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MOBULID RAYS IN THE ICCAT CONVENTION AREA: A REVIEW OF CURRENT KNOWLEDGE

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SUMMARY

Biological information for mobulid rays is summarised for the ICCAT Area. At least five valid species occur in this area, although taxonomic uncertainties means that the number of accepted species may change over time. Management regulations applying to mobulids would be applied most effectively at the family-level. Whilst life-history data are limited, mobulid rays have a low fecundity (single pup) and an extended reproductive cycle. The estimated rates of population growth are low (r_{max} = 0.022–0.045 year^{-1} and 0.022–0.085 year^{-1} for Mobula birostris *and* M. mobular, *respectively). Mobulids are of conservation concern, and all are listed on CITES (Appendix II) and CMS (Appendices I and II). Their population sizes in the ICCAT Area are unknown. Mobulids interact with ICCAT fisheries (purse seine fisheries and, to a lesser extent, longline), though fisheries data are incomplete. Available evidence indicates that mobulids are "a taxon of the greatest biological vulnerability and conservation concern for which there are very few data". Hence, ICCAT Recommendation 23-14 would be an appropriate precautionary measure to address the vulnerability of this taxon to overfishing.*

KEYWORDS

Devil rays, manta rays, shark fisheries, Atlantic Ocean, Mediterranean Sea

1. Introduction

Mobulid rays, also known as manta rays and devil rays (Order Myliobatiformes; Family Mobulidae), are pelagic rays that occur in shelf seas and oceanic waters. They occur primarily in tropical and subtropical waters, but extend occasionally into warm temperate zones. Mobulids are large-bodied, with the largest species attaining a disc width of >700 cm (Last *et al.*, 2016; Stevens *et al.*, 2018). Like many elasmobranchs, mobulid rays can

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form large aggregations and, combined with their large size, life-history characteristics, and spatial distributions that overlap with a range of fisheries, are often considered susceptible to overfishing (e.g. Palacios *et al.*, 2023). For general information on mobulid rays see Couturier *et al.* (2012) and Stevens *et al.* (2018).

Mobulid rays have been listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and in Appendices I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS). Under the CMS, "*Parties that are Range States of a migratory species listed in Appendix I shall prohibit the taking of animals belonging to such species*". Given this requirement is particularly relevant for those nations that are contracting parties to both CMS and ICCAT, a proposed recommendation to prohibit the retention of mobulid rays was presented at the Meeting of the Commission in 2023. This resulted in ICCAT Recommendation 23-14 (*Recommendation by ICCAT on mobulid rays (Family Mobulidae) caught in association with ICCAT fisheries*), for which the following text was agreed in Paragraphs 1 and 4:

> "*Contracting Parties, and Cooperating non-Contracting Parties, Entities or Fishing Entities (hereafter referred to as CPCs) shall prohibit retaining onboard, transhipping, landing or storing any part or whole carcass of all species of mobulid rays (family Mobulidae) taken in the Convention area in association with ICCAT fisheries*".
>
> "*CPCs shall, where possible, implement research on mobulid rays in the Convention area in order to identify potential mating, pupping, nursery, feeding and overwintering areas. Based on this research, CPCs shall consider implementing appropriate management measures, such as time and area closures, to provide additional protection for mobulid rays*".

It is also noted that the paragraphs relating to the prohibition on retaining and landing mobulid rays would not apply to those vessels operating only north of 47°N, or south of 47°S (see paragraph 7 of Recommendation 23-14), as those areas were outside the distributional range of mobulid rays.

Recommendation 23-14 also stated the following in Paragraph 8:

> "*The SCRS shall, in 2024, review existing data and information relating to the life history and conservation status of mobulid rays, and confirm whether they meet the definition of being a taxon of the greatest biological vulnerability and conservation concern for which there are very few data. Should this be the case, the SCRS shall advise on the appropriateness of applying precautionary management measures such as a prohibition on retention. The SCRS may also identify options for future research and data collection, as well as advise on other mitigation measures*"

Importantly, Paragraph 9 of Recommendation 23-14 also highlighted that "*This Recommendation shall become effective no later than 1 July 2025 only if there is a consensus on the interpretation of the SCRS advice at the 2024 Annual Meeting of the Commission*".

Consequently, there is a need to review existing data and information on mobulid rays in order to determine whether there is scientific evidence to support the proposed prohibition in the ICCAT area, as well as to better understand options for other mitigation measures, and to inform future data collection and research initiatives. The review of mobulid data conducted here aims to facilitate the discussions of SCRS so that they may adjudge whether mobulid rays are "*a taxon of the greatest biological vulnerability and conservation concern for which there are very few data*", and allow the SCRS to make an evidence-based decision on the appropriateness of precautionary management measures, including the proposed prohibition on retention. The reader is also referred to Cronin *et al.* (2024), who provided an overview of mobulid information for the Intersessional Meeting of the Subcommittee on Ecosystems and Bycatch.

2. Mobulid species in the ICCAT Convention Area

2.1 Taxonomy

Despite a number of recent[8] taxonomic studies (Poortvliet *et al.*, 2015; White *et al.*, 2018; Hosegood *et al.*, 2020; Chandrasekaran *et al.*, 2022), the taxonomy of mobulid rays is still somewhat uncertain, with the number of 'recognised' species ranging from 9–11, depending on the source (**Table 1**). As well as some species having been synonymised (**Table 2**), earlier studies often distinguished two genera (*Mobula* and *Manta*), with the various species currently considered to be in a single genus (*Mobula*). Due to the problematic identification and taxonomic nomenclature of the family, some published studies may refer to incorrect species. From a management and enforcement perspective, there is a rationale that any management measures are established at the family level, thereby alleviating potential future problems if there are further taxonomic revisions.

Mobulid rays occurring in the ICCAT convention area comprise:

- Oceanic manta ray *Mobula birostris* (with the Caribbean manta ray *Mobula* cf. *birostris* considered to be a potentially different species by some authors and also occurring in the ICCAT area)
- Spinetail devil ray *Mobula mobular* (includes what was also known as *Mobula japanica*[9])
- West Atlantic pygmy devil ray *Mobula hypostoma*
- East Atlantic pygmy devil ray *Mobula rochebrunei* (although some authors synonymise this species with *M. hypostoma*)
- Sicklefin devil ray *Mobula tarapacana*
- Bentfin devil ray *Mobula thurstoni*

The reef manta ray *Mobula alfredi* occurs in the Indo-west Pacific, but some studies have indicated that specimens may have been reported from the eastern Atlantic Ocean (Marshall *et al.*, 2009; Last *et al.*, 2016). The mobulid rays that do not occur in the ICCAT area comprise long-horned pygmy devil ray *Mobula eregoodoo*[10] (Indo-west Pacific), short-horned pygmy devil ray *Mobula kuhlii* (Indo-west Pacific) and Munk's pygmy devil ray *Mobula munkiana* (eastern Pacific).

2.2 Overview of mobulid rays in the northwestern Atlantic (FAO Area 21)

The northwestern Atlantic (FAO Area 21) extends northwards from 35°N (Cape Hatteras). The most frequently encountered mobulids in this area are *M. birostris* and *M. mobular*, with recent reported sightings of *M. tarapacana* off the US East Coast Atlantic to 40°N (Pate *et al.*, 2023). *Mobula hypostoma* has been reported as far north as Cape Hatteras (Coles, 1913[11]; as *M. olfersi*), and so may occur seasonally in the southernmost parts of this FAO Area, primarily in July.

Freedman and Roy (2012) examined the distribution of *M. birostris* off the eastern seaboard of the USA and, whilst most records were between Delaware to South Carolina, there were records as far north as New York (40°N). The sea surface temperature associated with the *M. birostris* records was 21.5°C on average (range = 15.5–29.2°C; Freedman and Roy, 2012).

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[8] See also Notarbartolo di Sciara (1987).

[9] Sometimes misspelt as *Mobula japonica*.

[10] Sometimes referred to as *Mobula eregoodootenkee* (see Notarbartolo di Sciara *et al.*, 2020a for discussion).

[11] See also Campbell and Munroe (1974).

A detailed study by Farmer *et al.* (2022) collated extensive data on the occurrence of mobulids along the east coast of the USA (thus including FAO Areas 21 and 31), but the study focused on *M. birostris* and species-specific sightings for the various species by FAO area were not indicated. In terms of *M. birostris,* Farmer *et al.* (2022) noted that the majority of sightings were at latitudes of 26–30°N (FAO Area 34) and recorded from March to May, whilst those sightings north of 35°N (and so in FAO area 21) were usually reported from June to September. Species distribution modelling indicated that the distribution of *M. birostris* was influenced most strongly by sea surface temperature (allowing a northward shift in the population during summer). Within their preferred thermal range (20–30°C, peaking at ca. 23°C), the occurrence of *M. birostris* was also influenced by factors that would relate to productivity (e.g. the presence of thermal and tidal fronts, bathymetric slope, and concentrations of chlorophyll a), with such features occurring in various nearshore and shelf edge habitats, as well as the inside edge of the Gulf Stream (Farmer *et al.*, 2022).

2.3 Overview of mobulid rays in the central western Atlantic, including the Caribbean and Gulf of Mexico (FAO Area 31)

Mobulids are more frequent in the warmer waters of the central western Atlantic (FAO Area 31), including the Caribbean Sea, Gulf of Mexico and around Florida. At least five mobulid species occur in this region, namely *M. birostris, M. hypostoma*, *M. mobular*, *M. tarapacana* and *M. thurstoni* (Del Moral-Flores *et al.*, 2020; Ehemann *et al.*, 2022; Pate *et al.* 2023), with possibly a sixth species also occurring, namely the Caribbean manta ray *Mobula* cf. *birostris* (Marshall *et al.*, 2009; Hinojosa-Alvarez *et al.*, 2016). There is, however, some uncertainty as to the exact species ranges. For example, specimens of *Mobula* cf. *hypostoma* that appeared to match the description of *M. hypostoma* but were of a much larger size had been reported from Venezuela (Ehemann *et al.*, 2017), but these specimens were subsequently corrected as relating to *M. mobular* (Ehemann *et al.*, 2022). Within this FAO area, records of *M. hypostoma* have come mostly from the Gulf of Mexico and southeastern USA, although there have been some records from the southern Caribbean Sea (Morales-Saldaña and Ehemann, 2024).

Coral spawning events, such as reported on the West Flower Garden Bank in the northwestern Gulf of Mexico, may provide seasonal feeding habitats for *M. birostris*, *M. hypostoma* and *M. tarapacana* (Childs, 1997), and the spatial distributions of mobulids may be influenced by seasonal changes in productivity and prey availability. The Flower Garden Banks National Marine Sanctuary may also serve as a nursery area for *M. birostris* and *Mobula* cf. *birostris* (Stewart *et al.*, 2018). Pate and Marshall (2020) indicted that there was also a potential nursery area for *M. birostris* along the coast of Florida, but the extent of this area is unclear.

Whilst primarily associated with pelagic waters in coastal and shelf seas (and oceanic areas for some species), mobulids have also been reported in estuarine and lagoonal ecosystems and outside harbours, including in Florida (Adams and Amesbury, 1998) and Jamaica (Bancroft, 1929), though they may simply be occasional, short-term vagrants in such habitats.

Notabartolo di Sciara and Hillyer (1989) studied mobulid rays in the waters off Venezuela, with this work initiated after reported collisions between hydrofoils and marine megafauna. Two mobulid species were observed, namely *M. birostris* and *M. tarapacana*, whilst *M. hypostoma* (which is present in the area), was not observed. In terms of *M. birostris*, results indicated that this species was observed from March to December, mostly in shallow waters, and with aggregations of up to 50 individuals. Overall, there were 98 sightings in the study involving 295 individuals (90.2% of all mobulids identified). The main sites where *M. birostris* was observed were the waters between Isla Margarita, Isla Cubagua and the Araya peninsula, and in the coastal waters from along the Puerto la Cruz coastline (near the islands of Borracho, Chimanas, Picuda, and Caracas). Notabartolo di Sciara and Hillyer (1989) also noted that individuals in coastal waters swam more slowly, whilst the movements of individuals observed offshore were faster and more directional. In terms of *M. tarapacana,* this species was observed from April to November, mostly in deeper waters, and sightings were generally of individual fish. Overall, there were 21 sightings in the study, with 32 individuals (9.8% of all mobulids).

There have been a range of other published studies of mobulids within this FAO Area, including Surinam (de Boer *et al.*, 2015). Other studies of mobulids in this area, but that are summarised in other sections of the paper, include Hacohen-Domené *et al.* (2017), Trujillo-Córdova *et al.* (2020), and Garzon *et al.* (2021).

2.4 Overview of mobulid rays in the southwestern Atlantic (FAO Area 41)

At least five mobulid species occur in this region, namely *M. birostris, M. hypostoma*, *M. mobular*, *M. tarapacana* and *M. thurstoni* (e.g. Gadig *et al.*, 2003). The Caribbean manta ray *Mobula* cf. *birostris*, which may or may not be a valid species (see preceding sections), has also been reported from Brazil, in the northern part of this FAO Area (Bucair *et al.*, 2021a).

Mobulids are found along much of the coastline, and also around offshore islands, such as the Archipelago of Fernando de Noronha (Brazil; Bucair *et al.*, 2021b, 2022), and the Archipelago of Saint Peter and Saint Paul (Brazil; Mendonça *et al.*, 2012, 2018, 2020; McCallister *et al.*, 2020). In terms of coastal habitats, the use of estuarine areas by *M. birostris* has been reported from the Amazon area (Bucair *et al.*, 2024) and from Paranaguá (southern Brazil, ca. 25.5°S; Medeiros *et al.*, 2015, 2021). The latter study indicated that *M. birostris* was present from October to May, peaking in the austral summer (January to March), with fishers considering the area to be used by gravid females, and as a nursery. In contrast, Luiz *et al.* (2009) reported that *M. birostris*, which may be more tolerant of cooler water, was seen most frequently in the austral winter (June to August) in the Laje de Santos Marine State Park (24.25°S), just further south. Although nursery areas for other mobulids within the southwestern Atlantic have not been identified, Casas *et al.* (2006) reported on the occurrence of a pregnant *M. thurstoni* bearing a 34 cm disc width embryo off the southeastern coast of Brazil.

Whilst mobulids are considered to be seasonal in some areas, they can occur over much of the year in more equatorial waters to the north, such as around the Fernando de Noronha Archipelago (Brazil, ca.3.85°S; Bucair *et al.*, 2021b).

In terms of the more southerly records of mobulids in FAO Area 41, Cousseau and Menni (1983) reported *M. hypostoma* from Mar del Plata, Argentina (ca. 38°S), Milessi and Oddone (2003) reported *M. birostris* from Uruguayan waters outside the Río de la Plata (34º 48' S), and Mas *et al.* (2015) reported mobulids as far south as 38°S.

2.5 Overview of mobulid rays in the northeastern Atlantic Ocean (FAO Area 27)

There are limited reports of mobulid rays in the northeastern Atlantic Ocean (FAO Area 27), with most information available based on observations made around the Azores, where three mobulid species have been reported, namely *M. birostris, M. mobular* and *M. tarapacana* (Sobral and Afonso, 2014; Das and Afonso, 2017). Of these, *M. tarapacana* is the most abundant, *M. birostris* frequent, and an individual from the *M. mobular-M. japanica* complex also observed (Sobral and Afonso, 2014). This study also noted that aggregations of *M. tarapacana* were observed in the summer, with the species recorded over offshore banks and reefs, whilst *M. birostris* was more solitary and was observed over both coastal and offshore banks and reefs.

In terms of the continental margin of western Europe, Lozano Rey (1928) reported a specimen of *Mobula mobular* from Cadíz (36° 32’N), although this has since been determined as being *M. birostris* (Notarbartolo di Sciara *et al.*, 2020b). Nobre (1935) reported *Dicerobatis giornae* from the Algarve, which is a junior synonym of *M. mobular,* although the species identification may be uncertain, noting that only a part of the fish was available for study. Indeed, Nobre (1935) wrote "”*fragmento do exemplar que encontrei no Algarve devia ter aproximadamente 1.2 m de diametro a avaliar pelas dimensões da cabeça; a côr dela era dum castanho escuro*" ("The fragment of the specimen that I found in the Algarve must have been approximately 1.2 m in diameter judging by the dimensions of the head; the colour was dark brown"). Nobre (1935) also noted *Mobula* sp. from the Canary Islands (c. 28°N) and Madeira (c. 32°N).

Early accounts of the fishes of western Europe (Moreau, 1881; Lozano Rey, 1928) did not report *Mobula* from the northern coast of Spain or the Atlantic coast of France, although *M. mobular* has been listed in the ichthyofauna of Galicia (Bañón *et al.*, 2010). Further north, there is one historical record of a dead, stranded *M. mobular* from southern Ireland in1830 (O'Riordan, 1968), but this may be considered an extralimital record. The more oceanic *M. birostris* has been reported from the Ormonde seamount (Gonçalves *et al.*, 2004), which lies towards the southern limits of this FAO Area, as well as from Cadíz.

2.6 Overview of mobulid rays in the Mediterranean Sea (FAO Area 37)

The most frequent mobulid species occurring in the Mediterranean Sea (FAO Area 37) is *M. mobular,* although some published studies (e.g. Capapé *et al.*, 2015; Rafrafi-Nouira *et al.*, 2015; Hemida *et al.*, 2016; Sakalli *et al.*, 2016; Gökoğlu and Teker, 2022) have also referred to *M. japanica*, which is currently considered a junior synonym of *M. mobular*.

Moreau (1881) reported two species of mobulid as occurring off Nice (southern France), namely *Cephalopterus giorna* and *C. massena*, although these are both considered junior synonyms of *M. mobular*. Whilst most studies on mobulids in the Mediterranean Sea relate to *M. mobular* (or *M. japanica*), there have been occasional instances of larger individuals that are considered to be *Mobula birostris* (Notarbartolo di Sciara *et al.*, 2020b), with these taken in the Bay of Rosas (Spanish Mediterranean coast), off Marseilles (France) and Oran (Algeria; Pellegrin, 1901), with another example from just outside the Mediterranean Sea (Cadíz, southern Spain).

Mobula mobular is relatively widespread in the Mediterranean Sea, with records from the northwestern Mediterranean (Moreau, 1881; Lozano Rey, 1928; Banaru *et al.*, 2010), Algeria (Hemida *et al.*, 2002, 2016; Hussein and Bensahla-Talet, 2019), Tunisia (north coast: Capapé *et al.*, 2015; Rafrafi-Nouira *et al.*, 2015; Gulf of Gabes: Bradaï and Capapé, 2001), Strait of Messina (Celona, 2004; Canese *et al.*, 2011), Adriatic Sea (Scacco *et al.*, 2009; Bello *et al.*, 2012; Holcer *et al.*, 2013; Fortuna *et al.*, 2014), eastern Mediterranean (Abudaya *et al.*, 2018), and Turkish waters (Kabasakal *et al.,* 2024), including the Gulf of Antalya (Başusta and Özbek, 2017; Gökoğlu and Teker, 2022), Iskenderun Bay (Yaglioglu *et al.*, 2013; Sakalli *et al.*, 2016) and off Samandağ (Sakalli, 2017).

Some studies have indicated seasonal occurrence of *M. mobular.* For example, Celona (2004) noted that females were seen in the Strait of Messina in late spring and summer. Holcer *et al.* (2013) compiled sightings and capture data from the Adriatic Sea, for which most observations were from the summer. Similarly, Notarbartolo di Sciara *et al.* (2015) used aerial sightings data to monitor *M. mobular* in Italian waters, with most records from the summer and no sightings in the winter. Whilst seasonal differences are likely, it should also be recognised that datasets based largely on sightings data may not be fully reflective of seasonality in distribution and horizontal movements, as sea state may impact census methods, and there could also be seasonal changes in vertical distribution.

There have been some localised, seasonal target fisheries for *M. mobular* in the waters off the Gaza strip in the eastern Mediterranean (Abudaya *et al.*, 2018). This study reported on 304 individuals being landed across the 2014–2016 fishing seasons, which occurred between February and April. It was also reported that >90% of males had sperm-filled claspers, leading Abudaya *et al.* (2018) to postulate that this part of the eastern Mediterranean Sea could be a mating area.

Other studies of mobulids in this area include Capapé and Zaouali (1976), and Notarbartolo di Sciara and Serena (1988).

2.7 Overview of mobulid rays in the central eastern Atlantic (FAO Area 34) and southeastern Atlantic (FAO Area 47)

There are limited, contemporary studies of the mobulids occurring across the central eastern Atlantic (FAO Area 34) and southeastern Atlantic (FAO Area 47), and information for these areas is combined here. At least five mobulid species occur in these waters (*M. birostris, M. mobular, M. tarapacana,* and *M. thurstoni*, as well as *Mobula hypostoma* (= *M. rochebrunei* of some authors). Marshall *et al.* (2009) discussed potential records of *M. alfredi* from the eastern Atlantic (from the Canary Islands, Cabo Verde, and Senegal), although the validity of these records could usefully be reappraised.

In an earlier account, Blache *et al.* (1970) reported six mobulids in the tropical seas off western Africa, namely *M. mobular* (also as *M. japanica* (as *M. rancureli*)), *M. birostris* (as *Manta birostris*), *M. tarapacana* (as *M. coilloti*), *M. thurstoni* (as *M. lucasana*) and *Mobula rochebrunei*.

Amandè *et al.* (2010) reported on various mobulid species being taken by the European Union (EU) purse seine fleet operating off west Africa. The species observed were *Mobula tarapacana* (as *Mobula coilloti*; n = 26 in free-school sets), *Mobula mobular* (including *Mobula mobular* and *Mobula rancurelli*, the latter a junior synonym of *M. japanica*; n = 9 in free-school nets; n = 1 in FAD associated sets) and *Mobula birostris* (n = 4 in free school nets; n = 7 in FAD associated sets). Clavareau *et al.* (2018) also reported *Mobula birostris* (n = 62) and *Mobular mobular* (which were separated between *M. mobular* (n = 57) and *M. japanica* (n = 94)) from the bycatch of the French purse seine fleet operating off west Africa from Mauritania to Angola.

Mobulids are also taken in artisanal and national fisheries along the west coast of Africa. For example, Doherty *et al.* (2023) reported five mobulid species in Republic of Congo which, in decreasing order of importance, were *M. thurstoni* (n = 451; 75.4%), *M. mobula* (n = 121; 20.2%), *M. hypostoma* (n = 15; 2.5%), *M. tarapacana* (n = 6; 1.0%) and *M. birostris* (n = 5; 0.8%). These data were collected from 507 sampling days across a period of three years.

In terms of reported occurrences of the various mobulid species over the area, *Mobula birostris* has been reported from Cabo Verde (Garzon *et al.*, 2023), Ascension (Wirtz *et al.*, 2017), and St Helena (Beard *et al.*, 2021). *Mobula mobular* has been reported from northern Angola (Weir *et al.*, 2012). *Mobula tarapacana* has been reported from St Helena (Wirtz *et al.*, 2017; Beard *et al.*, 2021), and Democratic Republic of São Tomé and Príncipe (Vasco-Rodrigues *et al.*, 2016). *Mobula thurstoni* has been reported from the Republic of Congo (Weir *et al.*, 2012), Democratic Republic of São Tomé and Príncipe (Vasco-Rodrigues *et al.*, 2016), and Cabo Verde (Ratão *et al.*, 2017). *Mobula hypostoma* has been reported from shallow waters in the Gulf of Guinea (de Boer *et al.*, 2024).

Whilst published data are more limited for the coastline of western Africa, various oceanic islands appear to be especially important for some species of mobulid, and there may be year-round presence in some such areas, albeit with seasonal peaks in sightings (Garzon *et al.*, 2023).

Other studies of mobulids in this area include Cadenat (1959, 1960) and Cadenat and Rancurel (1960).

2.8 Species distribution modelling

Species distribution modelling of *M. mobular* in the tropical Atlantic indicated that the species associated with seasonal upwellings in shelf seas and oceanic areas (Lezama-Ochoa *et al.*, 2020), with the model outputs indicating important areas for this species including the Angolan upwelling system, the coastal and offshore waters of Ghana, and off both Mauritania and Guinea.

Hacohen-Domené *et al.* (2017) undertook Maxent habitat modelling for *M. birostris* off the Yucatán peninsula (Mexico) and found that the presence of this species would, depending on the time of year, correlate with a range of factors. Important factors included sea surface temperature (especially when SST >27°C), primary productivity, depth, distance from shore, and bottom slope. It should also be recognised that the underlying presence data in this study was based on sightings information, which may be influenced by environmental conditions. Concentrations of chlorophyll a, and bathymetric slope were also identified as important factors influencing the distribution of *M. birostris* in a study by Garzon *et al.* (2021).

3. Feeding ecology

Mobulid rays are mainly planktivorous, feeding on euphausiids, mysids, sergestid shrimps, copepods, and larval stages of various invertebrates, although small fish and cephalopods may also be consumed (Notarbartolo di Sciara, 1988; Sampson *et al.*, 2010; Croll *et al.*, 2012; Rohner *et al.*, 2017; Medeiros *et al.*, 2022).

Whilst dietary data are limited for the wider Atlantic, studies on the trophic ecology of mobulids in the Indo-Pacific have, based on isotopic ratios, found a high degree of inter- and intra-specific diet overlap (Stewart *et al.*, 2017).

4. Life-history characteristics

There have been few quantitative studies on the life-history of mobulid rays, thus all species are data-limited and some key life-history parameters are based on estimates.

4.1 Reproduction

Mobulids are viviparous and generally produce a single pup, though specimens carrying two pups have been reported occasionally (Rambahiniarison *et al.*, 2018). The gestation period and length of the reproductive cycle, including any resting years, is unknown for many species but, based on *M. alfredi* from the western Indian Ocean, the gestation period may be inferred as being one year, and the reproductive cycle 1–2 years (Marshall and Bennett, 2010). Dulvy *et al.* (2014) also considered longer reproductive cycles. Whilst, in general, only a single pup is produced, the overall sex ratio is not significantly different from the expected 1:1 sex ratio (Rambahiniarison *et al.*, 2018).

Published studies on the size at maturity are limited (Notabartolo di Sciara, 1988; White *et al.*, 2006; Rambahiniarison *et al.*, 2018 ; Serrano-López *et al.*, 2021), especially when relating to those species and stocks in the Atlantic Ocean.

4.2 Age and growth

There are no published age and growth estimates for mobulids in the ICCAT area. An exploratory study has examined growth of *M. mobular* (as *M. japanica*) from Baja California (eastern Pacific), with this study using caudal vertebrae from below the origin of the dorsal fin that were then cleaned, sectioned and stained with crystal violet solution (Cuevas-Zimbrón *et al.*, 2013). Whilst recognising the small sample size (especially for some size classes) and the absence of detailed validation and verification, the band pairs were used to derive initial age estimates. The maximum observed age in this study was 14. In contrast, sightings data have been used to estimate a minimum longevity of at least 31 years for *M. alfredi* (Dulvy *et al.*, 2014).

Whilst an age at maturity of 3–6 years has been estimated for *M. alfredi* (see review by Couturier *et al.*, 2012), the age at maturity for mobulids may be higher. Based on an estimated size at maturity of 217.8 cm and the von Bertalanffy growth parameters (VBGP) given by Cuevas-Zimbrón *et al.* (2013), *M. mobular* would be expected to be mature at about 8 years of age, with this value close to the estimated age at maturity of 8–10 used by Dulvy *et al.* (2014).

4.3 Size-mass relationships

In general, more data for mobulids are reported in terms of disc width (or disc length) as opposed to total length. Size and mass data are often limited and, whilst many descriptive accounts have provided relevant information, it is not always clear as to whether the disc width has been measured over the body (including curvature) or as straight-line distance. Similarly, some available mass data may relate to total weight, gutted weight or dressed weight, and the accuracy and resolution of the measuring balances used for such large fish are often uncertain. Consequently, more detailed analyses of size-mass relationships could usefully be undertaken.

Abudaya *et al.* (2018) provided data for *M. mobular* in the eastern Mediterranean Sea, with the relationship between disc width (D, cm) and weight (W, g) being $W = 0.000004 \times D^{4.3917}$. It should be noted that underlying data for this study had clusters of points at either end of the overall size range, but with a few more widely scattered data points across the intervening size range (**Figure 1**).

Whilst outside the ICCAT area, Rambahiniarison *et al.* (2018) provided data for three mobulids from the Philippines (western Pacific; **Figure 1**), namely *M. thurstoni* ($W = 0.005414 \times D^{3.189}$), *M. mobular* (as *M. japanica*; $W = 0.065060 \times D^{2.641}$) and *M. tarapacana* ($W = 0.000734 \times D^{3.486}$). Notabartolo di Sciara (1988) provided data for mobulids from the Gulf of California (eastern Pacific), including *M. thurstoni, M. mobular* (as *M. japnica*) and *M. tarapacana*, although data were limited for the latter species. Other relevant width-mass relationships have been provided for *M. thurstoni* in Indonesian waters (Bintoro *et al.*, 2021) and *M. hypostoma* in Venezuelan waters (Tagliafico *et al.*, 2014), although the latter study was based on a low sample size. Further information on these relationships are provided in **Table 3**. Whilst Karim *et al.* (2012) gave a size-mass relationship for *M. birostris*, this was reported in relation to `fork length`, which is not a standard measurement for batoids, and so was excluded here.

Collating data for *M. mobular* from other data sources allowed for a further relationship to be derived, although the correlation was lower than reported in other studies, which may relate to the factors discussed above. The correlation coefficient was improved when those data points that could be extracted from Abudaya *et al.* (2018) were also included (**Figure 2**).

The estimated weight at disc width was calculated from all ten relationships, and the resultant data used to derive an additional curve, with the resulting *a* and *b* parameters potentially an alternative approach if applying a more generic set of conversion parameters for mobulid rays (**Figure 3**).

4.4 Summary of life-history data

Life-history data are incomplete for most species of mobulid ray in the ICCAT area, although more complete data are available for *M. mobular* (**Table 4**) and *M. birostris* (**Table 5**).

5. Population growth rates

Dulvy *et al.* (2014) estimated the maximum population growth rate (r_{max}) of manta ray[12] as being 0.116 year^{-1} (95th percentiles: 0.089–0.139) and, whilst it was sensitive to the estimated length of the reproductive cycle (which is not known exactly), the median r_{max} was among the lowest that had been estimated for various sharks and rays. Given the limited life-history data available for the various species of mobulid, derived estimates of population growth rates should be considered as being indicative. A subsequent study by Pardo *et al.* (2016), that re-analysed the age and growth data of Cuevas-Zimbrón *et al.* (2013) found that the estimated r_{max} for *M. mobular* (as *M. japanica*) was 0.077 year^{-1} (95th percentile = 0.042–0.108 year^{-1}) and, alongside some deep-water squaliform sharks, was the among the lowest of all the elasmobranchs considered.

Based on updated estimates of life history, the annual rate of population change for *M. birostris* was, on average, 2–4% based on the intrinsic rate of population increase (r_{max}) derived from the six methods outlined by Cortés (2016) (J. Carlson, unpublished). These six methods have been used to quantify extinction risk within a conservation framework for a variety of aquatic species. The results for *M. birostris* (**Table 5**) showed that r_{max} ranged from 0.022–0.045 year^{-1}, with an average of 0.033 year^{-1} (± 0.010). The assumption of r_{max}, through the Euler–Lotka equation and its associated derivations, assumes no resource limitations and therefore density independence. Using similar information for *Mobula mobular* (**Table 5**) resulted in an estimated r_{max} that ranged from ca. 0.022–0.085 year^{-1}, with an average of 0.048 year^{-1} (± 0.021).

6. Stock structure

Whilst there have been some tagging and genetic studies on mobulids, information with which to identify stock units of mobulids in the ICCAT area is limited, and more focused work in this work area is required.

7. Population trends

There are limited data on population trends of mobulid rays in the ICCAT convention area. Fortuna *et al.* (2014) used aerial surveys (designed primarily for cetaceans and sea turtles) to collect population data for *M. mobular* in the Adriatic Sea. The estimated numbers in the Adriatic Sea in this study ranged from 1,595 (coefficient of variation (CV) = 25%, uncorrected estimate) to 3,255 (CV = 56%; corrected for availability bias), but longer-term data sets and more extensive spatial coverage would be required to infer population trends.

Aerial surveys conducted in the Sardinian Sea, central and southern Tyrrhenian Sea, and Ionian Sea have also been used to monitor *M. mobular* (Notarbartolo di Sciara *et al.*, 2015). This study used a dataset of 298 sightings and then estimated population size. The uncorrected population estimates were 6,074 (CV = 13.4%; design-based) and 6,092 individuals (CV = 12.7%; model based), whilst the estimates corrected for availability bias were 12,396 (CV = 52.75%, design-based) and 12,722 individuals (CV = 52.57%; model-based).

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[12] This study was based on data for *M. birostris* and *M. alfredi*, which were considered to be in a different genus (*Manta*) at that time.

A study by Ward-Paige *et al.* (2013) used reported sightings data from two surveys collating information from divers, namely the 'eManta survey' and data from the Reef Environmental Education Foundation (REEF). Data from the former indicated a decline in the size of mobulid schools observed by divers in many parts of the world. The latter dataset resulted in no significant change being observed in the western Atlantic over the period 1993 and 2012. The utility of the underlying data for informing on population trends for particular stocks of mobulid rays is, however, uncertain.

Outside of the ICCAT area, declines in mobulid rays have been reported from elsewhere in the world, including South Africa (eastern seaboard), as observed from bycatch in protective nets (Carpenter *et al.*, 2023), the eastern tropical Pacific as observed in bycatch data (Griffiths and Lezama-Ochoa, 2021), Arabian Sea as inferred from landings data (Moazzam, 2018), and in Mozambique documented by diver sightings (Rohner *et al.,* 2013).

8. Movements and behaviours

This section summarises briefly some of those behaviours and movement patterns that may help inform on any future studies examining the 'susceptibility' of mobulids to capture in ICCAT fisheries, including vertical movements, aggregating behaviour, sexual segregation, and species associations.

8.1 Vertical movements

Electronic tagging studies of *Mobula mobular* (n = 3) conducted by Canese *et al.* (2011) in the Mediterranean Sea indicted that *M. mobular* spent most time in surface waters (<10 m deep) during both day and night (49 ± 25%, and 47 ± 25%, respectively). Overall, 81.5% (± 20%) of their time was in the upper 50 m of the water column, with occasional dives to depths of 600–700 m, but most time was spent in waters where the sea temperature was in the range of 20–29°C, (Canese *et al.*, 2011).

Whilst outside the ICCAT area, *M. mobular* (as *M. japanica*) in the eastern Pacific Ocean have also been found to spend a large part of the day (50.5%) and night (63.3%) in the upper 5 m of the water column, and the majority of the day (89.5%) and night (96.8%) in the upper 50 m (Croll *et al.*, 2012), so occupying waters of 20–30°C. The observed movements of *M. mobular* were potentially linked to the distribution of an important prey species - the euphausiid *Nyctiphanes simplex* (Croll *et al.*, 2012).

Within the Atlantic Ocean, *M. tarapacana* has been shown to make both extensive horizontal (latitudinal) movements, and also to make deeper dives (Thorrold *et al.*, 2014). Indeed, the results from this study showed that *M. tarapacana* would descend to depths of ca.1,800 m (where the minimum water temperatures were 3.6–4.4°C), with 49 such dives observed for those tags that provided data. These deep dives occurred during both day and night, although deep dives during the day were usually longer (130 ± 47 min.) than those observed at night (87 ± 26 min.), and the descent and ascent velocities were faster during the day (Thorrold *et al.*, 2014). Such diving behaviours could be related to foraging on organisms in the deep scattering layer.

Although outside the ICCAT area, a telemetry study conducted on *M. alfredi* in the Red Sea revealed their protracted vertical use of the water column (Braun *et al.*, 2014). Almost all tagged individuals mostly occupied the first 10 m of the water column throughout the day, but occupied deeper depths (mostly deeper than 150 m and down to 432 m) at night. The extended vertical use of a reef-associated species suggests that *M. alfredi* may play an important role in linking energy pathways between epi- and mesopelagic habitats (Braun *et al.*, 2014), which may also be the case for other mobulids.

8.2 Aggregating behaviour

Mobulids may show varying levels of aggregation, which may depend on the species, location and season (Palacios *et al.,* 2023). Coles (1916) considered that, at least off the eastern seaboard of the USA, that *M. hypostoma* (as *M. olfersi*) would migrate in large schools, but that *M. birostris* was more solitary.

Sightings data for *M. mobular* in the western Mediterranean indicated that 82% of sightings were of individual animals, although one group of 18 individuals was observed. In contrast, aerial surveys for whale shark *Rhincodon typus* and *M. birostris* off the Yucatán peninsula reported an average density of 8 ind.100 km^{-2} (SD = 13) for *M. birostris*, with a group size of up to 120 in an area of 1.2 km^2 also observed (Trujillo-Córdova *et al.*, 2020).

In terms of the types of aggregation that may be exhibited by mobulids, these may include aggregations for feeding, courtship and mating, predator avoidance, thermal refugia as well as aggregations around cleaning stations (Palacios *et al.*, 2023). The aggregating behaviour of mobulids may be of particular management concern for some fisheries, notably purse seine and driftnet fisheries, where they can be captured in large numbers during one fishing event (Lezama-Ochoa *et al.,* 2019).

8.3 Sexual segregation

Some studies have reported a preponderance of females in some areas (e.g. Bancroft, 1929), with skewed sex ratios also reported for mobulids from areas outside the ICCAT area (Harty *et al.*, 2022).

8.4 Species associations

In addition to associating with various cleaner fish, sucker fish (Echeneidae) and pilotfish *Naucrates ductor*, mobulid rays often associate with other megafauna, such as whale sharks and cetaceans, and may also occur with a range of commercially important pelagic species, including bluefin tuna *Thunnus thynnus* and Mediterranean spearfish *Tetrapturus belone* (e.g. Celona, 2004). Notabartolo di Sciara and Hillyer (1989) noted that mobulids associated with common dolphin, seabirds, hammerhead sharks, and other batoids (e.g. *Aetobatus* sp.). That many pelagic species may aggregate in, for example, areas of high biological productivity and prey availability, means that mobulids may occur in areas of interest to commercial fisheries.

9. Interactions with fisheries

Mobulid rays can be a relatively frequent species observed in bycatch studies for some pelagic fisheries, including those under the auspices of ICCAT management, with relevant information on capture methods, at-vessel and post-release mortality, and mitigation methods summarised below.

9.1 Capture methods

Surface driftnets: Banaru *et al.* (2010) reported *M. mobular* being caught in surface driftnets set overnight in the northern Mediterranean Sea (90–120 mm mesh size, 8–10 m driftnet height, 3–11.3 km driftnet length). During the study period (2000–2003), *M. mobular* (n = 59) were found in 50 trip reports from a total of 2,393 trips (2.1% occurrence), indicating that catches were largely of individual fish, and these were discarded alive. In Turkish waters, the catches in a surface driftnet fishery targeting swordfish *Xiphias gladius* had a bycatch of *M. mobular*, which accounted for 0.29% (by individuals) and 1.96% (biomass) of the catch (Akyol *et al.*, 2012).

Mobular mobular has been reported as being caught in gillnets (16 mm mesh size) when light fishing to catch pilchards and mackerel (Rafrafi-Nouira *et al.*, 2015). Earlier studies of bycatch in an Italian driftnet fishery for swordfish (1990–1991) found that *M. mobular* accounted for 0.17–0.55% of the catch (by numbers), and 0.48–7.98% in terms of biomass (Di Natale *et al.*, 1995).

Purse seine: Mobulids are usually reported as an incidental catch in purse seines, but can also be taken in relatively high numbers (e.g. Lezama-Ochoa *et al.*, 2019, Croll *et al.*, 2016). For example, Başusta and Özbek (2017) reported on 30 individuals being taken in the Gulf of Antalya (Turkey), and Sakalli, (2017) reported on ca. 300 individuals being caught by purse seine off Samandağ (southeastern Turkey). The exact number in the latter study was uncertain as live individuals were released. Abudaya *et al.* (2018) reported than purse seine vessels would seasonally target mobulid rays in the waters off the Gaza strip.

The EU purse seine fleet operating off west Africa catches at least three species of mobulid ray, with rays generally discarded. Initial studies indicated that *M. birostris* was observed in 3.61% of sets observed between January 1995 and January 1996 (260 sets in total; Santana *et al.*, 1998). The estimated bycatch of rays (including mobulids and other myliobatiform rays) has been estimated at about 0.2 t and 1.4 t per 1000 t of landed tuna for FAD associated sets and free-school sets, respectively (Amandè *et al.*, 2010). A subsequent study by Torres-Irineo *et al.* (2014) also indicated the presence of mobulids in the catches of the EU purse seine fleet, including free-school and FAD-associated sets. The latter authors reported *M. birostris*, *M. mobular* (and also *Mobula rancurelli*, which is a junior synonym of *M. japanica*), and *M. tarapacana* (including data for *M. coilloti,* a junior synonym of *M. tarapacana*). Further information for the French purse seine fishery operating off West Africa is provided by Clavareau *et al.* (2018).

The smaller number of mobulid rays captured in FAD-associated nets noted above (Amandè *et al.*, 2010) is also in keeping with studies in the Indian and Pacific Oceans (e.g. Romanov, 2002), with a review of bycatch taken in purse seines by Hall and Roman (2013) noting "*Manta and devil rays seldom associate with floating objects, but they are sometimes captured in school and dolphin sets*".

Longline: Mobulids are generally an occasional bycatch in pelagic longline fisheries, although captures are influenced by a range of factors, including depth and season (Mas *et al.*, 2015). Pan *et al.* (2022) reported that *M. mobular* was observed in longlines set in the tropical waters of the central Atlantic for both bigeye tuna *Thunnus obesus* (0.04% of sets) and bluefin tuna (0.09% of sets), but were all discarded alive. In the southwestern Atlantic Ocean, *Mobula hypostoma* was recorded as bycatch only infrequently in Brazilian longline fisheries, and was mostly discarded, although some appeared on the market (Amorim *et al.*, 1998). Similarly, mobulids are occasionally caught in Uruguayan longline fisheries, accounting for 0.0–0.33% of all individuals caught, depending on area and longline type (Marín *et al.*, 1998; Mas *et al.*, 2015).

A low incidence of mobulid rays has been reported for Japanese longline fisheries (1995–1998), with just single individuals observed in the central Atlantic and northwestern Atlantic fishing areas (Matsunaga and Nakano, 2000), although some rays were reported at higher taxonomic levels. Parra *et al.* (2023) also reported a low incidence of mobulid rays in Portuguese longline fisheries, with *M. tarapacana* and *M. birostris* accounting for 0.006% and 0.004% of individual animals caught. A low incidence of *M. birostris* has been reported in Cuban longline fisheries, where this species accounted for 0.002% of elasmobranchs caught (Ruiz-Abierno *et al.*, 2021).

Nonetheless, some studies have indicated more frequent interactions with longline gears. Rey and Muñoz-Chápuli (1992) undertook a longline study off west Africa in 1985, and caught 48 *Mobula* spp. (4.7% of the studied elasmobranchs and swordfish catch). In this study, most mobulids (n = 42) were caught as individual fish per sampling unit (length of line), although there were three occasions where two mobulids were captured on the same sampling unit. Consequently, Rey and Muñoz-Chápuli (1992) considered that the catch distribution of mobulid rays was random (with a light grouping tendency), whereas the catch distributions along the sampling units of most sharks showed a clearer pattern of intraspecific clustering.

Observer data from Moroccan fisheries in the Mediterranean Sea indicated that the estimated bycatch levels of mobulids were greater in longline, followed by trawl and then purse seine (El Arraf *et al.*, 2024). Longline fisheries for bluefin tuna *Thunnus thynnus* in Maltese waters indicated that *M. mobular* could account for 0.3 % (by individuals) and 1.0% (biomass) of the overall catch (Burgess *et al.*, 2010).

Tuna traps: *Mobula mobular* has been reported as a bycatch in tuna traps used in the Mediterranean Sea (Vacchi *et al.*, 2002; Storai *et al.*, 2011[13]). In one study, a total of 15 individuals were reported, thus accounting for 36% of all elasmobranch bycatch (Storai *et al.*, 2011). In contrast, Neves dos Santos *et al.* (2001) considered *M. mobular* as a 'rare' bycatch species in tuna traps off Portugal.

Pelagic freezer trawl: Zeeberg *et al.* (2006) examined the bycatch taken by a pelagic freezer trawl fishery that targeted small pelagic fish off northwestern Africa. Mobulid rays (given as *M. birostris*) were a part of the bycatch, with estimated numbers shown in **Table 6**. Observer data were available for all five months studied for two of the four study years, with an estimated annual catch of mobulids ranging from 66.1 (in 2002) to 563.3 (in 2004).

Bottom-set gillnets: Mobulids can also be an incidental catch in bottom-set gillnets in fisheries targeting demersal fish species. For example, Perez and Wahrlich (2005) noted that *Mobula* sp. were caught (and discarded) in fisheries off southern Brazil for blackfin goosefish *Lophius gastrophysus* that used anchored gillnets (mesh size = 280 mm stretched mesh) in waters of 132–607 m deep. In total, this study reported 809 individual mobulids from the 14 trips observed, and mobulids accounted for ca. 1% of the elasmobranch bycatch.

Harpoons: Traditionally, coastal artisanal fisheries have targeted mobulid rays using harpoons (Croll *et al.*, 2016), including those fisheries using harpoon to fish for a range of large pelagic fish that may be encountered close to the surface (Di Natale, 1998). Such gears were also used in early recreational fisheries operating in some areas (Holder, 1908; Coles, 1916; Bancroft, 1929; Harris, 2024).

Other: Hemida *et al.* (2002) reported specimens of *M. mobular* being caught in Algerian waters by 'trawl' and 'seine', but the exact gear types used are somewhat uncertain.

9.2 At-vessel mortality

Purse seine: Clavareau *et al.* (2018) indicted that the overall at-vessel mortality (AVM) of mobulids taken in the French purse seine fishery operating off west Africa ranged from 12.76% *(M. mobular*, as *M. japanica*) and 28.07% (*M. mobular*) to 43.53% for *M. birostris*. However, these authors also noted that the observed mortality varied over the study area and trips, with *M. birostris* exhibiting 84.2% mortality in some areas.

In a subsequent analysis, Clavareau *et al.* (2020) reported AVM of 62.6% (FAD-associated purse seine sets) and 29.9% (purse seine catches of free-swimming tuna schools; FSC) for *M. mobular,* and 56.2% (FAD) and 22.6% (FSC) for *M. birostris* in the Atlantic. Comparable data for purse seine fisheries in the Indian Ocean were generally lower, being 29.7% (FAD) and 31.4% (FSC) for *M. mobular,* and 32.6% (FAD) and 18.4% (FSC) for

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[13] See also Boero, F. and Carli, A. 1979. Catture di elasmobranchi nella tonnarella di Camogli (Genova) dal 1950 al 1974. *Bollettino dei Musei e degli Istituti Biologici dell'Universita di Genova*, 47: 27–34.

M. birostris. The reasons for these differences are unclear, but size of fish encountered may be one factor (Clavareau *et al.*, 2020).

Whilst based on a single capture event, Sakalli *et al.* (2016) reported that eight out of nine *Mobula mobular* (as *M. japanica*) were released alive after capture by purse seine, with a corresponding AVM of 11.1%.

Longline: Longline-caught mobulids have shown a low rate of AVM (e.g. 100% discarded alive: Pan *et al.*, 2022), whilst other studies have reported AVM ranging from 0–1.5% (Coelho *et al.*, 2011, 2012) to 5.8% (Mas *et al.*, 2015).

Other gears: In relation to tuna traps, Storai *et al.* (2011) reported one bycatch event of 12 *M. mobular*, of which eight were released alive.

9.3 Post-release mortality

Despite the low AVM reported in some fisheries, various authors have indicated the requirement for improved estimates of post-release mortality (PRM), given that the large size of mobulids and that handling associated with releasing such large fish can result in damage (e.g. Mas *et al.*, 2015). There are, however, limited data on the PRM of mobulids taken in ICCAT fisheries.

Stewart *et al.* (in review) measured PRM for *M. tarapacana* (n = 9), *M. mobular* (n = 2), and *M. thursoni* (n = 1) in the Atlantic Ocean using satellite tags. All individuals were released either manually or using cargo nets, with time on deck ranging from three to ten minutes. All but two individuals (one *M. mobular* and one *M. tarapacana*) died after release. In combining these data with satellite tags from the Eastern Pacific and New Zealand, the authors found that post-release mortality varies, and that that mortality is significantly associated with time spent on deck. As a result, the study makes recommendations for best handling practices to prioritize rapid release.

Although outside the ICCAT area, Francis and Jones (2017) tagged and released nine *M. mobular* (reported as *M. japanica*). Of the seven tags that reported data, the four that had been entangled in the purse seine all died within 2–4 days of their release, whilst the three individuals that had been brailed aboard all survived release.

9.4 Capture-induced parturition

There are numerous reports of mobulid rays either giving birth or aborting when caught (e.g. Coles, 1913, 1916; Notabartolo di Sciara, 1988). Whilst the survival rates of pups born prematurely is unknown, and may depend on a range of factors (e.g. developmental stage, and geographic location), this factor should also be considered in the interpretation of estimated rates of population growth.

9.5 Mitigation measures

Spatial management has often been suggested as a tool to afford protection to mobulid populations, especially when there are seasonally important feeding aggregations and nursery areas, and cleaning stations. Some such areas have been reported in the ICCAT Area (see Section 2), and the importance of such habitats has also been evidenced from comparable studies in the Indo-Pacific (Putra *et al.*, 2020; Venables *et al.*, 2020). In some cases, such areas may also provide economic benefits from ecotourism (Murphy *et al.*, 2018). However, the movements of mobulids may extend hundreds of kilometres, which may exceed the size of some protected area (Graham *et al.*, 2012). Additionally, mobulids are often found in association with biologically productive areas, including upwelling zones, frontal systems, seamounts, and around oceanic islands (Graham *et al.*, 2012; Mas *et* *al.*, 2015). Such productive areas may be important fishing grounds for a variety of tunas and other pelagic fish, and this would also be an important consideration for any marine spatial planning (Lezama-Ochoa *et al.,* 2020).

Whilst some areas of elevated biological productivity may be relatively site specific, such as those areas associated with geological and topographic features, some other productive oceanographic features may be more variable in their exact location, which would also need to be considered when considering options for static or dynamic spatial management.

Given the wide range in size and mass of mobulid rays, and their capture in multiple types of fishing gear, different approaches may need to be considered for bycatch mitigation and release guidelines. Hutchinson *et al.* (2017) developed some best practice guidelines for both purse seine and longline fisheries (summarised here in Annex 1 of this document), and such guidelines were used to inform bast handling practices for various RFMOs (including Western and Central Pacific Fisheries Commission (WCPFC) CMM 2019-05 and Annex 1 of ICCAT Recommendation 23-14). Simultaneously, there are ongoing efforts to improve species identification, which can be challenging for mobulids, include observer training workshops, distribution of identification guides and posters, and verification of species identification using genetic methods (Cronin *et al.,* 2023).

Cronin *et al.* (2023) recently reviewed bycatch mitigation strategies for mobulids, focusing on purse seine vessels, and considered the various stages of the fishing process, from pre-capture, pre-deck and on-deck. Avoiding fishing in areas where mobulids are seen is an important measure, but if mobulids are sub-surface or visibility is low, then such avoidance may not always be possible. In particular, large individuals can be difficult to remove from the vessel deck, and as a result may be more vulnerable to at-vessel and post-release mortality.

Cronin *et al.* (2023) noted that some vessels would lower the float line ("sink the corks") of the net to enable mobulids to escape, or use a range of stretchers (e.g. canvas slings, or cargo net) or a ramp or hinged gate to release mobulids back into the water. Some vessels also had a modified brailer or crane with a bycatch reduction device in the form of a sorting grid that could be used to release larger mobulid rays rapidly. Versions of these grids are currently being deployed and tested on purse seine vessels in the Pacific and Atlantic Oceans, and have the potential to decrease post-release mortality for large individuals (Murua *et al.*, 2022, Cronin *et al.,* 2024).

The use of aerial surveillance (e.g. spotter planes, helicopters or drones) has also been suggested as a useful approach to allow purse seine fleets to avoid and document areas with a high density of (near-surface) mobulids (Cronin *et al.*, 2023; Waldo *et al.*, 2024).

10. Productivity and susceptibility

Data on both the productivity and susceptibility of mobulid rays are limited, and this family was not included in the earlier Ecological Risk Assessments developed through ICCAT (Cortés *et al.*, 2010, 2015).

With regards the Indian Ocean, productivity-susceptibility analyses have flagged mobulid rays as being particularly vulnerable to drift gillnets, and also purse seine (Robertson *et al.*, 2022), and Griffiths and Lezama-Ochoa (2021) developed an ecological assessment for *M. mobular* in the eastern Pacific.

11. Summary of ICCAT data

ICCAT Task 1 catch data for mobulids are limited (**Table 7**) and likely to be incomplete, noting that many of the published studies documenting landings of mobulids (e.g. Başusta and Özbek, 2017; Abudaya *et al.*, 2018) are not contained in these data. The year when non-zero catch data were first reported was 2015, which suggests that earlier data are either lacking, had only been collated at a more generic level that cannot be definitively allocated to mobulid rays, or had not been reported to ICCAT. More data were submitted in 2017 than in other years, indicating that more consistent catch estimates had been submitted in that year.

These data have been summarised by gear type (longline, and purse seine), nation, sampling area, species, and catch type for the period 2015–2021 (**Table 8**). Reported annual catches of mobulids have averaged 5.2 $t.y^{-1}$ (range = 0.54–20.48 $t.y^{-1}$) over the period 2015–2022, though this value is skewed by the higher reporting in 2017. In more recent years (2018–2022), reported annual catches of mobulids have averaged 2.21 $t.y^{-1}$ (range = 0.00–2.21 $t.y^{-1}$) and 1.80 $t.y^{-1}$ (range = 0.51–2.95 $t.y^{-1}$) for purse seine and longline fleets, respectively.

Aggregated data (2015–2022) indicate that the majority of the reported mobulid catch comes from the purse seine fleet (73.4%), with the longline fleet accounting for 26.6%. This proportion is unlikely to reflect all sources of fishing mortality affecting mobulids, given that gillnet fisheries in shelf seas are also known to interact with these species. Overall, the majority of the reported catches were dead discards (72.8%), but some were reported as being landed (27.2%). Whilst no estimates of live discards have seemingly been reported in Task 1 data, observer programmes indicate the majority of mobulids are discarded alive (see below).

The main nations reporting catches of mobulids (aggregated data, 2015–2022) were France (43.6%), Venezuela (26.0%), Spain (15.7%), El Salvador (5.6%), and Curaçao (4.8%). Whilst these five nations accounted for >95% of the catches reported to ICCAT, this will be influenced by consistency in reporting estimated catches, and data are incomplete for several nations with known or expected interactions with mobulid rays.

The main areas from where catches of mobulids have been reported (aggregated data, 2015–2022) were in the northwestern Atlantic (BIL94A; 23.9%), northeastern Atlantic (BIL94B; 38.3%), and southeastern Atlantic (BIL97; 35.1%). Whilst these three areas accounted for >97% of reported catches, this will be influenced by national reporting, and thus not reflective of spatial variation in relative abundance.

The main mobulid taxa reported in catches (aggregated data, 2015–2022) were *M. mobular* (46.5%, comprising 36.3% of *M. mobular* and 10.2% reported as *M. japanica*), *M. birostris* (28.8%) and *M. tarapacana* (8.8%). However, 14.2% of landings were reported at the family-level (Mobulidae) and there were no reported landings of *M. hypostoma* (or *M. rochebrunei*).

In terms of reporting landings of mobulid rays, there was a total of 11.42 t reported to ICCAT over the period 2016–2022, with average annual landings over this period being 1.63 $t.y^{-1}$ (range = 0.51–2.95 $t.y^{-1}$). The majority of reported landings were from Venezuela (95.5%), with smaller quantities reported occasionally by Curaçao, El Salvador, Spain, Guatemala, and Panama.

Observer data providing data on the numbers of mobulid rays that were discarded alive or dead were available for three years (2019–2021; **Table 9**). When data for all species and years were aggregated, the overall percentage of mobulids being discarded alive was 92.9% for longline fleets and 78.1% for purse seine (**Table 10**).

12. FAO landings data

Reported landings data for mobulid rays (using the codes listed in **Table 1**) were extracted on 21 February 2024. These data (**Table 11**) related to just four nations reporting mobulids in landings data from the Atlantic Ocean.

Liberia reported landings of 'Mobulidae' that ranged from 100–931 $t.y^{-1}$ (1998–2005), which declined to 23 t in 2006, and with no reported landings since then. Mauritania also reported positive landings of Mobulidae (2–64 t per year) over a short period (2011–2014).

In terms of species-specific data, Spain reported positive landings of *M. mobular* (usually <5 $t.y^{-1}$) in the period 2004–2013, with a small amount also reported in 2019. Puerto Rico reported a landings value for *M. birostris* in a single year (0.46 t in 2011).

Given the reported landings of mobulids that have supported many of the published studies discussed in the present paper, it is apparent that FAO landings data are incomplete. This could relate to mobulid rays being reported under more generic categories (e.g. 'batoid fishes nei' (Batoidimorpha, Hypotremata, BAI) or 'sharks, rays, skates, etc. nei (Elasmobranchii, SKX)), or that they are unreported, especially when taken by artisanal fishers operating in coastal waters. Furthermore, these data do not include discards, and so are not representative of 'catch'.

13. Other threats

Given that mobulid rays spend a high proportion of the time in the upper parts of the water column, they may be subject to other anthropogenic activities, including vessel strike, entanglement in fishing line (from recreational fisheries), and entanglement in surface ropes (Croll *et al.*, 2016; Pate and Marshall, 2020; Pate *et al.*, 2020). Mobulids with lacerations that were suspected as being caused by propellor wounds have been reported in coastal areas by a range of authors (e.g. Adams and Amesbury, 1998; Pate and Marshall, 2020).

There have been limited studies of contaminant levels in mobulids (e.g. Essumang, 2009, 2010; Hauser-Davis *et al.*, 2021). Bordbar *et al.* (2023) examined metals and organic contaminants in a single specimen of *M. mobular* (a 130 cm disc width female) caught in Greek waters, for which the reported mercury concentration was 0.16 ± 0.01 $ug.g^{-1}$ wet weight (muscle) and 0.15 ± 0.003 $ug.g^{-1}$ (liver). Roubie *et al.* (2024) examined trace metals in the muscle and gill tissue of *M. mobular* ($n = 2$) from the Ionian Sea (Mediterranean Sea), with the mean mercury concentrations being 0.62 $ug.g^{-1}$ wet weight (muscle) and 0.13 $ug.g^{-1}$ (gill). Studies elsewhere have reported relatively low mercury concentrations in the muscle of mobulids, with all the samples analysed by Ooi *et al.* (2015) being ≤0.42 $mg.kg^{-1}$, and low concentrations also reported in *Mobula* spp. from both Brazilian waters (Hauser-Davis *et al.*, 2021) and Ghanaian waters (Essumang, 2009; cited by Hauser-Davis *et al.*, 2021).

Low concentrations of organic pollutants have also been observed (Zafeiraki *et al.*, 2019), but this was based on a single *M. mobular* of 80 cm (reported as body length, but may have been width). A subsequent study by Bordbar *et al.* (2023), who examined organic contaminants in a single specimen of *M. mobular* (a 130 cm disc width female) caught in Greek waters, found that organic contaminants were in low concentrations in the muscle, but that there were higher concentrations of some lipophilic organic contaminants in the liver. The impacts of such contaminant levels on the health of individual fish (and any embryos) is uncertain.

Mobulid rays are filter-feeding, and so there has been some concern over the potential for the ingestion of microplastics (Germanov *et al.*, 2019), although the extent and implications of this are uncertain.

Given that the distribution of mobulids has been linked with sea surface temperature, there is the potential for the distribution, seasonality, and local abundance of mobulids to be influenced by climate change and any resultant mismatches in predator-prey distribution (e.g. Sakalli, 2017).

14. Management measures and conservation instruments

Given concern over population levels and threats to this family of fish, for which there has been an international trade in their gill plates as well as local and regional consumption and trade of their meat (O'Malley *et al.*, 2017), there has been increasing focus of using conservation instruments to facilitate appropriate management measures relating to mobulid rays, noting the perceived vulnerability of this family of ray (Lawson *et al.*, 2017). Due to increasing concerns over the unregulated, international trade in gill plates, mobulid rays were listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Initially, two species (*M. birostris* and *M. alfredi*, which were both in the genus *Manta* at that time) were listed in Appendix II in 2013, with all mobulids listed in Appendix II in 2016.

In 2014, all the species that were recognised at the time were also listed in Appendices I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS). Under the CMS, "*Parties that are Range States of a migratory species listed in Appendix I shall prohibit the taking of animals belonging to such species*".

Various Regional Fisheries Management Organisations from oceanic areas outside the Atlantic have brought in prohibitions on the retention of mobulid rays, including the Indian Ocean Tuna Commission (IOTC; Resolution 19/03), Western and Central Pacific Fisheries Commission (WCPFC; CMM 2019-05), and Inter-American Tropical Tuna Commission (IATTC; Resolution C-15-04).

In 2015, the IATTC adopted Resolution C-15-04 'On the conservation of mobulid rays caught in association with fisheries in the IATTC Convention Area', under which "*Members and Cooperating Non-Members (CPCs) shall prohibit retaining onboard, transshipping, landing, storing, selling, or offering for sale any part or whole carcass of Mobulid rays*", although there are some provisions under which mobulid rays can be landed by small-scale fisheries for domestic consumption only.

The IOTC adopted Resolution 19/03 'On the conservation of mobulid rays caught in association with fisheries in the IOTC area of competence', which was based on the limiting life-history of the species, the 'ecological and cultural significance', the prior listings on CMS and CITES listings, and the recommendation from the Scientific Committee (SC21). This measure states that "*CPCs shall prohibit all vessels from intentionally setting any gear type for targeted fishing of mobulid rays in the IOTC Area of Competence, if the animal is sighted prior to commencement of the set*" and also that "*CPCs shall prohibit all vessels retaining onboard, transhipping, landing, storing, any part or whole carcass of mobulid rays caught in the IOTC Area of Competence*". Once again, there is some allowance for local consumption of mobulid rays from subsistence and artisanal fisheries.

The WCPFC adopted the conservation measure CMM 2019-05, entitled 'Conservation and Management Measure on Mobulid Rays caught in association with fisheries in the WCPFC Convention Area'. The text was broadly comparable to that used in the IOTC Resolution.

In 2018, the Commission for the Conservation of Southern Bluefin Tuna (CCSBT) adopted, and subsequently updated, the Resolution to Align CCSBT's Ecologically Related Species measures with those of other tuna RFMOs. Concerning Mobulid rays, this measure requires CCSBT members to abide by IOTC Resolution 19/03 and WCPFC CMM 2019-05 when their vessels fish in the Convention Areas of IOTC and WCPFC, respectively

There are also a range of other national and regional measures within fisheries legislation that afford protection to mobulid rays. For example, European Union (EU) regulation 2019/1241 includes a "prohibition to fish for, retain on board, tranship, land, store, sell, display or offer for sale" mobulid rays (European Union, 2019), with this also introduced into UK law. Additionally, Brazil and the USA have passed national legislation restricting the fishing and/or trade of mobulids (Lawson *et al.*, 2017).

With regards the Mediterranean Sea, the General Fisheries Commission for the Mediterranean (GFCM) has adopted Recommendation GFCM/42/2018/2 “on fisheries management measures for the conservation of sharks and rays in the GFCM area of application, amending Recommendation GFCM/36/2012/3”. Under this Recommendation, “*specimens of shark species listed in Annex II of the SPA/BD Protocol shall not be retained on board, transhipped, landed, transferred, stored, sold or displayed or offered for sale*”. The Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean included *M. mobular* on Annex II.

15. **Synthesis, data gaps and future work**

Stewart *et al.* (2018) identified a large number of research topics that could usefully be addressed to improve our knowledge of mobulids, including taxonomic issues (species identification, and cryptic diversity), life-history (age and growth, natural mortality, maturity, fecundity, and reproductive cycle), movements, habitat use and identification of ecologically-important areas (e.g. mating, pupping, and nursery areas), stock units, population trends and assessing population size (e.g. aerial surveys, photo-identification, and genomic approaches such as population structure analyses and close-kin mark-recapture), fisheries impacts (including incidental catch, at-vessel and post-release mortality, and bycatch mitigation) and other potential impacts (entanglement, vessel strike, pollutants, tourism impacts, and climate change).

Further studies to consider how changes in environmental conditions (e.g. predicted changes in sea surface temperature, chlorophyll density, and production) could usefully be undertaken in order to determine how the distribution of mobulids may be influenced by climate change.

Given that there is increased interest in the potential for aerial surveillance as an approach to notifying purse seine fleets which fishing grounds areas may have a high (or low density) of mobulids - and as an early alarm system to prepare recommended handling and release equipment (Cronin *et al.*, 2023; Waldo *et al.*, 2024), there may be potential to develop aerial surveillance programmes in some areas that could also provide standardised survey data for the local mobulid population, as well as informing on those areas where there is a higher risk of bycatch.

16. **Conclusions**

The taxonomy of mobulids is still somewhat uncertain, with recent changes in the number of recognised species and genera, and lack of consensus on the overall number of valid species. All species may be taken in pelagic fisheries and species identification is generally poor, including those fisheries under the management of ICCAT. Consequently, any management measures for mobulid rays would be better applied at the family-level (i.e. Mobulidae).

Mobulids are most frequent in tropical and subtropical waters, and so the latitudinal limits indicated in Recommendation 23-14 (which only applies to vessels operating between 47°N and 47°S) are appropriate to afford protection to the stocks of these species.

Given their large size, often aggregating behaviour, position in the water column, and association with other pelagic fishes, mobulids may be considered susceptible to capture in fishing activities. Whilst catch rates are often low in longline fisheries, they may be taken in larger numbers by purse seine fisheries. They may also be taken in fisheries that are largely outside the remit of ICCAT, including gillnet and driftnet fisheries in national waters.

Whilst the life-history of mobulids is not fully known, the low fecundity (typically one pup per pregnancy), extended reproductive cycle (potentially one litter every two or more years), and low estimated rates of maximum population growth means that mobulid rays should be considered as a taxonomic group with high biological vulnerability to overfishing. Initial published estimates of r_{max} for mobulid rays have ranged from 0.077 y^{-1} (Pardo *et al.*, 2016) to 0.116 y^{-1} (Dulvy *et al.*, 2014), and the estimated values shown in the present paper may be lower, at 0.033–0.048 y^{-1}. These values are within the range of r_{max} estimated by Cortés (2016) for some of the shark species for which a prohibition on retention has been agreed by ICCAT, including silky shark *Carcharhinus falciformis* (ICCAT Recommendation 23-14; $r_{max} = 0.062–0.237$ y^{-1}) and bigeye thresher *Alopias superciliosus* (ICCAT Recommendation 09-07; $r_{max} = 0.010–0.119$ y^{-1}), and those for which the prompt release of live individuals is required, such as porbeagle *Lamna nasus* (ICCAT Recommendation 15-06; $r_{max} = 0.042–0.161$ y^{-1}). Cortés *et al.* (2010) had previously estimated comparable rates of productivity for these species, being 0.010 y^{-1} (–0.006 to 0.025) for *A. superciliosus*, 0.048 y^{-1} (0.038 to 0.057) for *L. nasus,* and 0.063 y^{-1} (0.037 to 0.083) for *C. falciformis*. Consequently, mobulid rays should be considered as being of low biological productivity and of greatest biological vulnerability.

Furthermore, the FAO Expert Advisory Panels convened to consider the proposals to amend Appendices I and II of CITES concerning commercially-exploited aquatic species have stated that mobulid rays are of low productivity (FAO, 2013, 2016), with the most recent finding of this panel being "*there is little information about biological parameters of mobula rays. After reviewing the available parameter estimates for the species … the Panel concluded that these species meet the low productivity criteria. While some individual life history estimates suggest medium productivity (e.g. age of maturity*[14]*), the Panel considered its very low fecundity (one individual pup every 2–3 years) and the resulting estimate of maximum population increase and concluded that the species have a very low productivity*" (FAO, 2016).

Mobulid rays are of conservation concern throughout their range, having been listed in Appendix II of CITES, and in Appendices I and II of CMS. Additionally, mobulids are considered to be threatened on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, with the majority of species assessed as Endangered, including *M. birostris, M. hypostoma, M. mobular, M. tarapacana*, and *M. thurstoni*, and some Indo-Pacific species assessed as Vulnerable.

In addition to limited biological data, those data required to quantitatively assess mobulid populations are lacking for most areas, and temporal changes in population levels and current trajectories are uncertain. Furthermore, both ICCAT catch data and FAO landings data are largely incomplete. Indeed, the lack of landings data in international datasets is in contrast to published studies that have documented landings from within the ICCAT area. It is uncertain whether such data are held on national databases, and/or have been aggregated with data for other batoids.

Despite the lack of data on population trends for mobulids across the ICCAT area, the known interactions with ICCAT (and other) fisheries, and the low population productivity means that this family may be considered highly susceptible to depletion. Hence, precautionary management measures are justified and also in keeping with conservation instruments that are relevant to some ICCAT CPCs. Whilst there are limited data on post-release mortality, at-vessel mortality is often reported as being relatively low, and so a prohibition on retaining mobulid rays would, in conjunction with release best-practices, likely benefit the populations of these stocks.

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[14] See Section 3 for comments on some earlier estimates of the age at maturity.

Given the information above, mobulid rays should be considered as being a taxon "*of the greatest biological vulnerability and conservation concern for which there are very few data.*"

In some areas, mobulids are an important element of ecotourism, and so the economic value of these species and stocks, whilst not fully quantified, may be an important element of the 'natural capital' of some nations.

To summarise, in response to Paragraph 8 of ICCAT Recommendation 23-14:

- Mobulid rays clearly meet the definition of being a taxon of the greatest biological vulnerability and conservation concern for which there are very few data.
- Given the scarcity of data on fishery interactions and species' life histories, it is appropriate to apply precautionary management measures, such as a prohibition on retention.
- In order to address data gaps, it is particularly important that CPCs whose fisheries interact with mobulid rays fulfil their reporting obligations as laid out in Paragraph 2 of Recommendation 23-14.

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Table 1. Current list of mobulid species, FAO codes, and accepted scientific names according to the Catalog of Fishes, WoRMS and FishBase (all accessed 25 March 2024), Last (2016), Stevens *et al.* (2018) and whether they have been assessed by the IUCN (September 2022). Those species reported from the ICCAT convention area are indicated. Additional, relevant FAO codes include MAN for Mobulidae and RMV for *Mobula* spp.

Common name(s)	**Taxa**	**FAO code**	**Catalog of Fishes**	**WoRMS**	**FishBase**	**Last *et al.* (2016)**	**Stevens *et al.* (2018)**	**IUCN**	**Present in the ICCAT area**
Reef manta ray Alfred manta	*Mobula alfredi*	RMA	Yes	Yes	Yes	Yes	Yes	Yes	?
Giant manta ray Oceanic manta ray	*Mobula birostris*	RMB	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Caribbean manta ray	*Mobula* cf. *birostris*						Yes		Yes
Longhorned mobula, Long-horned pygmy devil ray [a]	*Mobula eregoodoo*	RME	Yes					Yes	No
	Mobula eregoodootenkee			Yes	Yes		Yes		No
Lesser devil ray West Atlantic pygmy devil ray	*Mobula hypostoma*	RMH	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Spinetail mobula	*Mobula japonica*				Yes				Yes
Shortfin devil ray Short-horned pygmy devil ray Kuhl’s devilray	*Mobula kuhlii*	RMK	Yes	Yes	Yes	Yes	Yes	Yes	No
Spinetail devil ray Devil fish	*Mobula mobular*	RMM	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Munk's devil ray, Munk’s pygmy devil ray, Pygmy devilray	*Mobula munkiana*	RMU	Yes	Yes	Yes	Yes	Yes	Yes	No
Lesser Guinean devil ray East Atlantic pygmy devil ray	*Mobula rochebrunei*	RMN		Yes	Yes		Yes		Yes
Chilean devil ray Sicklefin devil ray	*Mobula tarapacana*	RMT	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Smoothtail mobula Bentfin devil ray	*Mobula thurstoni*	RMO	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Total number of species			9	10	11	8	10	9	

Notes: [a] Different sources accept different scientific names as valid for this species

Table 2. List of mobulid species and synonyms. Adapted from FishBase.

Valid scientific name	**Original name and synonyms**
Mobula alfredi (Krefft, 1868)	*Ceratoptera alfredi* Krefft, 1868 *Manta fowleri* Whitley, 1936 *Manta pakoka* Whitley, 1936
Mobula birostris (Walbaum, 1792)	*Raja birostris* Walbaum, 1792 *Raja manatia* Bloch & Schneider, 1801 *Cephalopterus vampyrus* Mitchill, 1824 *Cephalopterus manta* Bancroft, 1829 *Manta americana* Bancroft, 1829 *Ceratoptera ehrenbergii* Müller & Henle, 1841 *Ceratoptera johnii* Müller & Henle, 1841 *Brachioptilon hamiltoni* Hamilton & Newman, 1849 *Cephaloptera stelligera* Günther, 1870
[a] *Mobula eregoodoo* (Cantor, 1849)	*Cephaloptera eregoodootenkee* Bleeker, 1859 *Mobula eregoodootenkee* (Bleeker, 1859)
Mobula hypostoma (Bancroft, 1831)	*Cephalopterus hypostomus* Bancroft, 1831 *Cephaloptera olfersii* Müller, 1834 *Cephaloptera massenoidea* Hill, 1862 *Ceratobatis robertsi* Boulenger, 1897
[b] *Mobula japanica* (Müller & Henle, 1841)	*Cephaloptera japanica* Müller & Henle, 1841 *Mobula rancureli* Cadenat, 1959
Mobula kuhlii (Müller & Henle, 1841)	*Cephaloptera kuhlii* Müller & Henle, 1841 *Dicerobatis draco* Günther, 1872
Mobula mobular (Bonnaterre, 1788)	*Raia mobular* Bonnaterre, 1788 *Raia fabroniana* Lacepède, 1800 *Raja cephaloptera* Bloch & Schneider, 1801 *Raja giorna* Lacepède, 1803 *Raja diabolus* Shaw, 1804 *Mobula auriculata* Rafinesque, 1810 *Apterurus fabroni* Rafinesque, 1810 *Cephalopterus massena* Risso, 1810 *Cephaloptera tatraniana* van Hasselt, 1823 *Cephalopterus edentula* Griffini, 1903 *Mobula japanica* (Müller & Henle, 1841)
Mobula munkiana Notarbartolo-di-Sciara, 1987	-
[c] *Mobula rochebrunei* (Vaillant, 1879)	*Cephaloptera rochebrunei* Vaillant, 1879
Mobula tarapacana (Philippi, 1892)	*Cephaloptera tarapacana* Philippi, 1892 *Mobula coilloti* Cadenat & Rancurel, 1960 *Mobula formosana* Teng, 1962
Mobula thurstoni (Lloyd, 1908)	*Dicerobatis thurstoni* Lloyd, 1908 *Mobula lucasana* Beebe & Tee-Van, 1938

Notes: [a] different sources list either *Mobula eregoodoo* or *Mobula eregoodootenkee* as the valid scientific name; [b] now considered to be a junior synonym of *M. mobular;* [c] some sources identify *Mobula rochebrunei* as a junior synonym of *M. hypostoma.*

Table 3. Disc width-weight conversion parameters for mobulid rays, based on [1] Tagliafico *et al.* (2014), [2] Abudaya *et al.* (2018), [3] Rambahiniarison *et al.* (2018), [4] Notabartolo di Sciara (1988), [5] data collated during the present study, and [6] Bintoto *et al.* (2021). Where necessary, parameters *a* and *b* have been converted to apply to disc width (cm) and mass (g).

Species	Area	N	Length range (cm)	a	b	r2	Source
M. hypostoma	Venezuela	3	32.6–71.4	0.004	3.296	0.99	[1]
M. mobular	Gaza	21	(ca. 173–305)	0.000004	4.3917	>0.9	[2]
M. japanica	Philippines	162	99.8–239.0	0.065060	2.641	0.93	[3]
M. mobular	Baja (E. Pacific)	27	131.6–228.5	0.001077599	3.4	0.96	[4]
M. mobular	Other sources	27	71–334	2.014	1.9716	0.674	[5]
M. mobular	Other and Gaza	46	71–334	0.229300	2.3938	0.781	[2,5]
M. tarapacana	Philippines	8	160.0–317.0	0.000734	3.486	0.98	[3]
M. tarapacana	Baja (E. Pacific)	7	ca. 247–305	0.019779342	2.92	0.99	[4]
M. thurstoni	Philippines	301	90.2–197.0	0.005414	3.189	0.97	[3]
M. thurstoni	Baja (E. Pacific)	105	21–177	0.029025295	2.78	0.98	[4]
M. thurstoni	Indonesia	37	126–229	0.003	3.2654	0.88	[6]
Mobula spp.	Average			0.0129	2.977		

Table 4. Summarised life-history parameters and rationale for *M. mobular*.

Life-history parameter		Value	Reference	Rationale
Age and Growth	L_{inf}	233.81	Cuevas-Zimbrón *et al.* (2013)	Cuevas-Zimbrón *et al.* (2013) used, noting that this was for *Mobula mobular* (as *M. japanica*) from the eastern Pacific. Dulvy *et al.* (2014) provided *K* values for other myliobatiform rays, with the value here averaged across the three species. Dulvy *et al.* (2014) indicated K may be in the range of 0.05–0.1 yr^{-1}. Pardo *et al.* (2016) used data from Cuevas-Zimbrón *et al.* (2013) and re-fitted. Size at birth was ca. 88 cm.
	k	0.28	Cuevas-Zimbrón *et al.* (2013)	
	t_0	–1.68	Cuevas-Zimbrón *et al.* (2013)	
	L_{inf}	–		
	k	0.086	Dulvy *et al.* (2014)	
	t_0			
	L_{inf}	299.9	Pardo *et al.* (2016)	
	k	0.12	Pardo *et al.* (2016)	
	t_0	–		
Longevity	T_{max} (years)	20	Couturier *et al.* (2012)	Based on sightings data for *Mobula birostris*, and comparable to the estimated longevity for *M. mobular* of 15–20 years (Pardo *et al.*, 2016)
	T_{max} (years)	14	Cuevas-Zimbrón *et al.* (2013)	Based on sample of aged vertebrae, could be an underestimate
	T_{max} (years)	31	Clark (2010; cited by Dulvy *et al.* 2014)	Based on sightings data for *Mobula alfredi*
Reproductive biology	Size at maturity (cm)	217. 8	Rambahiniarison *et al.* (2018)	Based on *Mobula mobular* (as *M. japanica*) from the Philippines
	Age at maturity (years)	8	Based on data from Cuevas-Zimbrón *et al.* (2013) and Rambahiniarison *et al.* (2018)	Given a 217.8 cm size at maturity, this would broadly equate with about 8 years of age (based on the VBGP given by Cuevas-Zimbrón *et al.* (2013; estimated length at age 8 = 218.3 cm). This value is close to the estimated 8–10 of Dulvy *et al.* (2014)
	Repro cycle (years)	2	Couturier *et al.* (2012); Dulvy *et al.* (2014)	Assumed 1 year gestation and 1 year resting
	L_0 - size at birth	95	White *et al.* (2006); Rambahiniarison *et al.* (2018)	Based on *Mobula mobular* (as *M. japanica*) from the Philippines and from Australia, which reported 90–100 cm (95 cm used as a midpoint)
	Fecundity (pups)	1	Couturier *et al.* (2012)	*M. mobular* has a litter size of 1, which is also typical of other mobulids (though litters of 2 have been reported occasionally for some species)
Length-weight relationship	a	0.001077599	Notabartolo di Sciara (1988)	Whilst from the Pacific, these values were derived from a study with a good sample size and size range, and the curve lies between the alternative options (Rambahiniarison *et al.*, 2018; Abudaya *et al.*, 2018)
	b	3.4		

Table 5. Estimated maximum population growth rate (r_{max}) for *M. birostris* and *M. mobular*, and input parameters. See Cortés (2016) for the original sources for the different methods.

	r_{max} (y^{-1})	
Method	***M. birostris***	***M. mobular***
Myers *et al.* (1997) equation applied incorrectly (Method 1)	0.045	0.085
Eberhardt *et al.*(1982) equation (Method 2)	0.022	0.040
Skalski *et al.* (2008) equation (Method 3)	0.028	0.048
Smith at el. (1998) equation (Method 4)	0.039	0.039
Demographic Invariant Method (Method 5)	0.042	0.056
The Euler-Lotka equation (Method 6)	0.022	0.022
Average	0.033	0.048
SD	0.010	0.021
Confidence limits	0.00826	0.01687
Input parameter	***M. birostris***	***M. mobular***
Age at maturity (A_{mat})	10.5	8
Litter size	1	1
Reproductive periodicity (years)	4	2
Maximum age (years)	45	31
Survivorship	0.965	0.950
Survivorship to A_{mat}	0.685	0.584
Natural mortality (M)	0.036	0.051

Table 6. Estimated numbers of mobulid ray taken by a pelagic freezer trawl fishery off northwestern Africa. Adapted from Zeeberg *et al.* (2006).

Month	**2001**	**2002**	**2003**	**2004**
July	-	0	-	98
August	-	46.5	-	405
September	-	19.6	0	28.4
October	58	0	32	28
November	-	0	4.6	3.9
Total	NA	66.1	NA	563.3

Table 7. Reported catches (tonnes) of mobulid ray (ICCAT Task 1 data; version of 31/01/2024; accessed 23 April 2024) for mobulids by gear type (LL = longline; PS = purse seine), nation, sampling area, species, and catch type (DD = dead discard; L = landed) for the years 2015–2021.

Gear	Nation	Area	Scientific name	Catch type	2015	2016	2017	2018	2019	2020	2021	2022	Total
LL	CAN	BIL92	*M. birostris*	DD		0.000	0.250						0.250
	VEN	BIL93	*M. birostris*	L		0.872							0.872
		BIL94A	*M. birostris*	L			1.013	1.620	1.815	0.511	2.945	2.129	10.035
PS	CUW	BIL94B	*M. birostris*	DD			0.058						0.058
			M. japanica	DD			0.270						0.270
			M. mobular	DD			0.238						0.238
				L			0.004						0.004
			Mobulidae	DD			0.296						0.296
				L			0.059						0.059
		BIL97	*M. birostris*	DD			0.183						0.183
			M. japanica	DD			0.459						0.459
			M. mobular	DD			0.387						0.387
			Mobulidae	DD			0.042						0.042
	SLV	BIL94B	*M. birostris*	DD			0.006						0.006
			M. japanica	DD			0.184						0.184
			M. mobular	DD			1.124						1.124
				L			0.088						0.088
			Mobulidae	DD			0.069						0.069
				L			0.014						0.014
		BIL96	*M. japanica*	DD			0.003						0.003
			M. mobular	DD			0.003						0.003
			Mobulidae	DD			0.001						0.001
		BIL97	*M. birostris*	DD			0.147						0.147
			M. japanica	DD			0.257						0.257
			M. mobular	DD			0.394						0.394
			Mobulidae	DD			0.060						0.060
	ESP	BIL94B	*M. birostris*	DD			0.162						0.162
			M. japanica	DD			1.445						1.445
			M. mobular	DD			2.482						2.482
				L			0.122						0.122
			Mobulidae	DD			1.096						1.096
				L			0.219						0.219
		BIL97	*M. birostris*	DD			0.061						0.061
			M. japanica	DD			0.689						0.689
			M. mobular	DD			0.300						0.300
			Mobulidae	DD			0.026						0.026

Table 7 (continued). Reported catches (tonnes) of mobulid ray (ICCAT Task 1 data; version of 31/01/2024; accessed 23 April 2024) for mobulids by gear type (LL = longline; PS = purse seine), nation, sampling area, species, and catch type (DD = dead discard; L = landed) for the years 2015–2021.

Gear	Nation	Area	Scientific name	Catch type	2015	2016	2017	2018	2019	2020	2021	2022	Total
PS	FRA	BIL94B	*M. japanica*	DD			0.148						0.148
			M. mobular	DD			0.197	1.366	4.222	0.000	0.149		5.934
			M. tarapacana	DD					0.150	1.206	0.000	0.000	1.356
			M. thurstoni	DD						0.000	0.357		0.357
		BIL97	*M. birostris*	DD	0.092						0.000		0.092
			M. japanica	DD	0.300		0.000						0.300
			M. mobular	DD	0.150		2.350	0.746	0.144	0.000	0.000	0.000	3.390
			M. tarapacana	DD						2.191	0.151	0.000	2.342
			M. thurstoni	DD						0.242	0.121	0.000	0.363
			Mobulidae	DD			3.992						3.992
	GTM	BIL94B	*M. birostris*	DD			0.000						0.000
			M. japanica	DD			0.013						0.013
			M. mobular	DD			0.007						0.007
			Mobulidae	DD			0.001						0.001
				L			0.000						0.000
		BIL97	*M. birostris*	DD			0.089						0.089
			M. japanica	DD			0.256						0.256
			M. mobular	DD			0.248						0.248
			Mobulidae	DD			0.034						0.034
	PAN	BIL94B	*M. birostris*	DD			0.003						0.003
			M. japanica	DD			0.074						0.074
			M. mobular	DD			0.221						0.221
				L			0.009						0.009
		BIL97	*M. birostris*	DD			0.118						0.118
			M. japanica	DD			0.200						0.200
			M. mobular	DD			0.266						0.266
			Mobulidae	DD			0.037						0.037
Total					0.542	0.872	20.475	3.732	6.331	4.150	3.723	2.129	41.956

Table 8. Reported catches (tonnes) of mobulid ray (ICCAT Task 1 data; version of 31/01/2024; accessed 23 April 2024) for mobulids summarised by gear type (LL = longline; PS = purse seine), nation, sampling area, species, and catch type (DD = dead discard; L = landed) for the period 2015–2021.

Year	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**	**Total**
Gear									
Longline		0.872	1.263	1.620	1.815	0.511	2.945	2.129	11.157
Purse seine	0.542		19.212	2.112	4.516	3.639	0.778	0.000	30.799
Total	0.542	0.872	20.475	3.732	6.331	4.150	3.723	2.129	41.956
Nation									
Canada		0.000	0.250		0.000				0.250
Curaçao			1.996						1.996
El Salvador			2.352						2.352
Spain			6.602						6.602
France	0.542		6.687	2.112	4.516	3.639	0.778	0.000	18.274
Guatemala			0.648						0.648
Panama			0.927						0.927
Venezuela		0.872	1.013	1.620	1.815	0.511	2.945	2.129	10.907
Total	0.542	0.872	20.475	3.732	6.331	4.150	3.723	2.129	41.956
Area									
BIL92		0.000	0.250		0.000				0.250
BIL93		0.872							0.872
BIL94A			1.013	1.620	1.815	0.511	2.945	2.129	10.035
BIL94B			8.608	1.366	4.372	1.206	0.506	0.000	16.058
BIL94C			0.000		0.000				0.000
BIL95									0.000
BIL96			0.008	0.000					0.008
BIL97	0.542		10.596	0.746	0.144	2.433	0.272	0.000	14.733
Total	0.542	0.872	20.475	3.732	6.331	4.150	3.723	2.129	41.956
Species									
M. birostris	0.092	0.872	2.091	1.620	1.815	0.511	2.945	2.129	12.077
M. japanica	0.300		3.997						4.297
M. mobular	0.150		8.441	2.112	4.366	0.000	0.149	0.000	15.218
M. tarapacana					0.150	3.397	0.151	0.000	3.698
M. thurstoni						0.242	0.478	0.000	0.720
Mobulidae			5.946					0.000	5.946
Total	0.542	0.872	20.475	3.732	6.331	4.150	3.723	2.129	41.956
Catch type									
Dead discards	0.542	0.000	18.946	2.112	4.516	3.639	0.778	0.000	30.533
Landings		0.872	1.529	1.620	1.815	0.511	2.945	2.129	11.423
Total	0.542	0.872	20.475	3.732	6.331	4.150	3.723	2.129	41.956

Table 9. ICCAT observer data (2019–2021) for mobulids in longline (LL) and purse seine (PS) fisheries giving the numbers discarded dead (DD), discarded alive (DL) and those of unknown (UNK) condition .

Gear	Species	Code	2019			2020			2021		
			DD	DL	UNK	DD	DL	UNK	DD	DL	UNK
LL	Mobulidae	MAN	0	4		0	11	20	0	10	
	Mobula japanica	RMJ		12		2	9	0	0	5	
	Mobula mobular	RMM	3	20		4	41	0		6	2
PS	Mobulidae	MAN				0	13	0	3	6	0
	Mobula japanica	RMJ	5	40	0	30	127	0	60	178	0
	Mobula mobular	RMM	39	157	0	51	187	0	50	167	0
	Mobula thurstoni	RMO				6	10	0	4	1	0
	Mobula tarapacana	RMT	4	15	0	30	83	0	7	46	3

Table 10. ICCAT observer data (2019–2021) for mobulids in longline (LL) and purse seine (PS) fisheries, giving the percentage of fish that were discarded alive, based on data in **Table 9** (specimens of unknown condition excluded).

Gear	Species	Code	2019	2020	2021	2019–2021 combined
LL	Mobulidae	MAN	100.0%	100.0%	100.0%	100.0%
	Mobula japanica	RMJ	100.0%	81.8%	100.0%	92.9%
	Mobula mobular	RMM	87.0%	91.1%	100.0%	90.5%
	TOTAL		92.3%	91.0%	100.0%	92.9%
PS	Mobulidae	MAN	-	100.0%	66.7%	86.4%
	Mobula japanica	RMJ	88.9%	80.9%	74.8%	78.4%
	Mobula mobular	RMM	80.1%	78.6%	77.0%	78.5%
	Mobula thurstoni	RMO	-	62.5%	20.0%	52.4%
	Mobula tarapacana	RMT	78.9%	73.5%	86.8%	77.8%
	TOTAL		81.5%	78.2%	76.2%	78.1%

Table 11. Landings (tonnes) of mobulids from the Atlantic as reported to FAO.

Year	Eastern Central Atlantic		NE Atlantic	Western Central Atlantic	Total
	Liberia*	Mauritania*	Spain**	Puerto Rico***	
1998	342	0	0	0	342
1999	802	0	0	0	802
2000	931	0	0	0	931
2001	106	0	0	0	106
2002	110	0	0	0	110
2003	100	0	0	0	100
2004	802	0	1	0	803
2005	435	0	3	0	438
2006	23	0	3	0	26
2007	0	0	2	0	2
2008	0	0	1	0	1
2009	0	0	3	0	3
2010	0	0	4	0	4
2011	0	11	5	0.46	16.46
2012	0	0	0	0	0
2013	0	2	1	0	3
2014	0	64	0	0	64
2015	0	0	0	0	0
2016	0	0	0	0	0
2017	0	0	0	0	0
2018	0	0	0	0	0
2019	0	0	0.11	0	0.11
2020	0	0	0	0	0
2021	0	0	0	0	0

*Landings reported as Mobulidae
**Landings reported as *Mobula mobular*
***Landings reported as *Mobula birostris*

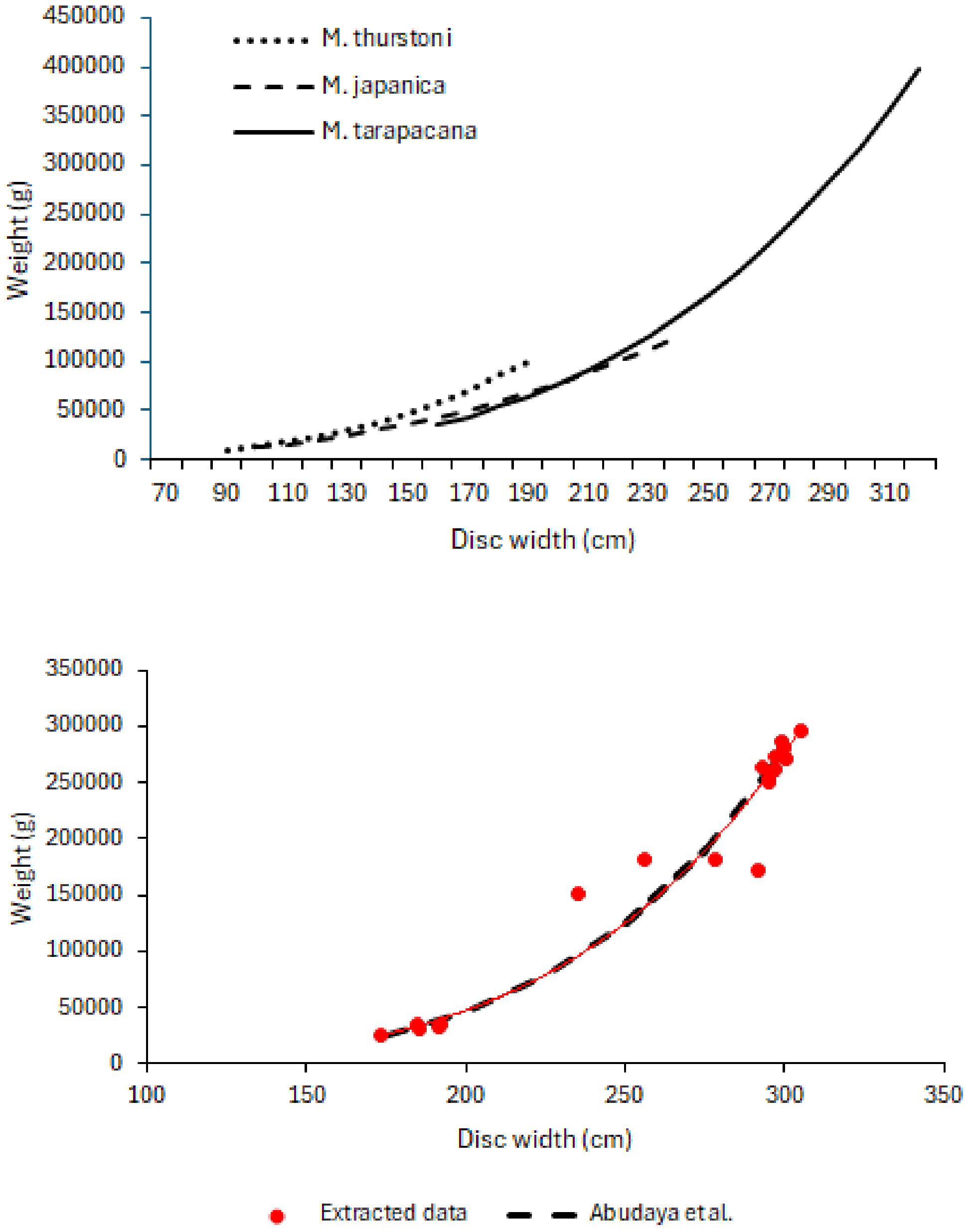
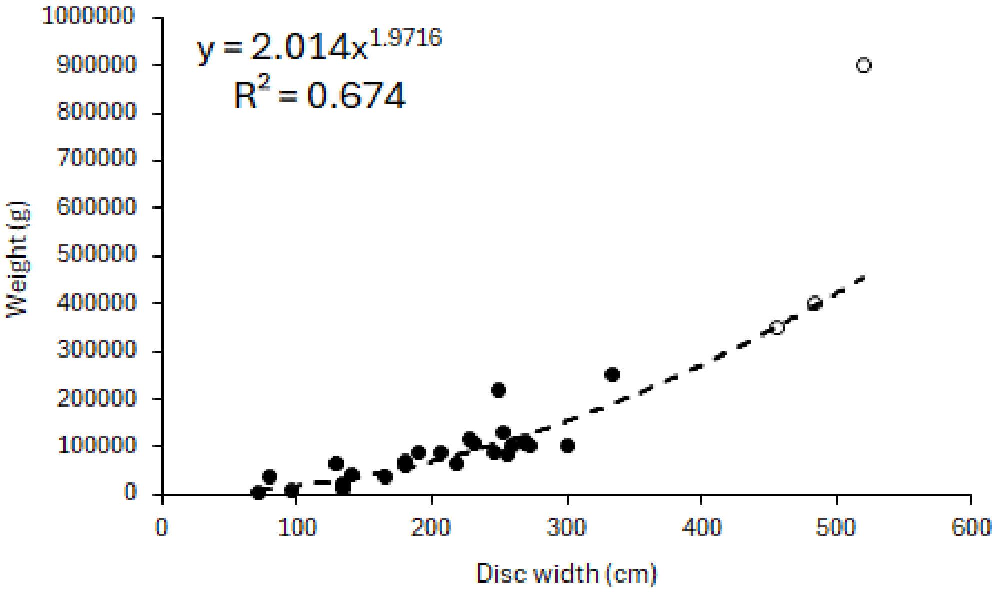


Figure 1. Relationships between weight and disc width for (top) mobulid rays from the Philippines (from Rambahiniarison *et al.*, 2018), and (bottom) *Mobula mobular* from Gaza (eastern Mediterranean; Abudaya *et al.*, 2018). Data points for the latter study were estimated from the original graph, though some overlying data points could not be differentiated. The lines represent the best fit lines from the extracted data points and the original length-weight relationship provided by Abudaya *et al.* (2018).



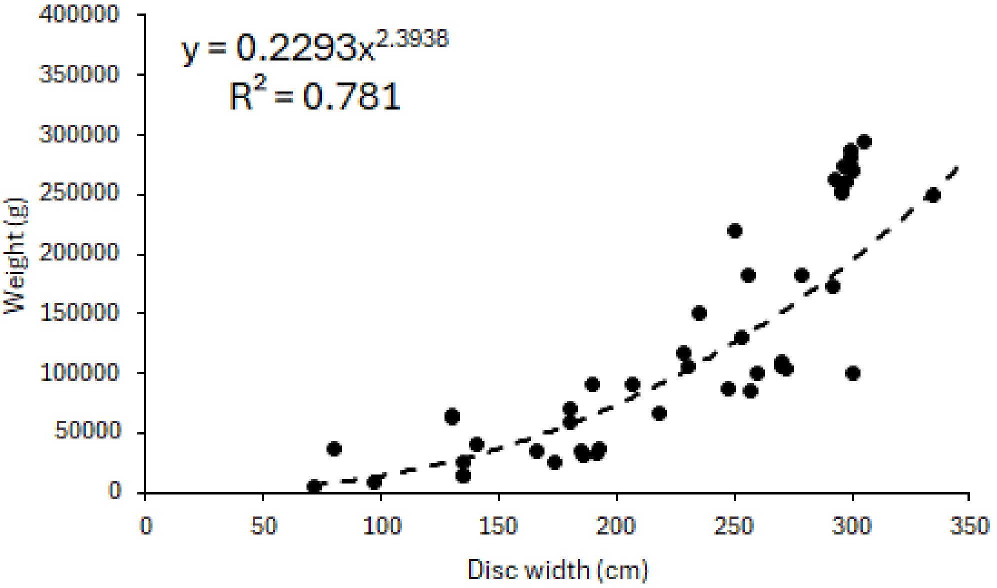


Figure 2. Relationships between weight and disc width for (top) *Mobula mobular* (filled circles and dashed line) and *M. birostris* (open circles) as derived from various studies, and (bottom) *M. mobular* using data points from various studies and data extracted from Abudaya *et al.* (2018). Weight information may include dressed weight for some studies, and the accuracy of weight information (including the type and resolution of the balances used) is uncertain.

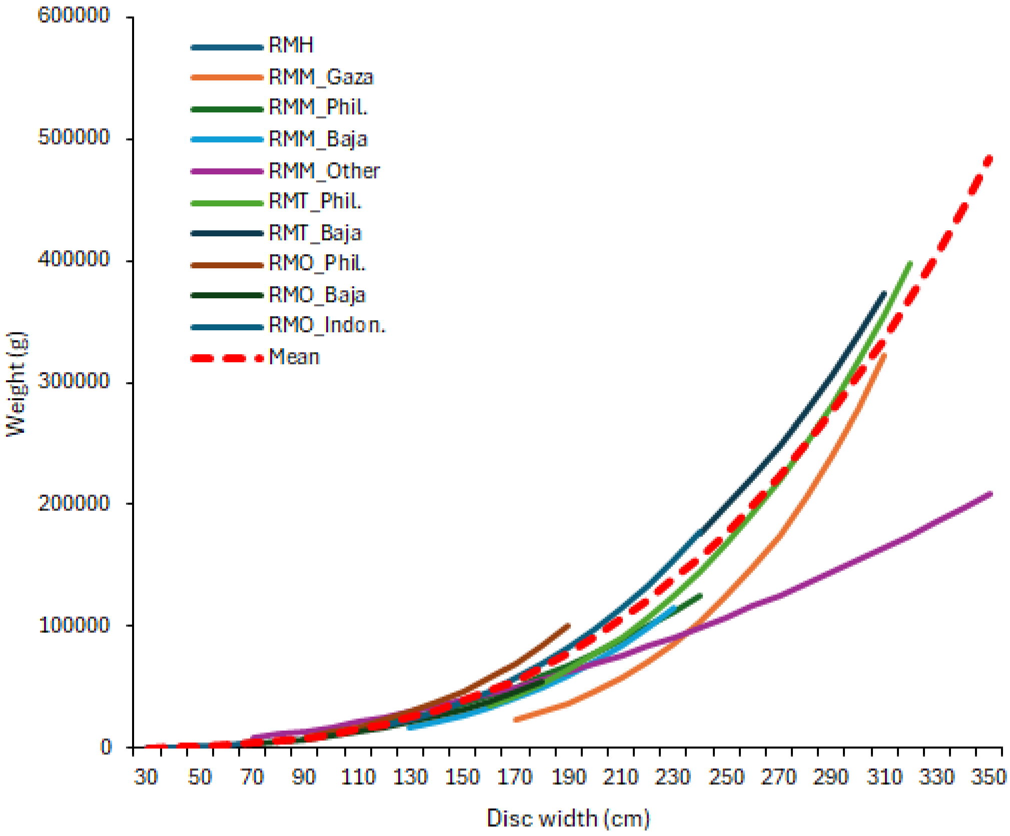


Figure 3. Relationships between weight and disc width for mobulid rays, including the best fit line (dashed line) based on the mean weight at disc width derived from the ten studies See **Table 1** and **Table 3** for details of species codes and parameters.

Annex 1: Handling guidelines for mobulid rays taken by purse seine and longline (adapted from Hutchinson *et al.*, 2017).

	Things to do	Things not to do
Purse seine	• Release mobulid rays from the net whilst they are still free-swimming (e.g. back down procedure, and dropping corks). • Release mobulid rays from the brailer immediately. • Small-sized (<30 kg) and medium-sized mobulid rays (30–60 kg) should be handled by 2–3 people, and carried by the sides of its wings or, preferably, using a specially designed stretcher. • Larger-sized mobulid rays (>60 kg) that are on the deck should be returned to the sea using an appropriate stretcher (e.g. cargo net, canvas sling, modified brailer) that can be placed under the animal and then lifted by crane. • If a large-sized mobulid ray is on deck, try to keep it out of direct sunlight and, if it cannot be released immediately, then use a deck hose and clean sea water supply to gently keep it wet. • Avoid fishing in those areas with known or predicted high densities of mobulid rays. • Reduce soak times when schools of mobulid rays are present. • If a mobulid ray is entangled in the net, then cut away the netting. • Check the equipment that would be used to release mobulid rays when fishing in areas where they may occur, and keep this equipment to hand.	• Do not leave a mobulid ray on deck until hauling is finished before returning it to the sea. They should be returned to the sea as soon as practicable. • Do not wrap wires or cables around or through the mobulid ray in in order to move or lift it. • Do not drag, carry, or pull a mobulid ray by the cephalic lobes or tail, and do not inserting your hands into the gill slits or the spiracles.
Longline	• Small-sized (<30 kg) mobulid rays should be brought on board gently, and as much of the gear removed as possible, by backing the hook out of its mouth. • If hooks are embedded in the jaw, either cut the hook with bolt cutters or cut the line at the hook and gently return the animal to the sea. • For medium- and large-sized mobulid rays (>30 kg), leave the ray in the water and use a de-hooker or long-handled line cutter to cut the gear as close to the hook as possible, and leaving as little line as possible attached to the animal. • Avoid fishing in those areas with known or predicted high densities of mobulid rays. • Reduce soak times when schools of mobulid rays are present. • Check the equipment that would be used to release mobulid rays when fishing in areas where they may occur, and keep this equipment to hand.	• Do not strike the mobulid ray against the side of the vessel in an attempt to get a ray off the line. • Do not attempt to remove a deeply hooked or ingested hook (gut-hooked fish) by pulling on the branch line or by using a dehooker. • Do not attempt to lift medium- to large-sized (>30 kg) mobulid rays onto the vessel. • Do not cut the tail. • Do not gaff a mobulid ray to bring it onto the vessel. • Do not drag, carry, or pull a mobulid ray by the cephalic lobes or tail, and do not inserting your hands into the gill slits or the spiracles. • Do not cut the jaw to recover hooks.