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Overfished and under conserved: life-history, ecology and supply chain of the Endangered whitespotted whipray (*Maculabatis gerrardi*) and sharpnose whipray (*Maculabatis macrura*) from south-east Asia

N. Clark-Shen[A,B,*], A. Chin[C,D], C. Gan[B], K. Xu-Ting Ting[E], C. Terence[A], J. Ng Zheng Kai[A], D. Wee[A] and N. Hutchinson[F]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
N. Clark-Shen
Tropical Future Institute, James Cook University, Singapore 387380, Singapore
Email: naomi.clarkshen@my.jcu.edu.au

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ABSTRACT

Context. The whitespotted whipray (*Maculabatis gerrardi*) and sharpnose whipray (*Maculabatis macrura*) are caught and traded in large volumes in south-east Asia and listed as Endangered by the IUCN. **Aims.** This study aimed to provide insights to their biology, ecology, fisheries, and markets. **Methods.** A total of 95 specimens from the species complex (*M. gerrardi* = 45, *M. macrura* = 40, and undetermined = 10) caught from Indonesia and Malaysia were examined, and an interview with a Singaporean seafood supplier was conducted. **Key results.** For *M. gerrardi*, the youngest mature male was 4 years old with 50% reaching maturity at 5.07 years, and the youngest mature female was 4 years old with 50% reaching maturity at 6.96 years. For *M. macrura*, the youngest mature male was 4 years old with 50% reaching maturity at 6.36 years, and the youngest mature female was 6 years old with 50% reaching maturity at 6.00 years, but with low sample size. The oldest specimen in the sample was 15 years old. *Maculabatis* spp. show asynchronous breeding with a littler size of one to five. There was no significant difference in the diets of both species, with *Decapoda* the dominant prey. The seafood supplier revealed that *Maculabatis* spp. are targeted by fisheries, and he perceives large declines in their population since he started in the business. **Conclusions and implications.** Considering the challenges distinguishing between the two cryptic species, life-history parameters that capture this species-complex as whole may be a more practical approach to management and are presented.

Keywords: age and growth, diet, elasmobranch, fishery, Indonesia, life-history, Singapore, stingray.

Introduction

Stingrays (Dasyitidae) are a diverse group of elasmobranchs (sharks, rays, skates, and sawfish) with many species filling the role of mesopredators (mid-ranking predators) in ecosystems (Ajemian *et al.* 2012; O'Shea *et al.* 2013). In this role, stingrays facilitate energy flows from benthic prey to mid-level and top-level predators, but also act as 'bioturbators' (i.e. disturbing sediments) playing a vital functional role in relation to nutrient dynamics in marine sediments (Flowers *et al.* 2021; Crook *et al.* 2022). Stingrays are also valuable to people through tourism, food, and trade (Haas *et al.* 2017; SEAFDEC 2017; Sahubawa and Pertiwiningrum 2020), yet despite these values and high exploitation, have received comparatively little conservation attention (SEAFDEC 2017; Dulvy *et al.* 2021).

South-east Asia is a region of particular conservation concern for rays, with 69.3% considered threatened with extinction compared to 51.3% of sharks (Clark-Shen *et al.* 2022). One genus of rays that are imperilled in south-east Asia are the *Maculabatis,* which includes the whitespotted whipray (*Maculabatis gerrardi*) and sharpnose whipray (*Maculabatis macrura*). These two cryptic species are targeted and caught as bycatch throughout their coastal habitats (SEAFDEC 2017; Sherman *et al.* 2020*a*, 2020*b*), and are threatened by poor fisheries management in general (Pomeroy *et al.* 2016; Clark-Shen *et al.* 2022). Both species are classified as Endangered by the International Union for Conservation of Nature (IUCN), with suspected population reductions of 50–79% over the past 75 years (Sherman *et al.* 2020*a*, 2020*b*). In Singapore, where this study was based, *Maculabatis* spp. are a preferred species for the local delicacy 'BBQ stingray' or 'ikan pari bakar' (Bahasa Melayu) and are imported to the country in high volumes from Indonesia and Malaysia (Clark-Shen *et al.* 2021).

Both *M. gerrardi* and *M. macrura* are widely distributed, the former extending from Oman to Taiwan, and the latter from Indonesia to the north-west Pacific (Last *et al.* 2016*a*). *M. gerrardi* reaches 116 cm disc width (DW), with males maturing at 48–58 cm DW and females at 62 cm DW (White 2007*a*; Last *et al.* 2016*a*, 2016*b*; Sherman *et al.* 2020*b*). *M. macrura* reaches at least 85 cm DW, with males maturing between 46–48 cm DW and females at 64 cm DW (Last *et al.* 2016*a*; Sherman *et al.* 2020*a*). However, detailed age and growth, reproductive, and diet data for both species are lacking. Insights into a species' ecology (i.e. diet), and life-history are fundamental to science-based management and conservation plans (Simpfendorfer *et al.* 2001; Harry *et al.* 2013; Fahmi *et al.* 2021). For example, some elasmobranchs show dietary shifts between age groups (Bornatowksi *et al.* 2014), and the sexes (Ba *et al.* 2013; Costa *et al.* 2015), highlighting the habitats in which they live (Simpfendorfer *et al.* 2001), and the type of prey that need to be protected to sustain different segments of the populations (Chiaradia *et al.* 2010). Life-history analysis such as age-growth reveals a species' intrinsic vulnerability: species that mature quickly, reproduce early, and have more young are better able to withstand exploitation and rebound than those that mature slowly, reproduce late and have few young (Hutchings 2002; García *et al.* 2008). To complement ecological and biological findings, leveraging Local Ecological Knowledge (LEK) by interviewing stakeholders in the industry can give insights to a species' fishery, population trends, supply chain, and potential management solutions (Acebes and Tull 2016; Ahmad *et al.* 2018). By documenting their life-history (age-growth, fecundity), ecology (diet), and collecting preliminary data on fisheries and supply chains, this research aimed to improve understanding of the *Maculabatis* genus from Indonesia and Malaysia and identify and potential conservation approaches.

Materials and methods

Sourcing animals and collecting biological data

Seventy four *Maculabatis* spp. (animals matching the description of both *Maculabatis gerrardi* and *Maculabatis macrura*; the only two species within the genus in Indonesia and Malaysia with distinctive white spots on their dorsal disc, pelvic fins and tail (Last *et al.* 2016*a*)), were sourced from a private seafood supplier in Singapore between February 2022 and April 2023. An additional 19 whole animals were sourced from Jurong Fishery Port in Singapore during this time, increasing the total sample size to 93 animals. Animal ethics approval was not necessary as animals were sourced following mortality from commercial fishing gear. For each animal, the import and/or catch location, as well as details of the fishing gear used in their capture were attained from the seafood supplier where possible. Each animal was photographed, sexed, weighed, and their disc width (DW), total length (TL), internasal width, head length, and tail length taken to the nearest mm as described by Last *et al.* (2016*a*). Animals were then assigned as either *M. gerrardi* or *M. macrura* according to morphological traits (see below) and dissected, and maturity was assessed according to gonad stage (Table 1). The liver, stomach, and a section of thoracic vertebrae were removed and stored frozen until further processing. Two additional vertebrae were also obtained directly from merchants processing large rays at Jurong Fishery Port in March and June 2023. These animals were not collected but their DW, sex and gonad stage was recorded. To supplement data on reproduction, data on gravid females encountered during routine surveys at Jurong fishery port in Singapore were collected; including the size of the mother and the number of embryos (determined by removing embryos through the cloaca).

Determining species

Morphology was used to determine whether animals were *M. gerrardi* or *M. macrura*. The morphological characteristics used to distinguish between these two species, per Last *et al.* (2016*a*), were ratios of: (1) total length to disc width; (2) internasal width to disc width; (3) head length to disc width; and (4) tail length to disc width (see Supplementary Material S1), although this last measurement is considered least reliable as some animals have cut or amputated tails, either by fishers, traders, or predators. Therefore, if animals matched at least two of the first three criteria for a particular species, they were assigned as that species. If animals matched one or fewer, they were not assigned a species but remained 'undetermined species of *Maculabatis* spp.' In the context of this study, 'undetermined species' refers to animals that could be either *M. gerrardi* or *M. macrura*; not the other species in the *Maculabatis* complex.

Stomach content analysis

Stomachs were excised and prey identified to the lowest taxonomic level possible (species, genus, family, or above). Contents suspected to be bait (e.g. portions with straight-edged cuts, attached to hooks) as well as sand/mud or rock (which are not prey but likely incidentally ingested) were excluded from further analysis (Jabado *et al.* 2015). Although some studies exclude indigestible parts from such analysis (e.g. shells, otoliths, and cephalopod beaks) (Potier *et al.* 2007; Bornatowski *et al.* 2014; Dicken *et al.* 2017), as they are not considered nutritionally valuable, they were included in this study as they were often the only identifiable parts of prey (Buckland *et al.* 2017). The percent frequency of occurrence

Table 1. Reproductive indices used to determine maturity stage.

Organ	Index	Description	Binary maturity condition
Female uterus	U = 1	Uteri uniformly thin and white tubular structure. Small ovaries and with no yolked ova	Immature
	U = 2	Uterus thin, tubular structure that is partly enlarged posteriorly. Small yolked ova developing in ovary	Immature
	U = 3	Uterus uniformly enlarged tubular structure. Yolked ova developing in ovary	Mature
	U = 4	Uterus enlarged with *in utero* eggs or embryos microscopically visible – pregnant	Mature
	U = 5	Uterus enlarged, flaccid and distended tubular structure – postpartum	Mature
Male clasper	C = 1	Pliable with no calcification	Immature
	C = 2	Partly calcified	Immature
	C = 3	Rigid and fully calcified	Mature

Adapted from Walker (2005).

(%FO), which is the proportion of individuals with a particular prey item, was calculated. To examine similarity and differences in diet between species, maturity, and sex, stomach contents were analysed using the Bray-Curtis coefficient (20 stress runs) and ADONIS (significance $P < 0.05$) were performed using the Vegan package (version 2.6-4, J. Oksanen *et al.*, see https://CRAN.R-project.org/package=vegan) on R-studio (ver. 1.2.5042). The software package PRIMER v6 (Clarke and Gorley 2006) was used to analyse similarity percentages (SIMPER) to examine where specific differences occurred.

Vertebral processing and age and growth validation

Vertebrae were sectioned and processed using methods described in Goldman (2005); tissue from vertebrae was removed with a scalpel, and five centra were sectioned, soaked in 5% sodium hypochlorite solution for up to 2 min (to remove remaining tissue), and then thoroughly rinsed with water and dried in an oven at 45–60°C until dry. The two largest centra were chosen and attached to a microscope slide with crystal bond adhesive glue and a heat pad set at 250°C. The centra were then sanded down using fine grain sandpaper (grit size 400CW) submerged in fresh water, until the middle of the centra was reached. The centra were then unglued from the microscope slide, reversed and re-attached, and the other side of the centra sanded down until a ~600-µm section at the middle of the centra remained. The centra were then examined and photographed under a dissecting microscope, and translucent and opaque bands (band pairs) were counted from the birthmark (Fig. 1); identified by a change in the angle of the corpus calcareum (age 0) (Caillet 2015). Annual deposition of band pairs was assumed, based on validation in other tropical whiptail stingrays (Jacobsen and Bennett 2010) and this species

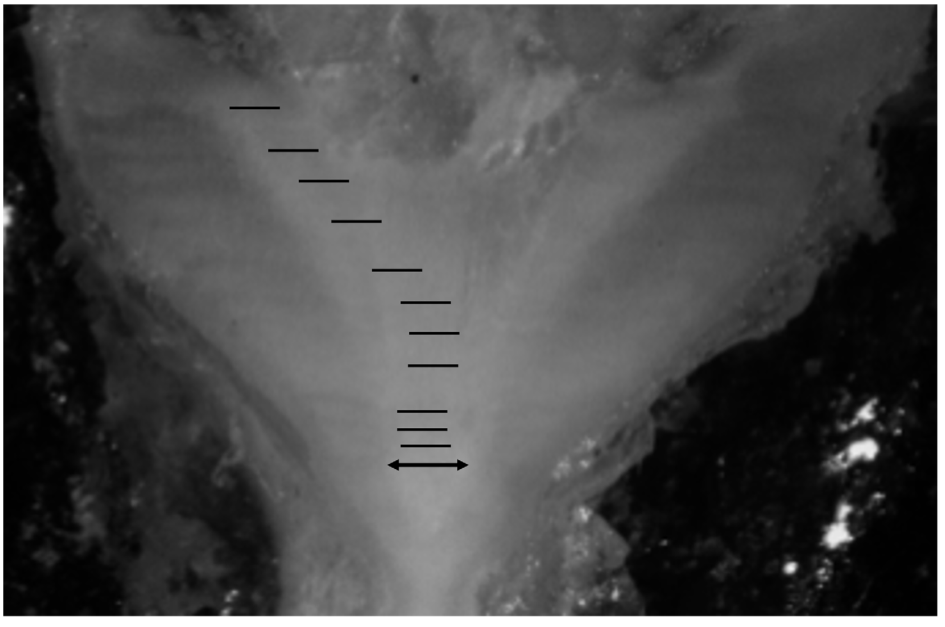

Fig. 1. Vertebral section from a 11-year-old female Maculabatis spp. measuring 786 mm DW.

living in a constant tropical environment with multi-annual depositions typically attributed to seasonal temperature changes (Smith 2013). Microsoft Powerpoint was used to adjust the saturation of vertebrae images to digitally resolve band pairs, and two readers determined age independently. A third independent reader helped to address discrepancies in the counts of band-pairs between the two initial readers. Each vertebra was also scored according to its readability: 0 = unreadable; 1 = bands visible but difficult to interpret; 2 = bands visible but most bands difficult to interpret; 3 = bands visible but a minority difficult to interpret; and 4 = all bands unambiguous (McAuley *et al.* 2006). Vertebrae with un-interpretable band counts were excluded from further analysis. The von Bertalanffy growth function (VBGF); (von Bertalanffy 1938), the logistic function, and the Gompertz function (Ratowsky 1990) were used to estimate growth parameters with growth curves generated in R-studio.

Interview about the fishery and species

We interviewed a private Singapore-based supplier of 74 of the stingrays through a semi-structured interview about the supply chain and perception of changes in the fishery over time (Supplementary Material S2). The interview was conducted in English, following human ethics guidelines, with no remuneration. Questions focused on: (1) the fisheries harvesting these rays; (2) trends in species harvested; (3) the supply chain; (4) the market; and (5) perceptions regarding future management. Questions were open-ended to encourage the supplier to express their own opinions. This research was undertaken with informed consent of those being interviewed under human ethics application H8683 as well as WWF's safeguards for engaging with stakeholders (WWF ESSF 2023).

Results

Species composition

Of the 95 *Maculabatis* spp. in the sample, five were caught in Malaysia and 90 were caught in Indonesia. Eighty five individuals could be identified to species, with the majority of animals identified as the whitespotted whipray (*M. gerrardi*, n = 45 [20 females, 25 males]), followed by the sharpnose whipray (*M. macrura*, n = 40 [19 females, 21 males]), and the remainder could not be determined (*Maculabatis* spp. n = 10 [4 females, 6 males]). Overall, there were more immature (n = 57) than mature (n = 38) individuals in the sample. The size-frequency distribution (Fig. 2) shows that the majority of the sample was dominated by individuals under 700 mm DW (mean DW = 520 mm).

Diet analysis

Of the total sample size (n = 95), the stomachs of two individuals were not retrieved, and 12 had empty stomachs, leaving 81 individuals for further dietary analysis. Based on %FO, crustaceans are the most important prey item for *Maculabatis* spp (Fig. 3). ADONIS revealed no significant difference in proportions of broad prey groups between sex (P = 0.27) or between species (P = 0.93). However, when analysing all *Maculabatis* spp. together, ADONIS revealed significant differences in the diet of mature and immature individuals (P = 0.002). SIMPER revealed that this difference arose from mature individuals consuming significantly more gastropods (P = 0.001) and fish (P = 0.008) compared to immature individuals, which consumed more crustaceans although the latter was not significant (P = 0.18). A more detailed breakdown of diet can be found in Supplementary Material S3.

Maturity and age-growth analysis

Males matured at smaller sizes than females for both *M. gerrardi* and *M. macrura* (Table 2; Fig. 4). Males and females exhibit a similar length-weight relationship, although females in the sample obtained larger sizes and weights (Fig. 5). Of the total sample size (n = 95) the vertebrae of 89 individuals (94%) yielded readable age bands. The oldest agreed age (between the readers) from the study for this species was 15 years old for female undetermined species of *Maculabatis* spp. (960 mm DW) and a male *M. gerrardi* (725 mm DW).

MCMC analysis (Supplementary Material S4) revealed that out of several potential growth models, the Logistic model was best when analysing *M. gerrardi* alone (k-value = 0.65 per year); the Von Bertalanfy was best when analysing *M. macrura* alone (k-value = 0.18 per year); and the Gompertz model was best performing when analysing all *Maculabatis* spp. together (k-value = 0.3 per year; Fig. 6). When analysing *M. gerrardi* alone, males and females had the same growth rate (k = 0.6 per year; Table 2), but males matured earlier (50% age-at-maturity = 5.07; Table 2) than females (50% age-at-maturity = 6.96; Table 2). When analysing *M. macrura* alone, males grew faster than females (k = 0.58 per year vs k = 0.17 per year; Table 2), but males matured later than females (50% age-at-maturity = 6.36 vs 50% age-at-maturity = 6.00; Table 2). When analysing all *Maculabatis* spp. together, males grew faster and matured earlier (k-value = 0.48 per year, 50% age-at-maturity = 5.88; Fig. 7; Table 2) than females (k-value = 0.1 per year, 50% age-at-maturity = 7.00; Fig. 7; Table 2). Fig. 8 visualises each individual's disc width, age, and maturity.

Reproductive analysis

There were two gravid females in this study. One was an *M. gerrardi* (11 years old, 680 mm DW), which carried two embryos in January (180 mm DW each; 26% the size of the mother). Considering the two embryos were well-developed at 180 mm DW, and the smallest ray provided from the fishery was 194 mm DW, this suggests length at birth likely

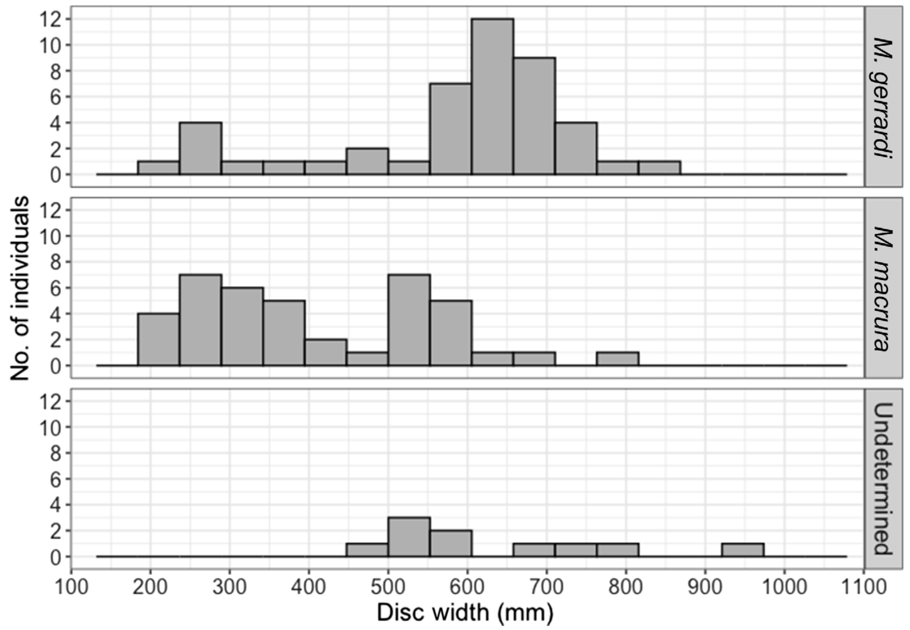

Fig. 2. Size-frequency distribution of the whitespotted whipray (*Maculabatis gerrardi*, *n* = 45), the sharpnose whipray (*Maculabatis macrura*, *n* = 40)), and Maculabatis spp. of undetermined species (*n* = 10) caught from fisheries in Indonesia (*n* = 89) and Malaysia (*n* = 5). The smallest individual was an *M. gerrardi* of 194 mm disc width (DW), and the largest individual was a *Maculabatis* spp. (undetermined species) of 960 mm disc width (DW). The entire sample had a mean size of 520 mm DW.

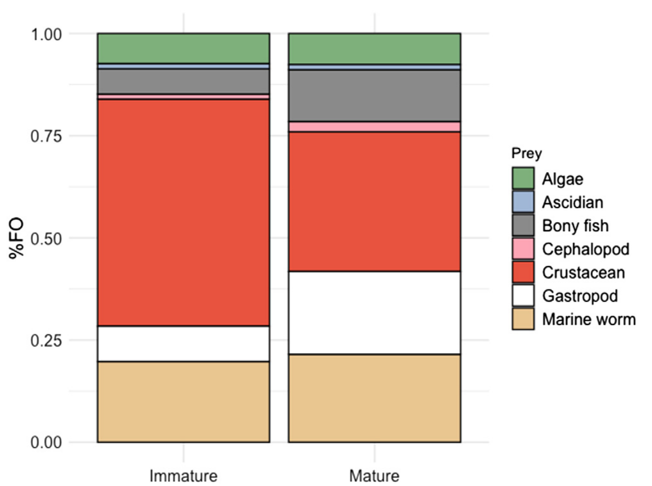

Fig. 3. Percent Frequency Occurance (%FO) of prey for 81 *Maculabatis* spp., including 42 whitespotted whipray (*Maculabatis gerrardi*), 32 sharpnose whipray (*Maculabatis macrura*), and seven undetermined species of Maculabatis spp. Analysis found no significant differences between the diets of *M. gerrardi* and *M. macrura*.

falls between 180 mm and 194 mm DW for this species. The second gravid female was an undetermined *Maculabatis* spp. (4 years old, 616 mm DW) at a very early stage (implanted egg) in June. Observed gravid females at Singapore's fishery ports (Table 3) reveal well-develop embryos in various months throughout the year. In addition, the nine mature *Maculabatis* spp. in this study for which ova diameter was recorded, showed various ovarian egg diameters across months. These observations suggest reproduction for these species is asynchronous (Fig. 8).

Interview with the supplier

The supplier has fished with their father since 7 years of age, and was involved in the seafood business since 16 years of age (~40+ years in this business).

The fishery and supply chain

The supplier's *Maculabatis* spp. are sourced from fisheries that use three primary methods: (1) rawai (bottom longline); (2) gillnets; and (3) 兄弟钩 in Mandarin/Hokien, which translates to 'brother hooks' (unbaited hooks are attached every inch along a straight line and dragged along the ocean floor). The latter are specifically for catching bottom-dwelling species and became widely used after the value of stingrays increased in the 1980s. Fishers know where to find *Maculabatis* spp., and animals are targeted, particularly *Maculabatis* spp. and *Himantura* spp. and other stingrays including *Pastinachus* spp. The bait used on longlines ranges from squid and herring (more costly) to various bycatch (a.k.a. 'trash') fish and eel flesh (less costly). Eel flesh is tough and stays on hooks for a long time. The longlines used to catch stingrays can range

Table 2. Summary of life-history results for *Maculabatis gerrardi*, *Maculabatis macrura*, and undetermined species of Maculabatis spp. which could be either of these two species.

Species	Males				Females			
	Smallest mature (mm DW)	Largest immature (mm DW)	50% age-at-maturity	*k*-value	Smallest mature (mm DW)	Largest immature (mm DW)	50% age-at-maturity	*k*-value
Maculabatis gerrardi	557	652	5.07	0.6 per year	592	673	6.96	0.6 per year
Maculabatis macrura	547	566	6.36	0.58 per year	593	616	6.00	0.17 per year
Maculabatis spp. (*M. gerrardi, M. macrura*, undetermined *Maculabatis* spp. combined)	547	652	5.88	0.48 per year	592	673	7.00	0.1 per year

The 50% age-at-maturity is based off the model of best fit (see Supplementary Material S4).

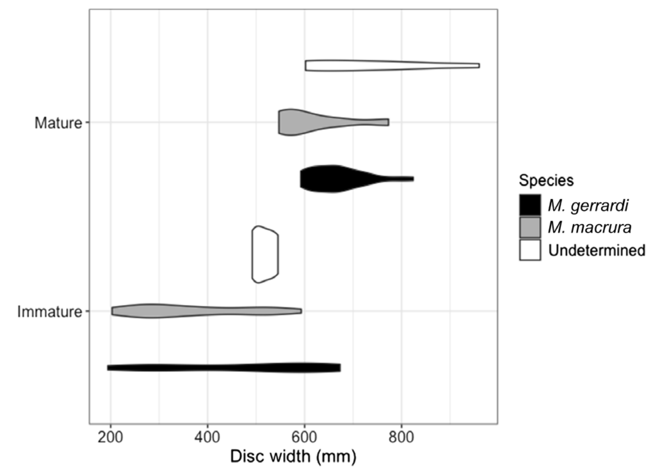

Fig. 4. Proportion by size range for immature and mature whitespotted whipray (*Maculabatis gerrardi*), sharpnose whipray (*Maculabatis macrura*), and undetermined species of Maculabatis spp.

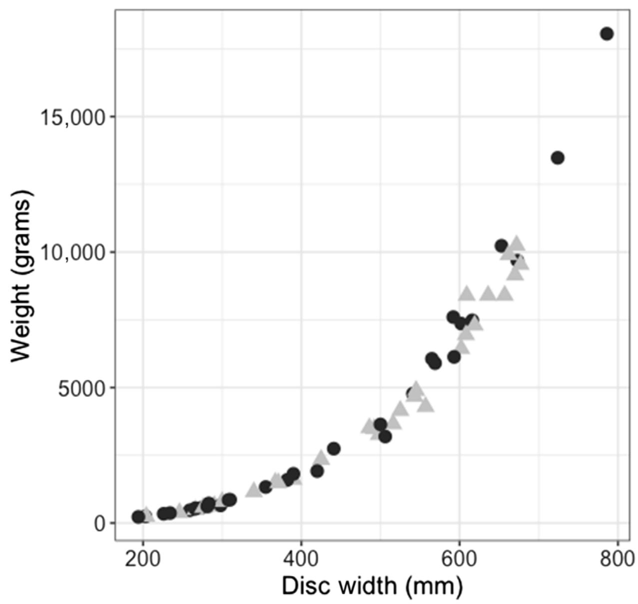

Fig. 5. Length-weight relationship for female (●, $n = 33$) and male (▲, $n = 30$) Maculabatis spp. for which weight was recorded.

in length from 200–300 m to 2–3 km. While many longline fisheries leave their gear out overnight, those targeting stingrays tend to check the gear more frequently (i.e. every 3–4 h) so the catch is fresher. Depending on when the stingray gets caught on the line, they may be dead or alive when hauled in. When stingrays are hooked and experience stress, sea lice (copepods) are attracted to them and parasitise them from the inside (copepods were observed on some dissected specimens in this study; on the liver and stomach). The supplier stated that no *Maculabatis* spp. are released as fishermen retain everything. There is no seasonality to catches of *Maculabatis* spp., ('the stingrays are always there'), but during the monsoon seasons boats do not go out as much.

The market for *Maculabatis* spp.

The market for stingrays in Singapore boomed in the 1980s. The main buyers of *Maculabatis* spp. are hawker centres (open-air complexes that house many food stalls) and wet markets (the latter of which eventually supply to hawker centres or sell direct to buyers to cook at home). At hawker centres, they are used for the local delicacy 'BBQ stingray' or 'Sambal stingray', known in Bahasa Malaysia as '*ikan pari bakar*'. *Maculabatis* spp. and *Himantura* spp. are a preferred species for this dish due to flesh quality and general availability. *Maculabatis* spp. and *Himantura* spp. have a high value, selling up to around SGD10 per kg (~USD7) wholesale and up to SGD18–20 per kg (USD13–14) retail. Smaller animals of these species (<6 kg) are preferred for BBQ/Sambal stingray, while larger specimens of these species are used for Asam Pedas (a Malay curry). Stingrays have become a mainstay for the supplier's business, accounting for 10–15% of business income.

Population trends and management

The supplier reports that *Maculabatis* spp. are primarily found on mudflats and have suffered a noticeable decline in a short

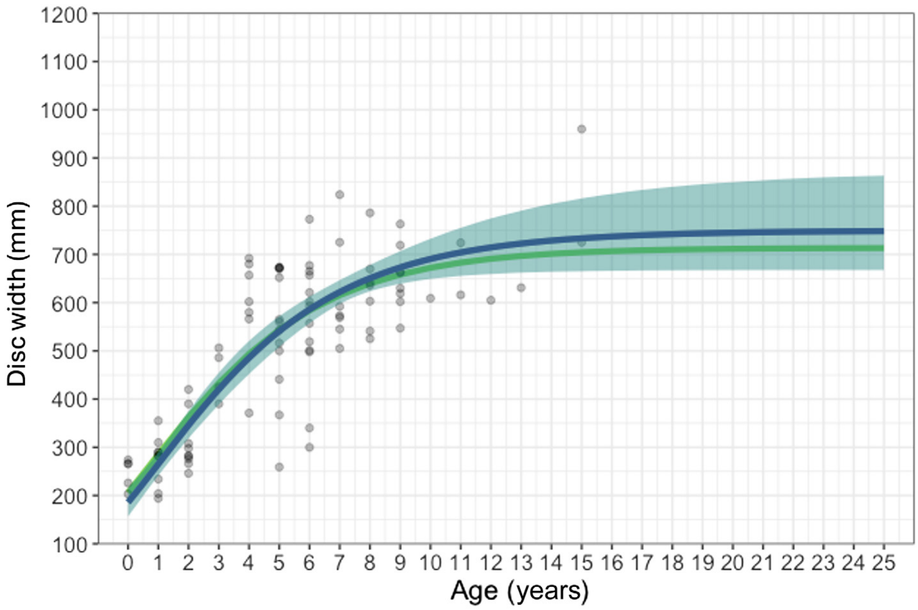

Fig. 6. Age-growth curve for 89 *Maculabatis* spp.: whitespotted whipray (*Maculabatis gerrardi*, *n* = 43), sharpnose whipray (*Maculabatis macrura*, *n* = 38), and undetermined species of *Maculabatis* spp. (*n* = 8) using vertebral band counts and the MCMC analysis performed using bayesian (blue line) and frequentist (green line) models. Circles (●) represent individual *Maculabatis* spp. with light shading indicating the 95% confidence intervals. A maximum age of 25 years was assumed for the genus.

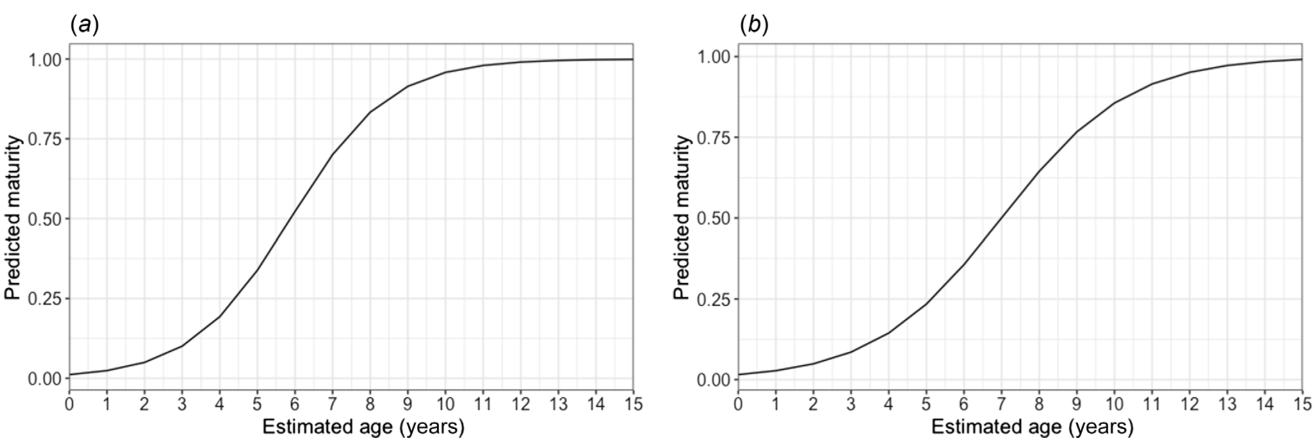

Fig. 7. Logistic generalised linear models (GLMs) of estimated ages of (*a*) male and (*b*) female *Maculabatis* spp. showing predictions of maturity at a given age. When all Maculabatis spp. are analysed together, the model predicts a 50% age-at-maturity of 5.88 years for males, and a 50% age-at-maturity of 7.00 years for females.

timespan (i.e. during their 45-years in this industry) although it was noted that *Himantura* spp. 'disappeared' before *Maculabatis* spp. did. The stage where it is no longer 'economical' to catch *Maculabatis* spp. is nearing (i.e. high effort to catch the animal, boats spending too long at sea, travelling farther). Fishermen source from all over the region: including from Banga Belitung to Kalimantan and even Papua; which now has cold rooms so rays can be stored and kept fresh until transfer. When/if *Maculabatis* spp. is no longer economical to catch, the supplier predicts that fishers will switch to alternative species such as *Neotrygon* spp. (which is less preferable and currently sells for less than *Maculabatis* spp. in Singapore). When asked 'what needed to be done to help [*Maculabatis* spp.],' the supplier replied 'a total fishing ban' but that this would be detrimental to fishers. While they acknowledged the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) would help *Maculabatis* spp., through trade regulation, they mentioned

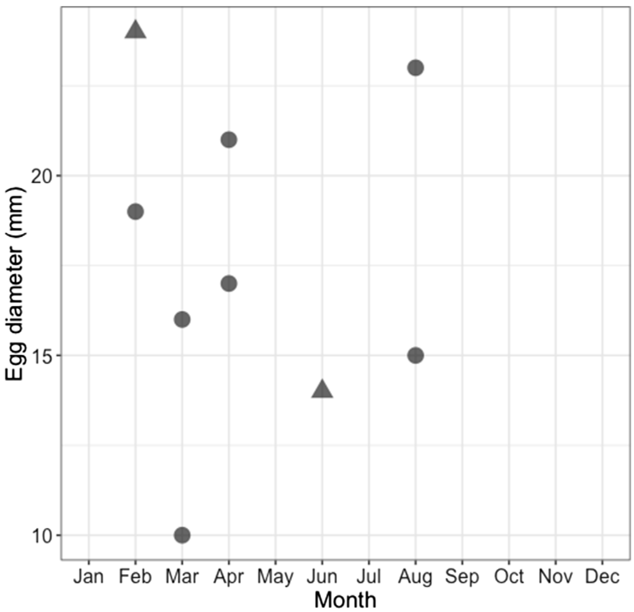

Fig. 8. Largest ovarian egg diameter by month for mature female (n = 9) Maculabatis spp. for which ova diameter was recorded, showing both gravid (▲) and non-gravid (●) females.

Table 3. Observations of gravid Maculabatis spp. during surveys of Jurong Fishery Port and Senoko Fishery Port in Singapore between 2017 and 2024.

Year	Month	Size of female (mm DW)	Number of embryos
2019	March	>800	3
2023	June	~600	2
2023	November	500–800	1
2024	January	600–700	5
2024	September	860	1
2024	October	~600	3
2024	November	~600	1

that the species is mainly traded between and consumed in Indonesia, Malaysia and Singapore, and so the trade may be too small-scale for CITES. The supplier also highlighted that any measure to protect *Maculabatis* spp. should apply to other stingrays, other marine animals (which are also in a terrible state), and the wider environment: 'we shouldn't play 'god' and protect some and not others . . . helping [*Maculabatis*] gerrardi is a starting point, but really everything needs help. Progress is too slow'. They believe only the younger generation will respond to a consumer campaign to stop eating stingray.

Discussion

This study found slight differences in life-history parameters compared to other studies. Previous research suggests that *M. gerrardi* males mature between 480 and 580 mm DW, and females at 630 mm DW (Last *et al.* 2016*a*, 2016*b*). However, our study found *M. gerrardi* matures at larger sizes, with males maturing between 557 and 652 mm DW, and females between 592 and 673 mm DW. Previous research suggests *M. macrura* males mature between 460 and 480 mm DW, and females at 640 mm DW (Last *et al.* 2016*a*). However, our study found *M. macrura* males maturing at larger sizes of between 547 and 566 mm DW, but females at smaller sizes from 616 mm DW.

Notably, for both *M. gerrardi* and *M. macrura*, previous research suggests males mature at smaller sizes (from 460 mm DW) than what our study found; the 11 males of similar size in our study (486–543 mm DW) were all immature. It may be that this previously published smaller size (460 mm DW) at maturity reflects fine-scale spatial variation in life history characteristics that has been widely recorded in chondrichthyans (e.g. grey sharpnose sharks, *Rhizoprionodon oligolinx*) in India (Purushottama *et al.* 2017)) vs Indonesia (White 2007*b*) or that attaining maturity by this size is possible, although rare. When considering results from this study, with results previously reported, it is apparent that *M. gerrardi* males may mature between 480 and 652 mm DW (from age 4 years in our study; 50% age-at-maturity = 5.07 years) and females between 592 and 673 mm DW (from age 4 years in our study; 50% age-at-maturity = 6.96 years), and *M. macrura* males mature between 460 and 566 mm DW (from age 4 years in our study; 50% age-at-maturity = 6.36 years) and females from 616 DW (from age 6 years in our study, with 50% age-at-maturity = 6 years). However, sample size (n = 2) for mature female *M. macrura* was very low and thus this latter finding is considered preliminary until further specimens can be analysed.

The oldest individual in this study was 15 years of age but this is not believed to represent the maximum age of the species. The sample was dominated by individuals under 700 mm DW (mean DW = 520 mm), which are on the smaller side considering *M. gerrardi* reaches 1160 mm DW and the *M. macrura* at least 850 mm DW. The Baraka's whipray (*Maculabatis ambigua*) from the Western Indian ocean is reported to reach ~900 mm DW and have a maximum age of 17 years (Temple *et al.* 2020) and the blackspotted whipray (*Maculabatis astra*) from Australia that reaches 920 mm DW, is reported to have a maximum age of 29 years and a generation length of 19 years (Jacobsen and Bennett 2011). Based on the latter a generation length of 19 years was estimated for the similarly sized *M. macrura*, and 25 years for the larger *M. gerrardi* (Sherman *et al.* 2020*a*, 2020*b*).

Despite exhibiting potential biological differences, *M. gerrardi* and *M. macrura* are morphologically similar. Given the taxonomic similarities between *M. gerrardi* and *M. macrura*, thus the difficulties in distinguishing the species, using age-growth parameters that reflect the life-history of both species combined (herein referred to as the 'species-complex') be a more practical approach to conservation and management. Using this approach of combining *M. gerrardi*, *M. macrura*, and undetermined species of *Maculabatis* spp., a conservative k-value of 0.1–0.6 for both sexes, with 50% age-at-maturity between 5.07 and 6.36 years for males, and 50 % age-at-maturity between 6.00 and 7.00 years for females, could be considered for the species-complex. Maturity may be possible from 460 mm DW (Last *et al.* 2016*a*), but more likely occurs from 547 mm DW and 4 years of age, with individuals likely mature when over 673 mm DW and 9 years of age. Rounding up for ease of application, the species-complex could be considered to reach maturity 4–9 years of age and from ~460–550 to 680 mm DW (Fig. 9).

When comparing these life-history values with other species of stingray, *Maculabatis* spp. has higher growth rates and faster maturity than the brown stingray (*Dasyatis lata*), which matures between 8.3 and 15 years old (Dale and Holland 2012). However, it has slower growth rates and maturity than the round stingray (*Urotrygon rogersi*), which matures at around 1 year with a *k*-value of 0.65 (Medjia-Falla *et al.* 2014) and the Baraka's whipray (*M. ambigua*), which matures at under 3 years old (Temple *et al.* 2020). *Maculabatis* spp.'s matures at a slightly younger age than their close relative the blackspotted whipray (*M. astra*), which had a 50% age-at-maturity of 7.32 years for males, and 8.67 years for females (Jacobsen and Bennett 2011).

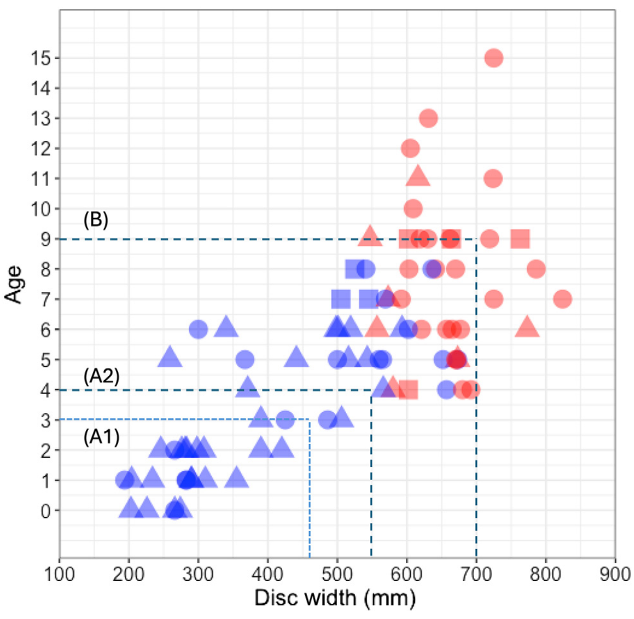

Fig. 9. Maturity (blue = immature, red = mature), relative to age and disc width (mm) for 89 Maculabatis spp.: *Maculabatis gerrardi* (*n* = 43, ●), *Maculabatis macrura* (*n* = 38, ▲), and undetermined species (*n* = 8, ■), using vertebral band counts. Previous research reports maturity from 460 mm DW (line A1 (Last *et al.* 2016*a*), which corresponds to ~3 years old in this study). This study found the youngest mature animal to measure 547 mm DW and the largest immature animal to measure 673 mm DW. Rounding to whole numbers for ease of reference for management application, *Maculabatis* spp. as a species-complex predominantly matures between 550 mm DW and 4 years old (line A2) to 680 mm DW and 9 years old (line B), after which they are likely all mature.

In this study, there were only two gravid females, one *M. gerrardi* with two well-developed embryos in January, an *M. macrura* at early-stage pregnancy with an implanted egg in June. The supplier from this study mentioned that larger specimens can carry more young, while a merchant at one of Singapore's fishery ports mentioned that two embryos is usually the norm for this species. Observation of *Maculabatis* spp. at fishery ports in Singapore reveal gravid females with well-developed embryos across seven different months; carrying between one to five embryos (average one to three pups). These observations, plus the largest ovarian egg diameter of dissected females, which show varying sizes across all months, suggest that *Maculabatis* spp. have asynchronous breeding with a litter size of one to at least five pups, but possibly more. There could be reproductive differences between *M. gerrardi* and *M. macrura*; however, these could not be determined from this study. With the exception of the *Maculabatis* spp. carrying five embryos in January, other observed pregnancies in this study typically involved one to three pups, which is also reported for the blackspotted whipray (*M. astra*) (Jacobsen and Bennett 2011) and may therefore represent the norm for species of this genus. One to three pups is considered low fecundity (Last and Stevens 2009; Gutteridge *et al.* 2013), and makes the species vulnerable to exploitation as they may not be able to rebound quickly. However, this study was unable to conclude gestation period or how many pregnancies females experience per year; if gestation is short and pregnancies are multiple, then this may increase their fecundity.

The relatively late maturity established in this study (50% age-at-maturity = 5.07–6.36 years for males, and 6.00–7.00 years for females) and potentially low fecundity for at least some pregnancies (one to five pups per gestation period), combined with the heavy fishing pressure this species-complex experiences in the south-east Asian region (SEAFDEC 2017; Clark-Shen *et al.* 2021), would explain the estimated population decline of 50–79% for *M. gerrardi* and *M. macrura* over the past 57 years (Sherman *et al.* 2020*a*, 2020*b*). The seafood supplier interviewed in this study confirmed that the species-complex is actively targeted by fisheries with large trade occurring between Indonesia, Malaysia, and Singapore, and noted that significant declines in their supply over a short-time have been observed, with the stage where it is no longer 'economical' to catch the species nearing. The supplier also emphasised that smaller individuals are preferred in Singapore for the local delicacy 'BBQ Stingray' and indeed, when looking at size classes of *Maculabatis* spp. observed at Singapore's fishery ports between 2017 and 2020 (Clark-Shen *et al.* 2021), 77.8% of *Maculabatis* spp. imports fell between 260 to 610 mm DW, which according to findings in this study, would mean they are predominantly immature with only a few maturing or recently matured individuals.

Both *M. gerrardi* and *M. macrura* are listed as Endangered by the IUCN Red List of Threatened Species (Sherman *et al.* 2020*a*, 2020*b*). The following five recommendations can improve conservation:

1. Considering these stingrays are actively targeted to supply demand, improved awareness among consumers in countries where demand is high (i.e. Singapore and Malaysia for meat, and Thailand for leather) could help to reduce the demand for these animals. An understanding of appropriate messaging would help with effectiveness of such outreach and campaign efforts.
2. The supplier highlighted that while a total ban on catching stingrays would help the animals, it would be 'too detrimental' for fishers. Thus, the release of certain animals based on maturity and size (Fig. 9) could be considered in countries where catch and supply is high (i.e. Malaysia and Indonesia) and demographic analyses (e.g. Grant *et al.* 2019) should be done to determine which segment of the population is most important to conserve through such measures.
3. A ban on the fishing gear used to specifically target stingrays in large volumes ('brother hooks' or 兄弟钩 in Mandarin/Hokien) would help to reduce targeted catch rates.
4. Trade regulations, whether regional (e.g. within south-east Asia, which the supplier suggests may be more relevant as he perceives demand is highest within this region), or international (CITES-Appendix II) should be explored. However, application to the entire group (e.g. all stingrays) will ensure pressure is not simply shifted to another species, as the supplier in this study predicts will happen if a species-specific approach is adopted. Trade restrictions should not only regulate the meat trade, but all parts including the skin because fresh skins from *Maculabatis* spp. are commonly sighted at Singapore's fishery port for trade up to Thailand.
5. Improved and considered protection (Chin *et al.* 2022) of often-neglected soft-substrate habitats, where these species of stingray live (as supported by the supplier interview and diet analysis in this study, as well as previous research (Last *et al.* 2016*a*)), is essential to give these animals and their ecosystem a reprieve from exploitation.

While this study has improved knowledge of south-east Asia's *Maculabatis* spp., there were several limitations. The challenges distinguishing *M. gerrardi* and *M. macrura* morphologically resulted in several specimens (10 of the total 95 vertebrae processed) being unassigned to a species, thus reducing the already small sample size. To overcome this, future studies could incorporate molecular work to compliment morphology. Due to the reliance on specimens already caught by fisheries, the sample lacked larger-sized individuals (>700 mm DW) and was biased toward the small size class, which are preferred for trading. Thus, the maximum age of this species remains unresolved, and the low number of mature, female *M. macrura* hindered reliable findings for this subgroup. Targeted sampling at fishery ports could resolve these two issues. Finally, the interview was conducted with only one person, which is a very low sample size, and future efforts should target a higher number of traders as well as fishers, to gather greater insights at different stages of the supply chain.

Supplementary material

Supplementary material is available online.

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Data availability. Data sharing is not applicable as no new data were generated or analyzed during this study.

Conflicts of interest. Andrew Chin is an Associate Editor for Pacific Conservation Biology but was not involved in the peer review or decision-making process for this paper. The author(s) have no further conflicts of interest to declare.

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Author affiliations

[A]Tropical Future Institute, James Cook University, Singapore 387380, Singapore.

[B]World Wide Fund for Nature (WWF), WWF-Singapore, Singapore.

[C]James Cook University, Centre for Sustainable Tropical Fisheries and Aquaculture, College of Science and Engineering, Douglas, Qld, Australia.

[D]Faculty of Marine Science and fisheries, Hasanuddin University, Makassar, South Sulawesi, Indonesia.

[E]The Dorsal Effect Pte Ltd, 22 Sin Ming Lane, Singapore.

[F]School of Science and Technology, Tropical Future Institute, James Cook University, Singapore 387380, Singapore.