

Biological Aspects, Stock and Conservation Status of Giant Oceanic Manta Ray, *Manta birostris* in the Indian Ocean(*)

DHARMADI¹⁾ & FAHMI²⁾

¹⁾ *Research Center for Fisheries Management and Conservation, Ministry of Marine Affairs and Fisheries. Jl. Pasir Putih I, Ancol Timur Jakarta 14430 Indonesia*

²⁾ *Research Center for Oceanography-Indonesian Institute of Sciences*

Email: darma_ancol@yahoo.com; fahmi_lipi@yahoo.com

ABSTRACT

The giant oceanic manta ray (*Manta birostris*) is a ray species of the Family Mobulidae, the largest type of rays in the world. A study on Manta rays from the Indian Ocean was conducted from April 2001 to August 2005 at Cilacap-Central Java and Tanjungluar-East Lombok fish landings. Catch data of Cilacap fishing port from 2006 to 2011 are also presented in this paper. The methodology utilized was direct observations and data collection by enumerators. The results show that Manta rays were caught as by-catch of tuna gillnet and tuna longline fishing in the Indian Ocean. There were three age groups (cohorts) of the *Manta birostris* caught in the Indian Ocean, i.e. size class between 200-300 cm disc width (DW) as a young group, 301-400 cm DW (subadult group), and 401-500 cm DW (adult group), respectively. The sex ratio of males to females of *Manta birostris* was 1:1 ($P>0.05$). Monthly production of *Manta birostris* during six years (2006-2011) indicated that the highest production occurred in the period between May and September. Almost all of the body of this species were utilised, for instance, the gill plates and cartilages were used for medicines, and meat for consumption. Based on IUCN Red List, the conservation status of *Manta birostris* is near threatened and vulnerable in South-East Asia.

KEY WORDS: biology, fisheries, conservation, *Manta birostris*, Indian Ocean

INTRODUCTION

The Giant Oceanic Manta ray (*Manta birostris*) and *Manta alfredi* were proposed to be listed in Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals in 2011 (FAO, 2013a). There is a paucity of reliable information on historical or recent changes in status of both species of *Manta*, both overall and within geographical regions. Fishery removals are poorly documented. *Manta birostris* resides in deepwater, pelagic zones, making periodic visits to cleaning stations at seamounts and coastal reefs. Each year, thousands of manta rays, primarily oceanic mantas, are caught and killed solely for their gill rakers. However the scale of production globally of either species is still unknown (FAO, 2013). *Manta birostris* can be reach at least 7.6 metres in disc width with a weight of about 2,400 kilograms (Kashiwagi *et al.* 2011). They are circumglobal and are typically found in tropical and subtropical waters, and can also be found in temperate waters. *M. birostris* undertake significant seasonal migrations and is capable of large migrations (> 1,000 km) although movements across ocean basins are rare (Marsall, *et al.*, 2011; Ebert & Stehmann, 2013).

In Indonesia, although the *Manta* is not a targeted species, those species are sought after by fishers because their high economic value, especially for the gill rakers. FAO (2013) reported that Manta rays are harvested for local consumption and also to supply international markets for skin, cartilage and, particularly gill rakers. Gill rakers fetch high prices because of the high demand for them. Heinrichs *et al.* (2011) estimated that an average of 61,000 kg of gill rakers is traded annually in some countries, with an estimated 30 percent coming from *M. birostris*. Nevertheless, *Manta* spp. is legally protected in only a few countries and in some small Marine Protected Areas (FAO, 2013).

The increase in demand for manta gills used in Chinese medicine has resulted from the change from a previously limited scale subsistence fishery in Indonesia into an expanding commercial fishery. The number of mantas caught each year has risen dramatically (Lewis, 2011). Due to their life history (slow growth, late age of sexual maturation and low fecundity), manta rays have limited capacity to recover from overfishing, and a decline of their populations has already been observed in certain areas of Indonesia where fishing pressure is high. According to Stevens *et al.*, (2000), some species of rays, including manta ray, need several decades to recovery their population after a period of intense exploitation. The Manta rays are only protected in a few range of states and there are no management measures in the area where the largest documented fisheries. It has also been stated that without regulation of international trade, all *Manta* spp. will probably qualify globally for Appendix I listing in the future (FAO, 2013).

The proportion of batoid group including Manta rays from all cartilaginous fish landed at the fish landing sites throughout Indonesia increased from 48.5% in 2006 to 50.4% in 2011. The Directorate General of Capture Fisheries reported that the production of the Family Mobulidae (*Mobula* spp.; *Manta* spp.) in 2005 was 200 tons and increased to 3,720 tons in 2011 (Anon, 2012). In Indonesian waters, Manta rays were caught as bycatch from tuna fishery that used longlines and gillnets. Last and Steven (1994) mentioned that in the Indian Ocean, Manta ray, *Manta birostris* (Fig. 1) was often caught by tuna gill nets. In Chennai, India, *M. birostris* was one of the elasmobranch species caught in the multispecies gillnet, trawling and hook and line fisheries between 2002 and 2006 (Mohanraj *et al.*, 2009). The catch composition of the family Mobulidae in the Indian Ocean was dominated by *Mobula japonica* (50%), followed by *M. tarapacana* (24%), *Manta birostris* (14%), *Mobula thurstoni* (9%) and *Mobula cf kuhlii* (2%) (White *et al.*, 2006a). Information on biological aspects of *M. birostris* caught in the Indian Ocean is still lacking and the catch data from Indonesia is not yet available. This paper aims to provide some biological information and insight on the conservation status of *Manta birostris*.

MATERIALS AND METHODS

This study was conducted from April 2001 to August 2005 at Cilacap-Central Java and Tanjung Luar-East Lombok fish landings (Fig. 2). Catch data of Cilacap fishing port from 2006 to 2011 are also presented in this paper. Direct observations and data collections by enumerators were used for the sampling methodology.

A total number of 85 individuals of oceanic manta ray (*Manta birostris*) caught by gill net and tuna longline were observed during the sampling period. Disc width frequency, sex ratio, relationship between disc width and clasper length of those species were analyzed. Clasper measurements in millimeters from the curve of the inside of the pelvic fin to the tip of clasper were taken. Carrier *et al.* (2004) states that the occurrence and progression of calcification (hardened and stiff) on clasper is a standard for determining the level of sexual maturity in cartilaginous fish. The data analyzed was based on daily data recording by enumerators from 34 tuna vessels operating in the Indian Ocean. Data analysis to determine the correlation between some parameters was measured using a statistical regression based on Minitab Release 13 software.

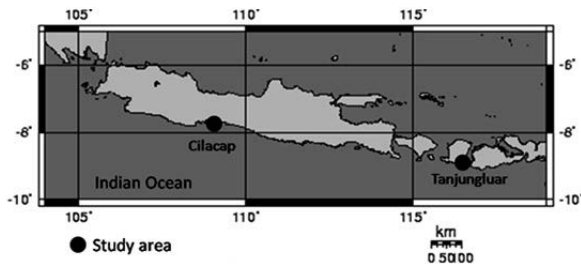


Fig. 2. Map of the study area and observed landing sites

Meanwhile, the stage maturity of claspers was determined based on macroscopic development, referring to Martin and Coillet (1988) as shown in Table 1.



Fig. 1. Morphology of Giant Oceanic Manta Ray (White et al., 2006).

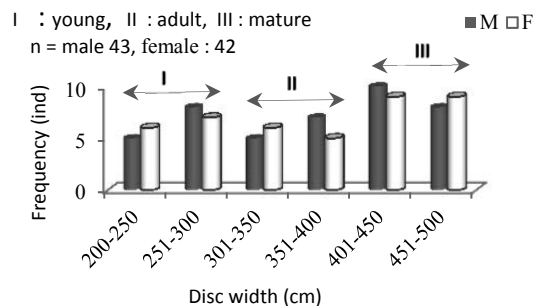
Table 1. Maturity stages male of elasmobranch (Martin and Coillet, 1988)

Stage	Macroscopic stage
Males	
1. Immature	Testes undeveloped. Claspers small and uncalcified.
2. Maturing, virgin	Testes enlarging but without prominent lobes, vas deferens becoming coiled. Clasper enlarging and undergoing Calcification progressing, thus becoming rigid.
3. Mature, non	Testes contain large bulging lobes due to reproductive sperm production. Vas deferens are tightly coiled. Clasper fully developed and rigid due to calcification.
4. Mature, sexually	Seminal vesicles full of mature spermatozoa. Testes with bulging lobes and clasper enlarged and rigid.

RESULTS

Disc width distribution

At least three age groups of the Giant oceanic manta ray (*Manta birostris*) were recorded from the Indian Ocean, i.e. the young, subadult, and adult groups. The low size distribution of *Manta birostris* was seen in the male group between 200 and 300 cm with 250 cm mode (for young group), and a group between 301 and 350 cm with a mode of 375 cm, whereas the highest distribution in disc width was in the adult group with size between 401 and 450 cm with a mode of 425 cm. The highest distribution of female disc width occurred at 401-450 cm with a mode of 425 cm, while the lowest distribution of disc width was at 351-400 cm with a mode of 375 cm



for subadult group (Fig.3).

Fig. 3. Disc width distribution of males and females for Giant oceanic manta ray (*Manta birostris*)

The relationship between disc width and clasper length of *Manta birostris* is showed in Fig.4. The figure shows that the disc width and clasper length relationship of *Manta birostris* was sigmoid. It means that the increase of total disc width was followed by the increase of clasper length until it reaches its maximum length. There are

three stages in the size of clasper development, according to the calcification process of the claspers, i.e. non-calcified = NC, non-fully calcified = NFC, and fully calcified = FC. The NC category was found in sizes between 207.6 and 271.6 cm with the clasper length between 3.4 and 4.7 cm; NFC was at a size ranging between 270.4 and 371.5 cm with the clasper length between 4.6 and 7.1 cm; and FC was between 370.2 and 461.4 cm with the clasper length between 7.5 and 12.5 cm, respectively.

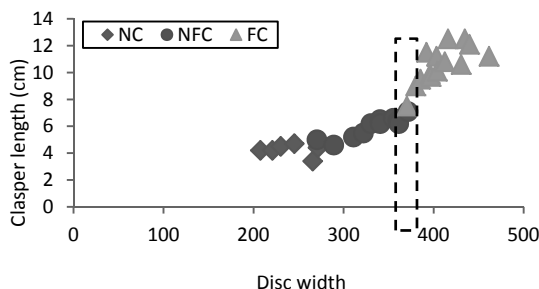


Fig. 4. Relationship between disc width and clasper length of Giant oceanic manta ray (*M. birostris*)

Sex ratio

The sex ratio between male and female of *Manta birostris* caught in the Indian Ocean from 2001-2005 was not significantly different from 1:1 ($p > 0,05$; Chi-square value = 0,012, degree of freedom = 1)

Catch Fluctuations

Catch fluctuations of giant oceanic manta ray (*Manta birostris*) from 2006 to 2011 are showed in Fig. 5.

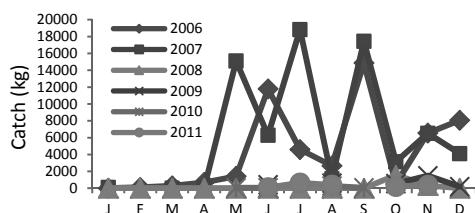


Fig. 5. Monthly catch fluctuation of *Manta birostris* caught by tuna drift gillnet from 2006-2011

Tabel 2. Annual production of *M. birostris*

	2006	2007	2008	2009	2010	2011
Production (kg)	51,470	82,610	42,926	3,242	411	1,703

Figure 5 shows that the catch fluctuations of *Manta birostris* caught in the Indian Ocean were relatively similar in six-year period between 2006-2011. The low catches occurred in January-April and rose in May-June, peaking in September and then decreasing significantly in August and October each year.

Fisheries

Manta birostris are commonly caught by tuna gillnet and tuna longline fisheries. The length of the gillnets used by fishers at Cilacap-Central Java ranged from 1200 to 3000 m and have stretched-mesh sizes of 10 to 14 cm. This fishing gear is set in offshore areas. Each fishing trip lasts for 15 to 25 days, depending on weather conditions and the size of catch. In some cases, for instance in Tanjungluar-East Lombok, gillnets are used in the first few days of a trip to catch pelagic fishes such as little tuna and skipjack tuna, which are then used as bait on longlines targeting large sharks. The fishing grounds of these fishers are usually within a day's travel from the landing sites.

The manta rays are utilised for their gill plates, meat, cartilage and skin. The increasing demand for the branchial filter plates of *Manta* spp. to be used in traditional Chinese medicines in Asia in the last decade has led to the increase of landings of these large rays in Indonesia.

The high value of branchial filter plates has also resulted in shifting the target from catching whales to catching *Manta* by fishers at the village of Lamakera in Eastern Indonesia (Dewar, 2002). The most abundant mobulid species caught by those fishers was *M. birostris*, followed by *Mobula tarapacana* and *Mobula thurstoni*.

The difference in catch composition between Lamakera fishery and those in the sites surveyed in this study is probably due to the differences in fishing methods. Fishers at Lamakera are using harpoons to catch rays close to the water surface, whereas gillnet fishers can also catch rays below the surface. Thus, *M. birostris* may occupy surface waters more than the other Mobulid species. On the other hand, fishers may select larger individuals to harpoon. Dewar (2002) reported that the annual catch of manta rays at Lamakera was estimated to be 1,500 individuals, which was similar to the estimated number of mobulid rays landed as bycatch annually at Tanjung Luar (White et al., 2006). Mobulids are also landed in the Manado region of North Sulawesi, where large trap nets are set in migratory channel of pelagic fishes and marine mammals in the Tangkoko Nature Reserve (Anon, 1997). The catches from these nets occurred between March 1996 and February 1997 and were reported to include 1,424 individual manta rays.

There is a lack of information on *Manta* spp. populations, and consequently it is very difficult to determine how the level of exploitation of this species in Indonesia may have affected their stocks. *Manta* spp are highly susceptible to fishing pressure due to their slow growth, late age at maturity and low fecundity. *Manta birostris* appear to be particularly susceptible to overfishing as their fecundity is the lowest of all elasmobranchs, i.e. their litter size is typically only one, and the gestation period is assumed to be between 1 and 3 years (Compagno and Last, 1999; Homma et al., 1999).

Conservation Status

Population sizes of *Manta birostris* are unknown, because until recently there is no study related to the population of this species in Indonesia. The biology characteristics of *Manta birostris* is slow reproductive rate, so that they are very vulnerable to overfishing. However, it has not yet been demonstrated that commercial harvesting is a major threat at this time. The International Union for Conservation of Nature (IUCN) lists this species as "Data Deficient," meaning it does not have enough information to assess its conservation status. However, IUCN declared giant manta rays as 'vulnerable with an elevated risk of extinction', meaning that manta rays could be threatened with extinction in the near future if conservation efforts are not implemented.

Intense fishing pressures and growing international consumer demand have caused manta ray (including *Manta birostris*) populations to decline by 30 percent worldwide, with some regions experiencing an 80 percent decline over the last 75 years. Data on the population trends and ecology are vital for effective conservation management plans. Knowledge about the characteristics of the specific sites that manta rays generally frequent may help to predict where aggregations might occur, which in turn may feed into management to regulate fishing and eco-tourism in these regions, or creation of sanctuaries for this species if deemed appropriate. In order to efficiently protect these gentle giant populations and their habitats, further data on their biology, ecology and behaviour are needed (Marshall and Bennett, 2010).

DISCUSSION

The Giant Manta Ray reaches disc width (DW) of at least 700 cm, with anecdotal reports up of to 910 cm DW (Compagno 1999, Alava et al., 2002). Size at maturity for the Giant Manta Ray may vary slightly throughout its geographical range, but males in southern Mozambique become mature at approximately 400 cm DW, while females appear to mature well over 400 cm DW (Marshall 2009). Last & Stevens (2009) reported that mature males and females of *M. birostris* found in the waters of Australia at a size of 375 cm DW and 380-410 cm DW, respectively. In this study, males and females of *Manta birostris* were found at a size of between 401-500 cm, and this group size was the most commonly caught. The size of this species was similar to those reported by Ebert and Stehmann (2013), where mature females and males found in the North Atlantic waters were at disc widths of 400 to 450 cm and 350 to 400 cm, respectively. Thus based on the results of this study, it can be said that most *Manta birostris* caught from the Indian Ocean in the years 2001-2005 were at mature stage.

In order to determine the growth parameters of a fish, one must look at body length frequency distributions (Sparre and Venema, 1992). This condition is also applicable to the Giant oceanic manta ray. In Indonesian waters, the giant oceanic manta rays are often caught by tuna drift gill nets. They easily get caught due to their large size, as they get entangled in nets. In general, the fishers operating in the Indian Ocean used fish nets with mesh sizes of 5 inches with targeting mainly skipjack tuna.

According to the development of the disc width, there was transition size at the clasper maturity stage. The transition size was related to a condition occurring when claspers were mature but not yet ready to reproduce until reaching full maturation (stage 3-4) at a size of between 361-385 cm disc width. The relationship between clasper length and body size is usually used to determine the size at which fish reach maturity in male genitals (Steven and McLoughlin, 1991). Grogan and Lund in Carrier et al.(2004) mentioned that the development of claspers in elasmobranchii is possibly due to the coordination of the development of the

necessary muscles to pump sperm and move the clasper. Although both the right and left claspers function in reproduction, only one is inserted into the cloaca of the female during copulation.

Comparative information on sex ratio in fish is needed to understand population development. Comparison of sex ratio is a very important aspect for the ability of individuals in the process of recruitment in the population (Anon., 2009). The recruitment process of a species will be successful if the ratio of males to females is in balance within a population (Sparre and Venema, 1992). This suggests that the sex ratio of *Manta birostris* was balanced during the research period. This situation can be caused by intrinsic factors, i.e. the male and female sex ratio at birth. The proportion of male to female at birth can be an important indicator in the process of reproduction of a fish population (Anon., 2005). Furthermore, Brykov et al., (2008) mentioned that the sex ratio is related to the amount of fish produced in the next generation and acts as a control on population size. While extrinsic factors such as fishing pressure, can lead to male and female population distribution becoming unequal. The imbalance in the number of male and female populations will result in the disruption of the recruitment process. The recruitment process of a species may also be influenced by water quality, availability of brood stock and the presence of prey (Dharmadi et al., 2013). In addition, differences in fishing techniques and fishing gear selection may also influence the sex ratio differences in the species caught. Up to present, there is no information about relationship between fishing methods and the ecology of Manta ray in Indian Ocean.

Fluctuations of Manta catches in the Indian Ocean waters were related to the frequency of fishing activities by fishers, and the number of fishing vessels used. Besides this, the catch are also affected by fishing techniques, fishing areas, and the weather conditions at sea. From January to April, the weather conditions at sea usually have strong winds and large waves, so fishers do not go to the sea as frequently. Therefore, there are not many *Manta birostris* landed in that period. However, from May to September, many fishers go to the sea because the weather conditions are favorable for them to operate fishing gear. This results in relatively high catches. The production of *Manta birostris* caught in the Indian Ocean decreased by 30.2% from 2006 to 2011 (Table 2). The significant decline in the annual catch of this species has given rise for concerns about the possibility of being driven to extinction. *Manta birostris* is known to occur in tropical tuna purse seine, longline and gillnet fisheries (White, Giles and Potter, 2006; Poisson et al., 2012). However, the relative importance of incidental catch in these fisheries compared with direct takes is still unknown.

CONCLUSIONS

Most *Manta birostris* caught in the Indian Ocean and landed at Cilacap and Tanjungluar were categorized as mature. However, the 30% decrease in catches of *Manta birostris* for the last six years indicates that the abundance of this species in the Indian Ocean has declined. Therefore, good management to control the catch of manta rays in the region should be implemented, and awareness of sustainable fisheries should be raised in order to maintain a viable population of manta rays in the Indian Ocean into the future.

ACKNOWLEDGEMENTS

Thanks are expressed to William White, as a counter part of the project, and also to Joko Riyanto for his invaluable assistance throughout the whole study. The project was funded by the Australian Center for Agriculture Research (ACIAR).

REFERENCES

- Alava, M.N.R., Dolumbaló, E.R.Z., Yaptinchay, A.A. and Trono, R.B. (2002). Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. Pp. 132-148. In: S.L. Fowler, T.M. Reed and F.A. Dipper (eds). Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop. Sabah, Malaysia, July 1997. Occasional paper of the IUCN Species Survival Commission No. 25.
- Anon. (2005). Prelude to intersex in fish. Identifying sensitive period for feminization. Environmental Health Perspective. Vol.113, No.10, October 2005. ehp.niehs.nih.gov/docs/2005/113-10/EHP113pa686PDF.PDF. [on line]. (Cited 2 February 2013).
- Anon., (2009). Male-biased sex ratio of fish embryos near a pulp mill : temporary recovery after a short-term shutdown (Research Article). www.encyclopedia.com, [online]. (Cited 25 April 2009).
- Anon, (1997). Fisheries Conservation Crisis in Indonesia: massive destruction of marine mammals, sea turtles and fish reported from trap nets in pelagic migratory channel. URL: <http://darwin.bio.uci.edu/~sustain/bio65/indonesia/indon97e.htm>. [online]. (Cited 1 January 2013).

- Anon (2012). Capture Fisheries Statistics of Indonesia. Ministry of Marine Affairs and Fisheries, Directorate General of Capture Fisheries. Vol.12, No.1. 134 p.
- Bucyznski, B., (2011). Giant Manta Ray Earns Protection Under International Treaty. Wikipedia, the free encyclopedia, [online]. (Cited 1 March 2013).
- Carrier, J. C., J. A. Musick, and M. R. Herthaus. (2004). *Biology of Sharks and their relatives*. Textbook. CRC Press. Washington D. C. 596 p.
- Compagno, L.J.V. (1999). Systematics and body form. Pp 1-42. In: W.C. Hamlett (ed.), *Sharks, Skates, and Rays: the Biology of Elasmobranch Fishes*. John Hopkins University Press, Baltimore.
- Dewar, H. (2002). Preliminary report: Manta harvest in Lamakera. Report from the Pflieger Institute of Environmental Research and the Nature Conservancy.
- Dewar H, Mous P, Domeier M, Muljadi A, Pet J, Whitty J. (2008). Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. *Mar Biol* 155:121–133.
- Dharmadi, Fahmi, & N.N. Wiadnyana (2013). Biological Aspects and Catch Fluctuation of Pelagic Thresher Shark, *Alopias pelagicus* from Indian Ocean. Paper presented in International workshop. Proceedings. The Design Symposium on Conservation of Ecosystem (SEASTAR2000). Kyoto University Design School. P. 77-85.
- Ebert, D.A and M.F.W. Stehmann (2013). Sharks, Batoids and Chimaeras of the North Atlantic. FAO Species Catalogue for Fishing Purpose. No.7. ISSN 1020-0682. 537 p.
- FAO (2013a). Report of the fourth fao expert advisory panel for the assessment of proposals to amend appendices I and II of cites concerning commercially-exploited aquatic species. Rome, 3–8 December 2012. FAO Fisheries and Aquaculture Report No. 1032 FIR/R1032 (En). ISSN 2070-6987. 168 p.
- FAO, (2013b). Convention on International trade in endangered species of wild fauna and flora. Sixteenth meeting of the Conference of the Parties. Bangkok (Thailand), 3 - 15 March 2013.
- Heinrichs, S., O'Malley, M., Medd, H. and Hilton, P. (2011). Manta Ray of Hope: global threat to manta and mobula rays. In: Manta Ray of Hope Project [online]. [Cited 13 March 2013]. www.mantarayofhope.com.
- <https://sites.google.com/site/projectmantasite/home/get.../reproduction>, (online). (Cited 12 March 2013)
- Last, P., and D. Stevens. (2009). *Sharks and Rays of Australia*. Second edition. SCIRO Publishing. 644 p.
- Lewis, S, (2011). Indonesia Manta Ray Project. Conservation through Research, Awareness and Education. Manta Trust. UK Registered Charity Number: 1145387
- Marshall, A.D. 2009. Biology and population ecology of *Manta birostris* in southern Mozambique. Ph.D Thesis, School of Biomedical Science, University of Queensland, Brisbane.
- Marshall, A.D., Bennett, M.B. (2010). Reproductive Ecology of the reef manta ray (*Manta alfredi*) in southern Mozambique. *Journal of Fish Biology* 77: 169-190.
- Marshall, A., Bennett, M.B., Kodja, G., Hinojosa-Alvarez, S., Galvan-Magana, F., Harding, M., Stevens, G. & Kashiwagi, T. (2011). *Manta birostris*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2 [online]. [Cited 13 March 2013]. www.iucnredlist.org.
- Martin, LK & Coilliet, GM. (1988). Aspects of the reproduction of the bat ray, *Myliobatis californica*, in Central California. *Copeia*, 1988 : 754-762.
- Mohanraj, G., Rajapackiam, S., Moha, S., Batch, H. and Gomathy, S. (2009). Status of elasmobranchs fishery in Chennai, India. *Asian Fisheries Science*, 22: 607–615.
- NOAA (2013). Recruitment process program. Alaska Fisheries Science Center. [online] [Cited 25 February 2013]. www.afsc.noaa.gov/RACE/recruitment.
- Sparre and Venema, (1992). Introduction to tropical fish stock assessment. Part 2. Exercises. FAO Fisheries Technical Paper. No. 306.2, Rev. 2.
- Stevens and McLoughlin, (1991). Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. *Australian Journal of Marine and Freshwater Research* 42: 151–199.
- Stevens, J.D., Bonfil, R., Dulvy, N.K., Walker, P.A., (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J. Mar. Sci.* 57, 476–494.

White, W.T., J. Giles, Dharmadi and I.C. Potter. (2006). Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. *Fisheries Research* 82, 65–73.

White, W.T. and Dharmadi. (2007). Species and size compositions and reproductive biology of rays (Chondrichthyes, Batoidea) caught in target and non-target fisheries in eastern Indonesia. The Fisheries Society of the British Isles. *Journal of Fish Biology* 70, 1809–1837.