

## ***Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays***

DONALD A. CROLL<sup>a,\*</sup>, HEIDI DEWAR<sup>b</sup>, NICHOLAS K. DULVY<sup>c</sup>, DANIEL FERNANDO<sup>d,e</sup>, MALCOLM P. FRANCIS<sup>f</sup>, FELIPE GALVÁN-MAGAÑA<sup>g</sup>, MARTIN HALL<sup>h</sup>, SHAWN HEINRICHS<sup>i</sup>, ANDREA MARSHALL<sup>j</sup>, DOUGLAS MCCAULEY<sup>k</sup>, KELLY M. NEWTON<sup>a</sup>, GIUSEPPE NOTARBARTOLO-DI-SCIARA<sup>l</sup>, MARY O'MALLEY<sup>c,m</sup>, JOHN O'SULLIVAN<sup>n</sup>, MARLOES POORTVLIET<sup>a,o</sup>, MARLON ROMAN<sup>h</sup>, GUY STEVENS<sup>e,p</sup>, BERNIE R. TERSHY<sup>a</sup> and WILLIAM T. WHITE<sup>q</sup>

<sup>a</sup>*Coastal Conservation Action Lab, University of California, Santa Cruz*

<sup>b</sup>*Southwest Fisheries Science Center, NOAA Fisheries*

<sup>c</sup>*Biological Sciences, Simon Fraser University*

<sup>d</sup>*Department of Biology and Environmental Science, Linnaeus University*

<sup>e</sup>*Manta Trust*

<sup>f</sup>*Fisheries, National Institute of Water and Atmospheric Research*

<sup>g</sup>*Centro Interdisciplinario de Ciencias Marinas*

<sup>h</sup>*Inter-American Tropical Tuna Commission*

<sup>i</sup>*Blue Sphere Media LLC*

<sup>j</sup>*Marine Megafauna Foundation*

<sup>k</sup>*Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara*

<sup>l</sup>*Tethys Research Institute*

<sup>m</sup>*WildAid*

<sup>n</sup>*Monterey Bay Aquarium*

<sup>o</sup>*Department of Marine Benthic Ecology and Evolution, Centre for Ecological and Evolutionary Studies, University of Groningen*

<sup>p</sup>*Environment Department, University of York*

<sup>q</sup>*Marine and Atmospheric Research, Commonwealth Scientific and Industrial Research Organization*

### ABSTRACT

1. Manta and devil rays of the subfamily Mobulinae (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 (matrotrophic 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 gill 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

---

\*Correspondence to: Donald A. Croll, Coastal Conservation Action Lab, University of California, Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060 USA. Email: dcroll@ucsc.edu

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 with a broad range of other, more complicated, marine conservation issues.

Copyright © 2015 John Wiley & Sons, Ltd.

Received 06 February 2015; Revised 28 July 2015; Accepted 13 August 2015

KEY WORDS: coastal; ocean; conservation evaluation; endangered species; fish; fishing

## INTRODUCTION

Marine organisms are subject to multiple anthropogenic threats (Stevens *et al.*, 2000; Lewison *et al.*, 2004; Dulvy *et al.*, 2014), and long-lived species with low fecundity (e.g. whales, seabirds, sea turtles, and sharks) are particularly vulnerable (Owens and 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 quantification of catch and management is limited or non-existent (Stevens *et al.*, 2000; Dulvy *et al.*, 2008, 2014).

Of the pelagic elasmobranchs, the 11 species of manta and devil rays, subfamily Mobulinae (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; White *et al.*, 2006a; Rohner *et al.*, 2013) and captured as bycatch in industrial fisheries (Paulin *et al.*, 1982; White *et al.*, 2006a). Between 1998 and 2009, mobulid landings increased more than an order of magnitude (from 200 to 5000 metric tons year<sup>-1</sup>) (Ward-Paige *et al.*, 2013). All eight of the mobulid species effectively evaluated for the IUCN Red List are threatened (endangered or vulnerable) 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 delayed, matrotrophic (ovoviparous) 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.*, 2014). Mobulid litter size is only one (Hoenig and Gruber, 1990, Stevens *et al.*, 2000), and interbirth intervals are estimated at 1–3 years (Notarbartolo-di-Sciara, 1988; Compagno and Last, 1999; Homma *et al.*, 1999; Marshall and Bennett, 2010). Marshall and Bennett (2010) estimated *Manta alfredi* gestation period at 12 months with a mix of annual and biennial pregnancies while Stevens (unpublished data) estimated one gestation every 5 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 per adult female per year for *M. alfredi*; Deakos *et al.*, 2011).

Maximum rate of mobulid population increase is also limited by delayed age at maturation. Pups are relatively large at birth, ranging from 27 to 49% of maternal size (Notarbartolo-di-Sciara, 1988; White *et al.*, 2006b; Marshall *et al.*, 2009). Information on age of maturation is limited, however, using unvalidated age/growth data from Cuevas-Zimbron (2007) and size at maturity from Serrano-López (2009), *Mobula japonica* appear to attain sexual maturity at 5–6 years. Marshall *et al.* (2011a) reported that *M. alfredi* matures at >8 and >3 years in females and males, respectively, while Clark (2010) reported the age of maturity of *M. alfredi* as 3–6 years.

Table 1. Characteristics of the family Mobulidae (Couturier *et al.*, 2012; IUCN, 2012)

Scientific common name	IUCN classification	Distribution	Habitat	Maximum size (DW)	Trend	Fishery
<i>Manta alfredi</i> Reef manta ray	vulnerable	Circumglobal, tropical and subtropical	coastal	550 cm	decreasing	targeted bycatch
<i>Manta birostris</i> Giant manta ray	vulnerable	Circumglobal, tropical and subtropical	coastal pelagic	900 cm	decreasing	targeted bycatch
<i>Mobula eregoodootenkee</i> Pygmy devil ray	near threatened	Tropical Indo-West Pacific and Northern Indian Ocean	coastal	100 cm	unknown	bycatch
<i>Mobula hypostoma</i> Atlantic devil ray	data deficient	Western Atlantic	coastal pelagic	120 cm	unknown	bycatch
<i>Mobula japonica</i> Spinetail devil ray	near threatened	Circumglobal, tropical, subtropical, temperate	coastal pelagic oceanic	310 cm	unknown	targeted bycatch
<i>Mobula kuhlii</i> Shortfin devil ray	data deficient	Indian Ocean and Western Central Pacific	coastal inshore	135 cm	decreasing	targeted bycatch
<i>Mobula mobular</i> Giant devil ray	endangered	Mediterranean and possibly North-eastern Atlantic	coastal pelagic	520 cm	decreasing	bycatch
<i>Mobula munkiana</i> Munk's devil ray	near threatened	Eastern Pacific	coastal inshore	110 cm	unknown	targeted bycatch
<i>Mobula rochebrunei</i> Lesser Guinean devil ray	vulnerable	Eastern Central and South Atlantic, possibly South-western Atlantic	coastal pelagic	133 cm	unknown	targeted bycatch
<i>Mobula tarapacana</i> Chilean devil ray	data deficient	Probably circumglobal, tropical, subtropical, temperate	coastal pelagic oceanic	370 cm	unknown	targeted bycatch
<i>Mobula thurstoni</i> Smoothtail devil ray	near threatened	Circumglobal, temperate and tropical	coastal pelagic oceanic	180 cm	unknown	targeted bycatch

There are no direct measurements of lifespan. Using unvalidated banding patterns in vertebral cartilage, Cuevas-Zimbrón *et al.* (2012) estimated *M. japonica* lifespan at >14 years. Summarizing published and unpublished photographic resighting data, Marshall *et al.* (2011a, b) estimated longevity of at least 20 and 30 years for *Manta birostris* and *M. alfredi*, respectively. These minimum estimates are probably below maximum longevity.

One approach to estimate the vulnerability to exploitation is to compare the maximum rate of population increase ( $r_{max}$ ). Dulvy *et al.* (2014) used generic *Manta* life history parameters to estimate median  $r_{max}$  at  $0.116 \text{ year}^{-1}$  (CI: 0.089–0.139). Compared with other chondrichthyans (median  $r_{max}$  of  $0.26 \text{ year}^{-1}$ ), mobulid median  $r_{max}$  is among the lowest (García *et al.*, 2008; Hutchings and Myers, 2012), and is more similar to marine mammals (median  $r_{max}$  of  $0.07 \text{ year}^{-1}$ ) than to coastal elasmobranchs or teleost fishes.

## 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, Supporting information).

It is challenging to quantitatively assess fisheries effects upon mobulids owing 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). Two types of fisheries interactions were defined: 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), these animals were included 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 US President Theodore Roosevelt set aside a week of his presidency to harpoon two *M. birostris* off south-western 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 and 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) (Bizzarro, 2001; Alava *et al.*, 2002). Since at least the 1990s a market for mobulid prebranchial gill plates for Asian medicines has emerged and expanded (Alava *et al.*, 2002; White *et al.*, 2006a; Couturier *et al.*, 2012). In Sri Lanka, wet gill plates are sold by fishers for \$US 9.10 – \$US 18.19 kg<sup>-1</sup> for *Mobula* spp. and \$US 27.29 kg<sup>-1</sup> for *M. birostris*, and dried gill plates are sold by intermediaries to exporters for

\$US 95.53 – \$US 113.76 kg<sup>-1</sup> (*Mobula* spp.) and \$US 136.80 to \$US 228.00 kg<sup>-1</sup> (*M. birostris*) (Fernando and Stevens, 2011). In Indonesia, shark and ray processors in Cilacap (Central Java) sell dried mobulid gill plates to exporters for ~\$US 71 kg<sup>-1</sup> (W. White, unpublished data). By comparison, the wholesale price for dried shark fins in the Guangzhou market, China is \$US 64 kg<sup>-1</sup> to \$US 963 kg<sup>-1</sup> (Whitcraft *et al.*, 2014a). These high prices have led to a rapid expansion of targeted mobulid fisheries, with dried gill plates being exported to mainland China from Sri Lanka, Indonesia, India, and the Philippines (Alava *et al.*, 2002; Chen *et al.*, 2002; White *et al.*, 2006a; Rajapackiam *et al.*, 2007; Couturier *et al.*, 2012). These countries are the main loci of targeted mobulid catches, which appear to be expanding in response to the export market for gill 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.* 2006a, A. Marshall, pers. obs.). Most have existed for



Figure 1. US President Theodore Roosevelt with *Manta birostris* harpooned recreationally off Florida in 1916 (Roosevelt, 1917).

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 gill 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 (Alava *et al.*, 2002; Acebes, 2009). Mobulids are taken with gaffs, harpoons, hook and line, and gill nets, and sold locally fresh or as dry meat, gill 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 1000 individuals year<sup>-1</sup>, 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 gill plates. Most fisheries operate off southern (Kerala, Tuticorin, and Chennai) (Mohanraj *et al.*, 2009; Fernando, 2012), and north-western (Mumbai) India (Raje *et al.*, 2009). *Mobula 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 gill 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 gill plate export has fuelled 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 and Stevens, 2011; Heinrichs *et al.*, 2011). Of these, 87% are *M. japanica* (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 and Stevens, 2011). Sri Lanka recently instituted a programme to phase out gill nets – the primary gear affecting mobulids.

### Mexico

Vaillant and Diguët (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 1980s, mobulids (primarily *M. japanica*, *Mobula munkiana* 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 gill 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 south-western 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. japanica*, existed in Taiwan from 1930 to 1960, with contradictory reports about its continued existence (Chen *et al.*, 2002; Camhi *et al.*, 2009).

### *Mozambique*

An artisanal harpoon fishery targeting *M. alfredi*, *M. birostris*, and *Mobula kuhlii* off southern Mozambique takes ~20–50 individuals year<sup>-1</sup> in a small (50 km<sup>2</sup>) 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 individuals year<sup>-1</sup> (White *et al.*, 2006a), 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 individuals year<sup>-1</sup>. Increasing value of mobulid gill 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 to depths of up to 130 m (Hall and 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 and 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 ~98 000 sets year<sup>-1</sup> (Table 2). Approximately 66% of sets occur in the Western and Central Pacific, 18% in the Eastern Pacific, 9% in the Indian Ocean, and 7% in the Atlantic Ocean (Table 2) (Molony, 2005; Pianet *et al.*, 2010, 2011; IATTC unpublished data). With the exception of the Eastern Pacific purse seine fishery, bycatch data for most tuna fisheries is limited (Hall and Roman, 2013). Furthermore, mobulids are usually not identified to species in bycatch reports (Hall and 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.

*Manta birostris*, *M. alfredi*, *M. munkiana*, *M. japonica*, *M. tarapacana*, *M. thurstoni*, *M. mobular*, and probably *Mobula eregoodootenkee* and *M. kuhlii* 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<sup>-1</sup>, see below), but global distribution of purse seine fisheries and the large number of sets presents concern for mobulid conservation. Collectively, it is estimated that approximately 13 000 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

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 <sup>-1</sup> (SE)	Mobulid capture rate (individuals set <sup>-1</sup> )	Average annual capture (individuals year <sup>-1</sup> )
Eastern Pacific	100	1996–2013	17 625	0.16	2774
Western and Central Pacific	~1–2	1994–2004	65 145 (6051)	0.12	7817
Indian	~8	1981–2008	8694 (659)	0.04	1936
Atlantic	~3	1991–2008	6975 (517)	0.08	558
Total/Weighted Mean			98 439	0.13	13 085

\*References for mobulid capture estimates provided in text.

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 and Roman, 2013). Of the mobulids captured, 67% were taken in school sets, with 29% in dolphin sets and 4% in floating object sets (Hall and Roman, 2013). Average mobulid capture rate (individuals set<sup>-1</sup>) was 0.38 set<sup>-1</sup> for school sets, 0.08 set<sup>-1</sup> for dolphin sets, and 0.02 set<sup>-1</sup> 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 year<sup>-1</sup>, with a range of 1100 to 6500. In terms of set types the estimates of mortality per year average 2022 individuals for schools sets, 638 individuals for dolphin sets, and 114 individuals for floating object sets. Much of the mobulid take happens in the Costa Rica Dome region of Central America but some coastal areas have sets with high mortalities as well (Figure 2).

#### 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 between 1994 and 2004 included mobulids, with these sets containing an average of 1.67 individuals set<sup>-1</sup>. Combining these rates provides an average bycatch of ~0.12 mobulids set<sup>-1</sup>. Jones and Francis (2012), using 1976–1982 data from the New Zealand skipjack tuna fishery, estimated a similar mobulid bycatch of 0.18 set<sup>-1</sup>. Molony (2005) estimated annual purse seine set effort (1994–2004) as 65 146 sets year<sup>-1</sup>, yielding an estimated annual bycatch of 7817 mobulids year<sup>-1</sup> (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 with others.

#### Indian Ocean

This fishery operates off north-eastern Africa (Hall and 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), it was estimated that 0.04 mobulids set<sup>-1</sup> were captured. Combining this with the average annual effort for this fishery yields an estimated total mobulid take of 1936 mobulids year<sup>-1</sup> (Table 2). Because school and floating object net sets occur in roughly equal numbers 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<sup>-1</sup> 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

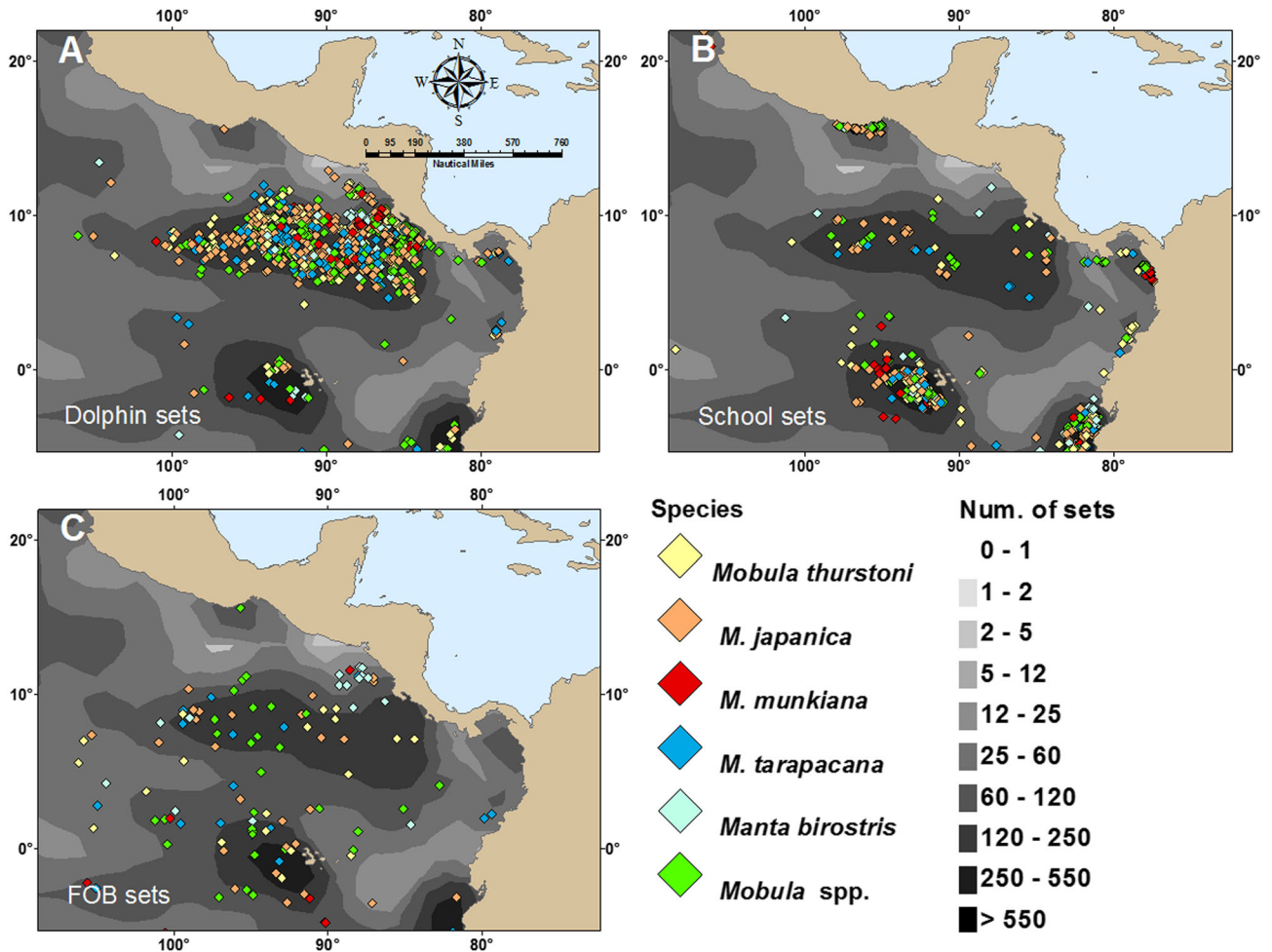


Figure 2. Mobulid bycatch in tuna purse seine fishery, eastern tropical Pacific 2005–2009: (A) sets on dolphin schools; (B) sets on fish schools; (C) sets on floating objects. Data from Hall and Roman (2013).

Somalia (Chassot *et al.*, 2010). Any mobulid catch near Somalia is not accounted for here.

### Atlantic Ocean

The Atlantic tuna purse seine fishery operates in the Eastern Atlantic, off western Africa primarily comprising vessels from France, Spain, and Ghana employing school and floating object sets (Hall and Roman, 2013). *Manta birostris*, *M. tarapacana* (reported as *M. coilloti*), *M. mobular*, and *M. japonica* (reported as *M. rancurelli*) are reported as bycatch (Amandè *et al.*, 2011). Forty-seven mobulids were observed captured in 598 purse seine sets (2003–2007), representing a bycatch rate of  $\sim 0.08$  mobulids set<sup>-1</sup> (Amandè *et al.*, 2010). Combining this with annual effort yields an estimated bycatch of 558 mobulids year<sup>-1</sup>; 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 and Cliff, 1993; Sumpton *et al.*, 2011):  $\sim 52.5$  *M. birostris* (probably *M. alfredi*) and  $\sim 14.2$  *Mobula* spp. are taken each year in South African protection nets (Dudley and Cliff, 1993). Entanglement and ship-strike have been identified as



important sources of mortality to other threatened marine megafauna (e.g. sirenians, baleen whales; Berman-Kowalewski *et al.*, 2010; Adimey *et al.*, 2014), 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 (Poortvliet *et al.*, 2015), but few have examined population genetic structure. Genetic population structure of, *M. birostris* (Hinojosa-Alvarez *et al.*, 2015) and *M. alfredi* (Kashiwagi *et al.*, 2012), and *Mobula japanica* (Poortvliet and Hoarau, 2013) are being investigated and recent development of genetic microsatellite markers (Poortvliet *et al.*, 2011) and sequencing of the entire mitochondrial genome of *M. japanica* (Poortvliet and 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 and Palumbi, 1994; Clarke *et al.*, 2006). Similar genetic tools are now being applied to mobulids to enhance visual guides used for gill plate identification to ascertain the source of mobulid gill 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 gill plates raise serious concerns. Given their limited reproductive capacity it is likely that even low catch rates can result in significant population declines (Dulvy *et al.*, 2008; Camhi *et al.*, 2009). 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 because of 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<sup>-1</sup> (O'Malley *et al.*, 2013). In contrast, the direct value of the manta ray gill plate trade is estimated at \$US 11 million annually (Heinrichs *et al.*, 2011; O'Malley *et al.*, 2013; Dulvy *et al.*, 2014). 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, New Zealand and the Maldives protecting all mobulids that occur in their waters (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*), 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.*, 2006a). *Mobula 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 probably most impacted by the gill 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, 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) are anticipated. However, most mobulids are globally dispersed and less likely to benefit from such protection. Three key actions that have the potential to provide significant conservation benefits are recommended:

#### **Reduce gill plate demand for medicinal use**

Approximately 61 000 kg of dried gill 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 gill plate trade centre, 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 gill plates does not have a long history of widespread traditional use, and almost all of the trade is centred 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 and Stevens, 2011; Heinrichs *et al.*, 2011), and relatively low targeted catch rates of mobulids before emergence of the gill plate market indicate that eliminating this market could greatly reduce mobulid fisheries.

#### **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 pose one of the most significant threats to mobulids. Although detailed

information of mobulid distribution is lacking, they seasonally aggregate in important productive regions, providing an 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 and 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 programme 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 focused non-profit organizations, and government agencies already exist and have proven effective in revising standard fishing practices to mitigate bycatch of marine mammals, seabirds, and sea turtles (Lewison *et al.*, 2004; Hall and Roman, 2013).

#### **Redirect and mitigate targeting and bycatch in artisanal fisheries**

Even in some countries where the gill 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 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 probably 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 gill 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 with 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.

## ACKNOWLEDGEMENTS

Project support provided by the Monterey Bay Aquarium.

## REFERENCES

- Acebes JMV. 2009. Historical whaling in the Philippines: origins of 'indigenous subsistence whaling', mapping whaling grounds and comparison with current known distribution: a HMAP Asia Project Paper. Working Paper No. 161. Asia Research Centre, Murdoch University, Perth, Western Australia.
- Adimey NM, Hudak CA, Powell JR, Bassos-Hull K, Foley A, Farmer NA, White L, Minch K. 2014. Fishery gear interactions from stranded bottlenose dolphins, Florida manatees and sea turtles in Florida, USA. *Marine Pollution Bulletin* **81**: 103–115.
- Alava MNR, Dolumbalo ERZ, Yaptinchay AA, Trono RB. 2002. Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. In *Elasmobranch Biodiversity, Conservation, and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997*, Fowler SL, Reed TM, Dipper, FA (eds). IUCN SSC Shark Specialist Group: Gland, Switzerland and Cambridge, UK; 132–148.
- Amandè MJ, Ariz J, Chassot E. 2008. Bycatch of the European purse seine tuna fishery in the Atlantic Ocean for the 2003–2007 period. Report IOTC-2008-WPEB-12. IOTC Ecosystem and By-catch Working Group, Bangkok, Thailand.
- Amandè MJ, Ariz J, Chassot E, Delgado de Molina A, Gaertner D, Murua H, Pianet R, Ruiz J, Chavance P. 2010. Bycatch of the European purse seine tuna fishery in the Atlantic Ocean for the 2003–2007 period. *Aquatic Living Resources* **23**: 353–362.
- Amandè MJ, Ariz J, Chassot E, Chavance P, Delgado de Molina A, Gaertner D, Murua H, Pianet R, Ruiz J. 2011. By-catch and discards of the European purse seine tuna fishery in the Atlantic Ocean: estimation and characteristics for 2008 and 2009. *Collective Volume Scientific Papers ICCAT* **66**: 2113–2120.
- Anderson RC, Adam MS, Goes JI. 2011. From monsoons to mantas: seasonal distribution of *Manta alfredi* in the Maldives. *Fisheries Oceanography* **20**: 104–113.
- Ayala L, Amorós S, Céspedes C. 2008. By-catch of Albatross and Petrel in Artisan Longline and gillnet Fisheries in northern Peru. Final report to the Rufford Small Grants for Nature Conservation. APECO, Lima, Peru.
- Baker CS, Palumbi SR. 1994. Which whales are hunted? A molecular genetics approach to monitoring whaling. *Science* **265**: 1538–1539.
- Berman-Kowalewski M, Gulland FMD, Wilkin S, Calambokidis J, Mate B, Cordaro J, Rotstein D, St. Leger J, Collins P, Fahy K, Dover S. 2010. Association between blue whale (*Balaenoptera musculus*) mortality and ship strikes along the California coast. *Aquatic Mammals* **36**: 59–66.
- Bizzarro J. 2001. The occurrence of mobulid (*Chondrichthyes: Mobulidae*) rays in the Gulf of California and their associated fisheries. A report to the Monterey Bay Aquarium, Monterey, California.
- Bizzarro JJ, Smith WD, Hueter RE, Tyminski J, Márquez-Farías JF, Castillo-Géniz JL, Cailliet GM, Villavicencio-Garayzar CJ. 2007. The status of shark and ray fishery resources in the Gulf of California: applied research to improve management and conservation. Technical Report 2009–01. Moss Landing Marine Laboratories, Moss Landing, California.
- Camhi M, Valenti S, Fordham S, Fowler S, Gibson C. 2009. The conservation status of pelagic sharks and rays: Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop. IUCN Species Survival Commission Shark Specialist Group, Newbury, UK.
- Canese S, Cardinali A, Romeo T, Giusti M, Salvati E, Angiolillo M, Greco S. 2011. Diving behavior of the giant devil ray in the Mediterranean Sea. *Endangered Species Research* **14**: 171–176.
- Chassot E, Dewals P, Floch L, Lucas V, Morales-Vargas M, Kaplan D. 2010. Analysis of the effects of Somali piracy on the European tuna purse seine fisheries of the Indian Ocean. IOTC Scientific Committee Report: IOTC-2010-SC-09. Indian Ocean Tuna Commission, Victoria, Seychelles.
- Chen C, Liu K, Joung S, Phipps MJ. 2002. Taiwan's shark fishery - an overview. In *Elasmobranch Biodiversity, Conservation, and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997*, Fowler

- SL, Reed TM, Dipper FA (eds). IUCN SSC Shark Specialist Group: IUCN, Gland, Switzerland and Cambridge, UK; 95–103.
- Clark T. 2010. Abundance, home range, and movement patterns of manta rays (*Manta alfredi*, *M. birostris*) in Hawai'i. PhD thesis, University of Hawai'i, Manoa.
- Clarke SC, Manussen JE, Abercrombie DL, McAllister MK, Shivji MS. 2006. Identification of shark species composition and proportion in the Hong Kong shark fin market based on molecular genetics and trade records. *Conservation Biology* **20**: 201–211.
- CMS (Convention on Migratory Species). 2014. Conservation of Migratory Sharks and Rays. UNEP/CMS/Resolution 11.20, 11th Meeting of the Conference of the Parties. Quito, Ecuador.
- Compagno LJV, Last PR. 1999. Mobulidae: devil rays. In: *FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific. Volume 3. Batoid Fishes, Chimaeras and Bony Fishes, Part 1 (Elopidae to Linophrynidae)*, Carpenter KE, Niem VH (eds). FAO: Rome, Italy; 1524–1529.
- Couturier LIE, Marshall AD, Jaine FR, Kashiwagi T, Pierce SJ, Townsend KA, Weeks SJ, Bennett MB, Richardson AJ. 2012. Biology, ecology and conservation of the Mobulidae. *Journal of Fish Biology* **80**: 1075–1119.
- Couturier LIE, Bennett MB, Richardson AJ. 2013. Mystery of giant rays off the Gaza strip solved. *Oryx* **47**: 480.
- Croll DA, Newton KM, Weng K, Galvan-Magana F, O'Sullivan J, Dewar H. 2012. Movement and habitat use by the spine-tail devil ray in the Eastern Pacific Ocean. *Marine Ecology Progress Series* **465**: 193–200.
- Cuevas-Zimbron E. 2007. Estudio preliminar de edad y crecimiento de la manta de espina, *Mobula japonica*. Master's thesis, Universidad Autonoma de Baja California, Ensenada, Baja California, Mexico.
- Cuevas-Zimbrón E, Sosa-Nishizaki O, Pérez-Jiménez JC, O'Sullivan JB. 2012. An analysis of the feasibility of using caudal vertebrae for ageing the spinetail devilray, *Mobula japonica* (Müller and Henle, 1841). *Environmental Biology of Fishes* **96**: 907–914.
- Deakos M, Baker J, Bejder L. 2011. Characteristics of a manta ray *Manta alfredi* population off Maui, Hawaii, and implications for management. *Marine Ecology Progress Series* **429**: 245–260.
- Dewar H. 2002. Preliminary Report: Manta Harvest in Lamakera. Pfleger Institute of Environmental Research, Oceanside, California.
- Dewar H, Mous P, Domeier M, Muljadi A, Pet J, Whitty J. 2008. Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Marine Biology* **155**: 121–133.
- Dudley SFJ, Cliff G. 1993. Some effects of shark nets in the Natal nearshore environment. *Environmental Biology of Fishes* **36**: 243–255.
- Dulvy NK, Baum JK, Clark S, Compagno LJV, Cortes E, Domingo A, Fordham S, Fowler S, Francis MP, Gibson C. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* **18**: 459–482.
- Dulvy NK, Pardo SA, Simpfendorfer CA, Carlson JK. 2014. Diagnosing the dangerous demography of manta rays using life history theory. *Peer J* **2**: e400.
- Elliott W. 1846. *Carolina Sports: by Land and Water: Including Incidents of Devil-Fishing*, Derby and Jackson: New York, NY.
- Fernando D. 2012. A study of India's manta and mobula ray fishery. Manta Trust, Sri Lanka.
- Fernando D, Stevens G. 2011. A study of Sri Lanka's manta and mobula ray fishery. Manta Trust, Sri Lanka.
- Francis MP. 2014. Survival and depth distribution of spinetail devilrays (*Mobula japonica*) released from purse-seine catches. NIWA Client Report No: WLG2014-2. Department of Conservation, New Zealand, Wellington, New Zealand.
- García VB, Lucifor LO, Myers RA. 2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceeding of the Royal Society of London B* **275**: 83–89.
- Gill T. 1908. The Story of the Devil Fish. *Smithsonian Miscellaneous Collections* **52**: 155–180.
- Gilman EL. 2011. Bycatch governance and best practice mitigation technology in global tuna fisheries. *Marine Policy* **35**: 590–609.
- Graham RT, Witt MJ, Castellanos DW, Remolina F, Maxwell S, Godley BJ, Hawkes LA. 2012. Satellite tracking of manta rays highlights challenges to their conservation. *PLoS ONE* **7**: e36834.
- Hall M, Roman M. 2013. Bycatches and non-tuna catches in the tropical tuna purse seine fisheries of the world. FAO Fisheries and Aquaculture Technical Paper No. 568. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Heinrichs S, O'Malley MP, Medd H, Hilton P. 2011. The global threat to Manta and Mobula Rays. Manta Ray of Hope, WildAid, San Francisco, California.
- Hinojosa-Alvarez S, Díaz-Jaimes P, Marcet-Houben M, Gabaldón T. 2015. *The complete mitochondrial genome of the Giant Manta Ray, Manta birostris*. *Mitochondrial DNA* **26**: 787–788.
- Hoenig JM, Gruber SH. 1990. Life-History patterns in the elasmobranchs: implications for fisheries management. In *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries*, Pratt Jr HL, Gruber SH, Taniuchi T (eds). US Department of Commerce, NOAA Technical Report NMFS 90: Washington DC; 1–16.
- Holcer D, Lazar B, Mackelworth P, Fortuna CM. 2013. Rare or just unknown? The occurrence of the giant devil ray (*Mobula mobular*) in the Adriatic Sea. *Journal of Applied Ichthyology* **29**: 139–144.
- Homma K, Maruyama T, Itoh T, Ishihara H, Uchida, S. 1999. Biology of the manta ray, *Manta birostris* Walbaum in the Indo-Pacific. In *Indo-Pacific Fish Biology: Proceedings of the 5th International Conference on Indo-Pacific fishes, Noumea, 1997*, Seret B, Sire J (eds). Ichthyological Society of France: Paris, France; 209–216.
- Hutchings J, Myers R. 2012. Life-history correlates of extinction risk and recovery potential. *Ecological Applications* **22**: 1061–1067.
- IUCN (International Union for Conservation of Nature and Natural Resources). 2012. The IUCN Red List of Threatened Species. Version 2011.2 www.iucnredlist.org [May 15, 2012].
- Jones E, Francis MP. 2012. Protected rays – occurrence and development of mitigation methods in the New Zealand tuna purse seine fishery. Client Report No. WEG2012-49.

- Department of Conservation, New Zealand, Auckland, New Zealand.
- Kashiwagi T, Broderick D, Lance SL, Bennett MB, Ovenden JR. 2012. Development and characterization of ten microsatellite loci for the reef manta ray *Manta alfredi*. *Conservation Genetic Resources* **4**:1055–1058.
- Lewison RL, Crowder LB, Read AJ, Freeman SA. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecology Evolution* **19**: 598–604.
- Marshall AD, Bennett MB. 2010. Reproductive ecology of the reef manta ray *Manta alfredi* in southern Mozambique. *Journal Fisheries Biology* **77**: 169–190.
- Marshall AD, Compagno LJV, Bennett MB. 2009. Redescription of the genus *Manta* with resurrection of *Manta alfredi* (Krefft, 1868)(Chondrichthyes; Myliobatoidei; Mobulidae). *Zootaxa* **2301**: 1–28.
- Marshall AD, Kashiwagi T, Bennett MB, Deakos MH, Stevens G, McGregor F, Clark TB, Ishihara H, Sato K. 2011a. *Manta alfredii*. The IUCN Red List of Threatened Species. Version 2013.2 www.iucnredlist.org [22 May 2014].
- Marshall AD, Bennett MB, Kodja G, Hinijosa-Alvarez S, Galvan-Magana F, Harding M, Stevens G, Kashiwagi T. 2011b. *Manta birostris*. The IUCN Red List of Threatened Species. Version 2015.2 www.iucnredlist.org [25 July 2015].
- McCauley DJ, DeSalles PA, Young HS, Papastamatiou YP, Caselle JE, Deakos MH, Gardner JPA, Garton DW, Collen JD, Micheli F. 2014. Reliance of mobile species on sensitive habitats: a case study of manta rays (*Manta alfredi*) and lagoons. *Marine Biology* **161**: 1987–1998.
- Mohanraj G, Rajapackiam S, Mohan S, Batcha H, Gomathy S. 2009. Status of Elasmobranchs Fishery in Chennai, India. *Asian Fisheries Science* **22**: 607–615.
- Molony B. 2005. Estimates of the mortality of non-target species with an initial focus on seabirds, turtles and sharks. EB WP-1. 1st Meeting of the Scientific Committee of the Western and Central Pacific Fisheries Commission Report No. WCPFC-SC1 EB WP-1, Noumea, New Caledonia.
- Molony B. 2008. Fisheries biology and ecology of highly migratory species that commonly interact with industrialised longline and purse-seine fisheries in the western and central Pacific. EB-IP-6 Report No. WCPFC-SC4-2008/EB-IP-6. Scientific Committee Fourth Regular Session Western and Central Pacific Fisheries Commission, Port Moresby, Papua New Guinea.
- Notarbartolo-di-Sciara G. 1988. Natural history of the rays of the genus *Mobula* in the Gulf of California. *Fisheries Bulletin* **86**: 45–66.
- O'Malley MP, Lee-Brooks K, Medd HB. 2013. The global economic impact of manta ray watching tourism. *PLoS ONE* **8**: e65051.
- Owens IPF, Bennett PM. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceeding of the National Academy Science USA* **97**: 12144.
- Paulin CD, Habib G, Carey CL, Swanson PM, Voss GJ. 1982. New records of *Mobula japonica* and *Masturus lanceolatus*, and further records of *Luvaris imperialis*. *New Zealand Journal of Marine and Freshwater Research* **16**: 11–17.
- Pianet R, Nordstrom V, Damiano A, Delgado de Molina A, Ariz J, Sabate I, Kouassi Y, Sow F. 2010. Statistiques de la pêche thonière Européenne et assimilée dans l'Océan Atlantique durant la période 1991–2008. *Collective Volume Scientific Papers ICCAT* **65**: 561–591.
- Pianet R, Delgado de Molina A, Dewals P, Lucas V, Floch L, Chassot E, Ariz J. 2011. Statistics of the main purse seine fleets fishing in the Indian Ocean (1981–2010). Tropical Tunas Working Party Report No. IOTC-2011-WPTT-13-24. Indian Ocean Tuna Commission, Male, Maldives.
- Poortvliet M, Séret B, Vernet AL, Goujon M, Dagorn L. 2014. Collaborative research: Development of a manual on elasmobranch handling and release best practices in tropical tuna purse-seine fisheries. *Marine Policy* **44**: 312–320.
- Poortvliet M, Hoarau G. 2013. The complete mitochondrial genome of the Spinetail Devilray, *Mobula japonica*. *Mitochondrial DNA* **24**: 28–30.
- Poortvliet M, Galván-Magaña F, Bernardi G, Croll D, Olsen JL. 2011. Isolation and characterization of twelve microsatellite loci for the Japanese Devilray (*Mobula japonica*). *Conservation Genetic Resources* **3**: 733–735.
- Poortvliet M, Olsen JL, Croll DA, Bernardi G, Newton K, Kollias S, O'Sullivan J, Fernando D, Stevens G, Galván-Magaña F, et al. 2015. A dated molecular phylogeny of manta and devil rays (Mobulidae) based on mitogenome and nuclear sequences. *Molecular Phylogenetics and Evolution* **83**: 72–85.
- Rajapackiam S, Mohan S, Rudramurthy N. 2007. Utilization of gill rakers of lesser devil ray *Mobula diabolus* - a new fish byproduct. *Marine Fisheries Information Service Technical and Extension Series* **191**: 22–23.
- Raje SG, Zacharia PU, Gopal-Raje S. 2009. Investigations on fishery and biology of nine species of rays in Mumbai waters. *Indian Journal Fisheries* **56**: 95–101.
- Rohner C, Pierce S, Marshall A, Weeks S, Bennett M, Richardson A. 2013. Trends in sightings and environmental influences on a coastal aggregation of manta rays and whale sharks. *Marine Ecology Progress Series* **482**: 153–168.
- Romanov EV. 2002. Bycatch in the tuna purse-seine fisheries of the western Indian Ocean. *Fisheries Bulletin* **100**: 90–105.
- Roosevelt T. 1917. Harpooning Devilfish. *Scribner's Magazine* **62**: 293–305.
- Serrano-López JN. 2009. Estudio comparativo de la reproducción de tres especies del género *Mobula* (Chondrichthyes: Mobulidae) en el suroeste del Golfo de California, Mexico. Masters thesis, Centro Interdisciplinario de Ciencias Marinas, La Paz, BCS, Mexico.
- Stevens G. 2011. Field Identification Guide of the Prebranchial Appendages (Gill Plates) of Mobulid Rays for Law Enforcement and Trade Monitoring Applications. The Manta Trust, Dorchester, Dorset, UK.
- Stevens JD, Bonfil R, Dulvy NK, Walker PA. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal Marine Science* **57**: 476–494.
- Sumpton WD, Taylor SM, Gribble NA, McPherson G, Ham T. 2011. Gear selectivity of large-mesh nets and drumlines used to catch sharks in the Queensland Shark Control Program. *African Journal of Marine Science* **33**: 37–43.
- Vaillant L, Diguët L. 1898. Sur le Cephaloptere du Golfe de Californie. *Bulletin du Museum National d'Histoire Naturelle* **4**: 127–128.
- Ward-Paige CA, Davis B, Worm B. 2013. Global population trends and human use patterns of *Manta* and *Mobula* rays. *PLoS ONE* **8**: e74835.

- Whitcraft S, Hofford A, Hilton P, O'Malley MP, Jaiteh V, Knights P. 2014a. Evidence of declines in shark fin demand, China. WildAid, San Francisco, California.
- Whitcraft S, O'Malley MP, Hilton P. 2014b. The continuing threat to Manta and Mobula Rays: 2013–14 Market Surveys, Guangzhou, China. WildAid, San Francisco, California.
- White W, Giles J, Potter I. 2006a. Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. *Fisheries Research* **82**: 65–73.

White WT, Clark T, Smith WD, Bizzarro, JJ. 2006b. *Mobula japanica*. The IUCN Red List of Threatened Species Version 2013.2. [www.iucnredlist.org](http://www.iucnredlist.org) [22 May 2014].

### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site.