PLANKTIVOROUS SHARKS AND RAYS

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SPECIES DIVERSITY, ECOLOGY, AND DISTRIBUTION

Planktivorous sharks and rays are an ecological grouping of at least 12 species, including nine rays and three sharks. The rays are all within the family Mobulidae and genus *Mobula*, including two currently recognised species of manta rays (formerly *Manta*). Species-level taxonomy is not fully resolved within this group, and one or two additional species may be delimited (Stewart et al., 2018; Hosegood et al., 2020). The three planktivorous sharks are Whale Shark (*Rhincodon typus*), Basking Shark (*Cetorhinus maximus*), and Megamouth Shark (*Megachasma pelagios*), which span the orders Orectolobiformes (Whale Shark) and Lamniformes (Basking Shark and Megamouth Shark). All three species are in monospecific families, so they are not closely related. Whale Shark and Basking Shark are considered in the top 50 'Evolutionarily Distinct and Globally Endangered' (EDGE) sharks and rays in the world (EDGE, 2017).

This group contains the largest sharks and rays, and indeed the largest poikilothermic vertebrates. Whale Shark reach 18–20 m in length, while the other two aforementioned shark species also exceed 7 m. The Oceanic Manta Ray (*Mobula birostris*) is the largest of all rays, growing to around 7 m in disc width (DW). The smallest species in this group are the four pygmy devil rays (Munk's Pygmy Devil Ray [*Mobula munkiana*], Atlantic Pygmy Devil Ray [*Mobula hypostoma*], Shorthorned Pygmy Devil Ray [*Mobula kuhlii*], and Longhorned Pygmy Devil Ray [*Mobula eregoodoo*]), which all attain maximum DW of ~1.3 m (Stewart et al., 2018; Notarbartolo di Sciara et al., 2020).

Planktivorous sharks and rays range from coastal to oceanic waters across a circumglobal distribution, with Basking Shark reaching the Arctic Circle in the north. Several other species also penetrate temperate waters, although the highest diversity is found in the tropics. All species inhabit or at least transit through equatorial waters at times.

These taxonomically disparate species are united by their dietary preferences, which centre on zooplankton and small fishes. The mechanisms of prey capture vary among species. The acrobatic mobulids are capable of backward somersaulting in dense zooplankton patches, using their specialised cephalic fins to channel prey into their mouths. Basking Shark can simply open its huge mouth in plankton-rich temperate waters to filter over 800,000 litres per hour while continuously swimming (Sims, 2008), and Whale Shark can use suction to take immense 'gulps' of zooplankton and fish eggs (Heyman et al., 2001).

The challenge faced by these sharks and rays is the low mean quantity of prey in warmer seas. Tropical oceans are characterised by poor primary productivity, with the highest densities found in upwelling and frontal zones. This then concentrates zooplankton patches, and the planktivores that feed on them. To ensure a net energy gain from feeding, planktivorous sharks and rays rely on locating these dense patches of prey, which vary in space, depth, and across the seasons. In many cases, even diel or tidal cycles strongly influence planktivore foraging ecology. For instance, individual Reef Manta Ray (*Mobula alfredi*) in Hanifaru Bay in the Maldives switched from non-feeding to feeding behaviour specifically when copepod densities exceeded 53.7 mg dry mass m^{-3}, with large groups forming to feed together when prey density was over 200 mg dry mass m^{-3} (Armstrong et al., 2021). Whale Shark will routinely migrate large distances to exploit predictable feeding opportunities, such as the broadcast spawning of finfish (Heyman et al., 2001), timing their movements to coincide with ephemeral spawning events (Graham, 2007).

The need to travel large distances to exploit patchy prey resources is likely to be an important driver of the extreme body sizes seen in this group, as large bodies confer energy-efficient movement and high energy storage capacity. Basking Shark tagged in northeastern United States (US) were tracked swimming thousands of kilometres south, some crossing the equator to the Brazilian coast (Skomal et al., 2009), while Whale Shark in aquaria routinely go through periods of apparently voluntary 'fasting', suggesting that this is a normal aspect of their ecology (Wyatt et al., 2019).

Similarly, there can be a need for substantial vertical movements in search of prey (Graham, 2007). Several members of this group are capable of exceptionally deep dives, with tagged Whale Shark exceeding 1,900 m depth (Tyminski et al., 2015), and multiple species have been tracked diving into the bathypelagic zone. Most of these species probably feed on deeper prey at times, with the piscivorous Sicklefin Devil Ray (*Mobula tarapacana*) thought to feed in the deep scattering layer below 800 m (Thorrold et al., 2014), and some individual Basking Shark spending up to five months at 250–1,000 m depth (Skomal et al., 2009).

The ecology of the Megamouth Shark is presumed to be generally similar to other planktivorous sharks and rays, but this huge species remains remarkably enigmatic. Only 261 sighting and landing records were documented from its discovery in 1976 up to 2021 (Yu et al., 2021). Megamouth Shark are thought to feed primarily on krill (euphausiids), possibly using ram filter-feeding (Tomita et al., 2011). The species has a distinctive, highly-reflective white band on its 'lip', which may reflect the light produced by bioluminescent prey species to in turn attract photosensitive zooplankton toward the shark's large mouth immediately beneath (Duchatelet et al., 2020).

MAJOR DRIVERS OF LOSS

Aside from the Megamouth Shark, which is rarely encountered or caught across most of its broad distribution (Yu et al., 2021), all planktivorous sharks and rays are threatened (Vulnerable or Endangered) on the IUCN Red List of Threatened Species. These listings indicate global declines exceeding 30–50% in these species.

Fisheries have been the primary driver of declines and remain a major ongoing threat to mobulid rays (Croll et al., 2016; Rohner et al., 2017; Moazzam, 2018; Carpenter et al., 2023). Since the early 2000s, the largest fisheries for planktivorous sharks and rays have grown to supply fins, meat, and gill plates to southeast Asian markets. Trade routes have meant that most industrialised fisheries have been in the Indian Ocean, southeast Asia, and western Pacific Ocean.

Organised fisheries for Basking Shark in northern Europe date back to at least the 18th Century. Basking Shark fisheries in Norway, Scotland, and Ireland landed an estimated 105,000 individuals between 1946–1997 (Sims, 2008). Whale Shark have also been caught opportunistically in fisheries since at least the 1850s, including for the international export of their fins, but large-scale directed fisheries only began in several countries during the 1980–1990s, when Whale Shark meat came to be regarded as a marketable delicacy in Taiwan (Pierce et al., 2021). Both species are now estimated to be at <50% of their pre-fishing populations globally (IUCN, 2023). Megamouth Shark constitute a regular non-target catch in Taiwanese drift gillnet fisheries, but mandatory release has been in place since 2020 (Yu et al., 2021). While targeted fishing for planktivorous sharks has now largely ceased, an unquantified level of non-target catch – which may be significant in some fisheries – is ongoing.

Mobulid rays are still routinely caught across much of their distribution by both large- and small-scale fleets (Stewart et al., 2018; Fernando & Stewart, 2021). At least 21 small-scale fisheries land mobulid rays as non-target catch in 15 countries, mainly in drift gillnets, purse seines, trawlers, and occasionally longlines (Croll et al., 2016; Alfaro-Cordova et al., 2017). Offshore, they are primarily caught in gillnet and purse seine fisheries (Stewart et al., 2018; Lezama-Ochoa et al., 2019; Fernando & Stewart, 2021). Industrial fisheries land considerable quantities of mobulids as non-target catch, estimated at ~13,000 individuals each year in the tropical tuna purse seiner fleet, which are mostly discarded (Croll et al., 2016; Lezama-Ochoa et al., 2019). Although formal stock assessments are lacking, mobulid rays are considered overfished in Sri Lanka, where mortality rates of Spinetail Devil Ray (*Mobula mobular*) were estimated to be two to six times higher than the upper bound of the maximum intrinsic rate of population increase for this species (Pardo et al., 2016; Fernando & Stewart, 2021). Across their range, mobulids taken in small-scale fisheries are often retained and sold for domestic consumption (Winter et al., 2020).

Mobulid gill plates are a valuable product in Hong Kong Special Administrative Region (SAR) and mainland China (Zeng et

Basking Shark, *Cetorhinus maximus* in the United Kingdom | Simone Caprodossi al., 2016; O'Malley et al., 2017), and drive many of the industrial fisheries for these species. Comprehensive assessments of the gill plate industry in China, prior to mobulid Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) listings (see below), showed that Guangzhou accounted for the majority of the trade from 2010–2013 (O'Malley et al., 2017). However, by 2015, the Guangzhou market had declined sharply (reportedly due to conservation campaigns and government policies) and was overtaken by Hong Kong SAR, where gill plate sales increased dramatically between 2011–2015. Another rapid assessment in 2016 found a higher proportion of dried seafood stores selling gill plates in Hong Kong SAR (30%) than in Guangzhou (6%; Hau et al., 2016), though stores in Guangzhou still sell large quantities of gill plates relative to other locations, such as Singapore and Macau (O'Malley et al., 2017; Wainwright et al., 2018).

Several planktivorous sharks and rays are now popular focal species in marine tourism, primarily based around diving or snorkelling with these animals at feeding or cleaning areas. The high economic value of these operations – Whale Shark tourism was valued at over USD 139 million annually (Ziegler & Dearden, 2021) – has helped to accelerate a shift from fishing to tourism in multiple locations, and has been explicitly used as a justification for species- and habitat-level protections in several countries. An economic analysis of shark and ray tourism in Indonesia, one of the largest fishing countries, indicated that tourism value was 1.45 times the value of shark landings (Mustika et al., 2020). Manta ray tourism was an important contributor to these results. Indeed, global manta ray tourism was valued at USD 140 million annually in 2013 (O'Malley et al., 2013). However, as tourism increases in some areas, it is vital to ensure that the development of this industry is a net positive for conservation efforts – a high level of snorkeller and diver pressures on specific reef habitats, such as mobulid cleaning stations and feeding sites, has the potential to cause both physical damage and chronic behavioural disruption (Murray et al., 2020; Germanov et al., 2022).

While many species within this group are relatively well-studied, there are still significant knowledge gaps related to threat assessment and prioritisation. Population sizes are still unknown in many areas and thought to be small in others (McKinney et al., 2017). Fisheries remain a threat, with incidental catch in particular being challenging to monitor and quantify. The lack of baseline data on the population-level abundance of these species makes the sustainability of even known catches difficult to assess. It is clear that fisheries can rapidly deplete populations; for example, Reef Manta Ray and Oceanic Manta Ray are no longer observed in parts of Indonesia where they were previously recorded.

Depleted planktivore populations are also at heightened susceptibility to other anthropogenic threats, such as pollution, climate change, and ship strikes.

As surface filter-feeders, these species are highly susceptible to plastic pollution, with Reef Manta Ray and Whale Shark estimated to ingest a respective 63 and 137 pieces of plastic per hour at some Indonesian locations (Germanov et al., 2019). Mortality estimates are challenging to obtain, given the delayed onset of obvious physical impacts (Rowat et al., 2021a), and added potential for sub-lethal effects (Germanov et al., 2018). Planktivorous sharks and rays are also likely to be susceptible to the impacts of climate change, such as rising sea surface temperatures and ocean acidification, which have the potential to reduce prey and habitat availability (Hays et al., 2005; Harris et al., 2020).

Ship strikes on Whale Shark are one of the largest contemporary threats to the species (Rowat et al., 2021b), as there is a high overlap of commercial shipping and the movements of this wide-ranging species (Womersley et al., 2022). This is also difficult to monitor, as short-term mortality is assumed to be high, and these individuals are presumed to sink where they are unlikely to be reported. With that knowledge, the frequent large propeller scars on live sharks in areas where Whale Shark are surface feeding near major shipping routes, such as the Arabian/Persian Gulf region and the Gulf of Mexico, indicate this is a serious risk to some of the few remaining large aggregation sites (Womersley et al., 2022). Similarly, Oceanic Manta Ray seasonally aggregate in highly active shipping lanes (Graham et al., 2012), and have to contend with fast-moving speed boats in some coastal areas (Pate & Marshall 2020; Strike et al., 2022).

CONSERVATION AND MANAGEMENT

As highly mobile species, planktivorous sharks and rays have also been listed on CITES Appendix II, Convention on the Conservation of Migratory Species of Wild Animals (CMS) Appendices I and II, and on Annex 1 of the Memorandum of Understanding on the Conservation of Migratory Sharks (Sharks MoU). Their CITES listing requires that trade of these species be demonstrably sustainable and traceable, while CMS listings encourage range states to improve and coordinate management of these species, and – for Appendix I species – to prohibit their take altogether. Regional fisheries management, national protections, and domestic trade restrictions vary between species and oceans.

The single exception to the above, the Megamouth Shark, is not listed in international agreements. Megamouth Shark is rarely caught outside Taiwan where their release – whether dead or alive – was mandated in 2020 (Yu et al., 2021). The lack of clear direct historical or contemporary threats to this species has resulted in a Least Concern classification on the IUCN Red List (IUCN, 2023).

Basking Shark and Whale Shark, while still subject to the ongoing threats noted above, have been legally protected throughout much of their range. Industrial fisheries no longer target these species, there is a low presence in contemporary trade, and safe live release is encouraged in major fisheries. However, net fisheries may still pose a significant risk to incidental capture in some regions, such as New Zealand for Basking Shark (Finucci et al., 2022) and the Arabian region for Whale Shark (Pierce et al., 2021), with unknown mortality levels. High levels of population decline in some regions, with a lack of clear drivers, remain highly concerning in both of these species (Pierce et al., 2021; IUCN, 2023). Both species are listed as Endangered on the IUCN Red List.

Mobulid rays are among the most threatened of all vertebrate groups worldwide, with all species listed as Vulnerable or Endangered. Many of these rays have low levels of national protection, are utilised extensively in domestic fisheries, and remain valuable in international trade (Fernando & Stewart, 2021). On national and local scales, 'manta' rays tend to have more protections in place than other *Mobula* species. One or both described manta ray species are specifically protected in over a dozen countries and territories (IUCN, 2023), including Australia, Ecuador, Indonesia, Malaysia, Maldives, Mexico,

Top: Spinetail Devil Ray landings in Negombo, Sri Lanka | Blue Resources Trust

Bottom: Spinetail Devil Ray gill plates set to dry prior to exports | Daniel Fernando | The Manta Trust

Federated States of Micronesia (Yap), Mozambique, Peru, Philippines, Thailand, the United Arab Emirates (UAE), and the US.

Mobulids are also listed on several regional fisheries agreements. In 2012, the General Fisheries Commission for the Mediterranean (GFCM) banned retention and mandated careful release for these species. The Inter-American Tropical Tuna Commission (IATTC) prohibited mobulid species caught by large-scale fisheries in the IATTC Convention Area from being retained or sold, and mandated prompt, careful release in 2015. The Western and Central Pacific Fisheries Commission (WCPFC) adopted safe release guidelines for mobulids in 2017, and subsequently adopted measures to ban their targeted fishing and retention from 2021. The Indian Ocean Tuna Commission (IOTC) adopted a ban on the retention of mobulids for commercial sale in 2019.

To allow recovery in these species, it is recommended that mobulid landings be prohibited, in line with several international agreements, so long as global populations remain threatened. Improved reporting of catch and discard data, regional and national limits on catch based on scientific advice and/or the precautionary approach, efforts to minimise incidental catch mortality and implementation of safe release protocols, and adherence to the commitments agreed through international treaties are needed. The IUCN SSG Global Devil and Manta Ray Conservation Strategy provides detailed information regarding priority conservation actions in this group (Lawson et al., 2017).

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Basking Shark incidentally caught in net | Ali Hood | The Shark Trust

Juvenile Whale Shark *Rhincodon typus* landed in the United Arab Emirates and transported on a truck to Dubai | Rima W. Jabado

Whale Shark *Rhincodon typus* feeding in Mafia Island, Tanzania | Simon J. Pierce

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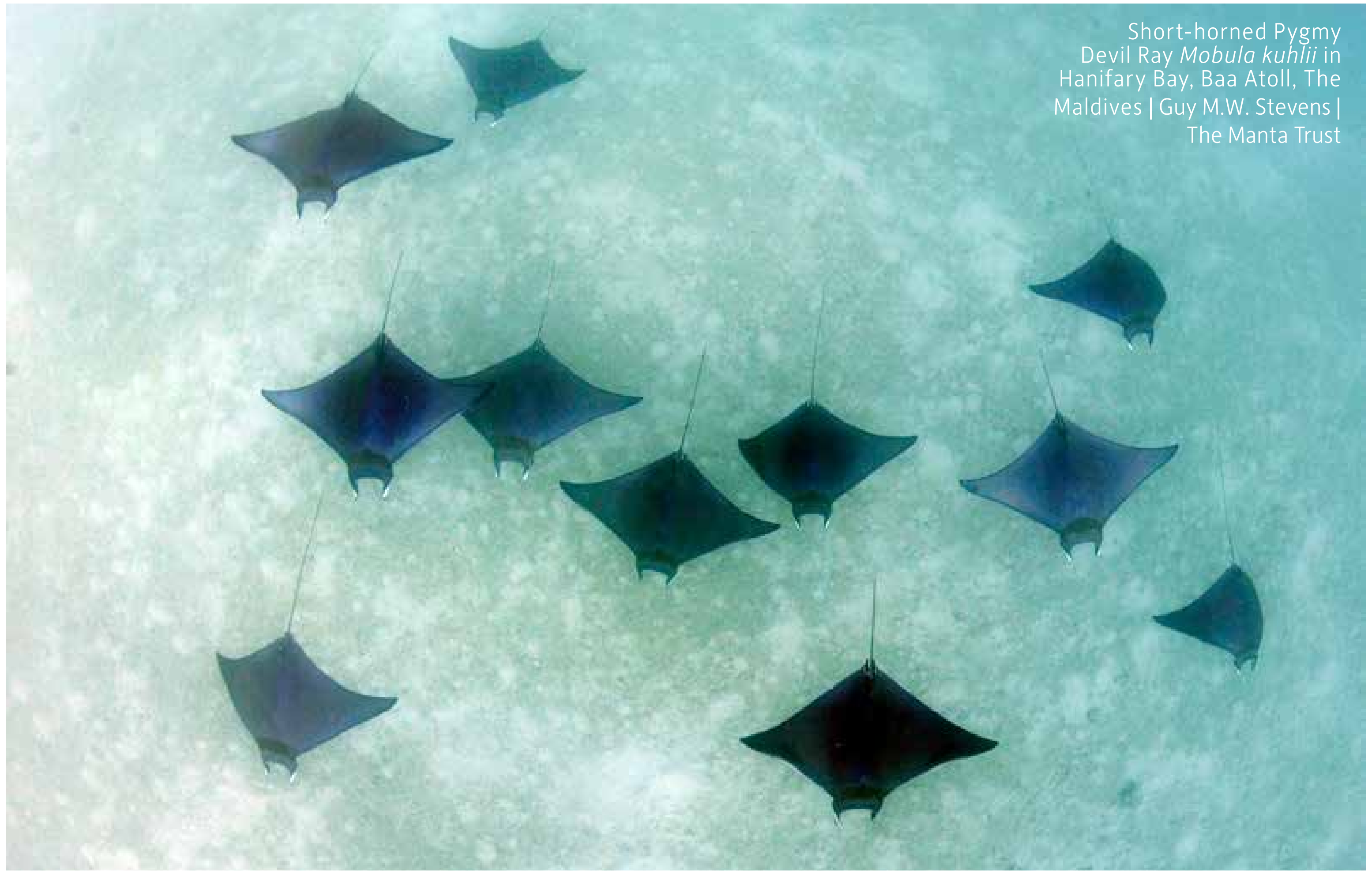

Short-horned Pygmy Devil Ray *Mobula kuhlii* in Hanifary Bay, Baa Atoll, The Maldives | Guy M.W. Stevens | The Manta Trust

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Spinetail Devil Ray *Mobula mobular* in Nosy Be, Madagascar | Simon J. Pierce