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

2  
3 **Nicholas K. Dulvy<sup>1\*</sup>, Sebastián A. Pardo<sup>1</sup>, Colin A. Simpfendorfer<sup>2</sup>, and John K. Carlson<sup>3</sup>**

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5  
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<sup>-1</sup>(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.

30 **Diagnosing the dangerous demography of manta rays using life history theory**

31

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43

44 **Keywords** | Chinese Traditional Medicine, CITES, data-poor fisheries, wildlife trade, life history  
45 invariant.

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**61 Introduction**

62 The rapid rise in demand for plant and animal products that are traded through international  
63 networks has globalised the reach of economically-powerful consumers to incentivize  
64 unsustainable depletion of biological resources (Berkes et al. 2006; Lenzen et al. 2012). Only in  
65 the past decade have we begun to reveal the enormous scale of trade in aquatic organisms  
66 (Clarke 2004). While we have long understood the challenges of poaching for the illegal ivory  
67 trade (Phillis et al. 2012), we are only now just beginning to reveal the enormous scale of trade in  
68 aquatic organisms, such as for the live food fish trade (Sadovy & Vincent 2002), and the dried  
69 product trade in shark fins (Clarke et al. 2006), seahorses (Foster & Vincent 2004), sea  
70 cucumbers (Anderson et al. 2011), and fish swim bladders (Clarke 2004; Sadovy & Cheung  
71 2003).

72 A recent emerging international trade in Manta and Devil ray gill plates is driving  
73 overexploitation elevating their extinction risk (IUCN/TRAFFIC 2013). There are two Manta  
74 rays (*Manta birostris* (Walbaum 1792), and *M. alfredi* (Krefft, 1868) and at least some of the  
75 nine Devil rays (*Mobula* spp.) reported in national catch statistics and international trade (CITES  
76 2007; Couturier et al. 2012; Ward-Paige et al. 2013). Manta and Devil rays are taken in targeted  
77 fisheries and also as a valuable retained bycatch in China, Ghana, India, Indonesia, Mexico,  
78 Peru, Philippines, Sri Lanka and Thailand (Couturier et al. 2012; IUCN/TRAFFIC 2013). Over  
79 the past decade the landings of Manta and Devil rays have risen more than 10-fold from less than  
80 200 metric tonnes (mt) per year in 1998 to a peak of over 5,000 mt in 2009 (Ward-Paige et al.  
81 2013). Manta and Devil rays are captured for their gill plates and a single mature animal can  
82 yield up to 7 kg of gillrakers which can be worth as much as \$680 per kg in Chinese Traditional  
83 Medicine (Heinrichs et al. 2011; IUCN/TRAFFIC 2013). Much of the international trade goes to  
84 southern China and other cities with large Chinese populations (Couturier et al. 2012; Heinrichs  
85 et al. 2011). One of the authors has seen Devil ray gill plates for sale for \$396.80 per kg (under  
86 the incorrect taxonomic name *Dasyatis Centroura*) in Vancouver, Canada 2013 (Figure 1). The  
87 trade is currently difficult to monitor because of a lack of international trade codes and species-  
88 specific catch and landings data. Despite this, ~21,000kg of dried *Manta* spp. gill plates are  
89 traded annually, derived from an estimated >4,500 individual Manta rays, and worth US \$5  
90 million (Heinrichs et al. 2011; O'Malley et al. 2013).

91

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

112

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

122

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

128

129

### 130 **Materials and methods**

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

139

140 We chose to estimate the extinction risk of Manta rays by calculating the maximum rate of  
 141 population increase using a variant of the Euler-Lotka model (García et al. 2008; Hutchings et al.  
 142 2012). This is one of the oldest and simplest life history models and is founded on the principle  
 143 that a breeding female only has to produce one mature female in her lifetime to ensure a stable  
 144 population size (Charnov & Zuo 2011; Myers & Mertz 1998; Simpfendorfer 2005):

145

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

146

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

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

156  
157 The existence of more than one species of Manta ray was only recently recognized (Marshall et  
158 al. 2009); furthermore, with the geographic overlap and similarity in body sizes we draw upon  
159 the data of both species, to evaluate a generic Manta ray life history.

160  
161 **Annual reproductive output ( $\tilde{\alpha}$ ).** One pup is produced per litter (rarely two) and gestation  
162 period is approximately one year (366–374 days in the Okinawa aquarium) (Couturier et al.  
163 2012). This suggests an annual breeding interval, but there may also be a chance of skipped  
164 breeding or multiannual reproductive cycles. There is evidence for a biennial cycle where 1 pup  
165 is produced every two years (Couturier et al. 2012; Marshall & Bennett 2010). Even more  
166 extreme example is the recent discovery of a complete absence of pregnant females for four  
167 years in the Maldives Islands, following three biennial cycles, which could be interpreted as one  
168 pup every five years (personal communication; Guy Stevens, Environment Department,  
169 University of York, UK). Similar patterns of skipped reproduction have been noted in Japanese  
170 waters (Tom Kashiwagi, School of Biomedical Sciences, University of Queensland, Queensland  
171 4072, Australia). Assuming an even sex ratio, a plausible range would be an annual reproductive  
172 output averaging 0.25 to 0.5 female pups per year, but consider extremes out to an annual  
173 reproductive output 0.1 (1 female pup every five years). Because of the modeling approach, we  
174 do not consider juvenile mortality and we expect Manta pups to have low mortality due to their  
175 extremely large size in comparison to other sharks and rays. Mortality patterns are strongly size-  
176 dependent in the ocean and hence larger individuals are likely to have much higher survival rates  
177 (Charnov et al. 2012; Gislason et al. 2010; Pope et al. 1994). Manta offspring are some of the  
178 largest offspring of any ectotherm in the ocean. The size of birth of Manta pups is 130-150 cm  
179 disc width, considering the maximum linear dimension this one of the largest of any  
180 elasmobranch. The maximum linear dimensions of offspring sizes of 274 elasmobranchs ranged  
181 from 6.8 cm in Cuban pygmy skate (*Fenestraja cubensis*) to 175 cm in the basking shark  
182 (*Cetorhinus maximus*), and the size at birth disc width of a Manta ray of 130-150 cm lies in the

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

185

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

189

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

193

194 There is no growth curve available for Manta rays, however we can draw some inference as to  
195 the plausible range because fish growth parameters are narrowly constrained and highly  
196 correlated because of fundamental life history tradeoffs (Charnov et al. 2012). The rate of  
197 somatic growth ( $k$ ) is negatively-related to the asymptotic maximum size ( $L_{\infty}$ ) within a narrow  
198 range (Jensen 1996). Hence, we review the von Bertalanffy growth curves of larger tropical  
199 batoids (>1 m) to guide the choice of a plausible range of  $k$  for Manta rays. The available growth  
200 rates for species with similar lifestyles, tropical and subtropical myliobatoid rays (Table 1) and  
201 the tropical planktivorous whale shark, reveals that most  $k$  values lie between 0.009 yr<sup>-1</sup> and 0.28  
202 yr<sup>-1</sup> (Table 1). It might be expected that this range of  $k$  would be on the high end for Manta rays  
203 because they reach a considerably larger size. While known from temperate regions, they are  
204 typically found in warm tropical and subtropical water. They are planktivores and hence can  
205 access a much larger food resource base and higher growth might be expected at high  
206 temperatures. There is some evidence that planktivores grow quickly because their feeding mode  
207 is more energetically profitable when individuals (and their gape) reach a larger size.  
208 Comparisons to whale shark would suggest Manta  $k$  values around 0.03-0.04 yr<sup>-1</sup> (Wintner  
209 2000).

210

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



213 been continuously resighted since 1979, providing a minimum estimate of longevity of 31 years  
214 (Clark 2010). The inferred Manta ray maximum age of >31 years is considerably higher than the  
215 19 to 25 years for *Aetobatis flagellum*, *Myliobatis californicus* and *Rhinoptera bonasus*, so a  
216 more plausible range for  $k$  might be 0.05-0.1 yr<sup>-1</sup>. Life history invariants can be used to estimate  
217 mortality from growth rate, assuming an  $M/k$  ratio of 0.4 which is more typical for elasmobranch  
218 fishes than the higher ratio of  $M/k = 1.5$  observed in teleost fishes and reptiles (Frisk et al. 2001).  
219 For a range of  $k$  of 0.05-0.1, then  $M$  is between 0.02 and 0.04.

220

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

230

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

243

244 **Results**

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

250  
251 The  $r_{max}$  decreases considerably when annual reproductive output is lower. The  $r_{max}$  is most  
252 sensitive to annual reproductive output  $\tilde{\alpha}$  compared to the age at maturation  $\alpha_{mat}$ , note the  
253 difference between each  $\tilde{\alpha}$  is greater than among growth rates or ages of maturation (Figure 2b).  
254 The sensitivity to annual reproductive output  $\tilde{\alpha}$  relative to age at maturation  $\alpha_{mat}$  becomes  
255 increasingly important when annual reproductive output is low (Figure 2b). There is a positive  
256 relationship between growth (and hence mortality) and  $r_{max}$  across species (Figure 3a), and larger  
257 species have lower  $r_{max}$  (Figure 3b).

258  
259 Of the 106 species for which we could calculate the maximum intrinsic rate of population  
260 increase, the Manta ray had one of the lowest  $r_{max}$  values (0.113). The  $r_{max}$  of deepwater sharks ( $n$   
261 = 14) is significantly lower than for continental shelf and oceanic pelagic species, as revealed by  
262 García et al. (2008). Aside from the deepwater sharks which are all intrinsically sensitive to  
263 overfishing (Simpfendorfer & Kyne 2009), in shallower water the species with the lowest  $r_{max}$   
264 were the temperate basking shark (*Cetorhinus maximus*)  $r_{max} = 0.109$ , followed by the Manta ray  
265 ( $r_{max} = 0.114$ ).

266  
267 We compared the maximum population growth rate  $r_{max}$  as calculated from the modified Euler-  
268 Lotka models and the population growth rate  $r$  (which equals  $\ln[\lambda]$ ) as calculated from age-  
269 structured models (Cortés 2002). We found both measure of population growth significantly  
270 related, but the slope of the relationship was 0.26 ( $\pm 0.09$  standard error) suggesting  $r_{max}$  is  
271 typically four times greater than  $r$  ( $F_{1,27} = 8.09$ ,  $p = 0.008$ , adjusted  $r^2 = 0.2$ ). Hence, in assessing  
272 the productivity of species against the criteria of Food and Agriculture Organization of the  
273 United Nations (Musick 1998), it might be more precautionary to estimate  $r$  as  $r_{max} / 4 = 0.029$   
274 (95% CI = 0.022-0.34), and hence Manta ray has “very low” productivity ( $<0.05$ ).

275 **Discussion**

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

290  
291 We find that the maximum rate of population increase is slightly higher than a recent estimate of  
292 the intrinsic rate of population increase,  $r = 0.042-0.05$  (Ward-Paige et al. 2013), compared to  
293 our median  $r_{max} = 0.11$ . The range of parameters we used encompassed those of Ward-Paige et  
294 al. (2013) and suggest the difference in  $r$  versus  $r_{max}$  may be due to differences in the method  
295 used to estimate natural mortality and that the rebound potential method consistently provides  
296 lower growth rate. We used an elasmobranch-specific mortality estimator (Frisk et al. 2001),  
297 whereas the other used an estimator based on fishes, molluscs and whales (Hoenig 1983). A  
298 more puzzling issue is why our approach reveals that Manta rays have one of the lowest  $r_{max}$  of  
299 any chondrichthyan, whereas the other suggests Manta rays may have an intermediate  $r$  (Ward-  
300 Paige et al. 2013). This issue is beyond the scope of this paper, and requires a simulation-based  
301 performance comparison of these kinds of models. While close, the difference in demographic  
302 estimates underscores the need for a better understanding of such rule-of-thumb mortality  
303 estimators and a comparison of the performance of different variants of simple scalar  
304 unstructured demographic models, such as the Euler-Lotka model, the rebound potential model,  
305 and Pope's *Fjeopardy* model (Pope et al. 2000; Simpfendorfer 2005; Smith et al. 1998).

306

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

315

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

336

337 Our analysis reveals that a key parameter to estimate in future field studies are the growth rate  $k$   
338 from a von Bertalanffy growth curve, fitted appropriately to size at age data (Pardo et al. 2013;  
339 Smart et al. 2013; Thorson & Simpfendorfer 2009). Hopefully, the growth rate  $k$  can be  
340 estimated for Manta rays, as has been done for other smaller tropical myliobatoids (Table 1).  
341 However, there is a real possibility that annuli may not be recoverable from Manta rays because  
342 mobulid vertebrate tend to be poorly calcified (personal communication, Wade Smith, Oregon  
343 State University, Corvallis, Oregon, USA). Hence mark-recapture tagging or resighting  
344 programmes may be the most pragmatic method of estimating a growth curve (Town et al.  
345 2013). As we have shown, natural mortality rate depends heavily on  $k$  and the ratio of  $M/k$ ,  
346 which is around 0.4 for elasmobranchs (Frisk et al. 2001). If it is not possible to estimate a  
347 growth curve for Manta rays in the near future then demographic modeling will be heavily  
348 reliant on our understanding of: (1) the overall pattern of maximum size ( $L_{\infty}$ ) and growth rate ( $k$ )  
349 in elasmobranchs, and especially tropical batoids, and (2) the  $M/k$  ratio. Future work should  
350 concentrate on understanding why the elasmobranch  $M/k$  ratio is around 0.4, by comparison the  
351 teleost and reptile  $M/k$  ratio is around 1.5 (Charnov et al. 1993). Why is this so? This ratio has a  
352 profound influence on the estimate of population growth rate and the sustainability of species,  
353 and hence understanding the life histories, ecological and environmental correlates of the  $M/k$   
354 ratio can only improve the predictive power of these simple demographic models.

355  
356 Other parameters that strongly influence the maximum intrinsic rate of population increase are  
357 the age at maturation and the annual reproductive rate. These parameters very poorly understood  
358 (Marshall & Bennett 2010). The Manta ray annual reproductive rate estimates of one pup per  
359 year are based on aquarium-held specimens under relatively ideal conditions, and hence these  
360 estimates are likely to be optimistic. There is unpublished evidence suggesting that annual  
361 reproductive rates may be much, much lower and variable among and within individuals. The  
362 proportion of pregnant females returning to long-term (6-8 years) study sites in the Maldives  
363 previously suggested a biennial reproductive mode, but in recent years no pregnant females have  
364 returned (Guy Stevens, Environment Department, University of York, UK; personal  
365 communication). The absence of returning pregnant females may indicate a spatial shift of  
366 returning females, but also may presage reproductive failure and hint at much lower and more  
367 variable annual rates of reproductive output than we have modeled here. We recommend that the

368 demographic rates of Manta rays be revised as greater detail of temporal and geographic  
369 variability come to light. The emerging observations of year-to-year variation in individual  
370 reproductive output may lead to variance in year-to-year population growth rate which can only  
371 serve to depress the long-term population growth rate further elevating extinction risk (Hutchings  
372 1999). And indeed such observations caution us to initiate and undertake local analyses of  
373 population structure and reproductive activity and to incorporate local variations into local  
374 demographic models and assessments contribution to CITES Non-Detriment Findings. Of course  
375 the greatest uncertainty, that we have entirely overlooked, is that future demographic estimates  
376 would benefit greatly from species-specific estimates of the key life history parameters: growth  
377 rate  $k$ , annual reproductive rate and age at maturity.

378  
379 Notwithstanding the current uncertainty in the life history of Manta rays, given their very low  
380 productivity coupled with low localized population size and predictable seasonal aggregations,  
381 the unregulated targeting of local Manta populations for their high-value gill plates is unlikely to  
382 be sustainable. The largest targeted fisheries and highest mortality occurs in Indonesia, Sri  
383 Lanka, India, Peru and Mozambique and these countries have little fisheries monitoring,  
384 regulation or effective enforcement. The time to local extinction depends on the size of the  
385 population and the rate of fishing mortality. The very low productivity of Manta rays mean that  
386 even a moderate level of fishing mortality of  $F = 0.2$  (survival = 0.81) would reduce a small  
387 population of 100 individuals to fewer than 10 within less than a generation span (11 years). The  
388 key challenge this poses is that it leaves little time to mount an effective conservation  
389 management response. These serial depletion fisheries are operated by low-income subsistence  
390 coastal fishers, often against a backdrop of collapsing fisheries. For such fishers the international  
391 market demand for valuable Manta and mobulid ray gill plates is likely to provide a desirable  
392 income. Such fisheries tend to be unregulated and even if there are protections these are difficult  
393 to enforce, which underscores the importance of international trade regulation.

394

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- 564
- 565

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

Species name	IUCN Status <sup>1</sup>	Sex	Maximum length (cm) <sup>2</sup>	Maximum age (years)	$L_{\infty}$	$k$	Reference
<i>a. Mobula japonica</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)

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

570 <sup>2</sup>Disc width (cm) for rays and total length (cm) for whale shark.

571 **FIGURE 1.**

572 Gill plates, tentatively identified as from the Sickie-fin Devil ray *Mobula tarapacana* (Philippi,  
573 1892), for public sale in downtown Vancouver, British Columbia, Canada on 26<sup>th</sup> April 2013:  
574 photo credit Nicholas K. Dulvy.

575



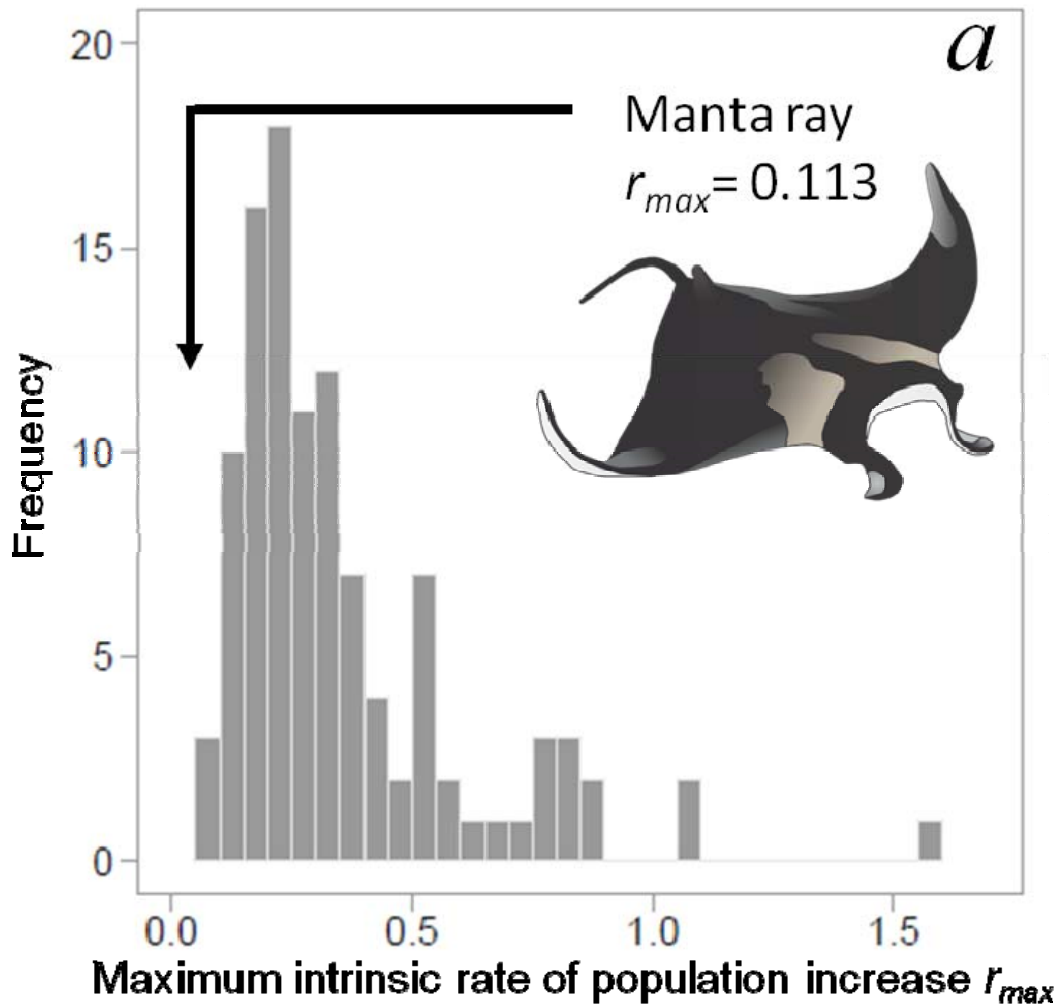


576 **FIGURE 2.**

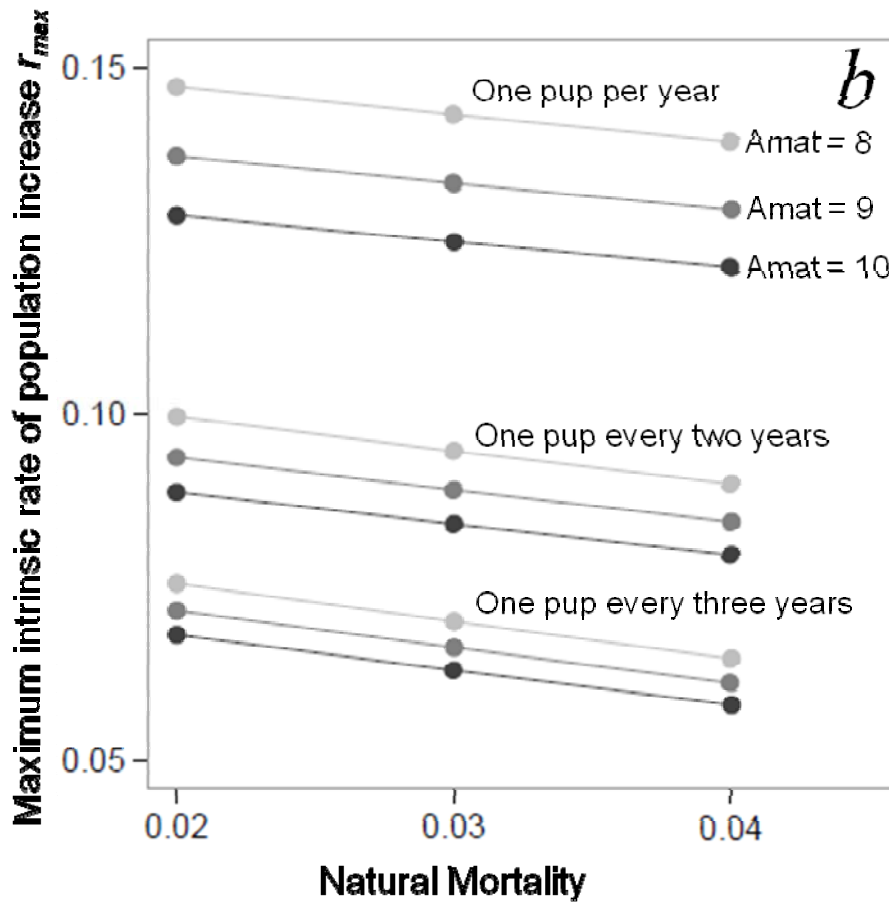
577 (a) Maximum intrinsic rate of population increase for 106 chondrichthyans, including the Manta

578 ray.

579



580 **FIGURE 2.**  
581 (b) Sensitivity of Manta ray maximum intrinsic rate of population increase to variation in  
582 growth rate, age at maturity and annual reproductive rate.  
583



584 **FIGURE 3.**  
 585 Maximum intrinsic rate of population increase versus, (a) growth rate, and (b) maximum size for  
 586 106 chondrichthyans on a logarithmic scale. Whale and basking sharks are highlighted for  
 587 comparison.

