High bycatch rates of manta and devil rays in the "small-scale" artisanal fisheries of Sri Lanka

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18   **Abstract**

19   **Background.** Expanding fisheries in developing nations like Sri Lanka have a significant impact
20   on threatened marine species such as elasmobranchs. Manta and devil (mobulid) rays have some
21   of the most conservative life history strategies of any elasmobranch, and even low to moderate
22   levels of bycatch from gillnet fisheries can lead to significant population declines. A lack of
23   information on life history, demographics, population trends, and fisheries impacts hinders
24   effective management measures for these species.
25   **Method.** We report on mobulid fishery landings over nine years between 2011 and 2019 across
26   38 landing sites in Sri Lanka. We collected data on catch numbers, body sizes, sex, and maturity
27   status for five mobulid species. We used a Bayesian state-space model to estimate monthly
28   country-wide catch rates and total annual landings of mobulid rays. We used catch curve
29   analyses to estimate total mortality for *Mobula mobular*, and evaluated trends in recorded body
30   sizes across the study period for *M. mobular, M. birostris, M. tarapacana* and *M. thurstoni*.
31   **Results.** We find that catch rates have declined an order of magnitude for all species across the
32   study period, and that total annual captures of mobulid rays by the Sri Lankan artisanal fishing
33   fleet far exceed the estimated annual captures of mobulids in all global, industrial purse seine
34   fisheries combined. Catch curve analyses suggest that *M. mobular* is being fished at rates far
35   above the species' intrinsic population growth rate, and the average sizes of all mobulids in the
36   fishery except for *M. birostris* are declining. Collectively, these findings suggest overfishing of
37   mobulid ray populations in the northern Indian Ocean by Sri Lankan artisanal fisheries. We
38   recommend strengthening the management of these species through improved implementation of
39   CITES, CMS, and regional fisheries management actions. In addition, we report on the
40   demographic characteristics of mobulids landed in Sri Lanka and provide the first record of *M.*
41   *eregoodoo* in the country.

1. Introduction

Small-scale and artisanal fisheries are increasingly recognized as having an equal or greater impact on marine resources than large-scale industrial fisheries, with recent studies suggesting that small-scale fisheries in developing countries employ over 90% of all fishers and are responsible for half of all fisheries landings (Shester & Micheli, 2011; Kelleher et al., 2012; FAO, 2015; Crona et al., 2015). Yet these fisheries are frequently unmonitored, often unregulated, and represent a widespread challenge to enforcement of fisheries management regulations. The most commonly utilised gear type in small-scale fisheries is the gillnet; due to ease of manufacture, deployment, recovery, repair, its relatively low cost, and the wide range of species that can be effectively captured (Anderson et al., 2020; Berninsone et al., 2020). However, their versatility also makes gillnets responsible for an extremely large proportion of the world's incidental capture and bycatch (Lewison et al., 2004; Peckham et al., 2007; Žydelis et al., 2009; Reeves, McClellan & Werner, 2011; Jabado, 2018; Arlidge et al., 2020). Further, because gill nets are often deployed for many hours or days at a time, the bycatch mortality associated with gillnet fisheries can be much higher than other gear types such as purse-seines and longlines (D'agrosa, Lennert-Cody & Vidal, 2000; Thorpe & Frierson, 2009; Broadhurst & Cullis, 2020). Efforts to phase out gillnets in favour of fishing gears with lower bycatch rates are often challenging (Squires, 2010; Rojas-Bracho & Reeves, 2013), particularly as alternatives generally result in lower capture and higher operational costs, a combination that is not favoured by low-income fishers or governments seeking to expand fishery revenue.

Sri Lanka, a small, developing island nation situated in the Indian Ocean, has a considerable proportion (27%) of its 21.4 million inhabitants living along its 1,770 km coastline (Emerton, Miththapala & Sutharkaran, 2021). With an Exclusive Economic Zone (EEZ) that covers an area greater than 517,000 km², fish products are an important and dominant source of protein, comprising 50% of total animal protein consumed by the population (MFAR, 2020). Fisheries are also an integral part of the culture and economy, directly employing over 224,610 marine fishers and contributing around 1.1% to GDP, resulting in focused efforts by the government to increase national fishing productivity (GoSL, 2019; MFAR, 2020). These include the provision of fuel and boat subsidies, in addition to the establishment of new fishery harbours, fish processing and canning factories, and larger vessels to engage in deep sea trawling. Nonetheless, the fisheries industry is still heavily reliant upon small-scale and artisanal fisheries, a large proportion (56%) using gillnets or gillnets in combination with longline or ringnets to target yellowfin and skipjack tuna (Hewapathirana, Gunawardane & Ariyaratne, 2019).

While tuna and billfish species fetch the highest prices for fishers, the Sri Lankan gillnet fleet captures a wide variety of bycatch species including marine mammals, turtles, elasmobranchs (Karunasinghe, Fernando & Samaraweera, 2000; Jayasinghe et al., 2019; Anderson et al., 2020). It is well documented that in small-scale fisheries, where almost all the catch is consumed or utilized, retained bycatch have a high value (Ardill et al. 2012), and fisheries in Sri Lanka are no

82   exception. While some bycatch is discarded at sea due to prohibitions on retention (e.g. marine
83   mammals, turtles, whale sharks, oceanic white-tip sharks and thresher sharks), other species,
84   most notably elasmobranchs, are retained and sold due to national and international demand for
85   their meat and derivatives.
86

87   Manta and devil rays (genus *Mobula*) consist of 9 extant species found in tropical, subtropical
88   and temperate waters worldwide (Notarbartolo di Sciara et al., 2017, 2020; Hosegood et al.,
89   2020). Collectively referred to as mobulids, they are among the largest of all rays and tend to
90   favour pelagic habitats (Couturier et al., 2012). Similar to many other elasmobranchs, mobulid
91   rays are highly susceptible to overexploitation due to their slow population growth rates driven
92   by low fecundity, matrotrophic reproduction, large size at birth, slow growth rates, late maturity,
93   and longevity (Couturier et al., 2012; Dulvy et al., 2014; Pardo et al., 2016). While significant
94   progress has been in describing the biology and ecology of mobulid rays over the last decade,
95   information on the biology and life history of most mobulid species is still extremely scarce
96   (Stewart et al., 2018a). The best-studied member of the genus is the reef manta ray (*Mobula*
97   *alfredi*), mostly due to its tendency to aggregate in coastal environments. Studies on the oceanic
98   manta ray (*M. birostris*) have also expanded in recent years, resulting in important baseline data
99   on movements, feeding ecology, courtship, and mating (Burgess et al., 2016; Stevens, Hawkins
100   & Roberts, 2018; Bessey et al., 2019; Beale et al., 2019; Trujillo-Córdova et al., 2020;
101   Armstrong et al., 2020). However, the rest of the devil rays have received far less scientific
102   attention, and consequently major knowledge gaps exist in reproductive biology, population
103   connectivity, geographic range, movements, habitat use, and foraging behaviour (Couturier et al.,
104   2012; Stewart et al., 2017, 2018a).
105

106   International demand over the last decade for mobulid gill plates – the cartilaginous structures
107   that filter plankton from the water column – has directly led to an increase in fishing effort and
108   retention of these species in bycatch fisheries (Croll et al., 2016; O'Malley et al., 2017). This
109   demand for dried mobulid gill plates, which are marketed as a form of Traditional Chinese
110   Medicine in east Asia, was fuelled by a rapidly expanding middle class alongside the depletion
111   of more desirable fish stocks (Graham-Rowe, 2011; Fabinyi, 2012; O'Malley et al., 2017).
112   Mobulid rays are highly susceptible to incidental capture in a wide range of fisheries and gear
113   types including gillnets, purse seines, trawl nets, and on occasion even long lines (Croll et al.,
114   2016). Together with their conservative life history characteristics, this has led to a number of
115   suggested population declines around the world (Ward-Paige, Davis & Worm, 2013; Dulvy et
116   al., 2014; White et al., 2015a; Lewis et al., 2015; Pardo et al., 2016), including in the western
117   Indian Ocean (Pacoureau et al., 2021). Sri Lanka is considered one of the largest mobulid
118   fisheries in the world (Ward-Paige, Davis & Worm, 2013; CMS Secretariat, 2015; Acebes &
119   Tull, 2016; Marshall et al., 2019) due to the expansive fishing fleet that ventures far beyond the
120   country's EEZ.
121

122 To improve implementation of international agreements to protect mobulid rays (e.g. Convention
123 on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the
124 Convention on Migratory Species of Wild Animals (CMS)) and support further national action,
125 we report on the catch and landing composition of mobulid rays encountered during surveys of
126 domestic fish markets from 2010 to 2020. We use Bayesian state-space models to estimate the
127 trends in catches across this period for each of four mobulid species and to estimate the total
128 landings of mobulids in the surveyed markets. Additionally, we use demographic analyses of
129 size and age distributions to infer total mortality and impacts of the fishery on mobulid rays.
130 Finally, we report demographic data including sex composition and size at maturity, contributing
131 to the limited available information on the reproductive biology of these species.

132 **2.   Methods**
133 *2.1 Study Sites*
134 We recorded mobulid ray landings over 1,346 surveys at 38 landing sites (combination of fishery
135 harbours and beach landing sites) in Sri Lanka between May 2010 and February 2020 (Fig. 1).
136 Data until March 2014 was collected by the project leader (DF), and from March 2014 to March
137 2020 by 15 research assistants with varying durations under the direct supervision of DF, who
138 performed quality control checks on all data collected and entered by research assistants. One
139 research assistant's morphometric measurements of mobulid specimens were deemed to be
140 unreliable based on several implausible values identified during quality control assessments and
141 therefore all measurements collected or entered by that researcher were eliminated from length-
142 based analyses. All species identification was confirmed by DF based on images collected in the
143 field by research assistants.
144
145 Sites encompassing both single-day (IDAY: Inboard Single-day Boats and OFRP: Outboard
146 engine Fiberglass Reinforced Plastic Boats) and multi-day (IMUL: Inboard Multi-day Boats)
147 vessels were monitored, providing us access to specimens caught both nearshore and offshore.
148 However, given the proximity of the continental shelf drop-off to shore (Karunarathna et al.,
149 2020), pelagic species are often encountered even by the single day vessels. Unless specimens
150 were counted as they were offloaded from a specific vessel, it was not possible to assign catches
151 to single or multi-day vessels. Consequently, we considered only combined landings for the
152 purposes of this study and do not distinguish between catches from single and multi-day vessels.
153
154 *2.2 Data Collection*
155 Whenever possible, unstructured and informal interviews were conducted with fishers,
156 auctioneers, and middlemen at the study sites to gather anecdotal information on mobulid
157 fisheries, vessels and fishing grounds (GPS coordinates), gear types, catch seasonality,
158 utilisation, and trade. We excluded implausible reported GPS coordinates that were on land.
159 Trade of gill plates as reported by Sri Lanka to the Convention on International Trade in
160 Endangered Species of Wild Fauna and Flora (CITES) were downloaded from the online trade
161 database (CITES Trade Database, 2021).
162
163 *2.3 Mobulid Landings, Demographic Analyses, and CPUE*
164 We identified all recorded individual mobulid rays to species level using the Guide to the Manta
165 and Devil Rays of the World (Stevens et al., 2019). When possible, we recorded the disc width
166 (DW) and disc length (DL) of individuals to the nearest centimetre. Due to constraints on the
167 size of the opening to ice holds onboard fishing vessels, most rays were landed cut in half
168 (vertically), or in several pieces for the largest bodied species (e.g. large *M. birostris* or *M.*
169 *tarapacana*). In such cases we derived measurements from each segment and added them
170 together to reconstruct a full DW.
171

172   Sexual maturity for males were recorded in two categories: immature having undeveloped
173   claspers not extending beyond the pelvic fin and mature with fully calcified claspers extending
174   beyond the posterior margin of the pelvic fin. We were unable to determine the maturity of
175   females since the internal reproductive organs were usually removed prior to storage in the ice
176   holds to slow down the rate of decomposition. Some individual specimens (including males)
177   could not be sexed as their entire reproductive organs were cut out during gutting. Other practical
178   complications included days when large numbers of rays were landed and piled on top of each
179   other making it impossible to accurately identify the gender of each individual specimen.
180
181   To account for potential data recording errors, we performed a logistic regression of DW to DL
182   and excluded from the dataset any entries where a recorded DW was more than three standard
183   deviations from the mean expected DW value based on the recorded DL. This resulted in the
184   exclusion of one *M. birostris*, ten *M. mobular*, and three *M. tarapacana* data points. We
185   estimated the size at maturity for males of each species by fitting a logistic regression to the DW
186   and maturity data and calculating the size at which a male has a 50% chance of being sexually
187   mature (DW_{50}). We performed logistic regressions in R (R Core Team, 2020) with the glm
188   function.
189
190   Due to the social dynamics of the fish markets and the speed at which mobulids were unloaded
191   from vessels, purchased, and moved out of the market, it was not possible to collect any standard
192   metrics of effort such as number of boats or number of fishing days in relation to the
193   corresponding number of landed mobulids. Furthermore, since mobulid rays are not as valuable
194   as target species such as tuna, the capture dynamics of mobulids are extremely complex. This
195   makes it extremely challenging to conceptualize, let alone collect, a valid metric of effort that
196   would explain landing rates and allow for a reliable catch per unit effort (CPUE) estimation.
197   Instead, we used the total number of registered single-day and multi-day vessels per year
198   reported by the national Ministry of Fisheries and Aquatic Resources Development, as a coarse
199   proxy for overall fishing effort in Sri Lanka (MFAR, 2020).
200
201   *2.4 Catch Time Series Analysis*
202   Since the fish markets were sampled irregularly throughout the study period, we chose to model
203   trends in landings using monthly estimates of daily mean landings. In other words, the model
204   estimated a mean landing rate for each month, around which daily, observed landings were
205   distributed. We modelled landings as count data from a negative binomial distribution and used a
206   state-space model to account for both observation error and true variability in the underlying
207   process (i.e. actual increases and decreases in catch rates that deviate from the overall trend). We
208   selected the negative binomial distribution to explain catch data as initial models using the
209   Poisson distribution resulted in overdispersion in the data relative to model estimates. The model
210   was described by the equations:
211

212 $$\ln\left(\hat{C}_{s,t}\right) = \ln\left(\hat{C}_{s,t-1}\right) + \mu_{s,t-1} \qquad \text{(eq. 1)}$$

213

214 where $\hat{C}$ is the overall mean daily catch rate (landed mobulids per day) for month t and species s,

215 which is determined by the mean daily catch rate for the previous month ($\hat{C}_{s,t-1}$) multiplied by

216 the change in catch rate $\mu_{s,t}$ (additive in log space). The species-specific monthly change in catch

217 rate $\mu_{s,t}$ is defined by:

218

219 $$\mu_{s,t} \sim N[\hat{\mu}_s, \sigma_{ts}] \qquad \text{(eq. 2)}$$

220

221 where $\mu_{s,t}$ is drawn from a normal distribution with mean $\hat{\mu}_s$ where $\hat{\mu}$ is the overall trend in

222 catches for species s and σ_{ts} is the process error term allowing for monthly variation around the

223 overall trend, estimated separately for each species. Each monitored fish market had a

224 hierarchically distributed persistent mean random effect throughout the time series in order to

225 estimate catches at markets during unsampled periods, such that:

226

227 $$\hat{M}_{m,s} \sim N[0, \sigma_{ms}] \qquad \text{(eq. 3)}$$

228

229 where $\hat{M}$ is the mean market random effect for each market m and species s, and σ_{ms} is the

230 process error term for the market effects, estimated separately for each species. The monthly

231 market effect was then hierarchically distributed around the mean market effect:

232

233 $$M_{m,s,t} \sim N[\hat{M}_{m,s}, \sigma_{ms,m}] \qquad \text{(eq. 4)}$$

234

235 where M is the market random effect for each market m and species s in month t, and $\sigma_{ms,m}$ is the

236 process error term defining the variability in the monthly market random effect around the mean

237 market random effect, estimated separately for each species and market. Put simply, this allowed

238 a market to have, for example, generally higher catch rates than the country-wide mean ($\hat{M}_{m,s}$)

239 but flexibility for the monthly catch rates to vary around that general effect ($M_{m,s,t}$). The mean

240 catch rate at each market was then calculated as:

241

242 $$\ln\left(C_{m,s,t}\right) = \ln\left(\hat{C}_{s,t}\right) + M_{m,s,t} \qquad \text{(eq. 5)}$$

243

244 where C is the mean catch rate for market m and species s in month t. Note that the *Market* effect

245 is therefore estimated in log space. Finally, the observed catches are distributed around the mean

246 catch rates using the negative binomial distribution such that:

247

248 $$catch_{m,s,t} \sim NegBin[p_{m,s,t}, n_{m,s,t}] \qquad \text{(eq. 6)}$$

249

250 $$n_{m,s,t} = \frac{C_{m,s,t} * p_{m,s,t}}{1 - p_{m,s,t}}$$ (eq. 7)

251

252 where *catch* is the observed catch at market *m* and species *s* in month *t*, *p* is the model-estimated
253 probability parameter for the negative binomial distribution for market *m* and species *s* in month
254 *t*, and *n* is the dispersion parameter for the negative binomial distribution, calculated as a
255 function of the mean catch rate *C* and probability parameter *p*.

256

257 We did not include market random effects for *M. thurstoni*, as only 93 specimens were recorded
258 over the full 10-year time series and were only recorded at 10 of 38 fishing ports. Instead, we
259 estimated a single country-wide mean monthly catch rate and applied that to all markets for *M.*
260 *thurstoni*. We did not include *M. kuhlii* in the catch estimation models as only 59 specimens were
261 recorded in total. We conducted posterior predictive checks to assess the fit of our final model, in
262 which we took draws from a random subset of the model estimated means for each month,
263 species, and market and compared these to observed catches. We ran the model with JAGS
264 (Plummer, 2003) using 3 chains with 400,000 iterations each, a burn-in of 200,000, and thinning
265 of 240. We assessed convergence of the model using visual inspection of chain convergence and
266 autocorrelation plots, and Gelman-Rubin diagnostics (Gelman & Rubin, 1992).

267

268 In order to estimate the total annual catch of each mobulid species we took random draws from
269 the model-estimated mean catch for each month, species, and market using the estimated
270 negative binomial parameters (similar to the posterior predictive checks). We sampled across the
271 full posterior distribution for each month, species and market and drew *n* samples for each
272 month, where *n* was the estimated number of fishing days that take place in that calendar month.
273 To calculate fishing days, we excluded public and religious holidays from the number of
274 calendar days that occur in each month and averaged this value across markets, as markets in
275 different regions of the country often observe different religious holidays.

276

277 We then summed the posterior draws for the entire month and across all markets for each species
278 to generate a monthly total for each species across all markets. Doing this for each posterior
279 draw allowed us to generate a distribution of monthly total catch rates for each species,
280 incorporating the uncertainty from the model fits into our estimates of total catch. Finally, we
281 summed catches across all months within complete years covered by the study period (2011 –
282 2019) to generate annual estimates of total catch.

283

284 In addition to estimating total annual catch of each species using the above model, for
285 comparison we conducted a simple extrapolation:

286

287 $$\bar{x}_{s,y} = \frac{x_{s,y}}{n_y} * F_y * m$$ (eq. 8)

288

289   where $\bar{x}$ is the estimated total catch of species *s* in year *y*, *x* is the recorded number of landed
290   mobulid rays of species *s* in year *y*, *n* is the number of survey days in year *y*, F is the estimated
291   number of total fishing days in year *y*, and *m* is the total number of surveyed landing sites
292   throughout the study period.
293
294   *2.5 Size Trend Analyses:*
295   We also assessed annual changes in the average size of each mobulid species landed, as changes
296   in size and age structure can be an indicator of fishing impacts on a population (Sharpe &
297   Hendry, 2009; Enberg et al., 2012). We aggregated DW's within years for each species and
298   estimated the linear trend in mean DW using a simple Bayesian linear regression coded and run
299   in R using JAGS (Plummer, 2003). A significant portion of the width data were collected by
300   research assistants, and we assume that measurements collected by assistants are likely to have
301   more observation errors than measurements collected by the project leaders. To account for this,
302   we included an additive error term to our linear models for DW data collected by the research
303   assistants. This additional error term was estimated by the model and allowed the data collected
304   by research assistants to be normally distributed around the mean annual DW with a standard
305   deviation that was greater than or equal to the standard deviation of width data collected by the
306   project leader. In short, this explicitly introduces into the model the expectation that the research
307   assistant's data were less precise than project leader data but allows for the situation where both
308   data sets were equally precise. It does not, however, allow for the research assistant data to be
309   more precise than project leader data in estimating annual mean DWs. For linear models, we ran
310   3 chains of 100,000 iterations each, a burn-in of 50,000, and thinning of 60.
311
312   *2.6 Total Mortality Estimation for Mobula mobular:*
313   A length-at-age relationship has previously been estimated for *M. mobular* (formerly *Mobula*
314   *japanica*) using vertebral band pairs (Cuevas-Zimbrón et al., 2013). This relationship was
315   subsequently used to convert DW data into age distributions, allowing for the estimation of total
316   mortality in a fished population in Baja California, Mexico (Pardo et al., 2016). We replicated
317   the methods applied in Pardo et al., (2016) to create a catch curve for *M. mobular* in the Sri
318   Lankan fishery. First, we converted DW data to ages using the estimated parameters from the
319   Von Bertalanffy growth curve with strong priors from Pardo et al., (2016). We chose to use
320   growth parameters estimated using strong priors as opposed to weaker or uninformative priors
321   because few large individuals were sampled in their study and the parameter values estimated
322   using strong priors were more consistent with expectations of maximum size for the species. We
323   used regression estimators to calculate total mortality *Z* in order to remain consistent with Pardo
324   et al., (2016) and provide comparable estimates of mortality for the same species in a different
325   fishery. Pardo et al., (2016) used an unweighted regression estimator of *Z* and truncated the right
326   tail of the age distribution (although they also compared estimates of *Z* without right truncation).
327   However, simulation studies of total mortality estimators have suggested that unweighted
328   regression estimators can be biased and warn against using them for analysing catch-curve data

329   (Smith et al., 2012). Instead, we used the recommended approach of weighted regression

330   estimators with no right truncation and considered the age of full recruitment to be the age of

331   maximum catch (Smith et al., 2012).

332   Following Pardo et al., (2016) we bootstrapped our age distributions to randomly include 80% of

333   the data in each bootstrap run. We conducted 20,000 bootstrap runs, identified the peak age

334   abundance within each subset of the data, and used the R package FSA (Ogle, 2017) to fit a

335   weighted regression estimator to the natural log of the number of individuals in each age class

336   beginning with the age of maximum catch. In addition to estimating Z for all years combined, we

337   conducted this analysis separately for width data collected in 2011, 2012, 2013, 2017, 2018,

338   2019, and 2020 to generate annual estimates of Z and evaluate whether total mortality has

339   changed over time.

340 **3. Results**
341 **3.1 Dynamics of the Fishery**
342 *3.1.1 Mobulid Fisheries*
343 Anecdotal information from fishers revealed that prior to 2010, mobulids were often released due
344 to low value and demand in comparison to other species. During this study, even as late as 2012,
345 it was observed that on rare occasions mobulid rays were being landed without their heads as
346 fishers had discarded them at sea to reduce space taken up in their holds and assuming that
347 traders were only interested in the meat. However, as fisher knowledge of the mobulid gill plate
348 trade and demand grew, the rays were landed whole.
349
350 Nonetheless, as mobulid rays are largely secondary catch, whether they were retained depended
351 on multiple factors, including the amount of target species captured, at which point during the
352 trip the mobulid rays were captured in the nets, and how much freezer space was available. Due
353 to limited capacity onboard vessels and the lack of refrigeration, fishers often stated that any
354 mobulids captured when heading out to sea were generally discarded in favour of catching target
355 species, and only retained them when returning back to shore in order to fill up their holds to
356 maximise profits and cover expenditures. Many fishers also claimed that mobulids are "heaty",
357 melting the ice onboard faster than other fish.
358
359 Furthermore, if mobulid rays were spotted in the water, nets would not be laid out as the rays
360 tend to entangle themselves due to their forward swimming nature coupled with the commonly
361 observed summersault behaviour exhibited when they encounter obstacles, including gillnets,
362 entrapping them even further. All this requires additional time for fishers to remove them from
363 the nets and repair any damage. There is also the potential for the entire net to be lost as many
364 mobulid species, except for *M. birostris*, tend to swim in schools resulting in multiple individuals
365 getting captured at the same time, dragging down the nets under their accumulated weight. The
366 fishers maintain that this is the reason they have to haul their nets in quickly when mobulids are
367 caught, since once they die, their weight compounded with their negative buoyancy can result in
368 fishers being unable to bring up the nets using only their hands, or sometimes even with a winch.
369 This results in the nets being cut and abandoned, causing significant financial losses considering
370 that the nets are usually approximately 50% of the investment placed into launching a fishing
371 vessel in Sri Lanka. Several times during the surveys we observed large *M. birostris* specimens
372 being towed in the nets back to port as it was too strenuous for the fishers to haul the individual
373 onboard at sea. Fishers also stated that the extremely rough skin of *M. birostris* caused damage to
374 their hands and were less appealing to bring onboard.
375
376 *3.1.2 Vessels and Fishing Grounds*
377 Fishing was predominantly conducted by three types of vessels; single-day boats fitted with
378 either outboard motors (maximum 40hp) or small inboard diesel engines that fish in coastal
379 waters for durations of up to 24 hours, and multi-day vessels with diesel inboard engines that fish

380   offshore and on occasion in the high seas for anywhere between around 30 to 90 days, depending
381   on weather conditions and catch. However, even in the case of single day vessels, there was a
382   high likelihood that they were fishing in deep waters due to the narrow continental shelf edge
383   around Sri Lanka that drops to over 200 meters in depth within 20 km of the shoreline, or in
384   some areas such as Trincomalee on the east coast, dropping to over 600 meters within the
385   harbour itself due to the presence of a deep-sea canyon. Only a few of these fisheries would have
386   been focusing effort at inshore coral reef habitats, and fishing at offshore coral reefs, such as Bar
387   Reef on the north-west coast, likely also took place.
388   We collected 78 reported GPS coordinates of fishing grounds from interviewed fishers and
389   excluded four of these as they were situated on land (three points in Sri Lanka, and one point
390   appearing on the border between China and Russia). Fishers in multi-day vessels often sailed
391   great distances to reach the most productive fishing grounds, with some claiming that Sri Lankan
392   waters were already over-fished, resulting in the need to venture into the high seas or even
393   neighbouring EEZ's including India, the Maldives, and sometimes as far as Indonesia,
394   Seychelles, and the Chagos Archipelago. This is corroborated by reported GPS coordinates of
395   catch locations from skippers of vessels that unloaded mobulids between 2011 and 2015 (Fig. 2).
396   Fishers at some landing sites on the west coast (predominantly in Beruwela) mentioned that the
397   Chagos Archipelago was especially good for shark fishing. Between 2010 and 2018, some
398   fishers reported that they had shifted their fishing behaviour in recent years to avoid venturing
399   too close to east Africa due to concerns over piracy surrounding the Somalian region.
400
401   *3.1.3 Gear Types*
402   Most vessels that we surveyed carried gillnets or a combination of both gillnets and longlines,
403   and reported deploying them depending on weather conditions, season, and species availability.
404   Mobulid rays were landed at 21 of the 38 monitored landing sites as non-discarded bycatch of
405   pelagic, or sometimes bottom-set, gillnet fisheries with mesh sizes ranging from 11.43 cm (4.5
406   inches) to 15.24 cm (6 inches) that were primarily targeting skipjack tuna (*Katsuwonus pelamis*),
407   yellowfin tuna (*Thunnus albacares*), and billfish. Only 3 records were logged of potential
408   capture by fishing lines (rather than nets): one *M. kuhlii* specimen by a longline, and two *M.*
409   *mobular* specimens, one by handline and the other was documented at the landing site with a
410   hook in its mouth. Across all surveys there were ten records of mobulid rays being captured
411   using hooks (similar to a harpoon but primarily used to drag large fish along the boat deck) when
412   encountered at the surface: six *M. birostris*, one *M. mobular*, and three *M. tarapacana*; all at
413   landing sites along the southern tip of Sri Lanka and prior to 2015.
414
415   *3.1.4 Catch Seasonality*
416   There appeared to be ambiguity among fisher claims regarding the effects of the monsoons on
417   mobulid catch. Some suggested there was a correlation while others said there was no influence
418   on the catch but rather a shift in numbers landed due to decreases of target species catch during
419   monsoonal periods. Either way, both agreed that the numbers landed generally increased during

420 the onset of the south-west monsoon (May to September) for ports along the west coast and
421 during the north-east monsoon (October to March) for ports on the east coast. We note that there
422 was no clear seasonal signal in the estimated mean landings rates from our state-space model, but
423 we did not include a spatial component, and country-wide averages may have masked alternating
424 peaks in landings between the east and west coasts of the country.
425
426 Multiple fishers on both sides of the island mentioned that the catch and presence of mobulid
427 rays were strongly correlated with the presence of krill, and that while the rays preferred deeper
428 waters, they (particularly *M. birostris*) would follow the krill to the surface. This information
429 was corroborated by whale-watching operators based at the Mirissa Fishery Harbour in the
430 South, who said they occasionally spotted manta rays feeding on krill at the surface.
431
432 *3.1.5 Mobulid Utilisation and Trade*
433 Only two of the surveyed communities (Negombo and Chilaw) were observed selling fresh
434 mobulid meat. At both sites, *M. tarapacana* was the most valued, followed closely by *M.*
435 *mobular*. Both *M. thurstoni* and *M. kuhlii* were considered the same as *M. mobular* (and often
436 not identified as separate species) and only fetched lower prices due to their smaller size. *Mobula*
437 *birostris* was almost never consumed fresh as it was said to have a "sandy" or "grainy" texture.
438 When not consumed fresh (and any excess), the meat was removed off the cartilaginous structure
439 and cut into strips, sun-dried, and sold as dry fish for consumption or animal fodder.
440
441 The highest value part of mobulid rays were their gill plates which were exported (see Table S1).
442 These cartilaginous structures are removed from the heads, cleaned by detaching gill filaments
443 and excess tissue, and then sun-dried. Due to the technical skills required to keep the plates intact
444 during removal (larger, intact gill plates fetch higher prices), together with the contacts required
445 to establish and maintain the supply chain and to avoid market saturation, each landing site had
446 at most around five middlemen that purchased gill plates. These middlemen were often the same
447 as those involved in the shark fin trade and often, both commodities went via the same supply
448 chain. These middlemen either purchased the heads of the mobulids or the entire specimen. They
449 would then extract the gill plates and resell any meat to retailers. The mobulids were always sold
450 by fishers via auctioneers, and on days where few individuals were landed, they were auctioned
451 off specimen by specimen. On days with high landings they were auctioned in bulk, by weight.
452 When individual specimens were auctioned, depending on the landing site, they were either sold
453 as one entire piece or in halves (as they were most frequently landed), or the head (containing the
454 gill plates) separate from the rest of the body. The sale prices varied significantly day to day and
455 appeared to be dependent on the number of rays landed on a given day and in relation to the days
456 prior to that, and taking into account the number of middlemen (purchasing power) present
457 during auctioning itself.
458
459 **3.2 Mobulid Landings and CPUE**

460   *3.2.1 Species Composition, Size Frequency, and Size at Maturity*
461   Most of our survey effort was focused at five of the primary landing sites: Mirissa fisheries harbour
462   (n = 172 survey days), Valaichchenai fisheries harbour (n = 170), Negombo (n = 135),
463   Valaichchenai landing sites (n = 145), and Valaichchenai fish market (n = 124). Nine additional
464   sites had more than 20 days of survey effort (range 22 – 86 survey days), and the remaining 25
465   sites had fewer than 20 days of survey effort (range 1 – 14 survey days). A total of 6,516 individual
466   specimens, comprising five species, were recorded over the 1,346 surveys (see Table 1). These
467   included pups of two *M. mobular* (one female: DW 74 cm; one male: unmeasured), of three *M.*
468   *tarapacana* (two females: DW 132 cm and 149 cm; one unknown gender: DW 117 cm), and four
469   *M. kuhlii* (three females: DW 35 cm, 49 cm, 62 cm, and 63 cm; one male: DW 63 cm). While there
470   were other small individuals of similar sizes of each species (Fig. 3), they could not be confirmed
471   to be pups (i.e. unable to confirm whether they were extremely small free-swimming individuals,
472   or fetuses that had been aborted in the nets or during handling). The smallest pregnant *M. mobular*
473   had a DW of 200 cm (see Fig. 4) (with another three pregnant with: DW of 205 cm, and two with
474   a DW of 209 cm), *M. tarapacana* had a DW of 304 cm (with another: DW of 326 cm), and *M.*
475   *kuhlii* had a DW of 128 cm (with another three: DW of 130 cm, 132 cm, and 138 cm). We note
476   that in June 2020 – after the sampling period included in our analyses – one *M. eregoodoo*
477   specimen was recorded, bringing the total number of *Mobula* species in Sri Lanka to six.
478
479   *3.2.2 CPUE Proxy*
480   The number of registered IMUL and IDAY fishing vessels show an overall increasing trend;
481   from 4,523 in 2010 to 5,833 in 2019, while the number of OFRP vessels remained fairly stable
482   after an initial increase in 2011 (see Table 2). Based on informal surveys and canvassing during
483   the study period, the majority of mobulid landings appeared to be associated with IMUL and
484   IDAY vessels that fish in the high seas and throughout the EEZ, while some of the more coastal
485   species such as *M. kuhlii* were more frequently landed by the OFRP vessels that tend to fish a
486   few kilometres offshore.
487
488   **3.3 Catch Time Series**
489   *3.3.1 State Space Models*
490   The median value of the overall trend in catches across all sampled years was -0.012 (95% CIs: -
491   0.048 - 0.021) for *M. birostris* with an 81.7% probability that the mean trend in catches was
492   negative; -0.013 (95% CIs: -0.038 - 0.015) for *M. mobular* with an 86.8% probability that the
493   mean trend in catches was negative; -0.010 (95% CIs: -0.031 - 0.018) for *M. tarapacana* with an
494   83.6% probability that the mean trend in catches was negative; and -0.015 (95% CIs: -0.038 -
495   0.008) for *M. thurstoni* with a 92.8% probability that the mean trend in catches was negative. In
496   all of our posterior predictive checks, observed numbers of mobulids landed at a specific market
497   fell within the prediction intervals based on model-estimated parameters (Fig. 5 and 6, and Fig.
498   S1 – S4).
499

500 Our catch reconstructions based on predictions from model-estimated catch rates are reported in
501 Table 3. Given the uncertainty around total catch estimates that use parameter estimates from
502 unobserved periods in the model, we report both 50% and 90% credible intervals (rather than
503 95%) to avoid reporting extraordinarily high catch estimates at the far-right tail of the predicted
504 distribution. Catch reconstructions from the model-estimated parameters and simple
505 extrapolations from average mobulid landings generally agreed well. Total estimated
506 countrywide catches of *M. birostris* (median estimates) ranged from a minimum of 1,025 (2017)
507 individuals to a maximum of 7,961 (2014), although both 50% and 90% credible intervals
508 suggest that total catches could be considerably higher. Median estimates of total *M. mobular*
509 catches range from 11,258 (2017) to 98,059 (2011); *M. tarapacana* from 4,867 (2019) to 13,966
510 (2013); and *M. thurstoni* from 533 (2017) to 2,915 (2011). We did not reconstruct total catches
511 from 2010 or 2020 as only a small portion of each year was sampled. The model estimated 2016
512 total catches although no simple catch extrapolations were made as no samples were collected
513 during 2016. In the case of *M. mobular, M. tarapacana* and *M. thurstoni*, total estimated catches
514 declined by an order of magnitude over the 10-year study period. *Mobula birostris* total
515 estimated catches decline by approximately 75% from 2011 to 2018, but roughly doubled from
516 2018 to 2019 (Table 3).
517

518 **3.4 Size Trends**
519 Bayesian linear models indicated a negative trend in the DW of landed individuals for all
520 sampled species except for *M. birostris* (see Fig. 7). *M. mobular* (N = 956) demonstrated a
521 decrease in mean DW of 2.8 cm per year (95% CI: 2.1 - 3.4 cm), *M. tarapacana* (N = 285) a
522 decrease of 2.4 (1.1 - 3.6) cm per year, and *M. thurstoni* (N = 68) a decrease of 2.2 (0.36 - 4.1)
523 cm per year. There was a 100% probability of a decline in body size of *M. mobular* and *M.*
524 *tarapacana*, and a 98.9% probability of decline in body size of *M. thurstoni* (i.e. 98.9% of
525 posterior estimates of the slope were negative). *M. birostris* (N = 121), in contrast, exhibited no
526 change in mean DW (median slope 0.5 cm increase, 95% CI: 3.5 cm decrease - 4.6 cm increase;
527 40% probability of decreasing body size). The additional uncertainty in DW measurements
528 estimated by the model for research assistants were generally negligible, although somewhat
529 higher for *M. birostris*. The median additional error term for *M. mobular* was 0.5 cm (0.024 - 2.5
530 cm), for *M. tarapacana* 1 cm (0.036 - 4.4 cm), for *M. thurstoni* 1.65 cm (0.056 - 8.2 cm), and for
531 *M. birostris* 10.7 cm (0.68 - 31.7 cm).
532

533 **3.5 Total Mortality estimates for Mobula mobular**
534 The size-to-age conversion using the Von Bertalanffy growth equation produced an age range
535 similar to *M. mobular* in Pardo et al., 2016 (maximum age 11.73 years). A small proportion
536 (0.049, n=40) of *M. mobular* in this study were below age zero, which is consistent with
537 occasional observations of foetuses aborted by pregnant females during capture. Our catch curve
538 analysis including all individuals across all years produced a median estimate of total mortality Z
539 = 0.671, with 95% bootstrapped confidence intervals of 0.359 – 0.909. Median estimates of Z for
540 individual years ranged from 0.256 (2017) to 0.795 (2019) (Fig. 8, Table 4). The majority of

541 bootstrap estimates fell above the 0.108 upper confidence interval for maximum intrinsic rate of
542 population growth estimated by Pardo et al., (2016) for *M. mobular*. Estimates from 2013 of Z
543 had the highest percentage (10.1%) of bootstrap estimates fall below 0.108, followed by 2012
544 (3.7%). All other years had 0 - 0.1% of bootstrap estimates below 0.108, which suggests that the
545 regional *M. mobular* population is experiencing mortality rates that far exceed the species'
546 intrinsic population growth rates.

547 **4. Discussion**
548 This study represents the first comprehensive evaluation of the mobulid fishery of Sri Lanka and
549 one of the most extensive and detailed examinations of mobulid bycatch in any fishery
550 worldwide. It provides an understanding of the scale of bycatch from this fishery and its probable
551 impact on mobulid populations across the Indian Ocean. We found multiple lines of evidence
552 suggesting that mobulid populations accessed by Sri Lankan fisheries are being exploited at
553 unsustainable levels, including an extremely high annual catch of mobulids, decreasing overall
554 catch rates in four species, high proportions of immature and juvenile individuals across four
555 species, decreases in body sizes in landed individuals of three species, and a catch curve analysis
556 of *M. mobular* indicating a total mortality rate far above the species' intrinsic maximum
557 population growth rate. Taken together, these findings suggest ongoing overfishing of mobulid
558 populations in the northern Indian Ocean and, most likely, associated population declines
559 (Pacoureau et al., 2021). This emphasises the urgent need for improved implementation of global
560 conservation measures, along with better regional and domestic fisheries management aimed
561 specifically at protecting mobulids, and other similarly vulnerable species.
562
563 *Catch trends*
564 Our catch reconstructions from state-space model fits reveal that Sri Lanka is one of the largest
565 mobulid landing nations in the world with median estimates of total catch landings between 2011
566 and 2019 indicating more than 1,000 *M. birostris*, 11,000 *M. mobular*, 5,000 *M. tarapacana*, and
567 500 *M. thurstoni* landed annually at the 38 fishing harbours, landing sites, and markets sampled
568 in this study. Our catch reconstructions suggest that annual mobulid landings in Sri Lanka have
569 declined by an order of magnitude over the past decade, and that total catch of mobulids in the
570 early 2010s may have exceeded 100,000 animals per year. There is cause to interpret these early
571 estimates of total catch with caution. First, the majority of the 38 landing sites in this study have
572 only been sampled since 2017 (Fig. S5). Our state-space model of catch rates estimates a
573 country-wide mean monthly catch rate and overall trend in catch rates, along with a persistent
574 random effect (or offset from the mean) for each sampled market. Therefore, catch rates are
575 estimated for all markets for the full survey period, and catch rates for the majority of markets
576 are estimated without data for 2010-2016. This assumes that all markets followed the overall
577 country-wide trend, which is informed primarily by catch rates at 8 markets that were sampled
578 relatively consistently over the full study period; an assumption that may or may not be valid.
579 Second, several of the markets sampled during the full study period were known to have some of
580 the highest overall mobulid catch rates (e.g. Negombo and Mirissa), which is why they were
581 initially targeted for sampling. Declines in catch rates at these markets may therefore bias the
582 overall catch reconstruction, inflating early estimates of total catch. Nevertheless, the markets
583 with continuous sampling throughout the study period demonstrate major declines in catch rates
584 (e.g. Fig. 5-6), and even the minimum catch estimates from the total catch reconstruction
585 demonstrate five- to ten-fold declines for most species. We also note that, despite the very high
586 upper credible intervals of the state-space model catch reconstructions, the model estimates and

587   simple extrapolations are generally closely aligned, and the state-space model posterior

588   predictive checks correspond closely to observed catches. These 38 sites include 10 of the 21

589   national fishery harbours where both single- and multi-day vessels land their catch in Sri Lanka,

590   and therefore these total catch reconstructions likely approach estimates of total mobulid

591   landings throughout the country. However, given there are a further 883 documented smaller fish

592   landing sites (MFAR, 2020) in Sri Lanka, it may be realistic to consider the upper bounds of the

593   credible intervals as plausible total catch estimates for the country.

594

595   The magnitude of these total catch estimates – even the lower estimates from 2017 onwards – are

596   exceptionally high considering the assumed small population sizes for mobulids (Stewart et al.

597   2018). To put these catch numbers in context, it was estimated that Indonesia landed between

598   1,050 and 2,400 *M. birostris* in their target fishery in 2002 (Dewar, 2002; Lewis et al., 2015),

599   Peru landed 1,985 mobulid rays over one year at their largest mobulid landing site while

600   estimates of the northern Peru region suggest ~8,000 individuals per year (Croll et al., 2016;

601   Alfaro-Cordova et al., 2017). The estimated global tuna purse seine mobulid bycatch is

602   approximately 13,085 individuals per year (Croll et al., 2016). Therefore, despite Sri Lanka's

603   fishery being classified as primarily small-scale artisanal, we would argue that it has significant

604   impacts on mobulid rays in the northern Indian Ocean that exceed the scale of industrial fishery

605   impacts in the region. Furthermore, the decline in catch rates despite an increase in the number of

606   registered offshore fishing vessels and a stable trend in the coastal vessels suggests that there

607   may have been an even larger decline in catch per unit effort during the nine-year study period,

608   although we acknowledge that the number of registered vessels is an imperfect proxy for fishing

609   effort. Inferences about the status of fished populations made using catch-only data are often

610   negatively biased and less accurate than stock-assessment methods that incorporate fishing

611   effort, indices of abundance, age or length structure, and other biological data (Carruthers,

612   Walters & McAllister, 2012). As we note here, effort data for this fishery is complex and

613   inadequate for inclusion in more integrated stock-assessment approaches, and biological data on

614   mobulid rays, including length-at-age relationships for all species but *M. mobular*, is extremely

615   sparse. Improving and collecting appropriate effort data in complex artisanal fisheries contexts

616   would allow for a more accurate accounting of catch per unit effort for these species and may

617   facilitate more robust stock-assessment approaches in the future. In addition, genomic tools such

618   as close-kin mark recapture (Bravington, Skaug & Anderson, 2016) could provide estimates of

619   abundance to further contextualize these catch estimates.

620

621   Three additional pieces of evidence indicate overfishing of the mobulid populations that are

622   accessed by Sri Lankan fishers. First, our catch curve analysis of *M. mobular* indicated total

623   mortality rates that far exceed estimates of the species' intrinsic maximum population growth

624   rates (r_{max}). These estimates fluctuated across years, although much of this variability may be due

625   to differences in sample size between years. Regardless of whether the catch curve analysis was

626   conducted at annual intervals or with combined age data across years, mortality rates ranged

627 from roughly two to six times higher than the upper bound of r_{max} estimates for the species
628 (Pardo et al., 2016). This suggests that fisheries mortality for the regional population of *M.*
629 *mobular* is exceptionally high and that the population is being overfished, which is consistent
630 with both declining catch rates and the magnitude of the total catch relative to expectations about
631 population size for the species. Second, we found strong evidence for a decline in average body
632 size in three mobulid species. Fished populations of elasmobranchs often exhibit decreases in
633 size structure, even in cases where fishing gear is not selective for larger size classes (Stevens,
634 2000). Because size-at-age relationships are only available for *M. mobular*, we were not able to
635 conduct catch curve analyses for any other species. However, the steady decline of average disc
636 width in *M. mobular*, *M. tarapacana*, and *M. thurstoni* of approximately 1-2% per year is similar
637 to size and weight declines of other heavily exploited elasmobranchs (Baum & Myers, 2004;
638 Clarke et al., 2013). While change in average size is a very coarse metric of size structure, these
639 changes seem to be driven by a decreasing number of larger individuals in our samples (Fig. 7),
640 which would be consistent with high mortality leading to a truncated age distribution. In contrast,
641 we found no change in the mean disc width of *M. birostris* across the study period. Given that
642 the vast majority of *M. birostris* landed in Sri Lanka are juveniles (76% of males and up to 96%
643 of the females), we would not necessarily expect a decline in average body size even if the
644 population is experiencing high levels of total mortality, as the average size of *M. birostris*
645 landed in Sri Lanka (278.6 cm) is not far from the lower bound of the estimated size at birth
646 (~180-200 cm) (Rambahiniarison et al., 2018; Stevens et al., 2019). The frequent landings of
647 juvenile *M. birostris* are concerning given the paucity of information on their juvenile life stage,
648 early life history, and nursery habitats, and suggest that Sri Lankan fishers may be accessing a
649 nursery habitat for the species. *Mobula birostris* are rarely encountered in shallow, coastal waters
650 around Sri Lanka, which may indicate that juveniles use an offshore or pelagic nursery habitat,
651 similar to one described in the northern Gulf of Mexico (Stewart et al., 2018b).
652
653 Declining population trends were further corroborated by gill plate middlemen who reported that
654 fewer individuals are being landed in recent years, and also by fishers who suggested that
655 mobulid (and shark) bycatch in gillnets have declined over the past two decades. The rapid
656 growth in the gill plate trade driving demand for mobulids, coupled with declines of more
657 desirable fish species including tuna, billfish, and sharks, further suggests that fishing effort for
658 mobulids was likely increasing during the study period and that the decline in CPUE may have
659 been even higher than the decline in total catches estimated by our models. Beyond recorded
660 landings, discards at sea may also be a significant source of unrecorded and unreported mortality
661 of mobulids in Sri Lankan fisheries. Fishers reported discarding mobulids when heading out to
662 sea in favour of more valuable target fish. While there is currently no information on the post
663 release survival probability of mobulids in gill nets, it is likely lower than survival rates in purse
664 seine and logline fisheries (Mas, Forselledo & Domingo, 2015; Francis, Jones & Library, 2016;
665 Ellis, McCully Phillips & Poisson, 2017). Evaluating post release survival rates of mobulids in

666 the Sri Lankan gill net fishery and other small-scale fisheries employing gill nets will be
667 important in understanding the full impacts of these fisheries on mobulid populations.
668
669 *Demographics and Ecological Inferences*
670
671 The size ranges of mobulids reported here were largely consistent with fishery-based
672 demographic characterizations of mobulids elsewhere in the Indo-Pacific (Notarbartolo-di-
673 Sciara, 1988; White et al., 2006; Rambahiniarison et al., 2018; Stevens et al., 2019). The
674 exception was *M. kuhlii*, for which we report a new maximum disc width of 138 cm (previously
675 122 cm: Stevens et al., 2019). The DW at which 50% of males were sexually mature (DW_{50})
676 reported here was within 10-15 cm of previous studies in the Philippines and Indonesia for all
677 species (see Table 5). We also report the first DW_{50} for *M. kuhlii*, which was approximately 10
678 cm smaller than the suspected size at maturity from the eight individuals recorded in Indonesia
679 (White et al., 2006). The sex ratios were approximately 1:1 for all species except for *M. kuhlii*,
680 which had a roughly 1.5:1 male:female ratio, although this could be due to small sample sizes
681 (Fig. 3). Interestingly, while landings of most species occurred throughout Sri Lanka, *M. kuhlii*
682 was landed most often at ports in the northwest of the island and along the west coast. *M. kuhlii*
683 were also predominantly captured by nearshore, coastal vessels, and a much higher proportion of
684 *M. kuhlii* were mature when compared to other species. This may indicate a more restricted,
685 coastal distribution than the other mobulid species throughout the shallow straits between Sri
686 Lanka and India.
687
688 Several interviewed fishers described mobulid rays conducting vertical migrations in search of
689 krill. Diel vertical migrations have been recorded in *M. birostris* from Peru and Mexico (Stewart
690 et al., 2016; Andrzejaczek et al., 2021), and euphausiids are known to be an important diet
691 component for mobulids (Notarbartolo-di-Sciara, 1988; Couturier et al., 2012; Rohner et al.,
692 2017; Stewart et al., 2017). Other large planktivores, such as blue whales, are frequently
693 encountered at the edge of the continental shelf feeding on sergestid shrimp (a predator of
694 euphausiids) and euphausiids that occur at depths of >300 m (de Vos et al., 2018). Given that
695 fishers predominantly deploy their nets at night, it is plausible that the mobulid rays are
696 following the diel migrations of euphausiids and encountering surface set gill nets, similar to the
697 capture patterns reported in the Philippines (Rohner et al. 2017).
698
699 There was ambiguity in responses of fishers regarding whether the seasonal monsoons in Sri
700 Lanka affected mobulid catch, with some stating they did and others not. Acoustic tagging
701 studies of reef manta rays in the Maldives, just south of Sri Lanka, have recorded east-west
702 migrations of the population between monsoon seasons to take advantage of monsoonal
703 upwelling that alternates from the eastern to western sides of the atolls (Harris et al., 2020).
704 Similar monsoonal upwelling and productivity cycles occur on either coast of Sri Lanka (Silva &
705 Davies, 1987; Vinayachandran, 2004; Suresh et al., 2016; Jinadasa et al., 2020), and it is possible

706 that mobulids may be exhibiting similar resource-driven seasonal migrations. Future studies
707 could evaluate the spatial distribution of catches across seasons in Sri Lanka, although we
708 caution that the monsoons have significant impacts on fishing distributions due to strong winds
709 and challenging weather conditions, which may obscure or confound ecologically-driven spatial
710 distributions of mobulids.
711
712 *Conservation and management of mobulid rays in Sri Lanka*
713
714 While several studies have reported on proxies for mobulid population trends (e.g., changes in
715 sighting rates (Ward-Paige, Davis & Worm, 2013; White et al., 2015b; Pacoureau et al., 2021)
716 and fisheries data (Lewis et al., 2015; Pardo et al., 2016)), accurate data on abundance and
717 absolute trends remain almost non-existent (Stewart et al., 2018a). Our study combines several of
718 these approaches for a single location (catch rates, catch curve analyses, and size trends), but we
719 remain unable to estimate absolute abundance trends. Nevertheless, it is clear that mobulid rays
720 are unable to withstand sustained, high rates of fishing (Dulvy et al., 2014; Pardo et al., 2016)
721 and Sri Lanka appears to be one more example where mobulid populations are likely in decline.
722 However, since 2013, amid growing concern for their globally threatened status (see Table S2),
723 some international precautionary measures were introduced.
724
725 The CITES convention provides the mechanism necessary to ensure that any trade of listed
726 species across international borders is permitted if it will not be detrimental to the survival of the
727 species. Given the 18-month delayed implementation to provide time to build capacity and
728 introduce necessary regulations, these listings came into force for *Manta* spp. in September 2014,
729 and for all *Mobula* spp. in April 2017. There was no indication from our surveys of fishers being
730 aware of, or adhering to, CITES export restrictions, and illegal gill plate exportations from Sri
731 Lanka, and interceptions of illegal shipments (mislabelled or lacking permits) in trade hubs such
732 as Hong Kong, continue to be recorded (Hau, Ho & Shea, 2016; HK-SAR, 2020; Sri Lanka
733 Customs, 2021).
734
735 Further, the inclusion of all mobulids on CMS requires Sri Lanka to enact domestic management
736 policies, including prohibiting the take of mobulids at the national level, while also encouraging
737 CMS Parties to improve regional coordination and cooperation to better protect these species.
738 Nevertheless, the declines in landings that we report cannot be attributed to this convention given
739 the poor implementation of CMS-listed elasmobranchs at a global level and the lack of any
740 national legislative framework to implement CMS in Sri Lanka (Lawson & Fordham, 2018).
741 Further, it should be noted that Sri Lanka as a Party to both Conventions would be unable to
742 trade gill plates given that catch ("take"), and therefore trade, is prohibited under CMS Appendix
743 I. However, the CITES Trade Database contains records of commercial gill plate trade, reported
744 by Sri Lanka, between 2015 and 2020 (Table S1), likely in contravention of CMS obligations.
745

746 There is a clear need for immediate management action to curtail the high rates of fishing
747 mortality of mobulid rays in Sri Lankan (and surrounding) waters. The national Department of
748 Fisheries and Aquatic Resources (DFAR) have initiated a programme to limit gillnets (the
749 primary gear type capturing mobulid rays). At present the prohibition is restricted to gillnets
750 longer than 2.5 km operating by vessels in the high seas (beyond the EEZ), as required by the
751 Indian Ocean Tuna Commission (IOTC) under Resolution 17/07 (IOTC, 2017). While the
752 revised National Plan of Action for Sharks in Sri Lanka 2018-2022 mentions the establishment
753 of a 2.5 km maximum length for gillnets for all multi-day (IMUL) and one-day (IDAY) vessels
754 under its intended activities, this restriction has not yet been implemented (MFAR, DFAR &
755 NARA, 2018) and may not have long-term consequences given the absence of a cap on the
756 growing number of registered fishing vessels (see Table 2). Given the lack of any other national
757 regulations to effectively manage these species, it is highly likely that overfishing of mobulid
758 rays will continue in Sri Lankan fisheries in the foreseeable future unless management action is
759 taken quickly.
760
761 The neighbouring countries of the Maldives and the Chagos Archipelago both prohibit fishing of
762 mobulid rays and could provide some protection if mobulid population distributions extend
763 across the northern Indian Ocean. However, with far-ranging Sri Lankan fisheries that access the
764 High Seas and at times even illegally fish within the sovereign waters of neighbouring nations or
765 MPAs (DFAR, 2013; BIOT, 2020; Kilgour, 2020), along with intensive and expanding fishing
766 pressure from other Indian Ocean countries such as India (Parappurathu et al., 2020), it is
767 unlikely that regional spatial protections implemented by other countries will provide sufficient
768 refuge from fishing pressure to prevent population declines. The mobulid conservation and
769 management measure (Resolution 19/03) introduced by the IOTC in 2019 (IOTC, 2019)
770 provides a regional framework for reducing mobulid fisheries captures. The measure includes a
771 retention ban for mobulid rays that will come into effect for all fisheries (including artisanal) by
772 January 2022. At present it is enforced only for commercial fisheries, with delayed
773 implementation for artisanal fisheries to enable time to increase awareness and improve
774 mitigation strategies. Given insufficient enforcement of CITES and the lack of implementation
775 of CMS in curbing mobulid landings in Sri Lanka, it remains to be seen whether the IOTC
776 measure can better address these impacts.
777
778 **5. Conclusions**
779
780 Based on the apparent population declines of mobulid rays in the Indian Ocean (Pacoureau et al.,
781 2021) and the extremely high rates of fishing mortality that we report here, it is clear that
782 implementation and – perhaps more importantly – enforcement of fisheries management actions
783 are urgently needed for mobulid rays in Sri Lanka and the northern Indian Ocean.

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795

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1088

Demographic characteristics of mobulid rays landed in Sri Lanka.

1   **Table 1:** Demographic characteristics of mobulid rays landed in Sri Lanka.

	Mobula birostris	*Mobula mobular*	*Mobula tarapacana*	*Mobula thurstoni*	*Mobula kuhlii*
Specimens recorded					
Females	107	1,598	388	41	18
Mature males	22	670	115	8	18
Immature males	73	1,077	224	32	11
Unknown males	1	3	0	0	0
Unsexed	96	1,550	387	12	12
Total*	**299 (4.6%)**	**4,898 (75.2%)**	**1,114 (17.1%)**	**93 (1.4%)**	**59 (0.9%)**
Size range (including pups)					
Females	180-478 cm	60-252 cm	132-326 cm	72-168cm	35-138 cm
Mature males	396-449 cm	184-242 cm	212-314 cm	138-160 cm	101-124 cm
Immature males	136-375 cm	62-222 cm	98-244 cm	65-145 cm	63-104 cm
Unsexed	168-308 cm	71-236 cm	115-300 cm	98.5-115.5 cm	75 cm
Size at 50% maturity (Fig. 4)					
Males	385.53 cm	202.51 cm	239.99 cm	142.78 cm	102.87 cm
Proportion of immature					
% of males immature	76% of 96 specimens	62% of 1,750 specimens	66% of 339 specimens	80% of 40 specimens	38% of 29 specimens
% of males smaller than DW_{50}	86% of 56 specimens	67% of 431 specimens	75% of 112 specimens	79% of 34 specimens	32% of 28 specimens
% of females smaller than DW_{50}[†]	96% of 53 specimens	83% of 406 specimens	87% of 117 specimens	97% of 31 specimens	56% of 18 specimens

2   * This excludes 53 specimens (0.8%) that were not identified to species level.

3   † DW_{50} for females from Rambahiniarison et al., 2018: *M. birostris*: 448.0 cm; *M. mobular*: 217.8 cm; *M. tarapacana*: 264.8 cm; *M. thurstoni*: 163.6 cm and the size
4   of the one recorded female specimen of *M. kuhlii* from Notarbartolo di Sciara et al., 2017: 116.8 cm (see Table 6). These figures are expected to be higher as they are
5   based on DW_{50} and not the DW of the smallest pregnant individual, however previous studies have shown delayed onset between maturity and pregnancy
6   (Rambahiniarison et al., 2018).

The number of registered fishing vessels from 2010 to 2019 as reported by the Ministry of Fisheries and Aquatic Resources Development (MFAR, 2020).

IMUL are inboard [engine] multi-day boats operating within and beyond the EEZ, while IDAY are inboard [engine] single-day boats operating within the EEZ, and OFRP are outboard engine fiberglass reinforced plastic boats operating in coastal waters.

1 **Table 2:** The number of registered fishing vessels from 2010 to 2019 as reported by the Ministry of Fisheries and Aquatic Resources
2 Development (MFAR, 2020). IMUL are inboard [engine] multi-day boats operating within and beyond the EEZ, while IDAY are
3 inboard [engine] single-day boats operating within the EEZ, and OFRP are outboard engine fiberglass reinforced plastic boats
4 operating in coastal waters.

	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
IMUL:	3,346	3,872	4,080	4,111	4,447	4,218	3,996	4,196	4,581	4,885
IDAY:	1,177	1,120	890	802	876	719	786	868	918	948
SUB-TOTAL:	**4,523**	**4,992**	**4,970**	**4,913**	**5,323**	**4,937**	**4,782**	**5,064**	**5,299**	**5,833**
OFRP:	18,770	22,890	23,160	23,134	23,982	24,028	24,282	22,394	24,132	23,404
TOTAL:	**23,293**	**27,882**	**28,130**	**28,047**	**29,305**	**28,965**	**29,064**	**27,458**	**29,631**	**29,237**

Annual catch reconstructions of mobulid rays in Sri Lanka.

Simple refers to the simple extrapolation described in equation 8. All other columns refer to the state-space model of fisheries landings: minimum and median values of the posterior distribution, and 50% and 90% credible intervals for each year and each species. Values represent the total model-estimated number of individuals landed across all sampled markets and landing sites. No data were collected in 2016, so the sample extrapolation was not possible in that year.

1 **Table 3:** Annual catch reconstructions of mobulid rays in Sri Lanka. Simple refers to the simple extrapolation described in equation
2 8. All other columns refer to the state-space model of fisheries landings: minimum and median values of the posterior distribution,
3 and 50% and 90% credible intervals for each year and each species. Values represent the total model-estimated number of
4 individuals landed across all sampled markets and landing sites. No data were collected in 2016, so the sample extrapolation was
5 not possible in that year.

Species/Year	Simple	Minimum	Median	50% Cis	90% Cis
Mobula birostris					
2011	5,714	610	4,461	2,736-8312	1,884-17987
2012	3,705	548	3,691	2,214-7,086	1,506-13,112
2013	5,217	532	4,317	2,650-8,049	1,854-16,426
2014	5,537	1,447	7,961	4,975-14,296	3,482-29,459
2015	0	104	2,691	1,467-5,398	877-11,336
2016	-	62	1,831	929-3,905	496-8,863
2017	502	62	1,025	611-1,925	398-4,067
2018	829	285	1,217	803-2,121	603-4,350
2019	2,885	713	2,785	1,920-4,810	1,421-10,018
Mobula mobular					
2011	251,547	25,222	98,059	68,577-163,796	52,453-319,592
2012	177,099	25,541	79,794	56,550-128,197	44,338-254,314
2013	205,820	19,717	59,238	42,477-95,140	33,256-180,457
2014	48,319	14,235	39,520	28,640-63,670	22,982-123,535
2015	14,227	4,134	18,076	12,249-30,149	9,122-55,762
2016	-	1,836	14,584	9,546-25,119	6,677-50,398
2017	12,258	2,550	11,258	7,922-17,804	6,249-31,888
2018	11,729	4,163	11,284	8,490-17,638	6,970-32,053
2019	15,294	4,462	12,075	8,968-18,863	7,464-35,053
Mobula tarapacana					
2011	32,568	3,611	13,023	8,852-21,861	6,743-47,131
2012	30,875	4,059	13,729	9,335-23,313	7,179-42,619
2013	32,723	3,321	13,966	9,332-23,491	7,327-46,587
2014	18,064	3,872	12,866	8,961-22,434	7,098-43,663
2015	9,485	1,313	8,192	5,515-14,626	4,069-30,786
2016	-	990	7,304	4,865-12,802	3,491-26,391
2017	4,622	1,519	5,966	4,165-9,923	3,130-20,078
2018	3,697	1,699	5,293	3,635-8,823	2,883-17,926
2019	4,347	1,148	4,867	3,510-8,405	2,740-17,768
Mobula thurstoni					
2011	2,857	981	2,915	2,434-3,495	2,061-4,100
2012	4,940	658	2,283	1,901-2,774	1,589-3,343
2013	1,897	361	1,603	1,345-1,930	1,117-2,338
2014	671	314	1,059	880-1,243	744-1,430
2015	0	65	825	631-1,019	456-1,216
2016	-	32	665	489-848	344-1,047
2017	201	80	533	400-672	302-795
2018	351	175	495	411-584	343-679
2019	593	164	559	459-674	388-778

Estimates of total mortality (Z) for *Mobula mobular*.

Bootstrap median estimates and 95% intervals for Z calculated using disc widths across all surveys (All) or using disc widths from individual years. P(Z>0.108) indicates the proportion of bootstrap estimates that were greater than the upper 95% confidence interval for r_{max} (0.108) estimated by Pardo et al (2016). We interpret that as the probability that total mortality exceeded the species' maximum intrinsic rate of population growth in a given year.

1   **Table 4:** Estimates of total mortality (Z) for Mobula mobular. Bootstrap median estimates and 95% intervals for Z calculated
2   using disc widths across all surveys (All) or using disc widths from individual years. P(Z>0.108) indicates the proportion of
3   bootstrap estimates that were greater than the upper 95% confidence interval for r_{max} (0.108) estimated by Pardo et al (2016). We
4   interpret that as the probability that total mortality exceeded the species' maximum intrinsic rate of population growth in a given
5   year.

Year	Median	95% Interval	P(Z>0.108)
All	0.671	0.359 - 0.909	1
2011	0.763	0.594 - 1.095	1
2012	0.319	0.091 - 1.792	0.963
2013	0.481	0 - 0.693	0.894
2017	0.256	0.134 - 0.578	0.999
2018	0.561	0.492 - 0.647	1
2019	0.795	0.519 - 0.934	1
2020	0.548	0.447 - 0.692	1

The size at maturity at which 50% (DW_{50}) of males are mature in this study (Fig. 4) compared with the other two published datasets from the region.

1 **Table 5:** The size at maturity at which 50% (DW_{50}) of males are mature in this study (Fig. 4) compared with the
2 other two published datasets from the region.

	DW_{50} (from this study)	DW_{50} Philippines (Rambahiniarison et al., 2018)	DW_{50} Indonesia (White et al., 2006)
Mobula birostris	**385.53**	381.9	375.2
Mobula mobular	**202.51**	205.8	201.6
Mobula tarapacana	**239.99**	252.1	248.6
Mobula thurstoni	**142.78**	158.4	153.8
Mobula kuhlii	**102.87**	---	115-119*

* Range at which maturity was attained (n=8 samples; insufficient to determine DW50).

Figure 1

Bathymetric (Amante & Eakins, 2009) map of Sri Lanka showing the continental shelf extent around the country, and locations of the 38 study sites.

Numbers in parentheses indicate multiple study sites in a given locality.
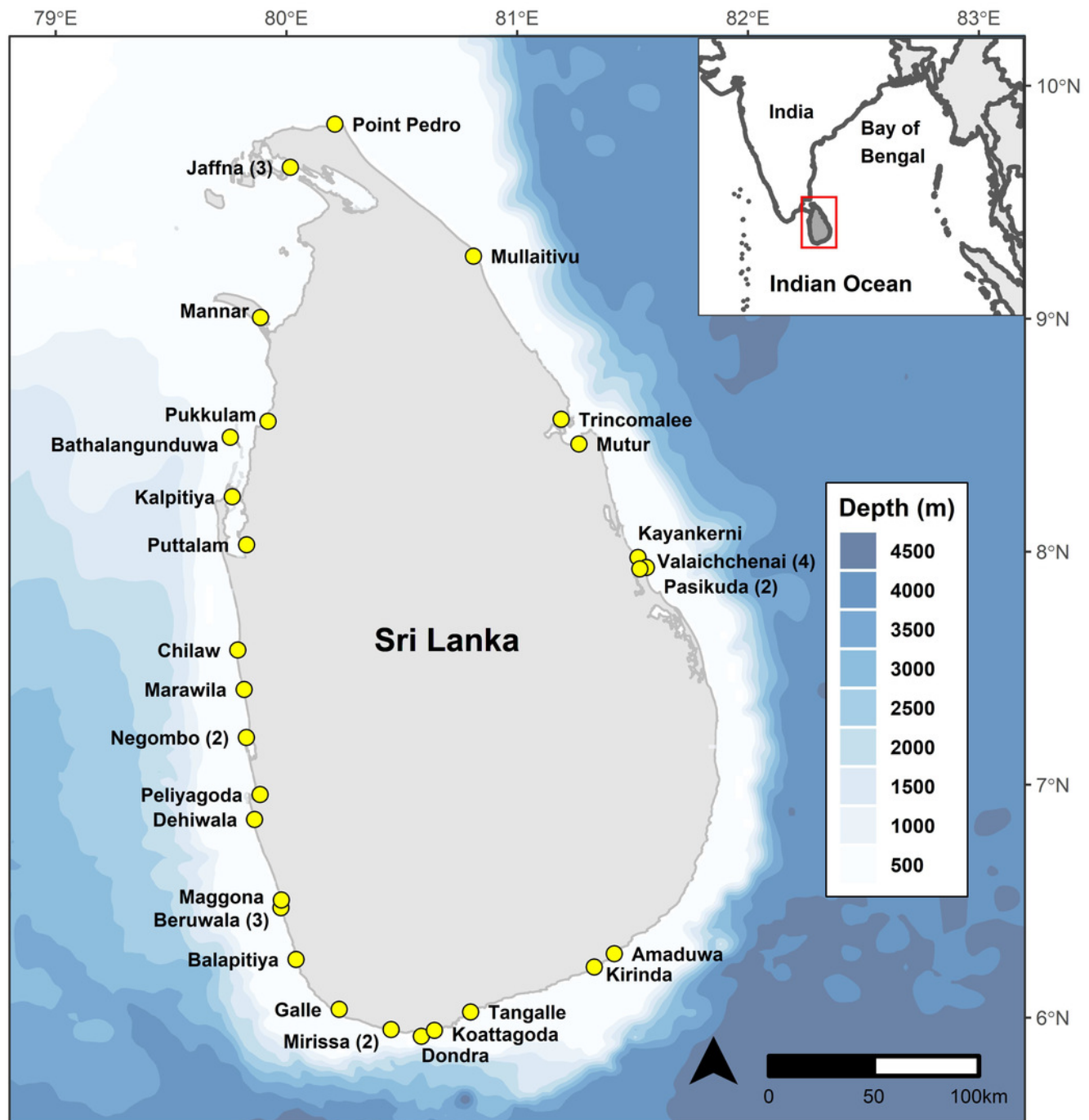
Figure 2

Distribution of reported fishing locations.

(A) Map showing the Exclusive Economic Zones (EEZs) with points (in red) displaying locations of mobulid fishing grounds, collected between 2011 and 2015. (B) Bathymetric (Amante & Eakins, 2009)map of Sri Lanka and neighbouring country EEZ's showing locations (in red) of mobulid fishing grounds, collected between 2011 and 2015. Implausible reported GPS coordinates (i.e. locations on land) were excluded.
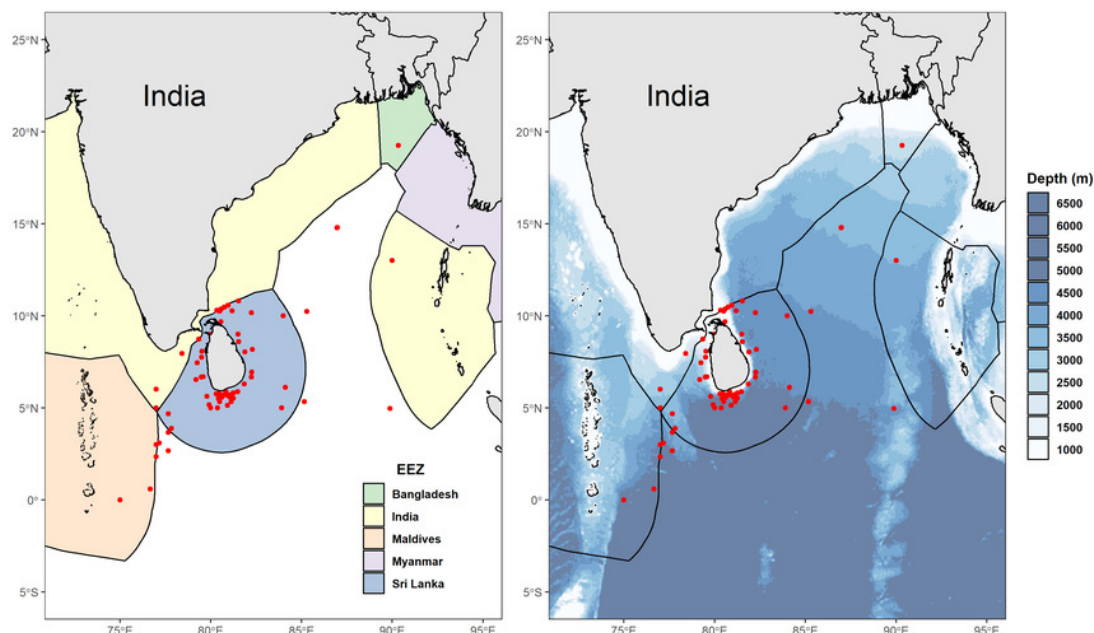
Figure 3

Mobulid size distributions.

Frequency histograms represent the distributions of males, females, and unsexed individual mobulid rays landed across the entire study period.
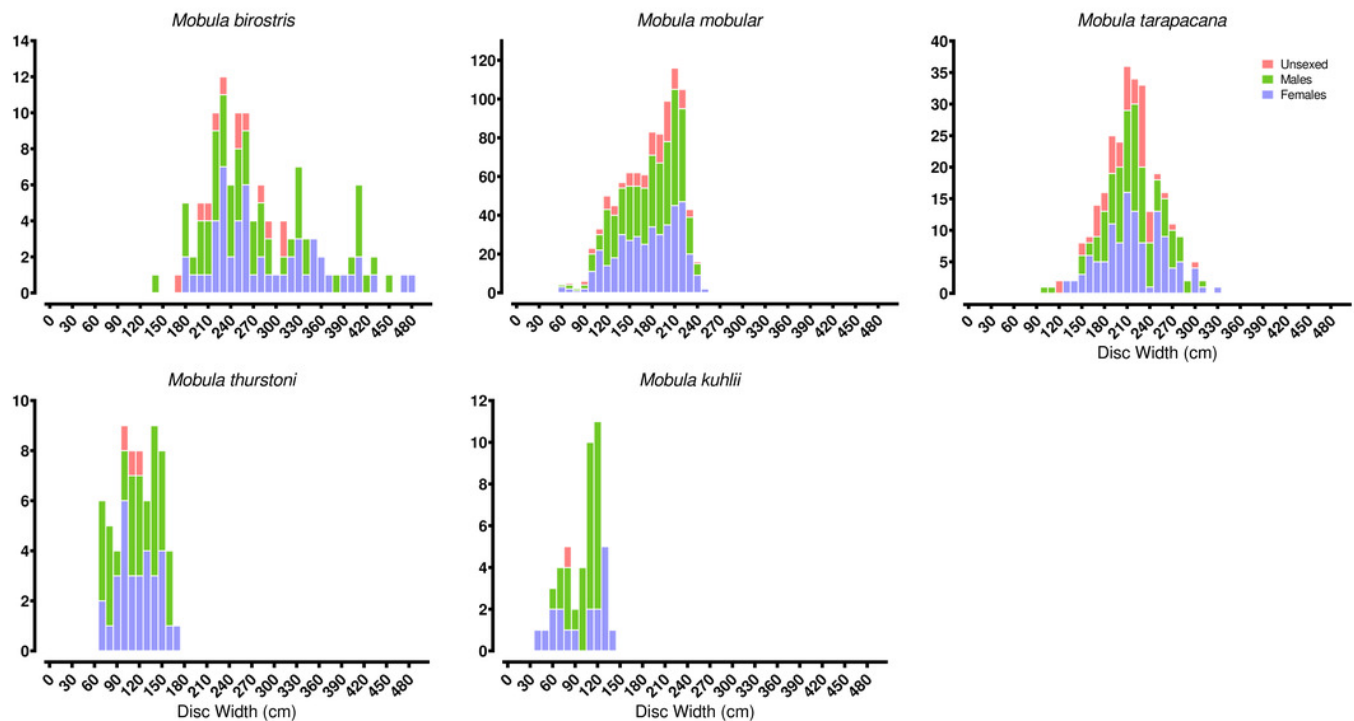
Figure 4

Size at maturity of the five mobulid species landed in Sri Lanka.

Points indicate individual male rays classified as mature (1) or immature (0) based on clasper length and calcification. Coloured curves indicate the logistic regression fit for size at maturity. Vertical black lines indicate the estimated disc width at 50% maturity (DW_{50}) for the five species (note the varying x-axis scale).
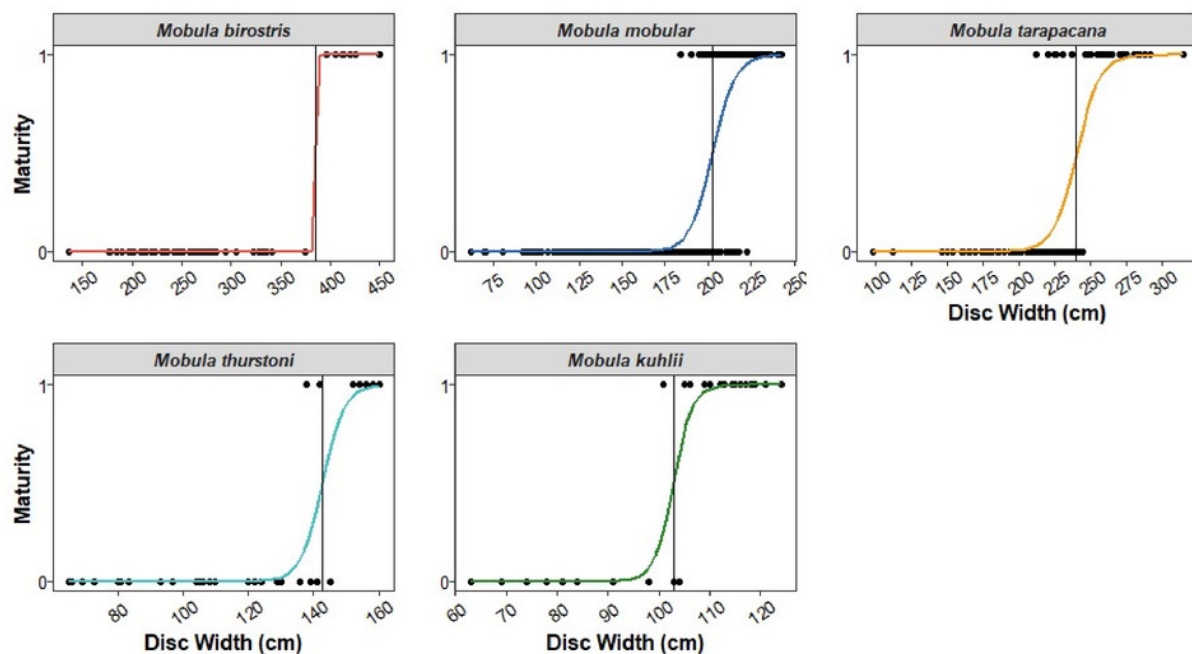
Figure 5

Overall country-wide model estimated mean monthly catch rates by species.

These values represent the mean catch rates before market-level random effects are applied. The black line indicates the median estimate of the posterior distribution, and the coloured polygons represent the posterior credibility intervals ranging from the 50% Cis (darkest) to 90% Cis (lightest). Squares along the bottom indicate months with sampling effort (at any market). Open squares indicate zero landings of the respective species, and filled squares indicate one or more recorded individuals landed.
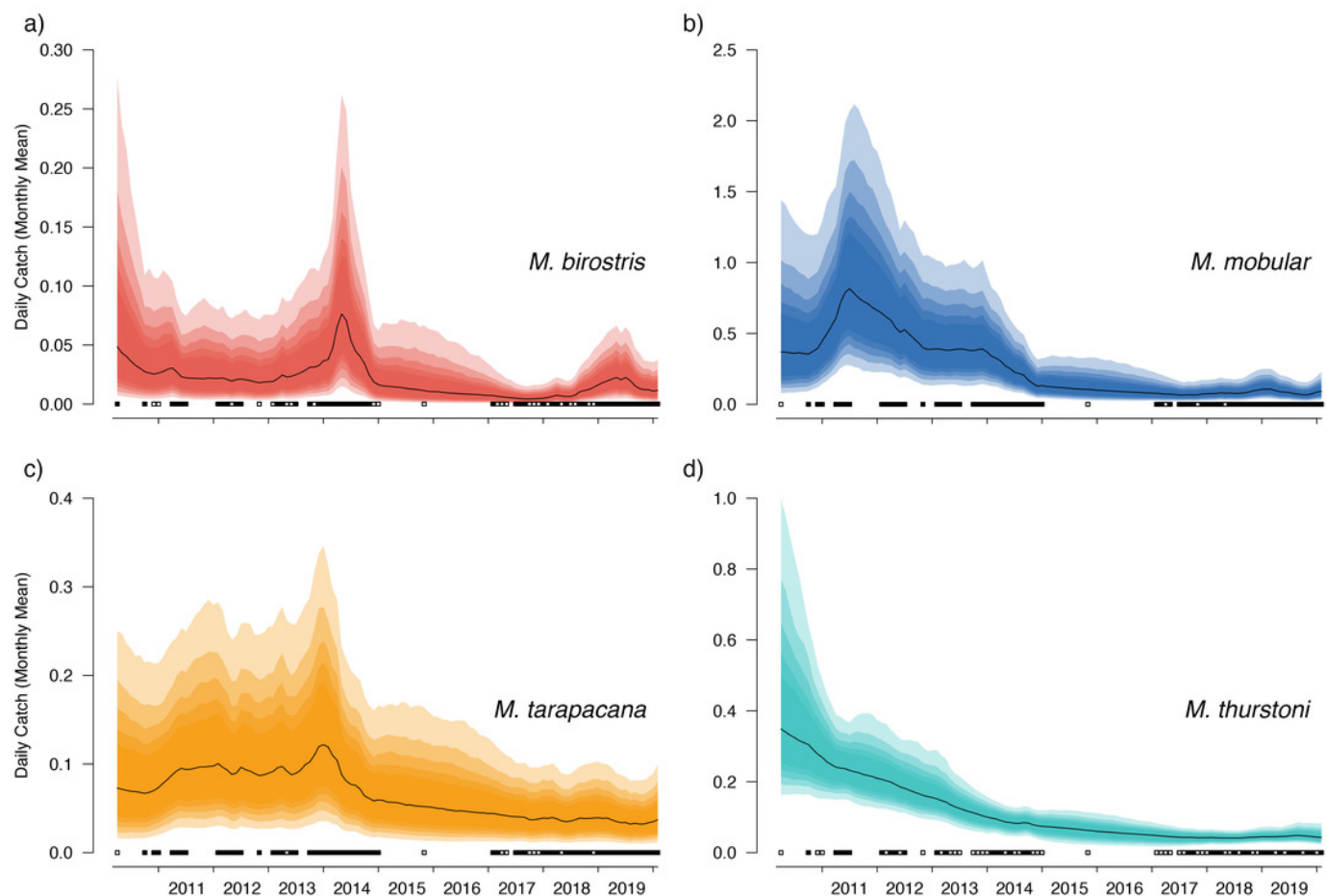
Figure 6

Catch trends for *M. mobular* from the landing sites with the six highest mean market random effects.

The black line indicates the median estimate of the posterior distribution, and the coloured polygons represent the posterior credibility intervals ranging from the 50% Cis (darkest) to 90% Cis (lightest). Squares along the bottom indicate months with sampling effort at each market. Open squares indicate zero landings of the respective species, and filled squares indicate one or more recorded individuals landed.
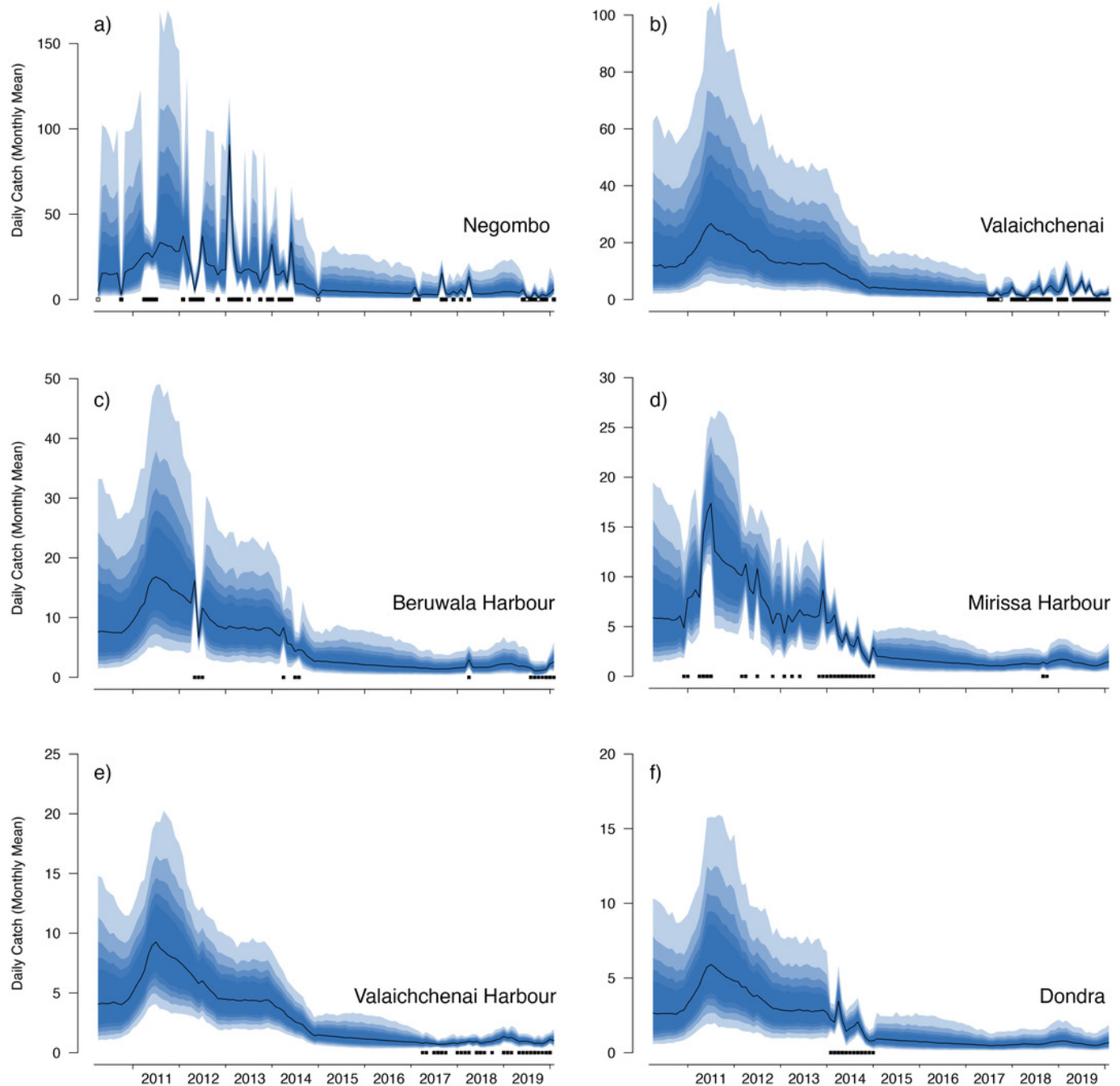
Figure 7

Size trends of mobulid rays captured in Sri Lankan artisanal fisheries.

For each panel, the open circles represent the recorded disc widths of individual a) *Mobula birostris* (N = 121), b) *M. mobular* (N = 956), c) *M. tarapacana* (N = 285), and d) *M. thurstoni* (N = 68). Observations are binned by year and jittered on the x-axis for clarity. The black line in each panel represents the regression line generated from the median model estimated parameters. The coloured lines represent the full Bayesian posterior distributions of estimated regression parameters, with each line representing one paired combination of slope and intercept from the posterior distribution.
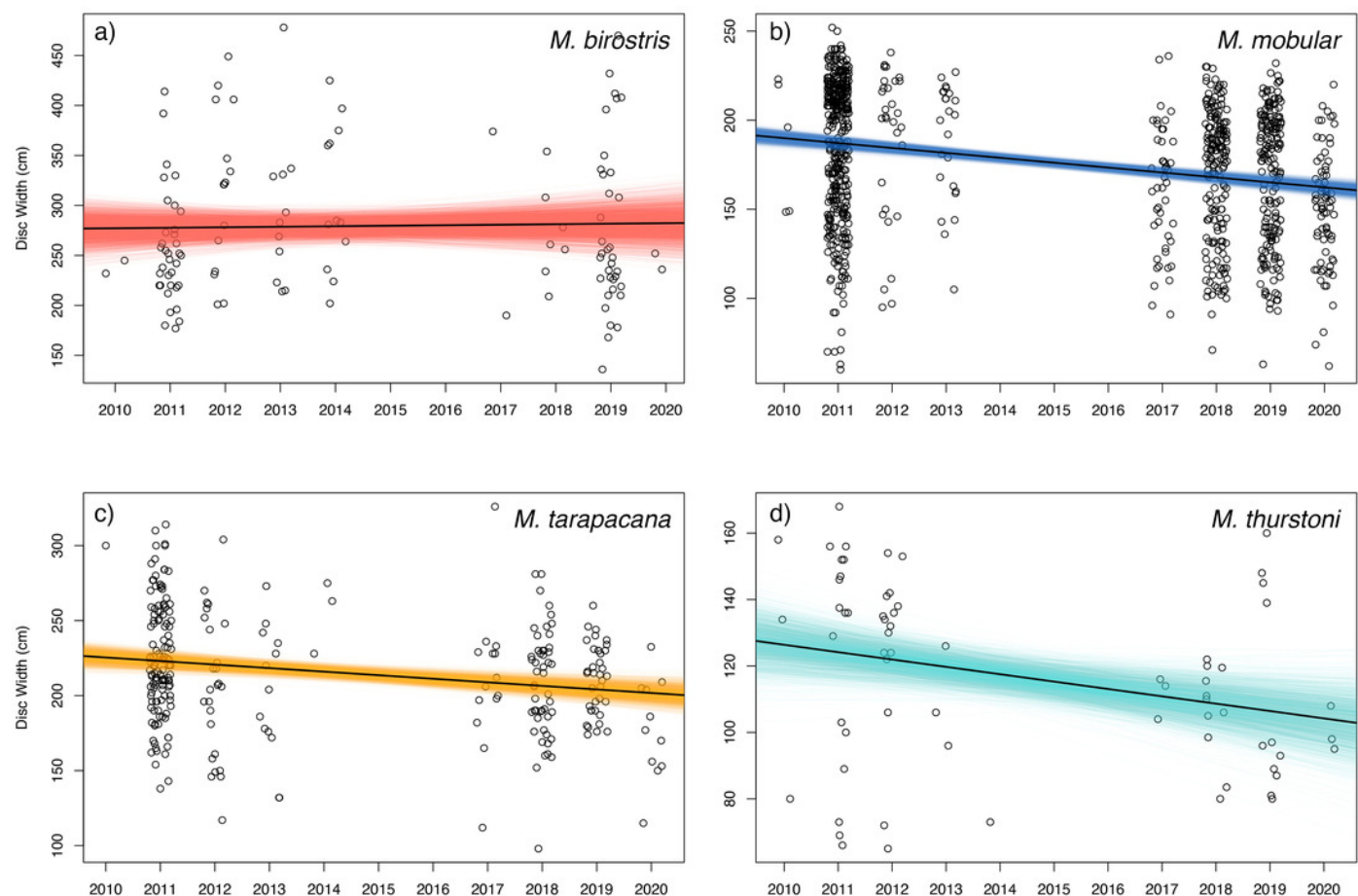
Figure 8

Total mortality estimates for *Mobula mobular*.

Shaded violin plots indicate the bootstrapped distributions of total mortality (Z) estimates from catch curve analyses using annual disc width records and disc widths from all years combined (All). Inset boxplots indicate the median (horizontal black line) 50% (white box) and 95% (vertical black line) bootstrap intervals. The solid horizontal line near the bottom indicates the median estimate of r_{max} for *M. mobular* from Pardo et al (2016), and dashed horizontal lines indicate the 95% confidence intervals of r_{max}. Numbers along the top indicate the sample sizes used to generate each estimate and bootstrap distribution.