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1 Diagnosing the dangerous demography of manta rays using life history theory

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6 **Background** | The directed harvest and global trade in the gill plates of Mantas, and other
7 mobulid rays, has led to increased fishing pressure and steep population declines in some
8 locations. The slow life history, particularly of the Manta rays, is cited as a key reason why such
9 species have little capacity to withstand directed fisheries. Here, we place their life history and
10 demography within the context of other sharks and rays.

11
12 **Methods** | Despite the limited availability of data, we use life history theory and comparative
13 analysis to estimate the intrinsic risk of extinction (maximum intrinsic rate of population increase
14 r_{max}) for a typical generic Manta Ray using a variant of the classic Euler-Lotka demographic
15 model. This model requires only three traits: von Bertalanffy growth rate, annual pup production
16 and age at maturity. To account for the uncertainty in life history parameters, we created
17 plausible parameter ranges and propagate these uncertainties through the model to calculate a
18 distribution of the plausible range of r_{max} values.

19
20 **Results** | The maximum population growth rate r_{max} of Manta ray is most sensitive to the length
21 of the reproductive cycle, and the median r_{max} of 0.11 year⁻¹(CI: 0.089-0.137) is one of the lowest
22 known of the 106 sharks and rays for which we have comparable demographic information.

23
24 **Discussion** | In common with other unprotected, unmanaged, high-value large-bodied species
25 with low or very low productivity, Manta (and other mobulid) rays are unlikely to sustain
26 unmonitored, unregulated exploitation, and may face increasing local and regional extinction
27 risk. We show that it is possible to derive important insights into the demography extinction risk
28 of some of the most data-poor species in the world with simple life history tools.

Diagnosing the dangerous demography of manta rays using life history theory

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Introduction

The rapid rise in demand for plant and animal products that are traded through international networks has globalised the reach of economically-powerful consumers to incentivize unsustainable depletion of biological resources (Berkes et al. 2006; Lenzen et al. 2012). Only in the past decade have we begun to reveal the enormous scale of trade in aquatic organisms (Clarke 2004). While we have long understood the challenges of poaching for the illegal ivory trade (Phillis et al. 2012), we are only now just beginning to reveal the enormous scale of trade in aquatic organisms, such as for the live food fish trade (Sadovy & Vincent 2002), and the dried product trade in shark fins (Clarke et al. 2006), seahorses (Foster & Vincent 2004), sea cucumbers (Anderson et al. 2011), and fish swim bladders (Clarke 2004; Sadovy & Cheung 2003).

A recent emerging international trade in Manta and Devil ray gill plates is driving overexploitation elevating their extinction risk (IUCN/TRAFFIC 2013). There are two Manta rays (*Manta birostris* (Walbaum 1792), and *M. alfredi* (Krefft, 1868) and at least some of the nine Devil rays (*Mobula* spp.) reported in national catch statistics and international trade (CITES 2007; Couturier et al. 2012; Ward-Paige et al. 2013). Manta and Devil rays are taken in targeted fisheries and also as a valuable retained bycatch in China, Ghana, India, Indonesia, Mexico, Peru, Philippines, Sri Lanka and Thailand (Couturier et al. 2012; IUCN/TRAFFIC 2013). Over the past decade the landings of Manta and Devil rays have risen more than 10-fold from less than 200 metric tonnes (mt) per year in 1998 to a peak of over 5,000 mt in 2009 (Ward-Paige et al. 2013). Manta and Devil rays are captured for their gill plates and a single mature animal can yield up to 7 kg of gillrakers which can be worth as much as \$680 per kg in Chinese Traditional Medicine (Heinrichs et al. 2011; IUCN/TRAFFIC 2013). Much of the international trade goes to southern China and other cities with large Chinese populations (Couturier et al. 2012; Heinrichs et al. 2011). One of the authors has seen Devil ray gill plates for sale for \$396.80 per kg (under the incorrect taxonomic name *Dasyatis Centroura*) in Vancouver, Canada 2013 (Figure 1). The trade is currently difficult to monitor because of a lack of international trade codes and species-specific catch and landings data. Despite this, ~21,000kg of dried *Manta* spp. gill plates are traded annually, derived from an estimated >4,500 individual Manta rays, and worth US \$5 million (Heinrichs et al. 2011; O'Malley et al. 2013).

We know little of the biology of Manta rays (*Manta birostris* (Walbaum 1792), and *M. alfredi* (Krefft, 1868), and less of the devil rays which is particularly problematic when their viability is threatened by rapidly emerging fisheries driven by international trade demand (Clarke 2004; Couturier et al. 2012). Both Manta rays were listed as Vulnerable on the International Union for the Conservation of Nature Red List of Threatened Species in 2011 because of the inferred global decline due to directed gill-plate fisheries and their inferred slow life history (Marshall et al. 2011a; Marshall et al. 2011b). Moreover, recognizing this threat, Brazil, Colombia and Ecuador successfully proposed *Manta* spp. for inclusion in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). These listings will come into force at the end of September 2014, by which time their international trade will only be allowed if: (1) specimens were legally sourced, and (2) the export is not detrimental to wild populations of the species (a non-detriment finding, NDF) (Vincent et al. 2013). Non-detriment findings rely on the ability to assess the sustainability of removals of individuals for the international trade from national populations. One of the principal challenges of assessing sustainability is that there is often a high degree of uncertainty in the population biology of species, and the pattern and rate of exploitation (Ludwig et al. 1993). However, decisions on the sustainability of fisheries and trade often have to be made without the benefit of sufficient information. Recent advances have made it possible to account for sources of uncertainty and this is increasingly an important part of the decision-making process in fisheries management and conservation (Baker & Clapham 2004; Magnusson et al. 2012; Peterman 2004).

One approach to dealing with uncertainty in life histories is to draw upon life history tradeoff rules that constrain the range of plausible trait values (Beverton & Holt 1959; Law 1979). There are fundamental constraints to the acquisition, allocation and metabolism of energy resulting in a narrow set of rules of life (Dulvy & Forrest 2010; Jennings & Dulvy 2008). These rules can be used to choose a plausible range of life history traits, which when combined with simple methods to propagate the uncertainty in the true trait value, can be used to provide powerful insights into demography and fisheries sustainability (Beddington & Kirkwood 2005). Recent work using a simple life history model suggests Manta rays are intrinsically sensitive and have low capacity to rebound from even low levels of fishing mortality (Ward-Paige et al. 2013).

Here, we examine the potential risk to Manta ray populations from fishing to supply the dried gill plate trade. Specifically, we calculate the maximum intrinsic rate of population increase (r_{max}) of Manta rays, and compare their demography to other sharks and rays. Our model and approach provides a demographic basis for evaluating the sustainability, or otherwise, of Manta fisheries, in the face of considerable uncertainty in their life history.

Materials and methods

We first outline the Euler-Lotka life history model and the three key parameters required to estimate the maximum rate of population increase r_{max} : the annual rate of production of female offspring ($\tilde{\alpha}$), age at maturity (α_{mat}), and the instantaneous natural mortality rate (M). Second, we describe plausible ranges for each of those parameters for a generic Manta ray life history. Third, we use a Monte Carlo procedure to propagate the uncertainty these three life history parameters through the Euler-Lotka model to calculate a distribution of the plausible range of Manta Ray maximum rate of population increase r_{max} . Finally, we compare the demography of the Manta Ray to the life histories and demography of 106 other sharks and rays.

We chose to estimate the extinction risk of Manta rays by calculating the maximum rate of population increase using a variant of the Euler-Lotka model (García et al. 2008; Hutchings et al. 2012). This is one of the oldest and simplest life history models and is founded on the principle that a breeding female only has to produce one mature female in her lifetime to ensure a stable population size (Charnov & Zuo 2011; Myers & Mertz 1998; Simpfendorfer 2005):

$$\tilde{\alpha} = (e^{r_{max}})^{\alpha_{mat}} - p(e^{r_{max}})^{\alpha_{mat}-1},$$

where $\tilde{\alpha}$ is the annual rate of production of female offspring. Here we calculated $\tilde{\alpha}$ as $l/i * 0.5$, where l is litter size and i is breeding interval, corrected for sex ratio i.e. 0.5). α_{mat} is age at maturity, and p is the adult survival rate, where $p = e^{-M}$, where M is the instantaneous natural annual mortality rate yr^{-1} . The simplicity of the model is that it requires only estimates of three biological parameters: annual reproductive output ($\tilde{\alpha}$), age at maturity (α_{mat}), and natural

mortality (M). Two of these parameters are highly uncertain ($\tilde{\alpha}$ and α_{mat}) and the other (M) is estimated indirectly, which can also result in uncertainty. Hence, we aim to estimate a range of r_{max} to encompass the widest range of life histories that are plausible for Manta rays and hence would encompass the true parameter values.

The existence of more than one species of Manta ray was only recently recognized (Marshall et al. 2009); furthermore, with the geographic overlap and similarity in body sizes we draw upon the data of both species, to evaluate a generic Manta ray life history.

Annual reproductive output ($\tilde{\alpha}$). One pup is produced per litter (rarely two) and gestation period is approximately one year (366–374 days in the Okinawa aquarium) (Couturier et al. 2012). This suggests an annual breeding interval, but there may also be a chance of skipped breeding or multiannual reproductive cycles. There is evidence for a biennial cycle where 1 pup is produced every two years (Couturier et al. 2012; Marshall & Bennett 2010). Even more extreme example is the recent discovery of a complete absence of pregnant females for four years in the Maldives Islands, following three biennial cycles, which could be interpreted as one pup every five years (personal communication; Guy Stevens, Environment Department, University of York, UK). Similar patterns of skipped reproduction have been noted in Japanese waters (Tom Kashiwagi, School of Biomedical Sciences, University of Queensland, Queensland 4072, Australia). Assuming an even sex ratio, a plausible range would be an annual reproductive output averaging 0.25 to 0.5 female pups per year, but consider extremes out to an annual reproductive output 0.1 (1 female pup every five years). Because of the modeling approach, we do not consider juvenile mortality and we expect Manta pups to have low mortality due to their extremely large size in comparison to other sharks and rays. Mortality patterns are strongly size-dependent in the ocean and hence larger individuals are likely to have much higher survival rates (Charnov et al. 2012; Gislason et al. 2010; Pope et al. 1994). Manta offspring are some of the largest offspring of any ectotherm in the ocean. The size of birth of Manta pups is 130-150 cm disc width, considering the maximum linear dimension this one of the largest of any elasmobranch. The maximum linear dimensions of offspring sizes of 274 elasmobranchs ranged from 6.8 cm in Cuban pygmy skate (*Fenestraja cubensis*) to 175 cm in the basking shark (*Cetorhinus maximus*), and the size at birth disc width of a Manta ray of 130-150 cm lies in the

upper 95th percentile of the distribution of maximum linear dimension of size at birth or hatch of these elasmobranchs (Cortés 2000; Goodwin et al. 2002; Jennings et al. 2008).

Age at maturity (α_{mat}). Male reef Manta rays (*M. alfredi*) mature at 3–6 years in Hawaii and female maturity is subject to considerable debate, and for our purposes is inferred to be 8-10 years (Marshall et al. 2011b).

Natural mortality (M) can be estimated indirectly from the von Bertalanffy growth coefficient (k) or can be assumed to be the reciprocal of lifespan, 1/maximum age (Charnov et al. 2012; Dulvy et al. 2004; Pauly 2002). Here we draw inferences from both approaches.

There is no growth curve available for Manta rays, however we can draw some inference as to the plausible range because fish growth parameters are narrowly constrained and highly correlated because of fundamental life history tradeoffs (Charnov et al. 2012). The rate of somatic growth (k) is negatively-related to the asymptotic maximum size (L_{∞}) within a narrow range (Jensen 1996). Hence, we review the von Bertalanffy growth curves of larger tropical batoids (>1 m) to guide the choice of a plausible range of k for Manta rays. The available growth rates for species with similar lifestyles, tropical and subtropical myliobatoid rays (Table 1) and the tropical planktivorous whale shark, reveals that most k values lie between 0.009 yr⁻¹ and 0.28 yr⁻¹ (Table 1). It might be expected that this range of k would be on the high end for Manta rays because they reach a considerably larger size. While known from temperate regions, they are typically found in warm tropical and subtropical water. They are planktivores and hence can access a much larger food resource base and higher growth might be expected at high temperatures. There is some evidence that planktivores grow quickly because their feeding mode is more energetically profitable when individuals (and their gape) reach a larger size. Comparisons to whale shark would suggest Manta k values around 0.03-0.04 yr⁻¹ (Wintner 2000).

The maximum age of Manta rays can be inferred from the longest period of resightings of individuals through photo identification projects (Town et al. 2013). In Hawai'i one female has

been continuously resighted since 1979, providing a minimum estimate of longevity of 31 years (Clark 2010). The inferred Manta ray maximum age of >31 years is considerably higher than the 19 to 25 years for *Aetobatis flagellum*, *Myliobatis californicus* and *Rhinoptera bonasus*, so a more plausible range for k might be 0.05-0.1 yr⁻¹. Life history invariants can be used to estimate mortality from growth rate, assuming an M/k ratio of 0.4 which is more typical for elasmobranch fishes than the higher ratio of $M/k = 1.5$ observed in teleost fishes and reptiles (Frisk et al. 2001). For a range of k of 0.05-0.1, then M is between 0.02 and 0.04.

We model parameters encompassing the following ranges: $k = 0.05$ -0.1, $M = 0.02$ to 0.04, age at maturity = 8-10 years and an annual reproductive rate of 0.25 to 0.5 female pups per year. To propagate the uncertainty inherent in these parameter ranges, we drew 10,000 values of each parameter from a random uniform distribution bounded by the plausible range of each. While life history traits are typically distributed around a mean value in a Gaussian manner, we choose a more conservative uniform distribution to explore the full range of parameter space. Maximum intrinsic population growth rate was calculated for the 10,000 triplets of $\tilde{\alpha}$, α_{mat} and M by iteratively solving for r_{max} using the `nlmminb` optimization function in R statistical software version 2.15 (R Core Team 2013).

We compared the Manta ray r_{max} to all available estimates ($n=106$), comprising 105 published estimates for chondrichthyans (García et al. 2008), to which we added the filter-feeding CITES-listed basking shark (*Cetorhinus maximus*) which has an M of 0.024 (based on a growth coefficient k of 0.067), age at maturity of 10, and an annual reproductive output of 1.5 females per litter every two years (assuming an 18 month pregnancy) (Pauly 2002). For plotting, we extracted all maximum sizes as the total length in centimeters, except for Myliobatiformes and Chimaeriformes for which we used disc width and fork length, respectively (García et al. 2008; Pauly 2002). There is wide geographic variation in maximum disc width and many *M. alfredi* individuals average around 400 cm increasing to 490 cm DW (Marshall et al. 2011c). The giant Manta ray consistently reaches a maximum size of over 700 cm DW with anecdotal reports of up to 910 cm DW (Marshall et al. 2009). Here, for graphical purposes we assumed a maximum size of 600 cm DW.

Results

Assuming that the range of life histories explored encompasses our current knowledge, then the median maximum intrinsic rate of population increase r_{max} for Manta ray is 0.11 (95% Confidence Interval = 0.089-0.137, Figure 2a). The lowest r_{max} value of 0.097 corresponds to an annual reproductive output, $\tilde{\alpha} = 0.25$, $\alpha_{mat} = 10$ years, and natural mortality, $M = 0.02$, and the highest r_{max} of 0.154 corresponding to $\tilde{\alpha} = 0.5$, $\alpha_{mat} = 8$ years, and $M = 0.04$.

The r_{max} decreases considerably when annual reproductive output is lower. The r_{max} is most sensitive to annual reproductive output $\tilde{\alpha}$ compared to the age at maturation α_{mat} , note the difference between each $\tilde{\alpha}$ is greater than among growth rates or ages of maturation (Figure 2b). The sensitivity to annual reproductive output $\tilde{\alpha}$ relative to age at maturation α_{mat} becomes increasingly important when annual reproductive output is low (Figure 2b). There is a positive relationship between growth (and hence mortality) and r_{max} across species (Figure 3a), and larger species have lower r_{max} (Figure 3b).

Of the 106 species for which we could calculate the maximum intrinsic rate of population increase, the Manta ray had one of the lowest r_{max} values (0.113). The r_{max} of deepwater sharks ($n = 14$) is significantly lower than for continental shelf and oceanic pelagic species, as revealed by García et al. (2008). Aside from the deepwater sharks which are all intrinsically sensitive to overfishing (Simpfendorfer & Kyne 2009), in shallower water the species with the lowest r_{max} were the temperate basking shark (*Cetorhinus maximus*) $r_{max} = 0.109$, followed by the Manta ray ($r_{max} = 0.114$).

We compared the maximum population growth rate r_{max} as calculated from the modified Euler-Lotka models and the population growth rate r (which equals $\ln[\lambda]$) as calculated from age-structured models (Cortés 2002). We found both measure of population growth significantly related, but the slope of the relationship was 0.26 (± 0.09 standard error) suggesting r_{max} is typically four times greater than r ($F_{1,27} = 8.09$, $p = 0.008$, adjusted $r^2 = 0.2$). Hence, in assessing the productivity of species against the criteria of Food and Agriculture Organization of the United Nations (Musick 1998), it might be more precautionary to estimate r as $r_{max} / 4 = 0.029$ (95% CI = 0.022-0.34), and hence Manta ray has “very low” productivity (<0.05).

Discussion

we show how life history theory can be used to guide the estimation of an important demographic parameter – the maximum intrinsic rate of population increase r_{max} – and likely sustainability of even the most difficult-to-study marine animals. The paucity of biological data for Manta rays is very typical of the many data poor fisheries of the world. But the absence of data should preclude or delay management. Our analysis shows that Manta rays have one of the lowest maximum intrinsic rates of population increase of any of the chondrichthyans studied to date. Our approach is designed not to estimate the one true value of the maximum intrinsic population growth rate but to calculate these values while understanding the sensitivity to the input parameters and accounting for uncertainty in those values. Despite some uncertainty in life history traits, the plausible range of Manta ray r_{max} estimates is narrow (Figure 2), because life history tradeoffs between maximum asymptotic size and the growth rate narrow the parameter space. It is likely that the range is narrower than we show because we could not account for the covariance of life history traits, if we were able to do so this would further narrow the plausible range of Manta ray r_{max} estimates.

We find that the maximum rate of population increase is slightly higher than a recent estimate of the intrinsic rate of population increase, $r = 0.042-0.05$ (Ward-Paige et al. 2013), compared to our median $r_{max} = 0.11$. The range of parameters we used encompassed those of Ward-Paige et al. (2013) and suggest the difference in r versus r_{max} may be due to differences in the method used to estimate natural mortality and that the rebound potential method consistently provides lower growth rate. We used an elasmobranch-specific mortality estimator (Frisk et al. 2001), whereas the other used an estimator based on fishes, molluscs and whales (Hoenig 1983). A more puzzling issue is why our approach reveals that Manta rays have one of the lowest r_{max} of any chondrichthyan, whereas the other suggests Manta rays may have an intermediate r (Ward-Paige et al. 2013). This issue is beyond the scope of this paper, and requires a simulation-based performance comparison of these kinds of models. While close, the difference in demographic estimates underscores the need for a better understanding of such rule-of-thumb mortality estimators and a comparison of the performance of different variants of simple scalar unstructured demographic models, such as the Euler-Lotka model, the rebound potential model, and Pope's *Fjeopardy* model (Pope et al. 2000; Simpfendorfer 2005; Smith et al. 1998).

Manta rays have very low productivities and even a low fishing mortality (F_{extinct}) would drive them to extinction. The Manta ray $r_{\text{max}} = 0.114$ falls within the ‘low’ category of the productivity classification used by CITES (0.05 to 0.15, Musick 1999). However, we highlight that the maximum population growth rate r_{max} reported here is typically four times greater than the intrinsic population growth rate r as derived from age-structured models (e.g. Cortés 2002). Hence, Manta rays are more likely to be classified as having “very low” productivity (<0.05). With additional field work, there is scope to refine and reduce the uncertainty in the estimates of Manta and Mobula ray productivity.

One might object to the calculation of r_{max} given such great uncertainty in basic life history of these data-poor species. However, the pragmatic reality is that we do not have the luxury of waiting for more data to become available. And indeed increasing effort is being paid to understanding safe biological limits for the exploitation of target and bycatch species (Dulvy et al. 2004; Pardo et al. 2012). At the most recent 16th Conference of the Parties of the Convention on the International Trade in Endangered Species both species of Manta ray were listed on Appendix II, which includes, “species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled”. Under this regulation Appendix II species can only be traded subject to three conditions, two of which pertain to the legality of capture and welfare (of live transported species), and the third relates to the sustainability (or otherwise) of trade – the so called Non Detriment Finding (Vincent et al. 2013). This finding confirms that the trade of specimens will not be detrimental to wild populations of the species. A key condition of the CITES listings of both Manta rays would be delayed by 18 months until 14th September 2014 (CITES 2013). By this date, any nation, party to the CITES, wishing to trade Manta ray gill plates needs to develop methods for assessing that proposed trade is sustainable and not detrimental to wild populations. There is very little time in which to gather new data and hence our simple modeling demographic model, constrained by life history tradeoffs and accounting for and propagating biological uncertainty, provides a much-needed first step toward developing methods to support the development of methods to assess the sustainability of exploitation and international trade.

Our analysis reveals that a key parameter to estimate in future field studies are the growth rate k from a von Bertalanffy growth curve, fitted appropriately to size at age data (Pardo et al. 2013; Smart et al. 2013; Thorson & Simpfendorfer 2009). Hopefully, the growth rate k can be estimated for Manta rays, as has been done for other smaller tropical myliobatoids (Table 1). However, there is a real possibility that annuli may not be recoverable from Manta rays because mobulid vertebrate tend to be poorly calcified (personal communication, Wade Smith, Oregon State University, Corvallis, Oregon, USA). Hence mark-recapture tagging or resighting programmes may be the most pragmatic method of estimating a growth curve (Town et al. 2013). As we have shown, natural mortality rate depends heavily on k and the ratio of M/k , which is around 0.4 for elasmobranchs (Frisk et al. 2001). If it is not possible to estimate a growth curve for Manta rays in the near future then demographic modeling will be heavily reliant on our understanding of: (1) the overall pattern of maximum size (L_{∞}) and growth rate (k) in elasmobranchs, and especially tropical batoids, and (2) the M/k ratio. Future work should concentrate on understanding why the elasmobranch M/k ratio is around 0.4, by comparison the teleost and reptile M/k ratio is around 1.5 (Charnov et al. 1993). Why is this so? This ratio has a profound influence on the estimate of population growth rate and the sustainability of species, and hence understanding the life histories, ecological and environmental correlates of the M/k ratio can only improve the predictive power of these simple demographic models.

Other parameters that strongly influence the maximum intrinsic rate of population increase are the age at maturation and the annual reproductive rate. These parameters very poorly understood (Marshall & Bennett 2010). The Manta ray annual reproductive rate estimates of one pup per year are based on aquarium-held specimens under relatively ideal conditions, and hence these estimates are likely to be optimistic. There is unpublished evidence suggesting that annual reproductive rates may be much, much lower and variable among and within individuals. The proportion of pregnant females returning to long-term (6-8 years) study sites in the Maldives previously suggested a biennial reproductive mode, but in recent years no pregnant females have returned (Guy Stevens, Environment Department, University of York, UK; personal communication). The absence of returning pregnant females may indicate a spatial shift of returning females, but also may presage reproductive failure and hint at much lower and more variable annual rates of reproductive output than we have modeled here. We recommend that the

demographic rates of Manta rays be revised as greater detail of temporal and geographic variability come to light. The emerging observations of year-to-year variation in individual reproductive output may lead to variance in year-to-year population growth rate which can only serve to depress the long-term population growth rate further elevating extinction risk (Hutchings 1999). And indeed such observations caution us to initiate and undertake local analyses of population structure and reproductive activity and to incorporate local variations into local demographic models and assessments contribution to CITES Non-Detriment Findings. Of course the greatest uncertainty, that we have entirely overlooked, is that future demographic estimates would benefit greatly from species-specific estimates of the key life history parameters: growth rate k , annual reproductive rate and age at maturity.

Notwithstanding the current uncertainty in the life history of Manta rays, given their very low productivity coupled with low localized population size and predictable seasonal aggregations, the unregulated targeting of local Manta populations for their high-value gill plates is unlikely to be sustainable. The largest targeted fisheries and highest mortality occurs in Indonesia, Sri Lanka, India, Peru and Mozambique and these countries have little fisheries monitoring, regulation or effective enforcement. The time to local extinction depends on the size of the population and the rate of fishing mortality. The very low productivity of Manta rays mean that even a moderate level of fishing mortality of $F = 0.2$ (survival = 0.81) would reduce a small population of 100 individuals to fewer than 10 within less than a generation span (11 years). The key challenge this poses is that it leaves little time to mount an effective conservation management response. These serial depletion fisheries are operated by low-income subsistence coastal fishers, often against a backdrop of collapsing fisheries. For such fishers the international market demand for valuable Manta and mobulid ray gill plates is likely to provide a desirable income. Such fisheries tend to be unregulated and even if there are protections these are difficult to enforce, which underscores the importance of international trade regulation.

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Table 1. Von Bertalanffy growth parameter estimates for species with similar life styles to the Manta rays; *a.* tropical myliobatoid rays larger than 1 m total disc width, and *b.* the tropical planktivorous whale shark.

Species name	IUCN Status ¹	Sex	Maximum length (cm) ²	Maximum age (years)	L_{∞}	k	Reference
<i>a. Mobula japanica</i>	NT	both	310	14	NA	0.28	(Cuevas-Zimbrón et al. 2012)
<i>Myliobatis californicus</i>	LC	M	158.7	6	199.1	0.0596	(Martin & Cailliet 1988)
<i>Myliobatis californicus</i>	LC	F	158.7	24	158.7	0.0095	(Martin & Cailliet 1988)
<i>Myliobatis californicus</i>	LC	F	158.7	24	156.6	0.099	(Martin & Cailliet 1988)
<i>Aetobatus flagellum</i>	EN	F	150	19	152.7	0.111	(Yamaguchi et al. 2005)
<i>Aetobatus flagellum</i>	EN	M	100	9	131.8	0.133	(Yamaguchi et al. 2005)
<i>Rhinoptera bonasus</i>	NT	both	102	18	123.8	0.075	(Neer & Thompson 2005)
<i>b. Rhincodon typus</i>	VU	NA	1370	NA	1400	0.026-0.051	(García et al. 2008; Pauly 2002)

¹IUCN Red List Categories: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient.

²Disc width (cm) for rays and total length (cm) for whale shark.

FIGURE 1.

Gill plates, tentatively identified as from the Sickie-fin Devil ray *Mobula tarapacana* (Philippi, 1892), for public sale in downtown Vancouver, British Columbia, Canada on 26th April 2013: photo credit Nicholas K. Dulvy.



FIGURE 2.

(a) Maximum intrinsic rate of population increase for 106 chondrichthyans, including the Manta ray.

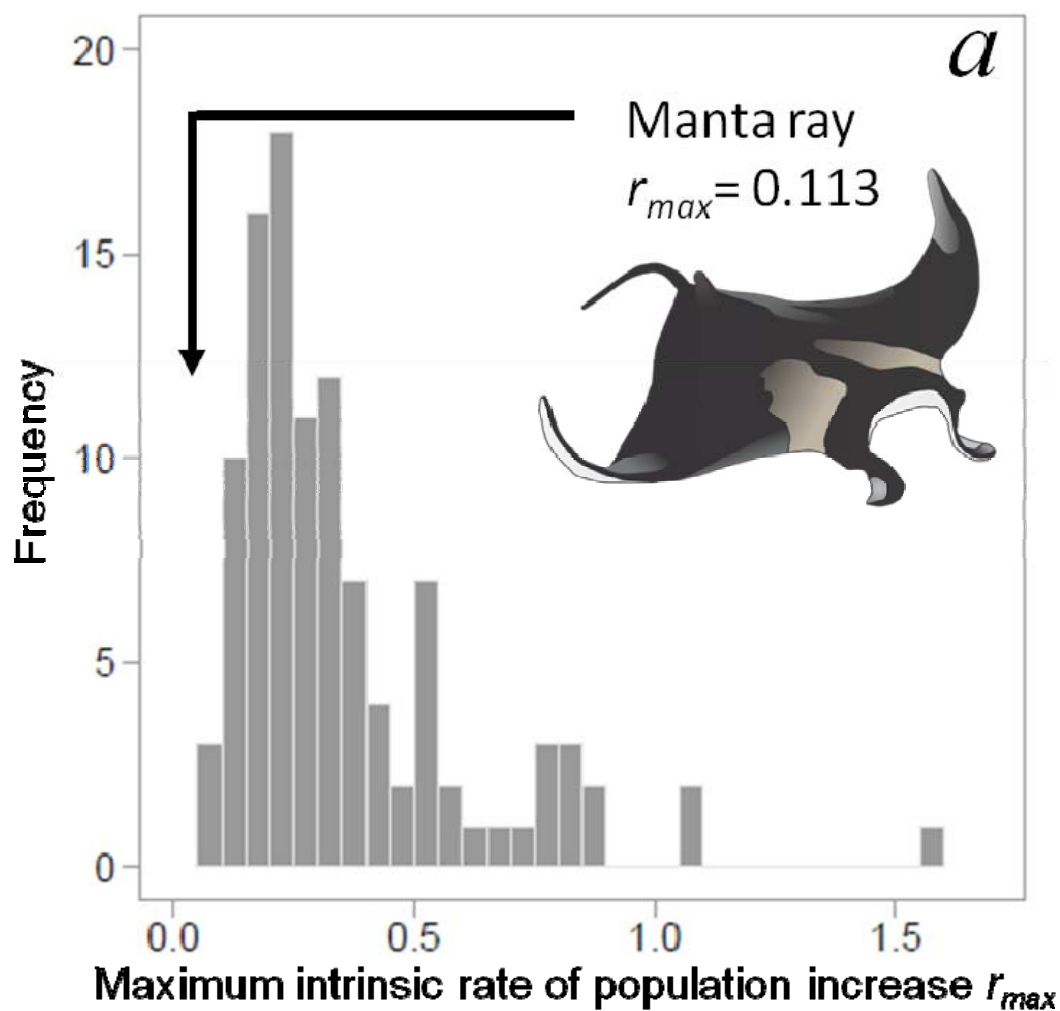


FIGURE 2.

(b) Sensitivity of Manta ray maximum intrinsic rate of population increase to variation in growth rate, age at maturity and annual reproductive rate.

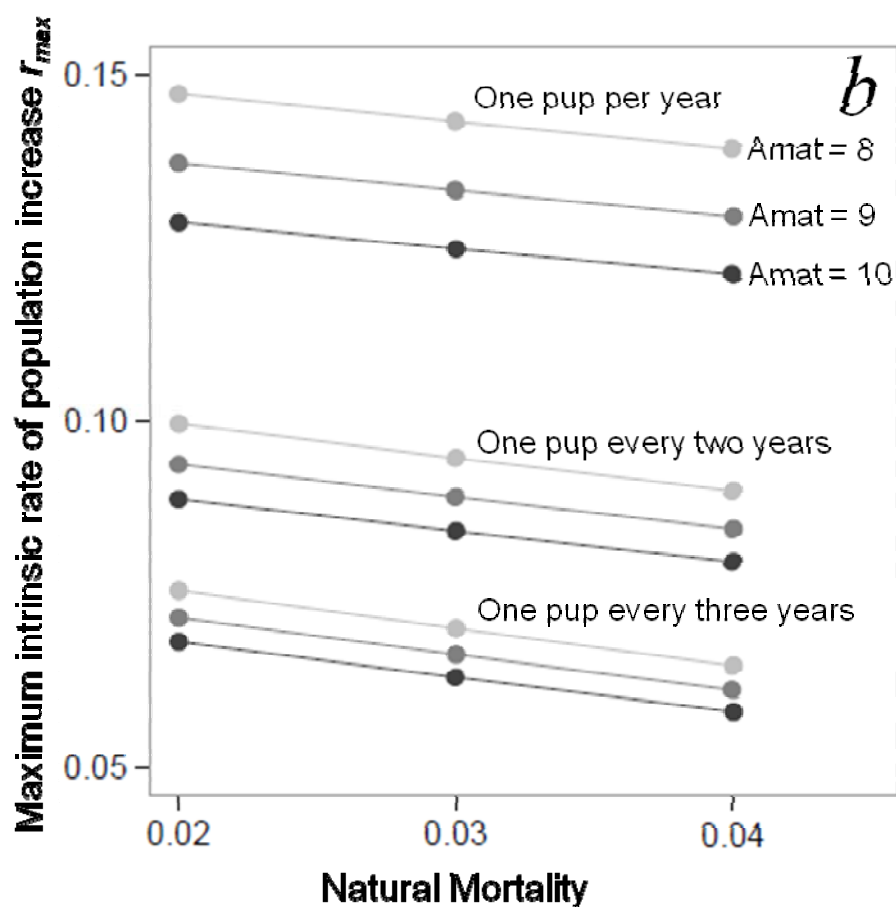


FIGURE 3.

Maximum intrinsic rate of population increase versus, (a) growth rate, and (b) maximum size for 106 chondrichthyans on a logarithmic scale. Whale and basking sharks are highlighted for comparison.

