Genetics of manta and devil rays
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Vulnerabilities and fisheries impact: the uncertain future of manta and devil rays

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Abstract

1. Manta and devil rays of the Family Mobulidae (mobulids) are rarely studied large pelagic elasmobranchs, with all eight of well-evaluated species listed on the IUCN Red List as threatened or near threatened.

2. Mobulids have life history characteristics (large body size, extended life span, ovoviviparous reproduction, extremely low fecundity, and delayed age of first reproduction) that make them exceptionally susceptible to overexploitation.

3. Targeted and bycatch mortality from fisheries is a globally important and increasing threat, and targeted fisheries are incentivized by the high value of the global trade in mobulid filter plates.

4. Fisheries bycatch of mobulids is substantial in tuna purse seine fisheries.

5. Thirteen fisheries in 12 countries specifically targeting mobulids, and 30 fisheries in 23 countries with mobulid bycatch were identified.

6. Aside from a few recently enacted national restrictions on capture, there is no comprehensive monitoring, assessment or control of mobulid fisheries or bycatch. Recent listing through the Convention on the International Trade in Endangered Species (CITES) may benefit mobulids of the genus *Manta* (manta rays), but none of the mobulids in the genus *Mobula* (devil rays) are protected.

7. The relative economic costs of catch mitigation are minimal, particularly compared to a broad range of other, more complicated, marine conservation issues.
Introduction

Marine organisms are subject to multiple anthropogenic threats (Dulvy et al. 2014b; Lewison et al. 2004; Stevens 2000), and long-lived species with low fecundity (e.g. whales, seabirds, sea turtles, and sharks) are particularly vulnerable (Owens & Bennett 2000). Pelagic elasmobranchs tend to be even more vulnerable because they have exceptionally low population growth rates, are often subject to targeted and bycatch in multiple fisheries, and the enumeration of catch and management is limited or nonexistent (Dulvy et al. 2008; Dulvy et al. 2014b; Stevens 2000).

Of the pelagic elasmobranchs, the 11 species of manta and devil rays, Family Mobulidae (mobulids) are among the most vulnerable. In addition to their k-selected life history traits, they have been directly targeted in small-scale fisheries (Notarbartolo di Sciara 1988; Rohner et al. 2013; White et al. 2006) and captured as bycatch in industrial fisheries (Paulin et al. 1982; White et al. 2006). Between 1998-2009, mobulid landings increased more than an order of magnitude (from 200 to 5000 metric tons year\(^{-1}\)) (Ward-Paige et al. 2013). All eight of the mobulid species effectively evaluated for the IUCN Red List are threatened or near threatened, with the remaining three listed as data deficient (Table 1). Four species are classified as declining, and the population trajectory of the remaining seven species is unknown (IUCN, 2012) (Table 1). Given these concerns, a logical first step to the conservation of mobulids is to evaluate their life history sensitivity and threats, and potential management solutions.

Life History

Like many elasmobranchs, mobulids have k-selected life history traits including slow growth, long life span, delayed reproduction, and low annual fecundity. The life history parameter that sets mobulids apart from other elasmobranchs and makes them vulnerable to overexploitation is their extremely low fecundity - among the lowest of all fishes (Dulvy et al. 2014b). Mobulid litter size is only one (Hoenig & Gruber 1990; Stevens et al. 2000), and interbirth intervals are estimated at 1-3 years (Compagno & Last 1999b; Homma et al. 1999; Marshall & Bennett 2010; Notarbartolo di Sciara 1988). Marshall and Bennett (2010) estimated *Manta alfredi* gestation period at 12 months with a mix of annual and biennial pregnancies while Stevens (unpub. data) estimated one gestation every five years in *M. alfredi* off the Maldives. Although variable across mobulids, most annual fecundities are ~0.5 pups per year, particularly for larger species (e.g. 0.56 pregnancies adult female\(^{-1}\) year\(^{-1}\) for *M. alfredi*: Deakos et al. 2011). Maximum rate of mobulid population increase is also limited by slow growth rates and late age at maturation. Pups are relatively large at birth, ranging from 27 to 49 % of maternal size (Marshall et al. 2009; Notarbartolo di Sciara 1988; White et al. 2006). Using age/growth data from Cuevas-Zimbrón et al. (2012) and size at maturity from Serrano-López (2009), *Mobula japonica* appear to attain sexual maturity at 5-6 years, while *M. alfredi* matures at >8 and >3 years in females and males, respectively (Marshall et al. 2011) or 3-6 years (Clark 2010).

There are no direct measurements of life-span, but the longest period between sightings of a photographically identified *M. alfredi* was 30 years (Couturier et al. 2014). Using banding patterns in vertebral cartilage, Cuevas-Zimbrón et al. (2012) estimated *M. japonica* life span at >14 years, while Homma et al. (1999) estimated *Manta birostris* life span at >19-20 years. These minimum estimates are likely well below maximum longevity.

One approach to estimate the vulnerability to exploitation is to compare the maximum rate of population increase (*r\(_{\text{max}}\)*). Dulvy et al. (2014b) used generic Manta life history parameters to estimate median *r\(_{\text{max}}\)* at 0.116 year\(^{-1}\) (CI: 0.089-0.139). Compared to other chondrichthyians (median *r\(_{\text{max}}\)* of 0.26 year\(^{-1}\)), mobulid median *r\(_{\text{max}}\)* is among the lowest (Garcia et al. 2008; Hutchings & Myers 2012), and is more similar to marine mammals (median *r\(_{\text{max}}\)* of 0.07 year\(^{-1}\)) than to coastal elasmobranchs or teleost fishes.
| Scientific name                      | Common Name                  | IUCN Classification | Distribution                                      | Habitat       | Maximum Size (DW) | Population trend | Fishery              |
|--------------------------------------|------------------------------|----------------------|---------------------------------------------------|---------------|-------------------|------------------|---------------------|
| *Manta alfredi*                      | Reef manta ray               | Vulnerable           | Circumglobal, tropical and subtropical           | Coastal       | 550 cm            | Decreasing       | Targeted and bycatch |
| *Manta birostris*                    | Giant manta ray              | Vulnerable           | Circumglobal, tropical and subtropical           | Coastal and oceanic | 900 cm          | Decreasing       | Targeted and bycatch |
| *Mobula eregoodootekee*              | Pygmy devil ray              | Near Threatened      | Tropical Indo-West Pacific and Northern Indian Ocean | Coastal       | 100 cm            | Unknown          | Bycatch             |
| *Mobula hypostoma*                   | Atlantic devil ray           | Data Deficient       | Western Atlantic                                 | Coastal and oceanic | 120 cm          | Unknown          | Bycatch             |
| *Mobula japonica*                    | Spinetail devil ray          | Near Threatened      | Circumglobal, tropical, subtropical, temperate  | Coastal and oceanic | 310 cm          | Unknown          | Targeted and bycatch |
| *Mobula kuhlii*                      | Shortfin devil ray           | Data Deficient       | Indian Ocean and Western Central Pacific         | Coastal       | 135 cm            | Decreasing       | Targeted and bycatch |
| *Mobula mobular*                     | Giant devil ray              | Endangered           | Mediterranean and possibly North Eastern Atlantic | Coastal and oceanic | 520 cm          | Decreasing       | Bycatch             |
| *Mobula munkiana*                    | Mun's devil ray              | Near Threatened      | Eastern Pacific                                  | Coastal       | 110 cm            | Unknown          | Targeted and bycatch |
| *Mobula rochebrunei*                 | Lesser Guinean devil ray     | Vulnerable           | Eastern Central and South Atlantic, possibly Southwestern Atlantic | Coastal       | 133 cm            | Unknown          | Targeted and bycatch |
| *Mobula tarapacana*                  | Chilean devil ray            | Data Deficient       | Probably circumglobal, tropical, subtropical, temperate | Coastal and oceanic | 370 cm          | Unknown          | Targeted and bycatch |
| *Mobula thurstoni*                   | Smoothtail Devil Ray         | Near Threatened      | Circumglobal, temperate and tropical             | Coastal and oceanic | 180 cm          | Unknown          | Targeted and bycatch |

Table 1. Characteristics of the Family Mobulidae (Couturier et al. 2012; IUCN 2012).
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Fisheries Impacts

The affinity of mobulids for productive habitats and distribution in the epipelagic zone (Croll et al. 2012; McCauley et al. 2014) makes them vulnerable to capture in an array of fishing gear. Mobulids have been reported as targeted or bycatch in both recreational and commercial harpoon, gill net, longline, trawl, purse seine, and trap fisheries throughout their range (Table S1). It is challenging to quantitatively assess fisheries effects upon mobulids due to inconsistencies in fishery data, species misidentification, the global and pelagic distribution of most species, sympatric distributions among mobulids, and the large number of fisheries with which they interact (Camhi et al. 2009). We define two types of fisheries interactions: targeted catch (mobulids are the primary or secondary target and are retained), and bycatch (mobulids are incidentally captured and discarded or retained and utilized). In some fisheries (e.g. tuna purse seine fishery), mobulids may be captured as bycatch but released alive (Poisson et al. 2014), but we included these as bycatch.

Targeted Fisheries

Mobulids have been targeted in recreational and small-scale commercial fisheries for centuries, with 19th and early 20th century accounts of museum and recreational expeditions for mobulids (Elliott 1846; Gill 1908; Roosevelt 1917). Indeed, in 1916 U.S. President Theodore Roosevelt set aside a week of his presidency to harpoon two M. birostris off Southwestern Florida (Roosevelt 1917) (Figure 1). One of the first accounts of targeted take of mobulids describes their capture as bait for finfish fisheries in the Gulf of California, Mexico (Gill 1908). Currently, at least 13 fisheries in 12 countries target mobulids (Table S1) with most of these fisheries being characterized as artisanal. Artisanal fishing, however, can have population-level impacts: Rohner et al. (2013) attributed an 88 % decline between 2003-2011 in M. alfredi off Praia do Tofo, Mozambique to artisanal harvest.

Small-scale fisheries have generally targeted mobulids for meat (consumed locally), cartilage (exported as filler for shark fin soup), and skin (exported for leather) (Alava et al. 2002; Bizzarro 2001). Since at least the 1990’s a market for mobulid prebranchial filter plates for Asian medicines has emerged and expanded (Alava et al. 2002; Couturier et al. 2012; White et al. 2006). In Sri Lanka, wet filter plates are sold by fishers for $US 9.10 - $18.19 kg⁻¹ for Mobula spp. and $US 27.29 kg⁻¹ for M. birostris, and dried filter plates are sold by intermediaries to exporters for $US 95.53 - $113.76 kg⁻¹ (Mobula spp.) and $US 136.80 to $228.00 kg⁻¹ (M. birostris) (Fernando & Stevens 2011). In Indonesia, shark and ray processors in Cilacap (Central Java) sell dried mobulid filter plates to exporters for ~$71 US kg⁻¹ (W. White, unpubl. data). As a comparison, the wholesale price for dried shark fins in the Guangzhou market, China is $64 US kg⁻¹ to $963 US kg⁻¹ (Whitcraft et al. 2014a). These high prices have led to a rapid expansion of targeted mobulid fisheries, with dried filter plates being exported to mainland China from Sri Lanka, Indonesia, India, and the Philippines (Alava et al. 2002; Chen et al. 2002; Couturier et al. 2012; Rajapackiam et al. 2007; White et al. 2006). These countries are the main loci of targeted mobulid catches, which appear to be expanding in response to the export market for filter plates (Heinrichs et al. 2011). Where available, regional information is provided in greater detail below.

Indonesia. Targeted mobulid harpoon fisheries have been documented across Indonesia including Lombok, Lamakera, Lamalera, and villages in the Alor region (Dewar 2002; White et al. 2006; A. Marshall, pers. obs.). Most have existed for generations, and focus on M. birostris with Mobula tarapacana and some Mobula thurstoni also taken (Dewar 2002). While traditionally taken for local consumption, the export market for dried filter plates and skin has likely driven increased fishing effort and technological innovation, leading to increased harvest and declines...
in local populations (Dewar 2002; Heinrichs et al. 2011).

**Philippines.** Targeted mobulid fisheries have existed for decades in the Philippines, primarily in the Bohol Sea region, emanating from Bohol, Camiguin, and Mindanao Islands (Acebes 2009; Alava et al. 2002). Mobulids are taken with gaffs, harpoons, hook and line, and gill nets, and sold locally fresh or as dry meat, filter plates, and skin (Alava et al. 2002). These fisheries target a range of mobulids including *M. birostris* and *M. japanica* (Camhi et al. 2009). Interviews with fishermen indicate villages take as many as 1,000 individuals year\(^{-1}\), and the number of villages and fishermen participating in the fishery expanded at least through 2002; concurrent with declines in catch rates, potentially indicating decreased populations (Alava et al. 2002). Concern for declining populations of whale sharks (*Rhincodon typus*) and *Manta* spp. in the Philippines prompted the prohibition of targeted fisheries in 2002 (Food and Agriculture Organization Order 193). However enforcement is difficult and *Mobula* species are not included in the ban (Camhi et al. 2009).

**India.** Mobulids are targeted in a number of small-scale fisheries off India and sold for dried meat and filter plates. Most fisheries operate off Southern (Kerala, Tuticorin, and Chennai) (Fernando 2012; Mohanraj et al. 2009), and Northwestern (Mumbai) India (Raje et al. 2009). *M. japanica* (identified as *Mobula diabolus*) are taken off Chennai in trawls with additional captures in gill net and hook and line fisheries (Mohanraj et al. 2009). A mechanized gill net fishery was initiated off Chennai in 2005 in response to increased demand for dried filter plates (Rajapackiam et al. 2007). Catch rate of elasmobranchs in coastal and shelf waters of India appears to be declining due to overfishing, and there is some evidence that the mobulid fishery may have collapsed (Fernando 2012).
Sri Lanka. Traditionally, mobulids were not fished in Sri Lanka due to the poor quality of their meat. However, demand for filter plate export has fueled targeted takes with >1000 M. birostris and >55 000 Mobula taken annually in gill net fisheries, representing over 50 % of global targeted mobulid catches (Fernando & Stevens 2011; Heinrichs et al. 2011). Eighty-seven percent are M. japonica (87 %), followed by M. tarapacana (12 %) and M. thurstoni (~1 %). Increasing take may be particularly problematic for M. birostris because 95 % of individuals taken were juveniles or sub-adults, and Sri Lankan fishers have reported decreased take (Fernando & Stevens 2011). Sri Lanka recently instituted a program to phase out gill nets – the primary gear impacting mobulids.

Mexico. Vaillant and Diguet (1898) described pearl divers in the Gulf of California, Mexico in 1898 taking “manta” to prevent them from entangling in diving equipment and using the carcasses for fishing bait. Since at least the early 1980’s, mobulids (primarily Mobula munkiana, M. japonica, and M. thurstoni) were taken in artisanal fisheries in the Gulf of California using harpoons and set gill nets (Bizzarro et al. 2007). Meat was sold fresh locally or dried; no export market for mobulids (including filter plates) has ever existed (Heinrichs et al. 2011). In 2004, capture, trade, and consumption of mobulids throughout Mexico was prohibited (NOM-029-PESCA 2004), resulting in reduced mobulid harvest in at least the southwestern Gulf of California (D. Croll, pers. obs.). However, individuals are still taken as bycatch in gill nets set for other species (Bizzarro et al. 2007; D. Croll, pers. obs.).

Taiwan. A targeted harpoon fishery for mobulids, primarily targeting M. japonica, existed in Taiwan from 1930 - 1960, with contradictory reports about its continued existence (Camhi et al. 2009; Chen et al. 2002).

Mozambique. An artisanal harpoon fishery targeting M. alfredi, M. birostris, and Mobula kuhlii off southern Mozambique takes ~20-50 individuals year⁻¹ in a small (50 km²) area (Couturier et al. 2012). Meat is consumed fresh locally (A. Marshall, pers. obs.).

Gaza, Palestinian Territories and Egypt. A purse seine fishery for Mobula mobular for local consumption off the Palestinian territory of Gaza recently gained notoriety after media coverage of a catch where ~500 individuals were landed (Couturier et al. 2013). A similar fishery is reported off the Egyptian Mediterranean coast near Alexandria (M. Abudaya, pers. comm.), despite the fact that M. mobular catch is prohibited in Egypt under the 1995 Barcelona Convention.

Bycatch Fisheries

Mobulids have been reported as bycatch in 30 small- and large-scale fisheries globally (Table S1).

Small Scale Fisheries

Mobulids have been reported as bycatch in 21 small-scale fisheries in 15 countries (Table S1) using driftnets, gillnets, traps, trawls, and long lines. Of particular concern is a small-scale driftnet fishery for skipjack tuna (Katsuwonus pelamis) off Indonesia with bycatch of M. japonica, M. tarapacana, M. birostris, M. thurstoni, and M. kuhlii where a partial survey of landing sites led to an estimated take of 1600 year⁻¹ (White et al. 2006), with fishery-wide bycatch
significantly greater. (Ayala et al. 2008) found 55 % of Northern Peruvian artisanal fishermen reported mobulid bycatch, contributing to an estimated bycatch of 8000 year⁻¹. Increasing value of mobulid filter plates has the potential to convert fisheries towards targeted take.

**Large Scale Fisheries**

Mobulids are reported as bycatch in nine large-scale fisheries in 11 countries (Table S1) using driftnets, trawls, and purse seines. The global tuna purse seine fishery may be a particularly important source of mobulid bycatch, with mobulids reported as bycatch in five tuna fisheries from eight countries (Table S1). Tuna purse seine nets extend from the surface up to 130m (Hall & Roman 2013) and are used in three types of sets of which school sets (sets directly on tuna schools, not aggregated under floating objects or associated with dolphins) have the greatest mobulid bycatch (Hall & Roman 2013). Mobulids and tunas have epipelagic tropical distributions in regions of high productivity, leading to a high degree of distributional overlap (Anderson et al. 2011; Croll et al. 2012).

Tuna purse seine fisheries operate in all tropical oceans with ~91,000 net sets year⁻¹ (Table 2). Approximately 70 % of sets occur in the Western and Central Pacific, 11 % in the Eastern Pacific, 10 % in the Indian Ocean, and 8 % in the Atlantic Ocean (Table 2) (IATTC 2012; Molony 2005; Pianet et al. 2010). With the exception of the Eastern Pacific purse seine fishery, bycatch data for most tuna fisheries is limited (Hall & Roman 2013). Further, mobulids are usually not identified to species in bycatch reports (Hall & Roman 2013). Regardless, existing data indicate that bycatch mortality may be large. This is of particular concern given the lack of information on mobulid stocks captured in these fisheries.

*M. birostris, M. alfredi, M. munkiana, M. japanica, M. tarapacana, M. thurstoni, M. mobular*, and likely *M. kuhlii* and *Mobula eregoodootenkee* have been reported as bycatch in purse seines (Hall and Roman, 2013). The frequency of mobulid capture and number of individuals captured per net set is generally relatively small (averaging less than 0.45 individuals set⁻¹, see below), but global distribution of purse seine fisheries and the large number of sets presents concern for mobulid conservation. Collectively, we estimate that approximately 13 900 mobulids are captured annually in global tuna purse seine fisheries (Table 2).

**Eastern Pacific.** The Eastern Pacific tuna purse seine fishery has 100 % of sets monitored, so mobulid bycatch can be directly determined. As the individuals have to undergo a process of encirclement, sacking up and brailing on board, all individuals captured are considered as mortalities although many individuals are alive when released. This reflects a precautionary approach, in the absence of evidence of post-release survival, and with the knowledge that the release methods used in many cases are clearly harmful (Hall & Roman 2013). Sixty-seven percent of mobulids were taken in school sets, with 29 % in dolphin sets and 4 % in floating object sets (Hall & Roman 2013). Average mobulid capture rate (individuals set⁻¹) was 0.38 set⁻¹ for school sets, 0.08 set⁻¹ for dolphin sets, and 0.02 set⁻¹ for floating object sets. Although the fishery operates across the Eastern Tropical Pacific, mobulid captures were concentrated in regions of high productivity and prey density (particularly euphausiids), which raises concerns about the concentration of impacts on subpopulations, if there is some degree of isolation (Figure 2). The estimates of mortality for the Eastern Pacific for the period 1993 – 2013 average almost 2800 individuals per year, with a range of 1100 to 6500. Much of mobulid take happens in the Costa Rica Dome region off Central America (Figure 2).
### Table 2: Estimated effort and mobulid bycatch in global tuna purse seine fishery*.

| Purse Seine Fishery   | Proportion of sets observed (%) | Time Period        | Number sets year$^{-1}$ (SE) | Mobulid capture rate (individuals set$^{-1}$) | Average annual capture (individuals year$^{-1}$) |
|-----------------------|---------------------------------|--------------------|------------------------------|-----------------------------------------------|-----------------------------------------------|
| Eastern Pacific       | 100                             | 1996-2011          | 10 347 (644)                 | 030                                           | 3618                                          |
| Western & Central Pacific Indian | ~1-2                           | 1994-2004          | 65 145 (6051)                | 012                                           | 7817                                          |
| Indian                | ~8                              | 1981-2008          | 8694 (659)                   | 004                                           | 1936                                          |
| Atlantic              | ~3                              | 1991-2008          | 6975 (517)                   | 008                                           | 558                                           |
| **Total/Weighted Mean** |                                |                    | **91 161**                   | **013**                                        | **13 929**                                    |

*References for mobulid capture estimates provided in text.

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**Figure 2.** Mobulid bycatch in tuna purse seine fishery, eastern tropical Pacific 2005-2009. A) sets on dolphin schools, B) sets on fish schools, C) sets on floating objects. Data from Hall and Roman (2013).
**Western and Central Pacific.** Observer data on mobulid capture are limited for the Western and Central Pacific tuna purse seine fisheries where >50% of the global tuna catch occurs (Molony 2008). Molony (2005) reported that 7.4% of sets observed 1994-2004 included mobulids, with these sets containing an average of 1.67 individuals set⁻¹. Combining these rates provides an average bycatch of ~0.12 mobulids set⁻¹. Jones and Francis (2012), using 1976-1982 data from the New Zealand skipjack tuna fishery, estimated a similar mobulid bycatch of 0.18 set⁻¹. Molony (2005) estimated annual purse seine set effort (1994-2004) as 65 146 sets year⁻¹, yielding an estimated annual bycatch of 7817 mobulids year⁻¹ (Table 2). While extrapolated from limited observer data, the relatively high mobulid bycatch rate and intensity of effort suggest this tuna fishery has a large mobulid bycatch compared to others.

**Indian Ocean.** This fishery operates off Northeastern Africa (Hall & Roman 2013), with mostly school and floating object sets (Romanov 2002). Only ~8% of fishing effort is monitored, but *M. birostris*, *M. tarapacana* (listed as *M. coilloti*), *M. mobular*, and *M. japanica* (listed as *M. rancurelli*) are reported as bycatch (Amandè et al. 2008). Using Amandè et al. (2008) reported bycatch of 77 mobulids across 1958 net sets (2003-2007), we estimate 0.04 mobulids captured set⁻¹. Combining this with the average annual effort for this fishery yields an estimated total mobulid take of 1936 mobulids year⁻¹ (Table 2). Because school and floating object net sets occur in roughly the same number in this fishery, these relatively low capture rates and total mobulid capture are most likely related to low densities of mobulids and fewer sets year⁻¹ rather than differences in gear or set types. Bycatch may be reduced by avoidance of coastal waters off the Western Indian Ocean since 2008 due to pirates off Somalia (Chassot et al. 2010). Any mobulid catch near Somalia is not accounted for here.

**Atlantic Ocean.** The Atlantic tuna purse seine fishery operating in the Eastern Atlantic, off Western Africa, is primarily comprised of vessels from France, Spain, and Ghana employing school and floating object sets (Hall & Roman 2013). *M. birostris*, *M. tarapacana* (reported as *M. coilloti*), *M. mobular*, and *M. japanica* (reported as *M. rancurelli*) are reported as bycatch (Amandè et al. 2011), and 47 mobulids were observed captured in 598 purse seine sets (2003-2007), yielding bycatch rate of ~0.08 mobulids set⁻¹ (Amandè et al. 2010). Combining this with annual effort yields an estimated bycatch of 558 mobulids year⁻¹; the lowest in number among the tuna purse seine fisheries (Table 2).

**Other Threats**

The distribution of mobulids in the upper portion of the water column makes them vulnerable to ship strike, collision with nearshore infrastructure (e.g. moorings, beach protection nets, offshore aquaculture facilities) and entanglement in fishing gear. Mobulids are regularly taken in shark nets set to protect beach bathers in South Africa and Australia (Dudley & Cliff 1993; Sumpton et al. 2011); ~52.5 *M. birostris* (likely *M. alfredi*) and ~14.2 *Mobula* spp. are taken year⁻¹ in South African protection nets (Dudley & Cliff 1993). Entanglement and shipstrike have been identified as important sources of mortality to other threatened marine megafauna (e.g. sirenians, baleen whales: Adimey et al. 2014; Berman-Kowalewski et al. 2010), and injuries from vessel strikes have been observed on mobulids (Couturier et al. 2012).

**Conservation Genetics**

Genetic studies have begun to elucidate mobulid taxonomic relationships, but few have examined population genetic structure. Genetic population structure of both *Manta* species, *M.
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birostris (Hinojosa-Alvarez et al. 2014) and M. alfredi (Kashiwagi et al. 2012), and M. japanica (Poortvliet et al. submitted) are being investigated and recent development of genetic micro-satellite markers (Poortvliet et al. 2011) and sequencing of the entire mitochondrial genome of M. japanica (Poortvliet & Hoarau 2013) promise to aid future studies. Understanding stock structure is critical to management and conservation.

DNA-based techniques are routinely used to identify the species from body parts of threatened species, and have been applied to evaluate the legality of cetacean meat sold at Japanese and Korean markets (Baker & Palumbi 1994; Clarke et al. 2006). Similar genetic tools are now being applied to mobulids to enhance visual guides used for filter plate identification to ascertain the source of mobulid filter plates sold globally at Asian medicine markets, and to enhance compliance with CITES treaties (Stevens 2011).

Conservation Recommendations

The conservation status, sensitive life histories, high mortality rates of mobulids in fisheries, and expanding markets for filter plates raise serious concern. Given their limited reproductive capacity it is likely that even low catch rates can result in significant population declines (Camhi et al. 2009; Dulvy et al. 2008). The population structure of most mobulid species is poorly known, and population status is difficult to assess due to lack of data on catch and life history. Global harvest of mobulids appears to be increasing; at the same time catch rates in some regions are declining, indicating potential overexploitation. Indeed, mobulid population declines have been reported in the Philippines, Indonesia, Mexico, India, and Mozambique (Couturier et al. 2012). Population declines in long-lived pelagic species are difficult to detect due to time lags in population trajectories, population structure uncertainty, and lack of fishery-independent population assessments (Lewison et al. 2004).

The importance of mobulids as a global food resource is minimal (Couturier et al. 2012), but their potential direct value as an ecotourism resource has been estimated at $US 73 million year⁻¹ (O’Malley et al. 2013). In contrast, the direct value of the manta ray filter plate trade is estimated at $US 11 million annually (Dulvy et al. 2014b; Heinrichs et al. 2011; O’Malley et al. 2013). Efforts to mitigate mobulid take come at relatively low direct cost but have the potential to yield significant direct and indirect local financial benefit.

Unfortunately, explicit management policies on mobulid capture are limited, with Mexico, Ecuador, Brazil, and the Maldives protecting all mobulids (Camhi et al. 2009; Whitcraft et al. 2014b). A handful of countries have established regulations protecting one or two mobulid species: Australia, European Union and, Philippines (M. birostris), Indonesia (M. birostris, M. alfredi), New Zealand (M. birostris, M. japanica), Croatia (M. mobular, M. birostris under the EU regulation), and Malta (M. mobular, M. birostris under the EU regulation). As early as 1988 international concerns about fisheries impacts resulted in a Fisheries Administrative Order (FAO 193), which prohibited the capture of mobulids in the Philippines (White et al. 2006). M. mobular has been listed as endangered by the IUCN and protected under international conventions, but only Malta and Croatia have passed protective regulations, and no actions have been taken to mitigate bycatch (Canese et al. 2011; Holcer et al. 2013). In 2004, CITES recognized mobulids as a vulnerable group (Camhi et al. 2009), and in 2013, Manta species (M. birostris, M. alfredi) were listed in Appendix II of CITES. Because M. japanica and M. tarapacana are likely most impacted by the filter plate trade (Heinrichs et al. 2011; Whitcraft et al. 2014b), at least these species should be added to CITES Appendix II. In November 2014, all mobulid species were listed in both Appendix I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS 2014).

Some species that are spatially-restricted seasonally may benefit from the establishment
of marine protected areas (e.g. *M. alfredi*, *M. birostris*). For example, we anticipate benefits for spatial protection established for *M. birostris* aggregating in specific sites within the Komodo Marine Park, Indonesia (Dewar et al. 2008) and off Yucatan, Mexico (Graham et al. 2012). However, most mobulids are globally dispersed and less likely to benefit from such protection. We recommend three key actions that have the potential to provide significant conservation benefits:

1. **Reduce filter plate demand for medicinal use**

   Approximately 61,000 kg of dried filter plates are traded annually at a value of $US 11.3 million (Heinrichs et al. 2011). They are predominately sold whole. Guangzhou, China is the mobulid filter plate trade center, with much of the market emanating from a handful of large suppliers (Heinrichs et al. 2011; Whitcraft et al. 2014b). Because the market for mobulid filter plates does not have a long history of widespread traditional use, and almost all of the trade is centered in Guangzhou, a focused education strategy to reduce consumer demand has the potential for relatively rapid success. In addition, international economic tools (e.g. boycotts, embargos) can also be used as conservation levers. The low value of mobulid meat (Fernando & Stevens 2011; Heinrichs et al. 2011), and relatively low targeted catch rates of mobulids prior to emergence of the filter plate market indicate that eliminating this market could greatly reduce mobulid fisheries.

2. **Mitigate bycatch in the commercial tuna purse seine fishery**

   Given the broad spatial distribution, intensity of effort, and reported bycatch, commercial tuna purse seine fisheries likely pose one of the most significant threats to mobulids. Although detailed information mobulid distribution is lacking, they seasonally aggregate in important productive regions, providing opportunity to decrease fishing intensity in regions of exceptionally high mobulid density with spatially discrete fishing prohibitions (Ward-Paige et al. 2013). Currently, there is considerable international interest in purse seine bycatch – primarily in the context of small tuna, billfish, marine mammals, sharks, and sea turtles. Expanding the focus to mobulids is realistic, given the potential for population-level impacts and their charismatic and widespread popular appeal.

   There is also considerable potential for technologies that reduce mobulid capture in net sets and release captured mobulids unharmed (Hall & Roman 2013). Most tuna fleets do not retain mobulids for commercial value, and there are previous examples of the technological solutions to mitigate dolphin bycatch in tuna purse seine fisheries (Gilman 2011). Indeed, an industry-supported program to develop methods for mobulid live release with tracking of post-release mortality has been initiated in the New Zealand skipjack tuna purse seine fishery (Francis 2014). There is reason for optimism for international agreement on mitigation of mobulid bycatch in the tuna purse seine fishing industry. Strong international governing bodies and alliances between industry, conservation non-profits, and government agencies already exist and have proven effective in revising standard fishing practices to mitigate bycatch of marine mammals, seabirds, and sea turtles (Hall & Roman 2013; Lewison et al. 2004).

3. **Redirect and mitigate targeting and bycatch in artisanal fisheries.**

   Even in some countries where the filter plate trade is not operating, targeting and bycatch of mobulid rays in artisanal fisheries can be significant. A strategy to reduce artisanal mobulid catch by initiating new fishery regulations, providing technical assistance for gear modification
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and improvement of live release techniques, and promotion of non-consumptive uses (e.g. diving ecotourism) could significantly reduce take. Education of the vulnerable status of mobulids and a realistic assessment of economic opportunities for mobulid conservation is important to ensure community cooperation.

Given increasing catches and extremely low fecundity, mobulid harvest rates are likely unsustainable as evidenced by declining populations. Sufficient information exists to support international efforts to mitigate mobulid harvest, requiring coordination between fisheries stakeholders (e.g. tuna purse seine industry, artisanal fishers), international trade organizations, non-governmental conservation groups, and consumer organizations (to reduce filter plate demand). While some international efforts have begun (e.g. IUCN Shark Specialist Group Global Mobulid Conservation Strategy, CMS, CITES), only five of 45 global marine conservation organizations (key in catalyzing government and industry to take effective measures) include mobulids in their fisheries conservation campaigns. The good news is that solutions are feasible and economic costs are minimal – particularly compared to a broad range of more complicated, marine conservation issues (e.g. fisheries overharvest, climate change). The challenge is to rally international support to effectively implement them.

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Supplementary material

Information on the scale, gear type, target species, fisher origin and location of fisheries capturing mobulids as target or bycatch (Supplementary Table S1) is available online. The authors are solely responsible for the content and functionality of this material. Queries (other than absence of the material) should be directed to the corresponding author.
