Diagnosing the dangerous demography of manta rays using life history theory

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^{-1}(CI: 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 this 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 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.

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

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13 *Mobula*.

14 **Introduction**

15   The rapid rise in demand for plant and animal products that are traded through international

16   networks has globalised the reach of economically-powerful consumers causing unsustainable

17   depletion of biological resources (Berkes et al. 2006; Lenzen et al. 2012). While we have long

18   understood the challenges of poaching for the illegal ivory trade (Phillis et al. 2013), we are only

19   now just beginning to reveal the enormous scale of trade in aquatic organisms, such as for the

20   live food fish trade (Sadovy & Vincent 2002), and the dried product trade in shark fins (Clarke et

21   al. 2006), seahorses (Foster & Vincent 2004), sea cucumbers (Anderson et al. 2011), and fish

22   swim bladders (Clarke 2004; Sadovy & Cheung 2003).

23   A recent emerging international trade in manta and devil ray gill plates is driving overexploitation

24   elevating their extinction risk (IUCN/TRAFFIC 2013). The high value of gill plates and the

25   international nature of the trade are driving roving bandit dynamics, incentivising serial depletion

26   and a globalized tragedy of the commons (Berkes et al. 2006). If the population growth rate of

27   manta rays is low this pattern of exploitation could lead to rapid depletions and local extinction of

28   manta populations. There are two described species of manta ray *Manta birostris* (Walbaum,

29   1792), and *M. alfredi* (Krefft, 1868) and at least some of the nine devil rays (*Mobula* spp.) are

30   reported in national catch statistics and appear in international trade (CITES 2007; Couturier et

31   al. 2012; Ward-Paige et al. 2013). Manta and devil rays are taken in targeted fisheries and also as

32   a valuable retained bycatch in China, Ghana, India, Indonesia, Mexico, Peru, Philippines, Sri

33   Lanka and Thailand (Couturier et al. 2012; IUCN/TRAFFIC 2013). Over the past decade the

34   landings of manta and devil rays have risen more than 10-fold from less than 200 tonnes (t) per

35   year in 1998 to a peak of over 5,000 t in 2009 (Ward-Paige et al. 2013). Manta and devil rays are

36   captured for their gill plates and a single mature animal can yield up to 7 kg of gillrakers which

37   can be worth as much as $680 per kg in Chinese medicine (Heinrichs et al. 2011;

38   IUCN/TRAFFIC 2013). Much of the international trade goes to southern China, and to Chinese

39   communities in other countries (Couturier et al. 2012; Heinrichs et al. 2011). For example, one

40   of the authors has seen devil ray gill plates for sale for $396.80 per kg (under the incorrect

41   taxonomic name *Dasyatis Centroura*) in Vancouver, Canada 2013 (Figure 1). The trade is

42   currently difficult to monitor because of a lack of international trade codes and species-specific

43   catch and landings data. Despite this, ~21,000kg of dried *Manta* spp. gill plates are traded

44   annually, derived from an estimated >4,500 individual manta rays, and worth US $5 million

45   (Heinrichs et al. 2011; O'Malley et al. 2013).

46 Many (46%) of chondrichthyans are Data Deficient (Dulvy et al. 2014), and in comparison to the

47 data-sufficient species we know little of the life history of manta rays *Manta birostris* (Walbaum

48 1792), and *M. alfredi* (Krefft, 1868). This is particularly problematic when their viability is

49 threatened by rapidly emerging fisheries driven by international trade demand, and CITES Non-

50 Detriment Findings are required for continued international trade (Clarke 2004; Couturier et al.

51 2012). Both manta rays were listed as Vulnerable on the International Union for the Conservation

52 of Nature Red List of Threatened Species in 2011 because of the inferred global decline due to

53 directed gill-plate fisheries and their inferred slow life histories (Marshall et al. 2011a; Marshall

54 et al. 2011b). Moreover, recognizing this threat, Brazil, Colombia and Ecuador successfully

55 proposed *Manta* spp. for inclusion in Appendix II of the Convention on International Trade in

56 Endangered Species of Wild Fauna and Flora (CITES). These listings will come into force on

57 14th September 2014, by which time their international trade will only be allowed if: (1)

58 specimens were legally sourced, and (2) the export is not detrimental to wild populations of the

59 species (a non-detriment finding, NDF) (Mundy-Taylor & Crook 2013; Vincent et al. 2013).

60 Non-detriment findings rely on the ability to assess the sustainability of removals of individuals

61 for the international trade from national populations. One of the principal challenges of assessing

62 sustainability is that there is often a high degree of uncertainty in the population biology of

63 species, and the pattern and rate of exploitation (Ludwig et al. 1993). However, decisions on the

64 sustainability of fisheries and trade often have to be made without the benefit of sufficient

65 information. Recent advances have made it possible to account for sources of uncertainty and this

66 is increasingly an important part of the decision-making process in fisheries management and

67 conservation (Baker & Clapham 2004; Magnusson et al. 2012; Peterman 2004).

68 One approach to dealing with uncertainty in life histories is to draw upon life history tradeoff

69 rules that constrain the range of plausible trait values (Beverton & Holt 1959; Law 1979). There

70 are fundamental constraints to the acquisition, allocation and metabolism of energy resulting in a

71 narrow set of rules of life (Dulvy & Forrest 2010; Jennings & Dulvy 2008). These rules can be

72 used to choose a plausible range of life history traits, which when combined with simple methods

73 to propagate the uncertainty in the true trait value, can be used to provide powerful insights into

74 demography and fisheries sustainability (Beddington & Kirkwood 2005). Recent work using a

75 simple life history model suggests manta rays are intrinsically sensitive and have low capacity to

76 rebound from even low levels of fishing mortality (Ward-Paige et al. 2013).

77 Here, we examine the potential risk to manta ray populations from fishing to supply the dried gill

78 plate trade. Specifically, we calculate the maximum intrinsic rate of population increase (r_{max}) of

79 manta rays, and compare their demography to other sharks and rays. Our model and approach

80 provides a demographic basis for evaluating the sustainability, or otherwise, of manta fisheries, in

81 the face of considerable uncertainty in their life history.

82 **Materials and methods**

83 We first outline the Euler-Lotka life history model and the three key parameters required to

84 estimate the maximum rate of population increase (r_{max}): the annual rate of production of female

85 offspring ($\tilde{\alpha}$), age at maturity (α_{mat}), and the instantaneous natural mortality rate (M). Second,

86 we describe plausible ranges for each of those parameters for a generic manta ray life history.

87 Third, we use a Monte Carlo procedure to propagate the uncertainty these three life history

88 parameters through the Euler-Lotka model to calculate a distribution of the plausible range of

89 manta ray maximum rate of population increase r_{max}. Finally, we compare the demography of the

90 manta ray to the life histories and demography of 106 other sharks and rays.

91 We chose to estimate the extinction risk of manta rays by calculating the maximum rate of

92 population increase using a variant of the Euler-Lotka model (García et al. 2008; Hutchings et al.

93 2012). This is one of the oldest and simplest life history models and is founded on the principle

94 that a breeding female only has to produce one mature female in her lifetime to ensure a stable

95 population size (Charnov & Schaffer 1973; Charnov & Zuo 2011; Myers & Mertz 1998;

96 Simpfendorfer 2005):

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

97 where $\tilde{\alpha}$ is the annual rate of production of female offspring. Here we calculated $\tilde{\alpha}$ as l/i

98 *0.5, where is l litter size and i is breeding interval, corrected for sex ratio i.e. 0.5). α_{mat} is age at

99 maturity, and p is the adult survival rate, where $p = e^{-M}$, where M is the instantaneous natural

100 annual mortality rate yr^{-1}. While local aggregations of manta rays may be sex-biased we assume

101 an even sex ratio at the, wider, species level. The simple elegance of the model is that it requires

102 only estimates of three biological parameters: annual reproductive output ($\tilde{\alpha}$), age at maturity

103 (α_{mat}), and natural mortality (M). Two of these parameters are highly uncertain ($\tilde{\alpha}$ and α_{mat}) and

104 the other (M) is estimated indirectly, which can also result in uncertainty. Hence, we aim to

105 estimate a range of r_{max} to encompass the widest range of life histories that are plausible for manta

106 rays and hence would encompass the true parameter values.

107 The existence of more than one species of manta ray was only recently recognized (Marshall et

108 al. 2009); furthermore, with the geographic overlap and in the absence of sufficient evidence to

109 differentiate the life history traits required by the model we thought it most defensible to evaluate

110 a generic manta ray life history.

111 **Annual reproductive output ($\tilde{\alpha}$).** One pup is produced per litter (rarely two) and gestation

112 period is approximately one year (366–374 days in the Okinawa aquarium) (Couturier et al.

113 2012). This suggests at least an annual breeding interval, but there may also be a chance of

114 skipped breeding or multiannual reproductive cycles. There is evidence for a biennial cycle where

115 1 pup is produced every two years (Couturier et al. 2012; Marshall & Bennett 2010). Even more

116 extreme example is the recent discovery of a complete absence of pregnant females for four years

117 in the Maldive Islands, following three biennial cycles, which could be interpreted as one pup

118 every five years (personal communication; Guy Stevens, Environment Department, University of

119 York, UK). Similar patterns of skipped reproduction have been noted in Japanese waters (Tom

120 Kashiwagi, School of Biomedical Sciences, University of Queensland, Queensland 4072,

121 Australia). It is worth noting that extended periods of 'non-pregnancy' may be an artifact of

122 occasional sightings and / or poor viewing angles (M. B. Bennett, University of Queensland,

123 Australia, pers. comm.). As is typical in demographic modeling we assume an even sex ratio.

124 Under these assumptions a plausible range would be an annual reproductive output averaging

125 0.25 to 0.5 female pups per year, but we considered extremes out to an annual reproductive

126 output 0.1 (1 female pup every five years). Because of the simple tractable nature of our

127 modeling approach, we did not have the opportunity to consider juvenile mortality. However,

128 juvenile survival may not be of overriding importance for overall population growth rate, because

129 they are likely to have low mortality and contribute relatively little to population growth rate

130 compared to sub-adults (Heppell et al. 1999). We expect manta pups to have low mortality due to

131 their extremely large size in comparison to other sharks and rays. Mortality patterns are strongly

132 size-dependent in the ocean and hence larger individuals are likely to have much higher survival

133 rates (Charnov et al. 2012; Gislason et al. 2010; Pope et al. 1994). Manta offspring are some of

134 the largest offspring of any ectotherm in the ocean. The size of birth of manta pups is 130-150 cm

135 disc width, considering the maximum linear dimension this is one of the largest of any

136 elasmobranch. The maximum linear dimensions of offspring sizes of 274 elasmobranchs ranged

137 from 6.8 cm in Cuban pygmy skate (*Fenestraja cubensis*) to 175 cm in the basking shark

138 (*Cetorhinus maximus*), and the size at birth disc width of a manta ray of 130-150 cm lies in the

139 upper 95th percentile of the distribution of maximum linear dimension of size at birth or hatch of

140 these elasmobranchs (Cortés 2000; Goodwin et al. 2002; Jennings et al. 2008). As survival

141 information becomes available, future models that account for age and stage-specific mortality

142 are likely to provide more nuanced insights into manta ray demography.

143 **Age at maturity (α_{mat}).** Male reef manta rays (*M. alfredi*) mature at 3–6 years in Hawaii and

144 female maturity is subject to considerable debate, and for our purposes is inferred to be 8-10

145 years (Marshall et al. 2011b).

146 **Natural mortality (M)** can be estimated indirectly from the von Bertalanffy growth coefficient

147 (k) or can be assumed to be the reciprocal of lifespan, 1/maximum age (Charnov et al. 2012;

148 Dulvy et al. 2004; Pauly 2002). Here we draw inferences from both approaches.

149 There is no growth curve available for manta rays, however we can draw some inference as to the

150 plausible range because fish growth parameters are narrowly constrained and highly correlated

151 because of fundamental life history tradeoffs (Charnov et al. 2012). The rate of somatic growth

152 (as indexed by the von Bertalanffy growth coefficient, k) is negatively-related to the asymptotic

153 maximum size (L_∞) within a narrow range (Jensen 1996). Hence, we review the von Bertalanffy

154 growth curves of larger tropical batoids (>1 m) to guide the choice of a plausible range of k for

155 manta rays. The available growth rates for species with similar lifestyles, tropical and subtropical

156 myliobatoid rays (Table 1) and the tropical planktivorous whale shark, reveals that most k values

157 lie between 0.009 yr^{-1} and 0.28 yr^{-1} (Table 1). It might be expected manta rays would have k

158 values toward the lower end of this range because they reach a considerably larger size than most

159 of these myliobatoid rays. While known from temperate regions, they are typically found in

160 warm tropical and subtropical water. They are planktivores and hence can access a much larger

161 food resource base and higher growth might be expected at high temperatures. There is some

162 evidence that planktivores grow quickly because their feeding mode is more energetically

163 profitable when individuals (and their gape) reach a larger size. Comparisons to whale shark and

164 the slower growing myliobatoid rays would suggest manta k values around 0.03-0.04 yr^{-1}

165 ([Wintner 2000](#)).

166 The maximum age of manta rays can be inferred from the longest period of resightings of

167 individuals through photo identification projects ([Town et al. 2013](#)). In Hawai'i one female has

168 been continuously resighted since 1979, providing a minimum estimate of longevity of the

169 *Manta alfredi* of 31 years ([Clark 2010](#)). The inferred manta ray maximum age of >31 years is

170 considerably higher than the 19 to 25 years for *Aetobatis flagellum, Myliobatis californicus* and

171 *Rhinoptera bonasus*, so a more plausible range for k might be 0.05-0.1 yr^{-1}. Life history invariants

172 can be used to estimate mortality from growth rate, assuming an M/k ratio of 0.4 which is more

173 typical for elasmobranch fishes than the higher ratio of $M/k = 1.5$ observed in teleost fishes and

174 reptiles ([Frisk et al. 2001](#)). For a range of k of 0.03-0.1, then M is between 0.012 and 0.04 yr^{-1}.

175 We model parameters encompassing the following ranges: k = 0.03-0.1, M = 0.012 to 0.04, age at

176 maturity = 8-10 years and an annual reproductive rate of 0.25 to 0.5 female pups per year. To

177 propagate the uncertainty inherent in these parameter ranges, we drew 10,000 values of each

178 parameter from a random uniform distribution bounded by the plausible range of each. While life

179 history traits are typically distributed around a mean value in a Gaussian manner, we choose a

180 more conservative uniform distribution to explore the full range of parameter space. Maximum

181 intrinsic population growth rate was calculated for the 10,000 triplets of $\tilde{\alpha}$, α_{mat} and M by

182 iteratively solving for r_{max} using the `nlminb` optimization function in R statistical software

183 version 2.15 ([R Core Team 2013](#)).

184 We compared the manta ray r_{max} to all available estimates (n=106), comprising 105 published

185 estimates for chondrichthyans ([García et al. 2008](#)), to which we added the filter-feeding CITES-

186 listed basking shark (*Cetorhinus maximus*) which has an M of 0.024 (based on a growth

187 coefficient k of 0.067), age at maturity of 10, and an annual reproductive output of 1.5 females

188 per litter every two years (assuming an 18 month pregnancy) ([Pauly 2002](#)). For plotting, we

189 extracted all maximum sizes as the total length in centimeters, except for Myliobatiformes and

190 Chimaeriformes for which we used disc width and fork length, respectively (García et al. 2008;

191 Pauly 2002). There is wide geographic variation in maximum disc width and many *M. alfredi*

192 individuals average around 400 cm increasing to 490 cm DW cm (Marshall et al. 2011c). The

193 giant manta ray consistently reaches a maximum size of over 700 cm DW with anecdotal reports

194 of up to 910 cm DW (Marshall et al. 2009). Here, for graphical purposes we assumed a

195 maximum size of 600 cm DW.

196 **Results**

197 Assuming that the range of life histories explored encompasses our current knowledge, then the

198 median maximum intrinsic rate of population increase r_{max} for manta ray is 0.116 (95%

199 Confidence Interval = 0.089-0.139, Figure 2*a*). The lowest r_{max} value of 0.079 corresponds to an

200 annual reproductive output, $\tilde{\alpha}$ = 0.25, α_{mat} = 10 years, and natural mortality, M = 0.04, and the

201 highest r_{max} of 0.15 corresponding to $\tilde{\alpha}$ = 0.5, α_{mat} = 8 years, and M = 0.012.

202 The r_{max} decreases considerably when annual reproductive output is lower. The r_{max} is most

203 sensitive to annual reproductive output $\tilde{\alpha}$ compared to the age at maturation α_{mat}, note the

204 difference between each $\tilde{\alpha}$ is greater than among growth rates or ages of maturation (Figure

205 2*b*). The sensitivity to annual reproductive output $\tilde{\alpha}$ relative to age at maturation α_{mat} becomes

206 increasingly important when annual reproductive output is low (Figure 2*b*). There is a positive

207 relationship between growth (and hence mortality) and r_{max} across species (Figure 3*a*), and larger

208 species have lower r_{max} (Figure 3*b*).

209 Of the 106 species for which we could calculate the maximum intrinsic rate of population

210 increase, the manta ray had one of the lowest r_{max} values (0.116). The r_{max} of deepwater sharks (n =

211 14) is significantly lower than for continental shelf and oceanic pelagic species, as revealed by

212 García et al. (2008). Aside from the deepwater sharks which are all intrinsically sensitive to

213 overfishing (Simpfendorfer & Kyne 2009), in shallower water the species with the lowest r_{max}

214 were the temperate basking shark (*Cetorhinus maximus*) r_{max} = 0.109, followed by the manta ray

215 (r_{max} = 0.114).

216 We compared the maximum population growth rate r_{max} as calculated from the modified Euler-

217 Lotka models and the population growth rate r (which equals ln[λ]) as calculated from age-

218 structured models (Cortés 2002). We found both measure of population growth significantly

219 related, but the slope of the relationship was 0.26 (± 0.09 standard error) suggesting r_{max} is

220 typically four times greater than r ($F_{1,27}$ = 8.09, p = 0.008, adjusted r^2 = 0.2). Hence, in assessing

221 the productivity of species against the criteria of Food and Agriculture Organization of the United

222 Nations (Musick 1998), it might be more precautionary to estimate r as r_{max} / 4 = 0.029 (95% CI =

223 0.022-0.35), and hence manta ray has "very low" productivity (<0.05).

224 **Discussion**

225 we show how life history theory can be used to guide the estimation of an important demographic

226 parameter – the maximum intrinsic rate of population increase r_{max} – and likely sustainability of

227 even the most difficult-to-study marine animals. Manta rays are data poor but compared to many

228 other chondrichthyans they are still relatively data rich. Of the 1100+ known species, manta rays

229 are among the 106 species for which we can calculate $r_{max.}$ Nevertheless, the paucity of life history

230 data for manta rays is very typical of the many data-poor fisheries of the world, particularly in the

231 tropics. But the absence of data should not preclude or delay management. Our analysis shows

232 that manta rays have one of the lowest maximum intrinsic rates of population increase of any of

233 the chondrichthyans studied to date. Our approach is designed not to estimate the one true value

234 of the maximum intrinsic population growth rate but to calculate these values while

235 understanding the sensitivity to the input parameters and accounting for uncertainty in those

236 values. Despite some uncertainty in life history traits, the plausible range of manta ray r_{max}

237 estimates is narrow (Figure 2), because life history tradeoffs between maximum asymptotic size

238 and the growth rate narrow the parameter space. It is likely that the range is narrower than we

239 show because we could not account for the covariance of life history traits, if we were able to do

240 so this would further narrow the plausible range of manta ray r_{max} estimates.

241 We find that the maximum rate of population increase is slightly higher than a recent estimate of

242 the intrinsic rate of population increase, r = 0.042-0.05 (Ward-Paige et al. 2013), compared to our

243 median r_{max} = 0.11. The range of parameters we used encompassed those of Ward-Paige et al.

244 (2013) and suggest the difference in r versus r_{max} may be due to differences in the method used to

245 estimate natural mortality and that the rebound potential method consistently provides lower

246 growth rate. We used an elasmobranch-specific mortality estimator (Frisk et al. 2001), whereas

247 the other used an estimator based on fishes, molluscs and whales (Hoenig 1983). A more puzzling

248 issue is why our approach reveals that manta rays have one of the lowest r_{max} of any

249 chondrichthyan, whereas the other suggests manta rays may have an intermediate r (Ward-Paige

250 et al. 2013). This issue is beyond the scope of this paper, and requires a simulation-based

251 performance comparison of these kinds of models. While close, the difference in demographic

252 estimates underscores the need for a better understanding of such rule-of-thumb mortality

253 estimators and a comparison of the performance of different variants of simple scalar

254 unstructured demographic models, such as the Euler-Lotka model, the rebound potential model ,

255 and Pope's *Fjeopardy* model (Pope et al. 2000; Simpfendorfer 2005; Smith et al. 1998).

256 Without the opportunity to consider juvenile survival rate our estimates of r_{max} may be slightly too

257 high. We implicitly assume that juveniles have the same survival rate as adults. However, a more

258 realistic assumption might be to assume that juvenile survival rate approaches adult survival rate

259 as described by survival to adulthood raised to the power of the age of maturity. Such an

260 approach to juvenile survival would result in smaller r_{max} values than we present here (E. L.

261 Charnov, University of New Mexico, pers. comm.).

262 Manta rays have very low productivities and even a low fishing mortality ($F_{extinct}$) would drive

263 them to extinction. The manta ray $r_{max} = 0.114$ falls within the 'low' category of the productivity

264 classification used by CITES (0.05 to 0.15, Musick 1999). However, we highlight that the

265 *maximum* population growth rate r_{max} reported here is typically four times greater than the

266 *intrinsic* population growth rate r as derived from age-structured models (e.g. Cortés 2002).

267 Hence,manta rays are more likely to be classified as having "very low" productivity (<0.05)

268 (FAO 2013). With additional field data, there is scope to refine and reduce the uncertainty in the

269 estimates of manta ray productivity.

270 One might object to the calculation of r_{max} given such great uncertainty in basic life history of

271 these data-poor species. However, the pragmatic reality is that we do not have the luxury of

272 waiting for more data to become available. And indeed increasing effort is being paid to

273 understanding safe biological limits for the exploitation of target and bycatch species (Dulvy et
274 al. 2004; Pardo et al. 2012). At the most recent 16th Conference of the Parties of the Convention
275 on the International Trade in Endangered Species both species of manta ray were listed on
276 Appendix II, which includes, "species that are not necessarily now threatened with extinction but
277 that may become so unless trade is closely controlled". Under this regulation Appendix II species
278 can only be traded subject to three conditions, two of which pertain to the legality of capture and
279 welfare (of live transported species), and the third relates to the sustainability (or otherwise) of
280 trade – the so called non-detriment finding (Vincent et al. 2013). A non-detriment finding
281 confirms that the trade of specimens will not be detrimental to wild populations of the species. A
282 key condition of the CITES listings of both manta rays has been a delay by 18 months until 14th
283 September 2014 (CITES 2013). By this date, any nation, that is party to the CITES, wishing to
284 trade manta ray gill plates (or other products) needs to develop methods for assessing that
285 proposed trade is sustainable and not detrimental to wild populations. There is very little time in
286 which to gather new data and hence our simple modeling demographic model, constrained by life
287 history tradeoffs and accounting for and propagating biological uncertainty, provides a much-
288 needed first step toward developing methods to support the development of methods to assess the
289 sustainability of exploitation and international trade.

290 Our analysis reveals that a key parameter to estimate in future field studies are the growth rate k
291 from a von Bertalanffy growth curve, fitted appropriately to size-at-age data (Pardo et al. 2013;
292 Smart et al. 2013; Thorson & Simpfendorfer 2009). Hopefully, the growth rate k can be estimated
293 for manta rays, as has been done for other smaller tropical myliobatoids (Table 1). However,
294 there is a real possibility that annuli may not be recoverable from manta rays because mobulid
295 vertebrate tend to be poorly calcified (W.,D. Oregon State University, Corvalis, USA, pers.
296 comm.). Hence, resighting programmes may be the most pragmatic method of estimating a
297 growth curve (Town et al. 2013). As we have shown, natural mortality rate depends heavily on k
298 and the ratio of M/k, which is around 0.4 for elasmobranchs (Frisk et al. 2001). If it is not
299 possible to estimate a growth curve for manta rays in the near future then demographic modeling
300 will be heavily reliant on our understanding of: (1) the overall pattern of maximum size ($L_\square$) and
301 growth rate (k) in elasmobranchs, and especially tropical and subtropical batoids, and (2) the M/k
302 ratio. Future work should concentrate on understanding why the elasmobranch M/k ratio is
303 around 0.4, by comparison the teleost and reptile M/k ratio is around 1.5 (Charnov et al. 1993).
304 Why is this so? This ratio has a profound influence on the estimate of population growth rate and

305   the sustainability of species, and hence understanding the life histories, ecological and

306   environmental correlates of the *M*/*k* ratio can only improve the predictive power of these simple

307   demographic models.

308   Other parameters that strongly influence the maximum intrinsic rate of population increase are

309   the age at maturation and the annual reproductive rate. These parameters very poorly understood

310   (Marshall & Bennett 2010). The manta ray annual reproductive rate estimates of one pup per year

311   are based on aquarium-held specimens under relatively ideal conditions, and hence these

312   estimates are likely to be optimistic. There is unpublished evidence suggesting that annual

313   reproductive rates may be much, much lower and variable among and within individuals. The

314   proportion of pregnant females returning to long-term (6-8 years) study sites in the Maldives

315   previously suggested a biennial reproductive mode, but in recent years no pregnant females have

316   returned (G. Stevens, Manta Ray of Hope, UK, pers. comm.). The absence of returning pregnant

317   females may indicate a spatial shift of returning females, but also may hint at much lower and

318   more variable annual rates of reproductive output than we have modeled here. We recommend

319   that the demographic rates of manta rays be revised as more details of the temporal and

320   geographic variability in reproductive output come to light. The emerging observations of year-

321   to-year variation in individual reproductive output may lead to variance in year-to-year

322   population growth rate which can only serve to depress the long-term population growth rate

323   further elevating extinction risk (Hutchings 1999). And indeed such observations caution us to

324   initiate and undertake local analyses of population structure and reproductive activity and to

325   incorporate local variations into local demographic models and assessments contribution to

326   CITES Non-Detriment Findings. Of course the greatest uncertainty, that we have entirely

327   overlooked, is that future demographic estimates would benefit greatly from species-specific

328   estimates of the key life history parameters: growth rate *k*, annual reproductive rate and age at

329   maturity.

330   Notwithstanding the current uncertainty in the life history of manta rays, given their very low

331   productivity coupled with small localized populations and predictable seasonal aggregations, the

332   unregulated targeting of local Manta populations for their high-value gill plates is unlikely to be

333   sustainable. The largest targeted fisheries and highest mortality occurs in Indonesia, Sri Lanka,

334   India, Peru and Mozambique and these countries have little fisheries monitoring, regulation or

335   effective enforcement. The time to local extinction depends on the size of the population and the

336 rate of fishing mortality. The very low productivity of manta rays mean that even a moderate

337 level of fishing mortality of $F = 0.2$ (survival $= 0.81$) would reduce a small population of 100

338 individuals to fewer than 10 within less than a generation span (11 years). The key challenge this

339 poses is that it leaves little time to mount an effective conservation management response. These

340 serial depletion fisheries are operated by low-income subsistence coastal fishers, often against a

341 backdrop of declining fish stocks. For such fishers the international market demand for valuable

342 *Manta* and mobulid ray gill plates is likely to provide a desirable income. Such fisheries tend to

343 be unregulated and even if there are protections these are difficult to enforce, which underscores

344 the importance of international trade regulation.

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526   238.

527 **Figure legends**

528 **FIGURE 1.**

529 Gill plates, tentatively identified as from the Sickle-fin Devil ray *Mobula tarapacana* (Philippi,

530 1892), for public sale in downtown Vancouver, British Columbia, Canada on 26th April 2013:

531 photo credit Nicholas K. Dulvy.

532 **FIGURE 2**

533 (*a*) Maximum intrinsic rate of population increase for 106 chondrichthyans, including the manta

534 ray. (*b*) Sensitivity of manta ray maximum intrinsic rate of population increase to variation in

535 natural mortality rate, age at maturity and annual reproductive rate.

536 **FIGURE 3.**

537 Maximum intrinsic rate of population increase versus, (a) von Bertalanffy growth rate k, and (b)

538 maximum linear dimension (cm) for 106 chondrichthyans on a logarithmic scale. Whale and

539 basking sharks are highlighted for comparison.

Growth estimates for tropical rays and whale shark

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.

1   Table 1. Von Bertalanffy growth parameter estimates for species with similar life styles to the manta rays; *a.* tropical myliobatoid rays

2   larger than 1 m total disc width, and *b.* the tropical planktivorous whale shark.

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

3   [a]IUCN Red List Categories: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern;

4   DD, Data Deficient.

5   [b]Disc width (cm) for rays and total length (cm) for whale shark

Figure 1

Image of Devil Ray gill plates for sale in Vancouver

Figure 1: 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.

Figure 2

Maximum intrinsic rate of population increase for 106 chondrichthyans, and the manta ray

Figure 2: (*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.
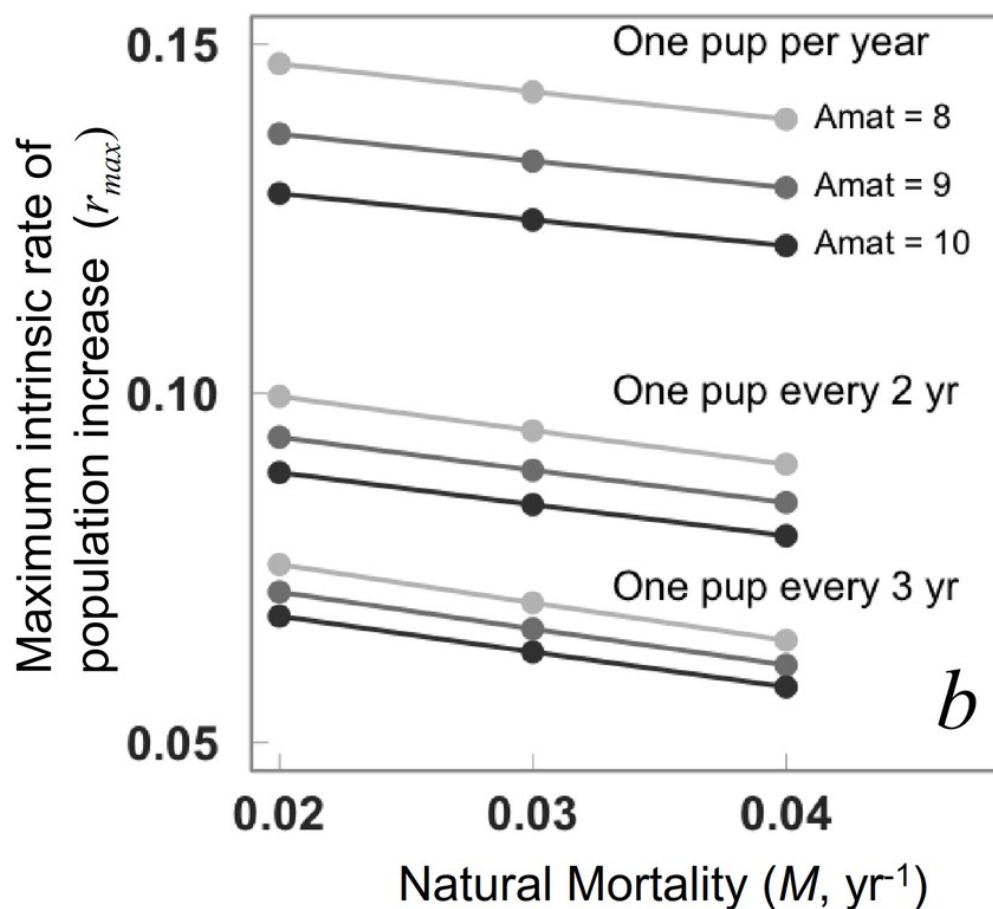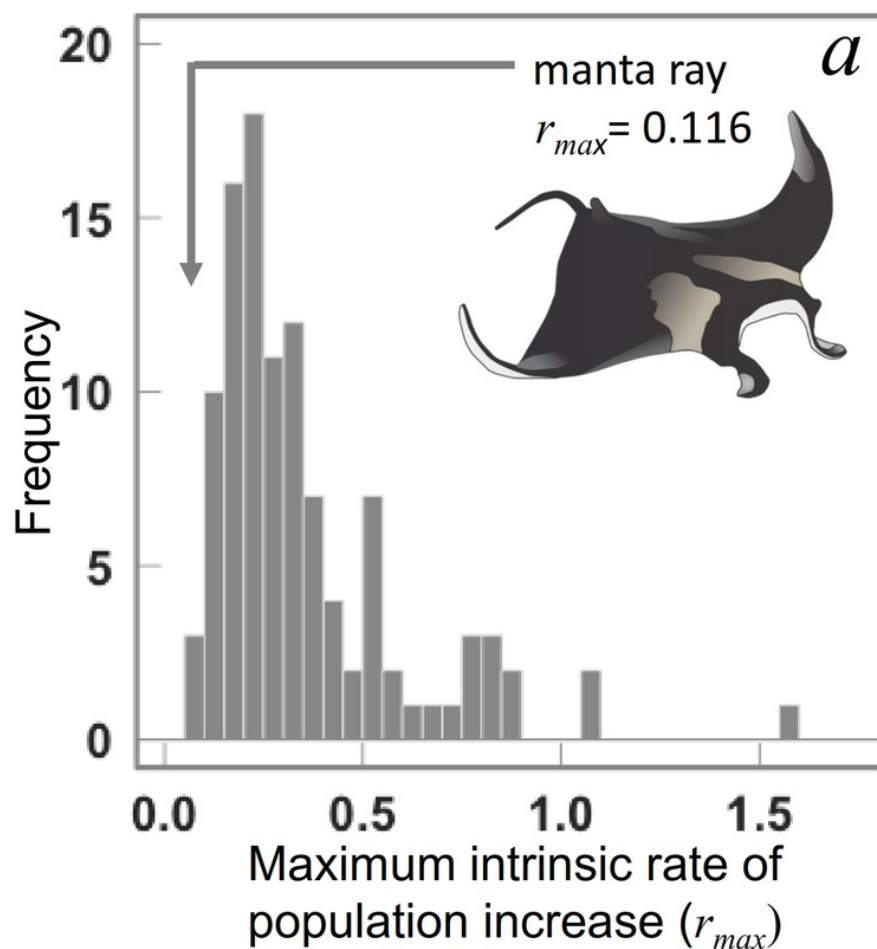
Figure 3

Manta rays have a low maximum intrinsic rate of population increases due to their low growth rate to a very large size.

Figure 3: 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. [b]