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REVIEW

Emergent research and priorities for shark and ray conservation

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ABSTRACT: Over the past 4 decades there has been a growing concern for the conservation status of elasmobranchs (sharks and rays). In 2002, the first elasmobranch species were added to Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Less than 20 yr later, there were 39 species on Appendix II and 5 on Appendix I. Despite growing concern, effective conservation and management remain challenged by a lack of data on population status for many species, human–wildlife interactions, threats to population viability, and the efficacy of conservation approaches. We surveyed 100 of the most frequently published and cited experts on elasmobranchs and, based on ranked responses, prioritized 20 research questions on elasmobranch conservation. To address these questions, we then convened a group of 47 experts from 35 institutions and 12 countries. The 20 questions were organized into the following broad categories: (1) status and threats, (2) population and ecology, and (3) conservation and management. For each section, we sought to synthesize existing knowledge, describe consensus or diverging views, identify gaps, and suggest promising future directions and research priorities. The resulting synthesis aggregates an array of perspectives on emergent research and priority directions for elasmobranch conservation.

KEY WORDS: Elasmobranch · Conservation priorities · Sharks · Rays

1. INTRODUCTION

Elasmobranchs, comprising more than 1200 species of sharks and rays, are one of the most ancient and evolutionarily distinct vertebrate radiations (Stein et al. 2018). Despite their evolutionary success, elasmobranchs are particularly sensitive to exploitation, owing to life history traits such as late maturity and few offspring. As a result, this group generally can only sustain relatively low levels of additional mortality caused by fishing (Stevens et al. 2000, Myers & Worm 2005). Overexploitation is currently driving an ongoing global decline of oceanic sharks and rays, resulting in a heightened risk of extinction of these species (Dulvy et al. 2021, Pacoureau et al. 2021). Similar declines in coastal elasmobranchs documented at re-

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gional scales mirror this general trend (e.g. Dudley & Simpfendorfer 2005, Roff et al. 2018, MacNeil et al. 2020). Elasmobranch products are mostly used for consumption (meat), dietary supplements (cartilage and oil), and their fins are highly valued as a luxury food item (primarily for shark fin soup). Almost all (99.6%) of known elasmobranchs are exploited and exposed to some form of directed (target) or incidental (bycatch) fisheries mortality (Dulvy et al. 2021). Yet stock assessments have only been completed for fewer than 58 populations, covering 45 species (Simpfendorfer & Dulvy 2017). Currently, 391 (32%) are listed as threatened (Critically Endangered, Endangered, or Vulnerable). However, more than one-third (37.5%) are likely to be threatened if Data Deficient species are assumed to be threatened in the same proportion as assessed species (Dulvy et al. 2021).

Public perception of sharks in particular includes both fascination and fear. On one hand, awe for these ancient ocean dwellers has inspired extensive basic scientific research, and their current plight has generated funding for conservation research worldwide. On the other hand, however, mitigation of inevitable human–wildlife conflicts with sharks can be overwhelmed by public fear of shark 'attacks', resulting in culling programs that may even target threatened species (Sabatier & Huveneers 2018), hampering conservation efforts (Simpfendorfer et al. 2011).

In the past decade, there has been a doubling in the number of studies addressing elasmobranch diversity, distribution, management, and conservation (Dulvy et al. 2021). A number of syntheses have summarized global hotspots of diversity (Lucifora et al. 2011, Dulvy et al. 2014), endemicity (Davidson & Dulvy 2017), evolutionary history (Stein et al. 2018), highlighted priority conservation and fisheries geography (Dulvy et al. 2017, Queiroz et al. 2019), and explored the importance of public perception in their conservation (Sabatier & Huveneers 2018). However, elasmobranch management, and in particular conservation, are still frequently hindered by gaps in basic and applied research, including key data on species biology, population status, scale and intensity of threatening processes, conflicts with human activities (public safety), and the effectiveness of conservation tools.

Given the urgent need for, and heightened interest in, elasmobranch research, conservation, and management, we sought input from scientists globally on the most important research questions to fill key knowledge gaps. Following previous initiatives on other taxa (Sutherland et al. 2006, 2009, Hamann et al. 2010, Lewison et al. 2012, Rees et al. 2016), we narrowed down a list of 20 priority questions addressing 3 broad categories that can be used to guide future research and conservation efforts: (1) status and threats, (2) population and ecology, and (3) conservation and management approaches (Box 1). For each section, we sought to synthesize what is known on the question, describe consensus or diverging views, identify

Box 1. Final list of questions used to generate this review

1. Status and threats (see Section 3.1)
1.1. How do we overcome data deficiency in elasmobranch population assessments? (see Section 3.1.1)
1.2. How can we improve life history estimations of elasmobranchs for fisheries management and conservation? (3.1.2)
1.3. What are the most effective and promising approaches for elasmobranch bycatch mitigation? (3.1.3)
1.4. How can we more accurately measure and monitor total global catch of elasmobranchs? (3.1.4)
1.5. Beyond fishing, what are the emerging threats to elasmobranchs? (3.1.5)
1.6 How can we reconstruct elasmobranch baselines to inform population decline estimations and recovery targets? (3.1.6)

2. Population and ecology (Section 3.2)
2.1. What are the knowledge gaps in global abundance and diversity of elasmobranchs? (3.2.1)
2.2. How can tagging technologies be applied more effectively to inform elasmobranch research and conservation? (3.2.2)
2.3. How can we more clearly define the ecological role of elasmobranchs? (3.2.3)
2.4. How can we improve knowledge of elasmobranch population structures? (3.2.4)

3. Conservation and management (Section 3.3)
3.1. What is the role of citizen science in elasmobranch conservation research? (3.3.1)
3.2. How can marine protected areas (MPAs) contribute to elasmobranch conservation? (3.3.2)
3.3. Under what conditions (ecological, environmental, social, and political) can elasmobranch fisheries be sustainable? (3.3.3)
3.4. What is the socio-economic role of elasmobranch fisheries? (3.3.4)
3.5. How can we quantify ecosystem services provided by elasmobranchs? (3.3.5)
3.6. What is the role of vessel tracking in assessing and enforcing fisheries interactions with elasmobranchs? (3.3.6)
3.7. What are the relative impacts of small-scale, industrial, and recreational fisheries on elasmobranch populations? (3.3.7)
3.8. How can we reconcile public safety and healthy elasmobranch populations? (3.3.8)
3.9. What are the species composition and population impacts of the shark fin trade? (3.3.9)
3.10. What are the impacts of regulations across elasmobranch species and jurisdictional scales? (3.3.10)

gaps, and suggest promising directions and priority future steps. This synthesis represents an unprecedented collection of perspectives from a global subset of elasmobranch experts with diverse scientific backgrounds. Through this effort, we aim to focus and prioritize research efforts, conservation approaches, and funding priorities for elasmobranch conservation.

2. MATERIALS AND METHODS

Five authors (S.J.J., F.M., F.F., T.D.W., C.B.) selected the elasmobranch experts for this survey by performing literature searches in Web of Science and Scopus. We searched for the top 100 authors with the most publications on elasmobranchs, as well as the top 100 authors with the most citations. In both Web of Science and Scopus, we used the following search terms: elasmobranch* OR batoid* OR shark* OR Selachi* AND marine* OR ocean*. We then combined the results of all searches, identified authors who overlapped among all searches, and created a single list of the top 100 elasmobranch researchers based on number of publications and citations (see Table S1; all 3 Supplements at www.int-res.com/articles/suppl/n047p171_supp.pdf).

Next, we emailed these experts, asking for feedback on a preliminary list of 20 questions identified as research needs in the field of elasmobranch biology/ecology/conservation compiled by the lead authors (S.J.J., F.M., F.F., T.D.W.) through literature review (Supplement 2). Experts were asked to rank what they considered to be the top 5 most important questions from 1–5, with 1 being the highest priority. We also asked if there were additional high-priority questions that we had not included in the preliminary list.

In total, 47 of the 100 experts we contacted responded. These respondents represented 42 different institutions in 18 countries. The majority (21) were from the USA, followed by Australia (4), the UK (3), Brazil, New Zealand, Canada, and France (2 each), and Spain, Costa Rica, Iceland, South Africa, Saudi Arabia, Taiwan, Singapore, Mexico, Brunei, Austria, and Switzerland (1 each) (Supplement 3). We revised the preliminary 20 questions (Supplement 2) based on the input from the 47 respondents and, using the priority rankings, maintained the top 20 while allowing for the possibility of new questions arising from the survey to down-vote original ones. The final list of 20 questions is reported in Box 1.

Following the initial survey, we asked 1–3 authors per question from the revised list to address each as a section. Given the strong bias toward North American and male experts from the initial survey (using publication and citation rates), we based author selection on both area of expertise and diversity (geographic, career stage, and gender), including authors outside of the initial 100 experts. The final 47 co-authors are based in 12 countries and represent expertise from every continent.

3. RESULTS

3.1. Status and threats

Elasmobranchs exhibit life history strategies, including slow growth and low fecundity, which result in lower maximum population growth rates than most marine teleost fishes (Myers & Worm 2005). However, high variation in life history traits amongst elasmobranch species results in a spectrum of sensitivity to exploitation. Nearly all (99.6%) elasmobranch species are threatened by targeted and incidental fisheries mortality (Dulvy et al. 2021), a management problem compounded by a scarcity of data on catch magnitude and location and limited management. Additionally, significant data deficiency on life history, biology, abundance, and population impacts (e.g. changes in catch per unit effort and fishing mortality) of elasmobranch species impairs population assessments and the ability to quantify species-specific responses to exploitation and additional conservation threats.

3.1.1. How do we overcome data deficiency in elasmobranch population assessments?

Data Deficient (DD) is a specific term used by the IUCN to characterize species for which we do not have enough data on abundance and distribution to complete conservation assessments. However, this term can be generalized to indicate the extent of knowledge gaps that exist on the life history, ecology, and biology of populations. Formerly, 46.8% of chondrichthyans were DD, but with the advances in research and production of new knowledge over the past decade, this level of data deficiency has now been drastically reduced, with 12.9% of species (155 of 1199) assessed as DD (Dulvy et al. 2021). This rate is lower than across the animal kingdom as a whole: 18.3% (14 912 of 81 569) of taxa on the Red List (2021–3rd update, 4 September 2021) are classified as DD. However, there is still a paucity of assessments at the population scale (Cortés et al. 2012, Simpfendorfer & Dulvy 2017). Less than 5% of elasmobranch species

have been assessed with direct or indirect fisheries stock assessment methods and a much lower proportion is expected at the population level, considering that most species have multiple populations, though the global number of elasmobranch populations is still undefined.

Overcoming data deficiency in elasmobranchs is difficult, as logistics and funding remain persistent challenges for research and monitoring; however, inferences on population status can be made by modeling risk based on life history traits and ecology, using the more data-rich species (e.g. Dulvy & Reynolds 2002). Importantly, elasmobranchs often have life history traits such as slow growth rates, large body size, and low reproductive output, which are generally associated with heightened population decline and extinction risk (Cortés 2000, Field et al. 2009, Dulvy et al. 2014, 2021, Walls & Dulvy 2021). These relationships can be used to help infer unknown extinction risk when the relevant life history traits of DD species are known (Dulvy et al. 2014, 2021, Walls & Dulvy 2021). Quantitative ecological analyses and risk assessments that describe overlaps between species distributions and known threats, such as fishing, can also be used to help infer the status of DD species (e.g. Maxwell et al. 2013). These approaches must be species-specific; for example, in the case of fishing, they must consider whether interactions with fishing gear will result in mortality (Cortés et al. 2010). Methodologies for data-limited stock assessments, such as catch-only, length-based, life-history based, and a variety of other methods (see Sections 3.1.2, 3.2.4, and 3.3.1), continue to improve and can aid in assessing data-limited elasmobranch populations (Jiao et al. 2011, Bradshaw et al. 2018, Carruthers & Hordyk 2018, Zhou et al. 2018). Many of these methods were developed for teleost fishes, and their applicability to elasmobranch life histories is an active area of research (Dureuil et al. 2021).

In synthesis, data deficiency in sharks and rays spans from information gaps in life history and ecology to the absence of the most basic abundance and distribution data for conservation assessment and fisheries management. Continued developments in data-limited assessment methods, particularly when combined with spatial data sets on environmental and human threats, will improve our quantitative understanding of DD sharks and rays and help alleviate the assessment gap in this ecologically important group. Advanced monitoring technologies such as environmental DNA (eDNA) and non-lethal animal detection approaches like baited remote underwater videos (BRUVs) and drone surveys are areas in fast expansion and promising avenues for obtaining independent population abundance indices. Similarly, increasing investment in data collection (see Sections 3.1.4, 3.1.6, 3.2.1, 3.2.4, and 3.3.1) and combining improved analytical techniques with alternative and non-conventional data (e.g. shark bite and sighting records from citizen science platforms) can boost our capability to characterize and predict spatio-temporal trends of distribution and abundance of elasmobranchs.

3.1.2. How can we improve life history estimation for fisheries management and conservation?

Life history studies have been biased towards commercially important species, primarily due to the need to conduct stock assessments and the ability to obtain samples from deceased animals. With research foci shifting from stock status evaluations towards more general conservation, a wider range of taxonomic groups are increasingly being studied, and non-lethal methods for collecting life history data are increasingly being sought (Hammerschlag & Sulikowski 2011, Dureuil & Worm 2015, Hillary et al. 2018).

Length-at-maturity and fecundity are commonly measured traits that are important for assessing population status. Both are still typically measured macroscopically through dissection, although non-lethal techniques including hormonal analysis and ultrasound have been employed (Awruch et al. 2008, Sulikowski et al. 2016). Further comparison of lethal and non-lethal methods is needed to evaluate consistency among approaches (Anderson et al. 2018). An additional priority is determining how fecundity translates into reproductive output. Studies that comprehensively document the uterine and ovarian cycles are needed to determine reproductive frequency with certainty (Walker 2005) rather than relying on assumptions based only on observations of gravid females (Natanson et al. 2019).

Recent studies on age and growth have cast doubt on the ability of growth zone counts on calcified structures such as vertebrae to accurately record age, especially in older individuals (Harry 2018, Natanson et al. 2018, Raoult et al. 2018). New technologies, such as near-infrared spectroscopy and eye lens dating, may pave the way for aging techniques that are not linked to growth zone counts (Nielsen et al. 2016, Rigby et al. 2018). New genomics techniques also provide promise for estimating lifespan in vertebrates (Mayne et al. 2019). Due to difficulties associated with aging and the confounding factor of

fishing mortality on most fish populations (Then et al. 2015), very little is known about natural mortality. Mark–recapture and telemetry studies are beginning to provide insights into this crucially important parameter (Kanive et al. 2015, Benson et al. 2018; Section 3.2.2), with recent research suggesting unified estimators that can be used for both teleost and elasmobranch populations (Dureuil et al. 2021).

Emergent methodologies and non-lethal sampling may provide solutions to some of the challenges in studying elasmobranch life histories. However, an ongoing priority is to establish or continue long-term monitoring programs, including surveys and tagging studies that provide high-quality empirical age, growth, and reproductive data (see Sections 3.2.2 and 3.3.1). Little is known about variability in life history at the population level or how traits respond to natural or human-induced change over long timeframes (Section 3.2.4). Hence, we suggest that greater effort should be directed toward field-based, modeling, and research synthesis studies targeted to fill this knowledge gap. Such information will be essential for improving the effectiveness of population assessment models and, ultimately, management and conservation strategies.

3.1.3. What are the most effective and promising approaches for bycatch mitigation?

Fisheries can have large impacts on elasmobranchs through incidental bycatch (Goñi 1998, Hall et al. 2000, Stevens et al. 2000, Baum et al. 2003, Dulvy et al. 2008, Gray & Kennelly 2018). Even moderate fishing mortality rates can result in population declines for some species (Musick et al. 2000, Kitchell et al. 2002, Rambahiniarison et al. 2018; Sections 3.1.4 and 3.3.7). Changes in fishing methods and gear can increase selectivity and mitigate bycatch of at-risk elasmobranchs (Hall et al. 2017). Of the most promising approaches, avoidance of temporally and spatially predictable elasmobranch bycatch 'hotspots' and changes in gear design have shown the most promise (Table 1).

Additional methods and data that could help improve elasmobranch bycatch assessment and management include (1) utilizing the increasingly available fishing vessel, animal tracking, and environmental data to identify unintended fisheries interactions and inform measures for reducing mortality through avoidance of shark hotspots (e.g. Queiroz et al. 2019); (2) identifying factors affecting post-release survival, such as fish handling, gear soak duration, environmental factors (dissolved oxygen, temperature), anatomical hooking position, and pelagic longline branchline length (Lyons et al. 2013, Butcher et al. 2015, Sepulveda et al. 2015, Musyl & Gilman 2019); (3) research and development of effective shark repellents that could inform gear modification (e.g. Sisneros & Nelson 2001, Kaimmer & Stoner 2008, Brill et al. 2009, Wang et al. 2019); and (4) accounting for cross-taxa conflicts from bycatch mitigation methods (e.g. long-line hook shape; Gilman et al. 2019a).

3.1.4. How can we more accurately measure and monitor total global catch of elasmobranchs?

Overexploitation is the primary threat to elasmobranchs (Dulvy et al. 2014, 2021), which are landed globally as targeted and untargeted catch across a range of latitudes and gear types (Fig. 1; Section 3.3.7). Unreported and inaccurately reported elasmobranch catch statistics contribute to underestimation and uncertainty in the numbers of these species taken each year in fisheries (Worm et al. 2013, Davidson et al. 2016, Cashion et al. 2019). Compounding the lack of catch data is a poor degree of taxonomic resolution of recorded catches. Better catch statistics are needed to address overfishing and inform better management. A key determinant of catch trajectories is the taxonomic resolution of catches, such that countries reporting catches in few aggregate categories are more likely to exhibit declining catch trends than countries with monitored catch differentiated into more and higher taxonomic resolution categories (Davidson et al. 2016). Together, these limitations make it challenging to accurately estimate fishing mortality rates and conduct reliable population assessments.

A straightforward, if tedious, method for estimating the global catch of elasmobranchs is to complement marine catch data from the FAO by reconstructing the unreported portion, and then identify its marine elasmobranch component, disaggregated to the lowest possible taxonomic level (Cashion et al. 2019; www.seaaroundus.org). This approach assumes (1) wherever fisheries occur, they must have a non-zero catch; and (2) that fisheries, as social activities, can be inferred indirectly, e.g. from fish consumption studies of coastal dwellers, the number of canoes along beaches, or weirs visible on satellite images (Pauly 1998, Pauly & Zeller 2016a). A reconstruction of FAO-reported and unreported global elasmobranch catches from 1950–2016 suggests that since 2000, estimated catch has peaked and is now maintained at a level of around 1.5 million t annually (Fig. 1).

Table 1. Methods to mitigate unwanted bycatch and mortality, and examples relevant to elasmobranchs

Bycatch mitigation approach	Elasmobranch example	Citations
Modify fishing gear	Increase gillnet tension and adjust mesh size. Use monofilament instead of wire for pelagic longline leaders. Use appropriate case-specific hook shape (e.g. circle or J) in pelagic longlines. Use finfish instead of squid for bait in pelagic longline fisheries. Use non-entangling fish aggregating devices (FADs) by tuna purse seine fisheries. Use bycatch reduction devices and grids in trawl fisheries.	Brewer et al. (2006), Werner et al. (2006), Zeeberg et al. (2006), Larsen et al. (2007), McAuley et al. (2007), Ward et al. (2008), Thorpe & Frierson (2009), Curran & Bigelow (2011), Filmalter et al. (2013), Restrepo et al. (2018)
Deterrents	Use UV lighting on gillnets. Use electropositive metals on longlines (and possibly other gears).	Hutchinson et al. (2012), Wang et al. (2019)
Modify fishing methods	Alter the case-specific depth and time-of-day of fishing. For instance, deep daytime pelagic longline sets for bigeye tuna avoid epipelagic sharks (but may overlap thresher shark vertical habitat). Remove shallower pelagic longline hooks to decrease catch rates of oceanic whitetip *Carcharhinus longimanus*, silky *C. falciformis*, and other epipelagic sharks. Employ seasonal closures on FAD sets, avoid sets on relatively small tuna schools, and ban sets on whale sharks and rays in tuna purse seine fisheries.	Moyes et al. (2006), Musyl et al. (2011), Dagorn et al. (2012, 2013), Gallagher et al. (2014), Forget et al. (2015), Hutchinson et al. (2015), Watson & Bigelow (2014), Restrepo et al. (2018)
Temporal and spatial management	Prohibit fishing at spatially and temporally predictable bycatch hotspots, or in areas or periods with relatively high ratios of bycatch to target catch.	Gilman et al. (2019a), Hays et al. (2019), Watson & Bigelow (2014)
Input and output controls	Limit fishing effort or catch. For instance, establish a seasonal limit on the catch of an overexploited species of shark	
Retention and discard bans	Intended to incentivize fishers to use more selective fishing methods and gear, prohibit the retention of at-risk taxa that have market value, e.g. for oceanic whitetip and silky sharks in tuna fisheries, or ban discarding species with low or no market value.	European Commission (2012), Condie et al. (2013), WCPFC (2012, 2013)
Compensatory mitigation (biodiversity offsets)	Meet bycatch mitigation through compensation to address non-fishery threats, or through a fee and exemption structure, similar to a 'polluter pays' system. For instance, governments could reduce or withhold subsidies or charge a higher license fee if bycatch thresholds are exceeded.	FAO (2010)
Avoid and remediate ghost fishing	Avoid producing abandoned, lost, and discarded fishing gear, and reduce the fishing efficiency of derelict gear. For example, degradable escape mechanisms are required in some trap fisheries.	Macfadyen et al. (2009)
Minimize stress and injury while captured and during handling and release	Release sharks and rays from within purse seine nets before pursing Release sharks in the water, leaving less than 1 m of trailing line Do not use 'lazy lines' to drag longline-caught sharks through the gear haulback	Poisson et al. (2014), Butcher et al. (2015), Hutchinson et al. (2015), Escalle et al. (2016), Hutchinson et al. (2019), Hutchinson & Bigelow (2019), Musyl & Gilman (2019), Zollett & Swimmer (2019)

Estimated catches in tropical climatic zones continue to grow (Fig. 1C), with dogfishes (Family Squalidae) increasingly dominating by weight (Fig. 1A). Estimated elasmobranch catches from nets (including trawls) have declined since the 1990s, increasingly displaced by line catch (Fig. 1B).

Accurately quantifying elasmobranch catch requires that these species be prioritized by national

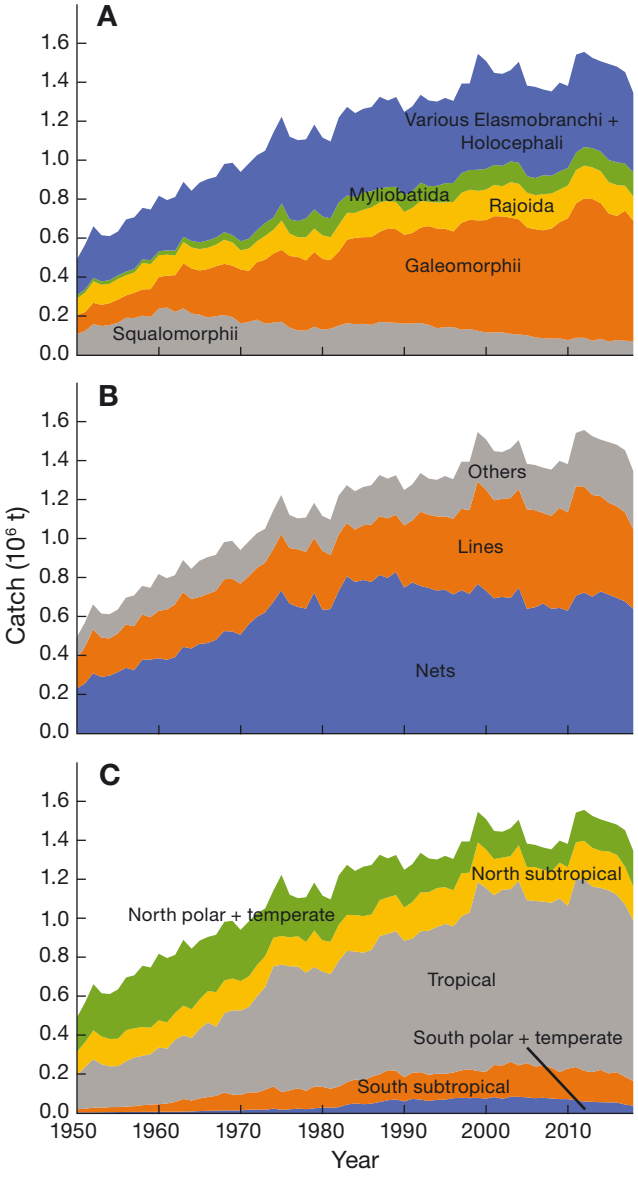

Fig. 1. Global marine catch of elasmobranchs. A reconstruction of FAO reported and unreported global elasmobranch catch over time by (A) major clade, (B) major groups of fishing gears, and (C) major climatic zones

agencies and Regional Fishery Bodies (RFBs), such that resources are invested to better monitor the fisheries in which elasmobranchs are taken as targeted catch as well as those that catch them incidentally. Future work should be focused on improving the taxonomic resolution of catch composition through observer training (Stevenson 2004, Tillett et al. 2012, Macbeth et al. 2018) and technologies such as species identification via artificial intelligence (AI; e.g. Angers et al. 2017). Further development and validation of indices for unreported catch, such as satellite imagery of coastal activity (Al-Abdulrazzak & Pauly 2014), remote fishing vessel tracking (Kroodsma et al. 2018; Section 3.3.6), and electronic monitoring of fisheries (van Helmond et al. 2020), will improve estimation of unreported catch. Finally, developing toolkits for assessing large-scale data-limited artisanal fisheries in developing countries will also help address a large unknown.

3.1.5. Beyond fishing, what are the emerging threats to elasmobranchs?

Emerging threats (the sources of stressors to elasmobranchs) besides fishing remain anthropogenic in nature. Impacts of coastal habitat loss and climate change stressors including ocean warming, acidification, and deoxygenation are expected to grow with increasing human population levels. These threats are compounded by uncertainties in future range shifts (e.g. Niella et al. 2020, Tanaka et al. 2021), also fueled by climate change (Hazen et al. 2013, Poloczanska et al. 2016).

Second to (but in addition to) overfishing, habitat loss and degradation resulting from coastal development, agriculture/aquaculture (such as mangrove destruction for shrimp farming), and indirectly through climate (Roff et al. 2016a) has been flagged as a threat for sharks and rays, jeopardizing over one-third (31.2%) of threatened species (Dulvy et al. 2014, 2021). This threat is particularly acute in coastal, estuarine, and riverine habitats, disproportionately affecting endemic species (Dulvy et al. 2014, 2021), freshwater species (Lucifora et al. 2015), and hence, nearshore nursery areas (Cuevas-Gómez et al. 2020). Mechanistic links between habitat preservation and restoration and population dynamics should be further explored.

Rising ocean temperature is expected to shift species distributions poleward (Perry et al. 2005, Pinsky et al. 2020), including elasmobranchs (Tanaka et al. 2021). To survive, species with limited distributions will need to evolve rapidly or exhibit phenotypic plasticity to adapt to these changes (Vila Pouca et al. 2018). A small number of studies (to date) on the effects of rising temperature and ocean acidification have reported changes in elasmobranch behavior, hunting rate, physiology, and even skeletal mineralization (Di Santo 2019). At the individual level, sharks are particularly vulnerable to elevated temperatures (Vila Pouca et al. 2018), which adversely affects their metabolic efficiency, digestion rates, and growth (Di Santo & Bennett 2011, Pistevos et al. 2015, Rosa et al. 2016). Exposure to elevated oceanic carbon dioxide

levels can result in reduced olfactory responses (Dixson et al. 2015, Pistevos et al. 2015) and changes in swimming rates, hunting and prey detection, as well as brain development and function (Green & Jutfelt 2014, Vila Pouca et al. 2018). Ocean deoxygenation (Oschlies et al. 2018) poses an additional challenge to elasmobranchs (Sims 2019) in open ocean and nearshore environments (Lawson et al. 2019). A greater understanding of oxygen uptake rates and fitness responses to environmental conditions is key to understanding deoxygenation impacts (Bouyoucos et al. 2019). Overall, there is a pressing need for an increased understanding of the mechanistic effects and population-level responses to climate-related threats. Based on current knowledge, 10.2% of threatened species are threatened by climate change (in addition to overfishing), mediated through 2 pathways: species shifting poleward (e.g. Tanaka et al. 2021) and species suffering from the loss and degradation of habitat, such as seen in the epaulette sharks (Dulvy et al. 2021, VanderWright et al. 2021).

Finally, pollution is currently a relatively minor and non-lethal stressor, affecting 6.9% of the 1199 assessed elasmobranch species, with little effect on shark and ray extinction risk compared to the overwhelmingly dominant threat of overfishing compounded by habitat loss/degradation and climate change (Dulvy et al. 2021). Similarly, global shark tourism has grown in the past 2 decades and shows mixed impacts on shark physiology, behavior, and ecology (Maljković & Côté 2011, Huveneers et al. 2013, Barnett et al. 2016) but has no effect on shark persistence and mortality. Although limited to a handful of primarily coastal species (Macdonald et al. 2017), shark tourism is expected to increase and eventually surpass shark fisheries in economic value (Cisneros-Montemayor et al. 2013), and therefore sustainable practices should be assessed and implemented.

3.1.6 How can we reconstruct elasmobranch baselines to inform population decline estimations and recovery targets?

The recent collection of scientific data reflects only a very small fraction of the history of degradation of the oceans (Lotze & Worm 2009). This imperfect understanding of the original state of our oceans and animal abundance biases our understanding of marine ecosystem change and often results in unambitious conservation targets (McClenachan et al. 2012). Elasmobranchs, in particular, have entered research agendas only in recent decades; hence, scientific data became available long after the initial onset of human impacts. However, several approaches have been developed to reconstruct elasmobranch baselines.

Preserved museum specimens and fossil assemblages can be used to reconstruct past elasmobranch community structure (White et al. 2019a). For example, museum collections of shark tooth weapons have been used to reveal the presence of species and reconstruct baseline communities in central Pacific islands (Drew et al. 2013). Research on pre-scientific accounts and museum collections has helped identify the presence of 2 sawfish species in the Mediterranean Sea, a region previously deemed to have unsuitable environmental temperatures for these species (Ferretti et al. 2016). Dermal denticles from sediment cores allowed reconstruction of pre-human elasmobranch community baselines in coral reef ecosystems (Dillon et al. 2017, 2021).

Historical naturalist accounts, exploratory fisheries surveys, and historical photographs compared to modern scientific records have been used to document the effect of exploitation on sharks in the last 2 centuries (Ferretti et al. 2010, Martin et al. 2016), including the local or functional extinction of historically abundant shark species from coral reef ecosystems and large oceanic expanses (Baum & Myers 2004, McClenachan 2009, Luiz & Edwards 2011, Ferretti et al. 2013, Dulvy et al. 2021). Yet in many cases, these are likely tail ends of depletions that began long before records began.

Space-for-time substitution models are often employed to understand the nature of relatively undisturbed shark populations. In remote coral reef ecosystems, SCUBA diving surveys have been used to produce densities ranging from 218 sharks km^{-2} in no-entry marine reserves of the Great Barrier Reef (Robbins et al. 2006) to 200 000 sharks km^{-2} in uninhabited atolls of the Line Islands (Sandin et al. 2008). These numbers, particularly the higher end, are likely methodological overestimates (Ward-Paige et al. 2010a, McCauley et al. 2012a) and were subsequently scaled back (Bradley et al. 2017). However, combining these data across multiple systems and analyzing them along human footprint gradients with other historical indices of abundance allows for the estimation of pre-exploitation densities (Nadon et al. 2012) and more robust quantifications of past population abundances (Bradley et al. 2017, Ferretti et al. 2018). In the Chagos Archipelago, this integrative approach suggested that population baselines previously set with SCUBA diving observations (Graham et al. 2010) were already altered states as a result of

the local and regional history of fishing and protection (Ferretti et al. 2018).

Understanding to what extent these remote systems represent baseline conditions for elasmobranch populations and community assemblages is now paramount (Stevenson et al. 2007, Sandin et al. 2008). For many present-day remote and uninhabited coral reef ecosystems, indirect effects of exploitation in the surrounding oceanic waters may have altered the structure and function of the ecosystems (through removal of broad-ranging predators and competitors) for decades before we could describe them scientifically (Ferretti et al. 2018). Furthermore, additional research is needed to understand the full extent of human impacts in coastal ecosystems, which have much longer exploitation histories than insular coral reef and oceanic ecosystems and do not offer simple equivalent spatial contrasts of human presence.

3.2. Population and ecology

Defining species in terms of distribution and genetic uniqueness is critical for assessing population units and implementing management actions for sharks. However, completing this foundational task is non-trivial since many shark species are migratory, dispersing relatively widely on a seasonal or ontogenetic basis. At the same time, even the most migratory species may exhibit strong site fidelity and natal philopatry (Jorgensen et al. 2010). As a result, gene flow can be sex-mediated and complex relative to spatial distribution, including cryptic sympatric speciation (e.g. Fields et al. 2016). Available genetic and tagging tools have been applied unevenly, leaving gaps in this critical knowledge of many less charismatic species. As a group, sharks are commonly cited as playing an important functional role in ocean ecosystem structure and function (Estes et al. 2016), yet this assertion remains untested for many species, and more studies are needed to document their trophic and ecological interactions across a range of systems (Heithaus et al. 2008, Bird et al. 2018).

3.2.1. What are the knowledge gaps in global abundance and diversity of elasmobranchs?

Eschmeyer's Catalogue of Fishes (Fricke et al. 2019) lists 1287 valid species of chondrichthyans (elasmobranchs and chimaeras), including 1231 species of elasmobranchs. Estimated distribution data for these species have become digitally available only over the past decade (Fig. 2). Recent map shapefiles are available for 1188 chondrichthyan species; the only species that could not be mapped are those known from a single depth or whose depth could not be inferred from relatives in their family (Dulvy et al. 2021).

From the distribution data sets that currently exist, several broad-scale patterns emerge. Like marine biodiversity overall (Tittensor et al. 2010, Jenkins &

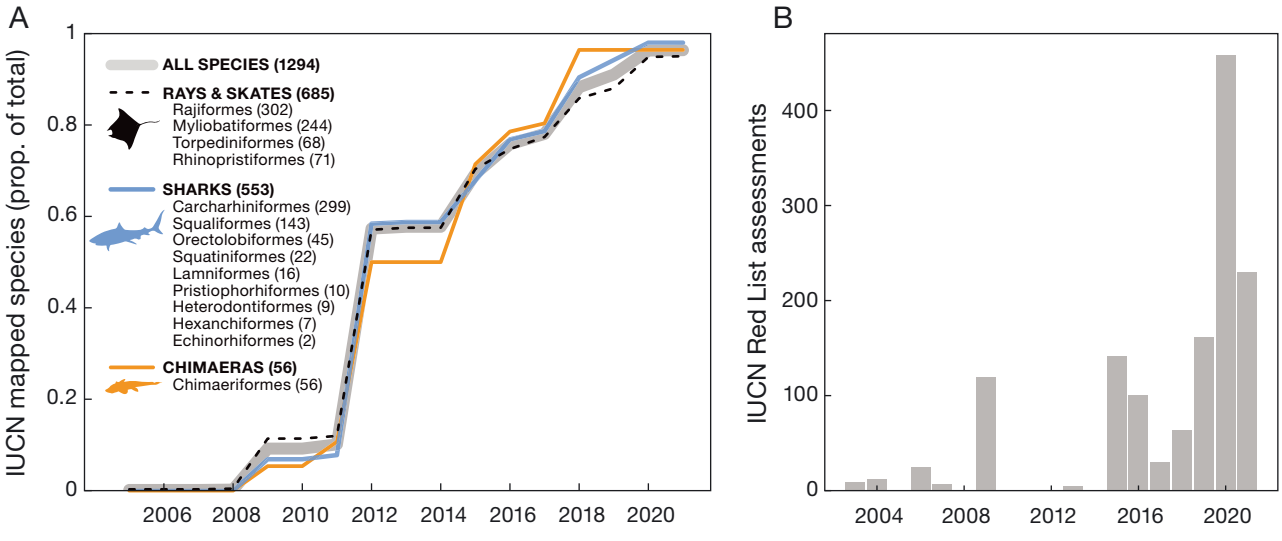

Fig. 2. Time series of available IUCN distribution and assessment data for chondrichthyans. (A) Accumulation curves for elasmobranchs and chimaera species range data availability. Representation of all major elasmobranch groups has grown remarkably in the last decade. Labelled species counts are the total described species for that taxonomic group (Fricke et al. 2019), not the number with available distribution data (IUCN 2021). (B) Current (end of 2020–2021) Red List assessment publication dates for chondrichthyans

Van Houtan 2016, Gagné et al. 2020), sharks (Lucifora et al. 2011, Guisande et al. 2013) and rays (Guisande et al. 2013) are most diverse on continental shelves near shore (Dulvy et al. 2014, 2021). More specifically, species richness for all 3 groups peaks at mid-latitudes (25–30° N and S) and in the extreme western Pacific (Lucifora et al. 2011, Guisande et al. 2013, Dulvy et al. 2014). The major global hotspots for threatened, small-ranged, and endemic chondrichthyans are in coastal southeast South America, in the South and East China Sea, off southeast Africa, and off eastern Australia (Davidson & Dulvy 2017, Stein et al. 2018). Obligate freshwater elasmobranchs are confined primarily to South America and secondarily to Southeast Asia, with one obligate freshwater species found in west Africa (Lucifora et al. 2015, Grant et al. 2019, Dulvy et al. 2021). To date, however, no fine-scale spatial data sets are available to determine spatial patterns within these broad regions.

As geographic range and population data are critical for assessing population and species status and crafting effective conservation (Lucifora et al. 2011, Dulvy et al. 2014, Stein et al. 2018; Sections 3.2.4 and 3.3.3), providing open-access distribution data for the remaining chondrichthyan species should be prioritized. However, extent of occurrence range maps can have limitations (Jenkins & Van Houtan 2016). IUCN shapefiles were based on the distribution of taxonomic specimens and surveys as summarized in natural history field guides (Dulvy et al. 2021) that include some interpolation based on expert opinion. They have coarse spatial resolutions (i.e. at the nation level) and are static in the context of species' range shifts. Shapefile polygons were drawn to include the entire ocean jurisdiction of nations where the species were deemed to occur, adjusted with known depth distribution ranges (for demersal species) and likelihood of occurrence in high-seas waters (for broad-ranging species) (Dulvy et al. 2021). Understanding to what extent these shapefiles are data-informed and tracking these sources is often challenging. Therefore, it is important that we increasingly transition toward standardized empirical approaches that can be readily updated with new data and methodology. Furthermore, while the IUCN shapefiles are useful for global and regional scale planning, national-scale conservation planning would benefit from the development of species distribution models based on both the global range map as well as local species occurrence data.

Empirically derived niche-based models that yield probabilistic distributions (Gagné et al. 2020, Reygondeau et al. 2020) may provide further insight into underlying environmental drivers of aggregated richness and distribution patterns (Sabadin et al. 2020) that may inform protected-area design. Such data products may also advance conservation applications, such as forensic analyses and enforcement of illegal, unreported, and unregulated (IUU) trade in chondrichthyans (e.g. Worm et al. 2013). These models need to clearly acknowledge the limitations and biases related to the availability of source records and state associated output uncertainty to avoid yielding inaccurate distributions when extrapolated beyond the region of interest (Raoult et al. 2021).

Assessments of population trends are heterogeneously distributed. Most population trend analyses have been performed for sharks of the orders Lamniformes and Carcharhiniformes (mainly Carcharhinidae and Sphyrnidae) (e.g. Baum et al. 2003, Ferretti et al. 2008, Hayes et al. 2009, Curtis et al. 2014, Kanive et al. 2021, Pacoureau et al. 2021). All other shark orders have fewer assessments (e.g. Hexanchiformes: Barbini et al. 2015; Squaliformes: Graham et al. 2001; Orectolobiformes: Bradshaw et al. 2008). Rays lag behind sharks, with most formal assessments conducted on large charismatic taxa (e.g. Mobulidae: Ward-Paige et al. 2013) or commercially important species (e.g. Rajiformes: Dulvy et al. 2000, Swain et al. 2013). Population trend estimations for Torpediniformes, Myliobatiformes, Rhinopristiformes, and Chimaeriformes are rare (although see Shepherd & Myers 2005, Ward-Paige et al. 2011, Ferretti et al. 2013, Carlson et al. 2007, and Barnett et al. 2012, respectively), even though some of these taxa may have intrinsically high vulnerability to overexploitation (Moore 2017, Yan et al. 2021). Habitat is another factor affecting the number of assessments. Most population-trend assessments are of demersal or neritic populations (e.g. Dulvy et al. 2000, Robbins et al. 2006, Carlson et al. 2007), which is not surprising given that the highest diversity of chondrichthyans occurs in coastal demersal and neritic habitats (Compagno 1990, Dulvy et al. 2021). Many oceanic populations have also been assessed (e.g. Ward & Myers 2005, Baum & Blanchard 2010, Clarke et al. 2013, Barreto et al. 2016, Pacoureau et al. 2021), which may be explained by the increasing economic importance of oceanic sharks given their prominence as incidental and increasingly target catch in tuna and billfish fisheries. Far less common are assessments of deep-water (e.g. Graham et al. 2001, Devine et al. 2006, Barnett et al. 2012) and euryhaline or freshwater populations (O'Connell et al. 2007, Lucifora et al. 2017).

Most chondrichthyan populations that have been assessed as sustainable occur in a few developed countries (Simpfendorfer & Dulvy 2017). At the same

time, most of the countries with the highest chondrichthyan catches are in the developing world (Worm et al. 2013, Davidson et al. 2016, Lucifora et al. 2019). This means that chondrichthyan populations in the developing world may be at high risk from overexploitation, and indeed there is disproportionate threat, with more than 75% of coastal species threatened in the tropics and subtropics (Dulvy et al. 2021). Collecting data and building capacity for analyzing those data in order to make informed management decisions is a major imperative for developing countries (Dulvy et al. 2017).

3.2.2. How can tagging technologies be applied more effectively to inform elasmobranch research and conservation?

Elasmobranchs have been electronically tagged (i.e. satellite, acoustic, or archival tags) across all oceans, and availability of data on position, behavior, and habitat use is increasing (Hussey et al. 2015a, Queiroz et al. 2019). A pervading motivation of such tagging studies is that movement data are needed to develop effective management and conservation strategies for these animals (Hays et al. 2019). Indeed, many studies have documented the spatial ecology of taxa relative to anthropogenic threats on both horizontal (Lyons et al. 2013, Queiroz et al. 2019, White et al. 2019b) and vertical (e.g. Coelho et al. 2015, Hutchinson et al. 2015, Carvalho et al. 2018, Musyl & Gilman 2019, Andrzejaczek et al. 2019) scales, enabled estimates of both natural and fishing mortality (Byrne et al. 2017, Benson et al. 2018), and/or assessed the efficacy of spatial management techniques such as marine protected areas (MPAs) (e.g. Espinoza et al. 2015, Carlisle et al. 2019; see Section 3.3.2 below).

For conservation strategies to be effectively implemented, however, a comprehensive understanding of a target species' spatiotemporal distribution is essential, which necessitates that a representative cross-section of the species (i.e. individuals of both sexes and a range of reproductive states, sizes, and body conditions) is tracked across its 3-dimensional range. Consequently, the cost, logistics, ethics (e.g. animal welfare considerations), and often opportunistic nature of tagging activities generate difficulties in obtaining such large and representative sample sizes of study species (Sequeira et al. 2019). As many species tend to segregate by sex and size (Sims 2006, Speed et al. 2010), sampling will often also be biased by the regional composition of the sample population. For assessing climate-related threats (Section 3.1.5), biologging technology provides a means to quantify tolerances (e.g. to deoxygenation; Jorgensen et al. 2009, Coffey & Holland 2015) and likely ranges of responses — an important knowledge gap for predicting shark and ray range shifts under future conditions (Hazen et al. 2013, Tanaka et al. 2021). Collaborative global initiatives that compile movement data collected in stand-alone studies (see Harcourt et al. 2019; Table 1) can facilitate the identification of areas (e.g. the high seas and in developing countries) and portions of a population that should be prioritized in future tagging efforts. Similarly, the data gaps in spatial distribution and home range highlighted in Section 3.2.1 offers good leads on where more telemetry effort should be focused. Early engagement with stakeholders involved in policy development and implementation is also paramount to allow tagging data to be translated into conservation outcomes (Lea et al. 2016, Hays et al. 2019). To better address elasmobranch conservation in the future, it will be important to (1) target data gaps by focusing efforts on hypothesis-driven tagging studies, (2) maximize the accessibility and utility of funded tagging efforts through promptly open-sourcing data sets, methods, and tag technologies, (3) develop novel applications for existing or lightly modified tagging technologies, and (4) pursue miniaturization of technologies to better study smaller and more threatened species.

3.2.3. How can we more clearly define the ecological role of elasmobranchs?

There is evidence that top-level predator sharks can play important roles in marine ecosystems (Heithaus et al. 2008, Ferretti et al. 2010, Estes et al. 2016, Roff et al. 2016a), and their removal through fisheries has often coincided with strong population responses of lower-level elasmobranchs. Ecological roles of elasmobranchs include top-down control of prey (Myers et al. 2007, Heithaus et al. 2008), nutrient cycling (Williams et al. 2018), facultative scavenging (Dudley et al. 2000, Drymon et al. 2019), biocontrol of invasive species (Diller et al. 2014), habitat modification (O'Shea et al. 2012), and possibly removal of weak and diseased individuals (Hammerschlag et al. 2016). Despite the potential for elasmobranchs to fulfill a broad range of ecological roles in marine ecosystems, data supporting the majority of these hypotheses are limited to relatively few case studies, and additional empirical data are needed. Furthermore, our understanding of the ecological role of

elasmobranchs has largely been limited to medium-sized and large sharks that are commonly encountered; in contrast, the ecological roles of smaller, deep-water, or less abundant elasmobranchs are unknown beyond more basic descriptions (Heupel et al. 2019, but see Moxley et al. 2019).

Substantial knowledge gaps exist for the context-dependence of ecological roles, which is important in terms of quantifying the consequences of elasmobranch removal or recovering elasmobranch populations. For example, we have little understanding of the role of fear in driving many of the large-scale and long-term ecosystem changes attributed to sharks (Heithaus et al. 2008, Ferretti et al. 2010, Jorgensen et al. 2019, Shea et al. 2020). Also unknown are factors affecting population sizes of key prey taxa (i.e. density-dependent processes) and potential compensatory reproduction relative to predation rate. The lack of clarity of these issues has led to diverging viewpoints on the role of sharks in driving trophic cascades (e.g. Grubbs et al. 2016, Roff et al. 2016b, Ruppert et al. 2016). Further, relying on dietary data alone to assess the potential for sharks to initiate trophic cascades may significantly underestimate the strength of aggregate effects on prey (Heithaus et al. 2008, Hammerschlag et al. 2019) by overlooking the real magnitude of risk effects (i.e. non-trophic interactions). Promising future directions in elucidating ecological and trophic roles include the use of BRUVs (e.g. Shea et al. 2020) or stable isotopes to resolve trophic complexity at top levels (Hussey et al. 2015b) and to infer resource use and ontogenetic patterns (e.g. Raoult et al. 2019), individual-based models to understand habitat use and spatial patterns (e.g. Papastamatiou et al. 2018), and systematic empirical studies of predator abundance and behavior (e.g. Jorgensen et al. 2019) at global scales.

3.2.4. How can we improve knowledge of elasmobranch population structures?

Knowledge of population structure is critical to management and conservation policies and actions. At the evolutionary level, population structure information is needed for estimating extinction risk in threatened species and for a rigorous application of criteria for IUCN Red Listing. At the demographic level, population structure informs the design of protected areas and recovery plans, and the delineation of management units. Studies assessing elasmobranch population structure have increased sharply in the past decade due to the development of genetics and genomics techniques. These approaches are becoming a crucial tool for informing conservation and management (Dudgeon et al. 2012, Domingues et al. 2018), as the resolution provided, especially by genomics, has led to more accurate identification of population structure even at small geographic scales (Pazmiño et al. 2017). Moreover, studies combining genetics and tagging (e.g. Jorgensen et al. 2010) provide a link between evolutionary and ecological structure. In addition to tagging, other non-genetic techniques such as mark–recapture (e.g. Kanive et al. 2015) or parasite load (e.g. Morris et al. 2019) inform ecological-scale population structure and should be used for cross-validation with genetic and genomic techniques.

Review of the literature shows that sharks have received disproportionately more attention than rays (Castillo-Páez et al. 2014, Dulvy et al. 2014, Shiffman et al. 2020), particularly for species that are charismatic, abundant, and/or affected by industrial fisheries (e.g. tiger shark, pelagic thresher; Cardeñosa et al. 2014, Carmo et al. 2019). Additionally, geographic gaps remain in several areas (e.g. Africa, South America).

The advent of next-generation sequencing methods offers an encouraging future for increasing knowledge on elasmobranch population structure (Johri et al. 2019). Genomic resources (e.g. species-specific data, reference genomes) combined with analytic and computational methods are constantly being developed (Naylor et al. 2012, Hara et al. 2018, Marra et al. 2019) and should be integrated with an improved sampling strategy to address the existing taxonomic and geographic gaps. Furthermore, training opportunities for researchers in developing countries and collaborative platforms and data repositories are needed to increase species and geographic representation in studies and ensure the best use of existing samples.

3.3. Conservation and management

International recognition of the need for shark conservation and management is increasing. Two comprehensive assessments of the status of sharks and rays have concluded that over one-third of species are threatened (Dulvy et al. 2014, 2021). Forty-five species of sharks and rays are now listed in the CITES and Convention on the Conservation of Migratory Species (CMS) Appendices, and several countries have now adopted national and international plans of action for the conservation and management of elasmobranch stocks. However, shark

and ray conservation faces implementation obstacles due to market drivers (e.g. shark fins), IUU fishing, and challenges with adoption of recommended management plans and effective enforcement. The political motivation for conservation is also dependent on perceptions of public safety and valuation of ecosystem services. How to best achieve effective conservation and management goals remains divisive (Shiffman & Hueter 2017, Porcher et al. 2019, Ferretti et al. 2020). A number of conservation strategies have been implemented or proposed ranging from market regulation (e.g. CITES Non-detriment Findings and fin trade regulations), to MPAs and shark sanctuaries, to an increased emphasis on species-specific stock assessments and subsequent implementation of catch quotas. Ultimately, science should be applied to select the best approach or portfolio of strategies to achieve the goal of shark and ray conservation. However, relevant data remain sparse, including assessments of the impacts of various fishing sectors, evaluations of the efficacy of MPAs and shark sanctuaries to sustain shark populations, and the analysis of the biological and harvest criteria for sustainability. Additionally, our understanding of the socio-economic factors surrounding market demand and how public perception can influence governance requires greater resolution to improve shark conservation and management.

3.3.1. What is the role of citizen science in elasmobranch conservation research?

Citizen science complements and expands our capacity to understand elasmobranchs and threats to their populations (Ward-Paige et al. 2010a, Davies et al. 2012, Vianna et al. 2014, White et al. 2015). By putting more eyes on the oceans, beaches, ports, and markets, data from millions of explorers (often posted on social media platforms) can provide insights on markets, movements, threats, and spatial and temporal trends (e.g. eOceans [previously eShark], www.eOceans.co; sharkPulse, http://sharkPulse.org; the Shark Sightings Database, https://www.sharktrust.org/sightings-database). These data have informed policies including shark sanctuaries (Ward-Paige et al. 2010a), CITES listings (Ward-Paige et al. 2013), IUCN Red List status (e.g. *Stegostoma tigrinum* and *Mobula alfredi*; Ward-Paige et al. 2010b, 2013), and conservation baselines (Ward-Paige et al. preprint doi:10.1101/2020.02.04.932236).

By adopting technological, big-data, and advanced analytical techniques, citizen science has the potential to expand elasmobranch monitoring and discovery — making it more collaborative, transparent, and accessible across geographic and cultural contexts. This is particularly important for elasmobranchs that are listed as DD, lack recent formal assessment, or cross political borders, as different regions may have varying resources and capacities. Additional values include education, support for science-based management, and collection of socio-economic data.

Citizen science programs vary greatly in effort and level of participant expertise. Therefore, bias and error in these data need to be considered and made explicit with respect to the questions being asked (Davies et al. 2012). For example, it was found that people with diving experience of around 20 dives can count sharks as accurately as those with 3000 dives (Ward-Paige et al. 2010b), which is important for reliable shark abundance estimates. In contrast, species identification is less precise and is more complex (e.g. influenced by interest, exposure, training) and requires additional validation techniques for species-specific analyses (Johnston et al. 2018). Finally, these data are often uncontrolled for observation effort, and efficiently estimating this aspect is paramount for extracting reliable indices of population abundance (Moro et al. 2020).

To fully harness citizen science to inform elasmobranch science and conservation, there is an urgent need to increase coordination, leadership, investment, and collaboration between scientists, government, and community groups. Novel platforms where scientists and citizen scientists process data and collaborate in real-time have exciting potential (Bargnesi et al. 2020). Going forward, breakthroughs will likely lie in harnessing the full potential of the integration of citizen science with traditional science and new technologies (eDNA, sensor technologies, image analysis, and AI developments).

3.3.2. How can MPAs contribute to elasmobranch conservation?

MPAs, defined here as marine spatial protections which restrict some or all fishing activity, may contribute to elasmobranch conservation by limiting targeted and incidental mortality and protecting areas of critical habitat within their boundaries. Widespread advocacy for MPAs as a tool for restoring elasmobranch populations has contributed to recent and rapid increases in their implementation. To date, 17 countries have created shark-specific MPAs, or shark sanctuaries, restricting targeted fishing for sharks

(and in some sanctuaries, rays) within their exclusive economic zones (EEZs) and thus providing enforceable ecosystem protection (Ward-Paige & Worm 2017).

Over the past decade, one-third of the growth of MPA extent has been motivated by shark conservation; however, fewer than 10 threatened species have less than 10% of their geographic range within a non-take MPA (Davidson & Dulvy 2017). Ongoing debate regarding the potential of MPAs for elasmobranch conservation centers on challenges associated with implementation, enforcement, and long-term monitoring (Daly et al. 2018) and the difficulty in attributing biological outcomes to MPA establishment (Ferraro & Pressey 2015). Research suggests that MPAs can be beneficial for some species, particularly those with restricted home ranges (Davidson & Dulvy 2017, White et al. 2017, Dwyer et al. 2020), but many countries lack the resources for successful enforcement and monitoring, and baseline population data for target species are often unavailable (Ward-Paige & Worm 2017; Section 3.2.1). Addressing these challenges is key to the implementation of effective spatial protection measures.

Ensuring that MPAs can contribute to elasmobranch conservation requires consideration of the biological, socio-economic, and political context in which they are established. Geographic regions should be prioritized based on clear objectives (e.g. protection of endemics) and the likelihood for success (Dulvy et al. 2017, Mizrahi et al. 2019), and MPA design should be informed by data on movement patterns and habitat use of target species (Knip et al. 2012, Chapman et al. 2015, Lea et al. 2016, Speed et al. 2016). Novel spatial approaches to elasmobranch assessment using widely available trawl survey data and other data sources may further help to constrain areas of fishery interaction and inform placement of spatial management measures to protect vulnerable populations. Further, considering the local socio-economic context, engaging stakeholders and emphasizing social outcomes (e.g. livelihood benefits) can help achieve the support and compliance necessary to realize the biological benefits of MPAs (MacKeracher et al. 2019, Mizrahi et al. 2019).

To date, many MPAs are ineffective in protecting vulnerable elasmobranchs due to weak regulations, lack of enforcement, and high fishing pressure inside the MPA (e.g. Dureuil et al. 2018). Ultimately, the potential for MPAs to contribute to elasmobranch conservation, particularly for highly mobile species (Gilman et al. 2019b), will be greatest if they are appropriately placed, co-designed and co-managed with relevant stakeholders, well-enforced, and complemented with other management measures that extend beyond the MPA boundaries (e.g. bycatch management, gear restrictions, and effort control; Curnick et al. 2020; Sections 3.1.3, 3.3.3).

3.3.3. Under what conditions can elasmobranch fisheries be sustainable?

The sustainable nature of elasmobranch take in fisheries has long been debated given their slow life histories (Holden 1973, Stevens et al. 1997, Walker 1998, Cortés 2004). An overview of sustainable take of sharks demonstrated that 39 stocks of 33 species were sustainably fished, representing 27% of global capture production as reported by the FAO and 9% of estimated total global catch (Simpfendorfer & Dulvy 2017). Some of these stocks appear to be sustainable despite the absence of management, providing a false sense of security. Hence, it is not enough for a stock to meet the biological criteria for sustainability, but it also requires an effective management process to be in place (Hilborn et al. 2015). It is also important to factor in current inconsistent definitions of 'sustainability' among fisheries management authorities (e.g. in selecting variable limit and target biological reference points for elasmobranch stocks) when objectively evaluating sustainability and management goals.

Conventional wisdom is that only the most productive species with fast life histories can be fished sustainably. Surprisingly, many species with low productivity (e.g. as measured by r_{max}; Pardo et al. 2016) can and do support sustainable fisheries, but good data collection and strict management systems must be in place to control fishing mortality, typically through science-based catch limits (Simpfendorfer & Dulvy 2017). The challenge is that most elasmobranchs are taken as incidental catch or in multispecies fisheries where fishing effort is inevitably optimized for productive target teleost species but is too high for the elasmobranch species (Worm et al. 2009, Burgess et al. 2013; Sections 3.1.3 and 3.1.4).

Proactive science-based management with species-specific precautionary catch limits is a bare minimum to ensure sustainability. To a first approximation, the size and development of the local economy and governance are leading indicators of the capacity to manage fisheries, maintain abundance, and avoid extinction of fisheries as a whole (Melnychuk et al. 2017) and of sharks specifically (Davidson et al. 2016, Simpfendorfer & Dulvy 2017). The challenge is to secure sustainable fisheries in developing countries that

have a lower capacity to implement sustainable catch limits, are home to more threatened species, and catch the bulk of the world's elasmobranchs (Dulvy et al. 2017, 2021, Booth et al. 2019, Lucifora et al. 2019). This will require research focused not only on the biological characteristics of species to support the setting of science-based catch limits, but also socio-economic research that considers approaches to implementing catch limits in nations and communities where sharks are integral to food security and livelihoods (e.g. Booth et al. 2020; Section 3.3.4).

3.3.4. What is the socio-economic role of elasmobranch fisheries?

Elasmobranch fisheries focus on meat for human and animal consumption and processing and trade of several commodities — fins, liver oil, cartilage, and skin — each with unique dynamics of demand and profitability, with shark meat and fins playing the most important economic roles. The declared economic value of global shark fisheries production is close to $2.6 billion USD (WWF 2021). The relatively well-documented trade in shark fins is economically important for traditional markets (~$1.5 billion USD from 2012 to 2019) (WWF 2021) but has no influence on food security. However, in response to declines in traditional fisheries productivity and changes in shark fishing regulations (e.g. finning bans), non-fin shark commodities, especially meat, are on the rise.

From 2001–2011, global trade in shark meat increased by more than 40% and likely continues to rise (Dent & Clarke 2015). Shark meat is an important source of protein in many parts of the world, especially in developing countries because of its low cost (Dulvy et al. 2017). Because shark meat is consumed locally and traded globally through complex networks — while often mislabeled — shark meat markets remain difficult to unveil (Prasetyo et al. preprint doi:10.1101/2020.12.08.416214). Tackling this uncertainty is a key challenge for the management of shark populations, as well as for ensuring the livelihoods of fishers and local communities. Since conservation measures for sharks (or population collapses) might negatively affect protein supplies for vulnerable human populations around the world, there is an urgent need for further studies of the food security dependencies on shark meat and alternatives for human populations.

Despite their relatively slow life history characteristics, research has shown that biologically sustainable elasmobranch fisheries do exist, though not always with adequate management in place (Simpfendorfer & Dulvy 2017; Section 3.3.3). Going forward, the key priorities for ensuring sustainable elasmobranch fisheries are (1) increasing capacity for science-based management to ensure sustainability of fisheries, (2) developing a better understanding of the global and domestic market for shark non-fin commodities, (3) increasing consumer access to information for seafood products, including transparency in supply chains and accurate product marketing, as well as the health implications of consuming shark meat, and (4) better understanding the social drivers of shark and ray fishing, local food security needs, and economic tradeoffs of management scenarios (Prasetyo et al. preprint doi:10.1101/2020.12.08.416214).

3.3.5. How can we quantify ecosystem services provided by elasmobranchs?

Ecosystem services are benefits humans gain from ecosystems or ecosystem components. Elasmobranchs provide several key ecosystem services that benefit society, either directly as a source of food (Dulvy et al. 2017), tourism (Gallagher & Hammerschlag 2011), and spirituality (Skubel et al. 2019), or indirectly by maintaining ecosystem connectivity (McCauley et al. 2012b) and influencing ecosystem structure (Estes et al. 2016) and function (Britten et al. 2016). There is also growing evidence suggesting that large predators (including sharks) may indirectly influence carbon sequestration, as the relationship between predators and herbivores/bioturbators is an important determinant of plant and microbe photosynthetic carbon pathways (Atwood et al. 2015). Further research investigating and quantifying the possible roles of elasmobranchs in climate mitigation through carbon sequestration (Atwood et al. 2015, Hammerschlag et al. 2019) is a key priority.

Elasmobranch fisheries, sustainable or not (see Section 3.3.4), can provide a source of food and livelihood for fishers. It is noteworthy, however, that elasmobranchs can hold significant socio-economic importance in terms of their value in diving tourism (Gallagher & Hammerschlag 2011, O'Malley et al. 2013, Zimmerhackel et al. 2018, Mustika et al. 2020). Studies have reported the value of sharks in dive tourism at various scales — from the individual organism level (Vianna et al. 2012) to national (Haas et al. 2017) — and commonly report these figures in terms of dollars (typically USD) calculated by incorporating expenditures on the tourism product and its associated activities (Huveneers et al. 2017).

Exposure to elasmobranchs through dive tourism may engender attitudes that promote conservation of sharks (e.g. Sutcliffe & Barnes 2018, Apps et al. 2018) and has led several countries with a large dependence on dive tourism to protect all sharks in their waters (Ward-Paige & Worm 2017). However, it remains unknown how pro-conservation attitudes translate into policy change elsewhere. One concern is that these mechanisms can work only for developed countries with appropriate tourism infrastructure. Another challenge is that only a small fraction of species is currently of importance to tourism (Macdonald et al. 2017). As such, at present, non-consumptive value can only be used directly to drive conservation for a small number of elasmobranchs. There are, therefore, future opportunities for expanding non-consumptive value to a broader set of species and geographies. To this end, key needs are to develop sustainable, context-appropriate ecotourism models and to elucidate the possible unintended consequences of tourism on sharks and rays. Evidence for the behavioral and physiological consequences of provisioning (feeding sharks during tours) on elasmobranchs, in particular, is mixed (Brena et al. 2015, Gallagher et al. 2015). Therefore, determining the specific ecotourism activities that lead to physiological or behavioral effects is a research priority.

Cultural, spiritual, and emotional values are also important and can drive economic and political decision-making processes (e.g. Friedrich et al. 2014); spiritual associations with sharks have long been a part of numerous indigenous and native island cultures, including the historical self-imposition of catch limits (Skubel et al. 2019). Bioinspiration is an often-overlooked ecosystem service of elasmobranchs. For example, novel materials have been engineered with shark skin-mimicking surfaces to design more aerodynamic drones, planes, and wind turbines (Domel et al. 2018).

3.3.6. What is the role of vessel tracking in assessing and enforcing fisheries interactions with elasmobranchs?

The conservation of elasmobranchs can be significantly improved by better understanding how these species overlap and interact with fisheries. Understanding fisheries interactions is crucial for identifying regions of conservation concern, assessing the impact of management actions, and detecting illegal fishing (McCauley et al. 2016, Queiroz et al. 2016). Unfortunately, reliable information on elasmobranch–fisheries interactions (e.g. catch, discards, and landings data) is not available for many regions and species. Major fisheries databases frequently contain sparse information for elasmobranchs, as most data is self-reported and penalties are rarely imposed for nations that withhold or misreport catch (Clarke et al. 2013, Campana 2016).

The recent proliferation of vessel tracking data and big data analytics offers valuable insight into the spatiotemporal overlap of elasmobranchs and industrial fisheries (Queiroz et al. 2016, 2019, White et al. 2019b). The global fishing effort of over 70 000 industrial vessels is now publicly accessible due to vessel tracking and transparency initiatives (Kroodsma et al. 2018). The resulting global fishing effort map was combined with satellite tracks of 1681 pelagic sharks to reveal substantial overlap between shark hotspots and global fishing effort (Queiroz et al. 2019). Additionally, vessel tracking can improve our design and enforcement of fisheries regulations, including shark sanctuaries or remote MPAs that restrict shark fishing (Bradley et al. 2019; Section 3.3.2). For example, illegal fishing within the Phoenix Islands Protected Area was detected using remotely sensed vessel tracks, leading to a 7-figure fine (McCauley et al. 2016). Vessel tracking-derived views of fishing activity alongside animal telemetry also revealed that a large MPA was effectively protecting grey reef shark populations from fisheries interactions (White et al. 2017). These tandem analyses of space use by elasmobranchs and humans may play a crucial role in guiding the placement of protected areas on the high seas, as are currently being considered by the United Nations (Heffernan 2018).

Future advances in vessel tracking (e.g. more consistent satellite coverage, more precise identification of vessel gear type; Park et al. 2020) and increased availability of catch and effort data sets will increase our ability to more precisely identify the regions where vessels and elasmobranchs not only overlap with specific gears but also interact directly leading to mortality (e.g. Queiroz et al. 2019). Current remote sensing studies often produce indices of spatial overlap between sharks and fisheries, but do not quantify interactions in terms of catch, bycatch, or mortality estimates (Murua et al. 2021, Queiroz et al. 2021). In order to fully realize the benefits of vessel tracking, effective policy regulating its consistent and transparent use must be expanded, as application is currently centered on large-scale pelagic fisheries and is limited or nonexistent in coastal and small-scale fisheries (SSF) (Kroodsma et al. 2018).

3.3.7. What are the relative impacts of small-scale, industrial, and recreational fisheries on elasmobranch populations?

Part of the grand challenge of more accurately assessing the global take of elasmobranchs (Section 3.1.4) will be differentiating the relative impacts of different fisheries sectors (i.e. large-scale/industrial, small-scale, and recreational) with each posing a different suite of challenges. While global elasmobranch landings as reported by the FAO are on the order of 100s of 1000s of t annually (Bonfil 1994, Catarci 2004), when bycatch and discards are considered, estimates soar to as high as 1.4 million t (Worm et al. 2013), 1.6 million t (Section 3.1.4, Fig. 1), or 1.7 million t (Clarke et al. 2006). Moreover, information on global landings of rays is much more limited (Dulvy et al. 2000, 2014, 2016, Saldaña-Ruiz et al. 2016). Satellite tracking of marine animals and fishing vessels show a high degree of spatial overlap between pelagic shark species and pelagic longlines (Queiroz et al. 2019), but these estimates are not yet translated into catch and catch rates indexes. While onboard observer schemes are well developed, coverage is variable, and political will and resources are needed to ensure adequate coverage. Electronic monitoring technologies are becoming quite well developed in this sector and offer great possibilities for augmenting observer coverage (Gilman et al. 2019a; Section 3.3.6).

The role and impact of SSF on elasmobranchs is less clear, as these fisheries are more difficult to monitor than large-scale industrial fisheries. Incidental catch in SSF often compounds the impact of large-scale fisheries for 62.3% of elasmobranch species assessed by the IUCN (Dulvy et al. 2021). SSF are thought to contribute up to one-third of global fish catch (Chuenpagdee et al. 2006), and more than half of the catch in developing countries (FAO 2020) where elasmobranchs constitute important fishery resources (Catarci 2004, Blaber et al. 2009, Cartamil et al. 2011, Saldaña-Ruiz et al. 2016, Hearn & Bucaram 2017; see Sections 3.3.3 and 3.3.4). Impacts differ from industrial fleets (e.g. Blaber et al. 2009, Cartamil et al. 2011, Humber et al. 2017, Temple et al. 2018) because SSF typically catch a greater diversity of species and tend to retain all species (Oliver et al. 2015). Improved data can be gathered from onboard observers (if vessels are large enough), landing surveys, or voluntary reporting (e.g. Doherty et al. 2014, Humber et al. 2017). In addition, remote camera monitoring has been trialed with some success (Bartholomew et al. 2018).

The impact of recreational fisheries globally is also difficult to monitor and govern because data are sparse outside of the USA and Australia (Fowler & Cavanagh 2005, Gallagher et al. 2017, Arlinghaus et al. 2019). Recreational vessels are estimated to account for ca. 1% (Pauly & Zeller 2016b) to 10% of global fish catch (Cooke & Cowx 2004), and sharks are often the target. In some localized areas, recreational catch of sharks may exceed that of commercial fisheries and may contribute to important ecological impacts (Fowler & Cavanagh 2005). Even in catch-and-release fisheries, sharks may still suffer from injury or post-release mortality (e.g. Kneebone et al. 2013, Whitney et al. 2017). Recreational fisheries would benefit from greater oversight and reporting (Arlinghaus et al. 2019), but this would likely have to include voluntary schemes. Top priorities for elucidating fishery impacts on elasmobranch populations include (1) clarifying the relative contributions of target catch and discards, (2) standardizing landings and bycatch reporting metrics, (3) increasing monitoring, particularly of small-scale and recreational fisheries (including through the use of novel technologies like electronic monitoring) with the goal of implementing management measures, and (4) enhancing reporting of historically overlooked species such as rays, skates, and sawfishes.

3.3.8. How can we reconcile public safety with healthy elasmobranch populations?

Increasing coastal human populations and aquatic activities have contributed to a rise in the global number of shark bites and stings from stingrays (Chapman & McPhee 2016), fueling public perception of increasing risk (Crossley et al. 2014, Sabatier & Huveneers 2018), even though risks from elasmobranchs remain low (e.g. Ferretti et al. 2015). Discrepancy in public understanding of risk assessment when comparing activities for which individuals have perceived control (e.g. risk of drowning while swimming) is common in low-probability–high-consequence events (Loewenstein et al. 2001, Sunstein 2002). Negative perceptions may impede conservation of globally endangered shark species (Thompson & Mintzes 2002, Treves & Bruskotter 2014).

Actual risk is geographically highly variable (Midway et al. 2019). Studies to date show per capita risk decreasing in some regions (Ferretti et al. 2015) and remaining unchanged in others (Midway et al.

2019), while a few locations have emerged as hotspots showing increasing occurrence and probabilities of shark bites (Chapman & McPhee 2016). Quantifying ocean activity and its effect on shark incidents, which differs from the common proxy of total population size, is crucial for estimating the probability of shark bites and remains a challenge (Ferretti et al. 2015). Unless effective mitigation (e.g. deterrence or avoidance) can be implemented, or human use of the marine environment changes, the number of shark bites, though extremely rare, is likely to continue rising with growing coastal human populations and ocean use, even if shark populations fail to recover.

The challenges in shark–human conflict are therefore to (1) learn from risk perception theories and psychology to educate the public about the actual shark bite risk and reduce fear that can lead to ineffective policies; (2) better quantify covariates to per capita risk in identified hotspots, including habitat destruction, variability in climate, and prey availability; (3) continue investing in new mitigation measures while ensuring adequate testing of their efficacy, and control the commercialization of untested products; and (4) proactively educate the public about the ability of mitigation measures to reduce risk and manage expectations.

3.3.9. What are the species composition and population impacts of the shark fin trade?

The strong demand and high market value of shark fins, for shark fin soup, remains a primary driver of global shark fisheries despite recent market declines. Recent surveys in the Hong Kong Special Administrative Region of the People's Republic of China, based on processed shark fin trimmings, revealed a total of 81 species/species complexes, with a small subset of pelagic and highly migratory species dominating the composition (Fields et al. 2018, Cardeñosa et al. 2018a; Fig. 3A). In contrast, a recent survey of small, low-value fins in Hong Kong revealed a different species composition dominated by coastal species (Cardeñosa et al. 2020; Fig. 3B). These surveys have shown that around 20–30% of the species in both large- and small-fin products are listed on Appendix II of CITES and around one-third are from species listed in IUCN Red List threatened categories (Fields et al. 2018, Cardeñosa et al. 2018a, 2020).

It is difficult to assess the precise extent to which international fin trade is driving shark mortality. The importance of the shark meat trade was recently highlighted by a global study, which revealed a 42% growth from 2000–2011, with South America and

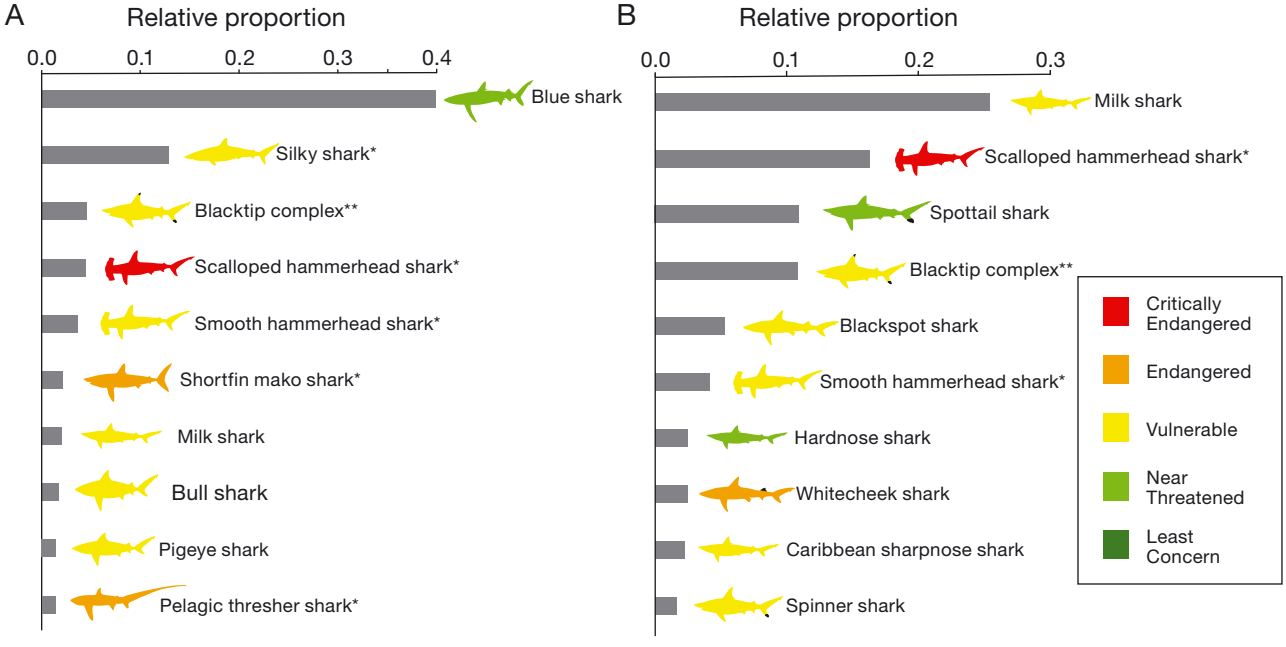

Fig. 3. Relative proportion of the top 10 species (or species complexes) represented in the Hong Kong shark fin retail market based on genetic identification of (A) 9200 shark fin trimmings collected between 2014 and 2017 and (B) 475 small, low-value fins. (*) Appendix II CITES-listed species; (**) blacktip complex comprising *Carcharhinus limbatus*, *C. amblyrhinchoides*, *C. leiodon*, and *C. tilstoni*

Europe as the largest consumers (Dent & Clarke 2015, Okes & Sant 2019; Section 3.3.4). Nevertheless, historically and at present, large volumes of shark trade represent threats to the populations of many shark species (Ferretti et al. 2020). Not all sharks enter the fin and meat trade because some individuals are caught and killed inadvertently as bycatch and may be discarded at sea (Gilman et al. 2008, Worm et al. 2013). Quantification of the fin trade alone suggests catches reached 300% above reported levels prior to Regional Fisheries Management Organization (RFMO) finning bans (Clarke et al. 2006), underscoring the importance of continuing shark trade monitoring programs. The critical threats to sharks require that these programs be scaled-up, appropriately targeted, properly resourced, and better linked to fishery management decision-making (Dent & Clarke 2015, Cardeñosa et al. 2018b, 2019, 2020).

3.3.10. What are the impacts of regulations across elasmobranch species and jurisdictional scales?

Among the described elasmobranch species, some 99.7% are threatened by target, bycatch, and catch-all industrial and/or subsistence fisheries, which take place in the waters of well over 100 countries and on the high seas (Dulvy et al. 2021; Sections 3.1.3, 3.1.4, 3.3.3, 3.3.4, 3.3.7). Only a small proportion of these fishing states have National Plans of Action (NPOA; under the voluntary FAO International Plan of Action for the Conservation and Management of Sharks) and even fewer have introduced national fisheries management measures specifically for elasmobranchs (Davidson et al. 2016). Many catches are not reported by species or taxonomic group, or reported at all, and taxon-specific trade data are extremely sparse (Cashion et al. 2019). More than 80 countries trade in elasmobranch products, with different trade routes for meat, fins, and other products, and some 80 elasmobranch species have been identified in the Hong Kong retail fin market (Cardeñosa et al. 2018a). Over 52 RFBs (advisory and management) could potentially contribute to the management of elasmobranch fisheries; 32 RFBs that are of potential relevance for species listed in CITES, including 14 RFMOs, 10 of which have adopted one or more Conservation and Management Measures (CMMs) for elasmobranchs. By early 2019, 6 Regional Plans of Action (RPOA), including the EU's, and 2 Regional NPOA guidance documents had been adopted; only 1 of the 6 was by an RFMO (Joint Technical Commission of the Maritime Front; CTMFM), while the others were a mixture of advisory RFBs and Regionals Seas Conventions and Action Plans (RSCAPs).

International consensus has been reached on the threatened status of a growing number of elasmobranch species. Under current taxonomy, 45 elasmobranchs are listed in CITES Appendix II (which requires international trade in their products between the 183 CITES Parties to be legal, sustainable, and traceable) and 7 sawfish species — of which 5 are recognized in current taxonomy — are listed in CITES Appendix I, which prohibits commercial trade. Due to catch prohibitions in a few RFMOs and national protected status for the CMS Appendix I species that occur in the waters of CMS Parties, many countries will not be able to trade legally in 4 species of sharks and 9 rays listed in CITES Appendix II. Despite these restrictions, the fins of the widely protected oceanic whitetip shark still comprise some 1% of the shark fin trade (Fields et al. 2018). Eight species of freshwater stingrays (Potamotrygonidae) from Colombia and all species of *Potamotrygon* from Brazil are listed in CITES Appendix III. This requires stingrays exported from those countries to have a certificate of origin and an export permit; however, smuggling of stingrays between countries and taxonomic issues may undermine the conservation value of these listings (Lucifora et al. 2022).

Despite international recognition of extinction threats to elasmobranchs, adoption of voluntary protection and mitigation measures has lagged. Of the approximately 150 migratory elasmobranch species, 39 are listed in the Appendices of the CMS. The 131 CMS Parties have committed to work collaboratively toward the conservation of CITES Appendix II-listed species and affirmed that Appendix I species are to be strictly protected. In 2018, only 28% of CMS parties had fully met their obligations to protect Appendix I species, and 33% had partly done so (Lawson & Fordham 2018). A similar but not identical list of species is in the Annex to the CMS Memorandum of Understanding of Migratory Sharks (Sharks MOU). Signatories to the Sharks MOU have agreed to facilitate the conservation of species listed in this Annex.

Work is also necessary to resolve ongoing disagreement between policy actions targeted to elasmobranch protection. Most notable are the management and conservation role of establishing shark sanctuaries in many nations' EEZs (Ward-Paige 2017) and banning shark fin trade as a means of mitigating targeted global shark catch for fins (Shiffman & Hueter 2017, Porcher et al. 2019, Ferretti et al. 2020). Shark sanctuaries and fin bans are often opposed to promoting sustainable shark fishing, even though these should not be considered mutually exclusive options.

4. DISCUSSION

The growing number of threatened elasmobranchs identified on the IUCN Red List and the growing number of species listed by international conventions, conservation agencies, and management bodies such as CITES and CMS, and under national legislations such as the United States Endangered Species Act demonstrates a growing global consensus on the threats to these taxa. Furthermore, some 12.9% of all chondrichthyan species are listed as DD, and their conservation status cannot presently be assessed (Dulvy et al. 2021). This is alarming since DD species more frequently become classified as threatened (versus not threatened) when data eventually become available (Dulvy et al. 2021). However, despite a growing conservation concern globally, effective conservation and management actions remain constrained by lack of political will, socio-economic constraints and trade-offs, and knowledge gaps, including limited data on population status, human–shark interactions, specific threats, and the relative efficacy of different management and conservation approaches. Finally, translating emerging and future science and conservation strategies into action requires sufficient political will to conserve sharks and rays.

In the face of rapidly escalating threats and limited funding, it is essential that priorities for research and action are identified for a suite of urgent environmental issues, including halting biodiversity loss. 'Horizon scanning' reviews and syntheses (e.g. Sutherland et al. 2019), like the one presented here, can increase the awareness of researchers, practitioners, and decision-makers and focus on priority areas, improving capacity to develop and implement solutions, and promote new collaborations and opportunities. Recent similar efforts have focused on specific elasmobranch taxa (e.g. Stewart et al. 2018) or identifying priorities for elasmobranch conservation (e.g. Dulvy et al. 2017, Stein et al. 2018). The UN Decade of Ocean Science for Sustainable Development (2021–2030) provides unprecedented opportunities for expanding research capacity broadly (Lubchenco & Gaines 2019). As such, prioritizing both fundamental research and management action, with input from a diverse group of experts, is especially timely.

Increasing global focus on elasmobranch conservation has unveiled a growing list of species that are threatened. Shark take continues to be driven, in part, by a high but declining demand for shark fins (Dent & Clarke 2015). At the same time, there is a growing market for shark and ray meat, likely as human population growth and declining premium fisheries fuel the need to consume generally lower value elasmobranch meat. Incidental catch also remains the most significant threat contributing to global take, with almost all chondrichthyan species taken unintentionally in fisheries (99%: 1082 of 1093; Dulvy et al. 2021). Technological advances for reducing incidental catch and increasing post-release survival are increasingly addressing the significant mortality threats posed by bycatch in commercial fisheries (Clarke et al. 2014). Our ability to quantify global catch increasingly relies on rapidly developing indirect and robust estimation methods, as under-reporting (or no-reporting) by countries to the FAO may underestimate global catch by up to a factor of 3 or 4 (Clarke et al. 2006, Okes & Sant 2019). Quantification of take at the species level is increasingly being improved in the shark fin market through forensic DNA analysis (e.g. Fields et al. 2018). Advances in genetic techniques and image recognition technologies hold promise for extending this ability to other market sectors, but economic barriers to monitoring at market sources in developing countries will need addressing. The challenge of linking elasmobranch products in aggregated markets (e.g. Asian market hubs) to their geographical source could be addressed with molecular techniques and probabilistic range mapping informed by robust tagging programs and citizen science photographic contributions. A large unknown is the growing potential of climate-related threats, which include direct physiological effects from warming, acidification, and deoxygenation as well as indirect effects such as range shifts (Dixson et al. 2015).

Assessments of species and populations have revealed considerable variability in elasmobranch stock productivity (Cortés et al. 2012). However, a massive gap remains between the number of populations exploited versus those assessed for sustainable management (Simpfendorfer & Dulvy 2017). A grand challenge remains to fill data gaps for DD species and populations requiring management and conservation. Research funding has disproportionately been directed toward relatively few charismatic species (Shiffman et al. 2020).

There is also a need to transfer lessons learned from these in-depth studies to other DD and more sensitive species, such as deepwater elasmobranchs (Kyne & Simpfendorfer 2010, Jabado et al. 2018), reef shark species (Osgood & Baum 2015), and rays — particularly guitarfishes and wedgefishes (Kyne et al. 2020), which are underrepresented in population

structure studies, landings data, and basic biological reference points. Addressing knowledge gaps on key aspects of elasmobranch biology requires further developments in data-poor methods, as well as technological, citizen science, data syntheses, and analytical advances. Electronic tagging studies and techniques are crucial to characterize multiple aspects of elasmobranch ecology. Unlike conventional tagging, electronic tagging has largely been confined to larger species due to large tag sizes and high cost. Miniaturization, lowering cost, and open-source/ 'DIY' techniques provide a path to extend techniques to smaller and less charismatic DD species (e.g. Wang et al. 2019). For rare and protected species, non-destructive techniques for delineating life history, population structure, and distribution and abundance estimation such as photographic (Kanive et al. 2015) and electronic tagging methods (Benson et al. 2018) and eDNA (Carrier et al. 2018) provide encouraging opportunities and potential. A top priority is to establish or continue long-term monitoring programs, including surveys and tagging studies that provide high-quality empirical data for data-poor species.

Implementation of effective management and conservation has lagged behind international recognition of extinction threats, even for data-rich threatened species. Existing international mandates for individual species protection at the international level depend largely on compliance with stated RMFO regulations (e.g. International Commission for the Conservation of Atlantic Tunas [ICCAT] species prohibitions). They are binding (enforceable) primarily at the point of trade across international boundaries, which is why CITES may be the most appropriate international mechanism for regulating trade restrictions (Campana 2016). Advances in seafood labeling and tracking will increasingly leverage these policies. Other approaches include MPAs and shark sanctuaries, which provide ecosystem protection primarily within nations' EEZs.

Enforcement remains a considerable challenge to the effectiveness of both ecosystem-level and species-based protective management (Jacoby et al. 2020). Emerging technologies to address enforcement include vessel tracking, remote imaging (including electronic monitoring of fisheries such as 'security' type camera observation), and forensic techniques. Particular attention should also be directed toward major global hotspots for threatened and small-ranged elasmobranchs (e.g. coastal Indo-Pacific and hotspots in Africa, South America, and North America). It is clear that there is no single silver bullet for better management, and that multiple approaches are needed to safeguard against depletion (Dulvy et al. 2017). Adoption of protective measures will also depend on the reconciliation of shark protection with the perception of public safety (Ferretti et al. 2015).

A call to action must also include addressing the human dimension of elasmobranch management and conservation through meaningful integration of stakeholders, including local and indigenous people at all stages of shark research, management, and conservation processes. The survey participants and author list in this study underscore a current lack of geographic, racial, and gender diversity in the field (also see Shiffman et al. 2020). Increasing diversity and participation in research, within academia, and across sectors and stakeholder groups is a key priority. Greater understanding of the social drivers of shark and ray fishing, local food security needs, barriers to education, collaboration, communication, enforcement decision-making as well as the economic tradeoffs of management scenarios are needed to ensure more sustainable conservation outcomes. Success will require the creation of opportunities to increase local ownership and linkages to management through novel participatory mechanisms, and a greater commitment to funding and development of local scientific and leadership capacities and gender equity. Combined, these actions will provide enabling conditions to secure a future for threatened species of sharks and rays.

Despite clear knowledge and data gaps, this review highlights the diversity of studies, programs, and data on elasmobranchs from a suite of geographies and ecosystems that can effectively move the needle towards more effective elasmobranch conservation. This compilation underscores the opportunities and requirements for more collaboration and data integration across elasmobranch research groups and programs, including multi-stakeholder collaboration and citizen science. Here, we have highlighted the current challenges for new analytical and technological development, as well as knowledge transfer across disciplines in assessing population status and threats, ecological dynamics, and conservation and management approaches. We hope that going forward, this synthesis of a large body of work and identification of research priorities will inspire renewed investments to better understand and preserve the legacy of one of the earth's oldest vertebrate lineages, representing some 500 million yr of evolutionary history, and its key roles in structuring and connecting food webs, ecosystems, and socio-ecological systems.

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