

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

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## ABSTRACT

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

**Methods.** Despite the limited availability of data, we use life history theory and comparative analysis to estimate the intrinsic risk of extinction (as indexed by the maximum intrinsic rate of population increase  $r_{\max}$ ) for a typical generic manta ray using a variant of the classic Euler–Lotka demographic model. This model requires only three traits to calculate the maximum intrinsic population growth rate  $r_{\max}$ : von Bertalanffy growth rate, annual pup production and age at maturity. To account for the uncertainty in life history parameters, we created plausible parameter ranges and propagate these uncertainties through the model to calculate a distribution of the plausible range of  $r_{\max}$  values.

**Results.** The maximum population growth rate  $r_{\max}$  of manta ray is most sensitive to the length of the reproductive cycle, and the median  $r_{\max}$  of 0.116 year<sup>-1</sup> 95th percentile [0.089–0.139] is one of the lowest known of the 106 sharks and rays for which we have comparable demographic information.

**Discussion.** In common with other unprotected, unmanaged, high-value large-bodied sharks and rays the combination of very low population growth rates of manta rays, combined with the high value of their gill rakers and the international nature of trade, is highly likely to lead to rapid depletion and potential local extinction unless a rapid conservation management response occurs worldwide. Furthermore, we show that it is possible to derive important insights into the demography extinction risk of data-poor species using well-established 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 causing unsustainable depletion of biological resources (Berkes *et al.*, 2006; Lenzen *et al.*, 2012). While we have long understood the challenges of poaching for the illegal ivory trade (Phillis *et al.*, 2013), 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). The high value of gill plates and the international nature of the trade are driving roving bandit dynamics, incentivising serial depletion and a globalized tragedy of the commons (Berkes *et al.*, 2006). If the population growth rate of manta rays is low, this pattern of exploitation could lead to rapid depletions and local extinction of manta populations. There are two described species of manta ray: *Manta birostris* (Walbaum, 1792), and *M. alfredi* (Kreffft, 1868). These mantas, and at least some of the nine devil rays and at least some of the nine devil rays (*Mobula* spp.), are reported in national catch statistics and appear in international trade (CITES, 2007; Couturier *et al.*, 2012; Ward-Paige, Davis & Worm, 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 ten-fold from less than 200 tonnes (t) per year in 1998 to a peak of over 5,000 t in 2009 (Ward-Paige, Davis & Worm, 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 markets (Heinrichs *et al.*, 2011; IUCN/TRAFFIC, 2013). Much of the international trade goes to southern China, and to Chinese communities in other countries (Couturier *et al.*, 2012; Heinrichs *et al.*, 2011). For example, 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, in 2013 (Fig. 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, ~21,000 kg 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, Lee-Brooks & Medd, 2013).

Many (46%) of chondrichthyans are Data Deficient (Dulvy *et al.*, 2014), and in comparison to the data-sufficient species we know little of the life history of manta rays *Manta birostris*, and *M. alfredi*. This is particularly problematic when their viability is threatened by rapidly emerging fisheries driven by international trade demand, and CITES Non-Detriment Findings are required for continued international trade (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



**Figure 1** Image of devil ray gill plates for sale in Vancouver. Gill plates, tentatively identified as from the sickle-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.

of the inferred global decline due to directed gill-plate fisheries and their inferred slow life histories (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 on 14th 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) (Mundy-Taylor & Crook, 2013; 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, Hilborn & Walters, 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, Punt & Hilborn, 2013; 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, Davis & Worm, 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 ( $\alpha_{\text{mat}}$ ), 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, Lucifora & Myers, 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 & Schaffer, 1973; Charnov & Zuo, 2011; Myers & Mertz, 1998; Simpfendorfer, 2005*):

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

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).

$\alpha_{\text{mat}}$  is age at maturity, and  $p$  is the adult survival rate, where  $p = e^{-M}$ , where  $M$  is the instantaneous natural annual mortality rate  $\text{yr}^{-1}$ . While local aggregations of manta rays may be sex-biased we assume an even sex ratio at the, wider, species level. The simple elegance of the model is that it requires only estimates of three biological parameters: annual reproductive output ( $\tilde{\alpha}$ ), age at maturity ( $\alpha_{\text{mat}}$ ), and natural mortality ( $M$ ). Two of these parameters are highly uncertain ( $\tilde{\alpha}$  and  $\alpha_{\text{mat}}$ ) and the other ( $M$ ) is estimated indirectly, which can also result in uncertainty. Hence, we aim to estimate a range of  $r_{\text{max}}$  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, Compagno & Bennett, 2009); furthermore, with the geographic overlap and in the absence of sufficient evidence to differentiate the life history traits required by the model we thought it most defensible 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 at least 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). An 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 (G Stevens, pers. comm., 2013). Similar patterns of skipped reproduction have been noted in Japanese waters (T Kashiwagi, pers. comm., 2013). It is worth noting that extended periods of ‘non-pregnancy’ may be an artifact of occasional sightings and/or poor viewing angles (Bennett, 2014). As is typical in demographic modeling we assume an even sex ratio. Under these assumptions a plausible range would be an annual reproductive output averaging 0.25–0.5 female pups per year, but we considered extremes out to an annual reproductive output 0.1 (1 female pup every five years). Because of the simple tractable nature of our modeling approach, we did not have the opportunity to consider juvenile mortality. However, juvenile survival may not be of overriding importance for overall population growth rate, because they are likely to have low mortality and contribute relatively little to population growth rate compared to sub-adults (Heppell, Crowder & Menzel, 1999). 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, Gislason & Pope, 2012; Gislason *et al.*, 2010; Pope, Shepherd & Webb, 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 is 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

**Table 1** Growth estimates for tropical rays and whale shark. 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 <sup>a</sup>	Sex	Maximum length (cm) <sup>b</sup>	Maximum age (years)	$L_{\infty}$	$k$	Reference
a.	<i>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, Kawahara & Ito, 2005)
	<i>Aetobatus flagellum</i>	EN	M	100	9	131.8	0.133	(Yamaguchi, Kawahara & Ito, 2005)
	<i>Rhinoptera bonasus</i>	NT	both	102	18	123.8	0.075	(Neer & Thompson, 2005)
b.	<i>Rhincodon typus</i>	VU	NA	1370	NA	1400	0.026–0.051	(García, Lucifora & Myers, 2008; Pauly, 2002)

**Notes.**

<sup>a</sup> IUCN Red List Categories: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient.

<sup>b</sup> Disc width (cm) for rays and total length (cm) for whale shark.

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, Dulvy & Reynolds, 2002; Jennings et al., 2008). As survival information becomes available, future models that account for age and stage-specific mortality are likely to provide more nuanced insights into manta ray demography.

### Age at maturity ( $\alpha_{mat}$ )

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,  $1/\text{maximum age}$  (Charnov, Gislason & Pope, 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, Gislason & Pope, 2012). The rate of somatic growth (as indexed by the von Bertalanffy growth coefficient,  $k$ ) is negatively-related to the asymptotic maximum size ( $L_{\infty}$ ) 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  $0.009 \text{ yr}^{-1}$  and  $0.28 \text{ yr}^{-1}$  (Table 1). It might be expected manta rays would have  $k$  values toward the lower end of this range because they reach a considerably larger size than most

of these myliobatoid rays. 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 and the slower growing myliobatoid rays would suggest manta  $k$  values around  $0.03\text{--}0.04\text{ yr}^{-1}$  (Wintner, 2000).

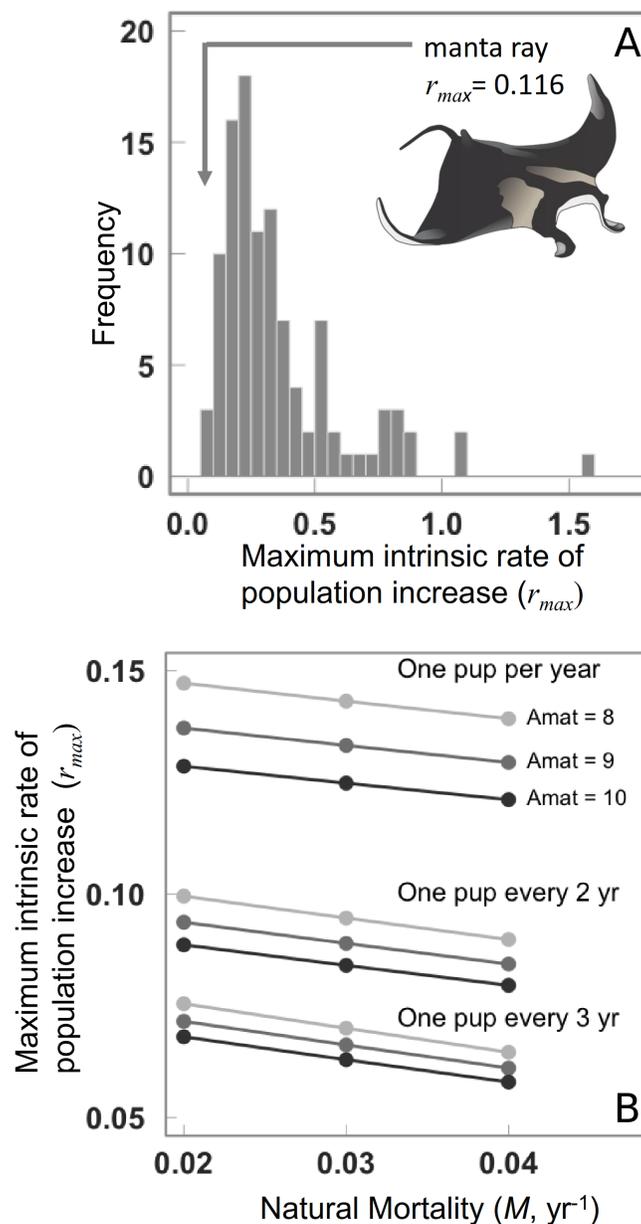
The maximum age of manta rays can be inferred from the longest period of resightings of individuals through photo identification projects (Town, Marshall & Sethasathien, 2013). In Hawai'i one female has been continuously resighted since 1979, providing a minimum estimate of longevity of the *Manta alfredi* 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  $0.05\text{--}0.1\text{ yr}^{-1}$ . 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, Miller & Fogarty, 2001). For a range of  $k$  of  $0.03\text{--}0.1$ , then  $M$  is between  $0.012$  and  $0.04\text{ yr}^{-1}$ .

### Estimation of maximum intrinsic population growth rate

We model parameters encompassing the following ranges:  $k = 0.03\text{--}0.1$ ,  $M = 0.012$  to  $0.04$ , age at maturity =  $8\text{--}10$  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  $\tilde{\alpha}$ ,  $\alpha_{\text{mat}}$  and  $M$  by iteratively solving for  $r_{\text{max}}$  using the `nLminb` optimization function in R statistical software version 2.15 (R Core Team, 2013).

### Manta $r_{\text{max}}$ compared to other sharks and rays

We compared the manta ray  $r_{\text{max}}$  to all available estimates ( $n = 106$ ), comprising 105 published estimates for chondrichthyans (García, Lucifora & Myers, 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, Lucifora & Myers, 2008; Pauly, 2002). There is wide geographic variation in maximum disc width and many *M. alfredi* individuals average around  $400\text{ cm}$  increasing to  $490\text{ cm DW cm}$  (Marshall, Dudgeon & Bennett, 2011). The giant manta ray consistently reaches a maximum size of over  $700\text{ cm DW}$  with anecdotal reports of up to  $910\text{ cm DW}$  (Marshall, Compagno & Bennett, 2009). Here, for graphical purposes we assumed a maximum size of  $600\text{ cm DW}$ .



**Figure 2** Maximum intrinsic rate of population increase for 106 chondrichthyans, and the manta ray. (A) Maximum intrinsic rate of population increase for 106 chondrichthyans, including the manta ray. (B) Sensitivity of manta ray maximum intrinsic rate of population increase to variation in natural mortality rate, age at maturity and annual reproductive rate.

## 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 rays is 0.116 (95th percentile = 0.089–0.139, Fig. 2A). The lowest  $r_{\max}$  value of 0.079 corresponds

to an annual reproductive output,  $\tilde{\alpha} = 0.25$ ,  $\alpha_{\text{mat}} = 10$  years, and natural mortality,  $M = 0.04$ , and the highest  $r_{\text{max}}$  of 0.15 corresponding to  $\tilde{\alpha} = 0.5$ ,  $\alpha_{\text{mat}} = 8$  years, and  $M = 0.012$ .

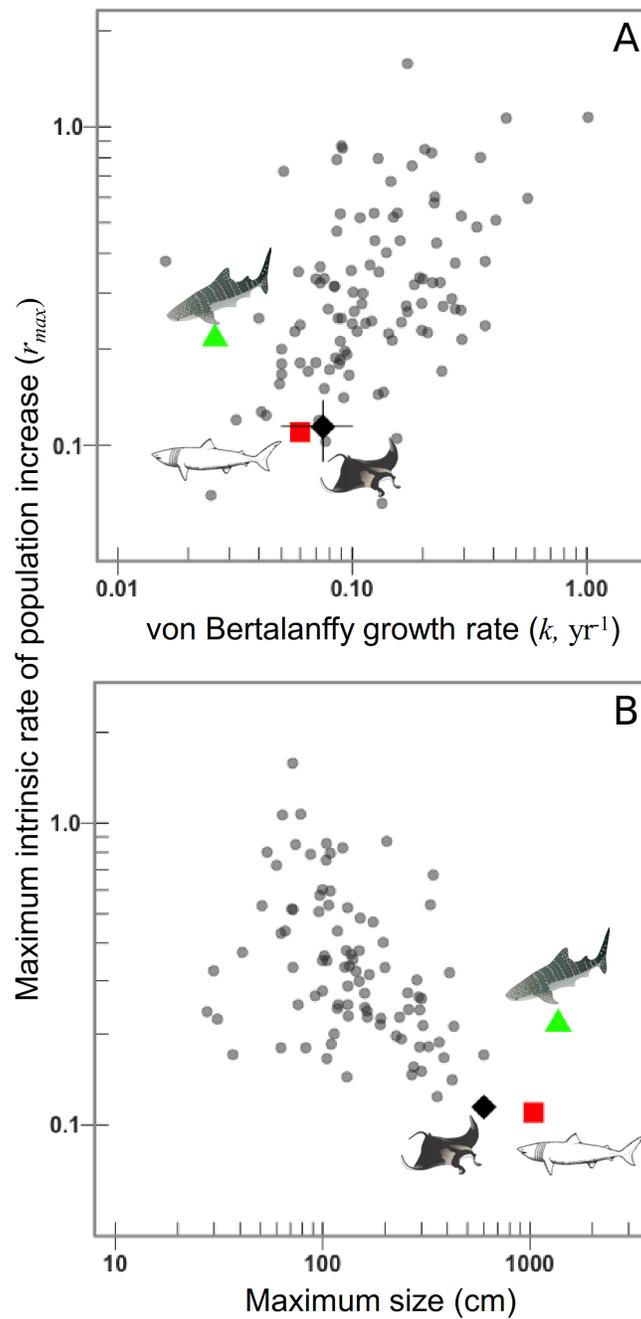
The  $r_{\text{max}}$  decreases considerably when annual reproductive output is lower. The  $r_{\text{max}}$  is most sensitive to annual reproductive output  $\tilde{\alpha}$  compared to the age at maturation  $\alpha_{\text{mat}}$ , note the difference between each  $\tilde{\alpha}$  is greater than among growth rates or ages of maturation (Fig. 2B). The sensitivity to annual reproductive output  $\tilde{\alpha}$  relative to age at maturation  $\alpha_{\text{mat}}$  becomes increasingly important when annual reproductive output is low (Fig. 2B). There is a positive relationship between growth (and hence mortality) and  $r_{\text{max}}$  across species (Fig. 3A), and larger species have lower  $r_{\text{max}}$  (Fig. 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  $r_{\text{max}}$  values (0.116). The  $r_{\text{max}}$  of deepwater sharks ( $n = 14$ ) is significantly lower than for continental shelf and oceanic pelagic species, as revealed by *García, Lucifora & Myers (2008)*. Aside from the deepwater sharks which are all intrinsically sensitive to overfishing (*Simpfendorfer & Kyne, 2009*), in shallower water the species with the lowest  $r_{\text{max}}$  were the temperate basking shark (*Cetorhinus maximus*)  $r_{\text{max}} = 0.109$ , followed by the manta ray ( $r_{\text{max}} = 0.116$ ).

We compared the maximum population growth rate  $r_{\text{max}}$  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 ( $\pm 0.09$  standard error) suggesting  $r_{\text{max}}$  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  $r_{\text{max}}/4 = 0.029$  (95th percentile [0.022–0.35]), 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  $r_{\text{max}}$ —and likely sustainability of even the most difficult-to-study marine animals. Manta rays are data poor but compared to many other chondrichthyans they are still relatively data rich. Of the 1100+ known species, manta rays are among the 106 species for which we can calculate  $r_{\text{max}}$ . Nevertheless, the paucity of life history data for manta rays is very typical of the many data-poor fisheries of the world, particularly in the tropics. But the absence of data should not 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  $r_{\text{max}}$  estimates is narrow (Fig. 2), because life history tradeoffs between maximum asymptotic size and the growth rate narrow the parameter space. It is likely that the range



**Figure 3** Manta rays have low intrinsic rates of population increase due to their slow growth to a very large size. Maximum intrinsic rate of population increase versus, (A) von Bertalanffy growth rate  $k$ , and (B) maximum linear dimension (cm) for 106 chondrichthyans on a logarithmic scale. Whale and basking sharks are highlighted for comparison. Manta ray mean (black diamond) and 95th percentiles.

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,  $r = 0.042\text{--}0.05$  (Ward-Paige, Davis & Worm, 2013), compared to our median  $r_{\max} = 0.116$ . The range of parameters we used encompassed those of Ward-Paige, Davis & Worm (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 population growth rate. We used an elasmobranch-specific mortality estimator (Frisk, Miller & Fogarty, 2001), whereas the other used an estimator based on fishes, molluscs and whales (Hoening, 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, Davis & Worm, 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  $F_{\text{jeopardy}}$  model (Pope et al., 2000; Simpfendorfer, 2005; Smith, Au & Show, 1998).

Without the opportunity to consider juvenile survival rate, our estimates of  $r_{\max}$  may be slightly too high. We implicitly assume that juveniles have the same survival rate as adults. However, a more realistic assumption might be to assume that juvenile survival rate approaches adult survival rate as described by survival to adulthood raised to the power of the age of maturity. Such an approach to juvenile survival would result in smaller  $r_{\max}$  values than we present here (EL Charnov, pers. comm., 2013).

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, Cooper & Dulvy, 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). A non-detriment 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 has been a delay by 18 months until 14th September 2014 (CITES, 2013). By this date, any nation, that is party to the CITES, wishing to trade manta ray gill plates (or other products) 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 coefficient  $k$  from a von Bertalanffy growth curve, fitted appropriately to size-at-age data (Pardo, Cooper & Dulvy, 2013; Smart et al., 2013; Thorson & Simpfendorfer, 2009). Hopefully, the growth coefficient  $k$  can be estimated for manta rays, as has been done for other smaller tropical myliobatoids. However, there is a real possibility that annuli may not be recoverable from manta rays because mobulid vertebrate tend to be poorly calcified (WD Smith, pers. comm., 2012). Hence, resighting programmes may be the most pragmatic method of estimating a growth curve (Town, Marshall & Sethasathien, 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, Miller & Fogarty, 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 ( $L_{\infty}$ ) and growth coefficient ( $k$ ) in elasmobranchs, and especially tropical and subtropical 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, Berrigan & Shine, 1993). 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 are 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 (G Stevens, pers. comm., 2013). The absence of returning pregnant females may indicate a spatial shift of returning females, but also may 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 more details of the temporal and geographic variability in reproductive output 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 coefficient  $k$ , 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 small localized populations 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 declining fish stocks. 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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## ADDITIONAL INFORMATION AND DECLARATIONS

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## Competing Interests

The authors declare there are no competing financial interests.

## Author Contributions

- Nicholas K. Dulvy conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Sebastián A. Pardo conceived and designed the experiments, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- Colin A. Simpfendorfer conceived and designed the experiments, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- John K. Carlson conceived and designed the experiments, wrote the paper, reviewed drafts of the paper.

## Data Deposition

The following information was supplied regarding the deposition of related data:

ChondroRmax140429.xls. Nick Dulvy. figshare.

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<http://dx.doi.org/10.6084/m9.figshare.1009215>—See more at: [http://figshare.com/preview/\\_preview/1009215#reserve\\_citation](http://figshare.com/preview/_preview/1009215#reserve_citation).

## REFERENCES

- Anderson SC, Flemming JM, Watson R, Lotze HK. 2011.** Serial exploitation of global sea cucumber fisheries. *Fish and Fisheries* **12**:317–339 DOI [10.1111/j.1467-2979.2010.00397.x](https://doi.org/10.1111/j.1467-2979.2010.00397.x).
- Baker CS, Clapham PJ. 2004.** Modelling the past and future of whales and whaling. *Trends in Ecology & Evolution* **19**:365–371 DOI [10.1016/j.tree.2004.05.005](https://doi.org/10.1016/j.tree.2004.05.005).
- Beddington JR, Kirkwood GP. 2005.** The estimation of potential yield and stock status using life-history parameters. *Philosophical Transactions of the Royal Society of London, Biological Sciences* **360**:163–170 DOI [10.1098/rstb.2004.1582](https://doi.org/10.1098/rstb.2004.1582).
- Bennett M. 2014.** Peer Review #1 of “Diagnosing the dangerous demography of manta rays using life history theory (v0.1)”. *PeerJ* DOI [10.7287/peerj.400v0.1/reviews/1](https://doi.org/10.7287/peerj.400v0.1/reviews/1).
- Berkes F, Hughes TP, Steneck RS, Wilson JA, Bellwood DR, Crona B, Folke C, Gunderson LH, Leslie HM, Norberg J, Nyström M, Olsson P, Österblom H, Scheffer M, Worm B. 2006.** Globalization, roving bandits, and marine resources. *Science* **311**:1557–1558 DOI [10.1126/science.1122804](https://doi.org/10.1126/science.1122804).

- Beverton RJH, Holt SJ. 1959.** A review of the life-spans and mortality rates of fish in nature and their relationship to growth and other physiological characteristics. *Ciba Foundation Colloquia on Aging* 5:142–180.
- Charnov EL, Berrigan D, Shine R. 1993.** The  $M/k$  ratio is the same for fish and reptiles. *American Naturalist* 142:707–711 DOI 10.1086/285565.
- Charnov EL, Gislason H, Pope JG. 2012.** Evolutionary assembly rules for fish life histories. *Fish and Fisheries* 14:213–224 DOI 10.1111/j.1467-2979.2012.00467.x.
- Charnov EL, Schaffer WM. 1973.** Life-history consequences of natural-selection—Cole’s result revisited. *American Naturalist* 107:791–793 DOI 10.1086/282877.
- Charnov EL, Zuo WY. 2011.** Human hunting mortality threshold rules for extinction in mammals (and fish). *Evolutionary Ecology Research* 13:431–437.
- CITES. 2007.** *Interpretation and implementation of the convention species trade and conservation issues. Conservation of sharks.* The Hague: Convention on the International Trade in Endangered Species, 62.
- CITES. 2013.** *Amendments to appendices I and II of the convention adopted by the Conference of the parties at its 16th meeting, Bangkok (Thailand), 3–14 March 2013.* Geneva: Convention on the International Trade in Endangered Species, 8.
- Clark T. 2010.** Abundance, home range, and movement patterns of manta rays (*Manta alfredi*, *M. birostris*) in Hawaiï, PhD, University of Hawaiï, Manoa.
- Clarke SC. 2004.** Understanding pressures on fishery resources through trade statistics: a pilot study of four products in the Chinese dried seafood market. *Fish & Fisheries* 5:53–74 DOI 10.1111/j.1467-2960.2004.00137.x.
- Clarke SC, McAllister MK, Milner-Gulland EJ, Kirkwood GP, Michielsens CGJ, Agnew DJ, Pikitch EK, Nakano H, Shivji MS. 2006.** Global estimates of shark catches using trade records from commercial markets. *Ecology Letters* 9:1115–1126 DOI 10.1111/j.1461-0248.2006.00968.x.
- Cortés E. 2000.** Life history patterns and correlations in sharks. *Reviews in Fisheries Science* 8:299–344.
- Cortés E. 2002.** Incorporating uncertainty into demographic modelling: application to shark populations and their conservation. *Conservation Biology* 18:1048–1062 DOI 10.1046/j.1523-1739.2002.00423.x.
- Couturier LIE, Marshall AD, Jaine FRA, Kashiwagi T, Pierce SJ, Townsend KA, Weeks SJ, Bennett MB, Richardson AJ. 2012.** Biology, ecology and conservation of the Mobulidae. *Journal of Fish Biology* 80:1075–1119 DOI 10.1111/j.1095-8649.2012.03264.x.
- Cuevas-Zimbrón E, Sosa-Nishizaki O, Pérez-Jiménez JC, O’Sullivan JB. 2012.** An analysis of the feasibility of using caudal vertebrae for ageing the spinetail devilray, *Mobula japonica* (Müller and Henle, 1841). *Environmental Biology of Fishes* 96:907–914 DOI 10.1007/s10641-012-0086-2.
- Dulvy NK, Ellis JR, Goodwin NB, Grant A, Reynolds JD, Jennings S. 2004.** Methods of assessing extinction risk in marine fishes. *Fish and Fisheries* 5:255–275 DOI 10.1111/j.1467-2679.2004.00158.x.
- Dulvy NK, Forrest RE. 2010.** Life histories, population dynamics, and extinction risks in chondrichthyans. In: Carrier JC, Musick JA, Heithaus MR, eds. *Sharks and their relatives II: biodiversity, adaptive physiology, and conservation.* Boca Raton: CRC Press, 635–676.
- Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LNK, Fordham S, Francis MP, Pollock CM, Simpfendorfer CA, Burgess GH, Carpenter KE, Compagno LVJ, Ebert DA, Gibson C, Heupel MR, Livingstone SR,**

- Sanciango JC, Stevens JD, Valenti S, White WT. 2014.** Extinction risk and conservation of the world's sharks and rays. *eLIFE* 3:e00590 DOI 10.7554/eLife.00590.
- FAO. 2013.** *Fourth FAO expert advisory panel for the assessment of proposals to amend Appendices I and II of CITES concerning commercially-exploited aquatic species.* Rome: Food and Agriculture Organization of the United Nations, 169.
- Foster SJ, Vincent ACJ. 2004.** Life history and ecology of seahorses: implications for conservation and management. *Journal of Fish Biology* 65:1–61 DOI 10.1111/j.0022-1112.2004.00429.x.
- Frisk MG, Miller TJ, Fogarty MJ. 2001.** Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences* 58:969–981 DOI 10.1139/f01-051.
- García VB, Lucifora LO, Myers RA. 2008.** The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society of London, B* 275:83–89 DOI 10.1098/rspb.2007.1295.
- Gislason H, Daan N, Rice JC, Pope JG. 2010.** Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries* 11:149–158 DOI 10.1111/j.1467-2979.2009.00350.x.
- Goodwin NB, Dulvy NK, Reynolds JD. 2002.** Life history correlates of the evolution of live-bearing in fishes. *Philosophical Transactions of the Royal Society of London, B* 356:259–267 DOI 10.1098/rstb.2001.0958.
- Heinrichs S, O'Malley M, Medd H, Hilton P. 2011.** Manta ray of hope: global threat to manta and mobula rays. Available at <http://www.mantarayofhope.com>.
- Heppell SS, Crowder LB, Menzel TR. 1999.** Life table analysis of long-lived marine species with implications for conservation and management. In: Musick JA, ed. *Life in the slow lane: ecology and conservation of long-lived marine animals.* Bethesda, Maryland: American Fisheries Society, 137–147.
- Hoening JM. 1983.** Empirical use of longevity data to estimate mortality rates. *Fisheries Bulletin* 81:898–903.
- Hutchings JA. 1999.** Influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. *Canadian Journal of Fisheries and Aquatic Science* 56:1612–1623 DOI 10.1139/f99-088.
- Hutchings JA, Myers RA, Garcia VB, Lucifora LO, Kuparinen A. 2012.** Life-history correlates of extinction risk and recovery potential. *Ecological Applications* 22:1061–1067 DOI 10.1890/11-1313.1.
- IUCN/TRAFFIC. 2013.** IUCN/TRAFFIC analyses of the proposals for CITES CoP15. Available at <http://www.traffic.org/cop16-table/>.
- Jennings S, Dulvy NK. 2008.** Beverton and Holt's insights into life history theory: influence, application and future use. In: Payne AI, Cotter AJR, Potter ECE, eds. *Advances in fisheries Science: 50 years on from Beverton and Holt.* Oxford: Blackwell Publishing, 434–450.
- Jennings S, Mélin F, Blanchard JL, Forster RM, Dulvy NK, Wilson RW. 2008.** Global-scale predictions of community and ecosystem properties from simple ecological theory. *Proceedings of the Royal Society B: Biological Sciences* 275:1375–1383 DOI 10.1098/rspb.2008.0192.
- Jensen AL. 1996.** Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 53:820–822 DOI 10.1139/f95-233.
- Law R. 1979.** Ecological determinants in the evolution of life histories. In: Anderson RM, Turner BD, Taylor LR, eds. *Population dynamics.* Oxford: Blackwell Scientific Publications, 81–103.

- Lenzen M, Moran D, Kanemoto K, Foran B, Lobefaro L, Geschke A. 2012.** International trade drives biodiversity threats in developing nations. *Nature* **486**:109–112 DOI [10.1038/nature11145](https://doi.org/10.1038/nature11145).
- Ludwig D, Hilborn R, Walters C. 1993.** Uncertainty, resource exploitation, and conservation—lessons from history. *Science* **260**:17–36 DOI [10.1126/science.260.5104.17](https://doi.org/10.1126/science.260.5104.17).
- Magnusson A, Punt AE, Hilborn R. 2013.** Measuring uncertainty in fisheries stock assessment: the delta method, bootstrap, and MCMC. *Fish and Fisheries* **14**:325–342 DOI [10.1111/j.1467-2979.2012.00473.x](https://doi.org/10.1111/j.1467-2979.2012.00473.x).
- Marshall AD, Bennett MB. 2010.** Reproductive ecology of the reef manta ray *Manta alfredi* in southern Mozambique. *Journal of Fish Biology* **77**:169–190 DOI [10.1111/j.1095-8649.2010.02669.x](https://doi.org/10.1111/j.1095-8649.2010.02669.x).
- Marshall A, Bennett MB, Kodja G, Hinojosa-Alvarez S, Galvan-Magana F, Harding M, Stevens G, Kashiwagi T. 2011a.** *Manta birostris*. Available at <http://www.iucnredlist.org/details/198921/0> (accessed 04 December 2012).
- Marshall A, Kashiwagi T, Bennett MB, Deakos M, Stevens G, McGregor F, Clark T, Ishihara H, Sato K. 2011b.** *Manta alfredi*. Available at <http://www.iucnredlist.org/details/195459/0> (accessed 04 December 2012).
- Marshall AD, Compagno LJV, Bennett MB. 2009.** Redescription of the genus *Manta* with resurrection of *Manta alfredi* (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). *Zootaxa* **2301**:1–28.
- Marshall AD, Dudgeon CL, Bennett MB. 2011.** Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. *Marine Biology* **158**:1111–1124 DOI [10.1007/s00227-011-1634-6](https://doi.org/10.1007/s00227-011-1634-6).
- Martin LK, Cailliet GM. 1988.** Aspects of reproduction of the bat ray *Myliobatis californica*, in Central California. *Copeia* (3):754–762 DOI [10.2307/1445398](https://doi.org/10.2307/1445398).
- Mundy-Taylor V, Crook V. 2013.** *Into the deep: implementing CITES measures for commercially-valuable sharks and manta rays*. Cambridge: TRAFFIC, 106.
- Musick JA. 1998.** Endangered marine fishes: criteria and identification of North American stocks at risk. *Fisheries* **2**:28–30.
- Musick JA. 1999.** Criteria to define extinction risk in marine fishes. *Fisheries* **24**:6–14 DOI [10.1577/1548-8446\(1999\)024<0006:CTDERI>2.0.CO;2](https://doi.org/10.1577/1548-8446(1999)024<0006:CTDERI>2.0.CO;2).
- Myers RA, Mertz G. 1998.** The limits of exploitation: a precautionary approach. *Ecological Applications* **8**:S165–S169 DOI [10.1890/1051-0761\(1998\)8\[S165:TLOEAP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)8[S165:TLOEAP]2.0.CO;2).
- Neer JA, Thompson BA. 2005.** Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. *Environmental Biology of Fishes* **73**:321–331 DOI [10.1007/s10641-005-2136-5](https://doi.org/10.1007/s10641-005-2136-5).
- O'Malley MP, Lee-Brooks K, Medd HB. 2013.** The global economic impact of manta ray watching tourism. *PLoS ONE* **8**:e65051 DOI [10.1371/journal.pone.0065051](https://doi.org/10.1371/journal.pone.0065051).
- Pardo S, Cooper AB, Dulvy NK. 2012.** *Critical review and analysis of existing risk-based techniques for determining sustainable mortality levels of bycatch species, DFO Can Sci Advis Sec Res Doc*. Ottawa: Fisheries and Oceans Canada. p v + 30.
- Pardo S, Cooper AB, Dulvy NK. 2013.** Avoiding fishy growth curves. *Methods in Ecology and Evolution* **4**:353–360 DOI [10.1111/2041-210x.12020](https://doi.org/10.1111/2041-210x.12020).

- Pauly D. 2002.** Growth and mortality of the Basking Shark *Cetorhinus maximus* and their implications for management of Whale Sharks *Rhincodon typus*. In: Fowler SL, Reed TM, Dipper FA, eds. *Proceedings of the international seminar and workshop, Sabah, Malaysia, July 1997*. Gland and Cambridge: IUCN Species Survival Commission Shark Specialist Group, 199–208.
- Peterman RM. 2004.** Possible solutions to some challenges facing fisheries scientists and managers. *ICES Journal of Marine Science* **61**:1331–1343 DOI [10.1016/j.icesjms.2004.08.017](https://doi.org/10.1016/j.icesjms.2004.08.017).
- Phillis CC, O'Regan SM, Green SJ, Bruce JEB, Anderson SC, Linton JN, Favaro B. 2013.** Multiple pathways to conservation success. *Conservation Letters* **6**:98–106 DOI [10.1111/j.1755-263X.2012.00294.x](https://doi.org/10.1111/j.1755-263X.2012.00294.x).
- Pope JG, MacDonald DS, Daan N, Reynolds JD, Jennings S. 2000.** Gauging the vulnerability of non-target species to fishing. *ICES Journal of Marine Science* **57**:689–696 DOI [10.1006/jmsc.2000.0729](https://doi.org/10.1006/jmsc.2000.0729).
- Pope JG, Shepherd JG, Webb J. 1994.** Successful surf-riding on size spectra: the secret of survival in the sea. *Philosophical Transactions of the Royal Society of London, B* **343**:41–49 DOI [10.1098/rstb.1994.0006](https://doi.org/10.1098/rstb.1994.0006).
- R Core Team. 2013.** *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Sadovy Y, Cheung WL. 2003.** Near extinction of a highly fecund fish: the one that nearly got away. *Fish and Fisheries* **4**:86–99 DOI [10.1046/j.1467-2979.2003.00104.x](https://doi.org/10.1046/j.1467-2979.2003.00104.x).
- Sadovy Y, Vincent AJ. 2002.** Ecological issues and the trades in live reef fishes. In: Sale PF, ed. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. San Diego: Academic Press, 391–420.
- Simpfendorfer CA. 2005.** Demographic models: life tables, matrix models and rebound potential. In: Musick JA, Bonfil R, eds. *Elasmobranch fisheries management techniques*. Rome: Food and Agriculture Organisation of the United Nations, 187–204.
- Simpfendorfer CA, Kyne PM. 2009.** Limited potential to recover from overfishing raises concerns for deep-sea sharks, rays and chimaeras. *Environmental Conservation* **36**:97–103 DOI [10.1017/S0376892909990191](https://doi.org/10.1017/S0376892909990191).
- Smart JJ, Harry AV, Tobin AJ, Simpfendorfer CA. 2013.** Overcoming the constraints of low sample sizes to produce age and growth data for rare or threatened sharks. *Aquatic Conservation-Marine and Freshwater Ecosystems* **23**:124–134 DOI [10.1002/aqc.2274](https://doi.org/10.1002/aqc.2274).
- Smith SE, Au DW, Show C. 1998.** Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **49**:663–678 DOI [10.1071/MF97135](https://doi.org/10.1071/MF97135).
- Thorson JT, Simpfendorfer CA. 2009.** Gear selectivity and sample size effects on growth curve selection in shark age and growth studies. *Fisheries Research* **98**:75–84 DOI [10.1016/j.fishres.2009.03.016](https://doi.org/10.1016/j.fishres.2009.03.016).
- Town C, Marshall A, Sethasathien N. 2013.** Manta Matcher: automated photographic identification of manta rays using keypoint features. *Ecology and Evolution* **3**:1902–1914 DOI [10.1002/ece3.587](https://doi.org/10.1002/ece3.587).
- Vincent ACJ, Sadovy de Mitcheson YJ, Fowler SL, Lieberman S. 2014.** The role of CITES in the conservation of marine fishes subject to international trade. *Fish and Fisheries* DOI [10.1111/faf.12035](https://doi.org/10.1111/faf.12035).
- Ward-Paige CA, Davis B, Worm B. 2013.** Global population trends and human use patterns of *Manta* and *Mobula* rays. *PLoS ONE* **8**:e74835 DOI [10.1371/journal.pone.0074835](https://doi.org/10.1371/journal.pone.0074835).

**Wintner SP. 2000.** Preliminary study of vertebral growth rings in the whale shark, *Rhincodon typus*, from the east coast of South Africa. *Environmental Biology of Fishes* **59**:441–451 DOI [10.1023/A:1026564707027](https://doi.org/10.1023/A:1026564707027).

**Yamaguchi A, Kawahara I, Ito S. 2005.** Occurrence, growth and food of longheaded eagle ray, *Aetobatus flagellum*, in Ariake Sound, Kyushu, Japan. *Environmental Biology of Fishes* **74**:229–238 DOI [10.1007/s10641-005-0217-0](https://doi.org/10.1007/s10641-005-0217-0).