharhinus falciformis	Silky shark	VU	Global	II
Alopias superciliosus	Bigeye thresher	VU	Global	II
Alopias pelagicus	Pelagic thresher	EN	Indian, Pacific	II
Alopias vulpinus	Common thresher	VU	Global	II

Table 3.2. tRFMO policy requirements grouped within approaches of the hierarchy for mitigating bycatch mortality.

Mitigation Approach	Example Requirement	Description/Notes
Avoid Does the policy direct fishers to avoid capture of a non-target species or group?	● Spatial management ● Close nursery or pupping area	Spatial or temporal management areas must be clearly defined; for instance, a responsibility to avoid shark nursery areas for the purpose of conservation
	● Temporal/seasonal management	Closure of fishing area during high-bycatch season or period of time
	● Alter the depth of fishing activity	E.g., setting longline hooks at a depth unlikely to capture species of interest
Minimize Does the policy direct fisheries to minimize the likelihood that a non-target species or group will be captured?	● Regulate set type for purse seiners	E.g., prohibit setting on whale sharks
	● Gear modifications to minimize capture: o Alternative bait less likely to attract bycatch o Shark repellant or deterrents o Alter mesh size of purse seine	Unlike a remediate approach, these interventions are designed minimize the likelihood of capture, not post-capture mortality
	● Alter Fish Aggregation Devices (FAD) design	FADs designed to reduce likelihood of entanglement
	● Alter timing of set	Deploying nets or lines at times of day when non-target species are less active((e.g., night setting)
	● Total allowable bycatch limit ● Effort limits	Bycatch limits allow bycatch up to a given threshold; do not avoid all bycatch
Remediate Does the policy direct fisheries to minimize the likelihood of mortality for a non-target species or group, given that it has been captured?	● Gear modification to minimize mortality: o Hook type / wire leader modification for longline gear	Unlike a minimize approach, these interventions are meant to increase survivorship; they are not meant to alter the likelihood of capture)
	● Retention rules: o Landing ban o Full or partial dead retention mandate	One or multiple species of conservation concern may be subject to a landing, retention and transshipment ban

	● Handling and release modification or guidelines ● Requirement to carry handling gear onboard	E.g., prohibition on gaffing mobulid rays
	● Finning regulations: o Fin-to-carcass ratio o Finning ban	The fin-to-carcass ratio requires that the total weight of fins onboard must not exceed 5% of the dressed weight of the carcasses
Research Does the policy direct further research or better data collection for a non-target species or group?	● Stock or population assessment	Stock assessments describe stock status; requires some knowledge of population status
	● Ecological risk assessment (Productivity-Susceptibility Analysis)	In data-poor situations, tRFMOs conduct risk-based prioritization analyses to identify species of highest priority
	● Study to gather data on: o Life history characteristics o Demography o Efficacy of mitigation technology or handling modification	E.g., research directive to study the effectiveness of other mitigation interventions at reducing capture or mortality
	● Increased observer coverage ● Data collection	E.g., a requirement to increase available data on a high-priority species via increasing observer coverage

Table 3.3 Gaps in tRFMO policies for the conservation and management of pelagic elasmobranchs in tRFMOs. Colors indicate existing single-species measures for that species in each tRFMO. CCSBT is not included in this figure, as it follows single-species policies of the other tRFMOs when fishing in their convention areas.



🟥 **No measures**	🟧 **Landing ban**	🟨 **Catch limit**	🟩 **Spatial management**	⬜ **Not eligible**

	IATTC	**ICCAT**	**IOTC**	**WCPFC**
Pelagic thresher	🟥	⬜	🟥	🟥
Bigeye thresher	🟥	🟧	🟧	🟥
Common thresher	🟥	🟧	🟥	🟥
Silky	🟧🟩	🟧	🟥	🟧
Oceanic whitetip	🟧	🟧	🟧	🟧
Shortfin mako	🟥	🟧🟨	🟥	🟥
Longfin mako	🟥	🟧	🟥	🟥
Porbeagle	🟥	🟥	🟥	🟥
Blue shark	🟥	🟨	🟥	🟥
Whale shark	🟥	🟥	🟧	🟧
Scalloped hammerhead	🟥	🟧	🟥	🟥
Great hammerhead	🟥	🟧	🟥	🟥
Smooth hammerhead	🟥	🟧	🟥	🟥
Reef manta ray	⬜	⬜	🟧	🟧
Oceanic manta ray	🟧	🟥	🟧	🟧
Longhorned pygmy devil ray	⬜	⬜	🟧	🟧
Atlantic devil ray	⬜	⬜	🟧	🟧
Shortfin devil ray	⬜	⬜	🟧	🟧
Spinetail devil ray	🟧	🟥	🟧	🟧
Munk's devil ray	🟧	⬜	⬜	⬜
Sicklefin devil ray	🟧	🟥	🟧	🟧
Bentfin devil ray	🟧	🟥	🟧	🟧

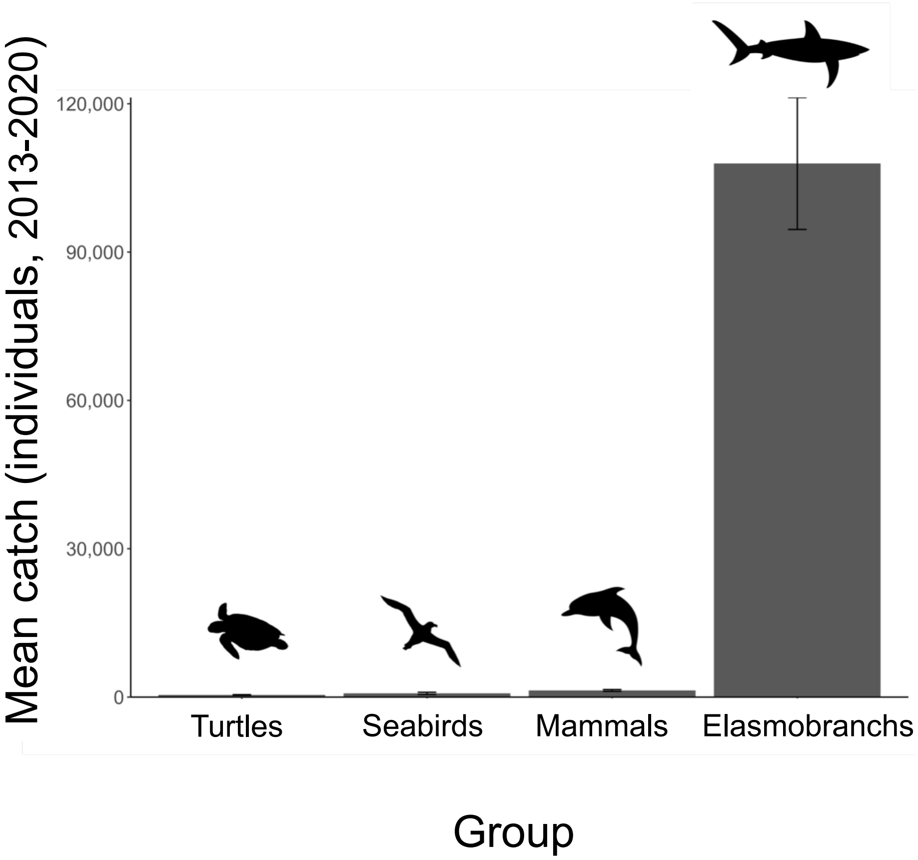


Fig 3.1. Annual mean bycatch ± SE in number of individuals reported in public domain data from WCPFC. Elasmobranchs make up the majority (97.6%) of reported megafauna bycatch from 2013-2020. Data from https://www.wcpfc.int/public-domain-bycatch).

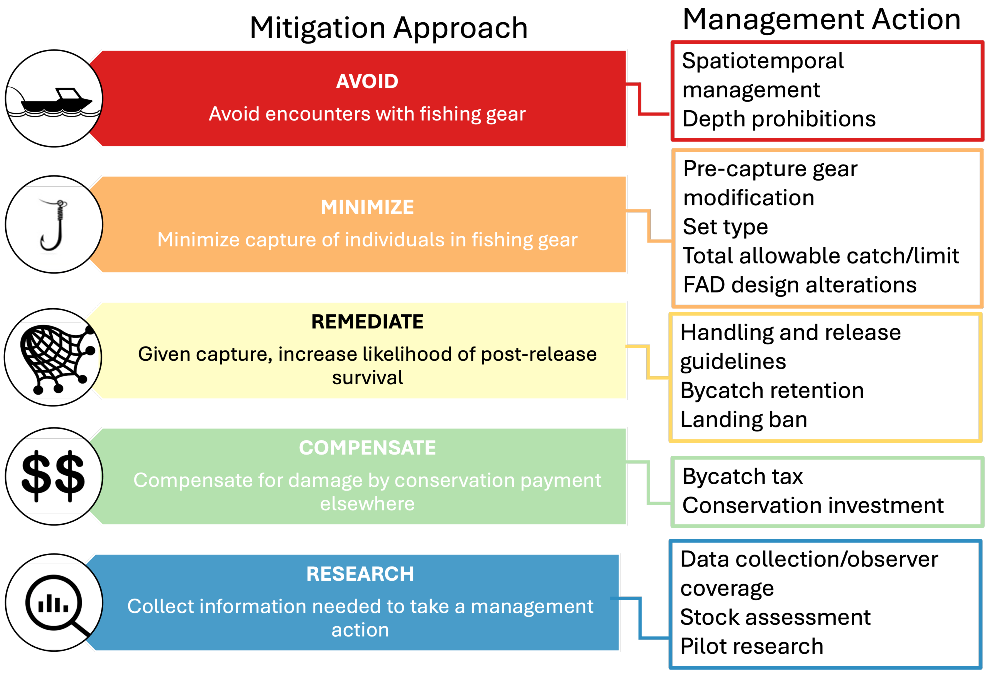


Fig. 3.2 Conceptual figure of bycatch mitigation approaches in fisheries, adapted from Milner-Gulland et al. (2018).

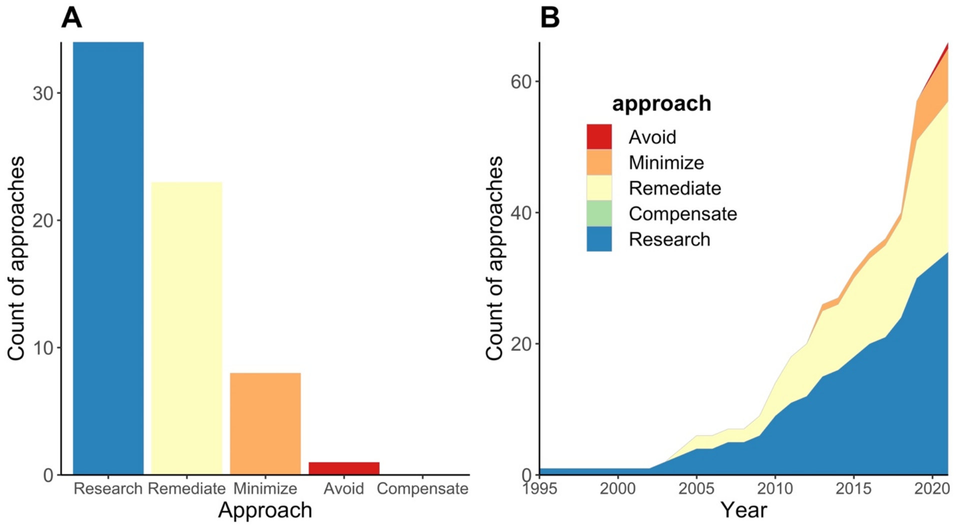


Fig 3.3. tRFMO policy approaches for pelagic elasmobranchs grouped by representation within the bycatch mitigation hierarchy**.** A) Mitigation hierarchy approaches represented within tRFMO policy for pelagic elasmobranchs; B) Cumulative adoption of pelagic elasmobranch bycatch mitigation approaches adopted by tRFMOs since their inception in 1995.

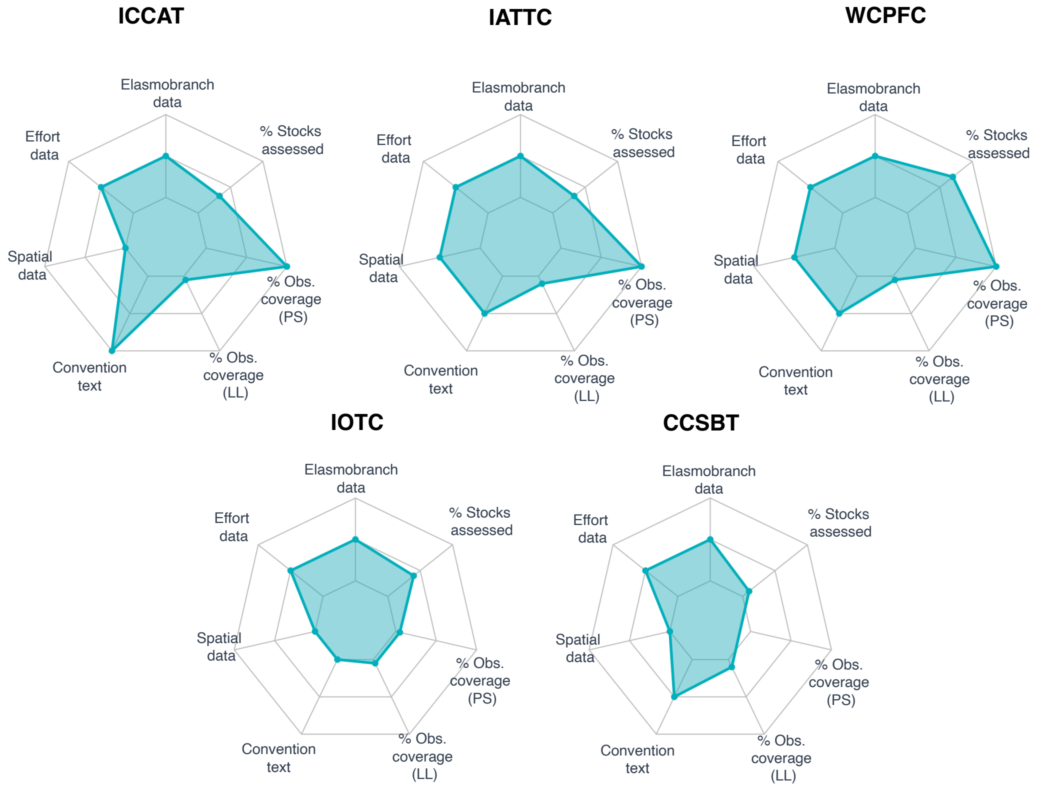


Fig. 3.4. Data collection and transparency gaps in tRFMOs. Scores for each category ranged from 0 to 2, and points farther from the inside of the circle represent higher scores. Radar spokes represent scores for the following rubric categories, clockwise from top: 1) transparency of elasmobranch bycatch data, 2) proportion of captured elasmobranch species with stock assessments, 3) mandated observer coverage for purse seine vessels, 4) mandated observer coverage for longline vessels, 5) inclusion of elasmobranchs in convention text, 6) public availability of spatial data for elasmobranch capture, and 7) availability of fishing effort data.

Table S3.1. Sections of tRFMO Convention texts related to non-target species and/or elasmobranchs.

tRFMO	Date of agreement	Agreement text relevant to elasmobranch bycatch
Commission for the Conservation of Southern Bluefin Tuna (CCSBT)	1994	*"Acknowledging the importance of scientific research for the conservation and management of southern bluefin tuna and the importance of collecting scientific information relating to southern bluefin tuna and* ***ecologically related species;****…'ecologically related species' means living marine species which are associated with southern bluefin tuna"*
International Convention for the Conservation of Atlantic Tunas (ICCAT)	1996	*"The Governments whose duly authorized representatives have subscribed hereto, considering their mutual interest in the populations of tuna and* ***tuna-like fishes and elasmobranchs that are oceanic, pelagic, and highly migratory*** *found in the Atlantic Ocean, and desiring to co-operate in maintaining the populations of these fishes at levels that will permit their long term conservation and sustainable use for food and other purposes, resolve to conclude a Convention for the conservation of these resources, and to that end agree as follows."*
Inter-American Tropical Tuna Commission (IATTC)	1949	*"Where the status of target stocks or* ***non-target or associated or dependent species is of concern****, the members of the Commission shall subject such stocks and species to enhanced monitoring in order to review their status and the efficacy of conservation and management measures."*
Indian Ocean Tuna Commission (IOTC)	1993	
Western and Central Pacific Fisheries Commission (WCPFC)	2004	*"… assess the impacts of fishing, other human activities and environmental factors on target stocks,* ***non-target*** *species, and species belonging to the same ecosystem or dependent upon or associated with the target stocks…"*

Table S3.2. Regulatory strength determined by tRFMOs for policy. tRFMOs use variable language within policy titles to indicate whether a policy is binding or non-binding.

	CCSBT	**IATTC**	**ICCAT**	**IOTC**	**WCPFC**
Title of binding policy	Resolution	Resolution, Conservation and Management Measure	Recommendation	Resolution	Conservation and Management Measure
Title of non-binding policy	N/A	N/A	Resolution	Recommendation	Resolution

Table S3.3. Eligibility for stock assessment and single-species policy**.** A species was considered eligible if its distribution overlapped with that of the tRFMO Convention Area.

Species	**IATTC**	**ICCAT**	**IOTC**	**WCPFC**	**CCSBT**
Alopias pelagicus	eligible	Not eligible	eligible	eligible	eligible
Alopias superciliosus	eligible	eligible	eligible	eligible	eligible
Alopias vulpinus	eligible	eligible	eligible	eligible	eligible
Carcharhinus falciformis	eligible	eligible	eligible	eligible	eligible
Carcharhinus longimanus	eligible	eligible	eligible	eligible	eligible
Isurus oxyrinchus	eligible	eligible	eligible	eligible	eligible
Isurus paucus	eligible	eligible	eligible	eligible	eligible
Lamna nasus	eligible	eligible	eligible	eligible	eligible
Prionace glauca	eligible	eligible	eligible	eligible	eligible
Rhincodon typus	eligible	eligible	eligible	eligible	eligible
Sphyrna lewini	eligible	eligible	eligible	eligible	eligible
Sphyrna mokarran	eligible	eligible	eligible	eligible	eligible
Sphyrna zygaena	eligible	eligible	eligible	eligible	eligible
Mobula alfredi	not eligible	not eligible	eligible	eligible	eligible
Mobula birostris	eligible	eligible	eligible	eligible	eligible
Mobula eregoodoo	not eligible	not eligible	eligible	eligible	eligible
Mobula hypostoma	not eligible	eligible	not eligible	not eligible	not eligible
Mobula kuhlii	not eligible	Not eligible	eligible	eligible	eligible
Mobula mobular	eligible	eligible	eligible	eligible	eligible
Mobula munkiana	eligible	not eligible	not eligible	not eligible	not eligible
Mobula tarapacana	eligible	eligible	eligible	eligible	eligible
Mobula thurstoni	eligible	eligible	eligible	eligible	eligible
Mobula rochebrunei	not eligible	eligible	not eligible	not eligible	not eligible

Table S3.4. Rubric for scoring data collection and transparency in tRFMOs.

Criteria ID	Category	Score: 0	Score: 1	Score: 2
1	**Precision of Elasmobranch Data**	no shark data available	Nominal (annual average) catch	Full catch data by set and flag (not aggregated)
2	**Fishing Effort Data**	no effort data	PS and LL effort data aggregated by 5 degree	PS and LL effort data aggregated by 1 degree
3	**Spatial Shark Catch Data**	no spatial data	PS and LL shark catch data aggregated by 5 degree	PS and LL shark catch data aggregated by 1 degree
4	**Inclusion in convention text**	not included	included as "non-target/ ecologically-related species"	included specifically as "elasmobranchs"
	Observer coverage (purse seine)	0-33%	34%-66%	67-100%
	Observer coverage (longline)	0-33		50%
5	**Observer coverage (purse seine)**	proportion (2021) mandated / 100%		
6	**Observer coverage (longline)**	proportion (2021) mandated / 50%		
7	**Proportion of species assessed**	# of species assessed with quantitative stock status assessment / # of species eligible*		

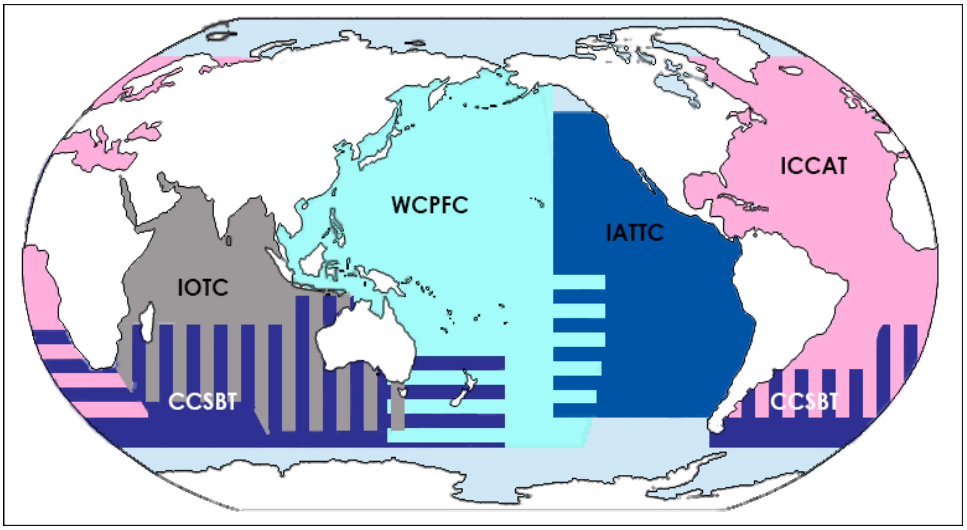


Fig. S3.1 Convention areas of the five tuna RFMOs: the Indian Ocean Tuna Commission (IOTC), the International Commission for the Conservation of Atlantic tuna (ICCAT), the Western and Central Pacific Fisheries Commission (WCPFC), the Inter-American Tropical Tuna Commission (IATTC), and the Commission for the Conservation of Southern Bluefin Tuna (CCSBT). Areas where colors overlap represent regions of joint jurisdiction. Data source: FAO.

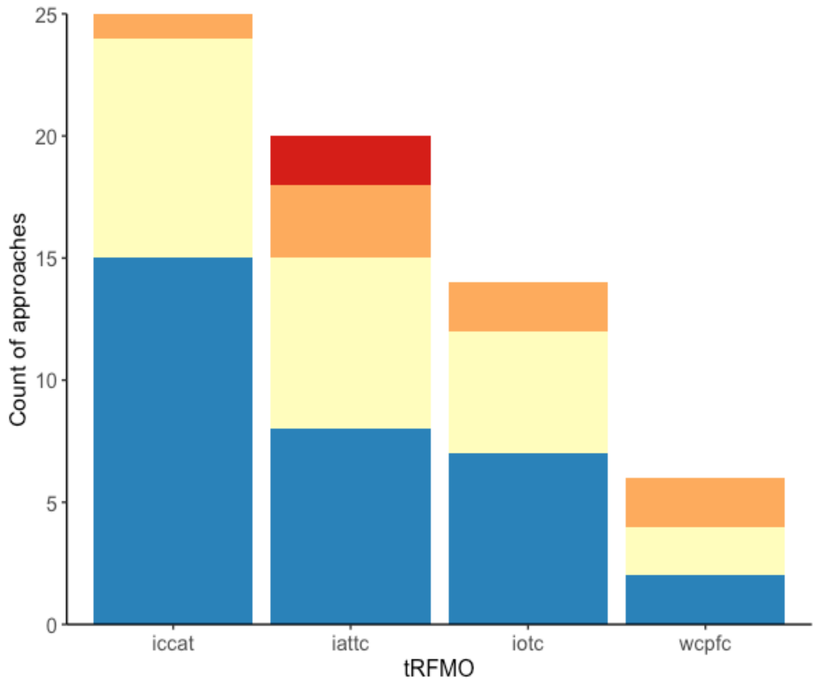
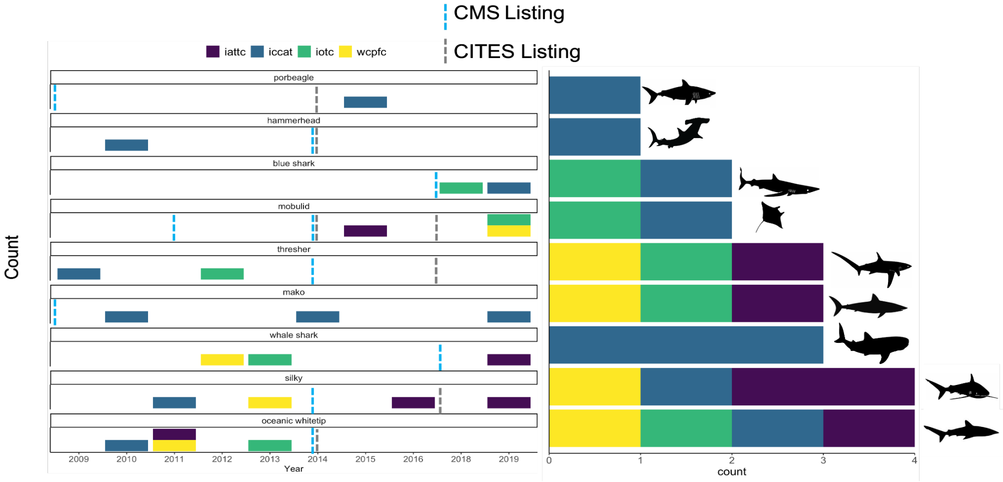


Fig. S3.2. Bycatch mitigation approaches across four tRFMOs. CCSBT is not included in this figure as it follows the policy of the other tRFMOs when fishing in their Convention Areas.



`**Figure S3.3.** Single-species policy adoption for pelagic elasmobranchs in tRFMOs presented as A) a timeline; dashed line represents effective data of CITES listing (listing on Appendix II of CITES for whale shark occurred in 2003 and is not pictured here) and B) Count of species-specific elasmobranch bycatch policies. Totals reported in this figure do not include CCSBT, as it follows the policies of other tRFMOs while fishing in their Convention Areas. Silhouettes from Phylopic (http://phylopic.org/).

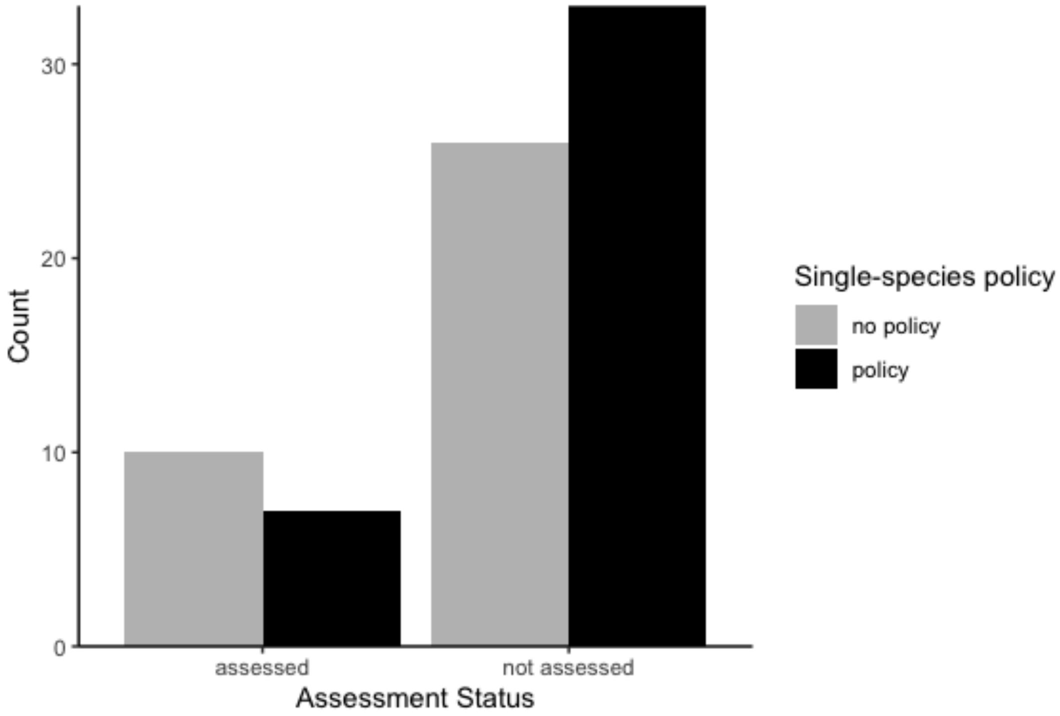


Fig. S3.4. A chi-squared test of independence for single-species policy adoption showed that there was no significant association between these the presence of a stock assessment and single-species policy adoption ($x^2 = 0.6367$, df = 1, $P = 0.42$).

CONCLUSION

Together, these studies present an interdisciplinary approach to describing and evaluating bycatch of oceanic sharks and rays in one of the world's largest and most impactful fisheries. In this dissertation, I demonstrate that oceanic elasmobranch catch is a substantially underreported but potentially significant conservation threat, particularly for the near third of the catch that is already overexploited (Chapter 1). Secondly, I demonstrate the utility of population genomics methods for delineating management and conservation units for one group of pelagic elasmobranchs, the Mobulids. This study shows that Mobulids cannot be considered one panmictic population, but instead have complex patterns of population structure and local selection that are important to protect and consider in conservation and management plans (Chapter 2). Finally, I show that current policies in the large international regulatory bodies that manage tuna fisheries are inadequate to avoid bycatch in these tuna fisheries, and that stronger policy is necessary to mitigate elasmobranch bycatch in tuna fisheries (Chapter 3).

Broadly, this thesis contributes to the notion that, despite long-held beliefs to the contrary, oceanic fish populations are not boundless. In fact, many elasmobranchs are at an elevated risk of extinction due to overfishing, and will continue to experience population declines under current levels of fishing pressure (Dulvy et al. 2008, Pacoureau et al. 2021). The large scope of pelagic elasmobranch catch identified by Chapter 1 combined with the policy deficits identified in Chapter 3 indicate that tuna fisheries are a high priority area for elasmobranch conservation. Both chapters point to substantial gaps in biological and fishery information that, if addressed, could allow for more informed management. But I also show in Chapter 3 that better scientific information (e.g., more stock assessments) does not necessarily lead to more or better policy adoption for elasmobranchs.

For this reason, reversing population declines for pelagic elasmobranchs will require more than just better data. Because much of this catch occurs on the high seas, in areas beyond national jurisdiction, this problem is more difficult to manage (Ostrom et al. 1999), and even more difficult to solve. Complicating an already complex problem is the powerful incentive of high prices inflated by economic subsidies that float industrial tuna fleets (Sumaila et al. 2016, Sala et al. 2018).

Despite these challenges, solutions to reduce the impact of tuna fishing on pelagic elasmobranchs exist, and have been recommended by scientists, conservationists, fishers, and managers for decades (Hall 1996, Jenkins 2007, Worm et al. 2013). Reducing fishing subsidies and associated capacity, implementing well-enforced large protected areas and spatiotemporal closures, cracking down on illegal and unregulated fishing, and adopting precautionary management for both targeted and bycatch elasmobranch populations would all be steps in the right direction (Pauly et al. 2002, Ban et al. 2014, Crespo et al. 2019, Maxwell et al. 2020, O'Leary et al. 2020). Designing interventions informed by population genomics and correctly scaled to population dynamics would help efficiently use scarce conservation resources. And implementing strong, avoidance-focused fishery policy can help set a top-down agenda for nations to consider non-target species as important as they do target species. Because these species do not respect international boundaries, international and national efforts must coordinate to support action at scales relevant to these species. Ultimately, protecting these species is a large and complex collective action problem. But solving that problem has benefits for biodiversity, food webs, human communities, and global ecosystems.

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Chapter 1

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