Effects of yearling, juvenile and adult survival on reef manta ray (*Manta alfredi*) demography

Isabel M Smallegange, Isabelle BC van der Ouderaa, Yara Tibiriçá

Background. The trade in manta ray gill plates has considerably increased over the last two decades. The resulting increases in ray mortality, in addition to mortality caused by by-catch, has caused many ray populations to decrease in size. The aim of this study was to ascertain how yearling and juvenile growth and survival, and adult survival and reproduction affect reef manta ray (*Manta alfredi*) population change, in order to increase our understanding of manta ray demography and thereby improve conservation research and measures for these fish.

Methods. We developed a population projection model for reef manta rays, and used published life history data on yearling and juvenile growth and adult reproduction to parameterise the model. Because little is known about reef manta ray yearling and juvenile survival, we conducted our analyses using a range of plausible survival rate values for yearlings, juveniles and adults.

Results. The model accurately captured the observed patterns of variation in population growth rate, lifetime reproductive success and cohort generation time in different reef manta ray populations around the world. Our demographic analyses revealed a range of population consequences in response to variations in demographic rates. For example, an increase in yearling or adult survival rates always elicited greater responses in population growth rate, lifetime reproductive success and cohort generation time than the same increase in juvenile survival rate. The population growth rate increased linearly with increasing yearling or adult survival rates, whereas lifetime reproductive success and cohort generation time increased at an accelerating rate with increasing yearling or adult survival rates. Hence, even a small increase in survival rate could increase lifetime reproductive success by almost one pup, and cohort generation time by up to several years. Elasticity analyses revealed that at the lowest adult survival rate (0.54 per year), the population growth rate is most sensitive to changes in the rate with which juveniles survive but stay juveniles (i.e. do not mature into adults), whereas at higher adult survival rates, such as those observed in populations off the coasts of Mozambique (0.68 per year) and Japan (0.95 per year), it is most sensitive to changes in the adult survival rate.

Discussion. It is important to gain an in-depth understanding of reef manta ray life histories, particularly of yearling and adult survival rates, as these can influence reef manta ray population dynamics in a variety of ways. For declining populations in particular, it is crucial to know which life stage should be targeted for their conservation. For one such declining population off the coast of Mozambique, adult annual survival rate has the greatest effect on population growth, and by increasing adult survival by protecting adult aggregation sites, this population's decline could be halted or even reversed.

1   **Effects of yearling, juvenile and adult survival on reef manta ray (*Manta alfredi*)**

2   **demography**

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16   **ABSTRACT**

17   **Background.** The trade in manta ray gill plates has considerably increased over the last two

18   decades. The resulting increases in ray mortality, in addition to mortality caused by by-catch, has

19   caused many ray populations to decrease in size. The aim of this study was to ascertain how

20   yearling and juvenile growth and survival, and adult survival and reproduction affect reef manta

21   ray (*Manta alfredi*) population change, in order to increase our understanding of manta ray

22   demography and thereby improve conservation research and measures for these fish.

23   **Methods.** We developed a population projection model for reef manta rays, and used published

24   life history data on yearling and juvenile growth and adult reproduction to parameterise the

25   model. Because little is known about reef manta ray yearling and juvenile survival, we conducted

26   our analyses using a range of plausible survival rate values for yearlings, juveniles and adults.

27   **Results.** The model accurately captured the observed patterns of variation in population growth

28   rate, lifetime reproductive success and cohort generation time in different reef manta ray

29   populations around the world. Our demographic analyses revealed a range of population

30   consequences in response to variations in demographic rates. For example, an increase in

31   yearling or adult survival rates always elicited greater responses in population growth rate,

32   lifetime reproductive success and cohort generation time than the same increase in juvenile

33   survival rate. The population growth rate increased linearly with increasing yearling or adult

34   survival rates, whereas lifetime reproductive success and cohort generation time increased at an

35   accelerating rate with increasing yearling or adult survival rates. Hence, even a small increase in

36   survival rate could increase lifetime reproductive success by almost one pup, and cohort

37   generation time by up to several years. Elasticity analyses revealed that at the lowest adult

38   survival rate (0.54 per year), the population growth rate is most sensitive to changes in the rate

39   with which juveniles survive but stay juveniles (i.e. do not mature into adults), whereas at higher

40   adult survival rates, such as those observed in populations off the coasts of Mozambique (0.68

41   per year) and Japan (0.95 per year), it is most sensitive to changes in the adult survival rate.

42   **Discussion.** It is important to gain an in-depth understanding of reef manta ray life histories,

43   particularly of yearling and adult survival rates, as these can influence reef manta ray population

44   dynamics in a variety of ways. For declining populations in particular, it is crucial to know which

45   life stage should be targeted for their conservation. For one such declining population off the

46   coast of Mozambique, adult annual survival rate has the greatest effect on population growth,

47   and by increasing adult survival by protecting adult aggregation sites, this population's decline

48   could be halted or even reversed.

49 **INTRODUCTION**

50 The global demand for plant and animal products is unsustainable (Berkes et al., 2006; Lenzen et

51 al., 2012), and trading in shark fins (Clarke et al., 2006), swim bladders (Sadovy & Cheung,

52 2003; Clark, 2004), sea cucumbers (Anderson et al., 2011) and seahorses (Foster & Vincent,

53 2004) occurs on a large scale. Since 1998, trading in products derived from manta and devil rays

54 has increased exponentially (Ward-Paige, Davis & Worm, 2013). Ray gill plates are a key

55 ingredient in traditional Chinese medicine, and cartilage serves as a filler in shark fin soup

56 (White et al., 2006; Ward-Paige, Davis & Worm, 2013). The exploitation of ray species has

57 resulted in population declines (Marshall et al., 2011a; Couturier et al., 2012), and increases their

58 risk of extinction. As a result, some rays, including the reef manta ray *Manta alfredi* and giant

59 manta ray *M. birostris*, are now listed as 'Vulnerable' on the International Union for

60 Conservation of Nature (IUCN) Red List of Threatened Species (Marshall et al., 2011a). Reef

61 manta rays have a slow life history, i.e. late maturity, a long gestation period and a low mean

62 lifetime reproductive success (Marshall et al., 2011a). Therefore, once a reef manta ray

63 population starts to decrease or contains critically few individuals (e.g. due to overfishing), it is

64 very difficult for the population to recover (Kashiwagi, 2014). Therefore, understanding how

65 manta ray populations' growth rates are affected by variations in demographic rates such as

66 growth, survival and fertility is particularly important (Couturier et al., 2014; Kashiwagi, 2014).

67 Recently, *M. alfredi* and *M. birostris* were listed on Appendix II of the Convention on

68 International Trade in Endangered Species of Wild Fauna and Flora (CITES), meaning that any

69 international trade in manta rays from September 2014 onward must be regulated. However, in

70 many countries, particularly developing ones (e.g. Sri Lanka and countries in East Africa, such

71 as Mozambique), manta ray populations are decreasing at an alarming rate (Marshall et al.,

72   2011a; Ward-Paige, Davis & Worm, 2013). Although manta ray ecotourism occurs in many of

73   these regions, only in 32% of them are manta rays protected (Ward-Paige, Davis & Worm,

74   2013). For example, despite their importance in ecotourism (Tibiriçá et al., 2011), manta rays are

75   not protected under Mozambique law, despite the fact that there has been an 88% decrease in

76   reef manta ray sightings off Praia do Tofo, Mozambique (Rohner et al., 2013). In addition, the

77   main reef manta ray aggregation areas off the coast of southern Mozambique are not inside

78   marine protected areas (Pereira et al., 2014), and there has been a rapid increase in the use of gill

79   nets by artisanal fisheries within inshore regions that are frequented by the rays, which has

80   significantly increased reef manta ray by-catch (Marshall, Dudgeon & Bennett, 2011b; Pereira et

81   al., 2014). A comprehensive understanding of reef manta ray demographics, and their responses

82   to different mortality regimes, is therefore urgently needed to improve conservation efforts and

83   management policies (Ward-Paige, Davis & Worm, 2013).

84   Although manta rays are often easy to approach, we currently do not have sufficient

85   demographic data to fully understand their population dynamics (Ward-Paige, Davis & Worm,

86   2013). If conservation management policies are to be effective, knowing which age classes

87   (yearlings, juveniles or adults) within a population are the most sensitive to disturbance is

88   essential. For example, demographic analyses of the population dynamics of other long-lived

89   organisms, such as turtles and killer whales (*Orcinus orca*), have revealed that population

90   persistence is most sensitive to adult survival, whereas protecting young (e.g. through protective

91   rearing schemes) has a much smaller impact on population persistence (Brault & Caswell, 1993;

92   Heppell, Crowder & Crouse, 1996). Therefore, a very small decrease in the annual survival rate

93   of juveniles and/or adults likely has serious repercussions on the persistence of populations of

94   long-lived species such as manta rays (Ward-Paige, Davis & Worm, 2013; Kashiwagi, 2014).

95   The aim of this study was to ascertain how yearling and juvenile growth and survival, and

96   adult reproduction and survival, affect populations of reef manta rays. To this end, we developed

97   a stage-structured population projection model (PPM) (Caswell, 2001) that we parameterised

98   using published life history data obtained from populations off the coasts of southern

99   Mozambique (Marshall, Dudgeon & Bennett, 2011b) and the Yaeyama Islands, Japan

100   (Kashiwagi, 2014). Sufficient data were available to parameterise growth and reproduction in the

101   PPM, but detailed information on the survival of yearling and juvenile reef manta rays is scarce

102   (Marshall et al., 2011a; Dulvy et al., 2014); therefore, we used the model to investigate how

103   different annual survival rates of yearlings, juveniles and adults affect the population growth

104   rate, mean lifetime reproductive success and cohort generation time. We assessed the

105   performance of the model by comparing the predicted values of these three population biology

106   descriptors with empirical observations. Subsequently, we conducted elasticity analyses for all

107   combinations of yearling, juvenile and adult survival rates to ascertain which demographic rate

108   (rate at which individuals survive and stay in the same life stage; survive and grow into the next

109   life stage; reproduce offspring) of which life stage (yearling, juvenile or adult) has the greatest

110   influence on the population growth rate. Elasticity analysis is widely used by conservation

111   biologists, because the results obtained can be used to prioritise conservation research and

112   management for those life stages that have the greatest effect on population growth (Benton &

113   Grant, 1999; Carslake, Townley & Hodgson, 2009). Because much less is known about yearling

114   and juvenile survival rates than adult survival rates (Marshall et al., 2011a; Dulvy et al. 2014),

115   investigating a range of yearling and juvenile survival rates will elucidate if and how reef manta

116   ray population responses vary with variations in survival rates. For all of the combinations of

117   yearling, juvenile and adult survival rates, we used the calculated population growth rates to

118   project a population of 500 individuals forward over a period of 10 years, in order to investigate

119   the population consequences of different yearling, juvenile and adult mortality regimes.

120

121   **METHODS**

122   *M. alfredi* **life cycle**

123   The life cycle of reef manta rays is generally divided into three life stages: yearlings, non-

124   reproducing juveniles and reproducing adults (Fig. 1) (Marshall et al., 2011a; Kashiwagi, 2014).

125   Male manta rays reach maturity after six years, and females are thought to mature at 8–10 years

126   of age; longevity is estimated to be at least 40 years (Marshall et al., 2011a). On average, adult

127   females produce one pup every two years, but fertility rates can range from one pup every one to

128   five years (Marshall et al., 2011a). Reef manta ray life history data have been collected from

129   various populations, including those off the coasts of Mozambique and the Yaeyama Islands,

130   Japan (Table 1). These two populations differ remarkably in their estimated annual survival rates

131   and population growth rates; the population off the coast of Japan is stable, and juveniles and

132   adults exhibit high survival rates (0.95 per year) (Kashiwagi, 2014), whereas the population off

133   the coast of Mozambique is declining, and the adult survival rate is estimated to be as low as

134   0.68 ± 0.147 SE (standard error) per year (Marshall, Dudgeon & Bennett, 2011b) (Table 1). In

135   the present study, we used the life history data of these two populations to serve as reference

136   points for our demographic analyses.

137

138   **Population model**

139   The population model was based on a three-stage life cycle (Fig. 1). The addition of further life

140   stages may have increased model accuracy, but these are the only currently distinguishable

141   stages in *M. alfredi*. The rate at which individuals survive and remain in the same life stage (as

142   opposed to growing into the next life stage) equals P_i, where i indicates Y (yearling), J (juvenile)

143   or A (adult), and was calculated following Caswell (2001):

144

145   $P_i = \sigma_i(1 - \gamma_i)$ (Equation 1)

146

147   where σ_i (i = Y, J, A) is the estimated survival rate for each life stage (Table 1). The parameter γ_i

148   is the transition rate from one life stage to the next (expressed per year); in this case, from

149   yearling to juvenile (γ_Y) or from juvenile to adult (γ_J). Each transition rate γ_i was calculated as γ_i

150   $= 1/D_i$, where D_i is the duration (in years) of either the yearling (i = Y) or juvenile life stage (i =

151   J) (Table 1). The rate (per year) at which individuals survive and grow into the next life stage is

152   defined as:

153

154   $G_i = \sigma_i\gamma_i$ (Equation 2)

155

156   where i indicates Y (yearling) or J (juvenile). The number of offspring produced each year equals

157   F_A. These equations result in the following population projection matrix, which has a projection

158   interval of one year:

159

160   $\mathbf{A} = \begin{bmatrix} P_Y & 0 & F_A \\ G_Y & P_J & 0 \\ 0 & G_J & P_A \end{bmatrix}$ (Equation 3)

161

162   **Parameterisation and model performance**

163   Following Kashiwagi (2014), and as is common practice (Caswell [2001]), the population model

164   was parameterised for females under the assumption that their growth and survival rates are not

165   too dissimilar to those of male reef manta rays. We set the stage transition rates γ_i in Equations 1

166   and 2 constant at $\gamma_Y = 1/D_Y = 1/1 = 1$ and $\gamma_J = 1/D_J = 1/8 = 0.125$ (Table 1), and assumed

167   that females produce one pup every two years, so that $F_A = 0.5$ per year. Because little is known

168   about yearling and juvenile survival rates (Marshall et al., 2011a; but see Kashiwagi, 2014), we

169   conducted each demographic analysis (explained in the next section) for all combinations of

170   values of yearling annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) within the

171   interval [0.5, 1] in increments of 0.005 (Table 1). We conducted each analysis using the observed

172   adult annual survival rate of reef manta rays off the coast of Mozambique, which is $\sigma_A = 0.68$

173   (Marshall, Dudgeon & Bennett, 2011b), a 20%-reduced adult annual survival rate of $\sigma_A = 0.54$,

174   and 20%- and 40%-increased adult annual survival rates of $\sigma_A = 0.82$ and $\sigma_A = 0.95$, respectively

175   (Table 1). The final value of $\sigma_A = 0.95$ is equal to the observed non-yearling annual survival rate

176   of reef manta rays in a stable population off the coast of Japan (Kashiwagi, 2014) (Table 1). To

177   assess the performance of our population model, we compared our predictions of population

178   growth rate, lifetime reproductive success and cohort generation time with the empirical

179   observations.

180

181   **Demographic analyses**

182   Firstly, we calculated the population growth rate λ from the dominant eigenvalue of matrix **A**

183   (Equation 3) for each of the abovementioned combinations of yearling, juvenile and adult annual

184   survival rates. Secondly, for each of the survival rate combinations, we performed an elasticity

185   analysis to investigate how sensitive the population growth rate λ is to perturbations of each of

186   the different growth, survival and fertility rates in the population projection matrix **A** (Equation

187   3). To this end, we calculated the elasticity matrix **E**, where each element on row *m* and column

188   *n* of matrix **E**, e_{mn}, represents the proportional contribution of each associated demographic rate

189   P_i, G_i and F_A in the population projection matrix **A** (Equation 3) to the population growth rate λ.

190   The elasticities were calculated as follows (Caswell, 2001):

191

192     $$e_{mn} = \frac{a_{mn}}{\lambda}\frac{\partial\lambda}{\partial a_{mn}}$$ (Equation 4)

193

194   where a_{mn} are the elements of **A**. The second part of the equation describes the sensitivities of λ

195   to changes in the elements a_{mn} of **A** (Caswell, 2001). The elasticities sum to 1, and give the

196   proportional contributions of the matrix elements to the population growth rate λ. Therefore, the

197   higher an elasticity value is relative to other elasticity values, the greater is the effect of the

198   associated demographic rate on the population growth rate.

199   Thirdly, for each combination of yearling, juvenile and adult annual survival rates, we

200   calculated mean lifetime reproductive success (R_0) by taking the dominant eigenvalue of the

201   matrix **R** = **FN**. The matrix **F** is a fertility matrix that describes the production of new

202   individuals:

203

204     $$\mathbf{F} = \begin{bmatrix} 0 & 0 & F_A \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$$ (Equation 5)

205

206   The matrix **N** is calculated as **N** = (**I** − **U**)$^{-1}$, where **I** is the identity matrix and **U** the transient

207   matrix that describes the growth and survival rates of the different stages:

208

$$\mathbf{U} = \begin{bmatrix} P_Y & 0 & 0 \\ G_Y & P_J & 0 \\ 0 & G_J & P_A \end{bmatrix} \qquad \text{(Equation 6)}$$

209

210

211 Fourthly, for each combination of yearling, juvenile and adult annual survival rates, we

212 calculated cohort generation time as the mean age of offspring production in a cohort of

213 yearlings (Caswell, 2009):

214

215 $T_c = \mathrm{diag}(\mathbf{FNe_Y})^{-1}\,\mathbf{FNUNe_Y},$ \qquad (Equation 7)

216

217 where the vector $\mathbf{e_Y}$ is a vector with 1 in the first entry (for yearlings) and zeros in the second and

218 third entries for juveniles and adults, respectively. Finally, we used the population growth rates

219 that were calculated at step one to project a population of 500 individuals forward over a period

220 of 10 years. All of the demographic analyses were conducted in MATLAB® R2014b

221 (MathWorks®, MA, USA).

222

223 **RESULTS**

224 **Model performance**

225 Overall, the predictions from our PPM matched the empirical observations well. Firstly, the

226 predicted values for the population growth rate λ ranged from 0.64 to 1.13, depending on the

227 values of yearling, juvenile and adult survival rates (Fig. 2; Table 2). This range includes the

228 range of observed population growth rate values, but also slightly exceeds the range of observed

229 values (Table 2). Similarly, the range of predicted values of lifetime reproductive success R_0

230   (0.06–6.20) (Fig. 3; Table 2) included the range of observed values of R_0, but the highest

231   predicted value of R_0 exceeded the highest observed value of R_0 (Table 2). The predicted values

232   for cohort generation time were very low (Fig. 4; Table 2), and much lower than the observed

233   cohort generation times in most cases (Table 2). Only when adult annual survival rate was at its

234   highest ($\sigma_A = 0.95$) (Fig. 4D) did the predicted cohort generation time match the observed value

235   (Table 2).

236

237   **Summary of the demographic analyses**

238   Because the results of our demographic analyses are complex, we first provide a summary to aid

239   in the interpretation of the specific results (below). Because little is known about survival rates of

240   yearling and juvenile reef manta rays, we explored the effects of a range of values of yearling

241   and juvenile annual survival rates on lifetime reproductive success, population growth rate and

242   cohort generation time. We also varied the adult annual survival rate from as low as 0.54, which

243   is 20% lower than the observed annual survival rate of adults (0.68 per year) off the coast of

244   Mozambique (Marshall, Dudgeon & Bennett, 2011b), to as high as 0.95 per year, which equals

245   the observed adult annual survival rate in the stable population off the coast of the Yaeyama

246   Islands (Kashiwagi, 2014). The effect of an increase in adult annual survival rate across this

247   range of values was straightforward: with increasing adult annual survival rate, the values of all

248   three population descriptors also increased. However, variations in yearling and juvenile annual

249   survival rates had different and varying effects on the population descriptors that we

250   investigated. In the case of population growth rate, changes in these two survival rates had

251   additive effects on the population growth rate, but interactive (multiplicative) effects on mean

252   lifetime reproductive success, whereas cohort generation time was unaffected by variations in the

253   juvenile annual survival rate. In addition, the effect of an increase in juvenile annual survival rate

254   was always of a far greater magnitude on population growth rate, mean lifetime reproductive

255   success and cohort generation time than the effect that the same increase in yearling or adult

256   annual survival rate had on these population descriptors.

257

258   **Specific results of the demographic analyses**

259   Calculating the population growth rate λ for all of the different values of yearling, juvenile and

260   adult annual survival rates revealed that for the observed adult annual survival rate of $\sigma_A = 0.68$

261   (Marshall, Dudgeon & Bennett, 2011b), populations can only persist if both yearling and

262   juvenile annual survival rates are high ($\sigma_Y > 0.7$ and $\sigma_J > 0.95$) (Fig. 2B; populations persist to

263   the right of the blue line, indicating population stability at $\lambda = 1$). When applying the lower value

264   of adult annual survival rate ($\sigma_A = 0.54$), populations can only persist if both yearling and

265   juvenile annual survival rates are almost at unity (Fig. 2A; populations persist to the right of the

266   blue line, indicating population stability at $\lambda = 1$). At higher values of σ_A ($\sigma_A = 0.82$ and $\sigma_A =$

267   0.95), populations can persist at much lower values of yearling and juvenile annual survival rates

268   (Fig. 2C, D; populations persist to the right of the blue line, indicating population stability at $\lambda =$

269   1), e.g. if $\sigma_A = 0.95$, the yearling survival rate (σ_Y) can be as low as 0.5, as long as the juvenile

270   survival rate is $\sigma_J = 0.8$ (Fig. 2D). Because the isoclines in each panel are neither horizontal nor

271   vertical, we can infer that for a constant value of σ_Y (or σ_J), the population growth rate depends

272   on what the value of σ_J (or σ_Y) is. However, because the isoclines in each plot are parallel, we

273   can infer that these effects are additive, and that therefore there is no interactive effect between

274   σ_Y and σ_J on λ (i.e. the magnitude of an effect of σ_Y on λ does not depend on the value of σ_J, and

275   vice versa).

276   We then investigated how variations in yearling, juvenile and adult survival rates affected

277 the elasticity of the population growth rate λ to each of the demographic rates of each life stage

278 in the PPM (Equation 3). This revealed that, depending on the survival rate values, λ was either

279 most sensitive to P_A, the rate at which adults survive and remain in the adult stage, or P_J, the rate

280 at which juveniles survive and remain in the juvenile life stage (Fig 2; white areas in each panel

281 denote survival rate values where λ is most sensitive to P_A, and grey areas denote survival rate

282 values for which λ is most sensitive to P_J). Interestingly, with increasing values of the adult

283 annual survival rate σ_A (going from Fig. 2A to Fig. 2D), the region of yearling survival rate (σ_Y)

284 values for which λ is most sensitive to P_A (white areas) increases, whereas the region of yearling

285 survival rate values for which λ is most sensitive to P_J (grey areas) decreases. These shifts

286 indicate that the elasticity results were independent of juvenile annual survival rate (σ_J); rather,

287 whether or not λ is most sensitive to perturbations in P_J or P_A critically depended on the values

288 of σ_Y and σ_A (Fig. 2).

289   We then investigated the effect of variations in yearling, juvenile and adult survival rates

290 on mean lifetime reproductive success. The results were qualitatively similar to those obtained

291 for the population growth rate: with increasing values of the adult annual survival rate σ_A,

292 populations can persist at ever lower values of yearling and juvenile annual survival rates (Fig. 3;

293 populations persist to the right of the blue line, indicating population stability at $R_0 = 1$). In

294 contrast to the results for population growth rate, however, the isoclines in each panel are not

295 parallel and are unevenly spaced (Fig. 3), indicating that the yearling and juvenile annual

296 survival rates σ_Y and σ_J have an interactive effect on lifetime reproductive success, i.e. the

297 magnitude of an effect of σ_Y on lifetime reproductive success depends on the value of σ_J, and

298 vice versa. The uneven spacing of the isoclines for each value of adult annual survival rate (Fig.

299   3) indicates that, with increasing values of yearling and juvenile annual survival rates, lifetime

300   reproductive success increases at an ever higher rate. This increase in lifetime reproductive

301   success is greater with increasing values of yearling or adult annual survival rates than with

302   increasing values of juvenile annual survival rates.

303   Regarding cohort generation time, for each value of adult annual survival rate (σ_A),

304   cohort generation time increases at an accelerating rate with increasing values of yearling annual

305   survival rate (σ_Y); hence, a slight increase in a high value of σ_Y results in a far larger increase in

306   cohort generation time than a slight increase in a low value of σ_Y. However, there is no effect of

307   juvenile annual survival rate (σ_J), because the increase in cohort generation time with increasing

308   values of σ_Y is the same for each value of σ_J (Fig. 4). Cohort generation time also increases at an

309   accelerating rate with increasing values of adult annual survival rate (σ_A); consequently, a slight

310   increase in a high value of σ_A results in a far larger increase in cohort generation time than a

311   slight increase in a low value of σ_A (Fig. 4).

312   Finally, we used the predicted population growth rates (Fig. 2) to project a starting

313   population of 500 individuals forward over 10 years to investigate the population consequences

314   of variations in yearling, juvenile and adult survival rates. The combinations of yearling, juvenile

315   and adult survival rate values at which populations are stable and the projected population size

316   remains at 500 individuals after 10 years (indicated by the green lines in Fig. 5) were the same as

317   those obtained from the population growth rate (Fig. 2) and lifetime reproductive success (Fig. 3)

318   analyses. In each panel in Fig. 5, combinations of survival rate values to the right of the green

319   line correspond to population increases. Comparing the different panels shows that the increase

320   in population size is greater at higher values of the adult annual survival rate (σ_A) (Fig. 5). The

321   lowest observed population size of reef manta rays off the coast of Mozambique is 149

322   individuals (Marshall, Dudgeon & Bennett, 2011b), and is indicated by red lines in Fig. 5.

323   Matching this lowest observed population size to our population projections reveals that it

324   corresponds to ever lower values of yearling annual survival rate (σ_Y) and juvenile annual

325   survival rate (σ_J) as the adult annual survival rate (σ_A) increases in value. This suggests that the

326   decrease in population size over 10 years is less at higher values of the adult annual survival rate

327   than at lower values.

328

329   **DISCUSSION**

330   **Model performance**

331   In this study, we developed a population model for reef manta rays that we used to conduct a

332   detailed analysis of reef manta ray demography. With this analysis, we aim to increase our

333   understanding of the drivers of population change in reef manta rays, and how perturbations to

334   demographic rates, such as a decrease in survival due to targeted fishing and by-catch, affect

335   their population fluctuations. Different techniques exist that relate the dynamics of populations to

336   the demographic rates of individuals, and include physiologically structured population models

337   (Metz & Diekmann, 1986), delay-differential equation models (Nisbet & Gurney, 2003),

338   individual-based models (Grimm & Railsback, 2005), integral projection models (IPMs)

339   (Easterling, Ellner & Dixon, 2000), and PPMs (Caswell, 2001). These methodologies all link

340   individual state to population structure, but differ in their mathematical approaches. Structured

341   population models such as PPMs and IPMs are particularly useful for investigating how

342   demographic changes affect population dynamics. They are closely and easily linked to field and

343   experimental data, and require relatively straightforward mathematical techniques from matrix

344   calculus (Coulson, 2012). IPMs have the added benefit that they can be used to investigate

345   simultaneous ecological and rapid evolutionary change in quantitative characters, life history

346   evolution and population dynamics (Smallegange & Coulson, 2013). However, IPMs are data

347   hungry, because their parameterisation requires extensive, long-term datasets on the life history

348   trajectories of individuals (Coulson, 2012). Because these data are currently not available for reef

349   manta rays, we developed a PPM that included the three life stages that can currently be

350   distinguished in reef manta rays: yearlings, juveniles and adults (Marshall et al., 2011a). Future

351   studies should, however, aim to develop a reef manta ray IPM that can take any evolutionary

352   responses in life history parameters to environmental change into consideration. We

353   parameterised our PPM using published life history data; therefore, the model outcomes

354   critically depended on the soundness and accuracy of these data. The data that we used to model

355   growth and reproduction are sound, as several studies on the growth and reproduction of reef

356   manta rays report very similar results (Marshall & Bennet, 2010; Marshall, Dudgeon & Bennett,

357   2011b; Kashiwagi, 2014). Less is known about individual survival in this species. Marshall,

358   Dudgeon & Bennett (2011b) studied adult survival in a reef manta ray population off the

359   southern coast of Mozambique, and our own preliminary, capture-mark-recapture analysis of

360   sight-re-sight data of adult reef manta rays off the southern coast of Mozambique (200 km south

361   of the study site of Marshall, Dudgeon & Bennett [2011b]) obtained an adult survival rate of 0.67

362   (± 0.16 SE) per year (I.B.C. van der Ouderaa & Y. Tibiriçá, unpublished data), which is not

363   significantly different to the value of 0.68 (± 0.15 SE) per year obtained by Marshall, Dudgeon

364   & Bennett (2011b). The survival of yearling and juvenile reef manta rays has been less studied,

365   as individuals at these life stages do not frequently visit the aggregation sites where demographic

366   data on adults are typically collected (Marshall, Dudgeon & Bennett, 2011b). For this reason, we

367   used a range of annual survival rate values for yearlings and juveniles.

368   Overall, we found that the performance of our model was satisfactory; mean lifetime

369 reproductive success and population growth rates observed in different reef manta ray

370 populations were all within the ranges that we predicted from our population model. However,

371 the predicted population growth rate and lifetime reproductive success values sometimes

372 exceeded the observed values; this was probably due to the fact that we also investigated the

373 population consequences of annual survival rates of yearlings, juveniles and adults that were

374 lower and higher than the observed survival rates. For the reef manta ray population off the coast

375 of the Yaeyama Islands, the annual survival rates of all three life stages, as well as the population

376 growth rate, have been estimated: the yearling annual survival rate is estimated to be 0.63 and

377 juvenile and adult annual survival rates are both estimated as 0.95 (Kashiwagi, 2014). The

378 population growth rate associated with these values as predicted by our population model was

379 ~1.01 (Fig. 2D; $\sigma_Y = 0.63$, $\sigma_J = \sigma_A = 0.95$), which is very close to the actual population growth

380 rate of the Yaeyama Islands reef manta ray population, which is estimated as 1.02 per year

381 (Kashiwagi, 2014). The only discrepancy between the predicted and observed values was cohort

382 generation time at the lower adult annual survival rates of $0.54 \leq \sigma_A \leq 0.82$ (Fig. 4A–C). At these

383 low survival rates, adults do not live very long, which lowers the average age at which adults

384 reproduce and results in a low cohort generation time. Cohort generation time values have

385 probably been obtained from stable populations (Marshall et al., 2011a; Ward-Paige, Davis &

386 Worm, 2013), in which annual adult survival rates are much higher. Indeed, at $\sigma_Y = \sigma_A = 0.95$

387 (as found for the stable reef manta ray population off the coast of the Yaeyama Islands

388 [Kashiwagi, 2014]), the predicted cohort generation time was 18.5 years, which is very close to

389 the observed generation time of 19.4 years (Ward-Paige, Davis & Worm, 2013). Overall, it is

390 rewarding that predictions from our population model match observations on the key population

391 descriptors of lifetime reproductive success, population growth rate and cohort generation time

392

393 **Demographic analyses**

394 The demographic analysis revealed that the effects of variations in yearling and juvenile survival

395 rates on population growth rate, mean lifetime reproductive success and cohort generation time

396 are not straightforward, but some general patterns did emerge. Firstly, an increase in yearling or

397 adult annual survival rate always elicited a greater response in population growth rate, mean

398 lifetime reproductive success and cohort generation time than the same increase in juvenile

399 annual survival rate. This suggests that a perturbation in yearling or adult annual survival rate

400 will have far greater consequences for reef manta ray population dynamics than the same

401 magnitude of perturbation in juvenile annual survival rate. Secondly, increases in any of the three

402 population descriptors with increasing yearling or adult survival rate values was either linear, in

403 the case of population growth rate, or was at an accelerating rate, in the case of mean lifetime

404 reproductive success and cohort generation time. The accelerating rates of increase are of

405 particular interest, because if yearling or adult annual survival rates are already high, a slight

406 increase can increase mean lifetime reproductive success by almost one pup (Fig. 3D), and

407 cohort generation time by a year to several years (Fig. 4D). Both of these effects can

408 significantly affect population structure and fluctuations. Therefore, in order to obtain an

409 accurate insight into reef manta ray population dynamics, accurate estimates of yearling and

410 juvenile survival rates should be obtained from natural populations.

411 One way of gaining a general insight into the population consequences of differences in

412 demographic rates is by using population models to project a population forward in time and

413   investigate its future size relative to its original size, which we did for a period of 10 years for all

414   combinations of yearling, juvenile and adult annual survival rates. The reef manta ray population

415   off the coast of Mozambique decreased by 88% between 2005 and 2011 due to variations in the

416   local environment, anthropogenic pressures and large-scale oceanographic influences (Rohner et

417   al., 2013). Our population projections confirm that the low observed adult annual survival rate of

418   adult reef manta rays off the coast of Mozambique of 0.68 per year (Marshall, Dudgeon &

419   Bennett, 2011b) nearly always results in population decline, unless yearling and juvenile annual

420   survival rates are close to unity. However, because reef manta ray by-catch has recently

421   significantly increased in this region (Marshall, Dudgeon & Bennett, 2011b; Pereira et al., 2014),

422   it is unlikely that the juvenile survival rate is close to unity. In the stable reef manta ray

423   population off the coast of the Yaeyama Islands, the yearling annual survival rate has been

424   estimated to be as low as 0.63, probably because of predation (Kashiwagi, 2014). If we assume

425   that this yearling annual survival rate also applies to the Mozambique population, the

426   Mozambique population is predicted to continue to decrease in size, even if the juvenile annual

427   survival rate is at unity (Fig. 5B). Therefore, unless the survival rates of reef manta rays in

428   populations off the coast of Mozambique increase (by reducing direct fishing and by-catch), it is

429   unlikely that this population will stop declining.

430

431   **Conservation implications**

432   Many manta ray populations across the globe are declining, according to the IUCN Red List for

433   Threatened Species (Marshall et al., 2011a; but see Kashiwagi [2014] for an exception). One

434   way of increasing our understanding of how such declines can be reduced or even halted is by

435   conducting elasticity analyses of a demographic model. The results of such analyses identify

436 which demographic rates of which life stages have the greatest effect on population growth. By

437 targeting conservation research and management on those rates and life stages, vulnerable

438 populations can be protected from further decline (Benton & Grant, 1999; Carslake, Townley &

439 Hodgson, 2009). Our elasticity analysis revealed that the population growth rate is most sensitive

440 to change in either the adult survival rate or the rate at which juveniles survive but stay in the

441 juvenile stage (i.e. do not mature into adults). To exemplify how the results of this analysis can

442 be used, we compared the values predicted by our analysis to the values obtained in two reef

443 manta ray populations off the coasts of Mozambique and the Yaeyama Islands. In the case of

444 Mozambique, the observed adult annual survival rate is 0.68 (Marshall, Dudgeon & Bennett,

445 2011b), and the observed population growth rate is estimated as 0.77 per year (Rohner et al.,

446 2013); according to our elasticity analysis (Fig. 2B), at these values, the population growth rate

447 will be most sensitive to changes in the adult annual survival rate. To prevent this population

448 declining further, the adult survival rate should be increased by reducing targeted and by-catch

449 fishing through the protection of aggregation sites that are often frequented by adults. Our

450 analyses indicate that if the adult survival rate increases to 0.95 per year, then the population

451 growth rate is close to unity and the Mozambique reef manta ray population would be stable.

452 Regarding the stable population off the coast of the Yaeyama Islands, the adult annual survival

453 rate is 0.95, and according to our elasticity analysis, this population will also be most sensitive to

454 changes in the adult annual survival rate. Although this population is not currently subject to

455 direct fishing pressure (Kashiwagi, 2014), our results predict that any changes in adult survival

456 will greatly affect it.

457   A previous demographic analysis that was based on a generic reef manta ray life cycle

458 and not on a specific manta ray population found that the intrinsic population growth rate r was

459   most sensitive to changes in the offspring production rate and not the mortality rate (Dulvy et al.,

460   2014). However, unlike our elasticity analysis, Dulvy et al.'s (2014) sensitivity analysis

461   investigated how *additive* perturbations in life history parameters affect the intrinsic population

462   growth rate, whereas we investigated how *proportional* perturbations in demographic rates affect

463   the long-term population growth rate. We used the second part of Equation 4 to run a sensitivity

464   analysis in order to investigate how *additive* perturbations affect the population growth rate, and

465   found that the population growth rate is most sensitive to perturbations in G_J or P_A, depending on

466   the values of yearling, juvenile and adult annual survival rates (Appendix: Fig. A1). However,

467   these results are not very informative, because the demographic rates in our population model are

468   measured in different units; survival rates are probabilities, and only have values of between zero

469   and unity, whereas reproduction rate has no such restrictions. Therefore, it is difficult to compare

470   the sensitivity of the population growth rate to changes in survival and growth rates with the

471   sensitivity of the reproductive rate. Therefore, we focus on the results of the elasticity analysis,

472   which suggest that reef manta ray populations off the coast of Mozambique and Japan are most

473   sensitive to perturbations in the adult annual survival rate. The demographic rates that comprise

474   our population matrix are determined by the underlying parameters σ_i (survival rate) and γ_i

475   (stage-specific transition rate); however, because the adult annual survival rate P_A equals σ_A and

476   is independent of γ_i, the population growth rate is indeed most sensitive to perturbations in adult

477   survival at high adult survival rates, which is typical for long-lived animals (Brault & Caswell,

478   1993; Caswell, 2001). This indicates that effective management and legislation is urgently

479   needed to avoid the local extinction of the reef manta ray population off the coast of

480   Mozambique. The following two approaches should be taken: (1) the species should be protected

481   against fishing, including accidental catch, at the national level; and (2) aggregation areas should

482 be protected. The behaviour of reef manta rays at cleaning stations makes targeted fishing a

483 potential threat, but also creates an opportunity for site-specific protection. By protecting

484 aggregation sites, adults, which are regular visitors to such sites (Marshall, Dudgeon & Bennett,

485 2011b; Kashiwagi, 2014), should exhibit increased survival rates, which will result in an increase

486 in the population growth rate.

487

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491

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Table 1. Life history data of different reef manta ray populations. Shown are annual survival rates, σ_i, duration of different life stages, D_i, where i = Y (yearlings), i = J (juveniles) and i = A (adults), and fertility rate of adults, F_A. Indicated are values estimated from data collected from populations off the coast of southern Mozambique and off the coast of Yaeyama Islands, Japan. Also shown are the values that were used in our demographic analyses.

	Explanation	Value in analyses	Observed value	Location of observation	Reference for observed value
σ_Y	Annual survival rate of yearlings	0.5 - 1.0	0.63	Japan	Kashiwagi, 2014
σ_J	Annual survival rate of juveniles	0.5 - 1.0	0.95	Japan	Kashiwagi, 2014
σ_A	Annual survival rate of adults	{0.54, 0.68, 0.82, 0.95}	0.68	Mozambique	Marshall, Dudgeon, & Bennett, 2011b
			0.95	Japan	Kashiwagi, 2014
D_Y	Duration of yearling stage (years)	1	1	not specified/ Japan	Marshall et al., 2011a; Kashiwagi, 2014
D_J	Average duration of (female) juvenile stage (years)	9	8-10	not specified/ Japan	Marshall et al., 2011a; Kashiwagi, 2014
D_A	Duration of adult stage (years)	31	31	not specified/ Japan	Marshall et al., 2011a; Kashiwagi, 2014
F_A	Average number of pups per year	0.5	0.5	Mozambique	Marshall & Bennett 2010

572

Table 2. Predicted and observed population descriptors for different reef manta ray populations. The population descriptors are: population growth rate (λ, expressed per year), mean lifetime reproductive success (R_0), and cohort generation time (T_c, years). Predicted values given are the minimum and maximum values from our demographic analyses (Fig. 2-4); observed values are taken from different locations around the world (locations are indicated).

	Predicted range	Observed value	Explanation of observed value	Location of observation	Reference for observed value
λ	0.64 - 1.13	0.77	Calculated from the observation of 88% decline between 2005 – 2011	Mozambique	Rohner et al., 2013
		0.98	Calculated from the observation of 80% decline over 75 years	not specified	Marshall et al., 2011a
		1.02	Estimated using POPAN models covering 1987 – 2009	Japan	Kashiwagi, 2014
R_0 [1]	0.06 – 6.20	0.72	Calculated using IUCN data (Marshall et al. 2011a) [1]: $T_c = 15$ and $\lambda = 0.98$	not specified	Marshall et al., 2011a
		0.02	Worst-case scenario calculated using slowest life history values[1]: $T_c = 19.4$ and $\lambda = 0.77$	not specified	Marshall et al., 2011a; Rohner et al., 2013
T_c	3.89 – 20.40	19.4	Mean of minimum (6.75 years) and maximum (32 years) age of adults	Tropical Easter Pacific & Atlantic; Hawaii	Ward-Paige, Ward-Paige, Davis & Worm, 2013
		15	Mean of minimum (10 years) and maximum (40 years) age of adults	not specified	Marshall et al., 2011a

[1] R_0 was calculated by taking the exponent of $T_c \times \log(\lambda)$ (Caswell 2001)

573

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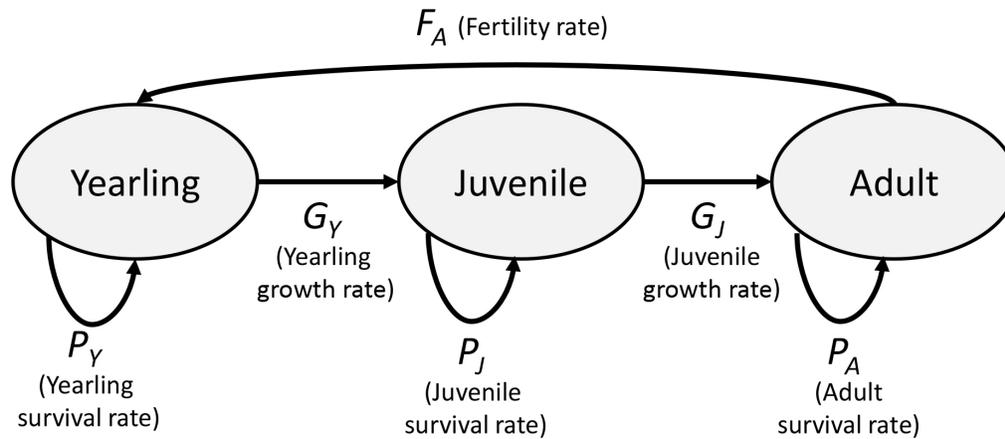
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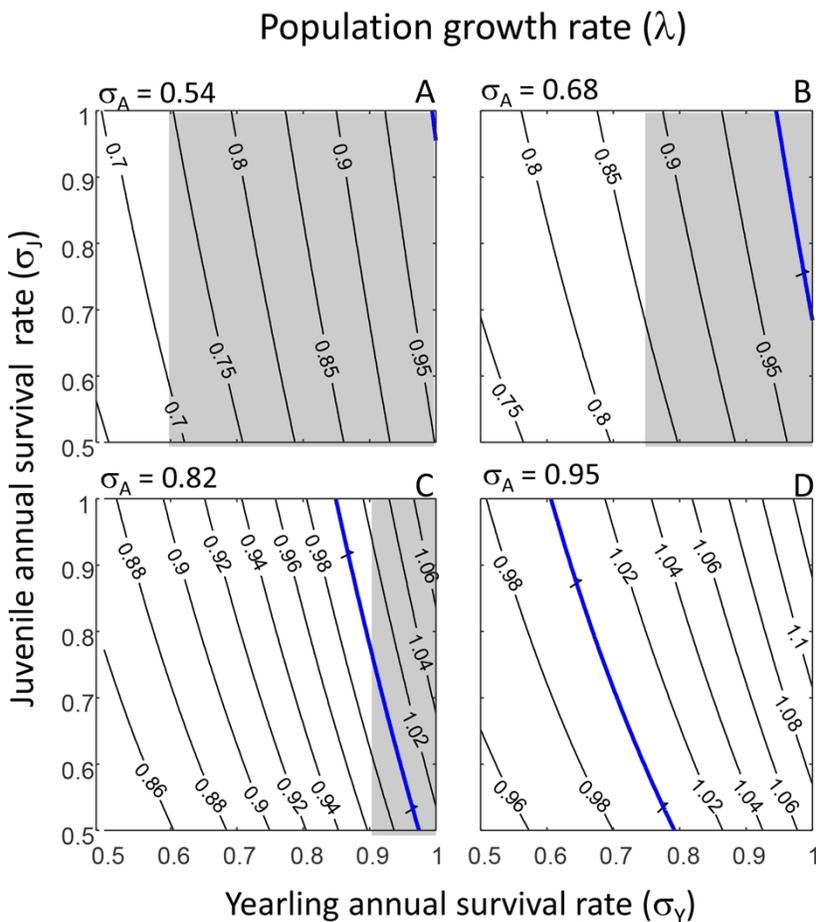
576 **Figure 1 Life cycle of *Manta alfredi*.** We distinguished three life stages: yearlings (Y), juveniles

577 (J) and adults (A). The rate at which individuals survive and remain in the same life stage equals

578 P_i, where i indicates Y (yearling), J (juvenile) or A (adult); the rate at which individuals survive

579 and grow to the next life stage equals G_i, where i indicates Y (yearling) or J (juvenile); the rate at

580 which adults produce yearlings equals F_A. See also Equations 1–3.

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582   **Figure 2 Population growth rate and elasticity results.** Predicted population growth rate λ in

583   relation to yearling annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) shown for

584   each of four values of adult annual survival rate (σ_A): $\sigma_A = 0.54$ (80% of observed rate) (A); σ_A

585     $= 0.68$ (observed rate) (B); $\sigma_A = 0.82$ (120% of observed rate) (C); and $\sigma_A = 0.95$ (140% of

586   observed rate) (D). In each panel, isoclines denote equal values of the population growth rate λ.

587   The blue line in each panel denotes population stability at $\lambda = 1$; values higher than $\lambda = 1$ denote

588   increasing populations and value lower than $\lambda = 1$ denote declining populations. The grey and

589   white areas in panels denote the elasticity results: white areas (panel D is all white) denote

590   parameter combinations where the population growth rate is most sensitive to P_A, the rate at

591   which adults survive and remain in the adult stage (Equation 3); grey areas denote parameter

592   combinations where the population growth rate is most sensitive to P_J, the rate at which juveniles

593   survive and remain in the juvenile life stage (Equation 3).

594

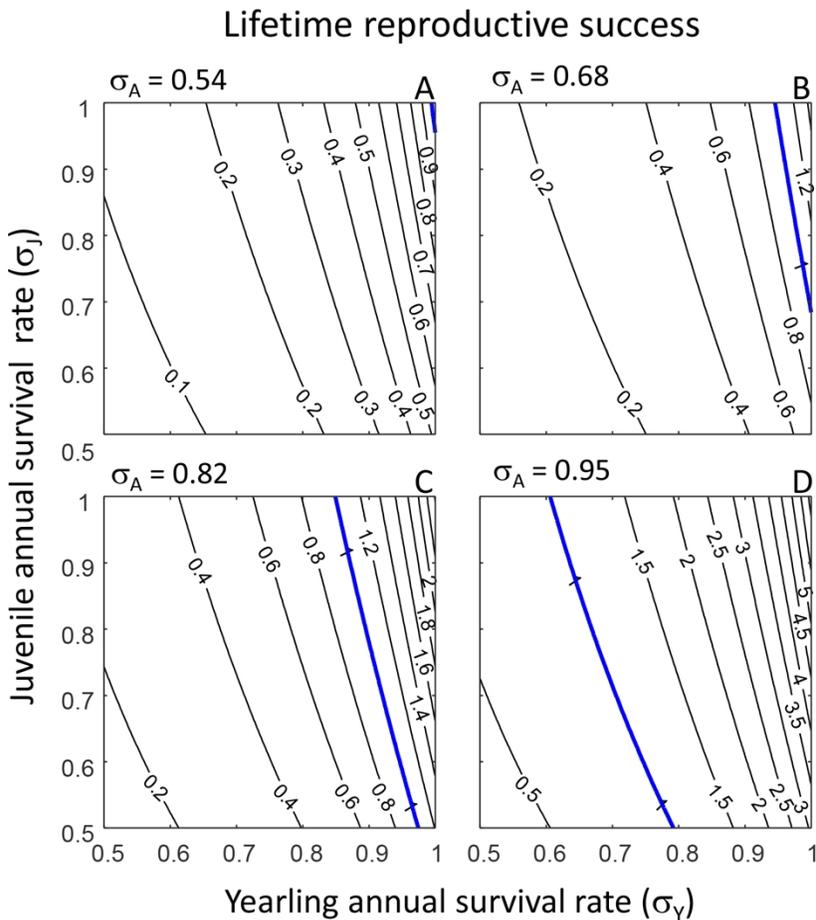



Figure 3 Mean lifetime reproductive success. Predicted lifetime reproductive success (R_0) in

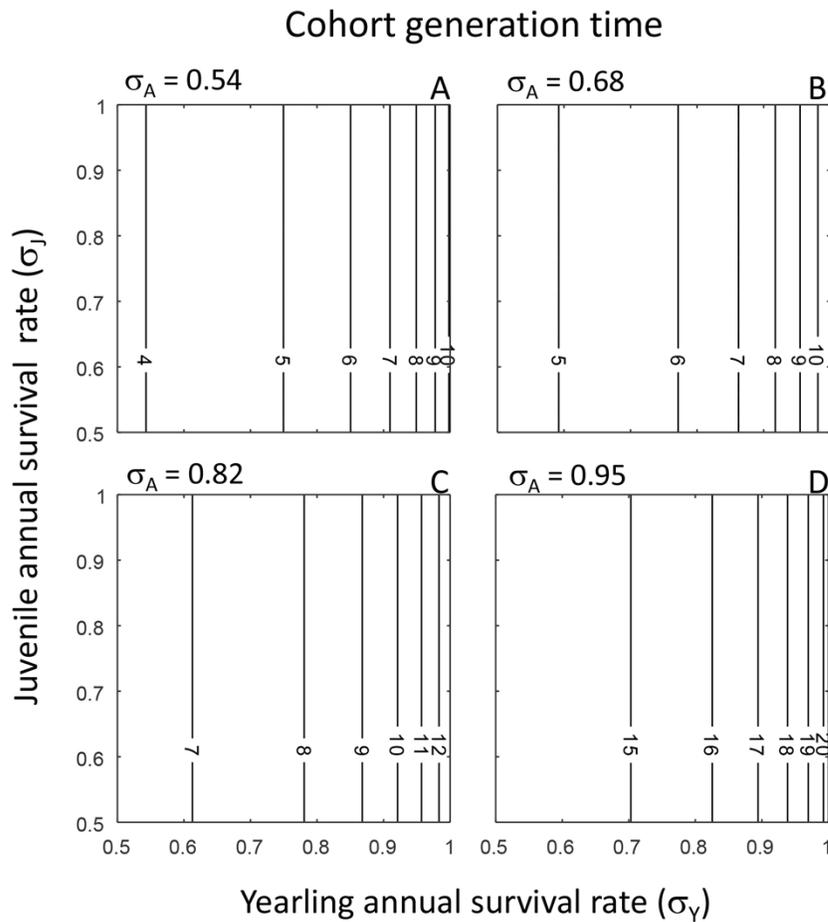
relation to yearling annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) shown for

each of four values of adult annual survival rate (σ_A): $\sigma_A = 0.54$ (80% of observed rate) (A); σ_A

$= 0.68$ (observed rate) (B); $\sigma_A = 0.82$ (120% of observed rate) (C); and $\sigma_A = 0.95$ (140% of

observed rate) (D). In each panel, isoclines denote equal values of lifetime reproductive success,

R_0. The blue line in each panel denotes population stability at $R_0 = 1$; values higher than $R_0 = 1$

denote increasing populations and value lower than $R_0 = 1$ denote declining populations.

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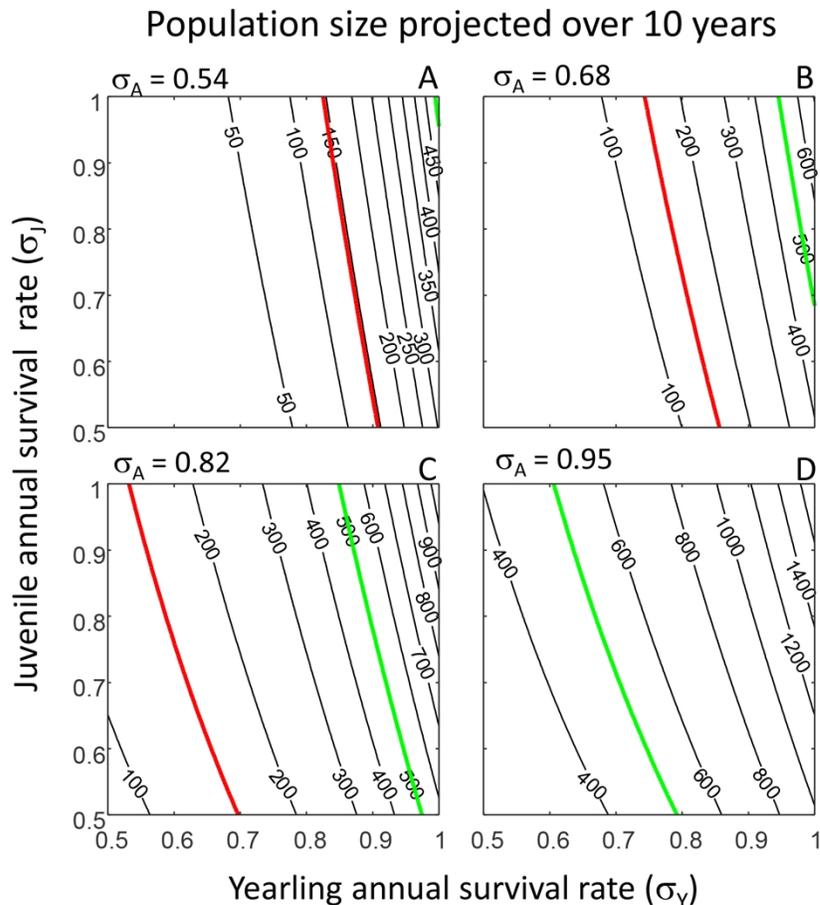
603 **Figure 4 Cohort generation time.** Predicted cohort generation time (T_c) in relation to yearling

604 annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) shown for each of four values of

605 adult annual survival rate (σ_A): $\sigma_A = 0.54$ (80% of observed rate) (A); $\sigma_A = 0.68$ (observed rate)

606 (B); $\sigma_A = 0.82$ (120% of observed rate) (C); and $\sigma_A = 0.95$ (140% of observed rate) (D). In each

607 panel, isoclines denote equal values of cohort generation time.

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609 **Figure 5 Population size projected over ten years.** A population of 500 individuals is

610 projected over ten years using the predicted population growth rate λ (Fig. 2). Projected

611 population sizes are shown in relation to yearling annual survival rate (σ_Y) and juvenile annual

612 survival rate (σ_J) for each of four values of adult annual survival rate (σ_A): σ_A = 0.54 (80% of

613 observed rate) (A); σ_A = 0.68 (observed rate) (B); σ_A = 0.82 (120% of observed rate) (C); and σ_A

614 = 0.95 (140% of observed rate) (D). In each panel, isoclines denote equal values of projected

615 population size. The green line in each panel denotes population stability where the projected

616 population size is equal to the initial size of 500 individuals; above and below this line,

617 populations are projected to increase or decrease respectively. The red line in each panel depicts

618   a population size of 149 individuals, which is equal to the lowest observed population size of

619   reef manta rays off the coast of Mozambique (Marshall, Dudgeon, & Bennett, 2011b).