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# Population dynamics of Bentfin devil ray, *Mobula thurstoni* (Lloyd, 1908), from Lakshadweep Sea, south-west coast of India

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Original Article

## Abstract

A demographic study was carried out on *Mobula thurstoni* covering 654 specimens' commercial fisheries along the Arabian Sea coast of southwestern India from January 2019 to December 2019. Overall sex ratio (M: F) did not deviate significantly from 1:1; females predominated the catches in almost all months. The asymptotic length ($L_\infty$) and growth constant (K) were 204.23 cm and 0.34 year$^{-1}$ respectively. The growth performance index (Ø) was estimated to be 4.152. The total instantaneous mortality rate (Z), natural mortality (M) and fishing mortality (F) were observed to be 0.98 year$^{-1}$, 0.51 year$^{-1}$ and 0.47 year$^{-1}$ respectively. The exploitation rate (E) (0.43) was close to the observed $E_{max}$ of 0.545 indicating the high harvest pressure on these species. Urgent management measures are required to ensure the sustainability of *M. thurstoni* fishery from Lakshadweep Sea, southwest Coast India.

***Keywords**: Mobula thurstoni, length-weight relationship, sex ratio, growth parameters, mortality parameters, exploitation*

## Introduction

The Bentfin devil ray, *Mobula thurstoni,* is circumglobally distributed and is found in tropical, subtropical and temperate waters of the Pacific, Atlantic and Indian Oceans (Couturier *et al*., 2012, Lawson *et al*., 2017). The bentfin devil ray occurs in neritic and oceanic waters from the surface to depths of 100 m (Notarbartolo-di-Sciara, 1988; Gadig *et al*., 2003; Croll *et al*., 2016; Weigmann, 2016; Fernando and Stewart, 2021).

*M. thurstoni* attains a maximum size of 220 cm (Disc Width) DW (Jabado and Ebert, 2015). Size at maturity is 150-163 cm DW for females and 150-158 cm DW for males (Notarbartolo-di-Sciara, 1988, White *et al*., 2006a, Rambahiniarison *et al*., 2018). They are aplacental viviparous, generally producing a single large pup; occasionally two are born at size intervals of 70-90 cm DW (Notarbartolo-di-Sciara, 1988; Rambahiniarison *et al*., 2018). *M. thurstoni* enlisted in the IUCN Red List as Endangered (Marshall *et al*., 2019) and has also been included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) since 2016.

Though they are enlisted in Conservation of Migratory Species of Wild Animals (CMS) and CITES, their fishery remains open and active around the globe. The meat from mobulid rays is often used locally or traded regionally for human consumption, animal feed, and shark bait (Fernando and Stevens, 2011; Heinrichs *et al*., 2011; Couturier *et al*., 2012; Croll *et al*., 2016). The gill plates in particular fetch a higher price tag in Asia and are used in Chinese medicine (O'Malley *et al*., 2017). Almost 99% of mobulid gill plates are destined for the markets of Guangzhou, China. They are sourced from over 20 countries and regions; among which the largest suppliers are Indonesia, Sri Lanka, India, China and Viet Nam (O'Malley *et al*., 2017). Thus mobulid fishery became directed as commercial export fisheries (Dewar, 2002; White *et al*., 2006b; Fernando and Stevens, 2011; Heinrichs *et al*., 2011; Acebes and Tull, 2016).

Mobulids, including the bentfin devil ray, are caught in at least 13 targeted artisanal fisheries in 12 countries. Some of the largest documented fisheries are in India, Indonesia, Mexico, Mozambique, Philippines, Sri Lanka, Taiwan, and Peru (Courturier *et al*., 2012; Ward-Paige *et al*., 2013; Croll *et al*., 2016). In some regions, directed artisanal fisheries land hundreds of bentfin devil rays per annum (Alava *et al*., 2002; Dewar, 2002; White *et al*., 2006b; Fernando and Stevens, 2011; Lewis *et al*., 2015; Acebes and Tull, 2016; Rambahiniarison *et al*., 2018). Overall, while many artisanal fisheries have grown into trade fisheries, some still target these rays mainly for food and local products (White *et al*., 2006b; Fernando and Stevens, 2011). In India, population reductions of devil rays are inferred based on their decline in catches in recent years. Catches indicate a clear depletion of stocks along the Kerala coast (Nair *et al*., 2013), so also in the Chennai and Tuticorin coasts (Kizhakudan *et al*., 2015) and Mumbai (Mohanraj *et al*., 2009).

The present study was carried out to understand the population dynamics of *M. thurstoni* aiming at the development of responsible sustainable fisheries management plans. The data generated from this study stand as a comprehensive study of the population dynamics of this species.

## Material and methods

A total of 654 specimens of *M. thurstoni* were collected at fortnight intervals for one year (January 2019 to December 2019) from commercial trawlers and purse seiners landed at Cochin Fisheries Harbour (Lat.09° 56' 327'' N, Long.76° 15' 764'' E), a major fish landing centre of the south-west coast of India. Disc Width (DW) was measured in cm and body mass (MB) was weighed (kg) separately for females and males. Males are easily distinguishable from females as they bear claspers. Measurements of 342 females and 312 males were taken for the study and were collected randomly to avoid any size bias in the analysis. Data was collected following the methodology of Gulland and Rosenberg (1992) on the length-based approaches to fish stock analyses published by the Food and Agricultural Organization (FAO).

The length data were grouped into 10 cm class intervals with the smallest mid-length of 84.5 cm. The length-weight relationships (LWRs) were calculated using the equation: $W = aL^b$ (Froese, 2006) and logarithmically transformed into $\log W = \log a + b \log L$, where W is the total weight (g), L = disc width (cm) and 'a' and 'b' are the regression parameters. When 'b' is equal to 3, the increase in weight is isometric; however, when 'b' is other than 3, the increase in weight is allometric (positive if $b > 3$; negative if $< 3$). The statistical significance level of the coefficient of determination ($r^2$) and the 95% confidence limit of parameters a and b (CI 95%) were estimated by least square linear regressions performed with the transformed equation. Extreme outliers were removed from the regression analyses according to Froese (2006). Statistical analysis was carried out using MS Excel 2010. At a significance level of 5% ($p<0.05$), all statistical analyses were taken into account. The chi-square test (Snedecor and Cochran, 1967) was applied to test the significant difference if any in the monthly sex ratio.

It was assumed that the *M. thurstoni* growth conformed to the von Bertalanffy growth (VBG) model (von Bertalanffy, 1938): $L_t = L_\infty (1- \exp [- K (t - t_0)])$. In the case of rays, disc width (DW) was considered as an indicator of growth; hence $L_\infty$ is the asymptotic length (cm), K is the growth constant (month$^{-1}$) and $t_0$ time (months) when the theoretical length is zero. The von Bertalanffy growth parameters, asymptotic length ($L_\infty$) and growth coefficient (K) were estimated from length-frequency data using the Electronic Length Frequency Analysis I (ELEFAN I) incorporated in FAO ICLARM Stock Assessment Tools II (FiSAT II) software (Gayanilo *et al*., 2005). Based on $L_\infty$ and K values, the growth performance index (Ø) and potential longevity (3/K) were estimated (Pauly and Munro, 1984). Instantaneous total mortality (Z) was estimated using the length-converted catch curve (Pauly, 1984); natural mortality (M) was determined by Pauly's empirical formula (Pauly, 1980). $\ln (M) = -0.0152 – 0.279 \ln (L_\infty) + 0.6543 \ln (K) + 0.463 \ln (T)$, T is the mean annual sea surface temperature of the water in which the fish occurs (27°C for the study area); instantaneous rate of fishing mortality (F) was computed as $F=Z-M$ and exploitation rate (E) was as $E=F/Z$ (Gulland, 1971). The $E_{max}$ (maximum yield per recruit) and $E_{50}$ (exploitation that retains 50% of the biomass) were predicted using relative yield per recruit (Y/R) and relative biomass per recruit (B/R) analysis using the knife-edge selection method (Pauly, 1984). From the length-converted catch curve, the length at first capture ($L_c$) was analysed. Growth parameters were used to determine the reproductive pulses per year, and the relative strength of each pulse using recruitment analysis (Moreau and Cuende, 1991). Growth and mortality parameters were used to perform Virtual Population Analysis (VPA) (Hilborn and Walters, 1992). Fishing mortality was considered as the terminal fishing mortality Ft. To understand how the population in different size classes might be affected by an increase in the fishing mortality, VPA was performed with different values of Ft.

Although, we estimated the length-weight relationship as well as age for males, females and pooled data separately; the growth and mortality parameters were done only for the pooled populations, to minimize any bias aroused because of the difference in the number of males and females obtained which might influence the results.

## Results

### *Length-Weight Relationship*

The length-weight relationship (LWR) of *M. thurstoni* females was $W = 0.006 L^{3.103}$ ($n = 342$, $r^2 = 0.955$, $p < 0.050$) and those for males was $W = 0.007 L^{3.048}$ ($n = 312$, $r^2 = 0.972$,

Table 1. Length-weight relationships of *M. thurstoni* from the south-west (SW) coast of India, based on $W=aL^b$

| | | Disc width (cm) | | Weight (kg) | | Regression parameters | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Sex | n | Min | max | min | max | a | 95% CL of a | b | 95% CL of b | $r^2$ |
| F | 342 | 85 | 193.4 | 4 | 100 | 0.006 | 0.005-0.007 | 3.103 | 3.031-3.174 | 0.955 |
| M | 312 | 83.5 | 193 | 4.6 | 98 | 0.007 | 0.006-0.008 | 3.048 | 2.989-3.106 | 0.972 |
| P | 654 | 83.5 | 193.4 | 4 | 100 | 0.007 | 0.006-0.007 | 3.078 | 3.031-3.125 | 0.962 |

n: number of specimen studied; min: minimum; max: maximum; a: the intercept of the relationship; b: the slope of the relationship $W = aL^b$; CL: Confidence limits; $r^2$: coefficient of determination

$p < 0.05$). LWR of combined sexes was found to be $W = 0.007\ L^{3.078}$ ($n = 654$, $r^2 = 0.962$, $p < 0.05$) (Table 1). In all cases, the exponent of length-weight relationship 'b' was higher than 3 (females 3.103; males 3.048 and pooled 3.078) and the 95% higher and lower confidence interval values were also above 3 indicating that the growth of *M. thurstoni* as isometric.

## *Exploited stock*

The exploited population of *M. thurstoni* from January 2019 to December 2019 was constituted of individuals ranging from 83.5 to 193.4 cm. The highest length class recorded among male and female populations was 160-169 cm and 150-159 cm respectively (Fig. 1 and 2). The fishery was dominated by individuals in the size range of 140 to 169 cm in both females and males (Fig. 3). The size class 150-159 cm (14%) constituted the largest share in females followed by 160-199 cm (11%) size class, whereas for males it was the 160-169 cm size class (18%) followed by 150-159 cm (15%) size class. The sex ratio was 1:1 which was not significantly different from 1:1 ($p > 0.05$).

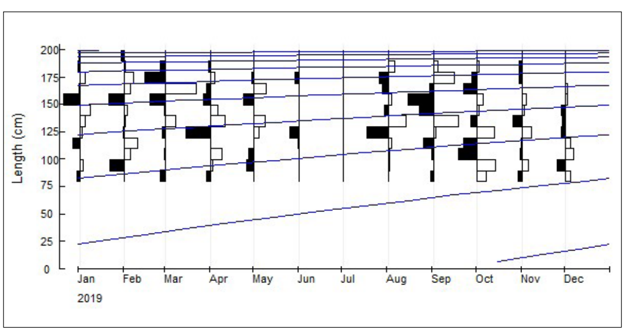


Fig. 1. Growth curve of the female population of *M. thurstoni* by ELEFAN 1 superimposed on the restructured length frequency diagram ($L_\infty = 204.23$ mm, $K = 0.3\ yr^1$ and $Rn = 0.163$)

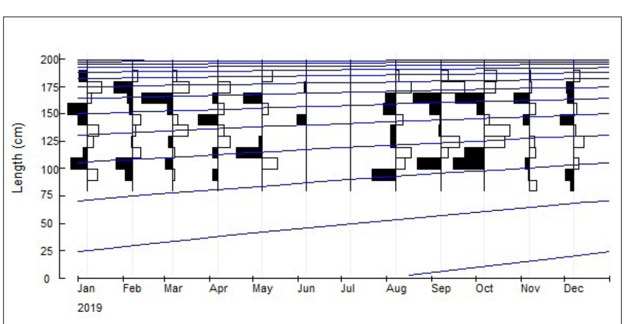


Fig. 2. Growth curve of the male population of *M. thurstoni* by ELEFAN 1 superimposed on the restructured length frequency diagram ($L_\infty = 204.23$ mm, $K = 0.3yr^1$ and $Rn = 0.101$)

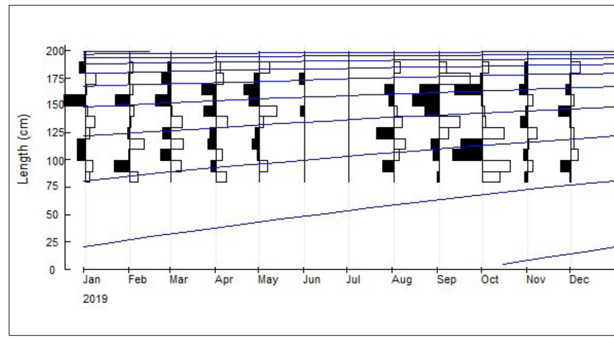


Fig. 3. Growth curve of the pooled population of *M. thurstoni* by ELEFAN 1 superimposed on the restructured length frequency diagram ($L_\infty = 204.23$ mm, $K = 0.3\ yr^1$ and $Rn = 0.105$)

## *Growth*

The estimated growth parameters in the female population of *M. thurstoni* (Table 2). The exhibited $t_0$ value, which employs the empirical equation Pauly (1979), was -0.543. The FiSAT (ELEFAN I) output of restructured length frequency data of the male population portrayed a superimposed growth curve fitted with the highest levels of Rn is given in Fig. 2. The VBGF for female *M. thurstoni* based on the growth parameters was expressed as: $L_t = 204.23\ [1–\exp^{-0.30\ (t+0.543)}]$.

For the male population (Table 2), the value of $t_0$ was found to be -0.543. The FiSAT (ELEFAN I) output of restructured length frequency data of the female population of *M. thurstoni* with superimposed growth curve fitted with highest levels of Rn is given in Fig. 3. The VBGF arrived at, based on the growth

Table 2. Growth parameters in male, female and pooled population of *M. thurstoni*

| | $L_\infty$ | K year$^1$ | Rn | Ø |
|---|---|---|---|---|
| Female | 204.23 | 0.3 | 0.163 | 4.097 |
| Male | 204.23 | 0.3 | 0.101 | 4.097 |
| Pooled | 204.23 | 0.34 | 0.105 | 4.152 |

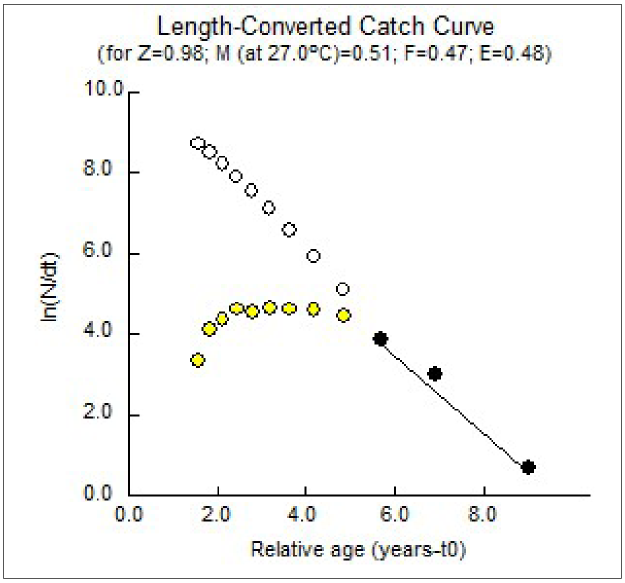


Fig. 4. Length converted catch curve of the pooled population of *M. thurstoni* (Z from catch curve = 0.90; M = 0.47; F = 0.43; E (F/Z) = 0.48)

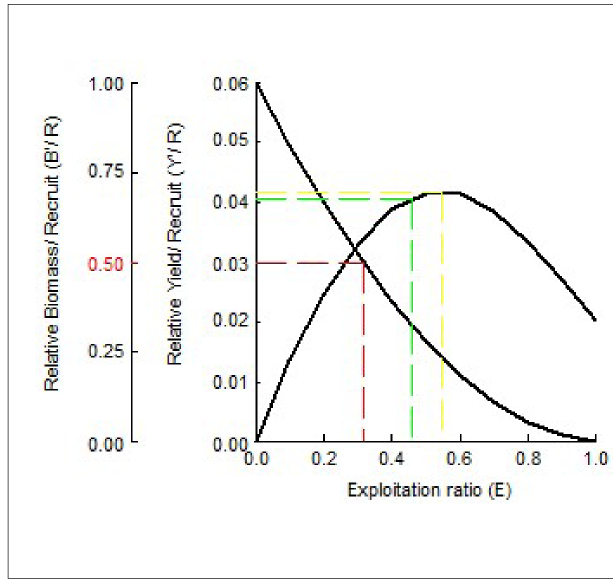


Fig. 6. Relative yield per recruit and biomass per recruit of *M. thurstoni* (Male and female pooled)

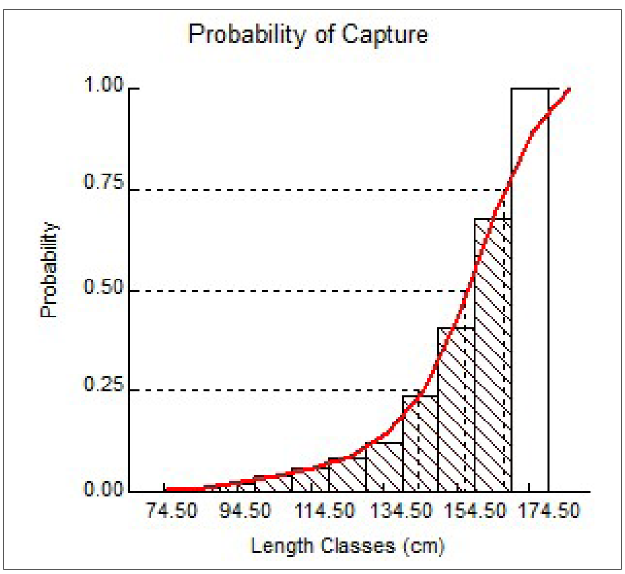


Fig. 5. Probabilities of capture pattern of *M. thurstoni* (Male and female pooled)

parameters in terms of male *M. thurstoni*, expressed as Lt = 204.23[1–exp$^{-0.30(t+0.543)}$)].

For the pooled population (combined sexes), the value of $t_0$ was found to be -0.542. Fig. 4 provides the FiSAT output of restructured length frequency data of the pooled population of *M. thurstoni* with a superimposed growth curve fitted with the highest levels of Rn. The VBGF in terms of pooled *M. thurstoni* population was expressed as Lt = 204.23 [1–exp$^{-0.34(t+0.542)}$].

The FiSAT output of mortality estimates of the pooled population of *M. thurstoni* by the catch curve method is depicted in Fig. 4. The total mortality (Z) was estimated to be 0.98 yr$^{1}$. The estimates of natural mortality (M) were determined as 0.51 yr$^{1}$. The values of the fishing mortality coefficient (F) and exploitation rate (E) were worked out as 0.47 yr$^{1}$ and 0.48 yr$^{1}$, respectively. Using the length converted catch curve method, the estimates of probabilities of capture were $L_{25}$ = 143.7 cm, $L_{50}$ = 156.46 cm and $L_{75}$ = 166.87 cm (Fig. 5) and the $L_c$ was found to be 61.3 cm. These values were subsequently used as inputs for the relative Y/R of Beverton and Holt (1957, 1966). The $L_c/L_\infty$ and M/K values used for Y/R analysis were 0.3 and 1.5 respectively. The relative yield per recruit and biomass per recruit in *M. thurstoni* is presented in Fig. 6. The relative Y/R reached a maximum at an exploitation rate of 0.545 yr$^{1}$ and thereafter decreased in the exploitation rate. It may be noted that the present exploitation rate E (0.43) is near the optimum exploitation rate of $E_{max}$= 0.545. The values of $E_{10}$ and $E_{50}$ were estimated as 0.46 and 0.315 respectively. The results of length-based virtual population analysis showed that F increases to a maximum of 0.9 at a body size of 154.5-164.5 cm (Fig. 7). The catch increases substantially from 114.5-144.5 cm size groups and attains a maximum at 154.5-174.5 cm.

## Discussion

Environmental factors play a major role in controlling the normal well-being and growth of fish. Fish living in various agro-climatic environments have different body parameters, and their growth parameters vary significantly. Depending on the value of 'b' of LWR, the growth in fishes can be said as isometric (b = 3), positive algometric growth (b > 3) and negative algometric

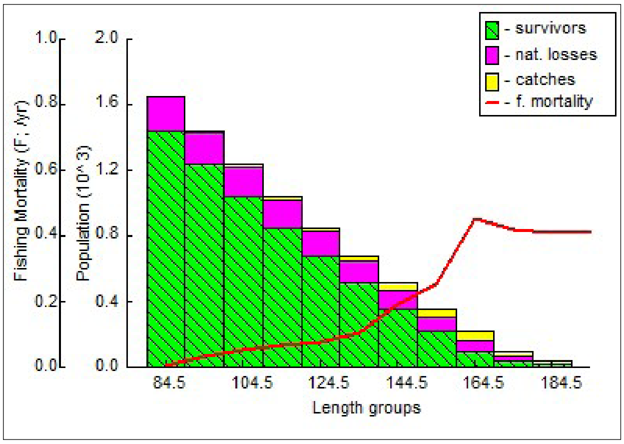


Fig. 7. Length-based virtual population analysis of *M. thurstoni* (Male and female pooled)

growth (b < 3) (Tesch, 1971; Ricker, 1975); however, Le Cren's Cube Law states that the value of 'b' remains 3 for ideal fish and follows isometric growth. The b values of female, male and pooled data were 3.103, 3.048, and 3.078, respectively, showing that *M. thurstoni* follows the cube law and exhibits isometric growth. The 'b' value obtained in our study is similar to *M. hypostoma* (b= 3.07) reported by Gonzalez-Gonzalez and Ehemann (2018) from Margarita Island, Venezuela.

Etim *et al.* (1999) opined that $L_\infty$ is the largest theoretical mean length that a fish could attain in its natural habitat and K is the speed with which it grows to gain this final size. Growth comparison is a multivariate problem that must be taken into consideration both the growth rate (K) and the asymptotic size ($L_\infty$). Thus, we used the overall growth performance index ø (Pauly and Munro, 1984) as it meets these criteria, to effectively compute and exhibit the least variance; when compared with other alternative indices. The growth parameters derived from this study are comparable to earlier works on similarly sized populations of *M. mobular*, *i.e.*, $L_\infty$: 233.8 cm, K= 0.280 year$^1$, $t_0$ = -1.68 (Cuevas Zimbron *et al.*, 2013); $L_\infty$: 299 cm, K=0.12 year$^1$, $t_0$ = -1.68 (Pardo *et al.*, 2016); $L_\infty$: 198.9 cm, K= 0.280 year$^1$, $t_0$ = -1.68 (Cuevas Zimbron *et al.*, 2012), $L_\infty$: 198.9 cm, K= 0.12 year$^1$, $t_0$ = -1.68 ( Pardo *et al.*, 2016); $L_\infty$: 707 cm, K= 0.1 year$^{-1}$, $t_0$ = -1.68 (Dulvy *et al.*, 2014) for *M. thurstoni* and *M. birostris* respectively. The value of the growth coefficient (K) obtained for *M. thurstoni* (0.3 year$^1$) falls well in tune with the values for batoids (0.07 to 0.45) reported by Cowley (1997). Although elasmobranchs are generally considered to possess slow growth rates, estimates of growth coefficients (k) encompass a broad range of values (Musick, 1999; Cailliet and Goldman, 2004). Branstetter (1990) delineated that growth rates among sharks remain slow if k is determined to be 0.1 year$^1$. On this basis, the present results ensure that *M. thurstoni* can be considered as a slow-growing elasmobranch.

Even at low levels of fishing mortality, life history characteristics indicate that mobulids would decline (F > 0.05). Higher rates of mortality were most likely observed in neonates and early juveniles, as is typical of many elasmobranchs (Cortés, 2004). Due to complete protection from commercial fishing and what appears to be low predation pressure, the Maui subpopulation of *M. alfredi* had higher survival rates than other subpopulations (Deakos *et al.*, 2011). According to estimates of Marshall *et al.* (2011), the local subpopulation of *M. alfredi* in Mozambique experiences a high fishing mortality rate, which may account for the species' estimated annual apparent survival of 0.6 to 0.7.

The size at first maturity for *M. thurstoni* was found to be 150-163 cm DW for females and 150-158 cm DW for males (Notarbartolo-di-Sciara, 1988; White *et al.*, 2006a; Rambahiniarison *et al.*, 2018). Fernando and Steward (2021) estimated the size at first maturity for male *M. thurstoni* found to be 142.7 cm. During the present study, it was observed that the exploited population of *M. thurstoni* was constituted by individuals ranging in size from 83.5 to 193.4 cm and that the fishery was dominated by individuals in the size range 150 to 179 cm in both sexes. The fact that immature individuals of *M. thurstoni* are also fished out indicates that recruitment fishing is taking place, damaging the reproductive potential and reducing the spawning stock of the species. The capture of small fish before they mature and breed also leads to a reduction in fisher productivity and profit.

Bentfin devil ray was the most commonly landed species in the mobulid fishery off Baja California Sur, Mexico (Notarbartolo-di-Sciara, 1988). By the early 1980s, there was concern about the sustainability of bentfin devil ray landings, with 72% of individuals reported as immature (Notarbartolodi-Sciara, 1988). By the late 1990s, the primary target had shifted to the pygmy devil ray (*M. munkiana*) and bentfin devil rays were a minor component of landings (Bizzarro *et al.*, 2009; Smith *et al.*, 2009). During the same period, bentfin devil rays were rarely encountered among elasmobranch landings from the more temperate northern Gulf of California (Bizzarro *et al.*, 2009). Recent landing data from this region are unavailable due to the ban on the capture of mobulid species, however, fisheries of these species continue to operate.

The bentfin devil ray was listed in Appendix I and II of CMS (Convention of Migratory Species) in 2014, reflecting the concerned Parties' commitments to strictly protect this species and work regionally towards its conservation. Mobulids were listed in Appendix II of CITES in 2016, which makes it mandatory that exports from CITES Parties must be strictly based on permits which ensures that they are sourced from legal and sustainable fisheries. *Mobula* species were included in the 'key shark species' list of the Western and Central Pacific Fisheries Commission

(WCPFC) in 2016 (for assessment only) and thereby adopted safe release guidelines in 2017.

Inter-American Tropical Tuna Commission (IATTC) (2015) prohibited mobulid fishery among large-scale fisheries in the IATTC Convention Area; and has to follow strict guidelines for its prompt and careful release at the earliest. Limited exceptions were given for small-scale fishery in Eastern Pacific Fisheries which are meant only for domestic consumption Mobulid landings have to be prohibited, in line with several international agreements, at least as long as the global populations are restored to a safer level.

The extremely conservative life history pattern of mobulid species makes them particularly vulnerable to over-exploitation and extremely slow to recover from depletion (Couturier *et al.*, 2012; Dulvy *et al.*, 2014) therefore maritime countries should adopt a precautionary approach in managing these species to avoid drastic population collapses. In India, population reductions are inferred based on general declines in devil ray catches in recent years. Despite increasing fishing efforts in several regions, catches indicate depletion of stocks in Kerala (Nair *et al.*, 2013), along the Chennai and Tuticorin coasts of Tamilnadu (Kizhakudan *et al.*, 2015) and Mumbai (Mohanraj *et al.*, 2009), Trawlers in Mumbai reported maximum landings of 6.3 t for *M. diabolos* (an invalid, perhaps generalized name for devil rays) in 1993- 95 surveys, declining to 4.8 t in 1996-98, and then to 3.1 t in 1999-2001 and 2002-2004 (Raje and Zacharia, 2009). This represents a 51% decline in landings over approximately ten years during which time fishing efforts almost doubled, from which local population declines could be inferred.

The present study unravels the high exploitation rate (E) (0.43) which was close to the observed $E_{max}$ of 0.545, indicating the high harvest pressure on *M. thurstoni*. The data generated on the population dynamics of *M. thurstoni* will stand as baseline information for the development of responsible sustainable fisheries management plans.

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## References

Acebes, J. M. V. and M. Tull. 2016. The history and characteristics of the mobulid ray fishery in the Bohol Sea, Philippines. *PLoS ONE*, 11(8): e0161444.

Alava, M. N. R., E. R. Z. Dolumbalo, A. A. Yaptinchay and R. B. Trono. 2002. Fishery and trade of Whale Sharks and Manta Rays in the Bohol Sea, Philippines. In: S. L. Fowler, T. M. Reed and F. A. Dipper (Eds.), Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997 on Elasmobranch Biodiversity, Conservation, and Management, IUCN SSC Shark Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK. 25: 132-148.

Beverton, R. J. H. and S. J. Holt. 1957. On The Dynamics of Exploited Fish Populations. *Gt. Britain. Fish. Invest. Ser.*, 19 (2):1-533.

Beverton, R. J. H. and S. J. Holt. 1966. Manual of methods for fish stock assessment. Part 2. Tables of yield functions. *FAO Fish. Tech. Pap.*, 38: 1-67.

Bizzarro, J. J., W. D. Smith, R. E. Hueter and C. J. Villavicencio-Garayzar. 2009. Activities and catch composition of artisanal elasmobranch fishing sites on the eastern coast of Baja California Sur, Mexico. *Bull. South. Calif. Acad. Sci.*, 108 (3): 137-151.

Branstetter, S. 1990. Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In: H. L. Pratt, S. H. Gruber and T. Taniuchi (Eds.), Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries. NOAA Technical Report 90, National Marine Fisheries Service, Washington, DC. p. 17-28.

Cailliet, G. M. and K. J. Goldman. 2004. Age determination and validation in Chondrichthyan fishes. In: J.C. Carrier, J. A. Musick and M. R. Heithaus (Eds.), Biology of Sharks and Their Relatives: CRC Press, New York. p. 399-477.

Cortés, E. 2004. Life-history patterns, demography and population dynamics. In: J. C. Carrier, J. A. Musick and M. R. Heithaus (Eds.), Biology of Sharks and their Relatives, CRC Press, New York. p. 449-469.

Couturier, L. I. E., A. D. Marshall, F. R. A. Jaine, T. Kashiwagi, S. J. Pierce, K. A. Townsend, S. J. Weeks, M. B. Bennet and A. J. Richardson. 2012. Biology, ecology and conservation of the Mobulidae. *J. Fish. Biol.,* 80 (5): 1075-1119.

Cowley, P. D. 1997. Age and growth of the blue stingray *Dasyatis chrysonota chrysonota* from the south-eastern cape coast of South Africa. *S. Afr. J. Mar. Sci.*, 18 (1): 31-38.

Croll, D. A., H. Dewar, N. K. Dulvy, D. Fernando, M. P. Francis, F. Galvan-Magana, M. Hall, S. Heinrichs, A. Marshall, D. Mc Cauley, K. M. Newton, G. Notarbartolo-di-Sciara, M. O'Malley, J. O'Sullivan, M. Poortvliet, M. Roman, G. Stevens, B. R. Tershy and W. T. White. 2016. Vulnerabilities and fisheries impacts: the uncertain future of Manta and Devil Rays. *Aquatic Conserv: Mar. Freshw. Ecosyst.*, 26 (3): 562-575.

Cuevas-Zimbron, E., O. Sosa-Nishizaki, J. C. Perez-Jimenez and J. B. O'Sullivan. 2013. An analysis of the feasibility of using caudal vertebrae for ageing the spinetail devil ray, *Mobula japanica* (Müller and Henle, 1841). *Environ. Biol. Fish.,* 96 (8): 907-914.

Deakos, M. H., J. D. Baker and L. Bejder. 2011. Characteristics of a manta ray *Manta alfredi* population off Maui, Hawaii, and implications for management. *Mar. Ecol. Prog. Ser.,* 429: 245-260.

Dewar, H. 2002. Preliminary report: manta harvest in Lamakera. Report from the Pfleger 887 Institute of Environmental Research, Oceanside, CA, 3 pp.

Dulvy, N. K., S. A. Pardo, C. A. Simpfendorfer and J. K. Carlson. 2014. Diagnosing the dangerous demography of manta rays using life history theory. *Peer. J.,* 2: p.e400.

Etim, L., P. E. Lebo and R. P. King. 1999. The dynamics of an exploited population of a Siluroid Catfish (*Schilbe intermedius* Rupell 1832) in the Cross River, Nigeria. *Fish. Res.*, 40: 295- 307.

Fernando, D. and G. Stevens. 2011. A study of Sri Lanka's Manta & Mobula Ray Fishery. *Manta Trust.,* 29 pp.

Fernando, D. and J. D. Stewart. 2021. High bycatch rates of manta and devil rays in the "small-scale" artisanal fisheries of Sri Lanka. *Peer. J.*, 9: p.e11994.

Froese, R. 2006. Cube law, conditon factor and weight-length relatonships: History, meta- analysis and recommendatons. *J. Appl. Ichthyol.*, 22: 241-253.

Gadig, O. B. F., R. C. Namora and F. D. S. Motta. 2003. Occurrence of the bentfin devil ray, *Mobula thurstoni* (Chondrichthyes: Mobulidae), in the western Atlantic. *J. Mar. Biol. Assoc. U. K.*, 83: 869-870.

Gayanilo, F. C., P. Sparre and D. Pauly. 2005. FAO-ICLARM stock assessment tools II: Revised version: User's guide. FAO Computerized Information Series (Fisheries) No. 8: FAO, Rome, 168 pp.

Gonzalez-Gonzalez, L. V. and N. R. Ehemann. 2018. Length-weight relationships of six elasmobranch species captured at the artisanal fishery of Margarita Island, Venezuela. *J. Appl. Ichthyol.*, 35 (2): 594-596.

Gulland, J. A. and A. A. Rosenberg. 1992. A review of length based approaches to assessing fish stocks. *FAO Fish. Tech. Pap.*, 323: 100 pp.

Gulland, J. A. 1971. The fish resources of the Ocean West Polyfleet Survey. *FAO Fish. Tech. Pap.*, 97: 428 pp.

Heinrichs S., M. P. O'Malley, H. Medd and P. Hilton. 2011. The global threat to Manta and Mobula Rays. San Francisco, CA: Manta Ray of Hope, Wild Aid, 21 pp.

Hilborn, R. and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. *Springer*, Boston, 570 pp.

Jabado, R. W. and D. A. Ebert. 2015. Sharks of the Arabian Seas: an identification guide. The International Fund for Animal Welfare, Dubai, UAE, 240 pp.

Kizhakudan, S. J., P. U. Zacharia, S. Thomas, E. Vivekanandan and M. Muktha. 2015. Guidance on National Plan of Action for Sharks in India. *CMFRI Marine Fisheries Policy Series,* 2: 1-102.

Lawson, J. M., S. V. Fordham, M. P. O' Malley, L. N. K. Davidson, R. H. L Walls, M. R.

Heupel, G. Stevens, D. Fernando, A. Budziak, C. A. Simpfendorfer, I. Ender, M. P. Francis, G. Notarbartolo-di-Sciara and N. K. Dulvy. 2017. Sympathy for the devil: a conservation strategy for devil and manta rays. *Peer. J.,* 5: p.e3027.

Le Cren, E. D. 1951. The length weight relationship and seasonal cycle in gonad weight and condition in perch (*Perca fluviatilis*). *J. Anim. Ecol.*, 21: 210-219.

Lewis, S. A., N. Setiasih, Fahmi, Dharmadi, M. P. O'Malley, S. J. Campbell, M. Yusuf and A. B. Sianipar. 2015. Assessing Indonesian manta and devil ray populations through historical landings and fishing community interviews. *Peer. J. Pre. Pr.*, 6: p.e1334v1.

Marshall, A. D., C. L. Dudgeon and M. B. Bennett. 2011. Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. *Mar. Biol.,* 158 (5): 1111-1124.

Marshall, A., R. Barreto, J. S. Bigman, J. Carlson, D. Fernando, S. Fordham, M. P. Francis, K. Herman, R. W. Jabado, K. M. Liu, S. A. Pardo, C. L. Rigby, E. Romanov, W. D. Smith and R. H. L. Walls. 2019. *Mobula thurstoni*. The IUCN Red List of Threatened Species. e.T60200A124451622.

Mas, F., R. Forselledo and A. Domingo. 2015. Mobulid ray by-catch in long line fisheries in the south-western Atlantic Ocean. *Mar. Freshw. Res.*, 66 (9): 767-777.

Mohanraj, G., S. Rajapackiam, S. Mohan, H. Batcha and S. Gomathy. 2009. Status of elasmobranchs fishery in Chennai, India. *Asian Fish. Sci.,* 22 (2): 607-615.

Moreau, J. and F. X. Cuende. 1991. On improving the resolution of the recruitment patterns of fishes. *Fishbyte,* 9 (1): 45-46.

Musick, J. A. 1999. Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals. American Fsheries Society Symposium 23. American Fisheries Society, Bethesda, Maryland, USA, 265 pp.

Nair, R. J., P. U. Zacharia, T. G. Kishore, K. S. Dinesh, K. V. Dhaneesh, K. S. Suraj and Siva G. Kumar. 2013. Heavy landings of mobulids reported at Cochin Fisheries Harbour, Kerala. *Mar. Fish. Infor. Serv. T & E Ser.*, 218: 19-20.

Notarbartolo-di-Sciara, G. 1988. Natural history of the rays of the genus Mobula in the Gulf of California. *Fish. Bull.*, 86 (1): 45-66.

O'Malley, M. P., K. A. Townsend, P. Hilton, S. Heinrichs and J. D. Stewart. 2017. Characterization of the trade in manta and devil ray gill plates in China and South-east Asia through trader surveys. *Aquatic Conserv: Mar. Freshw. Ecosyst.*, 27 (2): 394-413.

Pardo, S. A., H. K. Kindsvater, E. Cuevas-Zimbron, O. Sosa-Nishizaki, J. C. Perez-Jimenez and N. K. Dulvy. 2016. Growth, productivity and relative extinction risk of a data-sparse devil ray. *Sci. Rep.*, 6 (1): 1-10.

Pauly, D. and K. Munro. 1984. Once more on the comparison of growth in fish and invertebrates. *Fishbyte,* 2 (1): 1-21.

Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. *Ber. Inst. Meereskd. Christian-Albrechts- Univ. Kiel,* p. 1-136.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer.,* 39 (2): 175-192.

Pillai, S. K. 1998. A note on giant devil ray *Mobula diabolus* caught at Vizhinjam. *Mar. Fish Infor. Serv. T & E Ser.,* 152: 14-15.

Poortvliet, M., J. L. Olsen, D. A. Croll, G. Bernardi, K. Newton, S. Kollias, J. O'Sullivan, D. Fernando, G. Stevens, F. G. Magana and B. Seret. 2015. A dated molecular phylogeny of manta and devilray (Mobulidae) based on mitogenome and nuclear sequences. *Mol. Phylogenet. Evol.*, 83: 72-85.

Raje, S. G. and P. U. Zacharia. 2009. Investigations on fishery and biology of nine species of rays in Mumbai waters. *Indian J. Fish.*, 56 (2): 95-101.

Rambahiniarison, J. M., M. J. Lamoste, C. A. Rohner, R. Murray, S. Snow, J. Labaja, G. Araujo and A. Ponzo. 2018. Life history, growth, and reproductive biology of four mobulid species in the Bohol Sea, Philippines. *Front. Mar. Sci.*, 5: 1-17.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish population. *Bull. Fish. Res. Bd. Can.,* 191: 1-382.

Smith, W. D., J. J. Bizzarro and G. M. Cailliet. 2009. The artisanal elasmobranch fishery on the east coast of Baja California, Mexico: characteristics and management considerations. *Cienc. Mar.*, 35: 209-236.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. Sixth edition, Oxford and IBH Publ. Co., New Delhi, 53 pp.

Tesch, F. W. 1971. Age and growth. In: Ricker, W.E. (Eds.), Methods for Assessment of Fish Producton in Freshwaters. Blackwell Scientific Publications, Oxford. p. 99-130.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Hum. Biol.*, 10: 181-213.

Ward-Paige, C. A., B. David and B. Worm. 2013. Global population trends and human use patterns of Manta and Mobula rays. *PLoS ONE*, 8 (9): e74835

Weigmann, S. 2016. Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. *J. Fish. Biol.*, 88 (3): 837-1037.

White, W. T., J. Giles and I. C. Potter. 2006a. Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. *Fish. Res.*, 82: 65-73.

White, W. T., P. R. Last, J. D. Stevens, G. K. Yearsley, Fahmi and Dharmadi. 2006b. Economically important sharks and rays of Indonesia. Australian Centre for International Agricultural Research, 338 pp.

 