Using mechanistic models to assess temporary closure strategies for small scale fisheries

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1   ABSTRACT

Mechanistic models are particularly useful for understanding and predicting population dynamics in data deficient species. Data deficiency is a relevant issue in small scale fisheries as they are generally under studied and underrepresented in global fishing datasets. As overfishing remains a global issue, especially in small-scale fisheries, one commonly utilized conservation method is temporary closures The *Octopus cyanea* (blue octopus) fishery off the southwest coast of Madagascar is one such system that utilizes these closures, yet lacks sufficient data collection specific to this species to assess the viability of the population. This fishery is a key economic resource for the local community as blue octopus catch is sold by local fishers to international export markets adn is a major component of fisher income. To assess the sustainability of blue octopus, we parameterize a Levkovitch population matrix model using existing catch data. In this study, we show that this population was in a decline of 1.8% per month at the time of data collection. We also assessed the effects of different temporary closures and which of these management strategies would result in a sustainable population of blue octopus. To sustain the existing population of blue octopus, our model indicates that the fishery would need to close at least once every 5 months for one month. Increasing the frequencies of closure are predicted to significantly increase the octopus population at these sites. We show that if implemented correctly, temporary closures could be utilized to restore this population. Since this data was collected, the local communities of Madagascar have implemented various fishing restrictions to ensure sustainable fishing, indicating a need for further research into the effectiveness of these fishing closures. Therefore, our study provides insight into the underlying population dynamics of this fishery and provides survivability estimates of this species.

2   INTRODUCTION

Mechanistic models in ecology explicitly account for species life histories, behavioral, or other mechanisms to describe how a population or community may change over time (André, Haddon, and Pecl 2010; Briggs-Gonzalez et al. 2016). This is in contrast to statistical models that may be focused on correlating a response variable with different covariates and less focus on underlying mechanisms. Mechanistic models are important in situations without existing long-term data, when future conditions may not be similar to the past, and when different scenarios or actions need to be assessed (Crouse, Crowder, and Caswell 1987; Nowlis 2000; Gharouni et al. 2015). Thus, mechanistic models play a critical role in making informed conservation decisions, such as the management of small-scale fisheries. Worldwide, 32 million fishers make their livelihood in small-scale fisheries, a subsector in which 90 to 95% of fish is distributed for local consumption. These marine products are a vital source of nutrition for these communities ("HIDDEN HARVEST-The Global Contribution of Capture Fisheries" 2012).

The southwest region of Madagascar is one such area where subsistence fishing is an essential component to the diet and income of the local community. The ocean environments off the southwest coast of Madagascar are home to a wide variety of marine life, as sand beds, seagrass beds and coral reefs are all prominent biomes in the area. Increased urbanization in the region has led to higher fishing pressure which has in turn led to a decline in fish catch and biomass (Laroche et al. 1997). In fact, Madagascar has been calculated to be among the top countries for potential successful preservation based on the potential economic benefits and success of harvest regulation (MacNeil et al. 2020), especially in the western region of the country (Laroche et al. 1997). In the early 2000's, however, Madagascar began to move from local, subsistence fishing to selling catch to export markets (Humber et al. 2006), and there is evidence that up to 75% of all fish caught is now sold to outside entities for international export (Baker-Médard 2017).

Marine Protected Areas (MPAs) are regions in the ocean identified as being biologically important and fishing protections are therefore enforced. Before their establishment in Madagascar, governmental bodies had bans on certain types of fishing gear, implemented seasonal fishing regulations, and criminalized the harvest of endangered species. However, these strategies proved ineffective in execution and in their conservation goals (Humber et al. 2006). Both the government and nongovernmental organizations have since pledged to drastically increase the number of regions dedicated as MPAs through temporary fishing closures (Cinner et al. 2009; Oliver et al. 2015; Baker-Médard 2017).

One such class of MPAs that are currently being used in Madagascar are temporary closures. Temporary closures have a long history of use and have been seen to successfully rehabilitate stocks (Camp, Poorten, and

Walters 2015; Gnanalingam and Hepburn 2015). This method is flexible, logistically simple for fishers and enforcers to understand, and mitigates the financial loss from the fishery that can be seen with permanent closures (Nowlis 2000; Humber et al. 2006; Cohen and Foale 2013; Camp, Poorten, and Walters 2015; Gnanalingam and Hepburn 2015; Oliver et al. 2015). However, they are not always effective in their goal of replenishing stocks and this can depend on a wide range of factors. Ecological considerations about the life history of the target species, Allee effects, and changes to community structure and species interactions all play a role in how well the temporary closure will protect the fishery (Russ and Alcala 1998; Cohen and Foale 2013; Gnanalingam and Hepburn 2015; Gilchrist et al. 2020; Grorud-Colvert et al. 2021). Further, the characteristics of the fishery itself has been seen to influence fishery recovery. Fishing method, where the effort will be redistributed to, and fishing activity upon reopening have all been factors in negating the recovery made during the closure (Hiddink et al. 2006; Humber et al. 2006; Cohen and Foale 2013).

Since 2003, when this resource first began to globalize, cephalopods have become one of the largest classes of exports (Humber et al. 2006; Aina 2009; Barnes-Mauthe 2013). This has since added significant fishing pressure to Madagascar's cephalopod populations and yield from this fishery has decreased in the southwest Andavadoaka region (Humber et al. 2006). Cephalopods are a vital part of many ocean ecosystems and, compared to other fisheries, have a unique life history that can lead to distinct and variable population dynamics. Cephalopods act as both predators and prey in an ecosystem (Rodhouse and Nigmatullin 1996; Santos, Clarke, and Pierce 2001; Vase et al. 2021), situating them in a key role in food webs. They also provide rich nutrition and bioactive compounds to the oceanic microbial community (Catalán et al. 2006; Fitahia et al. 2018; Ibáñez et al. 2019; Van Nieuwenhove, Ratsimbazafy, and Kochzius 2019). Further, their abundance varies drastically with a wide range of ocean conditions including sea surface and bottom temperature, salinity, currents, and sediment type (Catalán et al. 2006; Ibáñez et al. 2019; Van Nieuwenhove, Ratsimbazafy, and Kochzius 2019). Compared to other exploited marine organisms, cephalopods have a short lifespan coupled with a fast reproduction rate and high fecundity. This explains their population's ability to quickly bounce back when short term MPAs are introduced into their habitat (Humber et al. 2006; Katsanevakis and Verriopoulos 2006; S. Benbow et al. 2014). However, once fishing resumes, populations suddenly and rapidly decline although in some examples, this could be attributed to heavy fishing pressure in the area right after reopening (Humber et al. 2006). Cephalopods are therefore extremely sensitive to both protection and harvest levels, and understanding how these volatile population dynamics will react to changes in fishing pressure is a key component to effective conservation of this resource.

Octopus cyanea, or blue octopus, is the most abundant cephalopod species in the western Indian Ocean and is caught in about 95% of local landings (Humber et al. 2006; Oliver et al. 2015). Like other cephalopod

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species, very little is known about their life history including natural death rate, larval survivability, and how much time this species remains in each stage of maturity. Further, age is difficult to determine from size alone as they have variable growth rates up to maturity (Wells and Wells 1970; Heukelem 1976; Herwig et al. 2012; Raberinary and Benbow 2012). Size limits have been shown to be the most effective method of conservation for cephalopods in general as it ensures individuals will breed before being harvested (Nowlis 2000; Emery, Hartmann, and Gardner 2016). To protect this species, size limits have been imposed on blue octopus catch in Madagascar, but these regulations are difficult in practice, as the fishing method used to harvest octopus involves spearing the octopus's den and extracting the octopus from the den. Blue octopus therefore typically die before size can be assessed (Humber et al. 2006). Further, the relationship between size and maturity stage is not strongly correlated (Raberinary and Benbow 2012) and as a result, size restrictions wouldn't necessarily protect individuals ready to reproduce and would be difficult to implement in the field. Therefore, temporary closures have been shown to be a more practical method of blue octopus conservation (S. Benbow et al. 2014), however this requires a deeper understanding of the characteristics of *Octopus cyanea* in this fishery in order to be properly instituted. Instituting effective temporary closures in octopus fisheries can be difficult due to their short lifespan, high mortality, and sensitivity to environmental conditions (Emery, Hartmann, and Gardner 2016). Lack of field data and difficulty of enforcement has also been a challenge in octopus fisheries, especially in Madagascar (Emery, Hartmann, and Gardner 2016; S. Benbow et al. 2014). This indicates that a thorough understanding of the life history of *O. cyanea* and the harvest methods employed by fishers is necessary to enact meaningful fishing restrictions. Currently, the octopus fishery in this region of madagascar is closed for the three months between June and August on a yearly basis (Sophie Benbow and Harris 2011; Westerman and Benbow 2014) which was decided in 2011. In this paper, we will also assess how this has affected *Octoups cyanea* stocks in the areas since.

As *O. cyanea* has an extended larval phase and there is no existing data on the age structure of this population of octopus, we will use a stage-based population matrix, otherwise known as a Lefkovitch matrix (Caswell 2001). Here, the life history of the study organism is grouped by stages (figure 1), where each unit of the matrix represents a distinct period of the organism's life where it is subject to different environments, pressures, or physical attributes that would alter the survival and reproductive output at that phase, but the amount of time between each stage is variable. This would simply create different inputs for the probability of remaining in the same stage, and the growth and fecundity inputs can be based on available data. Lefkovitch matrices have not yet been applied to *Octopus cyanea* populations and therefore could be a useful methodology to understand the dynamics of this population in the western Indian Ocean to better inform management strategies.

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In this paper, we have four goals: 1) we will fit a Levkovitch matrix to the limited available data on *Octopus cyanea* populations in southwestern Madagascar, 2) as well as create a theoretical estimation of the species' life history traits in different stages of its development and 3) determine the frequency and length in which these temporary closures should take place to maximize population health of the fishery and maximizing catch for the local community.
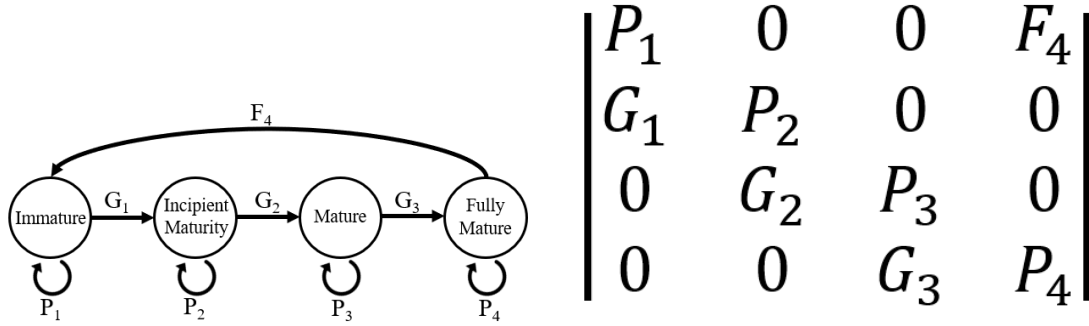

$$\begin{vmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{vmatrix}$$

Figure 1: A graph representing the life history of *O. Cyanea* and the subsequent Lefkivitch Matrix where i corresponds with each of the stages of maturity (Immature, Incipient Mature, Mature, and Fully Mature individuals, respectively). P_i corresponds to probability of surviving and staying within a stage. G_i is the probability of surviving and growing to the next stage. F_i is the reproductive output of stage i.

3   METHODS

3.1   Data

To inform our model, we used data collected by Raberinary and Benbow (2012) from landings ranging from the villages of Ampasilava in the south to Andragnombala in the north which spans about 30 kilometers of coastline. This study collected landing data from February 2005 to February 2006 through daily surveying fishers as they landed onshore within a two hour window. They recorded octopus weight, weight and length of gonads, sex, and a visual assessment of maturity class. A subsample of octopus were also collected for octopus length, and laboratory assessment of gonads for a confirmation of maturity class. They gathered this data on a total of 3253 octopuses, and for the purposes of this study, we will be modeling from the 1578 females collected. Despite there being no standardization for catch effort being available for this dataset, no other maturity stage study has been conducted on this population of *O. cyanea* and is therefore the best available data to fit a Lefkovitch matrix.

$$\begin{vmatrix} P_1 = 0.63 & 0 & 0 & F_4 = 26.7 \\ G_1 = 0.275 & P_2 = 0.322 & 0 & 0 \\ 0 & G_2 = 0.13 & P_3 = 0.393 & 0 \\ 0 & 0 & G_3 = 0.093 & P_4 = 0.331 \end{vmatrix}$$

Figure 2: Stage-based population matrix calculated using Wood's quadratic programming method and parameterized using data from Raberinary and Benbow (2012).

3.2 Model Parameterization

In order to parameterize this model, we used Wood's Quadratic Programming method (Caswell 2001). Other methods required longer time series than were available to us, were extremely sensitive to noise in the data, or simply resulted in matrices that had no reasonable biological interpretation (Caswell 2001). Figure 2 shows a preliminary stage-based matrix model based on Raberinary and Benbow (2012) data and calculated using the quadprog package in R (Turlach and Weingessel 2019). Model accuracy was assessed by comparing life history values inferred from the matrix with existing literature on *O. cyanea* life history (Table 1). As all of our values calculated from the matrix fell within the known attributes of this species, we were confident that this model gave an accurate mechanistic description for this population's underlying dynamics.

3.3 Model Analysis

Eigenvalues (λ) were then calculated from the matrix and future populations can be predicted by multiplying a population vector to incrementally higher powers of our matrix where the power of the matrix corresponds to the time length of the projection. We performed sensitivity analysis on the population matrix and eigenvalues using the r package popbio (Stubben and Milligan 2007). Further, as all of the parameters are scaled to a value between 0 and 1 except F_4, a unit change in these parameters will have a greater proportional effect on the eigenvalue than F_4. To address this, we also conducted elasticity analysis using the popbio package (Stubben and Milligan 2007). This will allow us to identify the groups within this octopus population whose protection will most benefit population growth, essentially creating focus points of conservation. Other life history traits that can be calculated from this matrix are stable stage distribution, reproductive value of each stage, average lifespan, and per-stage survivability. We then used the rage package in R to analyze various life history traits of this matrix, the output of which is included in the supplementary material (Jones et al. 2021).

Table 1: Existing research and information on the per-stage lifespan of *O. Cyanea*. Note: Heukelem and Fred (1976) estimate the time to maturity to be 10-13 months (i.e. stages 1-3 combined).

Stage	Duration	Sources
Egg	20-35 days	Van Heukelem, 1987. Guard and Mgaya, 2003.
Larval	28-56 days	Van Heukelem, 1987. Guard and Mgaya, 2003. Humber et al., 2006.
1: Immature	No existing estimate	
2: Incipient Maturity	No existing estimate	
3: Mature	No existing estimate	
4: Fully Mature	No existing estimate	
5: Post Laying	45-61 days	Heukelem and Fred, 1976. Van Heukelem, 1987.
Post larval Phase (stage 1-5)	9-18 months	Van Heukelem, 1987. Aina, 2019.

Finally, we calculated the minimum survivability increase necessary per stage to result in an increase of the overall population. We did this by increasing the P_i and G_i parameters by increasing percentages in each stage i until the overall eigenvalue (λ) became greater than one.

3.4 Management Scenarios

In order to determine optimal conservation strategies, we altered the survivability of *O. cyanea* by different rates from 0-10% survival increase of the species. Then, we simulated different closure scenarios for each survival increase, by altering the number of months between closures. We then multiplied higher powers of the original matrix uring months that were simulated to be "open fishing" and then when a closure was simulated, the matrix with increased survival was multiplied to the population for that month. We simulated these different scenarios in order to analyze all combinations of conservation strategies that result in stable *O. cyanea* populations. We also modeled how this fishery would act under the three month closure that is currently instituted in Madagascar. We simulated this scenario by increasing the survivability of the matrix by 1% increments and then multiplying this new matrix during the first three months of the year. After the closure, the orginial matrix was multiplied and the overall growth rate was calculated. This allowed us to analyze how much of a survivability increase would be necessary in these closures to result in a growing population of *Octopus cyanea*.

4 RESULTS

The resulting eigenvalue of our matrix was 0.982, indicating a population decline of 1.8% per month (Figure 3). Sensitivity analysis (Figure 4) showed that within each stage, the growth parameters (G_1 - G_3) had the largest effect on the eigenvalue compared to the parameters indicating staying within a stage (P_1-P_4).

Table 2: Stable stage distribution and reproductive value of each stage of this blue octopus population matrix given in Figure 2

Stage	Stable Stage Distribution (Dominant Eigenvector)	Reproductive Value (Left Eigenvector)
1 Immature	0.657	1.000
2 Incipient Maturity	0.274	1.279
3 Mature	0.061	6.491
4 Fully Mature	0.009	41.029

However, as all the parameters must necessarily be between 0 and 1 with the exception of the F_4 parameter, elasticity analysis provides an interpretation that weights all stages equally. The result of this analysis shows that percent changes in the fecundity metric can be as beneficial to the overall population growth as changes in the G parameters (Figure 5). Further, this analysis indicates that of all the stages, stage 1 has the most overall influence on the overall population growth. The stable stage distribution (Table 2) shows that 65% of the makeup of this population is immature individuals, while actively breeding individuals (fully mature) only make up less than 1% of the naturally occurring population. However, the reproductive output per stage (Table 2) shows that on average, an individual in this fully mature population is expected to have 41 times the number of offspring as those in stage 1.

Changing the survivability of each stage (Figure 6) showed that immature individuals (Stage 1) would need the smallest amount (5%) of survival increase in order to result in overall population growth. Stage 4, on the other hand, would require a survivability increase of 25% in order to create a viable population.

Our analysis of different closure scenarios (Figure 7) indicates closures less frequent than once every five months will be ineffective in ensuring a stable population, regardless of how much these closures decreased the deathrate of the species. Further, as our baseline growth rate was close to stable (-0.0184), it took a maximum of a 10% increase in the survivability of the population to ensure a sustainable population. Our pareto analysis (Figure 7) provides all the possible combinations of increased survival rates and frequency of closures that will result in a stable population. Suggested changes in overall survivability range from 2-10%, and the ranges of frequencies of closures span from permanent closure (every month) to once every five months. By analyzing the 3 month closure scenario, we found that these fishing restrictions must increase the survivability of the population by at least 7.4% in order to result in population growth.
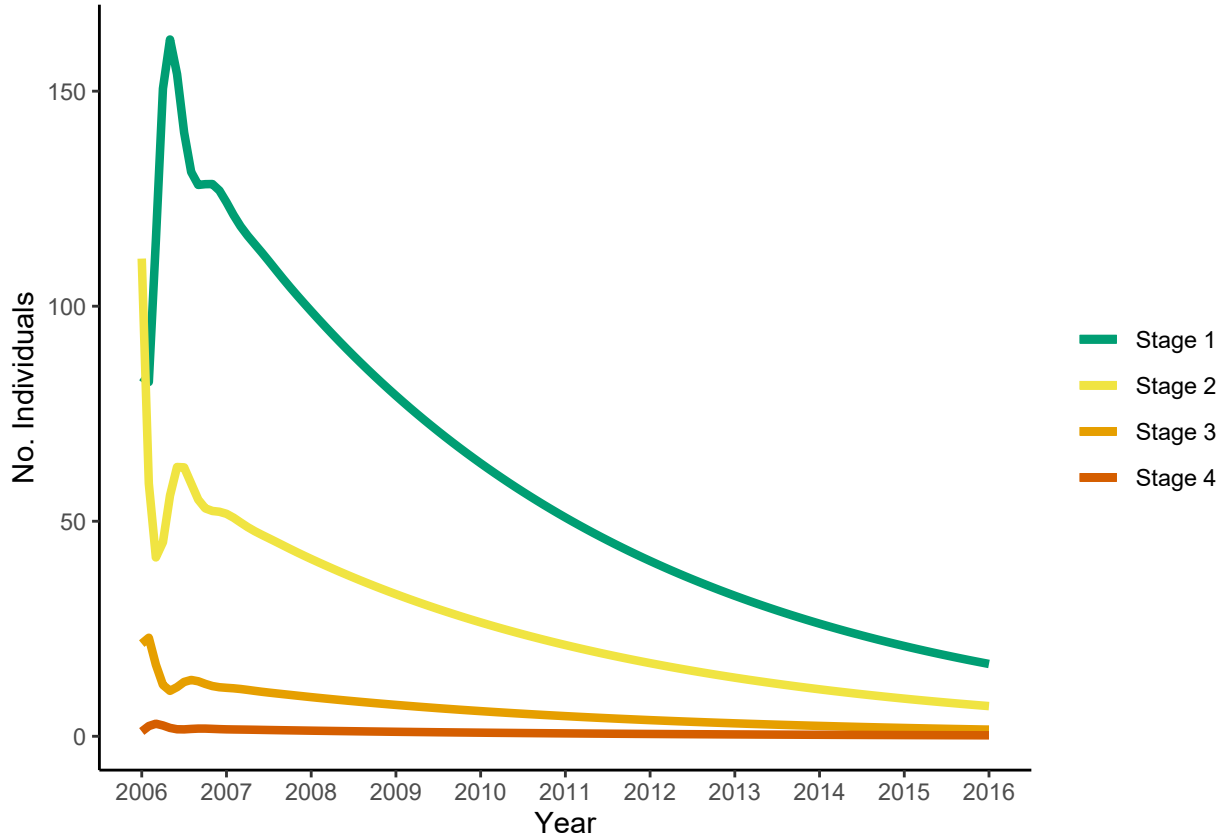
Figure 3: Ten-year projection of *O. cyanea* population based off of our calculated Lefkovitch matrix.

Table 3: The survivability (i.e. the proportion of individuals who survive from stage i to stage i+1) in each stage. Stages 1-4 were calculated by summing up the proportion of individuals surviving and staying within a stage every month (P_i) and the proportion of individuals surviving and growing every month (G_i). Larval survivability was calculated by dividing our estimated number of larvae surviving back to stage 1 (F_4) by 201,000 - the average estimated reproductive output of *O. cyanea* by (Guard 2009).

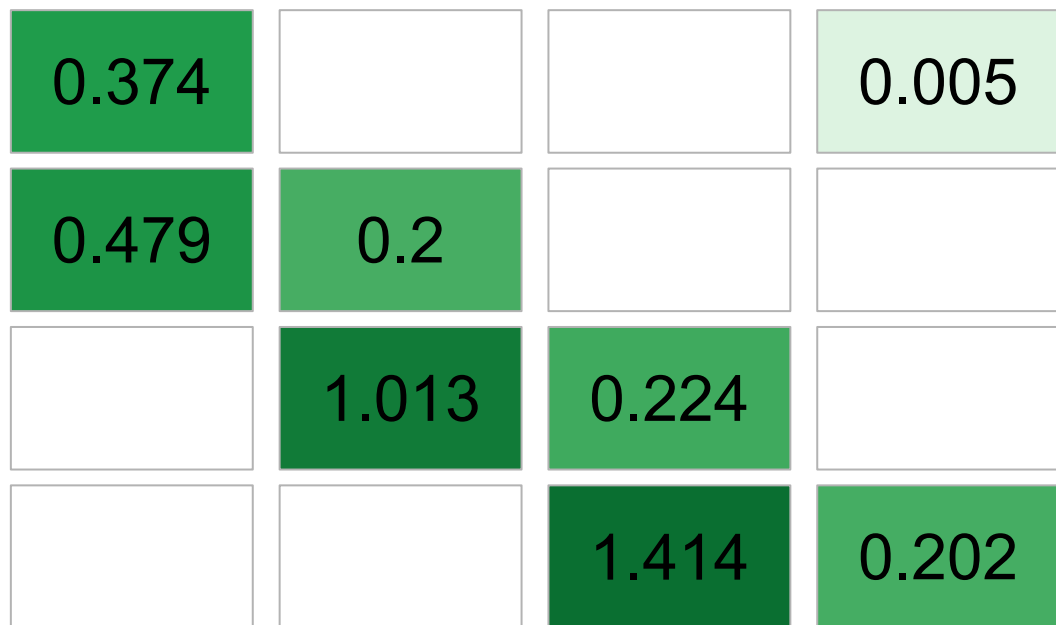| Stage	Survivability
1 Immature	0.9048003
2 Incipient Maturity	0.4519657
3 Mature	0.4859363
4 Fully Mature	0.3309474
Larval	0.0001328

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Figure 4: Sensitivity analysis of our matrix model - the change in the eigenvalue (λ) as a result of a unit change of each parameter in the model.
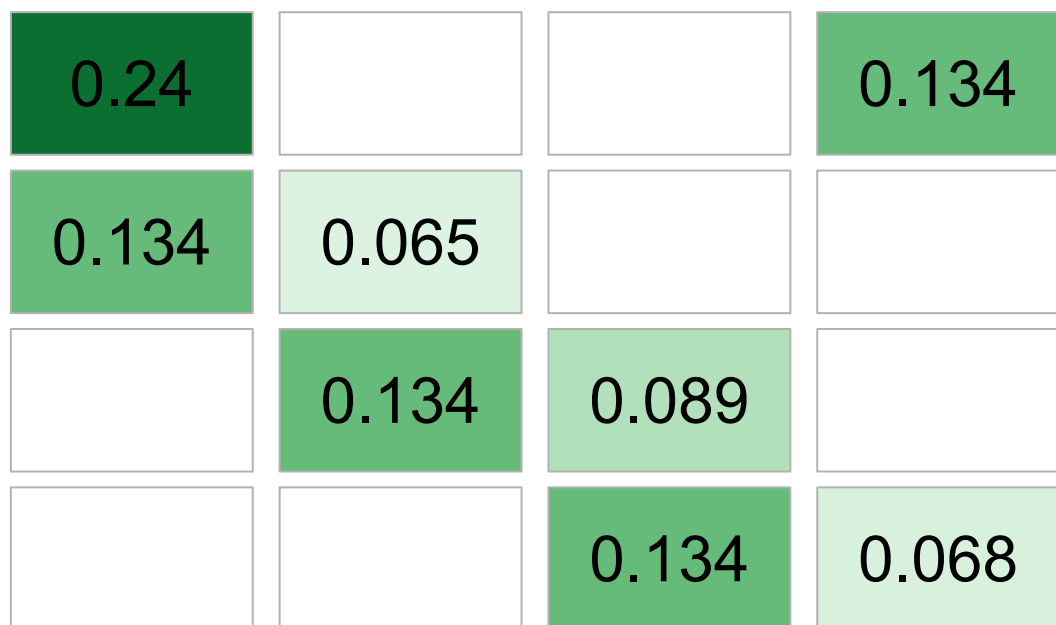
Figure 5: Elasticity analysis of our matrix model - the change in the eigenvalue (λ) as a result of a proportional change of each paramter in the model.
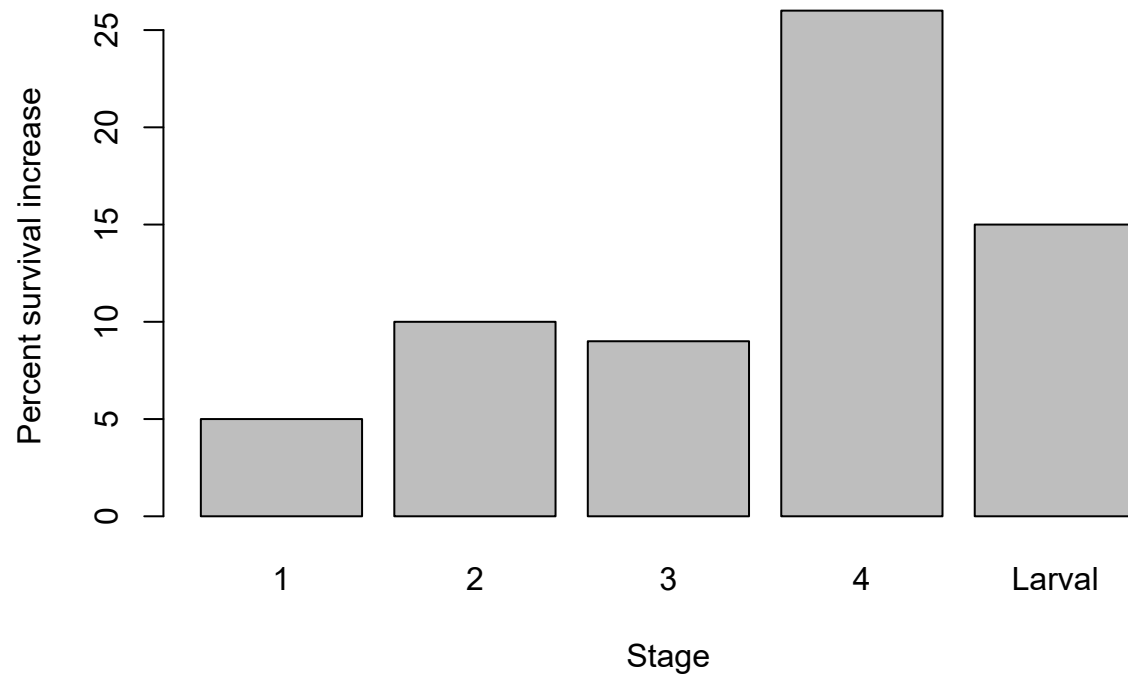
Figure 6: Minimum percent of per-stage survivability change needed to create population increase.
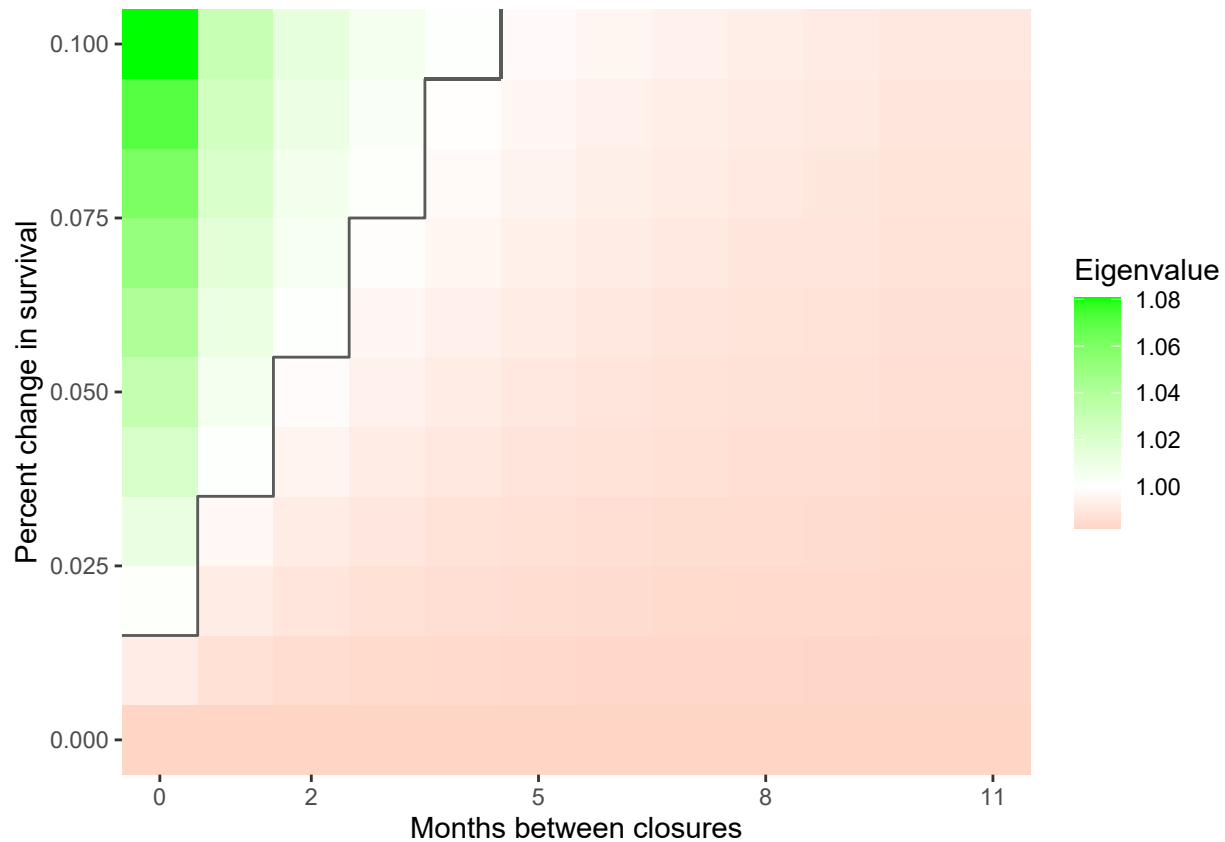
Figure 7: Paretto analysis of different management scenarios. The paretto front is represented by the black line. Green and white squares indicate theoretically successful management scenarios where red refers to the strategies that will not result in overall population growth. Frequency of closures refers to the number of months between a closure (i.e. 1 is closing every month and 12 being a closure for one month per year).

5 DISCUSSION

Our calculated growth rate of -0.0184 and resulting population projection further supports previous reports of declined catch (Humber et al. 2006; S. Benbow et al. 2014) and indicate a need for an assessment of possible action toward more sustainable practices. Decline in population presents an economical issue for individual fishers as their catch will become less lucrative and a recovery of this population will also result in economic gains from fishers in this community (Humber et al. 2006; S. Benbow et al. 2014; Oliver et al. 2015). Our model infers other information about the life history of this population as well, beyond its overall growth rate. As each column in the matrix represents a proportion of individuals within a stage either growing or staying within a stage (with the exception of the F_4 parameter), it also implies a per-stage survivability estimate (Table 3), life history parameters on which there has been no previous research. However, as the immature stage has a high survivability of 90.4%, this could indicate that although the fishing method employed in this region does not distinguish by octopus size, fishers may not be bringing this smaller catch to landing due to size limits preventing them from selling immature individuals (Humber et al. 2006). Further, as O. Cyanea have an approximately one month larval stage (Guard and Mgaya 2003), the fecundity parameter does not indicate the overall reproductive output of mature individuals, but the number of hatched offspring that will survive its larval stage and back the immature stage. This gives an estimation for larval survivability as female octopus have a fecundity ranging between 27,000 and 375,000 eggs (Guard 2009), our model indicates that only an average of 26.7 individuals will survive back into immaturity. There is no other larval survivability estimation that currently exists for this species.

Elasticity analysis shows that targeting of both the growth and reproductive parameters would have equal effect on the overall population growth, with the most influential parameter being the survival of stage 1 individuals. The sensitivity and elasticity analysis could potentially have conservation implications as they indicate which stages will have the greatest effect on the population if they are targeted for preservation practices. Previous research has indicated that catch size limits are very effective in preserving stocks of species with rapid growth and high death rates, but this is only if individuals do not enter the fishery until they have reached maturity (Nowlis 2000). However, as the fishing method employed by the local people does not discriminate based on stage, this is not an applicable suggestion for conservation practices. For this reason, even though our analysis of different stage survivabilities indicates that conserving immature individuals would be an effective tool for fostering population growth, this is not a realistic management practice in this fishery.

Based on our calculations of growth rate over different closure scenarios, we suggest implementing closures

at least once every five months, but the strictness of the closure (i.e. allowing some limited fishing) can be altered depending on how frequent these restricted fishing periods are implemented. There is no literature on the survivability of *O. cyanea* throughout their lifetime, particularly in this region. Therefore, the changes to survivability suggested by our analysis is in relation to their overall death rate not fishing rate, indicating a need for further research on the natural mortality rate of *O. cyanea* before any conservation action is taken. Our pareto analysis suggests a range of the simplest actions needed in order to ensure stability of this population. As all combinations of survivability increase and frequency of closure suggested by the analysis will result in stable *O. cyanea* populations, the specific strategy chosen should be decided based on which is most convenient and economically feasible to the local fisher community of southwest Madagascar. Among conservationists, there is a growing understanding that decision making is best left to those directly involved with resource extraction and implementing fishing restrictions upon a community without understanding their cultural practices can have detrimental effects upon the community, as well as be less effective in actually protecting natural resources (Humber et al. 2006; Baker-Médard 2017). Three month closures began to be implemented in the region in 2011 as this length of time was shown to improve octopus yeild and had limited negative effects on fisher income (Benbow and Harris 2011). As we don't have a current assessment of *Octopus cyanea* stocks in this fishery, this indicates a need to assess how effective these closures are in preserving the blue octopus of this region.

When implemented deliberately, establishing periodic closures is an effective and commonly-used strategy when implementing sustainable fishing practices (Humber et al. 2006; Oliver et al. 2015). As Madagascar has been committed to protecting its marine natural resources through increasing the number of marine parks, this study serves to highlight some of the available strategies to make population predictions and conservation strategies with limited data sources (Westlund 2017). Implementing fishing restrictions without regard for social norms can undermine cultural practices and in turn be detrimental to both the people and fishery, and halts the dissemination of traditional ecological knowledge (Okafor-Yarwood et al. 2022). For this reason, both the Madagascar government and scientific community has found a new emphasis on studying the complex social structures within the community in question in order to more effectively preserve resources along with peoples' livelihoods (Billé and Mermet 2002; Baker-Médard, Gantt, and White 2021). This has been shown to increase participation in conservation practices, therefore making them more effective.

The mechanistic methods utilized in this study allowed us to gain a baseline understanding of the growthrate and mortality of this population despite the limited data used to parameterize the model. Limitations of this study include the data collection process as even though daily collections occurred daily within a two-hour window, catch was not standardized by effort and therefore there could be catch fluctuations between

months that are not captured in the data. However, we can be confident that the catch represented is an accurate representation of the ratio of octopus in each stage. Further, matrix population models will converge or diverge based on their dominant eigenvalue, regardless of the initial population inputted in the model. Therefore, we can still conclude that the population at this time was in an overall decline, despite not knowing the exact number of individuals in this population. Another shortcoming of this study is that the only available stage data for this species and region was collected in 2006, and the community of southwest Madagascar has implemented several strategies since that time to improve the sustainability of their fish stocks in the region (Humber et al. 2006; Raberinary and Benbow 2012). Due to the time of data collection, this study does not reflect the current status of *Octopus cyanea*, but outlines the underlying population dynamics and serves to indicate the need for a more current assessment of *O. cyanea* stocks in the region. Finally, as we are using a Lefkovitch matrix to simulate population fluctuations, these models inherently make simplifying assumptions about the biology of the study species. For example, these models assume that all individuals within a stage are subject to the same growth and mortality rates. As this study uses data collected from a large geographic range (Raberinary and Benbow 2012), different individuals nesting in different regions may be subject to different selective pressures. Despite these limitations, the data provided is the best data available for fitting a Lefkovitch matrix to this species.

As cephalopod species tend to react faster to easing fishing pressure, a study of other fished species in the region is necessary to understand the effectiveness of MPAs. This study also highlights the need for further research into the life history patterns of *Octopus cyanea*. Specifically, studies on the natural mortality rate of this species, both in the larval and benthic stages, could better inform both our model and the greater understanding of how populations of this species grow. Further, a more contemporary study on the status of the octopus fishery of southwest Madagascar will paint a more accurate picture of how this population is faring under the current fishing pressure. These studies can also be used to build off of this one as more in depth data collection could be used to add spatial connectivity to our model, where we then can evaluate the accuracy of the assumption that every individual within a stage is subject to the same selective pressure. Finally, as the people of southwestern Madagascar are actively taking steps to preserve the health of their fisheries, we hope that studies such as these can serve to facilitate informed decision making when choosing how and when to impose fishing restrictions.

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