Spatial ecology and conservation of sharks, rays, and chimaeras

by

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Abstract

Patterns of biodiversity provide foundational information that can be used to inform conservation prioritization and action. For example, those places harbouring relatively greater numbers of threatened, endemic, or evolutionary distinct species may intersect with threats and conservation actions such as Marine Protected Areas (MPAs) or sustainable fisheries management. Here, I explore patterns of biodiversity, threat, and finally the conservation actions that, if implemented, could improve the status for the world's threatened marine species. First, I evaluated the contribution of MPAs and governance ability in protecting the world's threatened marine biodiversity. I found that 74 of the 338 threatened marine species in the database are neither adequately protected by MPAs nor found in countries with higher governance scores. Second, I focused on Class Chondrichthyes as a case study to evaluate the relationships between national landings trajectories and intrinsic ecosystem sensitivity and extrinsic drivers and threats. I found that global decline in Chondrichthyes landings was associated with overfishing, particularly in small tropical diverse ecosystems, rather than with management improvements. Third, I evaluated the degree to which MPAs protected imperilled endemic Chondrichthyan species. I found that only 12 of 99 imperilled endemics have at least 10% of their range overlapping with one or more strictly protected, no-take MPAs. However, over half of the threatened endemic Chondrichthyans can be protected given strategic MPA creation and fisheries management implementation in just 12 countries. Finally, to consider the conservation of a representation of unique assemblages, I delineated the unique shark and ray zoogeographic and phylogenetic regions. Globally, there are 41 zoogeographic and 12 phylogenetic shark and at least 50 and 28 ray regions, respectively. I suggest these regions be the focus for evaluating whether MPAs are ecologically representative. In conclusion, I incorporated biodiversity gradients, MPAs, fisheries management, and socio-economics to inform and improve conservation outcomes for threatened marine biodiversity.

Keywords: **fisheries; conservation planning; marine protected areas; socio-economic indictors; governance; phylogeny; biogeography; Gondwanaland**.

Dedication

To the most tenacious and hardworking people I know – my Mom and Dad.

Thank you for the continued love and support!

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Chapter 1. General Introduction

"Little in ecology, evolution, and conservation biology makes sense unless viewed within a geographic context"

Lomolino, Riddle, and Brown. *Biogeography,* 2010

Biodiversity gradients are non-random and are incongruent across different measures of biodiversity (Orme et al. 2005; Lennon et al. 2003). Likewise, patterns of threatening pressures, extinction risk, and conservation actions are non-random. Thus, intersection of biodiversity and threatening pressures can determine the locations of high biodiversity value that are exposed to relatively higher threatening pressures (Myers et al. 2000). Here, I determined conservation opportunities in the ocean by combining patterns of biodiversity and threatening pressures. I integrated principles from systematic conservation planning and biogeography to provide the basis for a more-coordinated international approach to marine species management and conservation.

1.1. Vulnerability, extinction risk and systematic conservation planning

Conservation biologists are faced with optimizing conservation outcomes due to limited financial and temporal resources. The vulnerability approach seeks to understand the intersection of biological priorities with exposure to threatening processes, offset by the socio-economic likelihood of conservation (Dulvy et al. 2003; Turner et al. 2003) (Fig 1.1, adapted from Turner et al. 2003). Here, vulnerability is defined as the ability of a species or socio-ecological system to withstand perturbations without a phase shift and is comprised of three elements: (1) intrinsic sensitivity, (2) extrinsic exposure, and (3) adaptive capacity, which in this thesis I consider to be the presence and strength of management (Fig. 1.1).

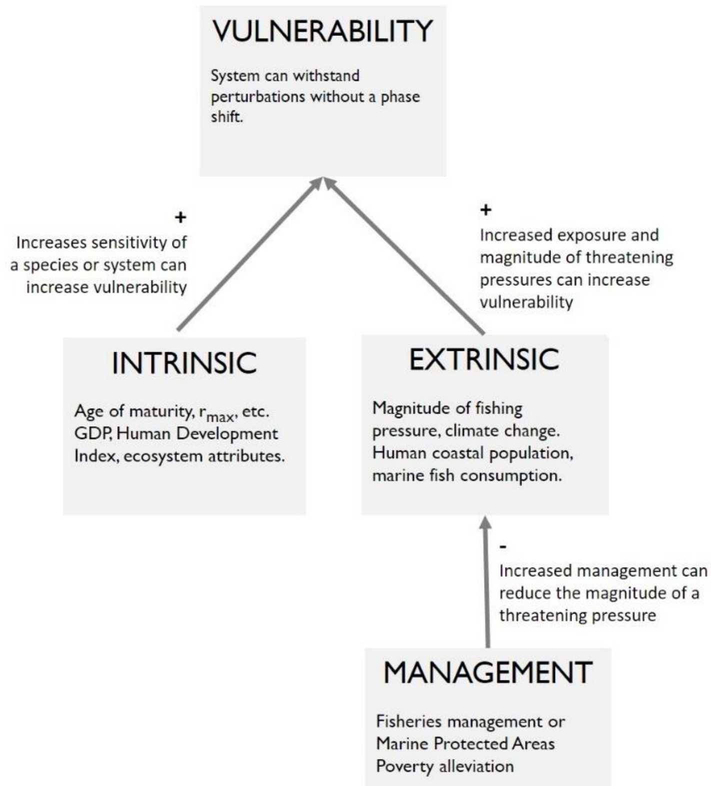

Figure 1.1 Vulnerability framework (adapted from Turner et al. 2003) that defines the vulnerability of a species or a socio-ecological system to perturbations as a function of intrinsic measurements (such as species life history or national socio-economic status), and extrinsic exposure (such as strength of threatening pressures, such as overfishing or climate change), and finally, the management that can modify the strength of threatening pressures (such as fisheries mangement, marine protected areas or climate change adaptivity).

A species' intrinsic sensitivity to extinction is generally non-random and can be predicted based on a species' biological and ecological characteristics (Cardillo et al. 2008). Intrinsic species traits include time-related (age of maturity, population growth rate, r_{max}) or size-related characteristics (maximum body size, geographic range size) (José Juan-Jordá et al. 2012; Hutchings et al. 2012). For example, those species with later ages of maturity, larger body sizes, or smaller geographic ranges are more sensitive to extinction (Cardillo et al. 2008; Davidson et al. 2012; Reynolds, Dulvy, et al. 2005). Those species more sensitive to extinction, based on intrinsic characteristics, may only be able to tolerate lower levels of exposure to threatening pressures, such as fishing or climate change. Hence, sensitivity interacts with the appropriate exposure process, e.g. large body size interacts with fishing pressure in marine fishes, whereas small-body size, and small geographic ranges of freshwater fishes interact strongly with habitat loss (Reynolds et al. 2005).

This vulnerability framework is enshrined within the International Union for the Conservation of Nature (IUCN) Red List Categories and Criteria. To date, 1,017 marine species are categorized with elevated extinction risk in one of three IUCN threat categories of Vulnerable, Endangered, or Critically Endangered. Of these threatened marine species, 183 are Chondrichthyes (sharks, rays, and chimaeras) meaning Chondrichthyes have the third highest proportion of threatened species of all groups (marine and terrestrial) assessed thus far (Hoffmann et al. 2008; Dulvy et al. 2014); preceded only by reef-building corals (33%) and amphibians (41%) (Hoffmann et al. 2010; Carpenter et al. 2008). Species categorized as Vulnerable, Endangered, or Critically Endangered are often prioritized for conservation action as they are in most urgent need of attention.

Systematic conservation planning also draws from the vulnerability framework to determine regional conservation priorities; i.e., those areas that that fall along the two axes of intrinsic and extrinsic measures (Fig. 1.2). The 'vulnerability' axis (equivalent to extrinsic measures) was defined to capture exposure to threatening pressures (Margules & Pressey 2000). The 'irreplaceability' axis (equivalent to intrinsic measures) was defined to capture locations with high numbers of small-ranged, hereafter "endemic" species. Endemic species are intrinsically vulnerable due to the potential for extinction from random, localized stochastic events, their limited spatial conservation options, and their relatively lower population densities (Brooks et al. 2006; Pimm et al. 2014). The systematic conservation planning framework, combined with the IUCN species assessment focus, seeks to determine the locations of areas of high intrinsic sensitivity and high exposure to threatening pressures, although see Brooks et al. 2006 for variations.

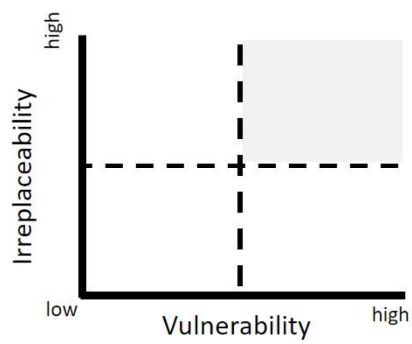

Figure 1.2 Systematic conservation planning framework (adapted from Margules & Pressey 2000). The systematic conservation planning framework aims to determine those areas of high intrinsic sensitivity (irreplaceability) and high exposure to threatening pressures (vulnerability) (corresponding to the shaded grey box), although see Brooks et al. 2006 for variations.

Systematic conservation planning became an important conservation tool, first in the terrestrial realm but with increasing application to the marine realm. Using the two axes of vulnerability and irreplaceability, Myers et al. (2000) found the locations where high numbers of endemic plants were highly exposed to threatening pressures. These areas, defined as 'hotspots', were concentrated globally and only covered 1.4% of the land surface area, contained almost half of the world's threatened plants, and covered 35% of threatened vertebrate species (Myers et al. 2000). These areas became the primary focus of terrestrial conservation action (Brooks et al. 2006).

Initial applications to the marine realm revealed hotspots of endemic cone snails, lobsters, hard corals, and reef fishes and evaluated the threatening pressures within each area (Roberts et al. 2002). A marine mammal prioritization scheme identified hotspots of threatened marine mammals (species categorized by the IUCN as Vulnerable, Endangered, or Critically Endangered) overlaid with distributions of threatening pressures (Davidson et al. 2012). Another analysis determined the distribution of pelagic species richness and the association of these species richness hotspots with fishing pressure (Trebilco et al. 2011). As the field of systematic conservation planning advances, however, conservation prioritization is no longer about prioritizing species or places, but rather actions (Brown et al. 2015). Therefore, there remains an opportunity to couple an understanding of the distribution of threatened, endemic marine species hotspots with an evaluation of existing management actions. Indeed, management is another dimension within the vulnerability framework, as the presence and effectiveness of management can modify the strength and magnitude of threatening pressures (Fig. 1.1).

1.2. Convention on Biological Diversity targets

Almost 200 countries agreed to meet the CBD's 20 Aichi Targets aimed to slow, reverse, or prevent the decline of biodiversity by 2020. Aichi Target 11 - "at least

…10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures…" - provided a benchmark for countries and resulted in the near-doubling of the area of global ocean designated as MPAs (Lubchenco & Grorud-Colvert 2015). In this thesis, I considered the coverage of MPAs and threatened species and in the last chapter delineate the ocean into regions that could be used to evaluated whether MPAs are ecologically representative.

Increasingly, research is considering the intersection between the 20 CBD Aichi Targets. For example, whether MPAs are contributing to CBD Aichi Target 12: "By 2020, the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained" (Venter et al. 2014; Butchart et al. 2015; Le Saout et al. 2013a). However, it remains less well-evaluated whether fisheries management (Aichi Target 6: "By 2020, all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, … fisheries have no significant adverse impacts on threatened species") is widespread or comprehensive enough to meet Aichi Target 12.

1.3. Marine protected areas and sustainable fisheries management

Marine Protected Areas (MPAs) appear to be the dominant management action or conservation tool for the protection of marine species. Although MPA designations have lagged behind increases in terrestrial protected area designations, in 2010 193 countries committed to protect 10% of their coastal waters within MPAs by the year 2020 (Convention on Biological Diversity (CBD) 20 Aichi Targets, Target 11). Progress was initially slow towards this target, however, the 10% target has undoubtedly motivated MPA expansion with a near doubling of ocean area designated since 2006 (Lubchenco & Grorud-Colvert 2015; Wood et al. 2008).

MPAs are not the sole conservation tool and sustainable fisheries management can have clear conservation benefits for species. For example, ending overfishing of targeted stocks could recover half of the world's threatened marine mammals, turtles, and birds that are threatened due to overfishing from bycatch (Burgess et al. 2018). Great White Shark (*Carcharodon carcharias*) populations showed increases in California after a prohibition on catches was implemented in 1994 (Burgess et al. 2014). Spiny Dogfish (*Squalus acanthias*) also recovered under strict catch quotas in the United States and the fishery re-opened in 2011 (COSEWIC 2011). Furthermore, sustainable fisheries management is a goal of the CBD Aichi Targets (Aichi Target 6: ensure sustainable fishing) and there are calls for conservationists to consider fisheries management as a conservation tool (Hilborn 2016; Salomon et al. 2011)

1.4. Goveranance and Conservation Likelihood

Although MPA and sustainable fisheries management coverage is an important goal for species protection, effective governance within a country is increasingly found to be associated with positive conservation outcomes (Amano et al. 2017; Gill et al. 2017). Governance capacity is both a measure of ability to manage successfully but also an indicator of the types of conservation interventions that could be successful in a region (Dickman et al. 2015; McClanahan et al. 2009). I used both dimensions of governance in this thesis, hereafter termed governance and conservation likelihood, respectively.

First, I used a measure of governance to define the attributes that are increasingly found to be the most important attribute of positive conservation outcomes. For example, higher protected area coverage of waterbirds has secured population increases, but only in countries with more effective governance (Amano et al. 2017). Budget and staff capacity were the strongest predictors of conservation outcomes within MPAs (Gill et al. 2017), meaning MPAs in areas of lower governance capacity lead to relatively lower conservation outcomes. Also, fisheries management has had success at recovering populations, like MPAs, sustainable fisheries mangement has been found to positively correlate with measures of a country's governance capacity (Melnychuk et al. 2016; Mora et al. 2009; Newton et al. 2007). Therefore, although there is a role for fisheries management in ensuring the seas have suitably low fishing mortality, without investment in human, scientific, and financial capacity, fisheries management outcomes may not be successful (Salomon et al. 2011; Melnychuk et al. 2016).

Second, I used conservation likelihood score (using the same metrics and methods as the governance score) as a measure of the conservation interventions that could be successful in a region. Countries with lower conservation likelihood scores represent areas where the population is likely to be more dependent on fishing for sustenance and therefore less resilient to changes in access to fisheries due to management action (Singh et al. 2017). For example, although MPAs may have long-term benefits for biological communities (e.g., increases in fisheries biomass), in the short term, MPAs may restrict access to fisheries resources leading increased fishing pressure outside of MPAs and illegal activities such as smuggling or poaching (Jaiteh et al. 2016). There are tradeoffs between poverty, current economic realities, and development versus biodiversity conservation (Blanchard et al. 2017; Singh et al. 2017; McClanahan et al. 2009). Additionally, fisheries management may be expensive, requiring higher socio-economic conditions for successful implementation and enforcement (Melnychuk et al. 2016). Therefore, countries with relatively lower governance may need conservation actions in the form of poverty alleviation, relief, scientific capacity building, consideration of alternative livelihoods, or preliminary data collection (Jaiteh et al. 2016).

Both metrics were calculated using relatively the same measurements. Based on the approach laid out by Dickman et al. (2015), my governance/conservation likelihood score included measurements that fall under three broad category classes: (1) strength of government: this combines scores of political stability, government effectiveness, control of corruption, and regulatory quality; (2) economy and welfare: this combines Gross Domestic Product (GDP), Purchasing Power Parity, and the Human Development Index (HDI); (3) human pressure: this combines measurements of annual human population growth, and human population 100 km from the coast (see Chapter 2 and Chapter 4 for details). The nine measures I introduced above were collated for each country using 2014 data. In those cases where no measurements were available, I used the most recent measurements (no later than 2011). Taiwan did not have an entry in this database; however, the Taiwan government calculated their HDI to be 0.882. Measurements were adjusted so that high positive values represented relatively higher governance. Therefore, variables such as such as human population density were multiplied by negative one (see Chapter 2 and Chapter 4 for details).

To create the governance score, each of the nine measurements were standardized to a mean of zero and a standard deviation of one. I then summed each of the measurements within each of the three categories, and then took the mean across the three categories. Several overseas territories were excluded from the analysis due to lack of data: Bassas da India, Bonaire, Curacao, Ile Europa, Juan de Nova Island, Falkland Islands, and New Caledonia. As well, Somalia had no information on government and economics and was excluded from the analysis. A final score was available for 180 nations.

1.5. Opportunities

I believed there was an opportunity to incorporate both management and governance/conservation likelihood directly into systematic conservation planning analyses. The inclusion of all these dimensions could not only identify the species and places, but also the specific management actions and governance realities that could be considered in the conservation of the world's threatened marine species. These additional dimensions were yet to be incorporated into a global, marine, conservation planning analysis.

1.6. Broad methods

1.6.1. How did I map species?

In this thesis, I used two databases of geographic ranges: Aquamaps and the IUCN Extent of Occurrence (EOO) range maps. The Aquamaps (aquamaps.org) geographic ranges are model-generated species distribution models with relative probabilities of occurrence ranging between 0 and 1. They were mapped to a 0.5 degree global grid. Relative environmental suitability decreases linearly with probability of occurrence (Klein et al. 2015). Less than 5% of the over 22,000 maps are reviewed by experts (Hara et al. 2017).

The IUCN EOO geographic range maps (iucnredlist.org) are expert-generated species distribution maps with a convex polygon drawn around all known locations. The maps were generated based on expert opinion of species presence, depth, and habitat preferences.

In Chapter 2, I used the Aquamaps database. I defined the geographic range of a species to include any cells with a probability of occurrence ≥60% for that species. I found this threshold created geographic ranges that matched the EOO maps more closely. The Aquamaps database has many more species distribution ranges (for example, 126 versus 30 ray-finned fish distributions) allowing the analysis to be extended to include more threatened marine species (Butchart et al. 2015). In Chapter 3, 4, and 5, I used the IUCN EOO maps as they are peer-reviewed.

1.6.2. How did I spatially define threats?

Almost a quarter of threatened marine species have exploitation listed as one of their threats (Fig. 1.2 from Dulvy et al. in prep., Maxwell et al., 2016). Fishing pressure is therefore the dominant threatening pressure in the ocean and can be mitigated through sustainable fishing practices or MPA protection.

In order to capture the spatial distribution of threatening pressures, I used the distribution of threatened species as a surrogate because a vulnerable species is a combinate of intrinsic sensitivity and extrinsic exposure. Previous analyses have defined the distribution of threat as areas of high threatening pressures such as pollution, vessel traffic, fishing pressure (i.e., impact maps from Halpern et al. 2008). Using the distribution of threatened species, however, allowed for the inclusion of all threatening pressures affecting that species, thus avoiding using the distribution of one measurement of threat as a surrogate (i.e., fishing pressure) and prevented the assumption that the magnitude of the threatening pressure translates to biodiversity loss (i.e., some populations may be more or less resilient) (Brooks et al. 2006).

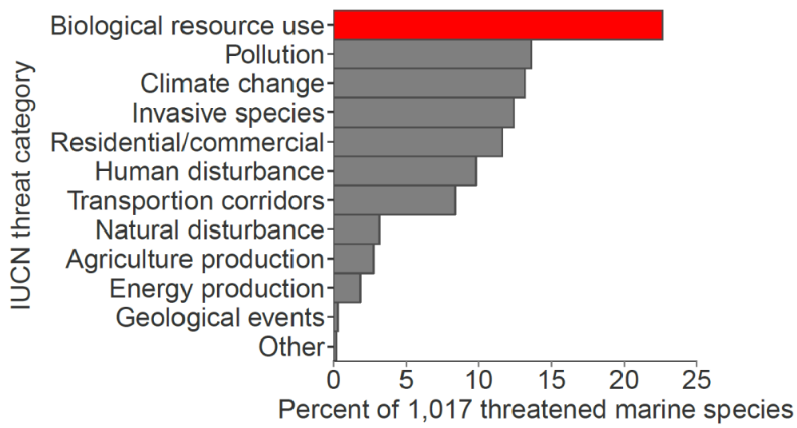

Figure 1.3 Threatening pressures for marine species categorized by the IUCN as threatened (Critically Endangered, Endangered, or Vulnerable). Almost a quarter of the 1,017 marine species are threatened from Biological Resource Use (i.e., fishing) (from Dulvy et al. in prep.).

I did not explicitly consider climate change in this thesis. Climate change may shift species distributions deeper or to higher latitudes (Dulvy et al. 2008; Sunday et al. 2012) therefore potentially shifting populations outside of either present-day, or proposed, MPAs. Future work will have to consider these shifts and ensure MPAs continue to capture biodiversity. However, present-day work and conservation efforts need to ensure that population sizes are robust enough to mitigate and adapt to climate change.

Whereas fishing pressure can be mitigated through MPAs, the role of MPAs in protecting species from climate change is more tenuous. For example, protecting coral species within MPAs protects those species that are less resilient to climate change (Cote & Darling 2010). Consequently, the Class Anthozoa was excluded from Chapter 2 as the majority of the decline in their geographic range size can be attributed to mass bleaching events (Kent Carpenter, pers. comm.) and there is little evidence to suggest climate change can be mitigated through MPAs for this group of species. Conservation of reef-building corals will require conservation planning focused on finding areas of climate refugia.

1.6.3. Which MPAs did I consider?

To evaluate protection from MPAs, I considered only the 1,388 marine parks categorized by the IUCN as 1a (strictly protected, no-take); hereafter “Marine Reserves”. I chose to consider only Marine Reserves as they have the attributes demonstrated to increase species biomass for large-bodied, vulnerable, exploited species, such as sharks (Costello & Ballantine 2015; Edgar et al. 2014). MPAs that allow for fishing have shown increases in total fish biomass, however, this is not true for larger species such as sharks (Gill et al. 2017). MPAs that allow entry have no distinguishable effect on shark biomass relative to fished areas (McCook et al. 2010; Dulvy 2006).

1.6.4. What are the intrinsic sensitivity and extrinsic exposure measures on a national scale?

I used the vulnerability framework to assess fisheries landings trajectories to understand whether measures of intrinsic sensitivity, extrinsic threatening pressures, or management are associated with landings declines. Broad measures of ecosystem intrinsic sensitivity include area, species richness, and number of endemic species (Brooks et al. 2006; Nesbitt & Moore 2016). The larger the ecosystem, or on a national scale a larger Exclusive Economic Zone (EEZ), potentially represents an ecosystem with larger population sizes of species or greater numbers of subpopulations. Increased subpopulations increase the stability of the metapopulation thereby reducing the risk of collapse or decline (Anderson et al. 2013; Mellin et al. 2014; Loreau et al. 2001). A larger area also correlates with increased species richness (Jaccard, 1912) and could therefore represent a country with more fisheries options or increased multi-species Maximum Sustainable Yield (Newton et al. 2007). Finally, the number of endemics within an ecosystem may be an indicator of intrinsic ecosystem vulnerability due to the correlation of elevated extinction risk with range size (Brooks et al. 2006; Pimm et al. 2014).

1.6.5. Why use sharks as a case study for marine biodiversity conservation and distribution?

Chondrichthyes are an ideal Class of organisms to answer biogeography and conservation questions: they are globally distributed, have a completed phylogenetic tree, have completed peer-reviewed distribution maps and IUCN assessments, have a high proportion of threatened species and are threatened from the dominant pressure in the ocean, and have been shown to be successfully conserved through MPAs and sustainable fisheries management (Dulvy et al. 2014; Simpfendorfer and Dulvy 2017; Curtis et al. 2014).

1.7. Main objectives of this thesis

My thesis can be grouped broadly into management evaluation and conservation opportunity. Under management evaluation, I analyzed the following:

Chapter 2; marine protected area and sustainable fisheries coverage for threatened marine species. Here, I evaluated the progress towards meeting intersecting international conservation targets for 338 threatened marine species in my database and considered opportunities for expanding conservation action.

Chapter 3; correlates of Chondrichthyan landings declines. Here, I evaluated the sustainability of global Chondrichthyan fisheries and identified the opportunities for improving sustainability on a nation-by-nation basis.

Under conservation opportunities, I analyzed the following:

Chapter 4; opportunities for MPA and fisheries management expansion. Here, I evaluated the current coverage of marine protected areas for threatened endemic

Chondrichthyan species and determined the opportunities for global marine protected areas and fisheries management expansion while considering the socio-economic realities that could influence conservation action and interventions.

Chapter 5; scaling up conservation. Here, I determine the global areas of distinct shark taxonomic and phylogenetic chondrichthyan assemblages that could be used to evaluate to what extent current and proposed MPAs are ecologically representative.

Chapter 2. Governing the gaps: safeguarding and sustaining threatened marine biodiversity inside and beyond Marine Protected Areas[1]

2.1. Abstract

The total ocean area designated as Marine Protected Areas (MPAs) has to more than double to meet Aichi Target 11 (10% of a nation's coastal waters protected by 2020). The race to meeting this area-based target, however, means countries may have sacrificed strategic placement of MPAs to protect threatened species (interdependent Aichi Target 12: to protect and improve the status of all known threatened species). Furthermore, MPAs are not the only area-based conservation measure -- sustainable fisheries management may play an important role limiting mortality of threatened species (Aichi Target 6: improve sustainable fisheries management). MPA and sustainable fisheries management have been documented to increase fish biomass but only in countries with more effective governance. Therefore, I assessed the coverage of both MPAs and governance ability with the distribution of the world's threatened marine species. I found that almost all of the threatened marine species in my database (334 out of 338) have less than 10% of their geographic range within global Marine Reserves (those MPAs that are strictly protected and no-take). I identified 74 'double-jeopardy' threatened marine species that are currently not adequately protected either by a Marine Reserve or within a country with relatively higher governance ability. Finally, I considered the conservation responsibility of countries for those double-jeopardy species and their access to resources and capacity for investment into capacity building, governance, fisheries sustainability, or MPA creation.

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[1] A version of this chapter is in preparation for publication with Brown, CJ., Holden, M., Jones, K., Klein, C., Kuempel, C., McGowan, J., Shumway, N., Stuart-Smith R., Possingham, H., Watson, J., and Dulvy, NK.

2.2. Introduction

Almost 200 countries agreed to meet the Convention on Biological Diversity's 20 Aichi Targets aimed to slow, reverse, or prevent the decline of biodiversity by 2020. Aichi Target 11 - the commitment to protect 10% of coastal marine areas - provided a benchmark for countries and resulted in the near-doubling of the area of global ocean designated as marine protected areas (MPA) (Lubchenco & Grorud-Colvert 2015).

Despite the global success in MPA expansion, the rapid growth in MPA coverage has led to growing concern for 'residual' MPA – those situated in places least desirable to extractive industries rather than based on biodiversity attributes of the region (Devillers et al. 2014; Jones & Santo 2016). The focus on MPA expansion, instead of strategic placement according to biodiversity value, means countries may have overlooked the interdependent and ultimate conservation outcome CBD Aichi Target 12 - 'to protect and improve the status of all know threatened species'.

There is an opportunity to expand MPAs to cover the distributions of threatened marine species that are not adequately protected (Butchart et al. 2015; Klein et al. 2015). For example, 12 of 99 imperiled, endemic shark and ray (Class Chondrichthyes) species are found within the global no-take and strictly protected MPAs despite 30% of total MPA area being designated for the explicit protection of sharks (Davidson & Dulvy 2017). The remaining 87 'gap' species, i.e., those that have either 0% or less than 10% of their geographic range within MPAs, could become the focus of MPA creation in order to better protect threatened sharks and rays and therefore achieve both Targets 11 and 12 (Venter et al. 2014; Butchart et al. 2012; Polak et al. 2016).

Although MPA coverage is an important goal for threatened species protection, effective governance within a country is increasingly found to be the most important attribute of positive conservation outcomes. For example, higher protected area coverage of waterbirds has secured population increases, but only in countries with more effective governance (Amano et al. 2017). Budget and staff capacity were the strongest predictors of conservation outcomes within MPAs (Gill et al. 2017), meaning MPAs in areas of lower governance capacity lead to relatively lower conservation outcomes.

Sustainable fisheries management can also play a role in conservation of species. Especially since the scale of MPA protection can be small compared to a species' activity space or home range. Consequently, a species may have the majority of it's range far outside the boundaries of MPAs and therefore be exposed to fishing pressure (Boonzaier & Pauly 2015). Fisheries management has had success at recovering populations, and, like MPAs, sustainable fisheries mangement has been found to positively correlate with measures of a country's governance capacity (Melnychuk et al. 2016; Mora et al. 2009; Newton et al. 2007). Therefore, although there is a role for fisheries management to play in ensuring the seas beyond MPA boundaries have suitably low fishing mortality, without investment in human, scientific, and financial capacity, fisheries management outcomes may not be successful (Salomon et al. 2011; Melnychuk et al. 2016).

Therefore, here I considered the intersection of MPAs and a national score of governance to identify the species, nations, and broad actions that could be implemented to protect the threatened marine biodiversity in my database (Fig. 2.1). Specifically, I asked four questions. (1) Which threatened marine species are not yet protected by global MPAs (i.e., gap species)? (2) Which threatened marine gap species occur in countries with lower governance scores (i.e., double-jeopardy species)? (3) Where are the global locations with the greatest numbers of gap and double-jeopardy species? (4) Which countries have the greatest conservation responsibility for gap and double-jeopardy species?

2.3. Methods

2.3.1. Threatened species included in the analysis

I considered all 1,017 marine species categorized by the International Union for the Conservation of Nature (IUCN) as threatened: Vulnerable, Endangered, or Critically Endangered (www.iucn.org; IUCN 2015). However, of these, I analysed only the subset of 491 threatened species with available Aquamaps, from 12 taxonomic Classes for analysis: 153 species of Anthozoa (corals and allies), 130 Elasmobranchii (sharks), 126 Actinopterygii (ray-finned fish), 29 Aves (marine birds), 23 Mammalia (marine mammals), 9 Holothuroidea (sea cucumbers), 8 Reptilia (marine reptiles), 7 Myxini (hagfishes), 2 Bivalvia (bivalves), 2 Gastropoda (snails, slugs), 1 Malacostraca (crabs, crustaceans, etc.,), and 1 Sarcopterygii (lobe-finned fish) (http://www.aquamaps.org/; Kaschner et al. 2016).

The Aquamaps geographic ranges are species distribution models with relative probabilities of occurrence ranging between 0 and 1, mapped to a 0.5 degree global grid cell. Relative environmental suitability decreases linearly with probability of occurrence (Klein et al. 2015). I defined the geographic range of a species to include any cells with a probability of occurrence ≥60% for that species. I found this size of geographic range matched the IUCN Extent of Occurrence areas (polygon around all known distributions) more closely.

2.3.2. Portion of geographic range outside of national jurisdictions

For pelagic species that have geographic ranges extending beyond national jurisdictions into international waters (such as the blue shark (*Prionace glauca*), blue whale (*Balaenoptera musculus*), or tunas (Scombridae spp.)) I excluded the portions of the ranges extending outside of global Exclusive Economic Zones (EEZ; national marine waters). I considered only national jurisdictions in this analysis because comparing national management to international management is not feasible. International jurisdictions will require consideration in future analyses

2.3.3. Dominant threatening pressure for threatened marine species

To determine the dominant threatening pressure for threatened marine species I linked the species from the spatial Aquamaps database to the IUCN Red List of Threatened species (iucnredlist.org). The IUCN database lists threatening pressures unique for each species based on 12 categories that include human pressures, natural disturbance, exploitation, habitat loss, and climate change (Salafsky et al. 2008). Most species have multiple threats associated with their IUCN listing and threats are not ranked. For example, a species could have both human exploitation and climate change listed. To determine the threatening pressure with the greatest number of species associated with that threat, I counted the number of species within each of the 12 categories of threat. From this analysis, I retained those taxonomic Classes where the majority of the species were threatened from fishing pressure, leaving 338 species in the analysis. Notably, the Class Anthozoa was excluded from the remainder of the analysis as the majority of the decline in geographic range size can be attributed to mass bleaching events and there is little evidence to suggest climate change can be mitigated through MPAs or sustainable fisheries management for this group of species (Kent Carpenter, pers. comm.).

2.3.4. Marine Protected Areas and Marine Reserves

To evaluate protection from MPAs, I used the World Database of Protected Areas (WDPA; UNEP-WCMC, 2016). The WDPA has 14,743 MPAs of any classification (for example whale sanctuary, shellfish management areas, historical sites, or strict no-take marine reserves) and of any IUCN parks category

(1a - strictly protected no-take marine reserve, to VI - protected area with sustainable resource use, or not reported/not assigned/not applicable). Duplicates were removed from the database if the name and the area were the same.

I considered only the 1,388 marine parks categorized by the IUCN as 1a (strictly protected, no-take; hereafter termed Marine Reserves; Figure 2.2a, Figure S.2a and b for distribution of all parks and IUCN categories). I chose to consider only Marine Reserves as these have the attributes demonstrated to protect and improve biomass for biodiversity protection (Costello & Ballantine 2015; Edgar et al. 2014).

2.3.5. Governance index

I developed a national governance index that broadly reflects the degree to which nations have the enabling socio-economic conditions that correlate with positive conservation outcomes for MPAs and sustainable fisheries management (Melnychuk et al. 2016). Based on the approach laid out by Dickman et al. (2015), my governance score included measurements that fall under three broad category classes: (1) strength of government: this combines scores of political stability, government effectiveness, control of corruption, and regulatory quality; (2) economy and welfare: this combines Gross Domestic Product (GDP), Purchasing Power Parity, and the Human Development Index (HDI); (3) human pressure: this combines measurements of annual human population growth, and human population 100 km from the coast (see Table S.1 for references). The nine measures I introduced above were collated for each country using 2014 data. In those cases where no measurements were available, I used the most recent measurements (no later than 2011). Taiwan did not have an entry in this database; however, the Taiwan government calculated their HDI to be 0.882. Measurements were adjusted so that high positive values represented relatively higher governance. Therefore, variables such as such as human population density were inversed (See Table S.1).

To create the governance score, each of the nine measurements were standardized to a mean of zero and a standard deviation of one. I then summed each of the measurements within each of the three categories, and then took the mean across the three categories. Several overseas territories were excluded from the analysis due to lack of data: Bassas da India, Bonaire, Curacao, Ile Europa, Juan de Nova Island, Falkland Islands, and New Caledonia. As well, Somalia had no information on government and economics and was excluded from the analysis. A final score was available for 180 nations.

I collated a direct measure of sustainable fisheries management effectiveness from the literature: the Fisheries Management Index (FMI) (Melnychuk et al. 2016). The Fisheries Management Index (FMI), is a score determined for 28 countries responsible for greater than 80% of the world's reported global landings and was derived from surveys pertaining to the management of ten targeted species. FMI is therefore an indicator of the effectiveness of management systems at meeting objectives for target fisheries (Melnychuk et al. 2016).

I correlated my national governance index against this direct measure of sustainable fisheries management effectiveness to verify that my governance index is strongly and positively associated with sustainable fisheries management effectiveness. I expected a linear or non-linear but positive correlation between my governance index (representative of the enabling socio-economic conditions) and the Fisheries Management Index (FMI) (a more direct measure of sustainable fisheries management). I used a Spearman's rank correlation to determine the strength and direction of the correlation.

2.3.6. Gap and double-jeopardy definitions

I categorized species into one of three categories based on the amount of their geographic range within Marine Reserves (Klein et al. 2015): (a) no protection (0% of geographic range), (b) poorly protected (0-10% of geographic range), and (c) adequate (≥10% of geographic range) (Figure 2.1). I followed previous definitions whereby “gap” species are those species with less than 10% of their range within one or more Marine Reserves, i.e., categories a plus b (Klein et al. 2015; Rodrigues et al. 2004).

To determine the percent of each species’ geographic range within a Marine Reserve I used ArcGIS version 10.3 and R version 3.2.4 (R Core Team 2015). I used a Cylindrical Equal Area projection and intersected each species’ geographic range with the global Marine Reserves spatial data. As species distribution models assume species are present throughout the entirety of a cell, if the geographic range of a threatened species is overestimated, protection by Marine Reserves will also be overestimated. If species are not equally distributed in each cell, my analysis will overestimate the protection afforded to species and likely represents a conservative (lower bound) estimate of the number of gap species.

To determine which threatened marine gap species are found in nations with a higher national governance index, I calculated the amount of each species’ range within each nation’s EEZ (VLIZ, 2012). I determined double-jeopardy species by calculating the sum of geographic range area inside EEZs with governance index scores greater or less than the median, expressed as a percentage of total geographic range. Species are considered double-jeopardy if the species had both: (1) less than 10% of its geographic range within one or more Marine Reserves and (2) less than 10% of its geographic range within one or more EEZs with a better than average governance score (greater than the median of all scores; see Table S.2 for sensitivity analysis).

2.3.7. Nation-specific weighted threat

I assessed the responsibility of nations to protect threatened marine species by calculating a nation-specific weighted threat score. The weighted threat (WT) of each nation was calculated as the sum of the proportion of each threatened species range within that country.

$$WT = \sum \frac{r}{R}$$

Where *r* is the area of each species' range within a country's national waters and *R* is the species' total range size (Rodrigues et al. 2014). As a sum across threatened species, a high value of WT represents a nation encompassing large portions of threatened species global ranges, and equates countries with few threatened but more endemic species and countries with many less endemic threatened species (Rodrigues et al. 2014).

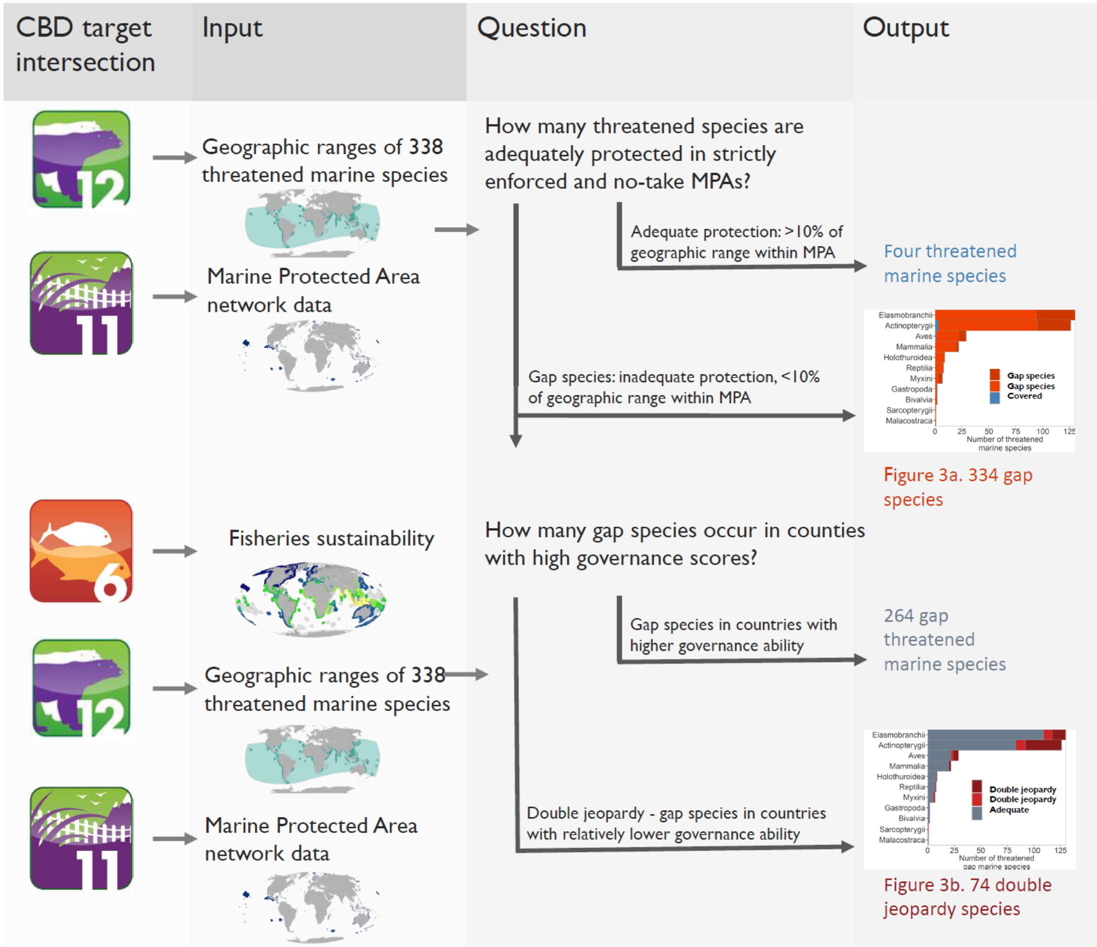


Figure 2.1 **Schematic diagram showing the flow of data, questions, and outputs. Threatened marine species that are not covered by global Marine Reserves are considered 'gap' species. Those gap species that are also found in countries with a low governance index scores are considered to be 'double-jeopardy' species.**

2.4. Results

2.4.1. Does access to resources translate to sustainable fisheries management?

I found that my governance score (Davidson & Dulvy, 2017; adapted from Dickman et al. 2015) is highly correlated with the Fisheries Management Index (FMI) (Melnychuk et al. 2016) that measures the degree to which countries have successful target fisheries management ($n = 25$, $r_s = 0.75$, $p < 0.001$) (Table 2.1). Therefore, I used the governance score for the 180 countries representing 62% of the world's EEZs that had enough data to assign a value. Some nations had incomplete data and hence were not assigned a score. Nations with no data were generally small islands but also include larger nations or archipelagos, such as Somalia, French Polynesia, Greenland, Pitcairn Islands, Cook Islands, Tokelau, and others; EEZs with no score were assigned as "No Data".

2.4.2. How many threatened species are adequately protected in strictly enforced, no-take MPAs?

Almost all (n = 334, 98%) of the world's threatened marine species included in this analysis are gap species, i.e., with less than 10% of their geographic range within Marine Reserves. Furthermore, a quarter (84 of 338 species) of the threatened marine species in this analysis have no part of their range overlapping with any Marine Reserve (Figure 2.3a). The majority of the species with no overlap are fishes (Elasmobranchii: 36 of 130 species; Actinopterygii: 31 of 126 species), but these unprotected threatened species also include Aves (7 of 29 species), Myxini (4 of 7), Mammalia (3 of 22), Reptilia (1 of 8), Gastropoda (1 of 2), and Malacostraca (1 of 1). Most species (249, 74%) are poorly protected with between 0.1 and 10% of their geographic range within Marine Reserves. Within taxonomic Classes, protection varied: Elasmobranchii (94 of 130 species poorly protected), Actinopterygii (92 of 126), Aves (21 of 29), Mammalia (19 of 22), Holothuroidea (9 of 9), Reptilia (7 of 8), Myxini (3 of 7), Bivalvia (2 of 2), Sarcopterygii (1 of 1), and Gastropoda (1 of 2).

Only four species have at least 10% of their range protected; three ray-finned fishes and one marine bird. The Distant Goby, *Lythrypnus insularis*, Socorran Soapfish, *Rypticus courtenayi*, and Black wrasse, *Halichoeres adustus,* and the Indian Yellow-nosed Albatross, *Thalassarche carteri,* have 34, 19, 11, and 11% of their geographic range within Marine Reserves, respectively. These species are found in Marine Reserves located in Australia, New Zealand, United States of America, New Caledonia, Cook Islands, Russia, Indonesia, and South Georgia and the South Sandwich Islands.

(a)

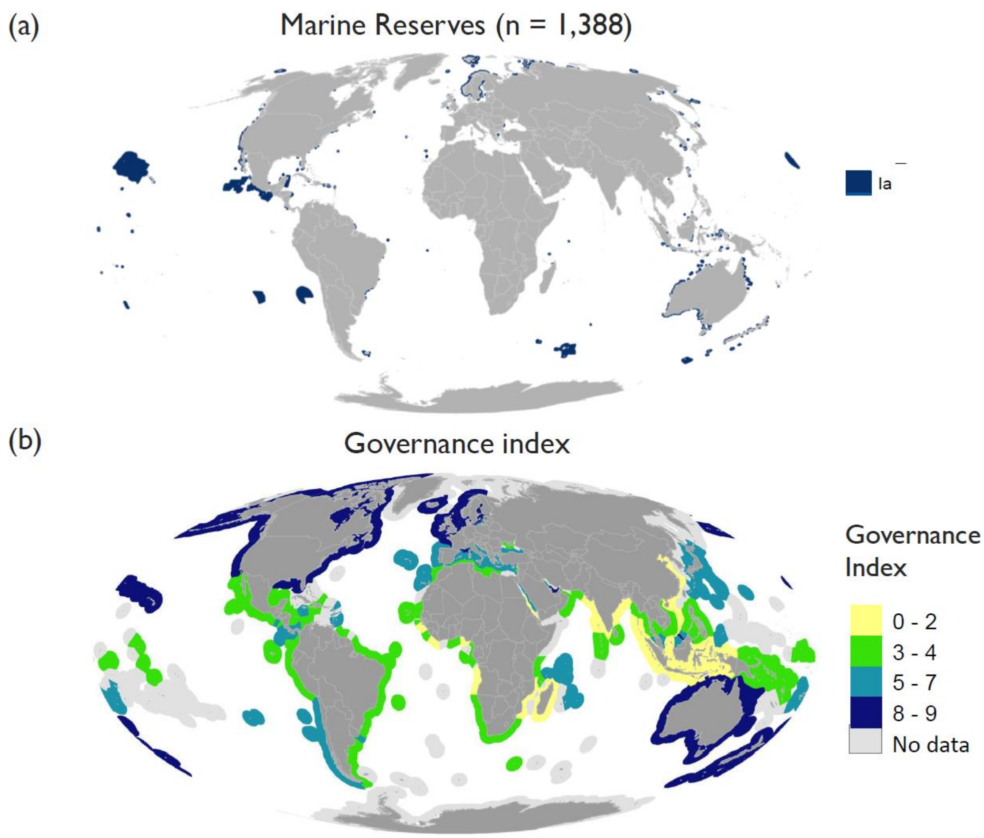


Figure 2.2 **Distribution of Marine Reserves and the national governance index. (a) Marine reserve (marine protected areas that are no-take and strictly protected, designated IUCN 1a). (b) National coastal and continental marine waters (Exclusive Economic Zones – EEZ) are shaded according to their governance index score. Darker blue colours represent those countries with the highest scores and therefore a greater availability of resources while the lighter yellow colours represent those nations with lower availability of resources. Gray nations did not have enough data available to generate a score.**

2.4.3. Double-jeopardy species - how many gap species occur in countries with relatively low governance scores?

There were seventy-four double-jeopardy species, meaning they had between 0 and 10% of their geographic range overlapping with Marine Reserves and 90-100% of their geographic range in countries with governance scores less than the median of all scores (Figure 2.3b, Table S.3). The greatest numbers of double-jeopardy species were within the Classes Actinopterygii (40 out of 123 species), Elasmobranchii (21 out of 130), and Aves (6 out of 28). I completed a sensitivity analysis to see how my definition of governance changed the number of double-jeopardy species. There were only nine double-jeopardy species when countries with low governance scores were considered as those with scores within the lower 25^{th} percentile. There were 155 double-jeopardy species when low governance scores were considered as those countries with scores within the lower 90^{th} percentile (Table S.2).

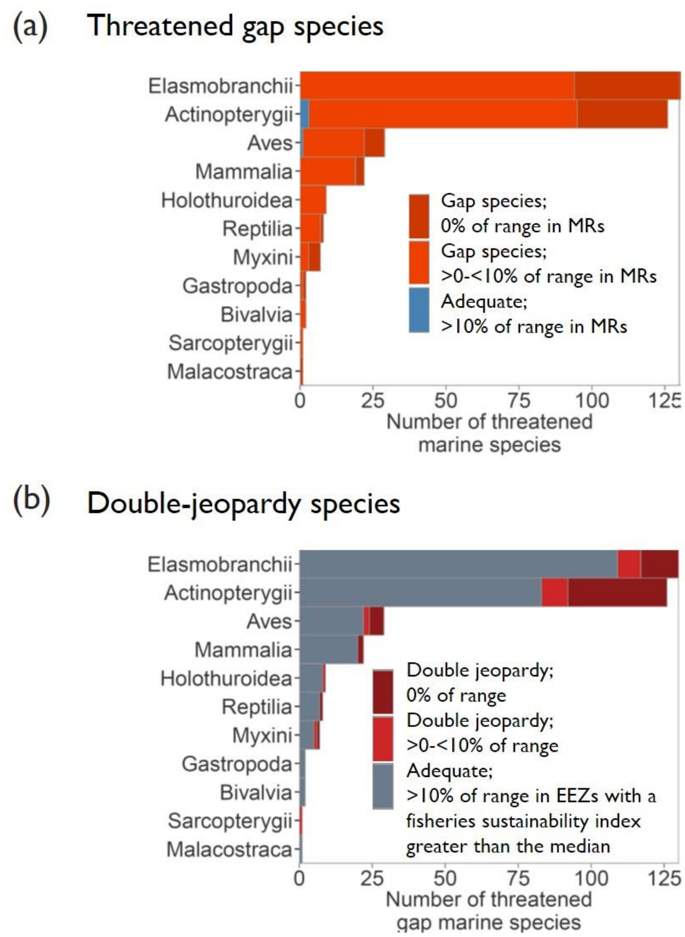


Figure 2.3 **Number of threatened marine species that wee not represented in global Marine Reserves or in countries with above median governance scores. (a) Number of threatened marine species within each Class with no part (dark orange), less than 10% (orange), and greater than 10% (blue) of their of their coastal and continental geographic range overlapping with Marine Reserves. Most species with no protection are Elasmobranchs and Ray-finned fish (Elasmobranchii: 36 of 130 species and Actinopterygii: 31 of 126 species), but also include marine Aves (7 of 29 species), Myxini (4 of 7), marine Mammals (3 of 22), Reptilia (1 of 8), Gastropoda (1 of 2), and Malacostraca (1 of 1). (b) Number of double-jeopardy species: those gap species within each Class with no part (dark red), less than 10% (light red), and more than 10% (grey) of their geographic range in one or more EEZs with governance scores greater than the median. The greatest numbers of double-jeopardy species are within the Classes Actinopterygii (40 out of 123 species), Elasmobranchii (21 out of 130), and Aves (6 out of 28).**

2.4.4. Where are the gap and double-jeopardy species?

Gap species are distributed in the continental shelf seas in most of the world's EEZs, with notable global locations in western Africa, western Pacific extending to Japan, South America, and eastern United States (Fig. 2.4a). The 74 double-jeopardy species are found in 100 nations: Galápagos (Ecuador), Mexico (Gulf of California), western Africa extending from Senegal to Angola, Madagascar, and South Africa, and the Coral Triangle nations (Fig. 2.4b).

The nations with the relatively higher responsibility for the double-jeopardy species are Ecuador (mainland and Galápagos I.), Brazil, Mexico, South Africa, China, Indonesia, Philippines, Madagascar, and Mozambique. These nations have between 0 and 14% of their EEZs designated as a Marine Reserve, with most (6 out of 9) having no Marine Reserves at all (Fig 2.5 (a), Table S.4). These nine nations have governance scores in the first (n=5) or second (n=3) quartile; Ecuador did not have enough data for a score (Table S.4).

Conversely, the ten countries that had the greatest conservation responsibility for adequately protected species (Australia, Indonesia, United States, Mexico, Japan, Canada, Brazil, New Zealand, Argentina, and China) (Fig 2.5 (b) "adequate", Table S.5). These ten countries have between 0 and 57% of their EEZ designated as a Marine Reserve, however, four had less than 1% designated. Half (n=5) had the highest governance scores and therefore have the resources and capacity to invest in effective fisheries management.

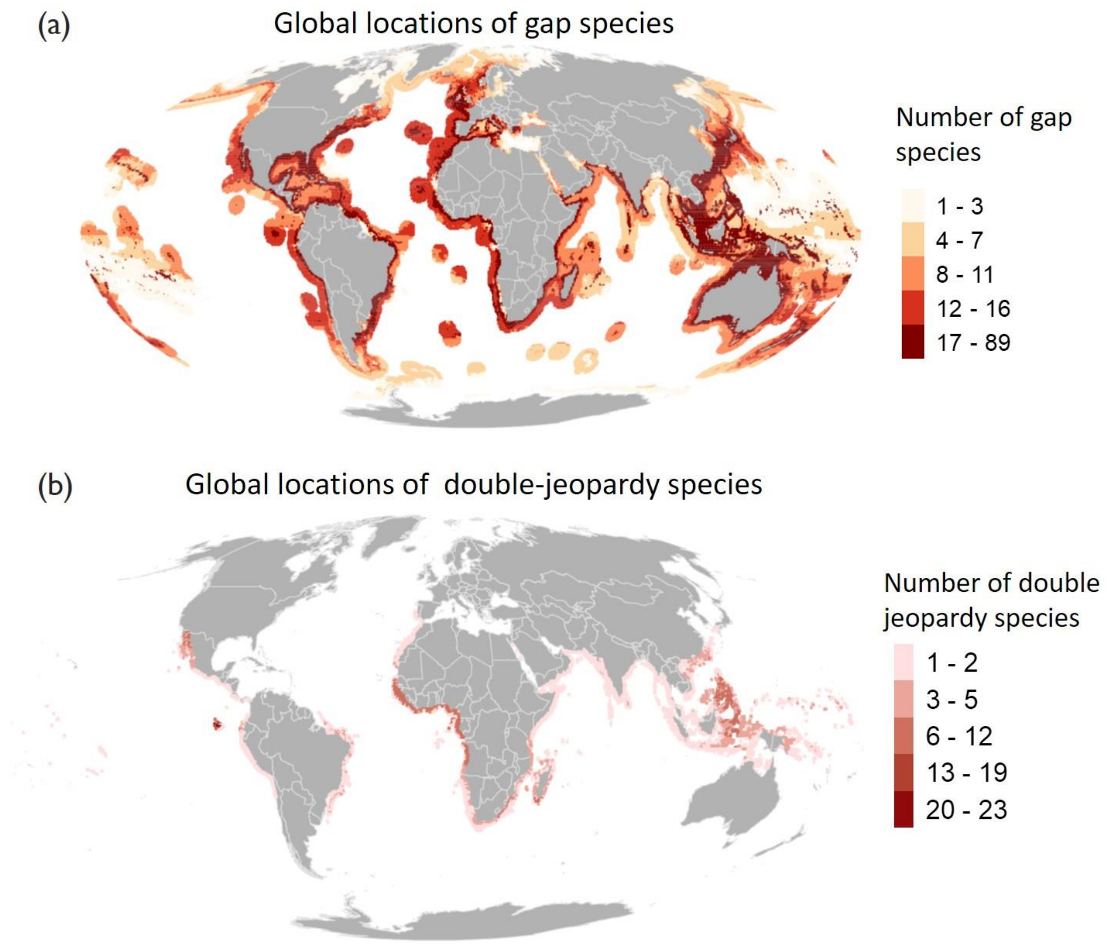


Figure 2.4 **Number of threatened marine species that are not represented in the Marine Reserves or in countries with higher governance scores. (a) Global locations of gap species (those with less than 10% of their geographic range overlapping with Marine Reserves). Darker colours represent larger numbers of gap species. (b) Global distribution of double-jeopardy species – those gap species with less than 10% of their geographic range within Marine Reserves and with less than 10% of their range within one or more EEZs with higher governance scores (greater than the median of all scores).**

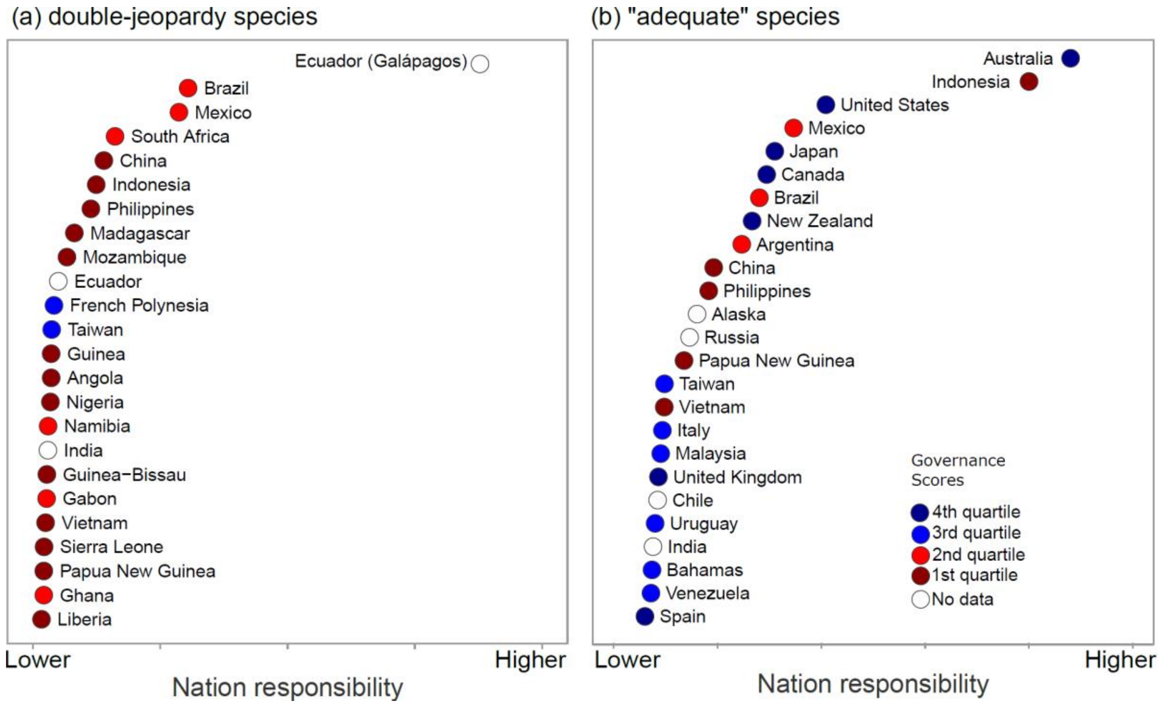


Figure 2.5 **Conservation responsibility and governance scores. (a) Twenty-five nations with the greatest conservation responsibility for double-jeopardy species. (b) Twenty-five nations with the greatest conservation responsibility for threatened marine species that were adequately protection (coverage greater than my marine reserve and governance thresholds). Nations are ordered from highest to lowest and coloured according to governance score.**

2.5. Discussion

This analysis of threatened species distributions, MPAs, and governance capacity yields three major findings. First, almost all of the 338 threatened marine species in my analysis have less than 10% of their geographic range overlapping with one or more Marine Reserves. These findings are in line with previous recommendations that the protected area network could be placed more strategically in order to protect threatened global marine biodiversity as per Convention on Biological Diversity Aichi Target 12 (Butchart et al. 2015; Venter et al. 2014; Le Saout et al. 2013).

Second, using the median governance score as a cut-off, 74 threatened marine species could be considered double-jeopardy species – meaning they are both gap species and species with between 90 and 100% of their geographic range within countries with relatively lower governance scores. These species could be considered priorities of those threatened species already in urgent need for conservation and management action.

Third, on a national level, ten countries have the highest conservation responsibility for the 74 double-jeopardy species (Fig. 2.5). These ten countries have opportunities for Marine Reserve expansions as some of these countries have less than 10% of their EEZ designated as a Marine Reserve. Further, these countries represent opportunity for investment in human and financial capacity as some of these countries have the lowest governance scores. These countries represent urgent conservation funding priorities in order to protect threatened species (Waldron et al. 2017; Waldron et al. 2013). Contrastingly, many species are found in countries with higher governance scores. These countries have the socio-economic attributes that correlate with and have the potential to translate into positive conservation outcomes. Therefore, these countries have the resources to dedicate to fisheries sustainability or implement effective MPAs but perhaps may currently lack the political will.

The success of fisheries management in contributing to biodiversity protection depends on the socio-economic factors that influence the strength and investment into management (Newton et al. 2007). Management effectiveness for targeted species is strongly influenced by Gross Domestic Product and by the number of stock assessments, the latter being data-intensive and expensive (Branch et al. 2011; Melnychuk et al. 2016). Expanding fisheries management to include ecosystem and biodiversity benefits will present significant challenges in species-rich, data-poor countries, however, there are multiple societal and ecological benefits to ending overfishing (Singh et al. 2017). It has been estimated that ending overfishing of targeted stocks could recover half of the world’s marine mammals, turtles, and birds that are threatened by bycatch (Burgess et al. 2018).

Reconciling the disparate, but interconnected, paradigms of conservation and fisheries management presents challenges. While the goals may be the same, trade-offs between MPAs and fisheries management exist (Salomon et al. 2011). Strictly protected Marine Reserves have clear conservation benefits for species biomass, especially for larger, exploited species such as sharks (Edgar et al. 2014; McCook et al. 2010) as well as strict fisheries management (Curtis et al. 2014). However, MPAs have been criticized for displacing fishing effort to other areas and potentially restricting access to fisheries for food-insecure populations, while fisheries management is potentially costlier and could present more implementation challenges in species-rich, data-poor regions. Nations with low governance will first need investment in poverty alleviation, infrastructure, social capital, and alternative incomes to achieve conservation outcomes (McClanahan 2008).

Future analyses will have to consider the amount of MPA protection for currently threatened species as more extensive protected area coverage may be required (Taylor et al. 2011). Although cumulative area coverage is a common metric within gap analyses (Klein et al. 2015; Rodrigues et al. 2004) future conservation research could incorporate measurements of MPA portfolio effects – i.e., coverage from many or one MPAs in order to quantify the trade-offs between risk while balancing the benefits of larger MPAs, and also trading off the cost of enforcement for larger versus smaller MPAs.

2.6. Supplemental material A

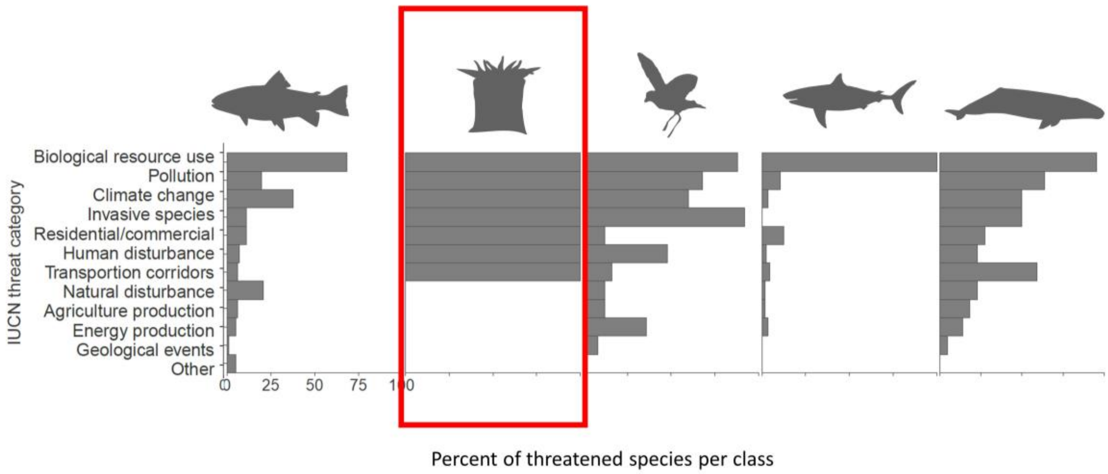
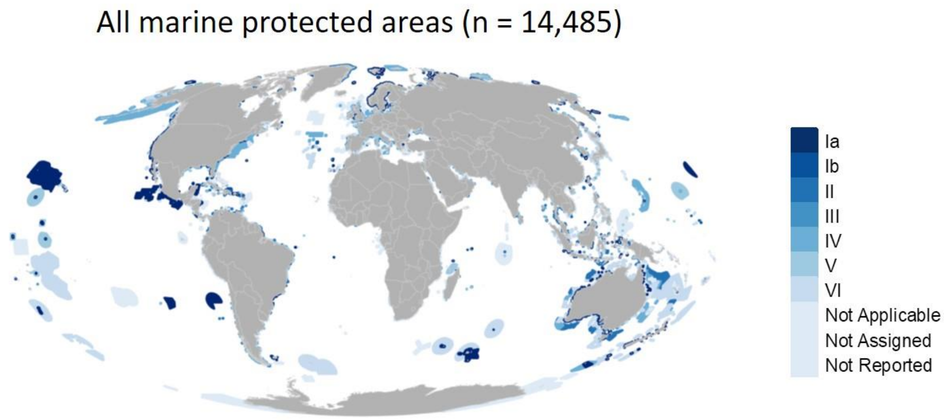


Figure S.1 Frequency of threatening pressures per taxonomic Class. Species in the Class Anthozoa were excluded from the analysis as the majority of declines in geographic ranges were due to mass bleaching events (Kent Carpenter pers. comm.).

(a)



(b)

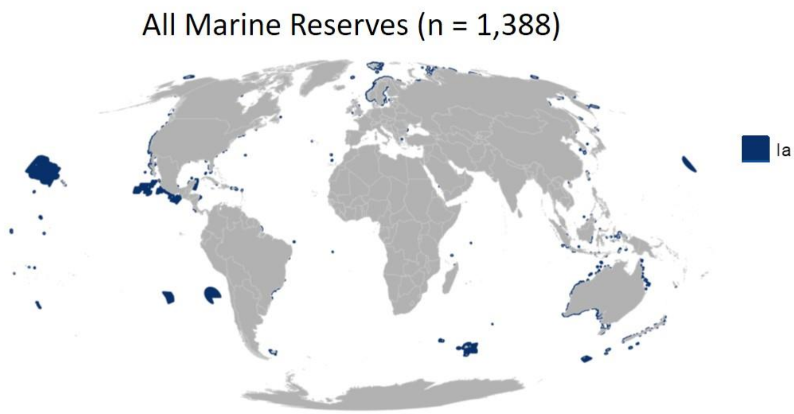


Figure S.2 Distribution of all **(a)** 14,743 Marine Protected Areas of any classification (for example whale sanctuary, shellfish management areas, historical sites, or strict no-take marine reserves) and of any IUCN parks category (1a - strictly protected no-take marine reserve, to VI - protected area with sustainable resource use, or not reported/not assigned/not applicable), and **(b)** the 1,388 marine parks categorized by the IUCN as 1a (strictly protected no-take; Marine Reserves) included in the analysis. Data compiled from the World Database of Protected Areas (WDPA; UNEP-WCMC, 2016).

Table S.1 Broad category classes, variables, and direction of relationship of measures that were included in the governance scores. Variables within each of the three broad category classes were standardized and summed. The final governance score was calculated as the mean of the sum of the three resulting scores.

Category	Variable	Direction and justification	Source
Governance	Political stability	Positive - political instability diverts attention from conservation, limits the will to work in that country and inhibits long-term planning	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
	Government effectiveness	Positive - effective governments are important for meaningful conservation	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
	Control of corruption	Positive - corruption restricts investment and distorts priorities	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
	Regulatory quality	Positive - need to implement and regulate sound conservation policies	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
Economics and welfare	GDP (Gross Domestic Product) per capita	Positive - allows a focus on conservation rather than urgent issues such as food security	World Bank's World Development Indicators for 2011 http://data.worldbank.org/data-catalog/world-development-indicators
	PPP (Purchasing power parity)	Positive - the local buying power of the US dollar affects operational costs of conservation	World Bank's World Development Indicators for 2011 http://data.worldbank.org/data-catalog/world-development-indicators
	Human Development Index	Positive - people are more likely to support and engage in conservation	FAO Aquastat http://www.fao.org/nr/water/aquastat/main/index.stm

Category	Variable	Direction and justification	Source
Human pressure	Annual human population growth	Negative - high growth rates place pressure on resources	World Bank's World Development Indicators for 2011 http://data.worldbank.org/data-catalog/world-development-indicators
	Coastal human population	Negative – higher coastal population places pressure on resources	Center for International EarthScience Information Network (CIESIN) http://sedac.ciesin.columbia.edu/data/set/nagdc-population-landscape-climate-estimates-v3
	Sea Around Us chondrichthyan landings	Negative – higher landings represent greater pressures on population	D. Pauly and D. Zeller, editors. 2015. Catch Reconstruction: concepts, methods and data sources. Online Publication. Sea Around Us (www.seaaroundus.org). University of British Columbia

Table S.2 Numbers of double-jeopardy species per marine Class based on different cutoffs of governance index.

	Higher goverance defined as those countries with governance scores:			
	greater than the lower 25th percentile of all scores	greater than the median of all scoes	greater than the upper 75th percentile of all scores	greater than the upper 90th percentile of all scores
Actinopterygii	6	40	59	72
Aves	-	6	8	11
Elasmobranchii	3	21	34	54
Holothuroidea	-	1	1	2
Mammalia	-	2	4	7
Myxini	-	2	2	6
Reptilia	-	1	2	2
Sarcopterygii	-	1	1	1
TOTAL:	**9**	**74**	**111**	**155**

Table S.3 List of double-jeopardy species, common name, and IUCN extinction risk status.

Class	Order	Family	Binomial	Common name	IUCN extinction risk status
Actinopterygii	Acipenseriformes	Acipenseridae	Acipenser sinensis	Chinese sturgeon	CR
Actinopterygii	Atheriniformes	Atherinidae	Atherinomorus lineatus	Lined silverside	VU
Actinopterygii	Clupeiformes	Clupeidae	Opisthonema berlangai	Galapagos thread herring	VU
Actinopterygii	Gobiesociformes	Gobiesocidae	Arcos poecilophthalmos	Galapagos clingfish	VU
Actinopterygii	Ophidiiformes	Bythitidae	Paradiancistrus cuyoensis	Cuyo coralbrotula	VU
Actinopterygii	Perciformes	Blenniidae	Ecsenius kurti	Kurt's coralblenny	VU
Actinopterygii	Perciformes	Chaenopsidae	Acanthemblemaria castroi	Galapagos barnacle blenny	VU
Actinopterygii	Perciformes	Chaenopsidae	Acanthemblemaria mangognatha	Revillagigedo barnacle	VU
Actinopterygii	Perciformes	Dactyloscopidae	Dactyloscopus lacteus	Milky sand stargazer	VU
Actinopterygii	Perciformes	Dactyloscopidae	Myxodagnus sagitta		VU
Actinopterygii	Perciformes	Dactyloscopidae	Platygillellus rubellulus	Shortfin sand stargazer	VU
Actinopterygii	Perciformes	Gobiidae	Lythrypnus gilberti	Galapagos blue-banded goby	VU
Actinopterygii	Perciformes	Haemulidae	Anisotremus moricandi	Brownstriped grunt	EN
Actinopterygii	Perciformes	Haemulidae	Xenichthys agassizii		VU
Actinopterygii	Perciformes	Haemulidae	Xenocys jessiae		VU
Actinopterygii	Perciformes	Labrisomidae	Gobioclinus dendriticus	Bravo clinid	VU
Actinopterygii	Perciformes	Labrisomidae	Malacoctenus zonogaster	Belted blenny	VU
Actinopterygii	Perciformes	Labrisomidae	Starksia galapagensis	Galapagos blenny	VU
Actinopterygii	Perciformes	Pomacentridae	Azurina eupalama	Galapagos damsel	CR
Actinopterygii	Perciformes	Pomacentridae	Neopomacentrus aquadulcis	Sweetwater demoiselle	EN
Actinopterygii	Perciformes	Pomacentridae	Stegastes beebei	Southern whitetail major	VU
Actinopterygii	Perciformes	Pomacentridae	Stegastes leucorus	Whitetail major	VU
Actinopterygii	Perciformes	Pomacentridae	Stegastes redemptus	Clarion major	VU
Actinopterygii	Perciformes	Scaridae	Scarus trispinosus		EN
Actinopterygii	Perciformes	Sciaenidae	Argyrosomus hololepidotus	Southern meagre	EN
Actinopterygii	Perciformes	Sciaenidae	Odontoscion eurymesops	Galapagos croaker	VU
Actinopterygii	Perciformes	Sciaenidae	Totoaba macdonaldi	Totoaba	CR
Actinopterygii	Perciformes	Scombridae	Scomberomorus concolor	Monterey Spanish mackerel	VU
Actinopterygii	Perciformes	Serranidae	Anthias salmopunctatus		VU
Actinopterygii	Perciformes	Serranidae	Epinephelus albomarginatus	White-edged grouper	VU
Actinopterygii	Perciformes	Serranidae	Mycteroperca jordani	Gulf grouper	EN
Actinopterygii	Perciformes	Serranidae	Mycteroperca rosacea	Leopard grouper	VU
Actinopterygii	Perciformes	Serranidae	Paralabrax albomaculatus	Camotillo	EN
Actinopterygii	Perciformes	Serranidae	Pseudanthias regalis		VU
Actinopterygii	Perciformes	Tripterygiidae	Lepidonectes corallicola	Galapagos triplefin blenny	VU
Actinopterygii	Pleuronectiformes	Soleidae	Zebrias lucapensis		VU
Actinopterygii	Scorpaeniformes	Triglidae	Prionotus miles	Galapagos gurnard	VU
Actinopterygii	Syngnathiformes	Syngnathidae	Hippocampus algiricus	West African seahorse	VU
Actinopterygii	Syngnathiformes	Syngnathidae	Hippocampus barbouri	Barbour's seahorse	VU
Actinopterygii	Syngnathiformes	Syngnathidae	Hippocampus comes	Tiger tail seahorse	VU
Aves	Ciconiiformes	Laridae	Larus saundersi	Saunder's gull	VU
Aves	Ciconiiformes	Phalacrocoracidae	Phalacrocorax capensis	Cape cormorant	EN
Aves	Ciconiiformes	Phalacrocoracidae	Phalacrocorax harrisi	flightless cormorant	VU
Aves	Ciconiiformes	Phalacrocoracidae	Phalacrocorax neglectus	bank cormorant	EN
Aves	Ciconiiformes	Sulidae	Morus capensis	Cape gannet	VU
Aves	Procellariiformes	Diomedeidae	Phoebastria irrorata	waved albatross	CR

Class	Order	Family	Binomial	Common name	IUCN extinction risk status
Elasmobranchii	Carcharhiniformes	Carcharhinidae	Glyphis gangeticus	Ganges shark	CR
Elasmobranchii	Carcharhiniformes	Carcharhinidae	Lamiopsis temminckii	Broadfin shark	EN
Elasmobranchii	Carcharhiniformes	Scyliorhinidae	Holohalaelurus favus		EN
Elasmobranchii	Carcharhiniformes	Scyliorhinidae	Holohalaelurus punctatus	African spotted catshark	EN
Elasmobranchii	Carcharhiniformes	Scyliorhinidae	Haploblepharus fuscus	Brown shyshark	VU
Elasmobranchii	Carcharhiniformes	Scyliorhinidae	Schroederichthys saurisqualus	Lizard catshark	VU
Elasmobranchii	Carcharhiniformes	Triakidae	Hemitriakis leucoperiptera	Whitefin topeshark	EN
Elasmobranchii	Myliobatiformes	Dasyatidae	Dasyatis margarita	Daisy stingray	EN
Elasmobranchii	Rajiformes	Rajidae	Gurgesiella dorsalifera	Onefin skate	VU
Elasmobranchii	Rajiformes	Rhinobatidae	Rhinobatos cemiculus	Blackchin guitarfish	EN
Elasmobranchii	Rajiformes	Rhinobatidae	Rhinobatos rhinobatos	Common guitarfish	EN
Elasmobranchii	Rajiformes	Rhinobatidae	Rhynchobatus luebberti	African wedgefish	EN
Elasmobranchii	Rajiformes	Rhinobatidae	Platyrhina sinensis	Fanray	VU
Elasmobranchii	Rajiformes	Rhinobatidae	Rhinobatos albomaculatus	Whitespotted guitarfish	VU
Elasmobranchii	Rajiformes	Rhinobatidae	Rhinobatos formosensis	Taiwan guitarfish	VU
Elasmobranchii	Rajiformes	Rhinobatidae	Rhinobatos irvinei	Spineback guitarfish	VU
Elasmobranchii	Squaliformes	Centrophoridae	Centrophorus lusitanicus	Lowfin gulper shark	VU
Elasmobranchii	Squatiniformes	Squatinidae	Squatina aculeata	Sawback angelshark	CR
Elasmobranchii	Torpediniformes	Narcinidae	Benthobatis kreffti		VU
Elasmobranchii	Torpediniformes	Narkidae	Electrolux addisoni	Ornate sleeper-ray	CR
Elasmobranchii	Torpediniformes	Narkidae	Heteronarce garmani	Natal electric ray	VU
Holothuroidea	Aspidochirotida	Stichopodidae	Isostichopus fuscus	brown sea cucumber	EN
Mammalia	Carnivora	Otariidae	Arctocephalus galapagoensis	Galapagos fur seal	EN
Mammalia	Cetacea	Phocoenidae	Phocoena sinus	vaquita	CR
Myxini	Myxiniformes	Myxinidae	Eptatretus taiwanae		EN
Myxini	Myxiniformes	Myxinidae	Myxine sotoi		VU
Reptilia	Squamata	Iguanidae	Amblyrhynchus cristatus	marine iguana	VU
Sarcopterygii	Coelacanthiformes	Latimeriidae	Latimeria chalumnae	Coelacanth	CR

Table S.4 Twenty-five EEZs with the highest conservation responsibility for double-jeopardy species, their governance index score and percent of EEZ designated as a Marine Reserve.

Country/Territory	ISO	Conservation responsibility for double jeopardy species - rank	Fisheries Sustainability Index score (based on quartile of scores: lowest, low, high, highest)	Percent of EEZ designated a Marine Reserve (MPA IUCN category 1a)
Galapagos	ECU	1		
Brazil	BRA	2	low	0.09
Mexico	MEX	3	low	14.47
South Africa	ZAF	4	low	
China	CHN	5	lowest	0.03
Indonesia	IDN	6	lowest	0.09
Philippines	PHL	7	lowest	
Madagascar	MDG	8	lowest	
Mozambique	MOZ	9	lowest	
Ecuador	ECU	10		
French Polynesia	PYF	11	high	
Taiwan	TWN	12	high	
Angola	AGO	13	lowest	
Guinea	GIN	14	lowest	
Nigeria	NGA	15	lowest	
Namibia	NAM	16	low	
India	IND	17		
Guinea-Bissau	GNB	18	lowest	
Gabon	GAB	19	low	
Vietnam	VNM	20	lowest	
Sierra Leone	SLE	21	lowest	
Papua New Guinea	PNG	22	lowest	
Ghana	GHA	23	low	
Liberia	LBR	24	lowest	
Equatorial Guinea	GNQ	25	lowest	

Table S.5 Twenty-five EEZs with the highest conservation responsibility for species with at least 10% of their range within one or more Marine Reserves and in one or more EEZs with governance index score greater than the median, their governance index score and percent of EEZ in a Marine Reserve.

Country/Territory	ISO	Conservation responsibility for adequate species, rank	Fisheries Sustainability Index score (based on quartile of scores: lowest, low, high, highest)	Percent of EEZ designated a Marine Reserve (MPA IUCN category 1a)
Australia	AUS	1	highest	1.16
Indonesia	IDN	2	lowest	0.09
United States	USA	3	highest	41.5
Mexico	MEX	4	low	14.47
Japan	JPN	5	highest	
Canada	CAN	6	highest	0.05
Brazil	BRA	7	low	0.09
New Zealand	NZL	8	highest	0.14
Argentina	ARG	9	low	
China	CHN	10	lowest	0.03
Philippines	PHL	11	lowest	
Alaska (USA)	USA	12		41.5
Russia	RUS	13		0.77
Papua New Guinea	PNG	14	lowest	
Taiwan	TWN	15	high	
Vietnam	VNM	16	lowest	
Italy	ITA	17	high	
Malaysia	MYS	18	high	0.02
United Kingdom	GBR	19	highest	
Chile	CHL	20		13.67
Uruguay	URY	21	high	
India	IND	22		
Bahamas	BHS	23	high	
Venezuela	VEN	24	high	
Spain	ESP	25	highest	

Chapter 3. Why have global shark and ray landings declined: improvement management or overfishing?[2]

3.1. Abstract

Global chondrichthyan (shark, ray, skate, and chimaera) landings, reported to the United Nations Food and Agriculture Organization (FAO), peaked in 2003 and have declined by almost 20% in the decade since. In the FAO's 2012 "State of the World's Fisheries and Aquaculture" report, the authors "hoped" the reductions in landings were partially due to management implementation rather than population decline. Here, I tested their hypothesis. Post-peak chondrichthyan landings trajectories from 126 countries were modelled against seven indirect and direct fishing pressure measures and 11 measures of fisheries management performance, while accounting for ecosystem attributes. I found the recent improvement in international or national fisheries management has not yet been strong enough to account for the recent decline in chondrichthyan landings. Rather, the landings' declines were more closely related to fishing pressure and ecosystem attribute measures. Countries with the greatest declines had high human coastal population sizes or high shark and ray meat exports and included Pakistan, Sri Lanka, and Thailand. While important progress has been made, country-level fisheries management measures do not yet have the strength or coverage to halt overfishing and avert population declines of chondrichthyans. Increased implementation of legally binding operational fisheries management and species-specific reporting is urgently required to avoid declines and ensure fisheries sustainability and food security.

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[2] A version of this chapter is published as:

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3.2. Introduction

Sharks, rays, skates, and chimaeras (Chondrichthyans, hereafter “sharks and rays”) are one of the most evolutionary distinct fish lineages and play important functional roles in marine environments (Stevens et al. 2000). They are commercially valuable for their fins, meat, liver oil, gill rakers, leather, and are an important source of food security. Shark and rays were once considered the less valued bycatch of more profitable fisheries stocks, such as tuna (Scombridae) and cod (Gadidae) (Stevens et al. 2005). The rising demand for products, coupled with the decline of valuable fisheries, however, resulted in rising catches and retention of shark and rays (Clarke, McAllister, et al. 2006; Lack & Sant 2011). Until recently, directed and bycatch shark and ray fisheries were subjected to little management and/or were of low management priority (Fischer et al. 2012; United Nations General Assembly 2007).

Concerns for the sustainability of shark and ray fisheries prompted advances in shark and ray fisheries management tools over the past twenty years. In 1999 for example, the United Nations Food and Agriculture Organization (FAO) recommended the development and implementation of National Plans of Actions for sharks (NPOAs hereafter referred to as *Shark-Plans*) by signatory nations to, preferably, be completed before 2001 (UN FAO 2013). These non-binding *Shark-Plans* had ten aims encompassing sustainability, threatened species, stakeholder consultation, waste minimization, ecosystem considerations, and improved monitoring and reporting of catch, landings, and trade. Aside from *Shark-Plans*, other global initiatives in chondrichthyan conservation and management over the past 20 years have included, but are not limited to: (i) the introduction of bans on fin removal and carcass disposal at sea (Biery & Pauly 2012; Clarke et al. 2013; Fowler & Séret 2010; Clarke, McAllister, et al. 2006); (ii) application of trade regulations of marine fishes through the Convention on the International Trade in Endangered Species (CITES) (Vincent et al. 2013); (iii) international agreements to prevent Illegal, Unregulated and Unreported fishing (Field et al. 2009; Witbooi

2014); and (iv) management and conservation of migratory sharks and rays through the Convention of Migratory Species Memorandum of Understanding for Sharks (CMS sharks MoU) (Fowler, 2012).

Despite the advances in shark and ray fisheries management, there were concerns that chondrichthyan fisheries were following the predictable pattern shown by unregulated, open-access fisheries: declining catch per unit effort, collapse, and serial depletion (Pitcher & Hart 1982; Lam & Sadovy de Mitcheson 2011). Indeed, shark and ray landings increased 227% from 1950 (the first year of data collection) to the peak year in 2003 and subsequently declined by almost 20% to 2011 (FAO 2013b). The authors of the 2010 State of the World's Fisheries and Aquaculture (SOFIA) expressed that they "hoped" this reduction in shark and ray landings was due to a rise in sustainable fisheries, and hence reduced catch, rather than population declines (FAO, 2010). There was little comment on shark and ray landings declines in the 2012 SOFIA report, however, the most recent SOFIA concluded, "a simple explanation for the recent [landings] trends is not possible" (FAO 2014).

Here, I tested FAO's hypothesis and assessed whether country-by-country variation in shark and ray landings from 2003 to 2011 was best explained by indicators of overfishing or fisheries management performance. I also accounted for ecosystem attributes as they have been shown to constrain fisheries catch (Chassot et al. 2010). If the hope expressed in the SOFIA 2012 report was correct, I expected landings reductions to be in response to management implementation. Conversely, if the interpretation was not correct, I expected landings reductions to be unrelated to management performance indicators and more closely related to direct and indirect measures of fishing pressure.

3.3. Methods

3.3.1. Analytical approach

The magnitude and trajectories of fisheries landings can be characterized as a function of exposure to fishing pressure, which can be modified by fisheries management performance and by the intrinsic sensitivity and resilience of the ecosystem (Fig. 3.1). A series of metrics can be used as indirect measures of fishing pressure including human coastal population size and density (Newton et al. 2007) and reliance on fish for income and dietary protein (Allison et al. 2009; Smith et al. 2010). The degree to which these indirect drivers translate into fishing pressure and mortality is modified by the form and strength of fisheries management control. Management control can be characterized with measurements such as scientific capacity, Gross Domestic Product (GDP), and the Human Development Index (HDI) (Mora et al. 2009; Pitcher et al. 2009; Allison et al. 2009). International and national protections, or more diffuse measures that are precursors to good management regimes, may promote reduced catch (Clarke et al. 2006). Metrics that are characteristic of lower intrinsic sensitivity at the ecosystem level could include larger ecosystem size, higher primary productivity (Chassot et al. 2010; Watson et al. 2013; Myers et al. 2001), higher species richness, or faster population growth rates (Dulvy et al. 2014; García et al. 2008).

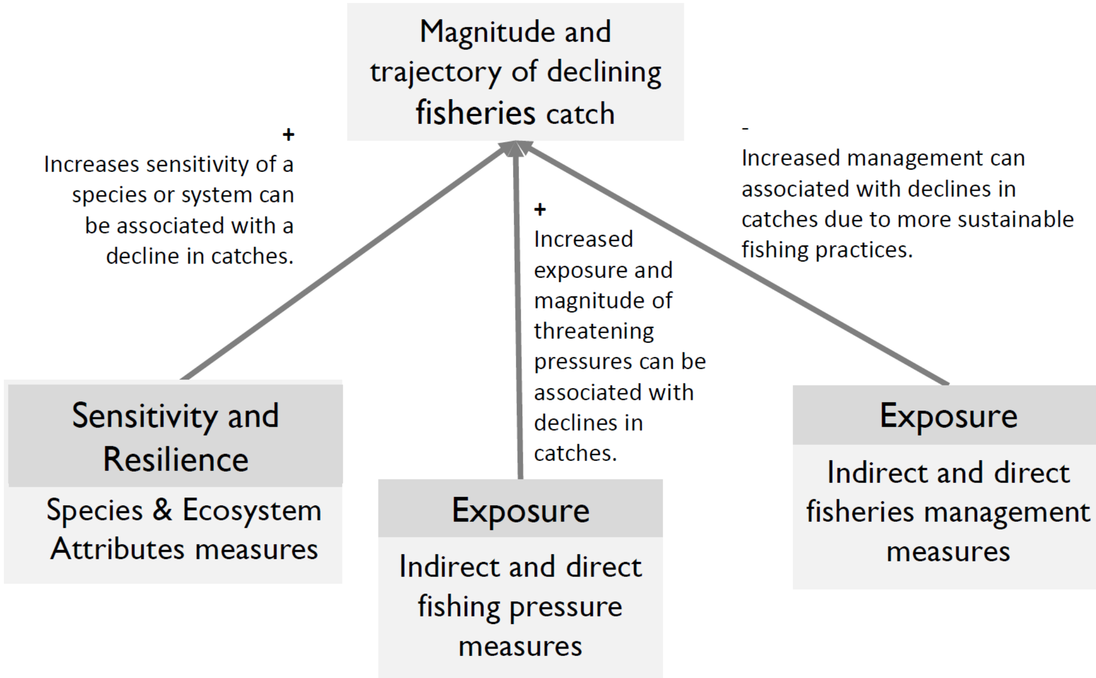


Figure 3.1 **Fisheries landings magnitudes and trajectories are a function of exposure to fishing, which is modified by the form and strength of fisheries management, but also the sensitivity and resilience of the ecosystem and species.**

I describe the collection of the response variable – the trajectory of the landed catch of chondrichthyans followed by the plausible explanatory variables broadly classed as exposure to (i) drivers of fishing pressure; (ii) fisheries management performance; and (iii) sensitivity and resilience of the surrounding ecosystem and species (see Table 3.1, Table S.6 for a summary of the measures used in this analysis).

3.3.2. Selection, filtering, and quality control of FAO landings data

I extracted all sharks, ray, skate, and chimaera reported landings by country from the earliest year of reporting (1950) to, at the time of this analysis, the most recent (2011) from the FAO FishSTAT database (FAO 2013b). Data for 2012 are now available. Chimaeras are included in this analysis; however, they are a small percentage of global landings. I used the “Sharks, rays, chimaeras” category of the “species by ISSCAAP” (International Standard Statistical Classification of Aquatic Animals and Plants) group. Within this broader group were 135 species and 30 aggregate non-species specific “nei” - not elsewhere indicated - reporting categories, which summed to 217,416 tonnes and 548,687 t in 2011, respectively, for a total of 766,103 t. Examples of nei categories include “sharks, rays, skates, etc., nei” and “threshers, nei”. The peak of the aggregate global shark and ray landings was 2003 at 895,743 t. In total, 155 countries/overseas territories reported to the FAO, however, countries that reported zero landings, as well as overseas territories, and the “Other nei” category were removed for the analysis, leaving 128 countries.

3.3.3. Response variable – country-by-country chondrichthyan landings trajectories

I calculated both the average and the change in reported landings. Average landings between 2003-2011 were calculated to account for the size of shark and ray fisheries (Fig. 3.2a). Change in reported landings was calculated as the absolute difference between averages of 2001-2003 and 2009-2011 (Fig. 3.2b).

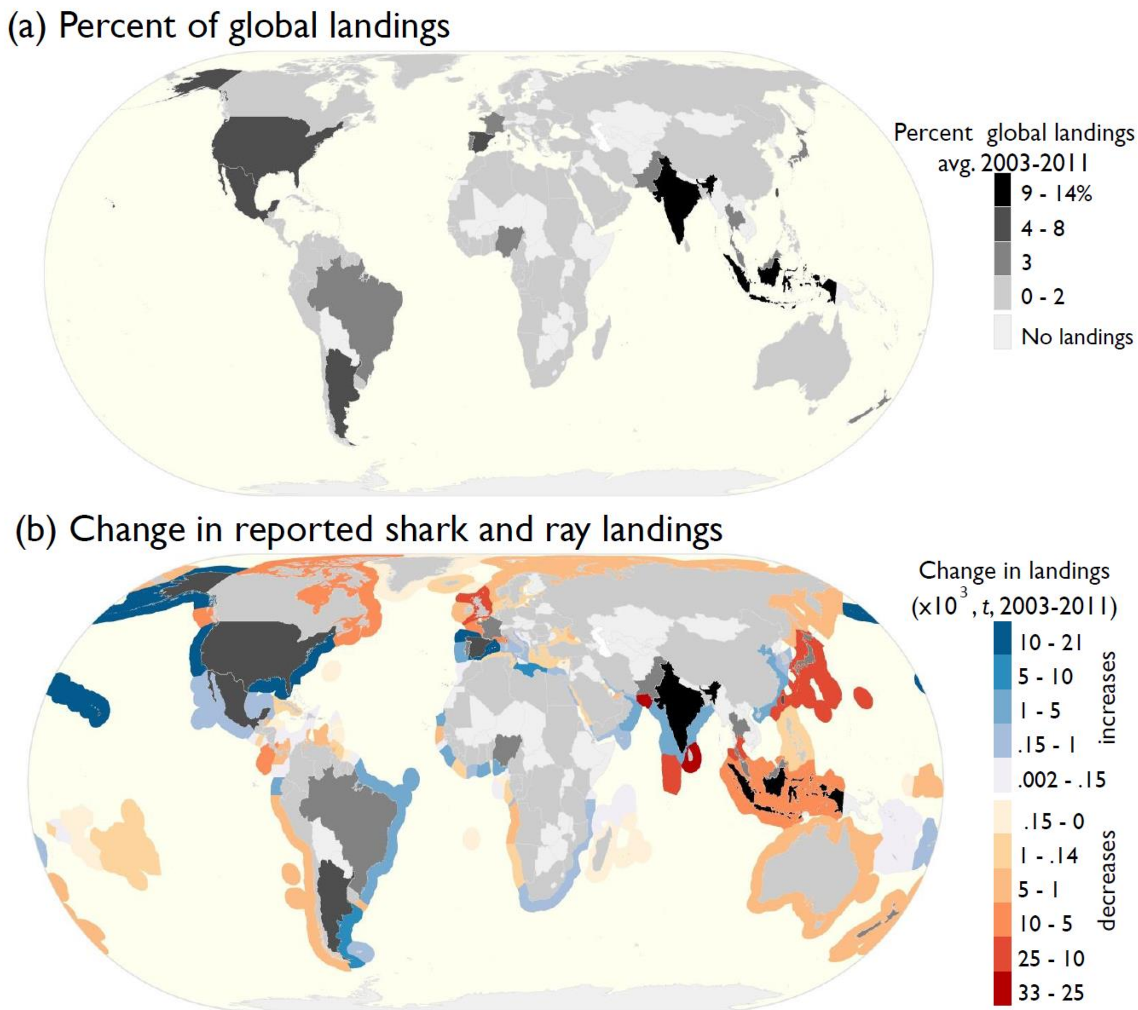


Figure 3.2 **Global distribution of (a) country-specific shark and ray landings averaged between 2003-2011 and mapped as a percentage of the total. Landings include fishing from overseas fishing and all categories ('nei' or species-specific), and (b) the change in landings between the averages of landings in 2001-2003 and 2009-2011. Mapped to the national waters that extend 200nm from the coast for visual purposes.**

3.3.4. Measures of fishing pressure

Indirect fishing pressure

Three indirect measures of fishing pressure were included in the analysis: coastal human population size, marine protein available for consumption, and percentage of threatened shark and ray species within national waters (Table S.6 Appendix B). Coastal human population size and the available marine protein for consumption is positively related to reduced biomass and measures of unsustainable fishing on coral reefs at island and country scales (Cinner et al. 2009; Newton et al. 2007; Dulvy et al. 2004). Coastal human population size was captured through nominal coastal settlement data and defined as the number of persons living in rural and urban areas within 100km of the country's coast as of 2011 (NASA Earth Data 2014). National marine protein supply was defined as grams per capita per day of marine fish protein available for consumption and represented reliance on marine resources (Allison et al. 2009; FAO 2013b). The dates of the marine protein supply estimates for each country ranged from 1969-2009; however, only 22 countries had entries earlier than 2009. The state of a country's shark and ray populations was likely to be captured by the percentage of threatened species within national waters. The percentage of shark and ray species classified by the IUCN as having an elevated risk of extinction (Vulnerable, Endangered, or Critically Endangered) within each country's national waters (EEZ - Exclusive Economic Zone that extends 200 nautical miles from the coast) was calculated (Dulvy et al. 2014).

Direct fishing pressure

Ideally, I would have included direct measures of fishing pressure such as fishing intensity, fishing effort, and fishing mortality estimates. The coverage of fisheries by stock assessments and other data intensive measures, however, are limited and only represent 16% of reported teleost fisheries (Ricard et al. 2012). Hence, the fisheries management performance measures included herein were not species-specific, mainly because there were few, and fewer yet that were consistent across the global scale. However, I believe that the measures I collated were salient because they were global, comparable, and supported by the international community and capture a country's progress towards sustainable shark and ray fishing within their national waters. I included and described four measures of exploitation pressure: overseas landings, the volume of shark and ray meat exports, the volume of fins exported to Hong Kong, and estimated Illegal Unreported Unregulated (IUU) fishing within national waters (Table S.6).

Overseas shark and ray landings were defined as those taken from beyond each country's EEZ from 2003-2011. My definition, however, only includes landings from outside the FAO major fishing areas as spatial mismatch between a country's EEZ and a FAO major fishing area exists with the boundaries of the latter extending farther beyond any EEZ. Therefore, my definition of overseas landings is a combination of international and national waters and removes overseas fishing (e.g. Belize landings from Indian Ocean) and hence, will be an underestimate. China, Hong Kong, Norway, and Zanzibar only reported landings from overseas waters.

The volume of shark and ray meat exports was included as a measure of fishing pressure as shark and ray meat is a globally traded commodity. I included the amount of shark and ray meat exports reported to the FAO under 13 commodity codes (FAO 2013b) between 2003-2009 which included fins and liver oil of mostly sharks, and also to a lesser extent rays, skates, and chimaeras. Spain, Taiwan, Canada, Japan, United Kingdom, and Indonesia reported the largest meat exports at 11 608 t, 4 684 t, 3 813 t, 3 748 t, 3 534 t and 3 497 t respectively. Meat exports between 2003 and 2009, on average, increased 277 t (Table S.7) with Uruguay and Taiwan reporting the largest increases (16,283 t, and 15,493 respectively). I used the volume of fins that countries exported to Hong Kong based on census trade statistics for 2011 (The Government of the Hong Kong Special Administrative Region of the People's Republic of China 2012). Note, this metric represented 50% of the global trade and included fins from high-seas catches, non-adjacent EEZs, and ignored import-reexport of fins, particularly from EU countries, and from those that are large trade entrépots such as UAE and Singapore (Clarke 2004a; Hareide et al. 2007; Clarke 2004b). IUU fishing estimates were calculated at the FAO major fishing region scale (MRAG and Fisheries Ecosystems Restoration Research 2008). Each country's value was calculated by summing the smaller estimate of IUU fishing for each FAO major fishing area that corresponded with a country's EEZ.

3.3.5. Measures of fisheries management performance

Indirect measures of fisheries management performance

Ideally, measures of fisheries management would have been country-by-country lists of the shark and ray fisheries management instruments implemented that ensured sustainable fishing. These instruments would have included science-based precautionary catch limits, prohibitions on catch (particularly of threatened species), reduction of bycatch, and habitat and spatial protections in place (Barker & Schluessel 2005). Such data are not readily or consistently available at the global scale for a comparative national analysis. The paucity of data could be due to poorly documented fisheries management but more likely reflects the lack of systematically applied shark and ray fisheries regulations (Fischer et al. 2012; Dulvy, Fowler, et al. 2014). I therefore developed a series of indirect management performance measures by country that described enabling conditions that promoted good management.

Fisheries management implementation and effectiveness are influenced by the economic and development status of a country (Melnychuk et al. 2016b). I therefore included GDP, Human Development Index (HDI), and percentage of Data Deficient (DD) species in this analysis. Countries with high income, or high development status, have significantly better fisheries management than low income countries (Mora et al. 2009; Gutiérrez et al. 2011; Pitcher et al. 2009).

GDP is the nominal value of the sum gross value of a country's economy and is positively correlated with overall management effectiveness (Mora et al. 2009). Countries with high HDI scores, a composite of health, education, and living standards metrics, are more successful at achieving sustainable fisheries (United Nations Development Programme 2011; Gutiérrez et al. 2011). Shark and ray species categorized as DD by the IUCN, are those that lack sufficient information to be assigned to a Red List category. Hence, the percentage of DD species within a country's EEZ was included as a measure of scientific capacity.

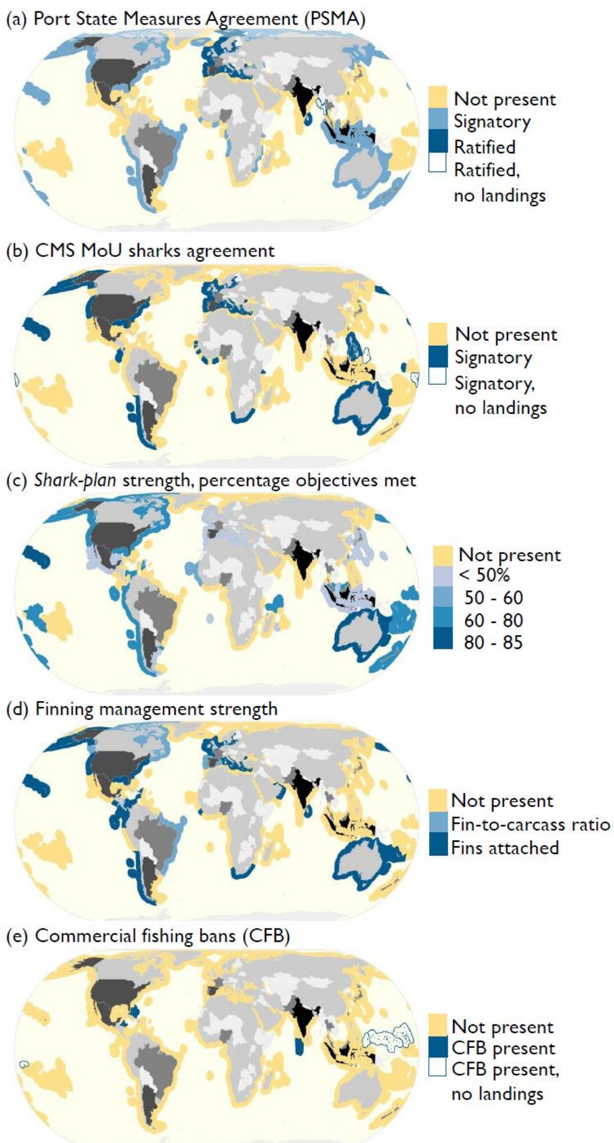


Figure 3.3 Spatial distribution of direct management measures finalized up to the year 2012 to correspond with FAO landings data. (a) Countries that are signatory to, or have ratified the PSMA. EU, Sri Lanka, and Myanmar (which did not report shark and ray landings) ratified the agreement. (b) Countries that were signatory to the CMS sharks MoU. Tuvalu and Palau signed the agreement and had not reported shark or ray landings. (c) The presence and strength of *Shark-Plans*; colours represent how well the document met the ten objectives of sustainable fishing. (d) The presence and strength of finning regulations; fins-attached > fin-to-carcass ratio > none. The variability of finning bans are not captured here (such as; South Africa's 8% fin-to-carcass (dressed weight) ratio for domestic vessels but 14% ratio for foreign vessels; or the variation in Australias finning regulations in territorial waters). (e) The location commercial fishing bans (CFB) for sharks.

Direct measures of fisheries management performance

I collated data for nine measures of direct fisheries management that were finalized up to 2012 (Table S.6). I categorized the uptake and implementation of international policies including the Port State Measures Agreement (PSMA), which is not specific to sharks and rays, and the Convention for Migratory Species Memorandum of Understanding (CMS sharks MoU). Three plus the 22 EU maritime countries had ratified, approved, or accessioned the PSMA (Figure 3.3a). Implementation of the PSMA results in ports with stricter regulations in order to prevent illegally caught fish from being unloaded. For sharks and rays, this translates to stricter enforcement on fishing that contravened regulations, such as finning or fishing illegally in another country`s EEZ. By 2011, 20 countries were signatory to the PSMA, meaning the agreement was not yet ratified (FAO 2013a). Twenty-three countries, plus the 22 EU maritime countries, were signatories to the CMS sharks MoU agreement, which had listed seven migratory shark species under Appendix 1: White (*Carcharodon carcharias*), Basking (*Cetorhinus maximus*), Whale (*Rhincodon typus*), Shorfin Mako (*Isurus oxyrinchus*), Longfin Mako (*Isurus paucus*), Spiny Dogfish (Northern Hemisphere) (*Squalus acanthias*), and Porbeagle (*Lamna nasus*). Species listed on Appendix I are to be the focus of a global or national Conservation Plan that “promotes the conservation of migratory sharks” (CMS, 2013). The objectives of the Conservation Plan include: (1) research and monitoring of populations, (2) ensuring directed and non-directed fisheries are sustainable, (3) promoting protection of critical habitat, (4) increasing public awareness, and (5) enhancing government cooperation (CMS 2013) (Fig. 3.3b). Support for CITES listings was not included in this analysis as membership to CITES was not specific to sharks and rays and voting direction of countries for listing species onto appendices was mostly not recorded (a motion generally passed before voting on a species to ensure voting anonymity).

Twenty-two finalized *Shark-Plans* were scored on a categorical three-point scale according to how comprehensively the ten objectives of sustainable shark fisheries and conservation were addressed (UN FAO 2013). For each country with a *Shark-Plan,* objectives were scored as to whether it was: met comprehensively (=2); mentioned, but not comprehensively addressed (=1); or not addressed (=0). The scores had a maximum score of 20 if all ten objectives were comprehensively addressed. The *Shark-Plans* performance scores ranged from five a low of five (Japan) to a high of 17 (Australia) meaning between 25 – 85% of the objectives met (Fig. 3.3c). I also counted the number of years since *Shark-Plan* completion up to the year of most recent FAO landings data (2011), with values ranging from one to ten years. There was a high positive correlation between completion year and the strength of *Shark-Plans* (Pearson`s, p=0.67) (Fig. S.3).

Finning is the act of cutting off a shark or rays' fins and dumping the carcass overboard (Biery and Pauly 2012; Clarke et al. 2006; Camhi et al. 2008). Finning mostly refer to sharks, but rays can have some of the most valuable fins (Dulvy, Fowler, et al. 2014). Finning bans were scored on an ordinal scale such that (up to 2011): (1) fins-attached, shark and ray fins not removed (n=16 countries plus 18 EU maritime countries) was a preferable management measure to, (2) fin-to-carcass ratio, fins separated from bodies but weight of fins must be a specific ratio of the bodies (n=4 plus 2 EU [Spain and Portugal]), which in turn was better than, (3) no finning ban (n= 86; Fig. 3.3d). Countries with finalized finning ban strategies were expected to initially report increased landings as carcasses, and not just fins, are brought back to port.

Shark "sanctuaries" (hereafter "commercial fishing bans") are a form of spatial protection as branded by environmental non-governmental organization the Pew Charitable Trust. Up to 2012, the following countries had declared commercial fishing bans: Palau, Maldives, Tokelau, Micronesia, Marshall Islands, Honduras, and Bahamas. Commercial fishing bans extend to a country's EEZ waters and ban commercial fishing for sharks, but not rays (Davidson 2012; PEW charitable trusts 2013) (Fig. 3.3e). They are neither no-take, nor no-entry, however, artisanal fishing or landed bycatch is permitted. Commercial fishing bans are included in this analysis, as opposed to all MPAs, to evaluate their stated goal of shark conservation.

Data collection and availability is an essential precursor to fisheries management. Therefore, I calculated the percentage of a country's landings reported to the species level, relative to the total (Table S.6; Fig. S.4). Finally, I included a score that evaluated compliance to UN Code of Conduct for responsible fisheries and was assigned to the 53 countries that reported more (96%) of the global marine catch (in 1999) (Pitcher et al. 2009). The ranking, however, was not included in the final analysis as the majority of countries I analyzed did not have a score.

3.3.6. Sensitivity and resilience of the species and surrounding ecosystem

Ecosystem and species attributes

I used measures of ecosystem area, species richness, and the number of endemic species to represent sensitivity and resilience (Table S.6). I used EEZ area as a measure of ecosystem size (VLIZ 2012; Chassot et al. 2010). There is a wide range of theoretical and empirical work that relates species richness and diversity to population stability (Anderson et al. 2013; Mellin et al. 2014; Loreau et al. 2001). The species richness of each nation's EEZ was calculated using the IUCN SSG (Shark Specialist Group 2013) Extent of Occurrence (EOO) distribution maps for 1,041 sharks and rays. I also included a measure of the number of endemic species with a country's waters. Endemicity was defined as species with range sizes within the lower quartile of total shark and ray range size (<121,509 km^2) (Pompa et al. 2011).

The larger the ecosystem, or on a national scale a larger Exclusive Economic Zone (EEZ), potentially represents an ecosystem with larger population sizes of species or greater numbers of subpopulations. Increased subpopulations increase the stability of the metapopulation thereby reducing the risk of collapse or decline (Anderson et al. 2013; Mellin et al. 2014; Loreau et al. 2001). A larger area also correlates with increased species richness (Jaccard, 1912) and could therefore represent a country with more fisheries options or increased multi-species Maximum Sustainable Yield (Newton et al. 2007). Finally, the number of endemics within an ecosystem may be an indicator of intrinsic ecosystem vulnerability due to the correlation of elevated extinction risk with smaller range size (Brooks et al. 2006; Pimm et al. 2014).

3.3.7. Statistical analysis

To measure the share of global shark and ray landings reported from countries with potentially sustainable fisheries, I calculated average reported landings from countries with each of five direct management measures: signatory to PSMA, signatory to CMS sharks MoU, *Shark-Plan*, finning ban, or a commercial fishing ban. I also considered combinations of the presence of management measures. A country was assigned a value ranging between no management measures present (=0) or all management measures present (=5). All reported landings were included regardless of location or reporting category. Finally, I determined the percentage of the decline reported from countries with any combinations of these management measures as I are seeking to understand if the decline in landings is associated with implemented management measures.

As a second step in the data analysis, I determined whether particular countries or reporting categories were influential upon the global trend in landings from 2003-2011 using a Jackknife analysis (see e.g., Juan-Jordá et al. 2011). Countries that reported large increases in landings may mask a steeper global decline, while countries with large declines may drive the global trend. To determine influence, I examined how the global trajectory from 2003-2011 changed in absence of the reported landings from each of the ten countries that reported the largest landings (2003-2011). I repeated this analysis for the top ten reporting landings categories, which included a combination of species and aggregate taxonomic categories.

To tackle the overall question of whether management or fishing pressure measures were associated with declining trajectories, I used Random Forest regression. Random Forest is an approach for assessing which explanatory variables account for the most variance in a response, without requiring assumptions about the nature of relationship between the two (Liaw and Wiener 2002). Each Random Forest model had 100,001 iterations, with the default value of the number of variables randomly sampled for each decision tree split, and data subsetted more than once (with replacement). Analyses were completed using the randomForest package (Liaw and Wiener 2002) for the statistical software R (R core team, 2012).

To compare and test the sensitivity of the results, I ran Random Forest models on four subsets of the data. The first model I ran with explanatory variables that included only those countries reporting a decline in catch. The second model included only landings from the large aggregate reporting category of "sharks, rays, skates, etc, in order to examine drivers of decline of only this subset of the catch. Because the EU countries have a largely coherent governance framework, I tested whether the global pattern was sensitive to the exclusion of these countries in the third model. In addition, because increased landings might arise from better reporting and management, I considered only those countries reporting an increase in landings separately from those showing declines in a fourth model.

Here, I am interested only in the interpretation of important variables. Therefore, I ranked explanatory variables according to variable importance measured by the Mean Standard Error (MSE) in descending order. MSE indicates the difference between model performance before and after permuting predictor variables. High MSE values denote the most important variables and indicate better model performance. If the predictor variable is associated with the response, the prediction accuracy will increase, whereas negative MSE values caution that randomly generated explanatory variables have greater prediction accuracy than the hypothesized predictors (Strobl et al. 2008). Partial dependence plots, the visual tool associated with Random Forest, show marginal effects of predictor variables on the response. The y-axis is the average predicted response across trees at the value of x.

3.4. Results

Just more than half (86) of the 147 countries and overseas territories reported reductions in shark and ray landings. The change in landings ranged between a 32,281 t decline (Pakistan) to an increase of 20,065 t (Spain). Across all reporting countries, the average change in landings was a 837 t decline, with a median of a 3 t decline. In total, across all reporting countries, the global landings declined by 129,642 t; with a 244,530 t change for countries reporting declines, and 114,888 t change for those countries reporting increases. Half of the decline in landings, regardless of reporting category or fishing location, occurred in just six countries: Pakistan (-32,281 t), Sri Lanka (-25,176 t), Thailand (-21,051 t), Taiwan Province of China (-18,919 t), and Japan (-15,471 t; Table 3.1a). Correspondingly, the broad FAO Fishing Areas regions with the greatest decline in landings occurred in the Western Central Pacific (49,920 t) and the Western Indian Ocean (45,928 t).

Over the same time period, the greatest declines in species-specific categories, were Spiny Dogfish (*Squalus acanthias,* Squalidae, -12,170 t), Whip Stingray (*Dasyatis akajei*, Dasyatidae, -4,557 t), Portuguese Dogfish (*Centroscymnus coelolepis,* Somniosidae, -3,510 t), Leafscale Gulper Shark (*Centrophorus squamosus,* Centrophoridae, -2,351 t), and Narrownose Smooth-hound (*Mustelus schmitti,* Triakidae, -1,070 t). Three of the five species exhibiting the greatest declines have been categorized by the IUCN as Vulnerable (Spiny Dogfish, Leafscale Gulper Shark) and Endangered (Narrownose Smoothhound).

The majority of these populations declined due to intensive fishing pressure. Consequently, Spiny and Portuguese dogfish, and Leascale gulper shark are currently managed with a zero Total Allowable Catch (TAC) in EU waters. In the United States, the Spiny Dogfish fishery re-opened in 2011 under quotas (Table 3.1b).

Table 3.1. **Countries and species reporting categories with the greatest changes between 2003-2011 in descending order. Only changes greater than a decline of 500 tonnes or less than an increase of 500t were included in the table for brevity. (a) The five countries that reported the greatest declines in landings, the reporting categories for each country, and associated management measures within that country. (b) Species-specific reporting categories with the greatest landings reduction, the countries that reported changes in those categories, and the associated management measures for that fishery.**

Table 3.1(a)

Country	Reporting Category	Diff. in landings ('03-'11, t)	Management
Pakistan	Requiem sharks nei	-19,161	"accessible fishery legislation of Pakistan did not contain any references to sharks" (Fischer et al. 2012)
	Rays, stingrays, mantas nei	-11,970	
	Guitarfishes, etc. nei	-1,150	
Sri Lanka	Sharks, rays, skates, etc. nei	-19,019	"a shark finning ban is the only fisheries management measure explicitly directed at sharks" (Fischer et al. 2012). Sri Lanka prohibited the catch, retention, transshipment, landing, storage, and/or sale of whole bodies or parts of common, bigeye, or pelagic thresher sharks (took effect in 2012) (Shark Advocates International 2012)
	Silky shark	-2,798	
	Blue shark	-1,366	
	Oceanic whitetip shark	-889	
	Thresher sharks nei	-698	
Thailand	Sharks, rays, skates, etc. nei	-10,665	"lack of data and trained staff, the absence of systematic monitoring and control of shark resources...and the absence of a baseline assessment on the status of shark populations" (Fischer et al 2012)
	Rays, stingrays, mantas nei	-10,387	
Taiwan, Province of China	Sharks, rays, skates, etc. nei	-24,536	NPOA - two stock assessments to be completed and a TAC (Total Allowable Catch) management scheme will be implemented if the shark resources declined significantly; finning management was introduced (2012) (Fishery Agency 2004). Since 2003 commercial fishing vessels were required to report Blue, Mako, and Silky shark catches separately (Fischer et al. 2012)
	Rays, stingrays, mantas nei	-1,319	
	Silky shark	1,058	
	Shortfin mako	1,855	

Country	Reporting Category	Diff. in landings ('03-'11, t)	Management
	Blue shark	3,562	
Japan	Sharks, rays, skates, etc. nei	-10,915	NPOA does not have specific measures for reduction of shark catches (Fisheries Agency 2009)
	Whip stingray	-4,557	

Table 3.1(b)

Reporting category	Country	Diff. in landings ('03-'11, t)	Management
Spiny dogfish	United Kingdom	-6,227	Spiny Dogfish were classified as Critically Endangered in the Northeast Atlantic. Their population was estimated to have fallen by 95% over 100 years. In the EU, in 2011, the TAC was set to zero to allow the population to recover (Fordham 2004). Canada has a quota on the Pacific and Atlantic coasts, however, the Atlantic quota was not based on scientific advice and there were no restrictions on bycatch or discards (DFO 2007). In the United States, the Spiny Dogfish fishery re-opened on May 1, 2011 under a quota (NOAA 2011)
	Canada	-5,382	
	New Zealand	-974	
	France	-881	
	Ireland	-865	
	Norway	-781	
	United States of America	3,907	
Whip stingray	Japan	-4,557	No information on management. IUCN classified as Near Threatened (Huveneers & Ishihara 2006)
Portuguese dogfish	United Kingdom	-1,672	IUCN classified the European populations of both the Portuguese and Leafscale Gulpher shark as Endangered (Stevens & Correia 2003; White 2003). In 2010, both populations were subject to a zero TAC in EU waters (OSPAR Commission 2010; Shark Trust n.d.)
	Portugal	-1,108	
Leafscale gulper	Portugal	-1,538	
Narrownose smooth-hound	Uruguay	-726	Classified as Endangered - no information on management (Massa et al. 2006)

Countries with the greatest increases in landings over the same period were Spain (20,065 t) then the United States (10,698 t), followed by Argentina (8,748 t), Libya (7,574 t), India (4,998 t) and Nigeria (4,944 t) (Table S.8). United States had the greatest increase when excluding my previously defined overseas landings. Spain reported the greatest landings increases mainly driven my increases of Blue Shark and to a lesser extent, the Cuckoo Ray (*Leucoraja naevus,* Rajidae) and Shortfin Mako, (*Isurus oxyrinchus,* Lamnidae). In terms of management, the Blue Shark and the Shortfin Mako fisheries currently have no catch limits in the EU; the Cuckoo Ray is subject to a combined Total Allowable Catch (TAC) for all species of skate and ray in EU waters. The greatest landings increase by FAO Fishing Area was recorded in the Eastern Central Atlantic (26,674 t) and Southwest Atlantic (20,083 t).

From a global perspective, the largest increase in categories was Blue Shark (62,907 t), “Stingrays, butterfly rays nei” (40,444 t), and to a lesser extent “Thresher sharks nei” (15,880 t), “Smooth-hounds nei” (6,113 t), “Dogfish sharks nei” (4,705 t) and Little Skate (*Leucoraja erinacea,* Rajidae; 4,520 t). Indonesia switched reporting, however, in 2005 from “sharks, ray, skates, etc., nei” and “rays, stingrays, mantas, nei” into 11 finer resolution reporting categories. Consequently, an increase in a reporting category may be the result of better reporting from Indonesia. Therefore, excluding Indonesia, the categories with the greatest increase are the Blue Shark (49,549 t), Little Skate (4,225 t), Shortfin mako (3,052 t), Thornback ray (3,042 t), “Smooth-hounds nei” (2,986 t), and “Dogfish sharks nei” (2,705 t).

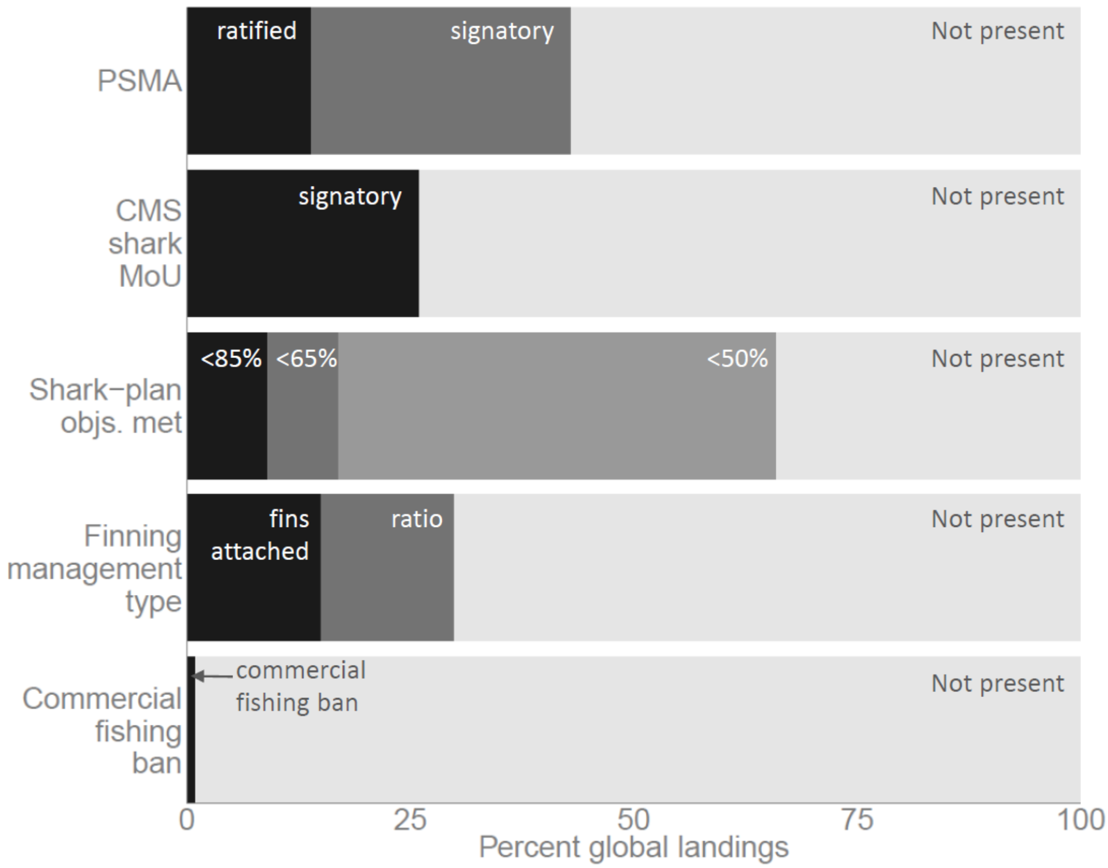


Figure 3.4 **The percentage of global shark and ray landings reported from countries with the management measures I considered: PMSA, CMS sharks MoU, *Shark-Plans*, finning management, or commercial fishing bans. The strongest management is represented by the black bar. The light grey bar represents the percentage of landings from countries that do not have/or are not party to the management measure.**

3.4.1. What percentage of global reported landings were reported from countries with management measures?

I found that a large share of the global shark and ray landings reported between 2003-2011 appear to be subject to one or more of the management measures I considered (Fig. 3.4). Over a quarter (29%) of the landings were from countries signatory to the Port State Measures Agreement (PSMA); however, only 14% were from countries that had ratified the PSMA. A quarter (26%) of the landings were from signatories of CMS sharks MoU. Both PMSA and CMS sharks MoU have an implementation bias skewed towards Northern hemisphere countries (Fig. 3.3 a,b). Two-thirds (64%) of landings were reported from countries with finalized *Shark-Plans*, but only 9% came from countries with relatively comprehensive *Shark-Plans*, i.e. those that met 65-85% of the objectives of sustainable fishing (Fig. 3.4). Ten percent of landings were reported from countries with the strongest finning bans -- a fins-attached policy. Countries with commercial fishing bans had contributed little to the global reported landings before commercial fishing ban implementation. Five out of the six countries with commercial fishing bans did not report any landings, the remainder accounted for less than one percent (0.56%) of the global landings prior to implementation. A quarter (27%) of the global shark and ray landings were from countries that did not report in any species-specific categories, while the majority of landings (75%) are from countries reporting less than a quarter of their landings to species-specific categories. Additionally, the bulk of the decline in global chondrichthyan catch (80%) occurred in countries with two or fewer of the considered management measures.

The countries with relatively stronger management measures in place showed modest declines in landings. Australia, United States and to a lesser extent Chile, and Uruguay, had *Shark-Plans* (addressing between 65-85% of the objectives) but three reported modest declines (<2,000 t) while the United States reported an increase in landings. The strongest finning policy, fins-attached, did show moderate signs of being associated with countries reporting a large share of the reductions; 30% of the decline was reported from countries with a fins-attached policy. This pattern was strongly influenced by Sri Lanka, which adopted fins-attached policy in 2001. Finally, 18 and 29% of the global decline was reported from countries signatory to CMS sharks MoU or PSMA, respectively.

3.4.2. Was the global trend sensitive to influential countries or reporting categories?

Ten countries accounted for two-thirds (62%) of global shark and ray landings from 2003-2011 (Fig. 3.5a). The global trend was less steep (5% shallower) when Taiwan's landings were removed (Fig. 3.5b). Indonesia reported the greatest landings, however, they remained stable over time and therefore had negligible effect on the global landings trend (Fig. 3.5 a,b). Spain reported the greatest landings increase and therefore, without their increased landings, the global trend would have been steeper (5% steeper) (Fig. 3.4b).

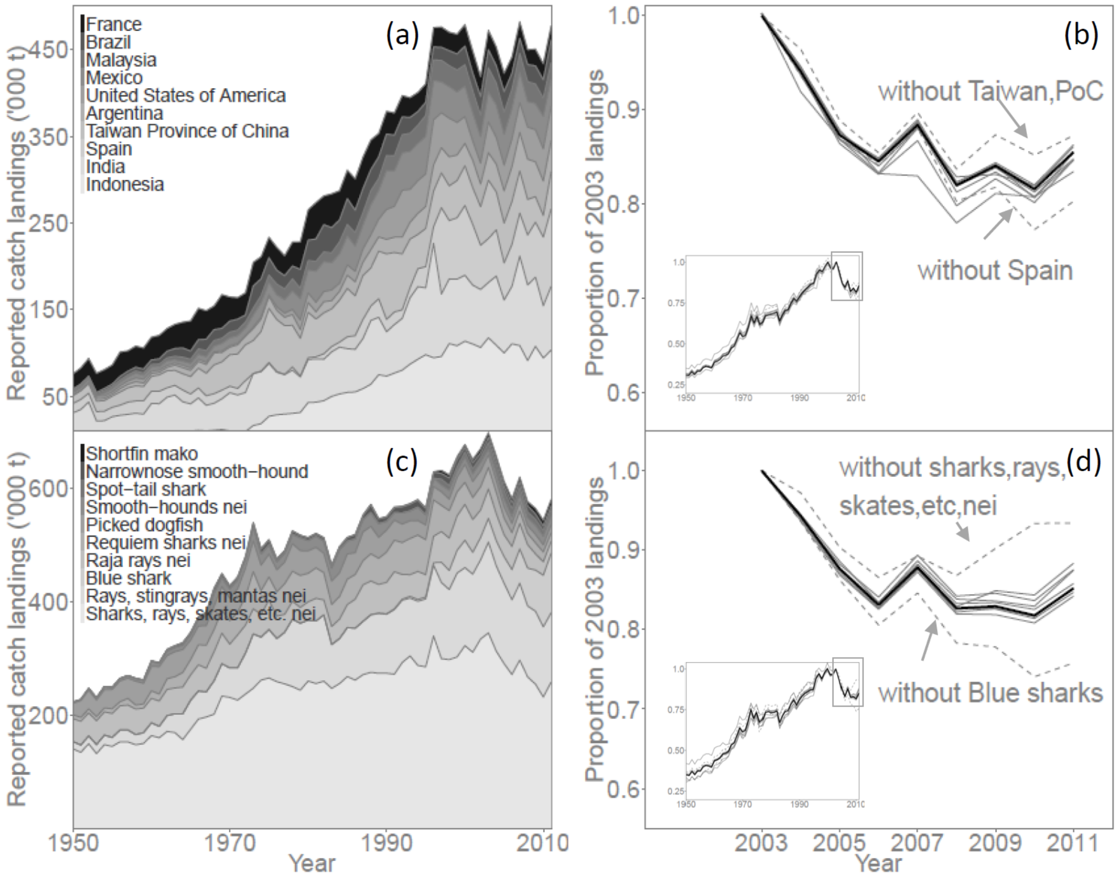


Figure 3.5 **Jackknife analysis to test the sensitivity of the global landings trend to influential countries or reporting categories: (a) ten countries that reported the greatest landings between 2003-2011, (b) the influence of these ten country's landings on the global trajectory as determined by recalculating the global trend in absence of their landings, (c) ten reporting categories with the greatest landings between 2003-2011, and (d) the influence of these ten reporting categories on the global trajectory as determined by recalculating the trend in absence of their landings. "Sharks, rays, skates, etc, nei" reported the greatest decline and therefore without this category the global trend would be less steep. Without the dramatic increase in Blue shark landings, the global trend would be steeper.**

Ten reporting categories accounted for four-fifths (83%) of global landings reported from 2003-2011 (Fig. 3.4c). The taxonomically undifferentiated category of “sharks, skates, rays, etc., nei” declined the most, and therefore this category drove the overall global trajectory (Fig. 3.5c). Excluding “sharks, rays, skates, etc., nei” revealed that the remaining landings would have been less steep (decline of 7%) (Fig. 3.5d). Contrastingly, the decline in global landings would have been greater had it not been ameliorated by the dramatic increase in Blue Shark landings. Without Blue Shark landings, the global decline would have been 25% (10% steeper than the global trend) (Fig. 3.5d). For this analysis, Indonesia’s landings were not included to get a more accurate picture of changes in landings, rather than changes due to reporting category shifts. When Indonesia is included, Blue Shark and “shark, ray, skate, etc., nei” still have the greatest influence (data not shown). Finally, the decline of reported landings in the “sharks, rays, skates, etc., nei” category cannot be accounted for in the increased reporting in the “Blue Sharks” category, i.e. due to change in reporting. Countries that reported declines in “sharks, rays, skates, etc., nei” are not those that reported increased Blue shark landings.

3.4.3. What measures were most important in describing landings trajectories?

Overfishing, rather than improved management, was the key driver of declines in shark and ray landings. The most important variables that explained landings trajectories were two measures of indirect fishing pressure: (1) human coastal population size, and (2) shark and ray meat exports (Fig. 3.6, Fig. S.5). The nature of the relationship suggested that countries with higher fishing pressure or trade, experienced greater declines in landings (Fig. 3.6, Fig.S.5). While the effect was weaker, countries that reported greater fin exports, or higher estimated IUU fishing in their waters, reported marginally bigger declines in landings. As expected, all three ecosystem and species attributes explained substantial variability in the majority of models. Specifically, small tropical countries exhibited steeper declines, i.e. those with smaller EEZs, higher endemicity, higher species richness. Average shark and ray landings reported between 2003-2011 were the most important across all model subsets, and had a positive relationship, however, this variable was only included to account for the size of fishery and therefore not included in the discussion.

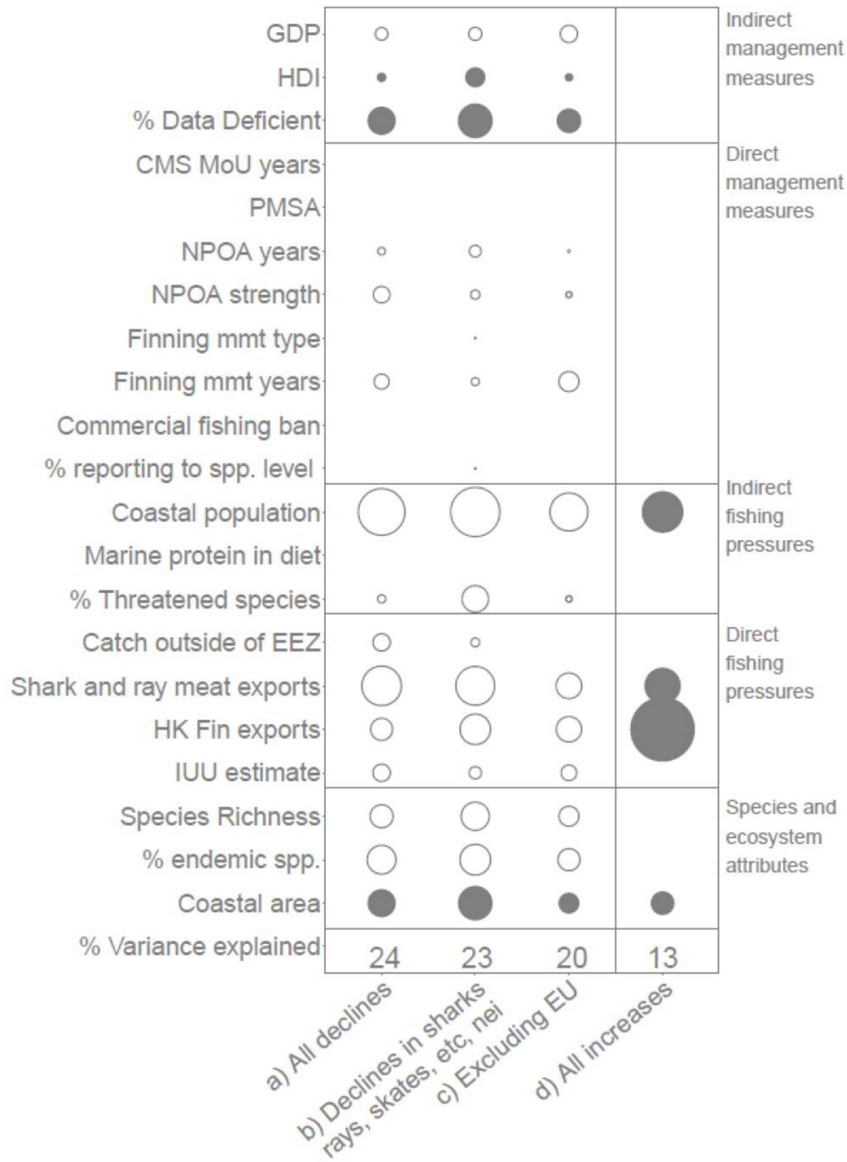


Figure 3.6 **Variable importance dot plot for all model subsets. Size of dot represents the Mean Standard Error associated with that variable from a Random Forest analysis. The larger the dot, the more important the variable is in describing the response. Hollow dots represent a negative relationship (Fig. S.5). Model output for: (a) all countries reporting a decline, (b) country-specific declines only within the "sharks, rays, skate, etc, nei" reporting category, (c) countries that reported a decline, with EU countries excluded, and (d) countries that reported an increase in landings.**

By comparison, the influence of the indirect and direct management measures was marginal as shown in the partial dependence plots (Fig. S.5). The most important management-related variable was a measure of the shortfall in scientific capacity: the percentage of Data Deficient species in the EEZ followed by *Shark-plan* year and strength, finning ban years, GDP, and HDI respectively. Countries with a low percentage of DD species, finning management in place for a longer period of time, and larger GDPs, and low HDI, reported marginally bigger declines (Fig. S.5). Five of the six unimportant variables were direct management measures and only one fishing pressure measure was unimportant - marine protein in diet.

3.5. Discussion

While the foundations for improved management have been laid, my analyses showed that the implementation was insufficient to account for the global reduction in shark and ray landings. Instead, it is more likely that the decline in shark and ray landings was due to reductions in fisheries catches, likely a result of population declines. The decline in shark and ray landings was strongly related to indirect and direct fishing pressure measures and only weakly related to measures related to fisheries management. My findings lead to six questions: (1) is there additional evidence for shark and ray population declines?; (2) Did aggregate reporting influence my interpretation?; (3) What are global priorities to promote shark and ray fisheries sustainability?; (4) Why did shark and ray landings decline?; (5) Why were shark and ray management efforts not reflected in landings trajectories?; and (6) What effective fisheries management progress has been made?

3.5.1. Is there additional evidence for shark and ray population declines?

There are two independent lines of evidence for widespread shark and ray population declines. First, a recent global analysis of the sustainability of the reported global catch (i.e. not accounting for discards or IUU fishing) suggests coastal species and large predators such as sharks were already heavily depleted by 1975 (Costello et al. 2012). By classifying FAO landings categories into 112 shark and ray fisheries, they found that the average biomass of these shark fisheries was 37% of that which would provide Maximum Sustainable Yield (B_{MSY}) (Costello et al*.*, 2012). If B_{MSY} occurs at 30-50% of unexploited biomass, then by 2009 the populations had, on average, declined by between 81% and 89% from the virgin population baseline (Dulvy, Fowler, et al. 2014; Costello et al. 2012). Second, the IUCN SSG estimates that 25% of all sharks and rays are threatened with elevated extinction risk (Vulnerable, Endangered, or Critically Endangered) primarily as a result of steep declines due to overfishing (Dulvy, Fowler, et al. 2014).

3.5.2. Did aggregate reporting influence my interpretation?

I caution that those countries with stable or increasing shark and ray landings may not have sustainable shark and ray fisheries. There were 62 countries (and overseas territories) reporting stable trajectories (±150 t) over the time period I examined and another 32 with increased landings. Stable or increased landings of aggregate species complexes has been shown to mask declines or disappearance of the most sensitive or more valuable species (Dulvy et al. 2000; Branch et al. 2013). For example, catches of skate species (Rajidae) reported as ‘skates and rays’ within British waters exhibited a stable trajectory. However, species-specific, fisheries-independent population trends revealed the disappearance of three of the largest skate species, and steep declines in the two largest remaining species. The declines had been masked by compensatory rises in the abundance of the smaller species (Dulvy et al. 2000). Furthermore, the poor taxonomic resolution of fisheries landings data masked the near extinction of the Angel Shark (*Squatina squatina*) from European waters. This species was recorded and sold under the product name “Monkfish”. The decline of the Angel Shark went almost entirely unnoticed because their dwindling catch was substituted with catches of anglerfish (*Lophius* spp.) sold under the same name (Dulvy and Forrest, 2010). Hence, accurate species-specific data on landed catch, and ideally discarded catch, are essential precursors to sustainable fisheries management.

The FAO strongly recommend that all landings be reported to a species-specific level (Fischer et al. 2012). Species-specific reporting has to be a condition of entry into fisheries or of fisheries licensing. Refining catches into species-specific categories will allow for better understanding of landings trends, lead to the improvement of management, and inform the true status of individual stocks (Stevens et al. 2000). Similarly, fins-attached regulation can improve statistical reporting as carcasses brought back to port can be more readily identified (Fowler & Séret 2010). Transitioning to species-specific reporting will require considerable investment in training, which may require foreign assistance from richer countries with well-developed fisheries management, or cost recover from the industry (Trebilco et al. 2010). I hope such activities are mainstreamed into the fisheries improvement activities of Development agencies and NGOs (Dulvy & Allison 2009).

3.5.3. What are global priorities to promote shark and ray fisheries sustainability?

My study highlights the necessity to focus on the sustainability of Blue Shark and “stingrays, butterfly rays nei” fisheries that have together increased by almost 100,000 tonnes over 2003-2011. First, ensuring the sustainability of Blue Shark catches is of high importance given evidence for increased retention and the substantial contribution to global catches in the past decade. In Chile, the retention of Blue Sharks increased almost sixty-fold between 1999-2009 (Bustamante & Bennett 2013). Globally, Blue Sharks fins are estimated to comprise 17% of the overall fin market weight in Hong Kong (Clarke, Magnussen, et al. 2006). Blue Sharks have comparatively higher rates of productivity than other sharks and hence have great potential to be fished sustainably (Kleiber et al. 2009). According to assessments by scientists associated with Regional Fisheries Management Organizations (RFMO's), Blue Shark catches are thought to be sustainable in the Atlantic and Pacific, although no country in this region has adopted quotas or fishing limits for Blue Sharks (Kleiber et al. 2009). There are concerns, however, that stock assessments are not reflecting the recent catch rate declines for Blue Sharks, by 5% per year since 1996-2009, in the North Pacific (Clarke et al. 2013). Unfortunately, these stock assessments are driven by the longest, rather than the most pertinent time series, the latter of which suggests steep declines in catch rate.

Second, the rise of landings in “stingrays, butterfly rays, nei” is mainly as a result of improved reporting by Indonesia. The rise in catches of rays (and skates) is concerning as they are often overlooked by management and are generally more threatened than sharks (Dulvy, Fowler, et al. 2014). Skates and rays (Batoids) are commercially exploited mainly for meat and the fins of the shark-like rays (Devil and Manta Rays, genus Mobula, are exploited for their gill plates). Steep declines have been noted for many skates and rays, including Sawfishes (*Pristidae* spp., Pristidae) (Dulvy, Fowler, et al. 2014), and the largest skates such as the Common Skate (*Dipturus ‘batis’* complex, Rajidae) (Brander 1981). Despite high risk and high exploitation rates, skates and rays were often overlooked in *Sharks-Plans,* and finning bans (UN FAO 2013).

3.5.4. Why did shark and ray landings decline?

I found that international demands for shark and ray meat products and human coastal population explained shark and ray declining trajectories. Therefore, the most plausible explanation for the shark and ray declining landings I observed is that local and international demands are driving fishing pressure and overexploitation.

Coastal human population size has repeatedly been shown to relate to indirect and direct measures of fishing pressure at a range of spatial scales from local to global. Catch rates, and direct and indirect effects of fishing are related to the number of islanders on coral reef islands (Jennings & Polunin 1996) and coastal human population density also relates to fisheries footprints and reef health at a regional (Mora 2008; Dulvy et al. 2004) and global scale (Newton et al. 2007). I also found that countries with high shark and ray meat exports reported larger declines, which indicates an important role of international meat trade in driving overfishing of sharks and rays (Clarke 2014).

3.5.5. Why were shark and ray management efforts not reflected in landings trajectories?

I showed that there has undoubtedly been an increase in national and international commitments and policies specific to chondrichthyan fisheries in the past two decades. My analyses showed, however, that important international commitments have yet to be realized in the form of concrete fishing limits or restrictions on fishing for sharks and rays. This result is probably because the measures I considered, with the exception of CITES, were not yet legally binding, far from comprehensive, lacked clear implementation guidelines, operated with vague wording, and lacked compliance monitoring (Fischer et al. 2012; Lack & Sant 2011). I highlight some of the shortfalls and limitations of the PMSA, CMS sharks MoU, *Shark-Plans*, finning bans, and commercial fishing bans that resulted in little or no effect on landings trajectories and provide suggestions for improvements.

Some of the international agreements and initiatives included in my analysis do not have widespread implementation. For example, the Port State Measures Agreement (PSMA) to combat IUU fishing is a new initiative (2009). To date, 26 countries plus the EU countries have signed, only five have ratified. Until ratified, the full potential of this agreement for improving fisheries sustainability cannot be realized. Addressing IUU fishing would have far reaching consequences for the sustainability of shark and ray fisheries (Doulman 2000). The global extent of IUU fishing for sharks and rays is unknown, however, the massive, uncontrolled catches of shark and rays in species-rich countries, in addition to the IUU fishing, remains to be a major problem for the persistence of shark and ray populations. IUU fishing has been noted to be a major problem in Indonesia and for vulnerable endemic sharks (FAO 2014; Fischer et al. 2012). Without controls on IUU fishing, it is estimated that fisheries management decisions are flawed subsequently leading to management goals not being met, and potentially, the overfishing of populations (Doulman 2000; FAO 2013a).

Similarly, CMS sharks MoU potentially had not affected fisheries trajectories as the agreement included a few highly migratory, pelagic species. As of 2012, the eight species listed in the CMS sharks Appendices represent less than 15% of threatened, migratory sharks and rays and no Endangered or Critically Endangered migratory shark or ray has been listed by CMS sharks (Fowler 2012). Also, the CMS needs a mechanism for compliance.

The national and regional *Shark-Plans* reviewed herein are non-binding and have been found to emphasize early stages of fisheries management such as communication, finning management, and forming partnerships rather than more direct catch and effort controls (Camhi et al. 2008). *Shark-Plans* that were more comprehensive (i.e. Australia, United States, Canada) represented relatively sound management policies already in place (Fordham, personal communication).

I found commercial fishing bans have been gazetted in countries with very small, or non-existent, commercial shark fisheries (as found in the past 60 years of the FAO landings records). Spatial protections that are strict and no-entry have been shown to increase predator biomass (Robbins et al. 2006). Commercial fishing bans, however, are not “no-entry” and countries often do not have the enforcement capacity to monitor large marine areas after implementation. For example, Palau has one enforcement boat to monitor the entire EEZ (Vianna, Gabriel, personal communication). Additionally, commercial fishing bans may have limited future conservation benefits as a result of having no protections or management plans in place for shark bycatch mortality (Campana et al. 2011) and mortality from artisanal fishing (Hawkins & Roberts 2004), which can be significant. Therefore, I suggest that commercial fishing ban designation be expanded to extend protection to rays and skates, to bycatch, and to not forestall national and international fisheries management initiatives that promote sustainable resource utilization.

Derogations or loopholes exist that undermine the implementation and effectiveness of finning regulations. First, the relative weight of a shark’s fins averages 3% but varies among species from 1.1 to 10.9% of the total weight of the animal (Biery & Pauly 2012). Second, the setting of a fin landing ratio is also complicated by the choice of denominator – whole carcass, gutted carcass or dressed carcass (head removed) (Biery & Pauly 2012). Hence, the use of a blanket 5% fin-to-carcass ratio (Fowler & Séret 2010) can allow for more sharks to be killed and disposed of further complicating mortality estimates (Biery et al. 2012). In addition, some countries have ratios higher than the recommended 5% and whether the percentage ratio refers to dressed carcasses or whole bodies is unclear (Fowler & Séret 2010). Third, countries may allow for exceptions. For example, on November 2012, the EU closed a loophole on a fins-attached rule that had been in effect since 2003. From 2003 to 2013, five EU countries were allowed to apply for Special Fishing Permits (SFP) exempting them from the fins-attached policy. This exception became the rule for Portuguese and Spanish fishing fleets, which held 220 (91%) SFPs issued in 2005/6 (Fowler & Séret 2010). Fins naturally attached policy is the most reliable and is the easiest finning ban strategy to enforce (Fowler & Séret 2010), and would permit better data collection.

3.5.6. What effective fisheries management progress has been made?

There have been considerable improvements in the management of shark and ray fisheries. First, Indonesia reports the largest landings of shark and rays to FAO and has made considerable progress in taxonomic resolution of their landings in the past decade. Prior to 2004, Indonesia reported 100,000 t of landings in two aggregate categories: “sharks, rays, skates, etc., nei” and “rays, stingrays, mantas nei” and in 2005 switched reporting into 11 family categories (Fischer et al. 2012). Currently, the majority of countries report in an aggregate ‘nei’ category which therefore presents vast opportunity for each country to improve this necessary step towards effective management. Second, a number of species have recovered under strict management regulations. For example, Great White Shark populations increased in California after a prohibition on catches was implemented in 1994 (Burgess et al. 2014). Spiny Dogfish also recovered under strict catch quotas in the United States and the fishery re-opened in 2011 (COSEWIC 2011). A third encouraging sign of progress includes seven West African countries that developed a regional plan of action for shark and ray fisheries management. While non-binding and lacking fishing quotas, this coalition has led to improved knowledge of the major shark fisheries, increased landings surveys, improved public awareness, improved understanding of sawfish status, and improved engagement with international conservation efforts such as the 2006 IUCN Red List assessment (Dulvy, Fowler, et al. 2014).

Similarly, South American countries (Chile, Columbia, Ecuador, and Peru) have worked together to develop a regional plan of action for the protection and management of chondrichthyans in this region (Gomez 2008).

3.6. Conclusion

I showed that the management measures I considered have had little influence on shark and ray fisheries landing trajectories. I interpret these findings, however, as a way to encourage the continued pressure on countries to sustainably manage their shark and ray fisheries. My analysis determined a number of countries and fisheries that deserve prioritization for conservation and management action. First, fisheries management development is necessary in the countries that report the greatest declines, such as Pakistan and Sri Lanka, and have little to no management in place. Second, countries reporting large increases, or a substantial portion of the world's landings, can become the focus of conservation and management efforts to forestall potential impeding population declines (such as Indonesia, Philippines, India, and Spain). Third, countries with relatively stronger management policies should improve further by sustainably managing fisheries that are of conservation concern and report landings to species-specific categories. These countries also should also work together in supporting developing countries with chondrichthyan management as shark and ray species are generally not confined to one national jurisdiction. Fourth, those fisheries with dramatic increases in landings need to be the focus of stock assessments and scientific management. Finally, I strongly suggest that countries implement the current scientific advice that includes, but not limited to, catch limits, bycatch limits, finning bans, stock assessments, and species-specific data collection.

3.7. Supplemental material B

Table S.6. Summary table of all predictor variables and definitions. Variables are organized according to their broad category class (Fig. 3.1)

Variable	Definition	Predicted impact on decline
Indirect fishing pressure measures		
Human coastal population size	Nominal value of persons living 100km from the coast	-
Marine protein in diet	Country specific index of grams/capita/day of marine fish protein available for consumption	-
Percentage of threatened species	Percentage of shark and ray species classified as Vulnerable, Endangered, or Critically Endangered in EEZ	-
Direct fishing pressure		
Catch outside of EEZ (tonnes)	Reported landings from FAO major fishing areas that do not overlap with a country's EEZ waters	-
Shark and ray meat exports	Avg. reported export of shark and ray meat from FAO between ('92-'03) in tonnes (see Appendix B Table 3.3).	-
Hong Kong fin exports	Country specific fin exports to Hong Kong in 2011	-
IUU fishing	Lower estimate of IUU fishing in EEZ waters	-
Indirect fisheries management		
Gross Domestic Product (GDP)	Value of a country's economy; standardized to US dollar	-
Human Development Index (HDI)	Composite index that captures a country's development status	-
Percentage of Data Deficient (DD) species	Percentage of shark and ray species classified as Data Deficient (DD) in EEZ	-
Direct fisheries management		
Port State Measures Agreement (PSMA)	Countries that have signed and ratified the PSMA to combat IUU fishing. PMSA was initiated in year 2009.	-
Convention of Migratory Species Memorandum of Understanding	Countries that have signed the CMS sharks MoU; an international agreement that lists 8 shark species.	-
Shark-Plans (National Plans of Action for sharks)	Duration: years the country had a finalized *Shark-plan.* *S*trength: how well the FAO's 10 objectives of sustainable fishing were met (Appendix B Table 3.1).	-
Finning ban	Duration: years finning regulation has been in place. Strength: the type of management plan (Appendix B Table 3.2).	-
Ban on commercial fishing	Ban on commercial fishing for sharks in EEZ.	-
Species specific reporting	Percentage of landings reported (avg. '03-'11) in species specific categories (see Appendix B Figure 3.2).	-
Sensitivity and Resilience: ***Ecosystem productivity and resilience***		
EEZ area	Area (km2) of a country's EEZ	+
Species productivity and resilience		
Species richness	Shark and ray species within a country's EEZ	+

Variable	Definition	Predicted impact on decline
Endemic richness	Shark and ray species, within a country's EEZ, with a range size less than the lower quartile of all species	-

Table S.7. Summary of commodity codes for shark and ray meat exports and total reported tonnes for 2003 and 2009 (most recent).

FAO FishSTAT commodity code	2003	2009
Shark fillets, fresh or chilled	15	12
Shark fillets, frozen	3,566	4,958
Shark fins, dried, salted, etc.	0	0
Shark fins, dried, unsalted	0	0
Shark fins, frozen	0	0
Shark fins, prepared or preserved	0	0
Shark fins, salted and in brine but not dried or smoked	0	0
Shark liver oil	51	40
Shark oil	42	40
Sharks nei, fresh or chilled	8,299	5,162
Sharks nei, frozen	40,098	81,339
Sharks, dried, salted or in brine	483	347
Sharks, rays, chimaeras nei, frozen	5,380	1,840
Sharks, rays, etc., dried, salted or in brine	0	0
Sharks, rays, skates, fresh or chilled, nei	89	747
Sharks, rays, chimaeras, nei fillets fresh or chilled	1	0
Sharks, rays, chimaeras, skates, nei fillets frozen	3,523	4,472
Skates, fresh or chilled	818	366
Skates, frozen	208	2,652
SUM	62,573	101,975

Table S.8. Countries reporting the greatest increase in landings between 2003-2011 in descending order. Only changes of greater than 100 tonnes (per reporting category) were included for brevity.

Country	Reporting category	Increase in landings ('03-'11, t)	Management
Spain	Blue shark	31,077	no catch limits in EU (Shark Trust, 2014)
	Rays, stingrays, mantas nei	2,450	NA
	Cuckoo ray	1,187	Combined TAC in place for all species of skate and ray in EU waters
	Shortfin mako	694	no catch limits in EU
	Thornback ray	578	minimum landing sizes have been implemented in some areas of the UK by Sea Fisheries Committees (Ellis, 2005); 2009 subject to TACs in EU waters (Shark Trust, 2014)
	Catsharks, etc. nei	434	no catch limits in EU
	Tope shark	401	no catch limits in EU
United States of America	Little skate	4,225	Currently, no specific management plan in place for Little Skate (NEFMC 2003)
	Picked dogfish	3,907	NOAA catch limits
	Rays, stingrays, mantas nei	3,610	NA
	Dogfish sharks nei	1,241	NA
Argentina	Rays, stingrays, mantas nei	3,822	NA
	Argentine angel shark	1,539	IUCN classified as Endangered; operating under Maximum Permitted Catch
	Plownose chimaera	1,502	unknown
	Yellownose skate	1,168	There are Total Allowable Catches (TACs), minimum sizes and overall annual quotas for skates, but they are not enforced (Kyne et al. 2007)
Libya	Dogfish sharks nei	6,432	NA
	Smooth-hounds nei	1,013	NA
India	Sharks, rays, skates, etc. nei	4,989	NA
Nigeria	Sharks, rays, skates, etc. nei	4,124	NA
	Rays, stingrays, mantas nei	820	NA

	Coastal pop.	Marine Diet	GDP	HDI	% spp. reporting	% DD	Finning mmt Years	NPOA years	NPOA strength	PSM years	CMS MoU years	FAO Code score	Landings (EEZ)	Outside EEZ	Meat exports	Fin exports	% THR	IUU est.	EEZ area	SR	% Endemic
Coastal pop.	1																				
Marine Diet	-0.01	1																			
GDP	0.39	0.12	1																		
HDI	-0.10	0.32	0.45	1																	
% spp. reporting	-0.29	0.27	0.08	0.50	1																
% DD	0.12	-0.08	0.06	-0.14	-0.19	1															
Finning mmt years	-0.31	-0.21	0.11	0.57	0.53	-0.31	1														
Shark-plan years	0.13	0.15	0.61	0.32	-0.11	0.29	0.08	1													
Shark-plan strength	-0.06	-0.06	0.11	0.47	0.06	0.24	0.38	0.62	1												
PSMA years	-0.03	-0.03	-0.04	0.45	0.43	-0.19	0.35	-0.03	0.40	1											
CMS MoU years	-0.13	-0.37	0.14	0.30	0.01	-0.05	0.15	0.31	0.42	0.27	1										
FAO Code score	-0.18	0.42	0.34	0.77	0.65	0.02	0.48	0.39	0.44	0.26	0.14	1									
Avg landings	0.80	-0.04	0.01	-0.22	-0.19	-0.05	-0.18	-0.10	0.08	0.09	-0.26	-0.25	1								
catch outside EEZ	0.42	0.29	0.87	0.25	-0.08	0.30	-0.16	0.58	-0.07	-0.23	-0.10	0.23	-0.02	1							
Meat exports	0.56	0.05	0.62	0.36	0.31	-0.03	0.32	0.41	0.26	0.38	-0.14	0.33	0.41	0.49	1						
Fin exports	0.83	-0.05	0.06	-0.18	-0.16	0.19	-0.18	-0.03	0.09	0.12	-0.34	-0.15	0.92	0.12	0.48	1					
% THR	0.12	-0.10	-0.13	-0.44	-0.55	0.07	-0.61	-0.14	-0.08	-0.23	-0.02	-0.32	0.19	-0.07	-0.32	0.12	1				
IUU est.	0.55	0.23	0.40	0.10	-0.55	0.42	-0.50	0.42	0.13	-0.28	-0.11	-0.05	0.29	0.56	0.13	0.36	0.28	1			
EEZ area	0.15	-0.13	0.15	0.26	0.13	-0.24	0.49	0.19	0.37	0.29	-0.15	0.34	0.22	-0.05	0.54	0.23	-0.02	-0.02	1		
SR	0.47	-0.03	0.27	0.02	-0.46	0.53	-0.21	0.47	0.31	-0.29	0.00	0.08	0.27	0.36	0.08	0.38	0.10	0.77	0.18	1	
% Endemic	0.25	0.17	0.16	0.30	0.13	0.32	0.16	0.31	0.28	-0.02	-0.13	0.50	0.20	0.22	0.21	0.36	-0.35	0.41	0.20	0.69	1

Figure S.3 Pearson's correlation table. Values highlighted blue represent positive correlations, red boxes are negative correlations. FAO Code of Compliance score was dropped from the analysis due to extensive NAs.

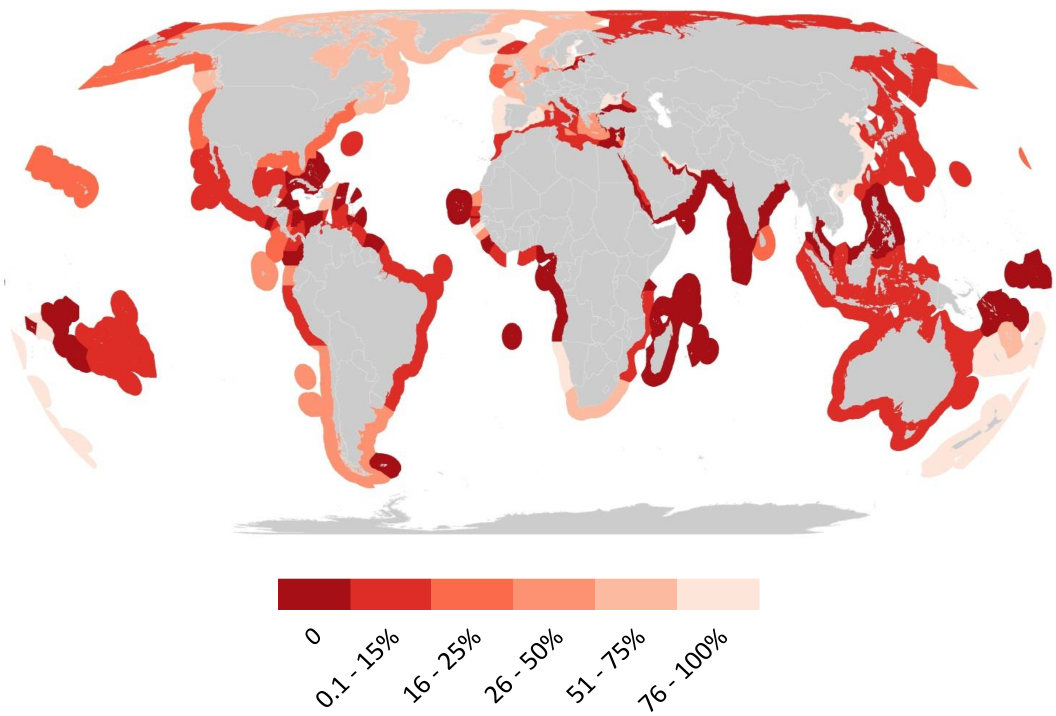
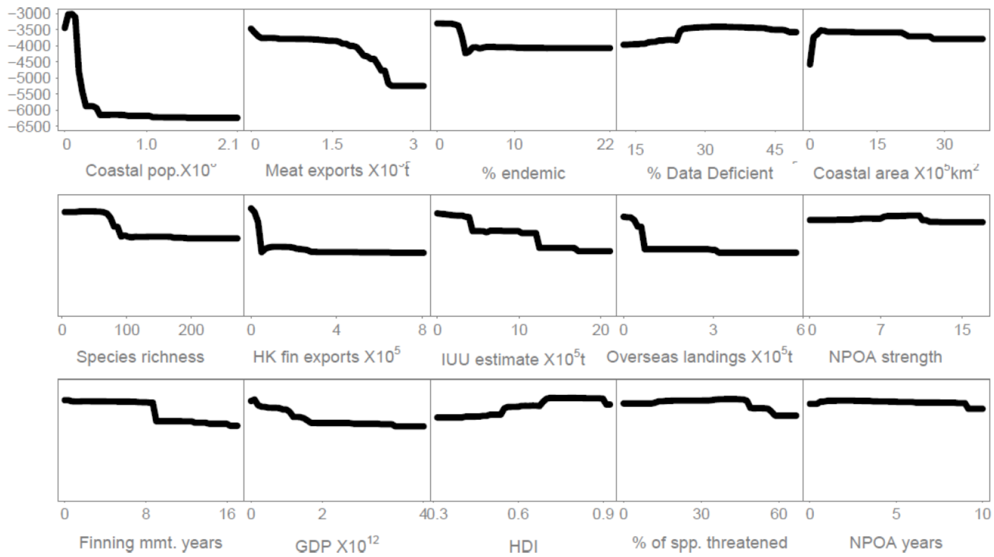


Figure S.4 **Distribution of the reporting resolution. Darker colours represent countries that report none of their shark and ray landings to the species level (India reports all landings in "sharks, rays, skates, etc, nei"). Lighter colours are those countries with better taxonomic resolution (greater than 75% of landings to species level). Countries that do not report shark and ray landings have no EEZ mapped.**

(a) All declines



(b) All increases

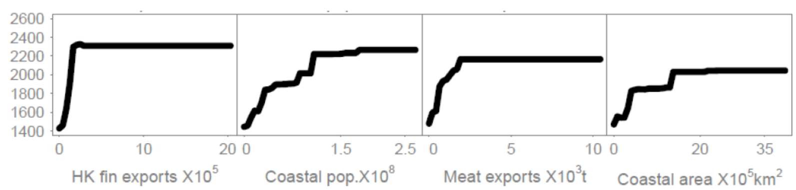


Figure S.5 Random Forest partial dependence plots of important variables from (a) the model that explained the most variance – all countries reporting a decline. Variables are order from left to right, top to bottom in terms of importance (see Figure 3.8, column one). (b) countries reporting an increase in landings.

Chapter 4.
Global marine protected areas to prevent extinctions[3]

4.1. Abstract

One goal of marine protected areas (MPAs) is to ensure that they represent a breadth of taxonomic biodiversity. Ensuring representation of species in MPAs, however, would require protecting vast areas of the global oceans and does not explicitly prioritize species of conservation concern. When threatened marine and terrestrial species are considered, a recent study found that only a small fraction of their geographic ranges is within MPAs. Those global marine areas, and what conservation actions beyond MPAs could be prioritized to prevent marine extinctions (CBD Aichi Target 12), remains unknown. Here, I use systematic conservation planning approaches to prioritize conservation actions for sharks, rays, and chimaeras (Class Chondrichthyes). I focused on chondrichthyans as they have the highest proportion of threatened species of any marine Class. I find that expanding the MPA network by 3% in 70 nations would cover half of the geographic range of 99 imperiled endemic chondrichthyans. My hotspot analysis reveals just 12 nations harbour over half (53) of the imperilled endemics. Four of these hotspot nations are within the top ten chondrichthyan fishing nations in the world but are yet to implement basic chondrichthyan fisheries management. Given their geopolitical realities, conservation action for some countries will require relief and reorganization to enable sustainable fisheries and species protection.

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4.2. Introduction

The most common assessment of marine protected area (MPA) progress is the amount of area protected (Wood et al. 2008; Lubchenco & Grorud-Colvert 2015), or the degree to which the MPA network represents a broad taxonomic swath of biodiversity (gap analysis) (Rodrigues, Andelman, et al. 2004; Klein et al. 2015) (i.e. Convention of Biological Diversity, CBD Aichi Target 11). A recent gap analysis found that most (97.4% of 17,348) marine species have less than 10% of their geographic range inside MPAs (Klein et al. 2015). To address this shortfall, MPAs would need to be expanded in almost every coastal country's waters as well as the open oceans (Klein et al. 2015). This expansion of MPAs would stretch limited funds and capacity for conservation action. Further, while representation is an important goal, it prioritizes species irrespective of conservation need and does not ensure extinctions are avoided as per the often overlooked CBD Aichi Target 12: "By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained" (Venter et al. 2014; Butchart et al. 2015; Le Saout et al. 2013a).

An approach that narrows the focus and scale of conservation and protects those species at greatest risk of extinction is the classic Myers et al. (2000) hotspot analysis (Myers et al. 2000; Margules & Pressey 2000; Rondinini et al. 2006; Possingham & Wilson 2005). Hotspots are those global areas with the greatest numbers of threatened and endemic species. In the terrestrial realm, this focus on threatened endemics narrowed the spatial scale of action to 1.4% of the land that, if protected, would represent over half of the threatened endemic plants and 35% of threatened vertebrate species (Myers et al. 2000). Until now it has not been possible to undertake a similar global marine hotspot analysis due to a lack of comprehensive IUCN (International Union for the Conservation of Nature) Red List assessments (Dulvy, Fowler, et al. 2014). Furthermore, MPAs are not the only tool to protect species - fisheries and conservation management outside of

MPAs can also protect biodiversity (Hilborn 2016; Shiffman & Hammerschlag 2016).

Here, I ask four questions: (i) by how much do we need to expand the current MPA network to avert the extinction of imperilled endemic chondrichthyans, (ii) which are the priority hotspot countries harbouring the greatest number of imperilled endemic chondrichthyan species, (iii) how can we improve fisheries and conservation management related activities in these hotspot countries, and (iv) what is the likelihood of conservation in each of the countries? I focused on 1,007 marine sharks, rays, and chimaeras (Class Chondrichthyes) for six reasons: (1) their threat status was comprehensively assessed by the IUCN (Dulvy, Fowler, et al. 2014), (2) they have the greatest percentage of threatened species in a taxonomic Class of marine organisms (Hoffmann et al. 2010) and at least 28 populations are locally or regionally extinct (Dulvy, Fowler, et al. 2014), (3) they are found in every ocean basin and across broad latitudes, (4) they are threatened by targeted and indirect overfishing, which is the leading threatening pressure in the ocean, (5) they have expert-generated, peer-reviewed Extent of Occurrence (EOO) maps, which are more suitable for conservation planning as they are not biased towards survey effort and are less likely to produce results with omission errors(Rodrigues 2011), and finally, (6) as of 2015, 29% of total ocean area protected was designated exclusively for shark conservation (Fig 4.1a) (Marine Conservation Institute 2016).

4.3. Methods

I used expert-generated, peer reviewed Extent Of Occurrence (EOO) geographic range maps for 1,007 marine chondrichthyan species that were taxonomically valid up to August 2011 (Dulvy, Fowler, et al. 2014). These maps are convex polygons around known locations, hence, I caution that my results are likely to contain commission rather than omission errors; that is, a species is shown to be present in an area when in fact it is not (Rondinini & Chiozza 2010). Notwithstanding the likelihood of commission errors, the use of these distribution maps for this type of analysis falls into the Best Practices for IUCN maps manual and priority countries should become the focus of local-scaled planning (IUCN 2011). All distribution maps were created through expert opinion from the International Union for the Conservation of Nature Shark Specialist Group (IUCN SSG). For this analysis, the Pita Skate (*Okamejei pita*) was not included due to its taxonomic uncertainty.

I used the IUCN Red List categories as a measure of extinction risk (Kyne 2016). This index considers all threats, such as: fishing pressure, coastal development, or pollution (Salafsky et al. 2008), however, future smaller-scale studies will be needed to identify the mechanism of the species endangerment and to tailor conservation action. Here, I focused on fishing pressure as this is the predominant threat to Chondrichthyan species (Dulvy, Fowler, et al. 2014).

To determine which species are imperiled and endemic, I used three definitions of marine endemism commonly used in the literature, those species within the: (1) 25^{th} percentile (183,616 km^2), (2) less than 500,000 km^2(Dulvy, Fowler, et al. 2014; Roberts et al. 2002), and (3) 50^{th} percentile (595,749 km^2) of EOO geographic range sizes (Davidson et al. 2012; Pompa et al. 2011) resulting in 252, 468, and 504 species, respectively. I defined imperiled species as those categorized by the IUCN as Vulnerable, Endangered, or Critically Endangered plus those Data Deficient (DD) species predicted to be threatened. Almost half (46.8%) of chondrichthyans are categorized as DD (Dulvy, Fowler, et al. 2014), meaning that not enough information was available to assign them to a IUCN Red List category, however, these DD species may be threatened. Indeed, based on body size and ecological characteristics 68 out of the 487 DD species are predicted to be threatened with extinction (Dulvy, Fowler, et al. 2014). Therefore, I included the distribution of predicted threatened DD species that meet my endemism criteria (n=35). The final number of imperiled endemic chondrichthyan species for each definition, is 57, 92, and 99, respectively. I used the median

(Figure S.6) definition of endemicity for the remaining analyses and the hotspot locations revealed were robust to the definition of endemism (Figure S.7 a,b,c).

A total of 99 chondrichthyans are both endemic and imperiled (Fig 4.1b). Over half (n=58) of these 99 are batoids (skates, stingrays, guitarfishes, wedgefishes, and rays; Order Rajiformes). The remaining imperiled endemics include 22 groundsharks (Order Carcharhiniformes), three dogfish (Order Squaliformes), eight carpet sharks (Order Orectolobiformes), three horn sharks (Order Heterodontiformes), and five angel sharks (Order Squatiniformes). Eighty percent (n=79) of the imperiled endemics are coastal and continental species while the remainder (n=20) are deepwater.

I used the MPAtlas (Marine Conservation Institute 2016) to determine how much of the world's marine protected areas are designated for, and protecting, sharks, rays, skates, and chimaeras (Class Chondrichthyes). To determine the ocean area protected, I excluded proposed parks and those without the year the park was created. Any marine designation was included as a marine protected area (MPA) such as whale sanctuaries, sites of community importance, and shellfish management areas for a total of 12,157 MPA sites. Fifteen sites were designated as "shark sanctuaries" and were used to calculate the percent of total area designated exclusively for sharks (Fig 4.1a). In the main text, I excluded the Southern Ocean Marine Sanctuary (designated in 1994) from the area calculations as it covers the marine portion of Antarctica and is unusually large sanctuary at about 65 million km^2. If I included this large ocean area, the amount of MPA designated exclusively for sharks in 2015 would be 9.3%.

To determine the number of imperiled endemic species with at least 10% of their EOO within MPAs, I subdivided the MPAtlas to include (1) any park that was designated (n=12,582), (2) any park designated as no-take (all or part, IUCN category 1a-VI or not reported) and those designated exclusively for sharks (n=988), and finally, (3) only those areas designated as no-take (all or part, IUCN category 1a-VI or not reported, n=973). Despite the differences in the number of parks and ocean area, I found little difference in the number of imperiled endemics protected - 24, 12, and 12, respectively (Table S.10). To calculate the area coverage from any MPA, I eliminated erroneous percentages that would arise from overlapping spatial protections (such as overlapping areas for trap/pot closures and national heritage sites in the eastern United States) by dissolving the boundaries of MPAs in ArcGIS version 10.3. I note that coastal (Knip et al. 2012), deepwater (Daley et al. 2015), or time-area closures for nursery populations of highly mobile sharks and rays (Heupel & Simfendorfer 2005; Wiegand et al. 2011) are shown to provide favourable conservation outcomes.

Almost ten percent (7.7%, n=973 of 12,582) of global MPAs entirely restrict fishing (no-take, part or all) although have varying enforcement and restrictions (IUCN protected area categories 1a -VI and those for which status is “not reported”) (Lubchenco & Grorud-Colvert 2015; Boonzaier & Pauly 2015). A much smaller subset, only 0.9% (n=110 of 12,582) of global MPAs, entirely restrict fishing (no-take) and are strictly enforced (IUCN protected area category 1a). These marine reserves have the attributes shown to increase biomass and hence contribute to avoiding extinctions (Edgar et al. 2011; Costello & Ballantine 2015). I found that only the Kermadec Spiny Dogfish (*Squalus raoulensis*) is entirely within a strictly the recently designated, strictly protected marine reserve (IUCN protected area classification 1a): Kermadec Islands in New Zealand. A portion of the EOO (16%) for Narrowbar Swellshark (*Cephaloscyllium zebrum*) is found within the Coral Sea marine reserve in Australia.

I used Marxan (Ball et al. 2009) to determine which global areas could be prioritized for protected area expansion if I extended coverage to 25, 50, and 75% of the range of all 99 imperiled endemics. I integrated area as cost (Ban et al. 2010) and a cell was considered protected (n=206 out of 1,132 cells) if at least half of the cell overlapped with a no-take MPA. Marxan is iterative and therefore I used the best scenario, out of 100, selecting those cells with the highest frequency of selection. I chose a boundary length modifier of one as I am interested in expanding from the current no-take MPA network rather than create disconnected new ones. I ran 100 iterations for each scenario and found that 2.2%, 3.3%, and 4.5% of the world's ice-free EEZ would need to become the focus of MPA expansion or creation to cover 25%, 50%, and 75% of each of the 99 imperiled endemic chondrichthyans EOOs (Fig 4.2a for cells selected to protect 50% of EOO). Some countries, particularly small countries, would have to protect large proportions of their EEZ such as Egypt, Uruguay, and Brunei.

I defined hotspots (Myers et al. 2000) as areas with the number of imperiled endemic chondrichthyan species on two spatial scales, (i) per hexagonal grid cell (23,322 km^2) and, (ii) per Exclusive Economic Zone (EEZ), 200 nautical miles from the coast (Fig 4.3a). I assigned cells to an EEZ based on the location of the center of the cell. I calculated the percent area of hotspot using ocean area from NOAA (Eakins & Sharman 2010). I also calculated how many non-endemic, imperiled species have parts of their ranges that overlap within hotspots and how many species have parts of their distributions in the hottest hotspots. All spatial overlay analyses were completed using ArcGIS version 10.3. Hexagons sometimes extended beyond the boundaries of some EEZ's (for example Uruguay), therefore, on occasion some hexagons have a higher number of species than is found within the country's EEZ.

The majority of hotspots are found in national coastal waters. Only five hotspot cells are oceanic; three are adjacent to Western Australia's southwest tip near Geographe Bay, while two are outside of Brazil's EEZ near the mouth of the Amazon River. Three cells fall within the Senkaku/Diayudao/Diaoyutai Islands, which is a disputed territory between Taiwan, China, and Japan. Another two cells are in a disputed marine area between Chile and Peru.

The most important hotspot countries (hereafter "hottest hotspots") are those with counts of between four to 14 imperiled endemic species per cell (Fig 4.2b, 4.3a).

These areas cover less than one percent (0.56%) of the global ice-free ocean's surface or 1.25% of global EEZ waters and contain a portion of the EOO of 54% (n=53) of the imperiled endemic species.

I ranked countries according to the total number of imperiled endemics within a country's national waters (EEZ) as this generally represents the scale of fisheries management. I also retained the number of species per cell to highlight the countries with high numbers of overlapping imperiled endemic species. Countries, such as Uruguay, have many imperiled endemics homogeneously distributed throughout a small EEZ (Fig 4.3a). However, most other priority countries, as typified by Australia, have many non-overlapping imperiled endemics throughout their EEZ (Fig 4.3a). Hence, it is unlikely that any one national MPA will serve to protect all the imperiled endemics a nation is responsible for.

To evaluate the sustainability and conservation initiatives in hotspot countries I compiled country-level chondrichthyan fisheries management measures that are global and comparable (Davidson et al. 2015) (Fig 4.3b, Table S.11). While these are not ultimate measures of fisheries management, the challenge is to find consistent measures that indicate or approximate good local management. I used four measures: (1) strength and number of years since a finning management regulation was finalized, (2) strength and number of years since a *Shark-plan* (National Plans of Action for sharks) was finalized, (3) whether a country is a signatory to the Convention of Migratory Species Memorandum of Understanding (CMS MoU sharks), and (4) whether a country is signatory to, or has ratified the Port State Measures Agreement (PSMA). These indirect and direct measures are intended to give a broad analysis of the state of chondrichthyans fisheries and may or may not be relevant to imperiled endemic species. For example, Rajiformes are not included in any country's finning policy (rays and skates can be "winged" at sea).

I used a modified conservation likelihood framework to broadly determine the types of interventions needed for the different hotspot countries. First, I determined how likely conservation actions would be successful in a country following the methods outlined by Dickman et al. (2015). Governance included political stability, government effectiveness, control of corruption, regulatory quality. Economic and Welfare included Gross Domestic Product (GDP), Purchasing Power Parity, and Human Development Index (HDI). Human Pressure included annual human population growth, human population 100 km from the coast, and Sea Around Us reconstructed chondrichthyan landings (see Table S.12 for references). I used 2014 measurements and in those cases where no measurements were available, I used the most recent measurements (no later than 2011). Taiwan does not have an entry in this database; however, the Taiwan government calculated their HDI to be 0.882.

To create the governance score, each of the nine measurements were standardized to a mean of zero and a standard deviation of one. I then summed each of the measurements within each of the three categories, and then took the mean across the three categories. Several overseas territories were excluded from the analysis due to lack of data: Bassas da India, Bonaire, Curacao, Ile Europa, Juan de Nova Island, Falkland Islands, and New Caledonia (these areas each only have one imperiled endemic in their waters). As well, Somalia had no information on governance and economics respectively and was excluded from the analysis. Second, I summed a standardized score of the presence and strength of the management and conservation measures that I considered. My presence of management axis is my derivative of the "environmental susceptibility" axis found in the original McClanahan et al. 2009 (McClanahan et al. 2009) framework where a higher score for management presence and strength represents a lower environmental susceptibility.

4.4. Results

I first asked, how well does the global MPA network protect the most imperiled and irreplaceable chondrichthyan species? Here, I defined imperiled as those chondrichthyan species categorized by the IUCN Red List as Critically Endangered, Endangered, Vulnerable, or Data Deficient but predicted to be threatened (Dulvy, Fowler, et al. 2014). I defined irreplaceable species (Brooks et al. 2006) as those species with limited spatial conservation options (endemics with EOO < median) (Fig 4.1b). I found that only 12 of the 99 imperiled endemics have at least 10% of their range within a no-take MPA (IUCN category 1a-VI or not reported) but only one species – the imperiled Kermadec Spiny Dogfish (*Squalus raoulensis*) – is entirely within in a no-take and strictly protected MPA (IUCN protected area category 1a; Fig 4.1c, Table S.9, S.10).

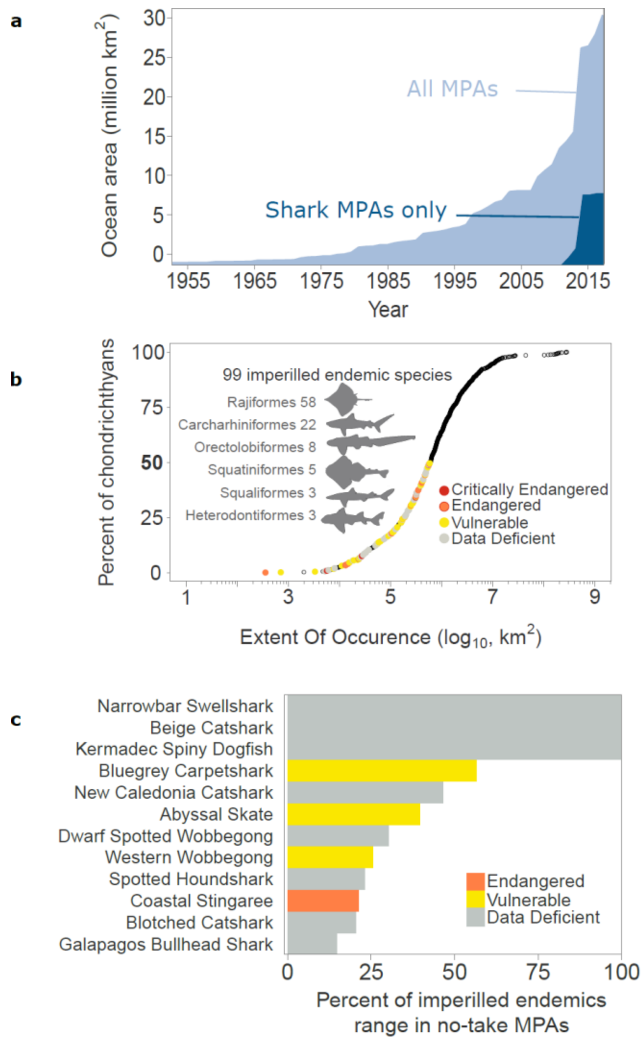

Figure 4.1 **The representation of the most imperilled and endemic chondrichthyans in the world's marine protected areas. a, Stacked plot of total ocean area designated with any spatial protection excluding those exclusively for sharks (all mpas – light blue), and those exclusively for sharks (shark mpas only - dark blue). b, Cumulative percent gain in species geographic range size measured as Extent Of Occurrence (EOO) $\log_{10}$ km^2 of 1,007 marine chondrichthyans, the endemic cutoff (median EOO), the IUCN Red List categories for endemic species, and the taxonomic composition of the 99 imperilled endemics. b, The 12 imperilled endemic species with >10% of their EOO within a no-take MPA of any IUCN protected area category (1a-VI or not reported). The bar colour represents the IUCN extinction risk category, grey bars represent Data Deficient species that are predicted to be threatened based on body size and ecological traits. Only the Kermadec Spiny Dogfish is found within a no-take, strictly protected MPA (IUCN protected area category 1a).**

I identified the locations that, if protected, would provide protection for the 99 imperilled endemic chondrichthyans. I used Marxan (Ball et al. 2009) software to identify planning units that meet conservation targets for each species while minimizing cost (area) and expanding from the current no-take MPA network (of any IUCN protected area category) (Marine Conservation Institute 2016). The exact amount of EOO that should be covered in order for long term persistence requires a consideration of life cycle. Conservatively, I chose to protect 100% of the EOO of each of the 99 species and found that this conservation target could be achieved by protecting 13% of the world's ice-free EEZ areas (Exclusive Economic Zone). These areas harbour not only imperiled endemic chondrichthyans, but also contain portions of the EOO of 78% (n=114) of the world's imperiled, non-endemic chondrichthyans. Alternatively, I found that protecting half of the EOO for each of the 99 species would only require expanding the MPA network to 3% of the global ice-free EEZ areas - well within the 2020 10% CBD target (Fig 4.2a).

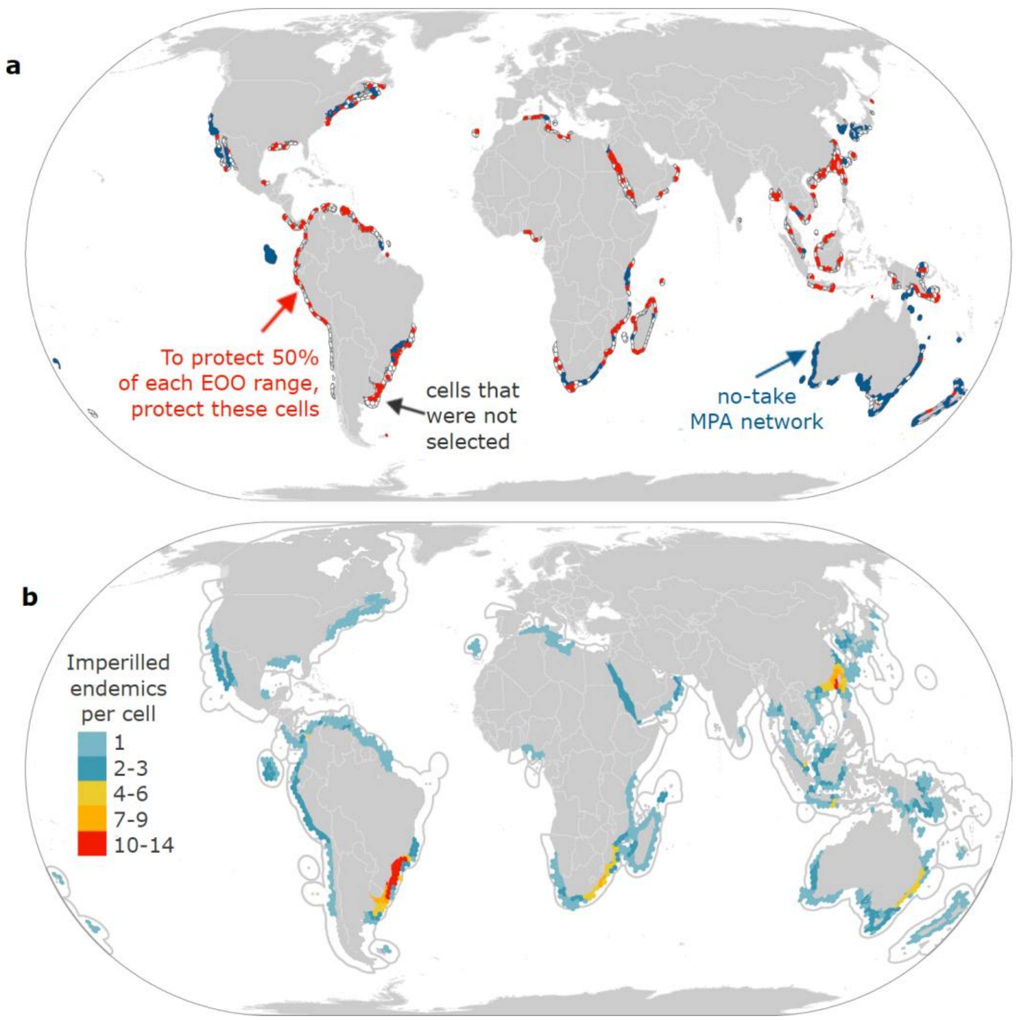

Figure 4.2 Spatial conservation options for two systematic conservation planning approaches. a, Species conservation targets; locations for MPA creation or expansion to protect 50% of the geographic range of all 99 imperilled endemic chondrichthyans (using Marxan): (red) planning units selected (white) planning units not selected, (blue) planning units currently designated as a no-take MPAs. b, Hotspots; global locations of the highest numbers of imperilled endemic chondrichthyans within a country's national waters (EEZ). Warm colours represent areas with high numbers of overlapping imperilled and endemic chondrichthyans, cool colours show where there are fewer numbers of species per cell. Hottest hotspot countries are those with between 4 -14 imperilled endemics per grid cell.

Covering half the 99 chondrichthyan species EOO, would require MPA expansion in 70 nations. Therefore, I ask: what narrower suite of countries could protect the greatest number of imperiled endemics? I found that focusing on hotspots of imperiled endemics (between 4-14 species per cell) narrowed the scope of conservation action to just 12 countries in four locations (Fig 4.2b, 4.3a): (1) eastern and northern South America (Columbia, Brazil, Uruguay, Argentina), (2) western Indian Ocean (South Africa, Mozambique), (3) western Pacific (Taiwan Province of China, Japan, China, and the Senkaku Island conflict zone between Taiwan Province of China, Japan, and China), and (4) the Indo-Pacific (Australia, Indonesia, Philippines). These 12 countries harbour over half of the imperiled endemics (n=53) and cover only 1.25% of global EEZ waters. Hotspot locations were robust to different definitions of endemism (Fig. S.6, S.7).

MPAs alone are likely not enough to secure the conservation of imperiled chondrichthyans, not least due to the median size of global MPAs is 3.3 km^{2}, (Boonzaier & Pauly 2015) and their average geographic range size is over half a million km^2 (Fig 4.1b). Assuming MPAs alone are insufficient, how can we improve fisheries and conservation management related activities in hotspot countries? I found that the implementation and strength of fisheries management is highly variable in these countries and reveal some simple steps that would support chondrichthyan conservation (Fig 4.3b, Table S.11). Of the 12 hotspot countries I identified as priorities, half have regulations to ban finning (cutting the fins off a shark and dumping the body overboard), but only four countries have the more comprehensive fins-attached regulation (shark brought back to port with fins naturally attached). Just over half (58%) of these hotspot countries have finalized a *Shark-Plan* (a non-binding plan to sustainably manage chondrichthyan fisheries), three of these countries have a *Shark-Plan* that meets greater than 50% of the objectives of sustainable fishing. Only two countries are signatory to the Convention on Migratory Species MoU Sharks agreement (CMS MoU *sharks* – a non-binding agreement to develop a conservation plan for listed species); six countries have taken meaningful steps towards curbing Illegal, Unreported, and

Unregulated fishing by becoming parties to the Port State Measures Agreement (PSMA), but only four ratified this critical agreement (Fig 4.3b). Finally, hotspot countries Brazil, Indonesia, Taiwan, and Argentina are among the top ten chondrichthyan fishing (Pauly & Zeller 2015) countries in the world (Fig 4.3c).

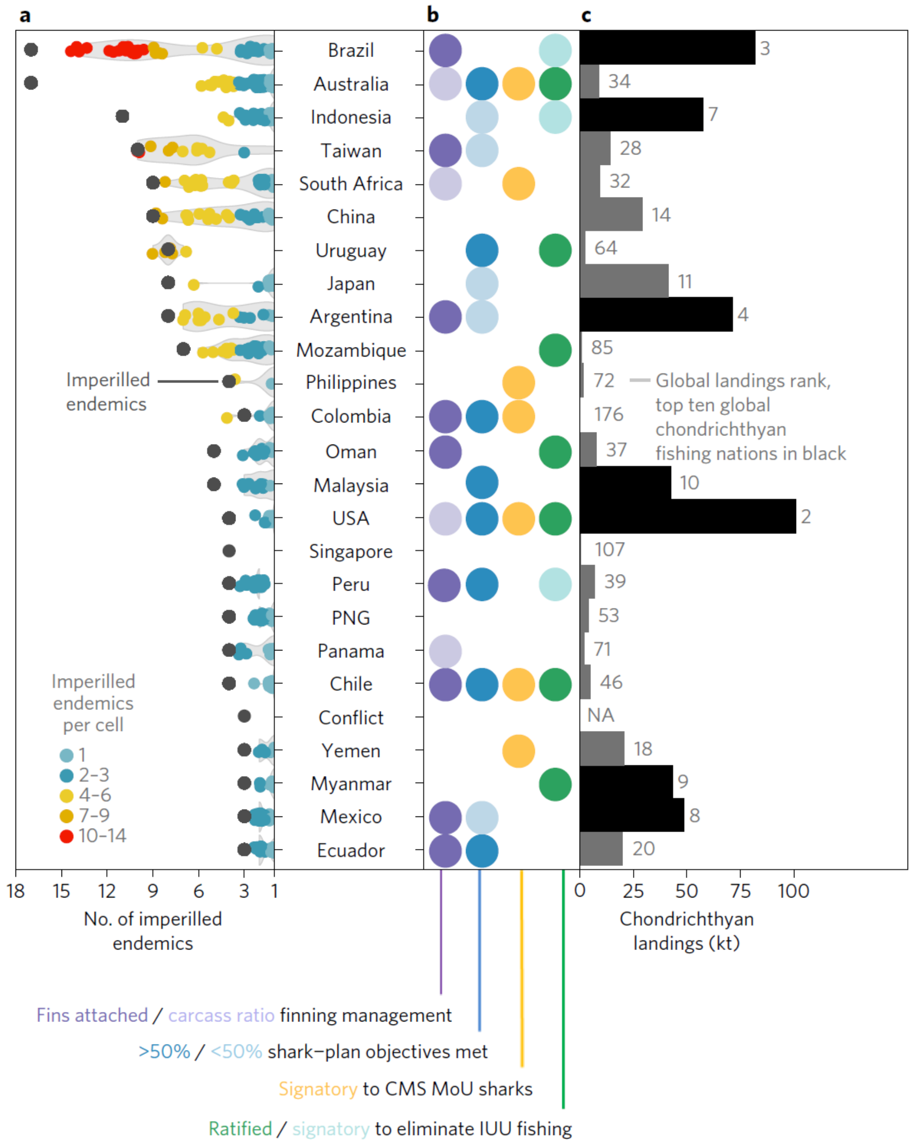

Figure 4.3 **Fisheries management and conservation needs beyond MPAs. a, The number of imperilled endemics in each country per cell (coloured points) and within the entire EEZ (black). b, Presence and strength of each of the fisheries management and conservation measures. Saturated colours across the four management measures represent a country (i) with the more desirable fins-attached regulation, (ii) an adequate Shark-plan, (iii) is a signatory to CMS MoU sharks, and (iv) has ratified the legally binding Port State Measures Agreement to deter Illegal, Unregulated, and Unreported fishing. c, Reported chondrichthyan landings (tonnes) from Sea Around Us Project catch reconstructions and the countries within the top ten chondrichthyan fishing nations in the world (black bars).**

What is the likelihood of conservation in each of the priority nations? I assessed the geopolitical realities that could influence conservation success in these 70 nations and distinguish four broad classes of interventions (Dickman et al. 2015; McClanahan et al. 2009). I created a composite conservation likelihood score from 10 national measures including governance, economics & welfare, fishing and human pressure (Fig 4.4, Table S.12). I found Australia, South Africa, and the United States have relatively higher conservation likelihood scores and management but also a high percent of planning units selected for MPA creation. In these countries, conservation and management action may be more successful (Fig 4.4 [1]). Despite having relatively high conservation likelihood scores, Panama, and Japan have relatively low chondrichthyan fisheries and conservation management (Fig 4.4 [2]). Argentina, and Brazil have high conservation value (high numbers of imperiled endemics and planning units selected for MPA expansion) but low conservation likelihood scores and hence conservation actions could be enabled with further capacity building. Malaysia, Papua New Guinea, Mozambique, and Indonesia have opportunity for expanding conservation action (fisheries and conservation management, as well as MPA expansion) but require considerable relief and reorganization to enable this transition. While China presents a unique conservation challenge with nine imperiled endemics and little evidence of chondrichthyan fisheries and conservation management (Fig 4.4 [4]).

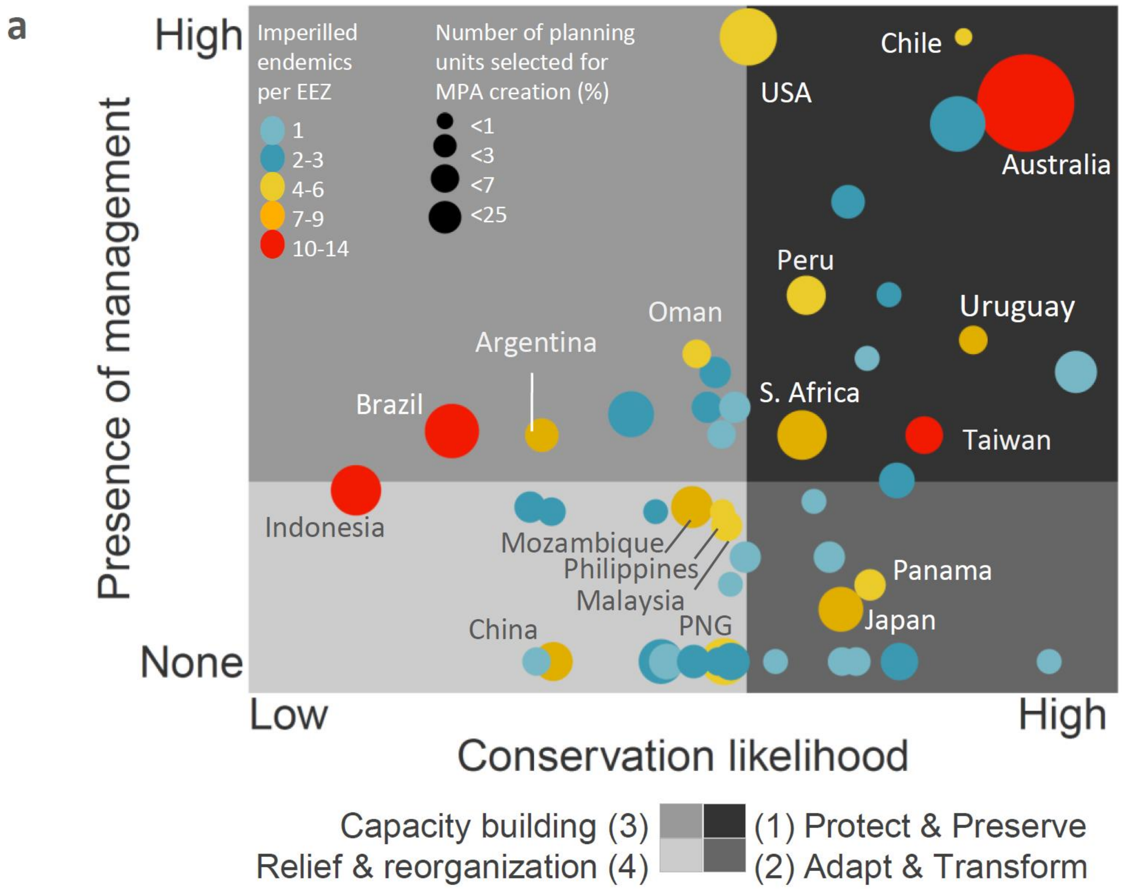

Figure 4.4 **Priority countries, conservation likelihood, and the presence and strength of the chondrichthyan management. Quadrants are delimited by the median index scores. Conservation and management action is more feasible in countries with relatively higher conservation likelihood scores (quadrant 1). Conservation value is represented by the combination of the percentage of Marxan planning units identified for MPA expansion (radius of each point; from Figure 4.2a), and the number of imperilled endemics (point colour; from Figure 4.2b) within that country's national waters.**

4.5. Discussion

Area-focused protection goals galvanized rapid gains in MPAs over the past decade (Lubchenco & Grorud-Colvert 2015; Boonzaier & Pauly 2015; Wood et al. 2008; Devillers et al. 2014; Jones & Santo 2016). Yet, I find that this approach has failed to protect those imperiled endemic chondrichthyan species most in need of conservation action. I found that a reconfiguration could ensure future MPAs contribute to avoiding extinctions - similar to the approach taken by the Alliance for Zero Extinction to focus effort on terrestrial species (Butchart et al. 2012; Venter et al. 2014). Further, only a small fraction (0.9%) of the global MPA network is fit for the purpose of avoiding extinctions for chondrichthyans, therefore, new MPA designations could include a higher fraction of strictly enforced no-take areas (Gell & Roberts 2003; Edgar et al. 2014; Watson et al. 2014; Costello & Ballantine 2015). This could be complimented by widespread fisheries management improvements to minimize mortality on threatened species and ensure sustainability of others (Wiegand et al. 2011).

The greatest challenge is to secure fisheries and conservation improvements in counties with lower conservation likelihood and hence adaptive capacity (Allison et al. 2009). Climate change has led to a massive engagement of aid and development organizations to enable coastal adaptation. Following this template, there is a clear need to mainstream fisheries management and marine conservation within development aid, poverty alleviation, and adaptation activities (McClanahan et al. 2009; Turner et al. 2003; Allison et al. 2009).

4.6. Supplemental material C

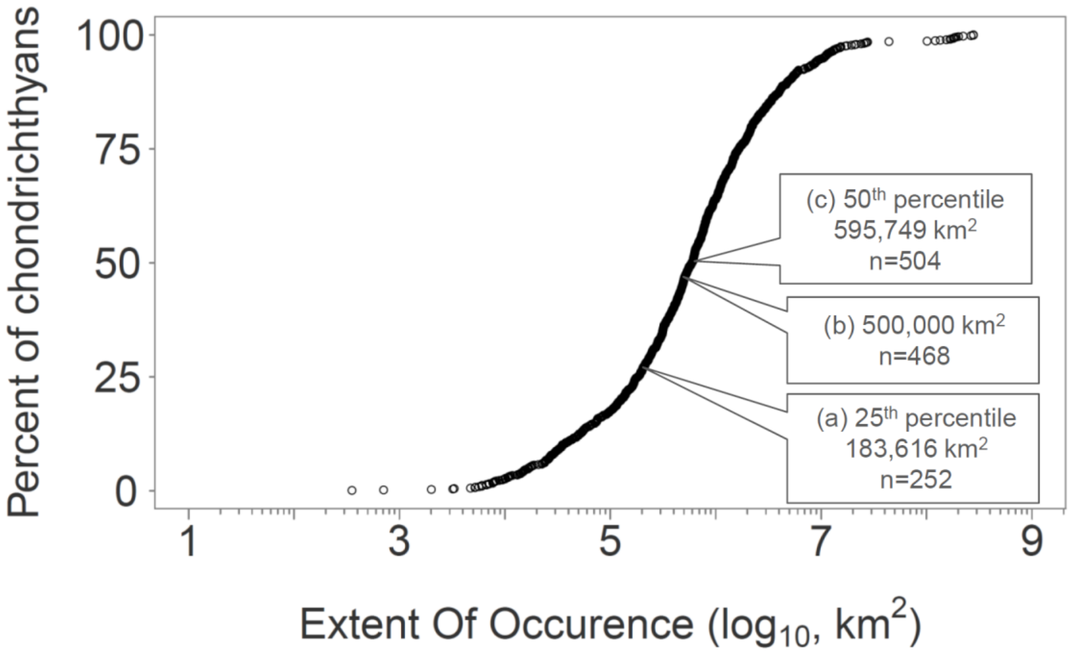

Figure S.6 **Extent Of Occurrence (EOO) geographic range area curve for all 1,007 marine chondrichthyan species and endemic definition cutoffs. Call-outs demark the subset of the data for my three definitions of endemism. a, 25^{th} percentile (183,616 km^2), b, 500,00 km^2, and c, 50^{th} percentile (595,749 km^2). Irrespective of IUCN threat category, 252, 468, and 504 species fall under the three definitions respectively.**

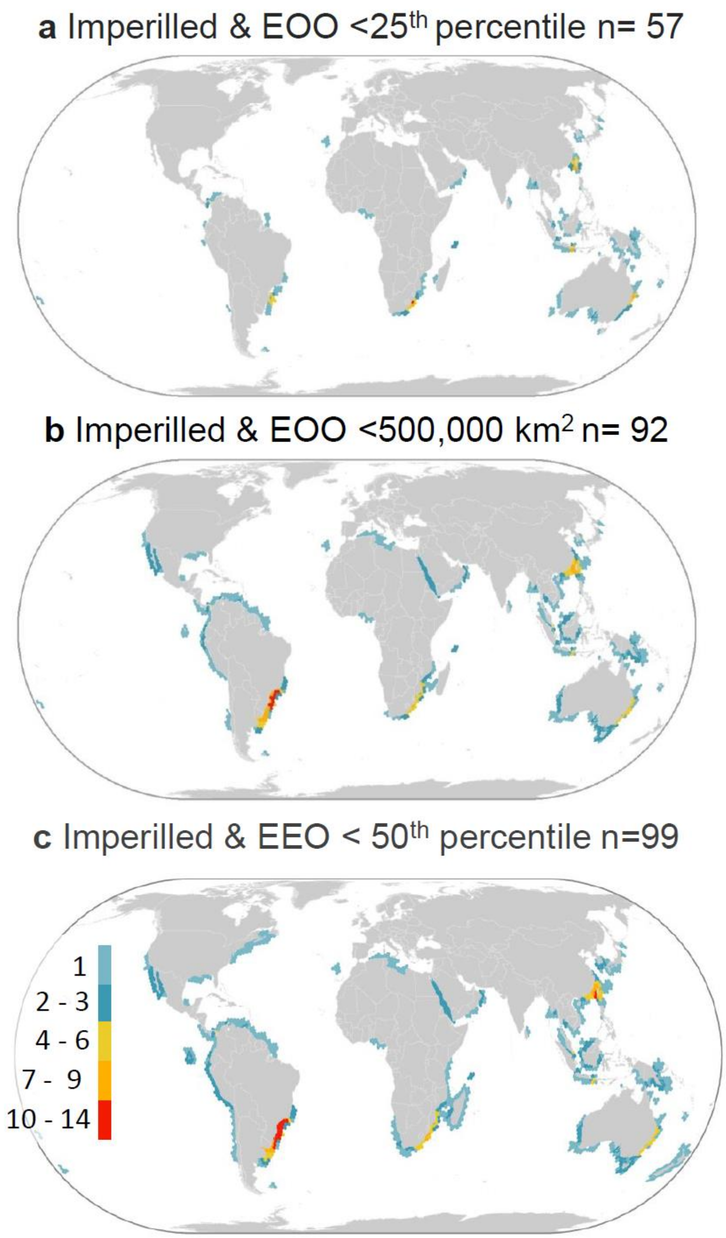

Figure S.7 **Distribution of hotspot for the three endemic definitions. Hotspot locations for imperilled endemics with distributions less than or equal to the a, 25th percentile, b, 500,000 km² and c, 50th percentile.**

Table S.9. Protected area name, country of origin, and amount of coverage for the 12 imperiled endemic species with at least 10% of their EOO within MPAs or marine reserve (no-take and IUCN protected area category 1a). Also included are the ten species with between 1-8% of their EOO within MPAs. For display purposes, only those entries with values greater than one percent are shown.

Country	MPA name	No-take status (Part or All)	IUCN MPA category	Species name	IUCN Red List category	EOO area (km2)	% EOO protected
Australia	Abrolhos	Part	VI	*Orectolobus hutchinsi*	DD	18,512	8
Australia	Abrolhos	Part	VI	*Orectolobus parvimaculatus*	DD	18,512	18
Australia	Central Eastern	Part	IV	*Brachaelurus colcloughi*	VU	2,619	2
Australia	Central Eastern	Part	IV	*Dipturus australis*	VU	2,664	2
Australia	Central Eastern	Part	IV	*Urolophus bucculentus*	VU	4,225	2
Australia	Central Eastern	Part	IV	*Urolophus sufflavus*	VU	2,622	2
Australia	Coral Sea	Part	II	*Brachaelurus colcloughi*	VU	8,821	6
Australia	Coral Sea	Part	II	*Cephaloscyllium zebrum*	DD	18,310	100
Australia	Coral Sea	Part	II	*Hemiscyllium hallstromi*	VU	6,351	2
Australia	Coral Sea	Part	II	*Parmaturus bigus*	DD	6,064	100
Australia	Eastern Recherche	Part	II	*Asymbolus funebris*	DD	9,889	18
Australia	Flinders	Part	VI	*Urolophus bucculentus*	VU	4,059	1
Australia	Freycinet	Part	VI	*Urolophus bucculentus*	VU	6,033	2
Australia	Freycinet	Part	VI	*Urolophus viridis*	VU	4,579	1
Australia	Great Barrier Reef	Part	VI	*Brachaelurus colcloughi*	VU	44,598	28
Australia	Hamelin Pool	All	Ia	*Orectolobus parvimaculatus*	DD	1,117	1
Australia	Jurien	Part	VI	*Orectolobus parvimaculatus*	DD	1,851	2
Australia	Moreton Bay	Part	IV	*Brachaelurus colcloughi*	VU	3,247	2
Australia	Moreton Bay	Part	IV	*Dipturus australis*	VU	2,720	2
Australia	Moreton Bay	Part	IV	*Myliobatis hamlyni*	EN	1,040	7
Australia	Moreton Bay	Part	IV	*Urolophus sufflavus*	VU	1,685	1
Australia	Murray	Part	II	*Urolophus orarius*	EN	6,066	4
Australia	Perth Canyon	Part	VI	*Orectolobus hutchinsi*	DD	3,241	1
Australia	Perth Canyon	Part	VI	*Orectolobus parvimaculatus*	DD	1,041	1
Australia	Shark Bay	Part	VI	*Orectolobus hutchinsi*	DD	6,692	3
Australia	Shark Bay	Part	VI	*Orectolobus parvimaculatus*	DD	6,124	6

Country	MPA name	No-take status (Part or All)	IUCN MPA category	Species name	IUCN Red List category	EOO area (km2)	% EOO protected
Australia	South-west Corner	Part	II	*Asymbolus funebris*	DD	1,382	2
Australia	South-west Corner	Part	II	*Bathyraja ishiharai*	DD	14,211	47
Australia	South-west Corner	Part	II	*Orectolobus hutchinsi*	DD	14,741	7
Australia	Tasman Fracture	Part	VI	*Urolophus bucculentus*	VU	10,014	4
Australia	Tasman Fracture	Part	VI	*Urolophus viridis*	VU	10,368	3
Australia	West Cape York	Part	VI	*Brachaelurus colcloughi*	VU	11,341	7
Australia	Western Eyre	Part	VI	*Urolophus orarius*	EN	27,835	16
Australia	Western Kangaroo Island	Part	VI	*Urolophus orarius*	EN	2,335	1
Ecuador	Galapagos Marine Reserve	Part	VI	*Heterodontus quoyi*	DD	44,016	15
Ecuador	Galapagos Marine Reserve	Part	VI	*Triakis maculata*	VU	137,204	26
Mexico	El Vizcaíno	Part	VI	*Zapteryx exasperata*	DD	3,244	1
Mozambique	Bazaruto	Part	Not Reported	*Paragaleus leucolomatus*	DD	1,220	2
New Caledonia	Natural Park of the Coral Sea	Part	VI	*Aulohalaelurus kanakorum*	VU	8,803	56
New Zealand	Kermadec	All	Ia	*Squalus raoulensis*	DD	66,831	90
New Zealand	Kermadec Islands	All	Ia	*Squalus raoulensis*	DD	7,526	10
South Africa	Pondoland	Part	IV	*Electrolux addisoni*	CR	1,214	4
South Africa	Pondoland	Part	IV	*Scylliogaleus quecketti*	VU	1,214	1

Table S.10. Differences in EOO area protection across three subsets of the MPA data: (1) 24 species have greater than 10% of their range protected when all areas (n=12,582) designated with any protection such as shellfish management or sites of cultural importance are considered, (2) 12 species have greater than 10% of their range protected when those sites designated as no-take (part or all) or any IUCN protected area category (1a-VI or not reported) and those areas designated exclusively for shark conservation (n=15) are considered, and (3) 12 species have greater than 10% of their range protected when those areas designated as no-take (part or all) or any IUCN protected area category (n=973) are considered.

Common Name	Binomial	IUCN Red List status	(1) % of EOO in any MPAs (n=12,582)	(2) % EOO in no-take MPAs and those designated exclusively for sharks (n=988)	(3) % EOO in no-take MPAs (n=973)
Narrowbar Swellshark	*Cephaloscyllium zebrum*	DD	100	100	100
Beige Catshark	*Parmaturus bigus*	DD	100	100	100
Kermadec Spiny Dogfish	*Squalus raoulensis*	LC	100	100	100
New Caledonia Catshark	*Aulohalaelurus kanakorum*	VU	59	56	56
Abyssal Skate	*Bathyraja ishiharai*	DD	47	47	47
Bluegrey Carpetshark	*Brachaelurus colcloughi*	VU	43	40	40
Dwarf Spotted Wobbegong	*Orectolobus parvimaculatus*	DD	37	30	30
Spotted Houndshark	*Triakis maculata*	VU	26	26	26
Western Wobbegong	*Orectolobus hutchinsi*	DD	32	23	23
Coastal Stingaree	*Urolophus orarius*	EN	36	21	21
Blotched Catshark	*Asymbolus funebris*	DD	20	20	20
Galapagos Bullhead Shark	*Heterodontus quoyi*	DD	16	15	15
Yellowback Stingaree	*Urolophus sufflavus*	VU	13	0	0
Greenback Stingaree	*Urolophus viridis*	VU	14	0	0
Sydney Skate	*Dipturus australis*	VU	15	0	0
Sandyback Stingaree	*Urolophus bucculentus*	VU	17	0	0
Horn Shark	*Heterodontus francisci*	DD	18	0	0
Maltese Skate	*Leucoraja melitensis*	CR	24	0	0
Wedgefish spp.	*Rhynchobatus sp. nov. A*	VU	25	0	0
Southern Fiddler Ray	*Trygonorrhina melaleuca*	EN	42	0	0
Winter Skate	*Leucoraja ocellata*	EN	44	0	0
Spotted Shovelnose Ray	*Aptychotrema timorensis*	VU	44	0	0
Maugean Skate	*Zearaja maugeana*	EN	54	0	0
Gulf of Mexico Smoothhound	*Mustelus sinusmexicanus*	DD	58	0	0

Table S.11. Descriptions of fisheries and conservation management measures considered.

Variables	Definition
Finning ban	*Finning* regulation is an enabling step towards better management and regulates the act of cutting off a shark or ray's fins and then dumping the body overboard. Strength of fin ban refers to type of regulation where fins-attached is more enforceable than fin-to-carcass ratio which is better than no regulation.
Shark-Plans (National Plans of Action for sharks)	*Shark-Plans* is a document that all chondrichthyan nations were recommended to develop that outlines how they will sustainably manage and prevent extinctions of chondrichthyans species in their national waters. Strength refers to how well the document met the FAO recommended 10 objectives of sustainable fishing
Convention of Migratory Species Memorandum of Understanding (CMS MoU)	CMS MoU for sharks is a non-legally binding international agreement that currently lists 29 chondrichthyan species on Annex 1 which aims to achieves to maintain a favourable conservation status for listed species.
Port State Measures Agreement (PSMA)	A legally binding agreement whereby countries aim to prevent, deter, and eliminate Illegal, Unreported, and Unregulated fishing. Countries have signed or ratified the PSMA. PSMA was initiated in year 2009.
Sea Around Us catch reconstructions	Reconstructed chondrichthyan catches (tonnes) per country

Table S.12. Ten variables in three broad category classes included in the conservation likelihood score (adapted from Dickman et al. 2015). Variables for each category were standardized and summed. Final score was calculated as the mean of the summed variables for each category.

Category	Variable	Direction and justification	Source
Governance	Political stability	Positive - political instability diverts attention from conservation, limits the will to work in that country and inhibits long-term planning	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
	Government effectiveness	Positive - effective governments are important for meaningful conservation	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
	Control of corruption	Positive - corruption restricts investment and distorts priorities	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
	Regulatory quality	Positive - need to implement and regulate sound conservation policies	World Bank Group: Governance Matters VIII 2011 database http://databank.worldbank.org/data/views/variableselection/selectvariables.aspx?source=worldwide-governance-indicators
Economics and welfare	GDP (Gross Domestic Product) per capita	Positive - allows a focus on conservation rather than urgent issues such as food security	World Bank's World Development Indicators for 2011 http://data.worldbank.org/data-catalog/world-development-indicators
	PPP (Purchasing power parity)	Positive - the local buying power of the US dollar affects operational costs of conservation	World Bank's World Development Indicators for 2011 http://data.worldbank.org/data-catalog/world-development-indicators
	Human Development Index	Positive - people are more likely to support and engage in conservation	FAO Aquastat http://www.fao.org/nr/water/aquastat/main/index.stm
Human pressure	Annual human population growth	Negative - high growth rates place pressure on resources	World Bank's World Development Indicators for 2011 http://data.worldbank.org/data-catalog/world-development-indicators

Category	Variable	Direction and justification	Source
	Coastal human population	Negative – higher coastal population places pressure on resources	Center for International EarthScience Information Network (CIESIN) http://sedac.ciesin.columbia.edu/data/set/nagdc-population-landscape-climate-estimates-v3
	Sea Around Us chondrichthyan landings	Negative – higher landings represent greater pressures on population	D. Pauly and D. Zeller, editors. 2015. Catch Reconstruction: concepts, methods and data sources. Online Publication. Sea Around Us (www.seaaroundus.org). University of British Columbia

Table S.13. Priority countries, number of imperiled endemic chondrichthyan species, and country specific fin exports to Hong Kong (2011), meat exports, and mean imports as reported to the FAO.

Country	Number of imperilled endemics within country's EEZ	Fin exports to Hong Kong in 2011 (kg)	FAO meat exports (2009, tonnes)	FAO meat imports (2009, tonnes)
Australia	17	65,575	66	554
Brazil	17	133,297	0	21,231
Indonesia	11	805,919	1,425	85
Taiwan	10	922,272	23,054	3,629
China	9	9,368	984	5,666
South Africa	9	109,594	1,822	663
Argentina	8	190,538	3,631	0
Japan	8	209,204	5,399	617
Uruguay	8	30,402	17,223	21,717
Mozambique	7	5,528	0	0
Malaysia	5	28,199	33	96
Oman	5	12,402	35	6
Chile	4	28,523	1,810	0
Panama	4	36,943	5,190	53
Papua New Guinea	4	16,579	0	0
Peru	4	198,877	1,492	2,910
Philippines	4	35,062	45	481
Singapore	4	1,091,803	3,820	3,943
United States	4	253,303	639	306
Colombia	3	32,137	0	511
Conflict Zone Senkaku Island	3	NA	NA	NA
Ecuador	3	206,926	5	0
Mexico	3	319,244	322	3,546
Myanmar	3	NA	NA	0
Yemen	3	422,498	110	10
Chile/Peru	2	NA	NA	NA
Djibouti	2	NA	NA	NA
Egypt	2	16,356	1	9
Eritrea	2	NA	NA	NA
Galapagos Islands	2	NA	NA	NA
Grenada	2	NA	NA	NA
Madagascar	2	21,757	4	0
New Zealand	2	153,664	2,489	0
Saudi Arabia	2	3,906	10	0
Seychelles	2	5,224	1	NA
South Korea	2	112,471	1,581	21,063
Sudan	2	460	NA	NA
Thailand	2	33,098	1,095	217
Venezuela	2	20,956	NA	467
Vietnam	2	9,900	700	900

Chapter 5. Where are the taxonomic and phylogenetically distinct marine regions of Chondrichthyes?[4]

5.1. Abstract

Over a hundred years ago, the naturalist and biogeographer Wallace divided the terrestrial world into six realms based on his observations of species assemblages between regions. A century later, quantitative research has upheld Wallace's qualitative observations and has shown that ten realms of distinct terrestrial assemblages of species exist. Additionally, by incorporating phylogenetic relationships into a biogeographic framework, recent analyses determined global realms of distinct biota, notably in Australia, Madagascar, and South America. While there are numerous oceanographic and habitat-based delineations, opportunities for defining the global biogeographic patterning of the ocean's biological diversity remain. Therefore, using the distribution of sharks and rays (Class Chondrichthyes) I ask a fundamental question in biogeography: where are the distinct faunal regions in the ocean? For the analysis, I used distribution data and a completed phylogenetic tree for 457 sharks (9 orders from the Superorder Squalomorphii and Galeomorphii) and 539 ray species (four orders from the one Superorder: Batoidea). I used multivariate analyses with data generated from a species presence matrix spanning the world's coastal and continental oceans. I determined that there are 23 zoogeographic (B_{sim}) and 10 phylogenetic (pB_{sim}) regions in the ocean for sharks and at least 23 and 11, respectively, for rays. The shark phylogenetic analysis divides the world's oceans first into (1) tropical and (2) temperate regions which are then further subdivided into (1) northern and southern sub-tropics, (2) northern and southern temperate zones, (3) western Atlantic and Pacific tropics, (4) Indo-west Pacific tropics, and

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[4] A version of this chapter is in preparation for publication with; Mazel, F. Mull, CG. Dulvy, NK. Many thanks to Vanessa Guerra and Dan A. Greenberg for help with CEDAR and R code in this chapter.

(5) western Africa. There are less distinct regions in (6) north and south sub-tropical limits, and (7) around archipelagos such as the Philippines, northern Madagascar, Seychelles, Canary Islands, and Azores. The phylogenetic analysis of rays divides the world's oceans into tropical regions: (1) Indo-West Pacific, and (2) tropical Atlantic and eastern Pacific, and then sub-tropical/temperate regions: (3) southern and northern temperate seas, and (4) southern sub-tropical (Australia), (5) freshwater South America, (6) subtropical limit (South Africa), and northern sub-tropical limit (Japan). Further work will need to investigate the mechanisms that delineate the faunal breaks for both the zoogeographic and phylogenetic regions I identified here.

5.2. Introduction

Past continental configurations may have acted as barriers to, or facilitated, species dispersal resulting in present day species assemblages that are more or less related than might be estimated based on current-day geographic distance alone (Lomolino et al. 2006). Defining and understanding zoogeographic regions, i.e., geographic patterns of similarity of species assemblages, might help elucidate these historical processes. Traditionally, zoogeographic regions were defined using expert opinion. For example, Alfred Wallace described the faunal boundary, now known as Wallace's Line, separating Asiatic and Australian species. Here, marsupials, many birds, and bats are found on one side of Wallace's line or the other, but not on both (Wallace 1876). Wallace also defined the six globally distinct terrestrial realms based on his knowledge of geographic ranges of the world's land species (Wallace 1876). Recently, using a measurement of beta diversity to estimate taxonomic assemblage turnover coupled with multivariate statistical analyses, Wallace's zoogeographic realms were upheld, with small changes to the exact location of Wallace's line (Holt & Lessard et al. 2013). These new multivariate techniques are providing quantitative lines of evidence to define zoogeographic regions, which can then be used to infer or test historical hypotheses relating to species distribution, evolution, and ecology (Kreft & Jetz 2010).

There are numerous ocean-wide delineations that mostly use physical and biological oceanographic features, rather than taxonomic distributions. None has yet incorporated phylogenetic information. For example, marine provinces were defined by Briggs (1974) as shallow endemic-rich areas with at least 10% endemic fish and in depths less than 200 metres. Longhurst provinces were categorized based on abiotic measures such as wind and water movements (Longhurst 1995). Marine Ecosystems of the World (MEOW) used expert opinion to reconcile many regionalization schemes to categorize the coastal and continental shelf at less than 200 m depth (Spalding et al. 2007). Finally, Large Marine Ecosystems (LMEs) are characterized by distinct bathymetry, hydrography, productivity and trophic interactions (www.lme.noaa.gov). A recent analysis incorporated quantitative measurements of species assemblage turnover using the distribution of 65,000 marine species and defined the global oceans into 30 distinct realms (Costello et al. 2017). This analysis provided support for many of the regions previously classified, as mentioned above, including matching nine of Spalding's 11 realms (Costello et al. 2017).

There are key historical events that have influenced the current-day distribution of marine species (Fig. 5.1). For example, 250 MYA there was one great ocean called Panthalassa; 180 MYA the supercontinent Pangea began to separate; 120 MYA the tropical Tethyan seaway divided Laurasia and Gondwanaland and connected oceans east to west. The Atlantic Ocean began opening 84 MYA, with the separation of Africa and South America (Gondwanaland); followed by the Weddellian Province (Antarctica, South America, and Australia) began to break-up 80 MYA. The Red Sea land bridge closed off the Tethyan seaway between the tropical faunas of the Indian Ocean and the Atlantic in 12-18 MYA, and finally

3.1 MYA the Isthmus of Panama closed (Kulbicki et al. 2013a; Lomolino et al. 2006).

There are numerous analyses of small radiations, e.g., littorinid snails, coral reef fish, and skates (Cowman et al. 2017; McEachran & Miyake 1990; Kulbicki et al. 2013b; Zinsmeister 1982). However, a global zoogeographic and phylogenetic analysis has yet to be completed for any major taxonomic group. Here, I determined the marine taxonomic and phylogenetic regions using a Class of marine vertebrates that are globally distributed and have a complete phylogeny. Chondrichthyes are one of three Classes of fishes and are among the oldest and most evolutionarily distinct vertebrate lineages; they are also fully aquatic and are found throughout the world's coastal seas and open oceans. I analyzed both taxonomic and phylogenetic beta diversity (phylogenetic turnover, pB_{sim}) in order to quantitatively delineate ecosystems based on shared taxonomic and phylogenetic distance, respectively (Graham & Fine 2008). I asked three questions. (1) Where are the taxonomically distinct regions? (2) Where are the phylogenetically distinct regions? Finally, (3) what are the species that characterize these regions? I believe this analysis is a step towards describing historical processes that may have shaped current-day patterns of shark and ray biodiversity.

5.3. Methods

5.3.1. Geographic ranges of sharks and rays

I used geographic range maps for Chondrichthyan species from the International Union for the Conservation of Nature (IUCN) (IUCN 2015). These maps are peer-reviewed Extent of Occurrence (EOO) geographic ranges, which are likely to include commission rather than omission errors (Rodrigues 2011). To visualize species distributions, phylogeny, and historical processes, I plotted species richness patterns of all 13 Elasmobranchii Orders (Table S.14).

I analysed sharks and rays separately as their lineages diverged early, (approximately 230 MYA) soon after the origination of Chondrichthyes 430 MYA, (Stein & Mull et al. 2018) (Figure 5.1) and, additionally, due to potential differences between shark and ray range sizes and dispersal ability. To understand if range size differences between sharks and rays influenced number of regions, I calculated the area of each species' EOO, using Cylindrical Equal Area projection, for sharks (Superorders: Galeomorphii and Squalomorphii) and rays (Superorder: Batoidea).

5.3.2. Phylogenetic data

I used the completed Chondrichthyan phylogenetic tree from Stein & Mull et al. (2017). Due to the computationally expensive nature of this analysis, I used one tree (see Table S.14 for variability in node ages of Orders using 100 randomly selected trees). The Order with the greatest node age variability was Echinorhiniformes (Bramble sharks, two species), with a mean node age of 121.26 (SD 46.5 MYA, Table S.14). I believe the results are not affected by the tree variability given that species without DNA sequence data or species with low node support were constrained to placement within their genus as defined by the IUCN (www.iucnredlist.org) or based on taxonomy from the Chondrichthyan Tree of Life (http://vertlife.org/sharktree) (Stein & Mull et al. 2018).

I removed the 17 wide-ranging, ocean-spanning species (consisting of: three Carcharhiniformes, 12 Lamniformes, one Orectolobiformes, one Squaliformes and three pelagic ray species: *Mobula birostris*, *Mobula alfredi*, and *Aetobatus narinari*). These species were not included, as the comparatively low species richness of pelagic areas would obscure the coastal and continental patterning. Additionally, although the phylogenetic tree consists of 1,077 Chondrichthyan species, distribution data were not available for all these species. My analysis therefore included those 457 shark species (Superorders Galeomorphii and

Squalomorphii) and 539 rays species (Superorder Batoidea, hereafter termed rays) with both phylogenetic and distribution data (IUCN, 2015; Stein & Mull et al. 2018).

5.3.3. Species presence and global grid

I divided the global ocean into two-degree, 3,429 hexagonal grid cells (~49,453 km^2) spanning both freshwater and coastal continental shelf marine areas, following methods in Holt & Lessard et al. (2013). I used *spatial join* within ArcGIS (version 10.3) to create a matrix of grid cell identification and species presence and absence. I created a pairwise, symmetrical matrix consisting of species and cell identification.

5.3.4. Beta diversity calculation

I used Simpson's beta diversity dissimilarity equation (B_{sim}, hereafter called taxonomic turnover) to calculate beta diversity and quantify change in taxonomic composition among species assemblages globally. This equation calculates the turnover portion of beta diversity, meaning that assemblages representing a high turnover of species are identified rather than assemblages that are nested (Baselga 2010). This equation has been used in recent terrestrial biogeographic analyses (see Holt & Lessard et al. 2013):

$$Bsim = 1 - \left(\frac{a}{\min(b,c) + a}\right)$$

where *a* is the number of species shared between two grid cells, and *b* and *c* are the number of species unique to each grid cell. Hence, a taxonomic turnover value of one represents cells with no shared species and therefore very high turnover consistent with a faunal break, while a low score represents high fauna similarity between two cells. This approach, however, ignores the detail of how closely or distantly related species are.

To capture evolutionary relationships, I used the same equation as above to calculate phylogenetic beta diversity ($pB_{sim},$ hereafter termed phylogenetic turnover). This equation quantifies the evolutionary dissimilarity of species assemblages by using Faith's metric of Phylogenetic Diversity (PD): the sum of branch lengths along a minimum spanning path on the phylogenetic tree (Faith 1992), where *a* is the sum of branch lengths that are shared between two grid cells, and *b* and *c* are the total length of phylogenetic branches unique to each grid cell. Therefore, a phylogenetic turnover value of one represents cells with no shared evolutionary history (i.e., areas of distantly or unrelated species) and, therefore, very high phylogenetic turnover, while a low score represents high shared evolutionary history. This methodology is different from Holt & Lessard et al. (2012) who, due to data availability constraints, used number of shared branches, as opposed to branch lengths, to calculate pB_{sim}.

5.3.5. Defining zoogeographic regions through hierarchical agglomerative clustering

To delineate taxonomic and phylogenetic regions, I used agglomerative hierarchical clustering, which aggregates grid cells with low dissimilarity and successively increases membership across homogeneous (low B_{sim} or $p\mathrm{B}_{sim}$) regions (Swenson 2014). I used a hierarchical approach to make inferences about relationships between clusters. There are seven linkage methods: unweighted pair group method using arithmetic averages (UPGMA), unweighted pair group method using centroids (centroid), weighted pair group method using arithmetic averages (McQuitty's), weighted pair group methods using centroids (median), Ward's method (minimum variance), single linkage (nearest neighbour) and complete linkage (furthest neighbour). They each calculate a new distance value between grid cells differently (Holt et al. 2013; Kreft & Jetz 2010; Swenson

2014). Therefore, to assess the fit of the resulting dendrogram, I correlated the original pairwise taxonomic and phylogenetic turnover matrix with the merging distances (dendrogram) calculated from each of the eight linkage methods. The resulting output, termed cophenetic distance correlation, is therefore an indication of fit, with a higher score indicative of a linkage method that produced a dendrogram highly correlated with the original data. All analyses were performed in R core team (2013) using the `dendextend` (Galili 2015), `tidyr` (Wickham & Henry 2018), `GMD` (Zhao et al. 2011; Zhao & Sandelin 2014) and `factoextra` (Kassambara & Mundt 2017) packages.

5.3.6. Linkage method and clustering diagnostics

Across all four analyses, the UPGMA linkage method had the highest cophenetic coefficient value, meaning that the resulting dendrogram best preserved the original information, similar the findings of other zoogeographical analyses (Kreft & Jetz 2010; Holt & Lessard et al. 2013). I found the cophenetic correlation coefficient for the UPGMA method across all four analyses to be: shark B_{sim} = 0.68, shark pB_{sim} = 0.60, ray B_{sim} = 0.72, ray pB_{sim} = 0.63.

5.3.7. Defining zoogeographic regions – number of clusters

To determine the number of clusters, I adopted an approach that focuses on maximizing the explained variance between clusters and minimizing the number of clusters. I sought to determine the number of clusters that explained 99% of the variation (Holt & Lessard et al. 2013). I choose a maximum of 50 clusters in order to generate patterns that are generalizable (Holt & Lessard et al. 2013). For all of the analyses, explaining 99% of the variation was not possible with fewer than 50 clusters. Therefore, I selected either 50 clusters, or the number of clusters where there was an increase in explained variance before the asymptote as, at this point, adding more clusters had diminishing returns with respect to explained variance (Salvador & Chan 2004). Cells that were assigned to a cluster with ≤10 grid cells in its membership were reassigned into the next closest cluster to create patterns that are generalizable (following Holt & Lessard et al. 2013).

5.3.8. Describing the spatially dominant species within each of the clusters

To characterize the species assemblages within the distinct phylogenetic regions I determined the wide-ranging species within each cluster. I chose those species that were present across the greatest number of cells within each cluster.

5.4. Results

5.4.1. Geographic range sizes of sharks and rays

Considering all species, the smallest range in the database is that of *Zearaja maugeana,* with a range size of 354 km^2, and the largest belongs to *Manta birostris* ($1.81*10^6$ km^2). As a group, skates and ray (n = 539 species, excluding pelagics) have a mean EOO area of 806,764 km^2, with a median of 276,536 km^2. For sharks, the smallest range in the database is that of *Atelomycterus baliensis* (258 km^2) and the largest is that of *Prionace glauca* ($2.78*10^8$ km^2). The mean EOO area (n = 457 species, excluding pelagics) is 2,352,304 km^2, with a median of 612,943 km^2.

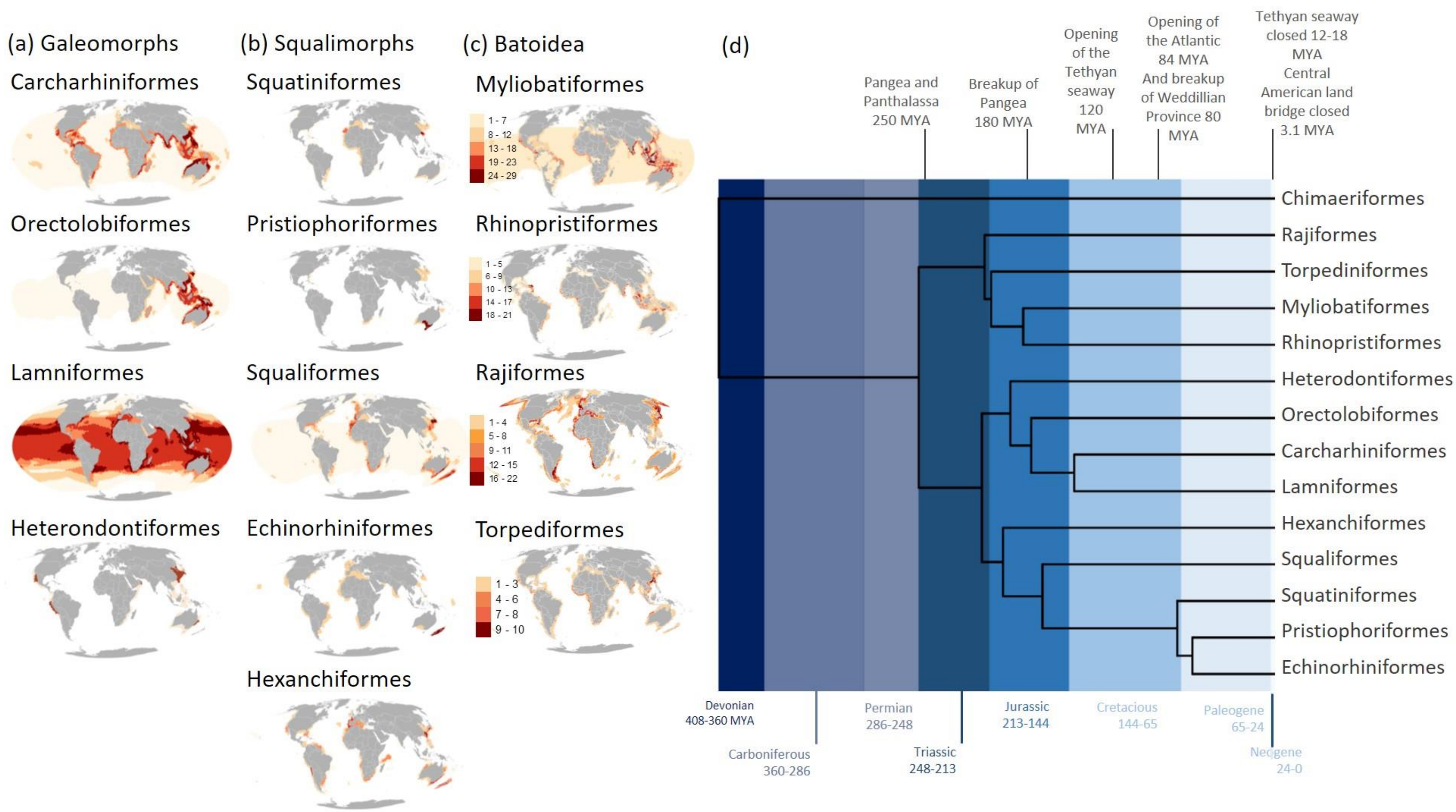


Figure 5.1 **Spatial and evolutionary data for sharks (a-b) and rays (c). Richness gradients of current-day species of (a) Galeomorphii, (b) Squalimorphii, and (c) Batoidea. (d) Geologic time scales and shark and ray Orders with historical geological events.**

5.4.2. Cluster selection

The optimal number of clusters, hereafter regions, varied across each analysis. The shark pB_{sim} analysis has the greatest amount of explained variance for the fewest regions (76% explained variance with 12 regions) while ray B_{sim} has the lowest explained variance, 57%, and the highest number of regions, 50. The shark B_{sim} analysis has more than three times the number of regions compared to phylogenetic shark regions ($p\mathrm{B}_{\mathrm{sim}}$): shark B_{sim} was divided into 41 regions, which explains 64% of the total variation (Fig S.8). Ray pB_{sim} was divided into 18 regions, explaining 73% of the total variation.

Eighteen of the 41 shark B_{sim} clusters had fewer than 10 cells; they were therefore reassigned to their closest branch, leaving 23 regions in total. For ray B_{sim}, I selected 50 regions that explained 57% of the variation; however, 28 of the regions had fewer than 10 cells and were reassigned to their closest branch, leaving 23 regions. Shark pB_{sim} had 12 regions, with two having fewer than 10 cells leaving ten regions all together. Finally, seven of the 18 ray pB_{sim} had fewer than 10 cells and were therefore reassigned to their closest branch, leaving 11 regions in all (Fig S.9).

5.4.3. Regions

Shark taxonomic turnover (B_{sim}) is marked in four fairly distinct regions: (1) southern South America from the Chilean coast around to Argentina, (2) southern temperate zone (New Zealand), southern sub-tropics and western Africa, (3) tropics with northern Pacific and Mediterranean, and finally (4) northern sub-tropics and northern Atlantic. Regions in the south along the southern end of Madagascar, western Australia, and Easter Island and in the north along the sub-tropics limit, i.e., southern Baja Mexico, Canary Islands and Azores and Southern Japan, likely represent areas of transition zones between tropical and temperate fauna and line up almost exactly along the Tropic of Capricorn (Fig. 5.2a).

The pattern of ray taxonomic turnover (B_{sim}) is more complicated and generated more than 50 regions. As such, there are more sub-regions within the broader patterns that I presented here (i.e., there are likely more regions nested within the tropics) (Fig. 5.2b). For rays, the first major split delineated six regions: (1) northern Atlantic off Newfoundland, (2) southern temperate seas, (3) southern sub-tropics and northern Atlantic, (4) southern sub-tropics, tropics, and southern inland South America, (5) eastern Pacific and northern inland Brazil, and (6) northern sub-tropics and temperate (Fig. 5.2b).

There are fewer phylogenetic regions. Shark phylogenetic turnover (pB_{sim}) divides the ocean into two major realms: (1) tropical, and (2) temperate (Fig. 5.3a). These realms are subdivided into (1) northern and southern sub-tropical, (2) northern and southern temperate zone, (3) western Atlantic and Pacific tropics, (4) Indo-west Pacific tropics, and (5) western Africa. There are less distinct regions in (6) north and south sub-tropical limits, and (7) regions around islands such as the Philippines, northern Madagascar, the Seychelles, Canary Islands, and the Azores (Fig. 5.3a). The Caribbean is more similar to temperate regions than tropical regions.

The pattern of ray phylogenetic turnover (pB_{sim}) divides the ocean into tropical and temperate regions (Fig. 5.4a). The tropical regions are further subdivided into two major tropical regions: (1) Indo-west Pacific, and (2) tropical Atlantic and eastern Pacific. The temperate regions are subdivided into: (1) southern and northern temperate seas, (2) southern sub-tropical (Australia), (3) freshwater Brazil, (4) subtropical limit (South Africa), and northern sub-tropical limit (Japan) (Fig. 5.4a).

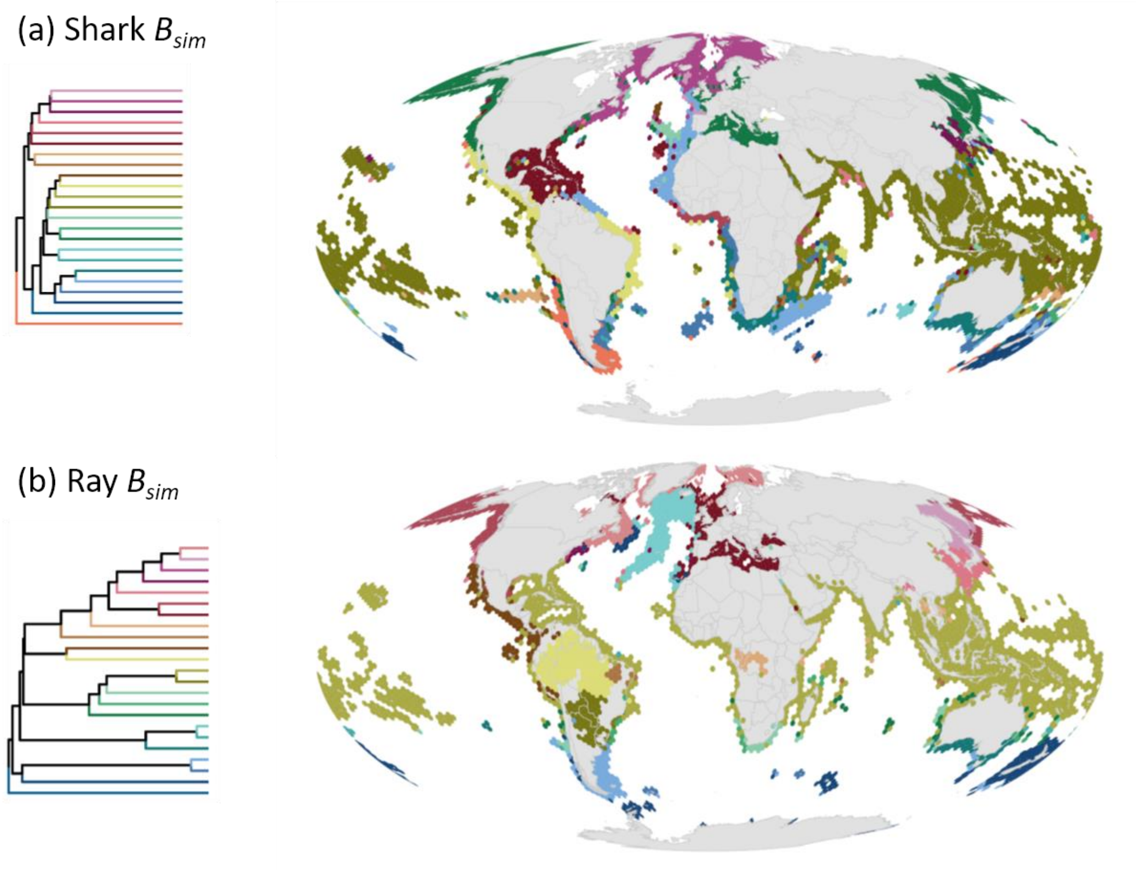


Figure 5.2 Species-level taxonomic regions of the world (B*sim*): (a) 23 regions for 457 sharks species, (b) 23 regions for 539 ray species. Dendrograms on the left show the relationships between regions; colours on the dendrograms match regions' colours on maps. Pelagic species are not included in the analysis.

5.4.4. Comparison of shark and ray regions

Taxonomic regions show similarities and differences between sharks and rays (Fig 5.2a, b). Similarly, the high latitudes provide a cold-water area for radiation that is seen for both sharks and rays: eight shark and nine ray taxonomic regions are found largely within the northern temperate seas. Further, both groups show turnover between regions located at the Tropics of Capricorn and Cancer. Sharks, however, show more taxonomic turnover within the tropics more broadly, and specifically along western Africa, the western Atlantic and the Caribbean (Fig. 5.2a,b). Comparatively, taxonomic turnover regions for rays are different as they have more structuring in the northern temperate seas (seven major realms across the Pacific and Atlantic) and have clear turnover and delineation in the tropics.

Both shark and ray phylogenetic regions show a clear west-east divide of the tropics (Atlantic/Caribbean, and Indo-west Pacific) and divisions between subtropical and temperate regions (Fig. 5.3 a,b; Fig. 5.4a,b). Specifically, sharks show more regions along the west coast of Africa up to the Canary Islands and the Azores, while rays have comparatively more structuring around South Africa. Hawaii has an assemblage that is more similar to the western tropics for sharks and the Indo-West Pacific for rays.

5.4.5. Comparison of taxonomic and phylogenetic regions

Comparison between phylogenetic and taxonomic turnover can provide insight into evolutionary relationships. For example, an area of low taxonomic turnover and low phylogenetic turnover represents an area of similar taxonomic composition of closely related species (Fig 5.3, quadrat (a)). An area of high taxonomic and high phylogenetic turnover represents areas of very distinct taxonomic comprised of distantly related species (Fig 5.3, quadrat (b)). An area with high taxonomic turnover but low phylogenetic turnover, reflecting an area of turnover of species with shared evolutionary history (Fig 5.3, quadrat (c)) perhaps due to vicariance events. Although these patterns are more visible for rays, we see: (a) is found in the tropics reflecting wide-ranging but closely related species such as ground sharks (*Carcarhinus* spp.) or stingrays (Dasyatidae), (b) is exemplified in northern Atlantic for rays with high taxonomic but low phylogenetic turnover (Rajidae) and to a lesser extent around South America for sharks, and (c) is exemplified in the faunas derived from a number of distinct assemblages, such as South Africa for rays with both high taxonomic and high phylogenetic turnover and to a lesser extent north Atlantic for sharks (Sleeper sharks and dogfish).

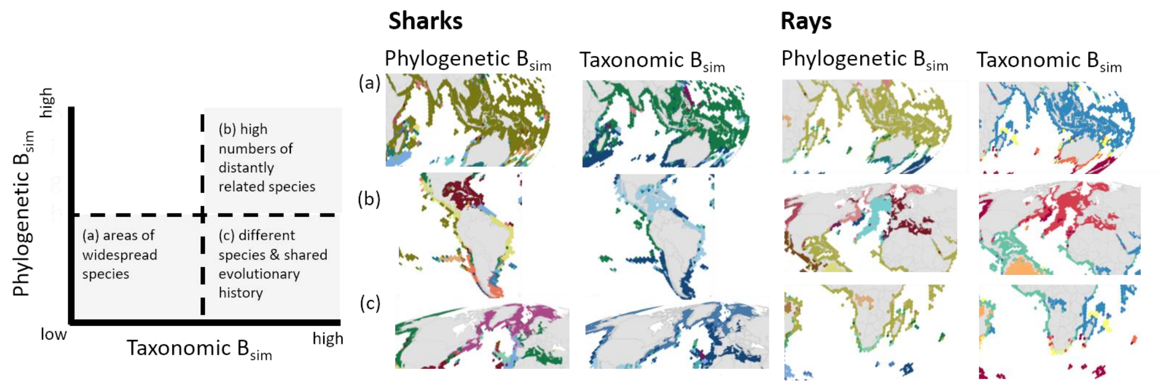


Figure 5.3 Comparison between taxonomic and phylogenetic turnover for sharks and rays. (a) A global region of low taxonomic turnover and low phylogenetic turnover represents an area of similar taxonomic composition with a shared evolutionary. (b) A global region of high taxonomic and high phylogenetic turnover representing areas of distinct taxonomic and evolutionary assemblages. (c) A global region with high taxonomic turnover but a homogenous phylogenetic region, thus reflecting an area of turnover of species with shared evolutionary history.

5.4.6. Species assemblages per cluster

Species composition of regions can provide insights into their ecology. For sharks, the two temperate regions can be characterized by the wide-ranging species spiny dogfish *Squalus acanthias* and Greenland shark *Somniosus microcephalus,* two species that are from the closely related families Squalidae and Somniosidae (both from the Order Squaliformes which has an amphi-tropical species richness gradient) (Fig 5.3a (1) and (2)).

The southern Australian and South American freshwater regions are geographically separate but are phylogenetically related. The southern Australia region comprises whip-tail stingrays Dasyastidae and round rays Urolophidae, both of which are closely related to the South American freshwater stingrays (Potomotrygon) (Fig 5.4a (1), (3), and (4)). Japan has a similar assemblage to South Africa, potentially due to closely related sleeper rays (Narkidae) (Fig 5.4a (7) and (8).

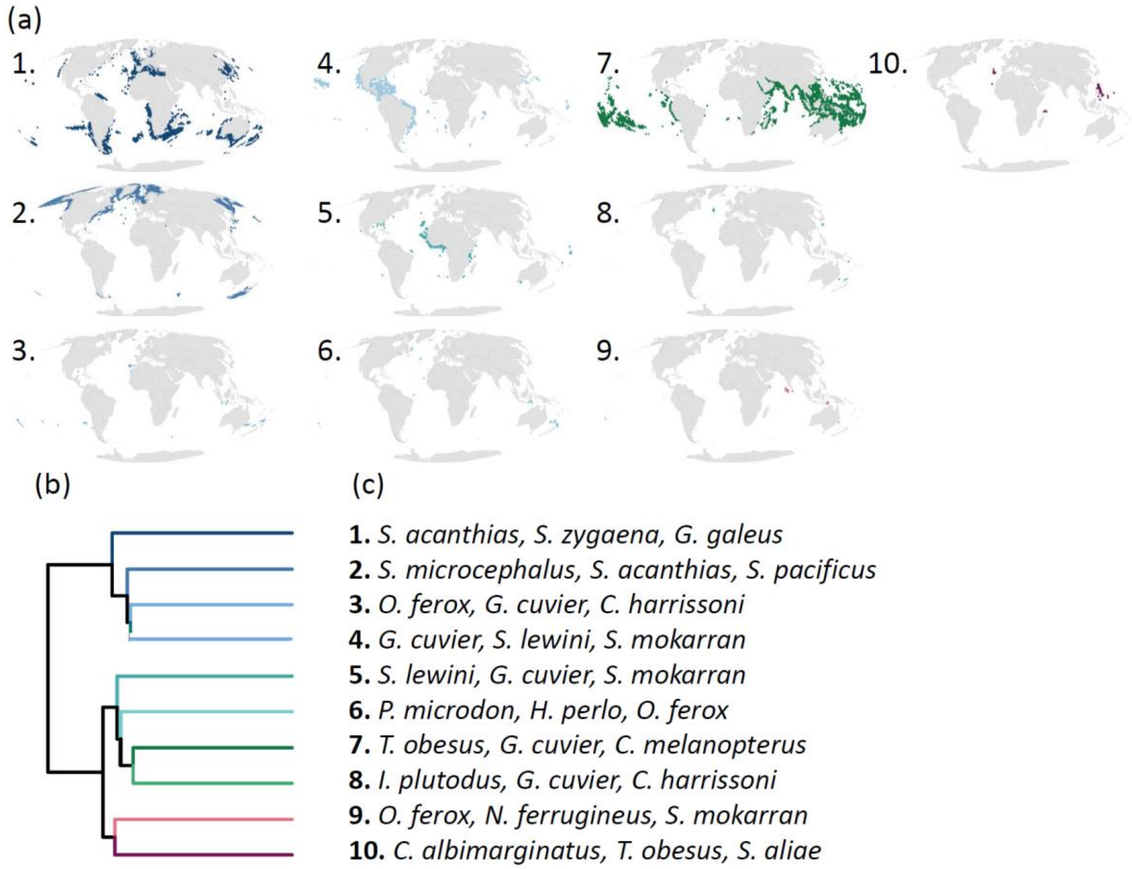


Figure 5.4 **Shark phylogenetic regions of the world (pB_{sim}). (a) 10 regions for 457 shark species. (b) Dendrogram shows the relationship between regions with a greater patristic distance representing a greater dissimilarity. (c) Spatially dominant species per region quantified as the sum of the number of grid cells of occurrence per region.**

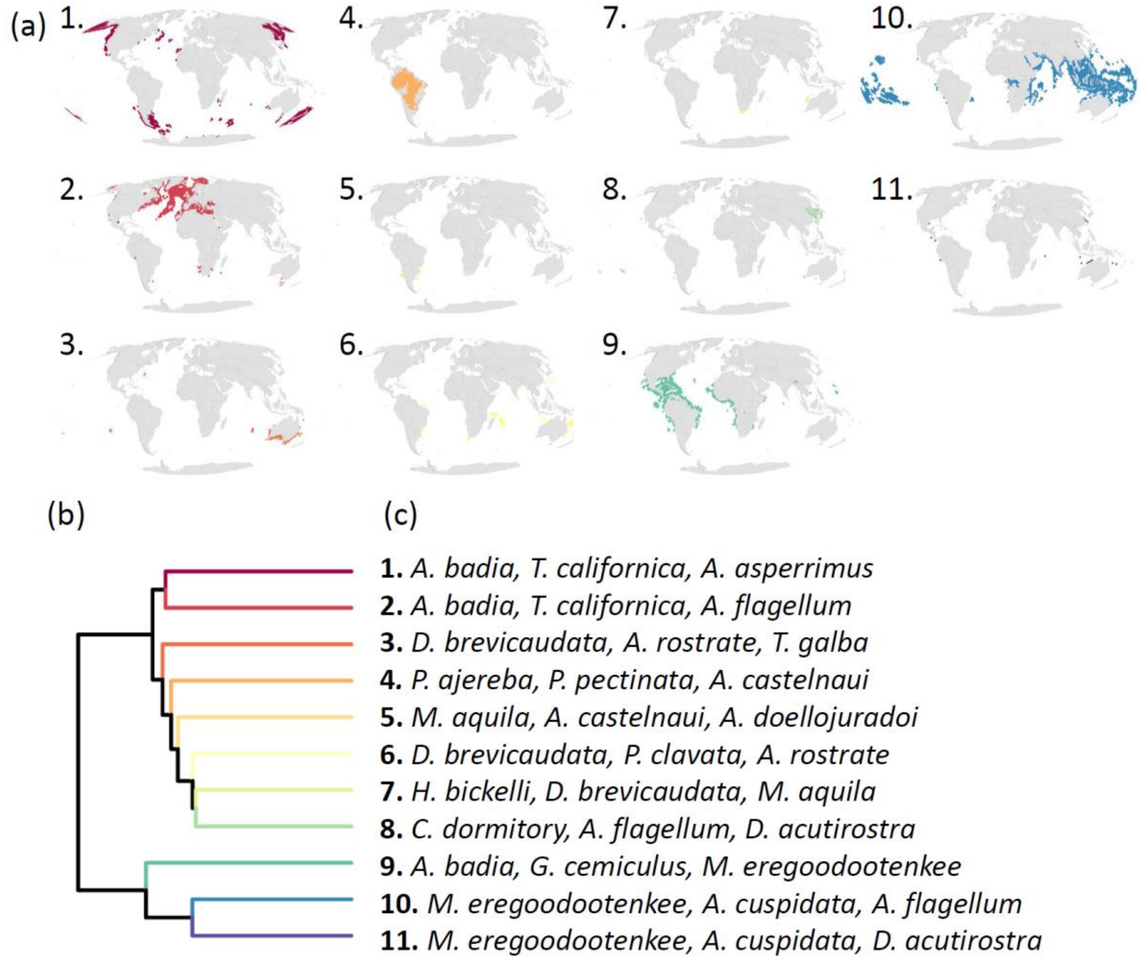


Figure 5.5 **Ray phylogenetic regions of the world (pB_{sim}). (a) 11 regions for 539 ray species. (b) Dendrogram shows the relationship between regions with a greater patristic distance representing a greater dissimilarity. (c) Spatially dominant species per region quantified as the sum of the number of grid cells of occurrence per region.**

5.5. Discussion

5.5.1. Main findings

I determined that there are 23 taxonomic (B_{sim}) and 10 phylogenetic (pB_{sim}) regions in the oceans for sharks and at least 23 and 11 for rays, B_{sim} and pB_{sim} respectively. Both sharks and rays have many more taxonomic than phylogenetically distinct regions. The greater number of regions for rays suggests a finer sub-structuring of geographic diversity in rays that is potentially due to their smaller geographic range size and potentially dispersal abilities and could reflect diversification through vicariance events. There are more than double the number of shark taxonomic regions versus shark phylogenetic regions, reflecting greater taxonomic differences in regions but more shared evolutionary history potentially driven by the recent radiations of the speciose Carcharhiniformes that diverged approximately 219 MYA and currently has the greatest number of species at 270 (Table S.14). Broadly, for sharks, the split between tropical Atlantic and Pacific could be due to the near absence of the very old lineages from the in the Indo-west Pacific (Hexanchiformes [263 MYA, 4 species], Squaliformes [233 MYA, 126 species], and Squatiniformes [157 MYA, 18 species] and the near absence of two old orders from the tropical Atlantic (Orectolobiformes [244 MYA, 36 species] and Heterodontiformes [260 MYA, 9 species]).

Both sharks and rays show distinct tropical and temperate patterning, both taxonomically and phylogenetically, and may potentially represent the long-term barrier that cold water presents to dispersal for tropical species (Hawkins & Devries 2009). Both shark and ray regions show higher taxonomic structuring in the north Atlantic than in the north Pacific, potentially reflecting the younger age of the Atlantic, the more structured current systems as shown in abiotic classifications, or higher speciation rates at higher latitudes (Rabosky et al. 2018). Gondwanaland and Weddellian province patterns are evident in the close relatedness of formerly connected, but now widely separated regions in South America, South Africa, and Australia and as has been found for chimaera species (Walker 1987). The Tethyan seaway, which used to span across the equator, could have facilitated movement of shark species and is potentially reflected in the lower dissimilarity values between the Indo-West Pacific, Mediterranean, and north Atlantic shark taxonomic regions (see Rajiformes, Fig. 5.1).

Contrary to expectations, many more zoogeographic and phylogenetic regions are identified in the ocean (for sharks and rays) than for any of the terrestrial Classes previously examined (11 realms and 20 regions for amphibians, birds, and mammals), with a higher degree of explanatory power (Holt & Lessard et al. 2013). The larger phylogenetic regions for sharks and rays may be reflective of the longer evolutionary ages of Chondrichthyans as compared to amphibians, birds, and mammals (Stein & Mull et al. 2018), stronger abiotic constraints, or evolutionary histories that have resulted in complex patterns.

5.5.2. Previous findings

Some of my regions are concordant with previously described patterns. For example, a study of South African skate species found that a distinct faunal group extends northwards from west South Africa along the cold Benguela current, while the warm Agulhas (eastern South Africa and Mozambique) has a different distinct faunal group (Compagno & Ebert, 2007). Phylogenetically, for rays, I see a similar pattern with distinct regions in (1) West Africa to Namibia, (2) the Benguela ecosystem (Namibia and western South Africa), (3) Angulhas current (eastern South Africa, Mozambique) and (4) Madagascar (Compagno & Ebert 2007a).

Another similarity with previous work is within Japan, where there is a division for both sharks and rays in the Sea of Okhosk. Previous analyses have described a division of skates occurring here due to the warm Kuroshio current meeting the cold Oyashio current coming from the north (McEachran & Miyake 1990).

5.5.3. Caveats

Although I chose species as the taxonomic scale of my analysis, higher-level taxonomic cuts (Order, Family) are shown to delineate regions that are largely concordant across these levels (Kreft & Jetz 2010).

Here, I used a completed phylogenetic tree and current-day geographic distributions. Therefore, my analysis is unable to account for the possibility that current-day species could have potentially been a part of a much larger family complex, or that current-day distribution could be a result of range contraction (Lomolino et al. 2006).

5.5.4. Next steps

I believe that my analysis provides the basis for future studies that can provide ecological, evolutionary, and historical insights into current patterns of biodiversity (Graham & Fine 2008; Kreft & Jetz 2010). Future studies could consider regionalization exclusively of endemic species to gain a greater understanding of the influence of historical biogeography on species distributions as the signal could be stronger in these patterns (Lomolino et al. 2006; Floeter et al. 2007; Kulbicki et al. 2013b; Cowman et al. 2017). Additional comparative studies could quantify the levels of endemism and relatedness between the biogeographical regions to understand why and when these regions were formed (Floeter et al. 2007). Further, consideration of salinity, depth, and other gradients could influence the distribution of species and allow a better understanding of the drivers of speciation (Compagno, Ebert, & Cowley, 1991). Finally, understanding and determining these patterns will be an important step toward better understanding the determinants of these regional boundaries (Ficetola, 2017) as well as the relative importance of contemporary climate and historical plate tectonics on zoogeographic and phylogenetic patterns through time (Mazel et al. 2017).

5.5.5. Conservation implications

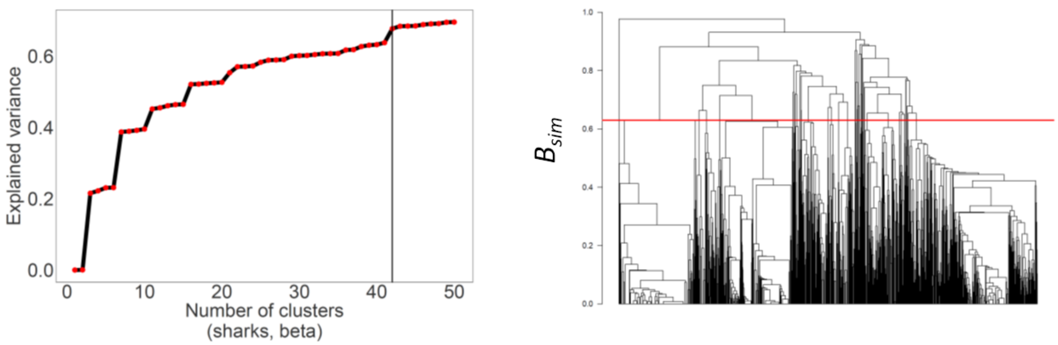
Finally, the Convention on Biological Diversity has laid out 20 targets for signatory countries to achieve by 2020. One target, Aichi Target 11, states that countries should protect “at least 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscape and seascape.” (www.cbd.int/). Progress towards this goal is often measured in terms of whether countries have meet the 10% goal (Lubchenco & Grorud-Colvert 2015; Wood et al. 2008). However, I believe that the taxonomic and phylogenetic regions could be used to measure progress towards MPAs being “ecologically representative,” specifically for sharks and rays. Further, the taxonomic and phylogenetic regions identified here could be used as conservation units and regions that are globally rare (i.e. geographically restricted regions with high numbers of endemic species) and overlap with high exposure to threatening pressure could be prioritized for conservation action.

5.6. Supplemental material D

Table S.14 Uncertainty in node age for orders across chondricthyans using 100 randomly selected phylogenetic trees.

Family	Mean node age across 100 trees (MYA)	Standard deviation across 100 trees	Superorder	Family	Mean node age across 100 trees (MYA)	Standard deviation across 100 trees	Superorder	Family	Mean node age across 100 trees (MYA)	Standard deviation across 100 trees	Superorder
Platyrhinidae	213.31	17.47	Batoidea	Heterodontidae	231.44	27.36	Galeomorphii	Centrophoridae	154.45	33.03	Squalimorphii
Rhinobatidae	205.88	20.85	Batoidea	Parascyllidae	202.76	25.22	Galeomorphii	Somniosidae	145.15	31.51	Squalimorphii
Zanobatidae	187.18	19.00	Batoidea	Scyliorhinidae	167.91	23.36	Galeomorphii	Oxynotidae	145.15	31.51	Squalimorphii
Hypnidae	156.93	28.77	Batoidea	Brachaeluridae	126.17	22.22	Galeomorphii	Chlamydoselachidae	139.85	12.39	Squalimorphii
Hexatrygonidae	135.70	13.11	Batoidea	Orectolobidae	126.17	22.22	Galeomorphii	Hexanchidae	139.85	12.39	Squalimorphii
Rajidae	132.12	20.01	Batoidea	Mitsukurinidae	124.73	22.40	Galeomorphii	Etmopteridae	138.58	30.95	Squalimorphii
Pristidae	131.11	28.41	Batoidea	Hemiscylliidae	118.02	15.56	Galeomorphii	Squalidae	131.21	29.80	Squalimorphii
Arhynchobatidae	122.54	25.21	Batoidea	Pseudotriakidae	104.79	21.59	Galeomorphii	Dalatiidae	131.21	29.80	Squalimorphii
Anacanthobatidae	122.54	25.21	Batoidea	Proscyllidae	104.79	21.59	Galeomorphii	Pristiophoridae	121.41	36.47	Squalimorphii
Gymnuridae	119.90	12.87	Batoidea	Triakidae	103.01	17.64	Galeomorphii	Echinorhinidae	121.26	46.49	Squalimorphii
Urolophidae	115.83	11.65	Batoidea	Leptochariidae	98.77	21.78	Galeomorphii	Squatinidae	116.04	40.45	Squalimorphii
Plesiobatidae	115.83	11.65	Batoidea	Alopiidae	91.40	19.09	Galeomorphii				
Myliobatidae	113.44	11.98	Batoidea	Hemigaleidae	90.20	14.72	Galeomorphii				
Narcinidae	110.71	19.74	Batoidea	Lamnidae	85.69	13.41	Galeomorphii				
Torpedinidae	102.12	9.17	Batoidea	Cetorhinidae	85.69	13.41	Galeomorphii				
Narkidae	101.85	13.14	Batoidea	Carcharhinidae	82.31	12.72	Galeomorphii				
Urotrygonidae	98.19	9.43	Batoidea	Sphyrnidae	82.31	12.72	Galeomorphii				
Rhynchobatidae	90.69	20.36	Batoidea	Odontaspididae	60.85	29.19	Galeomorphii				
Rhinidae	90.69	20.36	Batoidea	Pseudocarchariidae	51.36	30.55	Galeomorphii				
Potamotrygonidae	68.91	7.57	Batoidea	Megachasmidae	49.96	32.08	Galeomorphii				
Dasyatidae	68.91	7.57	Batoidea	Stegostomatidae	42.42	27.95	Galeomorphii				
Rhinopteridae	65.01	11.10	Batoidea	Rhincodontidae	40.13	27.82	Galeomorphii				
Mobulidae	65.01	11.10	Batoidea	Ginglymostomatidae	38.32	25.32	Galeomorphii				

(a) Shark B_{sim}



(b) Shark pB_{sim}

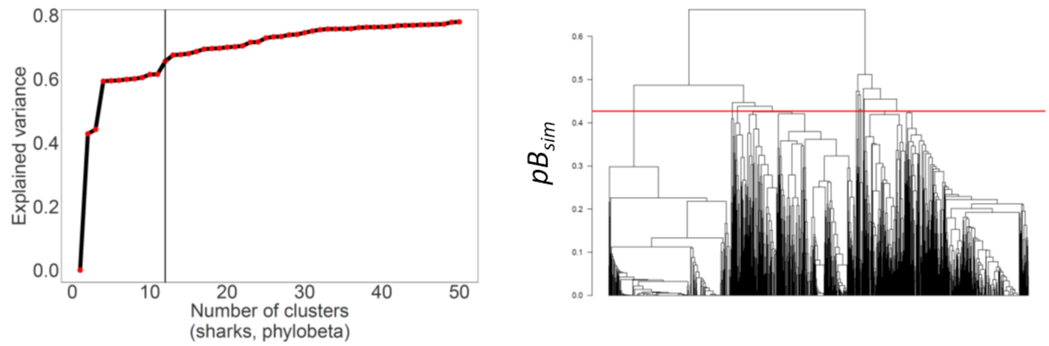


Fig S.8 **Sharks: Evaluation plots and dendrogram of (a) shark taxonomic B_{sim} and (b) phylogenetic pB_{sim}. Height of dendrogram represents the distance between leafs The red line represents the height at which the dendrogram was cut according to the number of clusters in the previous plot. A higher value represents regions that group together cells that are more dissimilar.**

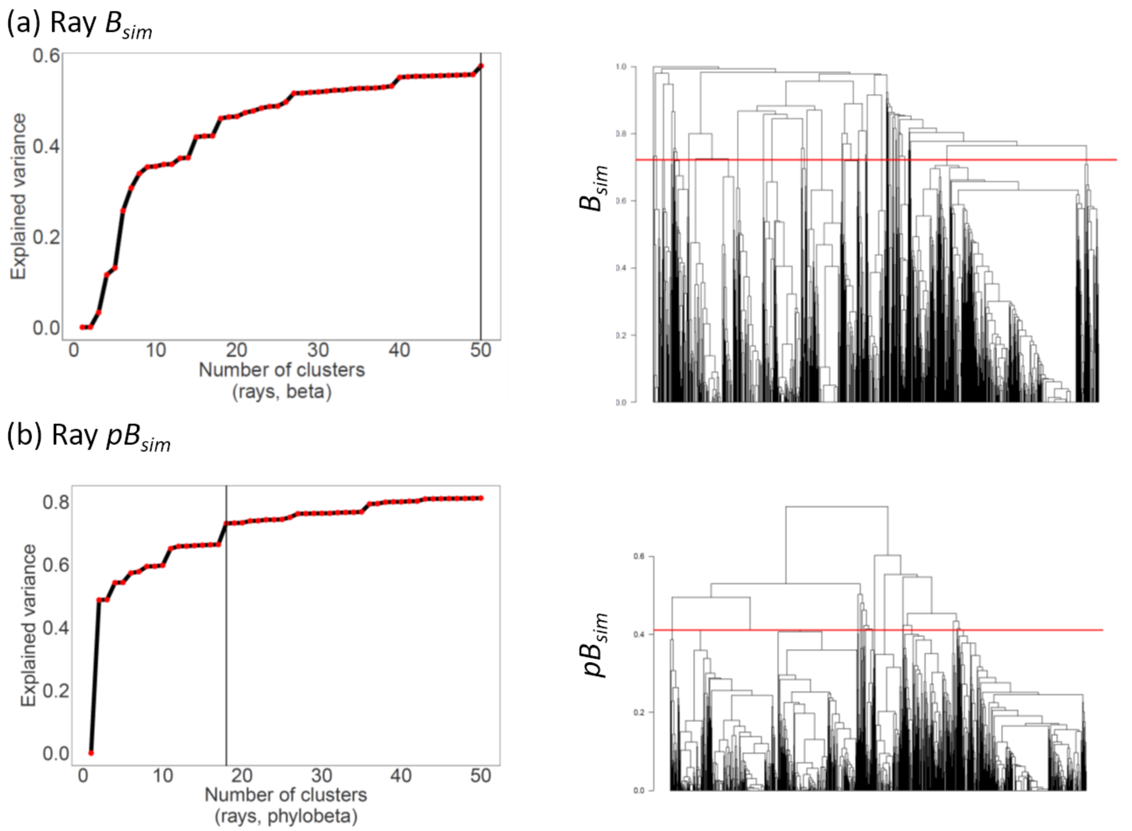


Fig S.9. **Rays: Evaluation plots and dendrogram of (a) ray taxonomic B_{sim} and (b) phylogenetic pB_{sim}. Height of dendrogram represents the distance between leafs The red line represents the height at which the dendrogram was cut according to the number of clusters in the previous plot. A higher value represents regions that group together cells that are more dissimilar.**

Chapter 6. General Discussion

My thesis has advanced our understanding of marine biodiversity gradients and conservation needs for a Class of exploited marine species.

6.1.1. MPAs and threatened species

My thesis builds off previous research that evaluated the progress towards the Convention on Biological Diversity's Aichi Targets. Previous work largely focused on evaluating progress towards Aichi Target 11 - 10% of coastal marine areas designated as MPAs by 2020 (Boonzaier & Pauly 2015; Lubchenco & Grorud-Colvert 2015; Wood et al. 2008). This target undoubtedly motivated countries to designate MPAs, however, there were concerns that the placement of MPAs should be more strategic and placed in a manner that considers the interdependent Aichi Target 12; preventing biodiversity loss. Consideration of both these targets led to an evaluation of global MPAs in the context of protecting threatened species (Butchart et al. 2015). Moving forward, countries need to commit to MPA creation, in the same manner that led to a near double of MPA area, that is strategic rather than opportunistic or performing no better than random (Watson et al. 2010; Deguise & Kerr 2005).

In chapters 2 and 3, I extended previous analyses and evaluated progress towards meeting both MPA area and threatened marine species protection (Butchart et al. 2015). I considered threatened marine species coverage within MPAs and broadly countries that could expand their MPAs to increase threatened marine species protection. Future analyses could consider species-specific requirements for MPA coverage and successful conservation outcomes. Meeting 10% of a species' range with MPAs should be considered a minimum target and may not be sufficient for increasing population sizes and improving conservation statuses of threatened species. Further, I considered a cumulative sum of a species' range within MPAs, future analyses could consider whether species are found within a portfolio of MPAs or few MPAs and consider the tradeoffs between this conservation strategy.

6.1.2. MPAs and fisheries management

In Chapters 3 and 4, I integrated sustainable fisheries management as part of the conservation toolbox. In this thesis, I considered the contribution of sustainable fisheries management towards threatened species protection, i.e., Aichi Target 6 - improving sustainable fisheries management. Additionally, I evaluated the sustainability of the world’s shark and ray fisheries on a nation-by-nation basis and found that declines are associated with measures of overfishing rather than management implementation. Future analyses could consider species-specific fisheries management requirements as here I considered fisheries management actions that were broad but comparable on a nation-by-nation basis. Further, I did not consider management actions in areas outside of national jurisdictions where fisheries management is governed through a collective of nations under Regional Fisheries Management Organizations. Migratory species with large ranges, much of which is outside of national jurisdictions, will need international coordination for MPAs and enforceable fisheries management to ensure sustainable fisheries and threatened species protection.

6.1.3. Governance and conservation interventions

I used governance (Chapter 2) and conservation likelihood (Chapter 3) to represent two dimensions of socio-economic conditions related to conservation outcomes. While named differently, they are both largely the same. I used governance as a measure to consider the effectiveness of conservation actions as countries with higher governance scores have better conservation outcomes (Amano et al. 2017; Gill et al. 2017). I used conservation likelihood, derived from largely the same variables and methods as the governance score, as a measure of the socio-economic realities in a country that influence the types of conservation actions that could be undertaken (Dickman et al. 2015; McClanahan et al. 2009). For example, areas of lower conservation likelihood may need to focus on scientific capacity building or poverty alleviation versus conducting data intensive fisheries stock assessments. The specific actions that are proven to be effective in areas of higher and relatively lower conservation likelihood, however, will need to be better understood.

6.1.4. Threatening pressures and costs

In this thesis, I considered the current-day distribution of threatened species, however, I did not consider potential shifting species distributions in lieu of climate change (Sunday et al. 2012; Dulvy et al. 2008). Future work could consider finding areas of climate refugia and of high biodiversity value as these areas could be important sites for capturing biodiversity in a changing climate.

Also, terrestrial analyses have considered the configuration of protected areas relative to cost (i.e., agricultural value of land). The authors found that protected areas have been placed in areas of lower cost as opposed to focused threatened species representation. With strategic placement, however, they found that 30 times more species could be protected within the same amount of area and cost as the current protected areas (Venter et al. 2017). In marine environments, future analyses could consider the MPA configuration that would optimize threatened species coverage, while reducing cost (i.e., lower cost would be areas of lower fishing pressure) and climate change refugia.

6.1.5. Fisheries landings trajectories and management actions

In Chapter 3, I provided multiple lines of evidence to show that global shark and rays landings have declined almost ~15% over the past decade due to widespread overfishing as opposed to reduced catches from fisheries management implementation. I completed a nation-by-nation review of comparable shark and ray fisheries management and highlight some of the key improvements in fisheries management that could be taken to improve either the data or the ability for countries to sustainably manage their shark and ray fisheries such as greater taxonomic resolution as countries with better reporting resolution have smaller declines in landings over time. Next steps will have to include using catch reconstructions to better determine declines in artisanal or commercial fisheries; artisanal and commercial fisheries will require different management interventions. Additionally, future research could focus on creating a predictive model that can determine which countries area currently reporting stable or increasing landings but have the attributes of unsustainable fishing.

6.1.6. Evolution in the oceans and evolutionary uniqueness

In Chapter 5, I build off of previous literature that defined the zoogeographic regions of the world based on reef fishes, skates, and a global analysis of 65,000 marine species (Cowman et al. 2017; Compagno & Ebert 2007b; Costello et al. 2017). In this chapter integrated taxonomic and phylogenetic information into a marine zoogeographic analysis. This analysis allowed for insight into how historical continental configurations could have influence the current-day biodiversity gradients, and for determining how patterns of the different dimensions of beta diversity vary across the seascape. I determined that the northern temperate seas provided a cold-water area for radiation that is seen for both sharks and rays, i.e., high number of taxonomic versus phylogenetic regions supporting previous findings that speciation in marine fish is faster at higher latitudes (Rabosky et al. 2018).

Future studies could consider regionalization exclusively of endemic species to gain a greater understanding of the influence of historical biogeography on species distributions as the signal could be stronger in these patterns (Lomolino et al. 2006; Floeter et al. 2007; Kulbicki et al. 2013b; Cowman et al. 2017). Additional comparative studies could quantify the levels of endemism and relatedness between the biogeographical regions to understand why and when these regions were formed (Floeter et al. 2007). Finally, there is an opportunity to expand our understanding of the relative importance of contemporary climate and historical plate tectonics on zoogeographic and phylogenetic patterns through time in marine environments (Mazel et al. 2017).

This analysis has also provided an opportunity to evaluate conservation action at another scale as Target 11 notes that MPAs should be "ecologically representative". In order for MPAs to be ecologically representative, each region I identified would have to have at least 10% of its area within MPAs (Butchart et al. 2015). Furthermore, in terms of conservation, the shark and ray regions I have identified here could become an alternative scale from which to study vulnerability. For example, some of the regions are geographically small, are comprised of high numbers of endemic species, and could therefore be vulnerable to threatening pressures such as overfishing or climate change.

6.2. Conclusion

Biodiversity loss is a wicked problem and cannot be stopped, however, conservation biology can provide the science to stem biodiversity loss. Much marine conservation research has previously focused on corals or reef-associated fish leaving our understanding of biodiversity and conservation needs to tropical regions. Further, marine hotspot research previously defined hotspots as areas of high species richness limiting the conservation focus to the species-rich Indo-west Pacific. Here, using a fully marine Class of organisms that spans the world's temperate and tropical regions I defined hotspots using Myers et al. (2000) original definition of areas of high number of threatened, endemic species. These hotspots show that there are alternative hotspots, not just the species-rich Indo-west Pacific, that are in need of immediate conservation action to stem biodiversity loss. Additionally, from my thesis, it seems clear that conservation efforts in many of these alternative regions will be challenging and will have to focus on capacity building, poverty alleviation, and supporting alternative livelihoods to see positive conservation outcomes.

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