Reef manta ray life history and demography: is it really all about survival?

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

Background. The trade in gill plates of devil and manta rays has increased greatly over the last two decades. The resulting increased mortality, in addition to mortality caused by by-catch, means that many ray populations are declining in size. The aim of this study was to ascertain the main demographic drivers of population change in reef manta rays (*Manta alfredi*) to increase our understanding of their demography and hence provide insight into potential conservation measures.

Methods. We developed a population projection model for reef manta rays and used published life history data to parameterise the model and also used these data as points of reference to compare our model output to. Because little is known about yearling and juvenile survival of reef manta rays, we conducted our analyses across a range of plausible survival rate values of yearlings, juveniles, and also adults.

Results. The model accurately captured observed patterns of variation in population growth rate, lifetime reproductive success and cohort generation time for different reef manta ray populations around the world. Varying the survival rates of the different life stages revealed that increasing adult annual survival rate always positively and additively affected population growth rate, lifetime reproductive success and cohort generation time. Variation in yearling and juvenile annual survival rate, however, had different and varying effects on the latter three population descriptors, highlighting the importance of obtaining accurate estimates of these survival rates from natural populations. Our elasticity analysis revealed that for both declining and stable populations, the population growth rate is most sensitive to changes in either juvenile or adult survival rate, depending on yearling and adult annual survival rate values.

Discussion. Many reef manta ray populations are declining, resulting in local extinction unless effective conservation measures are taken. Based on our detailed demographic analysis, we suggest that reef manta ray conservation would particularly benefit from focusing on increasing juvenile and adult survival.

Reef manta ray life history and demography: is it really all about survival?

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ABSTRACT

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Discussion. Many reef manta ray populations are declining, resulting in local extinction unless effective conservation measures are taken. Based on our detailed demographic analysis, we suggest that reef manta ray conservation would particularly benefit from focusing on increasing juvenile and adult survival.

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INTRODUCTION

The global demand and resulting trade in plant and animal products is causing unsustainable use of biological resources (Berkes et al., 2006; Lenzen et al., 2012). For aquatic species we are now only beginning to understand the great scale at which trading occurs in, for example, shark fins (Clarke et al. 2006), fish swim bladders (Clark 2004; Sadovy & Cheung 2003), sea cucumbers (Anderson et al., 2011) and seahorses (Foster & Vincent 2004). Since 1998, the trade of products derived from manta and devil rays has increased exponentially (Ward-Page, Davis & Worm 2013). The gill plates form the key ingredient in traditional Chinese medicine, whereas the cartilage serves as a filler in shark fin soup (White et al., 2006; Ward-Paige, Davis & Worm, 2013). The exploitation of these ray species has resulted in population declines (Marshall et al., 2011a; Couturier et al., 2012) and increases their risk of extinction. As a result, some rays, including the reef manta ray *Manta alfredi* and giant manta ray *M. birostris*, are now listed as 'Vulnerable' on the IUCN Red List of Threatened Species (Marshall et al. 2011a). Reef manta rays have a slow life-history, e.g. late maturity, a long gestation period and a low mean lifetime reproductive success (Marshall et al. 2011a). Therefore, once a reef manta ray population starts to decrease or reaches critically low numbers, e.g. due to overfishing, it will be very difficult for the population to recover (Kashiwagi, 2014). This means that understanding how manta ray population growth rates are affected by variation in demographic rates such as growth, survival and fertility rates, is particularly important (Couturier et al. 2014; Kashiwagi, 2014).

Recently, *M. alfredi* and *M. birostris* were listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This listing implies that any international trade of manta rays from September 2014 onward must be regulated. However, in many countries, particularly developing ones (e.g. Sri Lanka and countries in east Africa such as Mozambique), manta ray populations are decreasing at an alarming rate (Marshall et a. 2011a; Ward-Paige, Davis & Worm, 2013). Although manta ray ecotourism occurs in many of these regions, in only 32% of these are manta rays considered protected (Ward-Paige, Davis & Worm, 2013). For example, despite their importance for ecotourism (Tibiriçá et al., 2011), their large size and frequent inshore occurrence, manta rays are not protected under Mozambique law, even though there has been a 88% decrease in reef manta ray sightings off Praia do Tofo, Mozambique (Rohner et al., 2013). What is more, the main aggregation areas of reef manta rays off the coast of southern Mozambique are not inside marine protected areas (Pereira et al., 2014). At the same time, there has been a rapid increase in the use of gill nets by artisanal fisheries within offshore regions that are frequented by these rays, which has significantly increased reef manta ray by-catch (Marshall, Dudgeon & Bennett, 2011b; Pereira et al., 2014). In depth understanding of the demography of reef manta rays and their response to different mortality regimes is therefore urgently needed for improved conservation efforts and management policies (Ward-Paige, Davis & Worm, 2013).

Although manta rays are often easy to approach, the paucity of data hampers an in-depth understanding of their population dynamics (Ward-Paige, Davis & Worm, 2013). If conservation management policies are to be effective, knowledge regarding a population's sensitivity to disturbance is essential. For example, demographic analyses of the population dynamics of other long-lived organisms such as turtles have revealed that population persistence is most sensitive to adult survival, whereas the protection of young (e.g. through protective rearing schemes) has a much smaller impact on population persistence (Heppell, Crowder & Crouse, 1996). Therefore, a very small decrease in the annual survival rate of (sub)adults can have serious repercussions for the persistence of populations of long-lived species, including manta rays (Ward-Paige, Davis & Worm, 2013; Kashiwagi, 2014).

The aim of this study was to ascertain the demographic drivers of population change in reef manta rays (*Manta alfredi*). To this end we developed a stage-structured population projection model (PPM) (Caswell, 2001) and parameterised this model using published life history data from a population off the coast of southern Mozambique (Marshall, Dudgeon, & Bennett, 2011b) and off Yaeyama Islands, Japan (Kashiwagi, 2014) as points of reference for our demographic analyses. Detailed information on the survival of yearling and juvenile reef manta rays is scarce (Marshall et al. 2011a; Dulvy et al. 2014). We therefore used the model to investigate how different values of annual survival rates of yearlings, juveniles and adults affect *M. alfredi* population growth rate, mean lifetime reproductive success and cohort generation time. We assessed the performance of this model by comparing predicted values of the latter three population biology descriptors against empirical observations. We next conducted elasticity analyses for all combinations of yearling, juvenile and adult survival rates to investigate which demographic rate (i.e. growth, survival or fertility rate) has the greatest influence on the population growth rate. Elasticity analysis is widely applied by conservation biologists to aid in developing management strategies (Benton & Grant, 1999; Carslake, Townley & Hodgson, 2009). Because much less is known about yearling and juvenile survival rates than about adults survival rates (Marshall et al., 2011a; Dulvy et al. 2014), exploring a range of yearling and juvenile survival rates will provide insight into if and how reef manta ray population responses vary with variation in survival rates. Finally, for all these combinations of yearling, juvenile and adult survival rates, we used the calculated population growth rates to project a population of 500 individuals forward over a period of ten years to explore the population consequences of the different yearling, juvenile and adult mortality regimes.

METHODS

Life cycle

The life cycle of reef manta rays is generally divided into three life stages: yearlings, non-reproducing juveniles and reproducing adults (Fig. 1) (Marshall et al., 2011a; Kashiwagi, 2014). Male manta rays reach maturity after six years and females are thought to mature at 8–10 years of age; longevity is estimated to be at least 40 years (Marshall et al., 2011a). On average, adult females produce one pup every two years, but fertility rates can range from one pup every 1-5 years (Marshall et al., 2011a). Reef manta ray life history data are being collected from different populations, including ones off the coast of Mozambique and off the coast of Yaeyama Islands, Japan (Table 1). These latter two populations differ remarkably in estimated annual survival rates and population growth rates: the population off the coast of Japan is stable and juveniles and adults display high survival rates (0.95 per year) (Kashiwagi, 2014), whereas the population off the coast of Mozambique is declining and the survival rate of adults is estimated to be as low as 0.68 ± 0.147 SE (standard error) per year (Marshall, Dudgeon, & Bennett, 2011b) (Table 1). Here we used the life history data of these two populations to serve as reference points for our demographic analyses.

Population model

The population model was constructed using the three stage life cycle (Fig. 1). The addition of further life stages may have increased model accuracy, but these are the only currently distinguishable stages in *M. alfredi*. The rate at which individuals survive and remain in the same life stage (as opposed to e.g. growing into the next life stage) equals P_i, where i indicates Y (yearling), J (juvenile) or A (adult), and was calculated as (Caswell, 2001):

$$P_i = \sigma_i(1 - \gamma_i) \qquad \text{(Equation 1)}$$

where σ_i (i = Y, J, A) is the estimated survival rate for each life stage (Table 1). The parameter γ_i is the transition rate from one life stage to the next (expressed per year); in this case from yearling to juvenile (γ_Y) or from juvenile to adult (γ_J). Each transition rate γ_i was calculated as $\gamma_i = 1/D_i$, where D_i is the duration (in years) of either the yearling (i = Y) or juvenile life stage (i = J) (Table 1). The rate (per year) at which individuals survive and grow into the next life stage is defined as:

$$G_i = \sigma_i\gamma_i \qquad \text{(Equation 2)}$$

where i indicates Y (yearling) or J (juvenile). The number of offspring produced each year equals F_A. Putting it all together results in the following population projection matrix (with a projection interval of one year):

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

Parameterisation and model performance

As is common practice (Caswell, 2001), the population model is parameterised for females under the assumption that their growth and survival rates are not too dissimilar to those of male reef manta rays. We set the stage transitions rates γ_i in Equation 1 and 2 constant at $\gamma_\text{Y} = 1/D_\text{Y} = 1/1 = 1$ and $\gamma_\text{J} = 1/D_\text{J} = 1/8 = 0.125$ (Table 1), and we assumed that females produce one pup every two years so that $F_\text{A} = 0.5$ per year. Because little is known about yearling and juvenile survival rates (Marshall et al., 2011a; but see Kashiwagi, 2014), we conducted each demographic analysis (explained in the next section) for all combinations of values of yearling annual survival rate, σ_Y, and juvenile annual survival rate, σ_J, within the interval [0.5, 1] (in increments of 0.005) (Table 1). We conducted each analysis using the observed adult annual survival rate of reef manta rays off the coast of Mozambique of $\sigma_\text{A} = 0.68$ (Marshall, Dudgeon, & Bennett, 2011b); but also for a 20% reduced adult annual survival rate of $\sigma_\text{A} = 0.54$, and for a 20% and 40% increased adult annual survival rate of $\sigma_\text{A} = 0.82$ and $\sigma_\text{A} = 0.95$ respectively (Table 1). Note that the latter value of $\sigma_\text{A} = 0.95$ is equal to the observed non-yearling annual survival rate of reef manta rays in the stable population off the coast of Japan (Kashiwagi, 2014) (Table 1). To assess the performance of our population model, we compared our predictions on population growth rate, lifetime reproductive success and cohort generation time against empirical observations.

Demographic analyses

We first calculated the population growth rate λ from the dominant eigenvalue of matrix **A** (Equation 3) for each of the above mentioned combinations of yearling, juvenile and adult annual survival rate. Secondly, for each of these survival rate combinations, we performed an elasticity analysis to investigate how sensitive the population growth rate λ is to perturbation of each of the different growth, survival and fertility rates in the population projection matrix **A** (Equation 3). To this end, we calculated the elasticity matrix **E**, where each element on row *m* and column *n* of matrix **E**, e_{mn}, represents the proportional contribution of each associated demographic rate P_i, G_i, and F_A in the population projection matrix **A** (Equation 3) to the population growth rate λ. The elasticities were calculated as follows (Caswell, 2001):

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

where a_{mn} are the elements of **A**, and the second part of the equation are the sensitivities of λ to changes in the elements a_{mn} of **A** (Caswell, 2011). The elasticities sum to 1 and give the proportional contributions of the matrix elements to the population growth rate λ. Therefore, the higher an elasticity value is relative to other elasticity values, the greater is the effect of the associated demographic rate on the population growth rate.

Thirdly, for each combination of yearling, juvenile and adult annual survival rate we also calculated mean lifetime reproductive success, R_0, by taking the dominant eigenvalue of the matrix **R** = **FN**. The matrix **F** is a fertility matrix that describes the production of new individuals:

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

The matrix **N** is calculated as **N** = (**I** – **U**)$^{-1}$, where **I** is the identity matrix and **U** the transient matrix that describes the growth and survival rates of the different stages:

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

Fourthly, for each combination of yearling, juvenile and adult annual survival rate we calculated cohort generation time as the mean age of production of offspring in a cohort of yearlings (Caswell 2009):

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

where the vector $\mathbf{e_Y}$ is a vector with 1 in the first entry (for yearlings) and zeros in the second and third entry for juveniles and adults respectively. Fifth and finally, we used the population growth rates calculated at step one to project a population of 500 individuals forward over a period of ten years to explore the population consequences of variation in yearling, juvenile and adult survival rates. All demographic analyses were conducted in MATLAB® R2014b (MathWorks®, MA, USA).

RESULTS

Model performance

Overall, predictions from our population projection model matched empirical observations well. Firstly, predicted values for the population growth rate λ ranged from 0.64 to 1.13, depending on the values of yearling, juvenile and adult survival rate (Fig. 2; Table 2). This range includes the range of observed population growth rate values, but also slightly exceeds the range of observed values (Table 2). The latter is likely due to the fact that we also explored the population consequences of annual survival rates of yearlings, juveniles and adults that are lower and higher than observed survival rates (Table 1). Similarly, the range of predicted values of lifetime reproductive success R_0 (0.06 – 6.20) (Fig. 3; Table 2) includes the range of observed values of R_0, but the highest predicted value of R_0 exceeds the highest observed value of R_0 (Table 2). Again, this is likely due to the fact that we explored the population consequences of unrealistically high annual survival rates of yearlings, juveniles and adults, close to unity (Table 1). Predicted values for cohort generation time were very low (Fig. 4; Table 2), and mostly much lower than observed cohort generation times (Table 2). Only when high adult annual survival rate is at its highest ($\sigma_A = 0.95$) (Fig. 4D) did predicted cohort generation time match observed values (Table 2).

Demographic analyses

We first calculated the population growth rate λ for all different values of yearling, juvenile and adult annual survival rate. This showed that for the observed, adult annual survival rate of σ_A = 0.68 (Marshall, Dudgeon, & Bennett, 2011b), populations can only persist if both yearling and juvenile annual survival rate are high ($\sigma_Y > 0.7$ and $\sigma_J > 0.95$) (Fig. 2B: populations persist to the right of the blue line indicating population stability at $\lambda = 1$). At the lower value of adult annual survival rate $\sigma_A = 0.54$, populations can only persist if both yearling and juvenile annual survival rate are almost unity (Fig. 2A: populations persist to the right of the blue line indicating population stability at $\lambda = 1$). At the higher values of σ_A ($\sigma_A = 0.82$ and $\sigma_A = 0.95$) populations can persist at much lower values of yearling and juvenile annual survival rate (Fig. 2C, D: populations persist to the right of the blue line indicating population stability at $\lambda = 1$); e.g. if $\sigma_A = 0.95$, yearling survival rate, σ_Y, can be as low as 0.5 as long as juvenile survival rate $\sigma_J = 0.8$ (Fig. 2D). From the fact that the isoclines in each panel are neither horizontal nor vertical, we can furthermore infer that for a constant value of σ_Y (or σ_J), the population growth rate depends on what the value of σ_J (or σ_Y) is. However, because the isoclines in each plot are parallel, we can infer that these effects are additive and there is therefore no interactive effect between 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 vice versa).

Secondly, we checked how variation in yearling, juvenile and adult survival rate affected the elasticity of the population growth rate λ to each of the demographic rates in the population projection model (Equation 3). This revealed that, depending on the survival rate values, λ was either most sensitive to P_A or P_J, the rate at which adults, respectively juveniles, survive and remain in the adult, respectively juvenile life stage (Fig 2: white areas in each panel denote survival rate values where λ is most sensitive to P_A; grey areas denote survival rate values for which λ is most sensitive to P_J). What is noticeable is that with increasing values of adult annual survival rate σ_A (going from Fig. 2A to Fig. 2D), the region of yearling survival rate (σ_Y) values for which λ is most sensitive to P_A decreases whereas, at the same time, the region of yearling survival rate values for which λ is most sensitive to P_J, increases. These shifts also highlight the fact that the elasticity results are independent of juvenile annual survival rate (σ_J); instead, whether or not λ is most sensitive to perturbation of P_J or P_A depended critically on the values of σ_Y and σ_A (Fig. 2).

Thirdly, we investigated the effect of variation in yearling, juvenile and adult survival rate on mean lifetime reproductive success. The results are qualitatively similar to those observed for the population growth rate: with increasing values of adult annual survival rate σ_A, populations can persist at ever lower values of yearling and juvenile annual survival rates (Fig. 3: populations persist to the right of the blue line indicating population stability at $R_0 = 1$). In contrast to the results for population growth rate, the isoclines in each panel are non-parallel and unevenly spaced (Fig. 3), which indicates that yearling and juvenile annual survival rate σ_Y and σ_J have an interactive effect on lifetime reproductive success. That is, the magnitude of an effect of σ_Y on lifetime reproductive success depends on the value of σ_J and vice versa. The uneven spacing of the isoclines for each value of adult annual survival rate (Fig. 3) furthermore indicates that, with decreasing values of yearling and juvenile annual survival rates, lifetime reproductive success decreases at an ever slower rate.

Fourthly, we examined the effect of variation in yearling, juvenile and adult survival rate on cohort generation time. For each value of adult annual survival rate (σ_A), cohort generation time increases with increasing values of yearling annual survival rate (σ_Y). At the same time, however, there is no effect of juvenile annual survival rate (σ_J) as the increase in cohort generation time with increasing values of σ_Y is the same for each value of σ_J (Fig. 4). Overall, cohort generation time increased with increasing values of adult annual survival rate (σ_A) (Fig. 4).

Fifthly and finally, we used the predicted population growth rates (Fig. 2) to project a starting population of 500 individuals forward over ten years to investigate the population consequences of variation in yearling, juvenile and adult survival rate. The combinations of yearling, juvenile and adult survival rate values at which populations are stable and the projected population size remains 500 individuals after ten years (indicated by the green lines in Fig. 5) are the same as those observed in our analyses of population growth rate (Fig. 2) and lifetime reproductive success (Fig. 3). Values of yearling annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) values for which the projected population size equals the lowest observed population size of reef manta rays off the coast of Mozambique [149 (Marshall, Dudgeon, & Bennett, 2011b); indicated by the red lines in Fig. 5) both decrease with increasing values of adult annual survival rate (σ_A). This implies that the decline in population size over ten years is less at higher values of adult annual survival rate than at lower values of adult annual survival rate. Vice versa, for combinations of values of σ_J and σ_Y for which populations increase in size, the increase over ten years is higher at higher values of adult annual survival rate than at lower values of adult annual survival rate (Fig. 5).

DISCUSSION

Model performance

Here, we present a population model for reef manta rays, which we used to conduct a detailed analysis of reef manta ray demography. With this analysis we aim to contribute to an increased understanding of the drivers of population change in reef manta rays and how perturbations to demographic rates, such as a decrease in survival due to targeted fishing and by-catch, affect their population fluctuations. We started out by constructing a population projection matrix comprising the three life stages that can currently be distinguished in reef manta rays: yearlings, juveniles and adults (Marshall et al., 2011a). The performance of this model was satisfactory: mean lifetime reproductive success and population growth rates observed for different reef manta ray populations across the world were all within the range of population growth rates that we predicted from our population model. For the reef manta ray population off the coast of Yaeyama Islands, Japan, annual survival rates of all three life stages as well as the population growth rate have been estimated: yearling annual survival rate is estimated to be 0.63 and juvenile and adult annual survival rates are both estimated at 0.95 (Kashiwagi, 2014). The population growth rate predicted by our population model associated with these values is ~1.01 (Fig. 2D: $\sigma_Y = 0.63$; $\sigma_J = \sigma_A = 0.95$), which is very close to the actual population growth rate of the Yaeyama Islands reef manta ray population, which is estimated at 1.02 per year (Kashiwagi, 2014). The one discrepancy between prediction and observation was in case of predicted cohort generation time at lower adult annual survival rates of $0.54 \leq \sigma_A \leq 0.82$ (Fig. 4A-C). At these low survival rates, adults do not attain a high age, which lowers the average age at which adults reproduce and hence results in a low cohort generation time. Observations on cohort generation time are likely taken from stable populations (Marshall et al. 2011a; Ward-Paige, Davis & Worm, 2013), where annual adult survival rate is much higher; for example, in the stable reef manta ray population off the coast of Yaeyama Islands, Japan, adult annual survival rate (σ_A) equals 0.95 (Kashiwagi, 2014). Indeed, at $\sigma_A = 0.95$, predicted cohort generation times do match observed generation times. Overall, it is therefore rewarding that predictions from our population model match observations on the key population descriptors of lifetime reproductive success, population growth rate and cohort generation time.

Demographic analyses

Because little is known about survival rates of yearling and juvenile reef manta rays, we explored the effects of a range of values of yearling and juvenile annual survival rates on the three population descriptors lifetime reproductive success, population growth rate and cohort generation time. At the same time, we also varied adult annual survival rate from as low as 0.54, which is 20% lower than the observed annual survival rates of adults of 0.68 per year off the coast of Mozambique (Marshall, Dudgeon, & Bennett, 2011b), to as high as 0.95 per year, which equals the observed adult annual survival rate in the stable population off the coast of Yaeyama Islands, Japan (Kashiwagi, 2014). The effects of an increase in adult annual survival rate across this range of values was straightforward: with increasing adult annual survival rate, values of all population descriptors increased as well. However, variation in yearling and juvenile annual survival rate had different and varying effects on the population descriptors that we investigated. In case of population growth rate, changes in these two survival rates had additive effects on the population growth rate, but interactive (multiplicative) effects on mean lifetime reproductive success, whereas cohort generation time was unaffected by variation in juvenile annual survival rate. Also, the effect of an increase in juvenile annual survival rate was of a far greater magnitude on mean lifetime reproductive success and population growth rate than the effect that the same increase in yearling annual survival rate had on these population descriptors. All in all, this means that effects of variation in yearling and juvenile survival rates on population growth rate, mean lifetime reproductive success and cohort generation time are not necessarily straightforward. To obtain accurate insight into the dynamics of reef manta ray populations, our results therefore emphasize the importance of obtaining accurate estimates of yearling and juvenile survival rates from natural populations.

One way of gaining general insight into the population consequences of differences in demographic rates is by using the population model to project a population forward in time and examine its future size relative to its original size. We did so for a period of ten years for all combinations of yearling, juvenile and adult annual survival rates. The reef manta ray population off the coast of Mozambique has declined by 88% between 2005 – 2011 due to variation in the local environment, anthropogenic pressures and larger-scale oceanographic influences (Rohner et al., 2013). Our population projections confirm that the low, observed adult annual survival rate of adult reef manta rays off the coast of Mozambique of 0.68 per year (Marshall, Dudgeon, & Bennett, 2011b) indeed nearly always results in population decline, unless yearling and juvenile annual survival rate are near unity. However, given that fact that reef manta ray by-catch has recently significantly increased in this region (Marshall, Dudgeon & Bennett, 2011b; Pereira et al., 2014), it is unlikely that juvenile survival rates are close to unity. What is more, in a stable a reef manta ray population off the coast of Yaeyama Islands, Japan, yearling survival rate was estimated to be 0.63 (Kashiwagi, 2014). Hence, unless survival rates of reef manta rays in populations off the coast of Mozambique increase, e.g. by reducing direct and by-catch of manta rays, the prospects of these reef manta ray populations are dire.

Conservation

Many manta ray populations across the globe are declining according to the IUCN Red List for Threatened Species (Marshall et al., 2011a; but see Kashiwagi (2014) for an exception). One way of increasing our understanding of how such declines can be reduced or even halted is by conducting an elasticity analysis of a demographic model as the results can be used to develop adequate management strategies (Benton & Grant, 1999; Carslake, Townley & Hodgson, 2009).

Our elasticity analysis revealed that the population growth rate was either most sensitive to adult or juvenile annual survival rate. Which of these two rates was most influential depended on the values of yearling annual survival rate and adult annual survival rate. For example, in case of the reef manta rays off the coast of Mozambique, adult annual survival rate equals 0.68 (Marshall, Dudgeon, & Bennett, 2011b) and observed population growth rate is estimated at 0.77 per year (Rohner et al., 2013). At these values, the population growth rate is most sensitive to change in the adult annual survival rate according to our elasticity analysis (Fig. 2B). At higher values of adult annual survival rate, the range of values of yearling survival rate under which the population growth rate is most sensitive to perturbation of adult annual survival rate increases until the population growth rate is always most sensitive to perturbation of adult annual survival rate. For example, in the stable population off the coast of Yaeyama Islands, Japan, adult annual survival rate equals 0.95, and, according to our elasticity analysis, this population would also be most sensitive to a change in adult annual survival rate. Although currently this population does not suffer from direct fishing pressure (Kashiwagi, 2014), any exploitation or change in adult survival is likely to greatly affect this population. A previous demographic analysis based on a generic reef manta ray life cycle (hence not of a specific manta ray population) found that the intrinsic population growth rate *r* was most sensitive to change in offspring production rate (and not mortality rate) (Dulvy et al., 2014). However, unlike our elasticity analysis, this sensitivity analysis investigated how *additive* perturbations in life history parameters affected the intrinsic population growth rate, whereas we investigated how *proportional* perturbations in demographic rates affected the long-term population growth rate; hence no direct comparison can be made.

The demographic rates that comprise our population matrix are determined by the underlying parameters σ_i (survival rate) and γ_i (stage-specific transition rate). However, because the adult annual survival rate P_A equals σ_A and is independent of γ_i, population growth rate is indeed most sensitive to perturbation in adult survival at high adult survival rates, which is typical for long-lived animals. For example, there is a minimal impact of so-called "headstarting" of turtle hatchlings on the population growth rate. Elasticity analyses have revealed that targeting sub-adult and adult turtle survival would yield a higher rate of population growth, and thus form a more effective management strategy than the protective rearing of newborns (Crouse, Crowder & Caswell, 1987; Heppell, Crowder & Crouse, 1996). The importance of adult survivorship is also evident in northern fur seals *Callorhinus ursinus* (Trites & Larkin, 1989), marbled murrelets *Brachyramphus marmoratus* (Beissinger, 1995) and cheetahs *Acinonyx jubatus* (Crooks, Sanjayan & Doak, 1998). In the case of the reef manta rays off the coast of Mozambique, effective management and legislation is urgently needed to avoid its local extinction. Two main approaches should be taken: (1) the species should be protected at the national level against fishing, including accidental catch; (2) aggregation areas should be protected. The behaviour of reef manta rays at cleaning stations makes targeted fishing a potential threat, but also creates an opportunity for site-specific protection. By protecting aggregation sites, both juveniles and adults could profit from increased survival, resulting in a higher population growth rate. The importance of adult survival makes manta rays an unsustainable fishing resource. Their socio-economic value has yet to be realised to its full potential, but one thing is clear: manta rays are worth more alive than dead (O'Malley, Lee-Brooks & Medd, 2013; Ward-Paige, Davis & Worm, 2013).

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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	Marshall et al. 2011a
D_J	Average duration of (female) juvenile stage (years)	9	8-10	not specified	Marshall et al. 2011a
D_A	Duration of adult stage (years)	31	31	not specified	Marshall et al. 2011a
F_A	Average number of pups per year	0.5	0.5	Mozambique	Marshall & Bennett 2010

500

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)

501

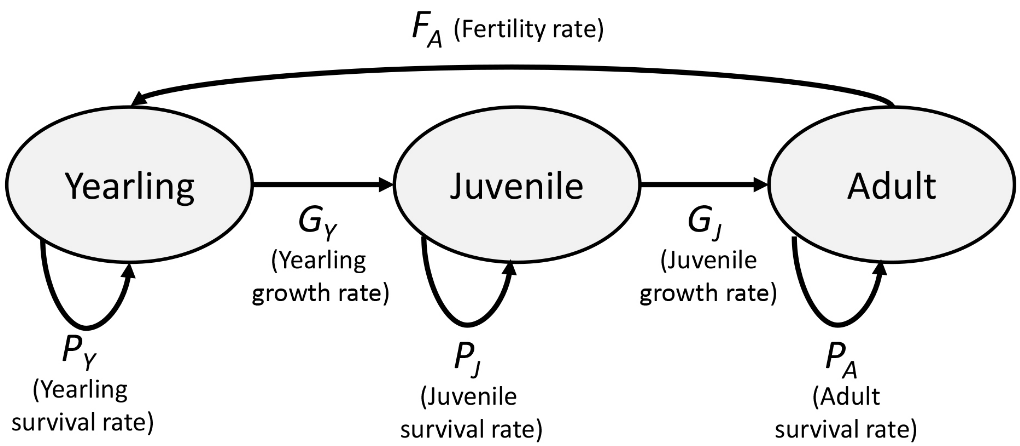

Figure 1 Life cycle of *Manta alfredi*. We distinguished three life stages: yearlings (Y), juveniles (J) and adults (A). The rate at which individuals survive and remain in the same life stage equals P_i, where i indicates Y (yearling), J (juvenile) or A (adult); the rate at which individuals survive and grow to the next life stage equals G_i, where i indicates Y (yearling) or J (juvenile); the rate at which adults produce yearlings equals F_A. See also Equations 1–3.

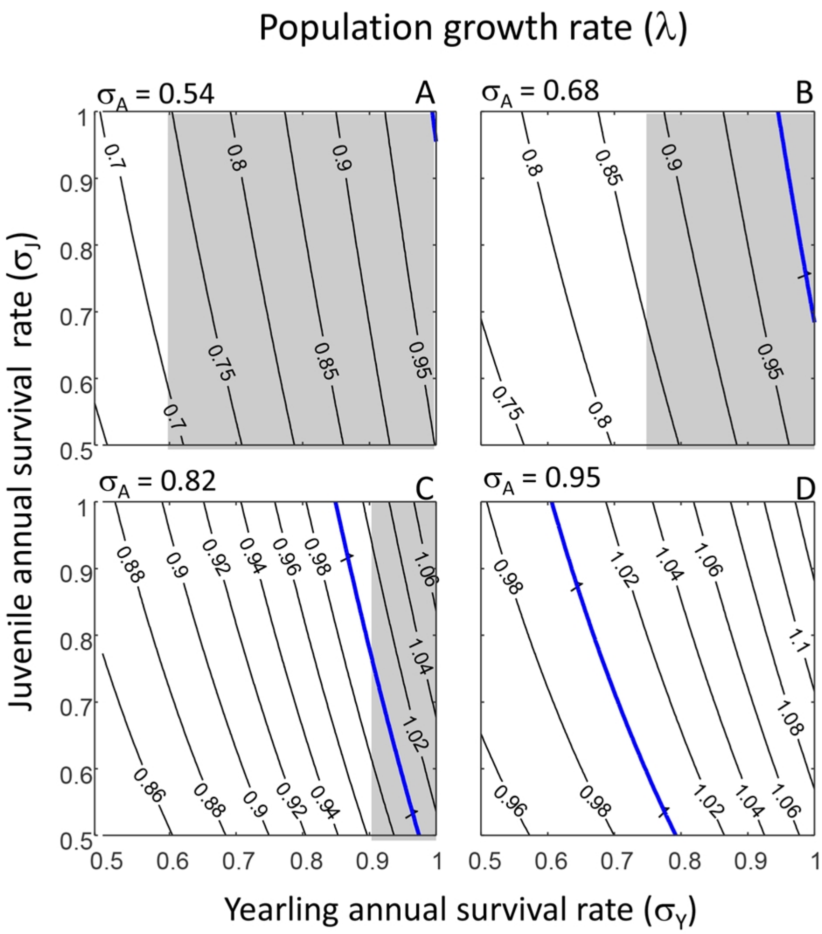

Figure 2 Population growth rate and elasticity results. Predicted population growth rate λ in relation to yearling annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) shown for each of four values of adult annual survival rate (σ_A): σ_A = 0.54 (80% of observed rate) (A); σ_A = 0.68 (observed rate) (B); σ_A = 0.82 (120% of observed rate) (C); and σ_A = 0.95 (140% of observed rate) (D). In each panel, isoclines denote equal values of the population growth rate λ. The blue line in each panel denotes population stability at λ = 1; values higher than λ = 1 denote increasing populations and value lower than λ = 1 denote declining populations. The grey and white areas in panels denote the elasticity results: white areas (panel D is all white) denote parameter combinations where the population growth rate is most sensitive to P_A, the rate at

which adults survive and remain in the adult stage (Equation 3); grey areas denote parameter combinations where the population growth rate is most sensitive to P_J, the rate at which juveniles survive and remain in the juvenile life stage (Equation 3).

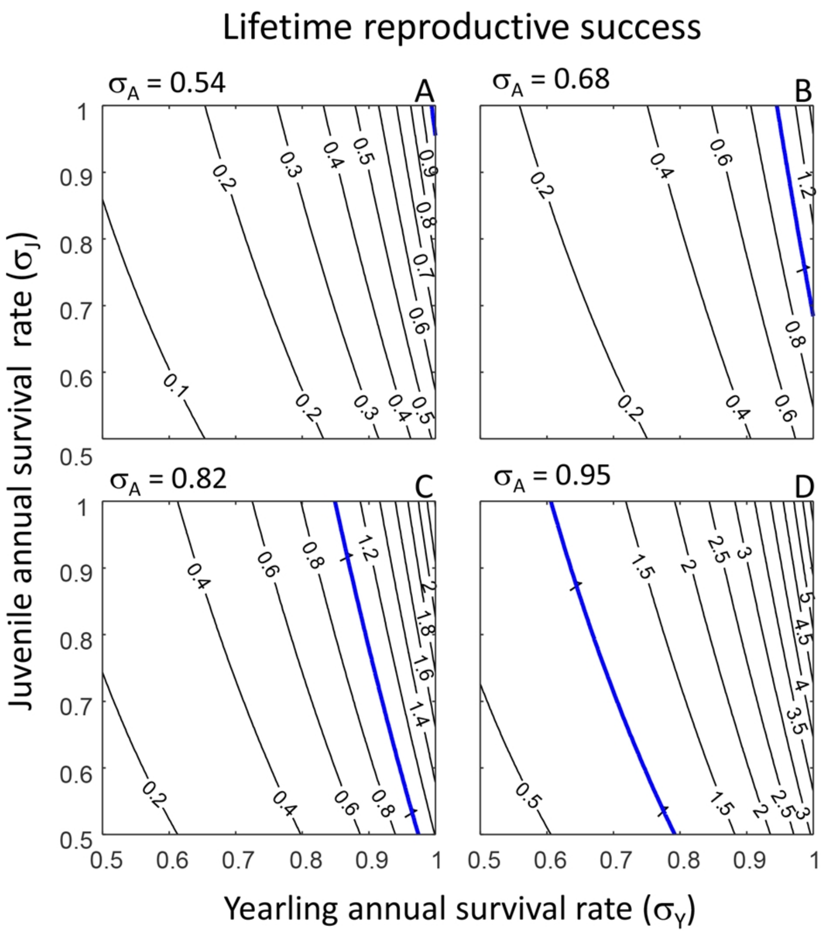

Figure 3 Mean lifetime reproductive success. Predicted lifetime reproductive success (R_0) in relation to yearling annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) shown for each of four values of adult annual survival rate (σ_A): σ_A = 0.54 (80% of observed rate) (A); σ_A = 0.68 (observed rate) (B); σ_A = 0.82 (120% of observed rate) (C); and σ_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.

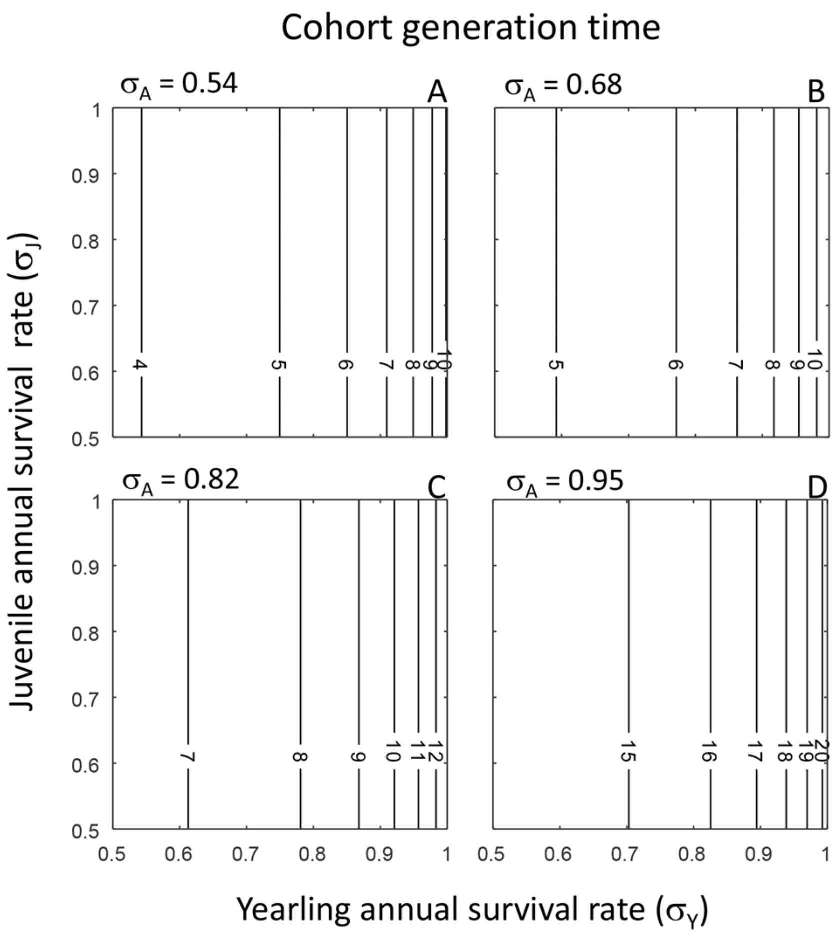

Figure 4 Cohort generation time. Predicted cohort generation time (T_c) in relation to yearling annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) shown for each of four values of adult annual survival rate (σ_A): σ_A = 0.54 (80% of observed rate) (A); σ_A = 0.68 (observed rate) (B); σ_A = 0.82 (120% of observed rate) (C); and σ_A = 0.95 (140% of observed rate) (D). In each panel, isoclines denote equal values of cohort generation time.

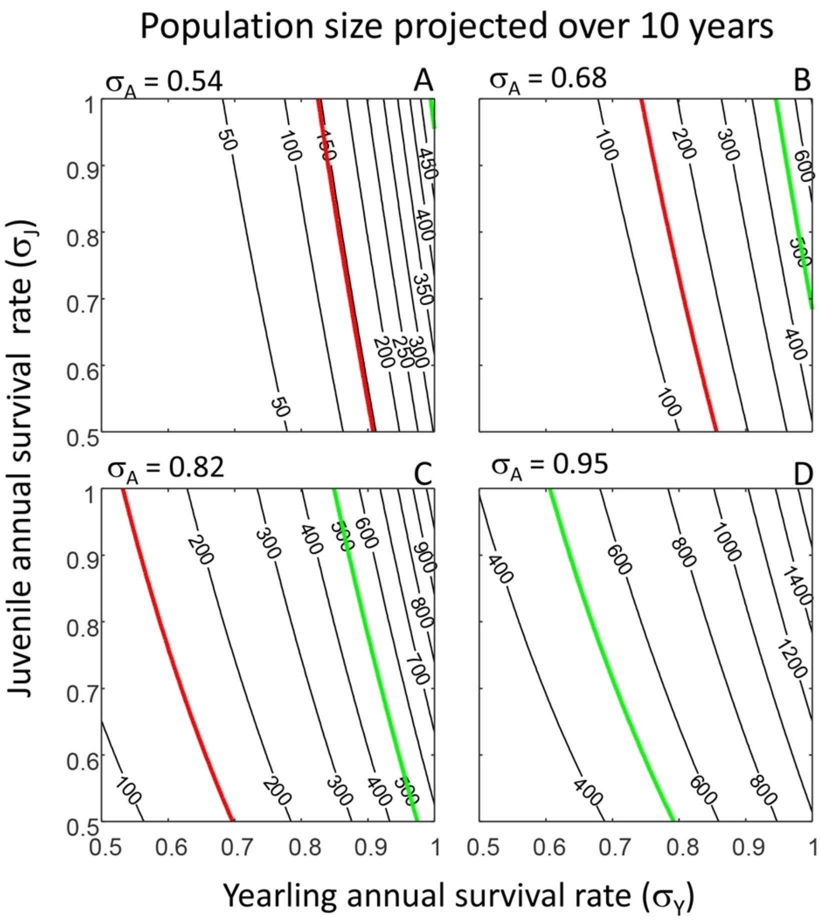

Figure 5 Population size projected over ten years. A population of 500 individuals is projected over ten years using the predicted population growth rate λ (Fig. 2). Projected population sizes are shown in relation to yearling annual survival rate (σ_Y) and juvenile annual survival rate (σ_J) for each of four values of adult annual survival rate (σ_A): $\sigma_A = 0.54$ (80% of observed rate) (A); $\sigma_A = 0.68$ (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 projected population size. The green line in each panel denotes population stability where the projected population size is equal to the initial size of 500 individuals; above and below this line, populations are projected to increase or decrease respectively. The red line in each panel depicts

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a population size of 149 individuals, which is equal to the lowest observed population size of reef manta rays off the coast of Mozambique (Marshall, Dudgeon, & Bennett, 2011b).