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

Sophie Wulfing, Easton White, Ahilya Sudarshan Kadba

2022-09-08

$_{\scriptscriptstyle 1}$ 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 11 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 five 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 16 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.

21 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). In order to protect fishing resources, Madagascar has instituted various conservation programs. 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

One such class of MPAs that are currently being used in Madagascar are temporary closures. Temporary

al. 2009; Oliver et al. 2015; Baker-Médard 2017).

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).

Therefore, assessments of each temporary closure is essential to insuring that they are effective in replenishing fish stocks.

Since 2003, when this marine resources in Madagascar 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 73 community (Fitahia et al. 2018). 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 84 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 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 in Madagascar (S. Benbow et al. 2014), however this requires a deeper understanding of the characteristics of Octobus cyanea in this fishery in order to be properly instituted. Instituting effective 100 temporary closures in octopus fisheries can be difficult due to their short lifespan, high mortality, and sensitivity to environmental conditions (Catalán et al. 2006; Emery, Hartmann, and Gardner 2016; Ibáñez 102 et al. 2019; Van Nieuwenhove, Ratsimbazafy, and Kochzius 2019). Lack of field data and difficulty of enforcement has also been a challenge in octopus fisheries, especially in Madagascar (Emery, Hartmann, and 104 Gardner 2016; S. Benbow et al. 2014). This indicates that a thorough understanding of the life history of 105 O. cyanea and the harvest methods employed by fishers is necessary to enact meaningful fishing restrictions. 106 Currently, the octopus fishery in this region of madagascar is closed for the three months between June and 107 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 duration of closure will affect Octoups cyanea stocks. 109 As O. cyanea has an extended larval phase and there is no existing data on the age structure of this 110 population of octopus, we will use a stage-based population matrix, otherwise known as a Lefkovitch matrix 111 (Caswell 2001). Here, the life history of the study organism is grouped by stages (figure 1), where each unit 112 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 114 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.

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.

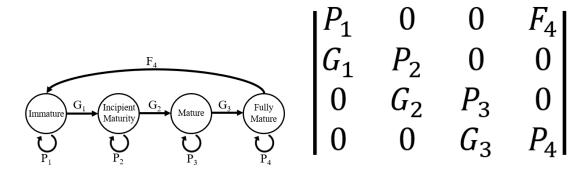


Figure 1: A graph representing the life history of O. Cyanea and the subsequent Lefkivitch Matrix where i corresponds with each of the stages of maturity (Immature, Incipient Mature, Mature, and Fully Mature individuals, respectively). P_i corresponds to probability of surviving and staying within a 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 127 the villages of Ampasilava in the south to Andragnombala in the north which spans about 30 kilometers of 128 coastline. This study collected landing data from February 2005 to February 2006 through daily surveying 129 fishers as they landed onshore within a two hour window. They separated each octopus into five age classes: 130 immature, incipient maturity, maturity, full maturity, and post laying. In this paper we ommitted stage 131 five, post laying, from this model as blue octopus only broad once, and stage five individuals therefore do 132 not contribute to population growth. They recorded octopus weight, weight and length of gonads, sex, and 133 a visual assessment of maturity class. A subsample of octopus were also collected for octopus length, and 134

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. As there is no previous estimate of the natural death rate of this population, the Lefkovitch matrix, survivability estimates and growth rate calculations for this model will also inlude the influence of fishing pressure. This data is reported in the appendix.

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

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 popoio (Stubben and Milligan 2007). Further, as all of the parameters

Table 1: Existing research and information on the per-stage lifespan of *O. Cyanea*. All existing estimates are from Heukelem (1976), Heukelem (n.d.), Guard and Mgaya (2003), Humber et al. (2006), Aina (2009). Note: Heukelem and Fred (1976) estimate the time to maturity to be 10-13 months (i.e. stages 1-3 combined).

| Stage | Existing Estimate | Estimate from Lefkovitch Matrix | Variance |
|--|----------------------|---------------------------------|-----------|
| Egg Larval 1: Immature 2: Incipient Maturity | 20-35 days | NA | NA |
| | 28-56 days | NA | NA |
| | No existing estimate | 2.699666 | 4.5885318 |
| | No existing estimate | 1.474724 | 0.7000867 |
| 3: Mature | No existing estimate | 1.646790 | 1.0651277 |
| 4: Fully Mature5: Post LayingPost larval Phase (stage 1-5) | No existing estimate | 1.494651 | 0.7393301 |
| | 45-61 days | NA | NA |
| | 9-18 months | NA | NA |

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 157 the popolio 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 159 of conservation. Other life history traits that can be calculated from this matrix are stable stage distribution, 160 reproductive value of each stage, and per-stage survivability. We will also use the R package Rage (Jones 161 et al. 2021) to calculate the age in each stage, life expectancy and longevity, the age and probability of 162 reaching maturity, and generation time of this population. We then used the rage package in R to analyze 163 various life history traits of this matrix, the output of which is included in the supplementary material. 164

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 length of annual closures by month. 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 including the three month closure that is currently being instituted.

176 4 RESULTS

The resulting eigenvalue of our matrix was 0.982, indicating a population decline of 1.8% per month with fishing pressure included (Figure 3). Sensitivity analysis (Figure 4) showed that within each stage, the 178 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) . However, as all the parameters represend proportions of individuals in a 180 stage and must necessarily be between 0 and 1 with the exception of the F_4 parameter, elasticity analysis 181 provides an interpretation that weights all stages equally. The result of this analysis shows that percent 182 changes in the fecundity metric can be as beneficial to the overall population growth as changes in the G 183 parameters (Figure 5). Further, this analysis indicates that of all the stages, stage 1 has the most overall 184 influence on the overall population growth. The stable stage distribution (Table 2) shows that 65% of the 185 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 187 (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. 189

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 two months in length or shorter 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
7.5% increase in the survivability of the population to ensure a sustainable population when utilizing three
month closures. This 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 2-7.5%, and the ranges of frequencies of closures span from permanent closure (every month) to
once every three months.

₂₀₁ 5 DISCUSSION

Our calculated growth rate of -0.0184 and resulting population projection further supports previous reports of overfishing (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

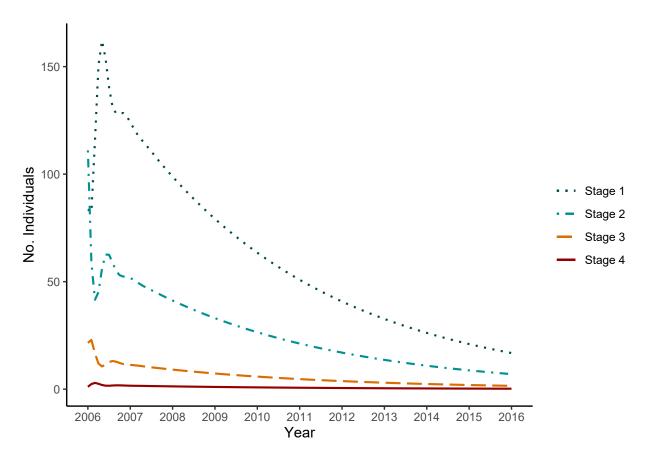


Figure 3: Ten-year projection of *O. cyanea* population based off of our calculated Lefkovitch matrix.

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 |

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

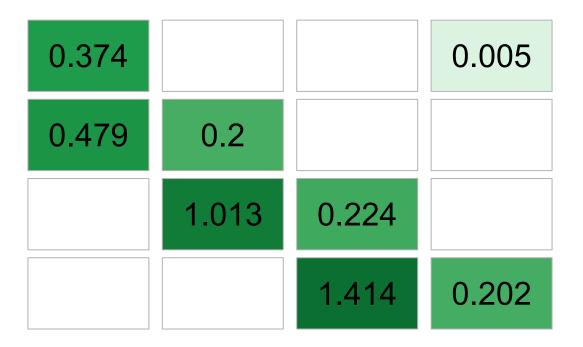


Figure 4: Sensitivity analysis of our matrix model - the change in the eigenvalue (λ) as a result of a unit change of each parameter in the model.

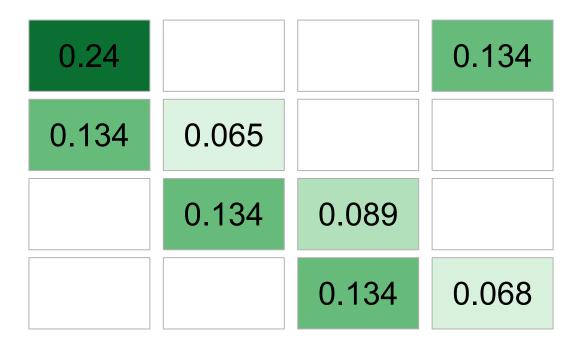


Figure 5: Elasticity analysis of our matrix model - the change in the eigenvalue (λ) as a result of a proportional change of each paramter in the model.

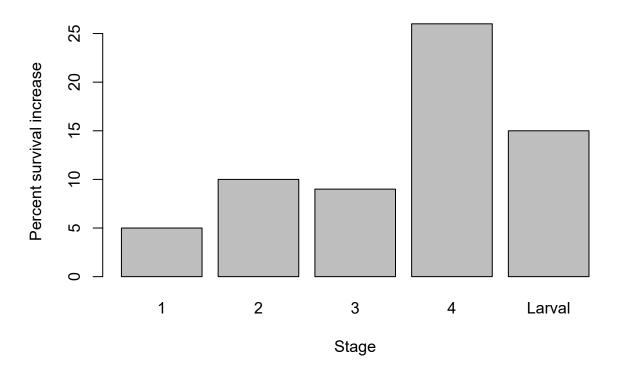


Figure 6: Minimum percent of per-stage survivability change needed to create population increase.

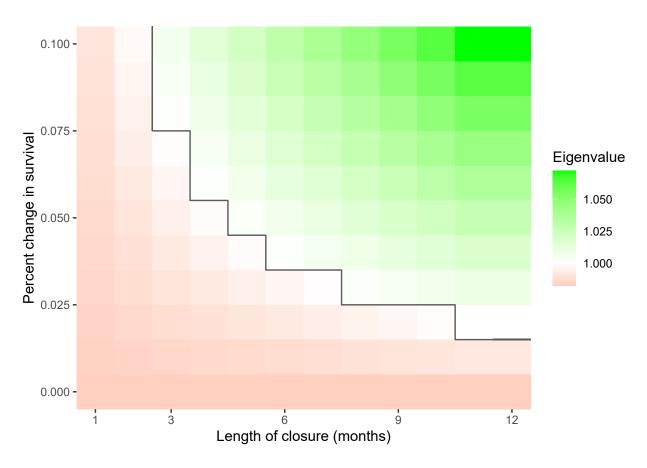


Figure 7: Analysis of different management scenarios. The black line separates the scenarios that succeed in sustaining the population from the scenarios that don't. Green and white squares indicate theoretically successful management scenarios where red refers to the strategies that will not result in overall population growth.

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 207 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 209 estimate (Table 3) and stage duration (MAKE AND INSERT FIG HERE OF STAGE DURATION), life history parameters on which there has been no previous research. However, as the immature stage has a high 211 survivability of 90.4% and a longer duration than the other stages of 2.7 months, this could indicate that 212 although the fishing method employed in this region does not distinguish by octopus size, fishers may not be 213 bringing this smaller catch to landing due to size limits preventing them from selling immature individuals 214 (Humber et al. 2006). Therefore, challenging our assumption of the data being properly stratified by size. 215 Further, as O. Cyanea have an approximately one month larval stage (Guard and Mgaya 2003), the fecundity 216 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 218 survivability as female octopus have a fecundity ranging between 27,000 and 375,000 eggs (Guard 2009), our 219 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. BUT Y DO U CARE 221

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 1 223 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 226 species with rapid growth and high death rates, but this is only if individuals do not enter the fishery until 227 they have reached maturity (Nowlis 2000). However, as the fishing method employed by the local people 228 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 230 individuals would be an effective tool for fostering population growth, this is not a realistic management 231 practice in this fishery. 232

Based on our calculations of growth rate over different closure scenarios, we suggest implementing closures
for at least every three 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 237 a need for further research on the natural mortality rate of O. cyanea before concluding if the three month closure is effective in sustaining fish stocks. Three month closures began to be implemented in the region in 239 2011 as this length of time was shown to improve octopus yield 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 241 fishery, this indicates a need to assess how effective these closures are in preserving the blue octopus of this region. Our analysis of different closure scenarios suggests a range of the simplest actions needed in order 243 to ensure stability of this population. As all combinations of survivability increase and frequency of closure 244 suggested by the analysis will result in stable O. cyanea populations, the specific strategy chosen should 245 be decided based on which is most convenient and economically feasible to the local fisher community of 246 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 248 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). 250 When implemented deliberately, establishing periodic closures is an effective and commonly-used strategy 251 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, 253 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 255 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 257 reason, both the Madagascar government and scientific community has found a new emphasis on studying 258 the complex social structures within the community in question in order to more effectively preserve resources 259 along with peoples' livelihoods (Billé and Mermet 2002; Baker-Médard, Gantt, and White 2021). This has 260 been shown to increase participation in conservation practices, therefore making them more effective. 261 The mechanistic methods utilized in this study allowed us to gain a baseline understanding of the growth rate 262 and mortality of this population despite the limited data used to parameterize the model. Limitations of this 263 study include the data collection process as even though daily collections occurred daily within a two-hour 264 window, catch was not standardized by effort and therefore there could be catch fluctuations between months 265 that are not captured in the data. As stage 1 had a high survival rate yet low duration, this challenges the assumption that the octopus caught are an accurate ratio of the octopus at each stage in the wild. Further, 267

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 269 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, 271 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 273 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. 275 cyanea stocks in the region. Finally, as we are using a Lefkovitch matrix to simulate population fluctuations, 276 these models inherently make simplifying assumptions about the biology of the study species. For example, 277 these models assume that all individuals within a stage are subject to the same growth and mortality rates. 278 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. INSERT SPATIAL 280 ISSUES HERE. Despite these limitations, the data provided is the best data available for fitting a Lefkovitch 281 matrix to this species. 282

As cephalopod species tend to react faster to easing fishing pressure, a study of other fished species in the 283 region is necessary to understand the effectiveness of temporary closures. This study also highlights the need for further research into the life history patterns of Octopus cyanea. Specifically, studies on the natural 285 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 287 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 variability to our model, where we then can 290 evaluate the accuracy of the assumption that every individual within a stage is subject to the same selective 291 pressure. Finally, as the people of southwestern Madagascar are actively taking steps to preserve the health 292 of their fisheries, we hope that studies such as these can serve to facilitate informed decision making when 293 choosing how and when to impose fishing restrictions. 294

- ²⁹⁵ Aina, Tantely Andriamaharo Ny. 2009. "MANAGEMENT OF OCTOPUS FISHERY OFF SOUTH WEST
- MADAGASCAR." United Nations University Fisheries Training Programme, Iceland [Final Project, 39.
- http://www.unuftp.is/static/fellows/document/tantely09prf.pdf.
- ²⁹⁸ André, Jessica, Malcolm Haddon, and Gretta T. Pecl. 2010. "Modelling Climate-Change-Induced Nonlinear
- Thresholds in Cephalopod Population Dynamics: CLIMATE CHANGE AND OCTOPUS POPULA-
- TION DYNAMIC." Global Change Biology 16 (10): 2866-75. https://doi.org/10.1111/j.1365-2486.2010.
- 301 02223.x.
- 302 Baker-Médard, Merrill. 2017. "Gendering Marine Conservation: The Politics of Marine Protected Areas
- and Fisheries Access." Society & Natural Resources 30 (6): 723-37. https://doi.org/10.1080/08941920.
- 2016.1257078.
- Baker-Médard, Merrill, Courtney Gantt, and Easton R. White. 2021. "Classed Conservation: Socio-
- Economic Drivers of Participation in Marine Resource Management." Environmental Science & Policy
- ³⁰⁷ 124 (October): 156–62. https://doi.org/10.1016/j.envsci.2021.06.007.
- ₃₀₈ Barnes-Mauthe, Michele. 2013. "The Total Economic Value of Small-Scale Fisheries with a Characterization
- of Post-Landing Trends: An Application in Madagascar with Global Relevance." Fisheries Research, 11.
- Benbow, S, F Humber, Ta Oliver, Kll Oleson, D Raberinary, M Nadon, H Ratsimbazafy, and A Harris. 2014.
- "Lessons Learnt from Experimental Temporary Octopus Fishing Closures in South-West Madagascar:
- Benefits of Concurrent Closures." African Journal of Marine Science 36 (1): 31–37. https://doi.org/10.
- ³¹³ 2989/1814232X.2014.893256.
- Benbow, Sophie, and Alasdair Harris. 2011. "Managing Madagascar's Octopus Fisheries. Proceedingsof the
- Workshop on Octopuscyanea Fisheries, 5-6 April 2011, Toliara." Blue Ventures Conservation Report.
- 316 Billé, Raphaël, and Laurent Mermet. 2002. "Integrated Coastal Management at the Regional Level: Lessons
- from Toliary, Madagascar." Ocean & Coastal Management 45 (1): 41–58. https://doi.org/10.1016/S0964-
- 5691(02)00048-0.
- 319 Briggs-Gonzalez, Venetia, Christophe Bonenfant, Mathieu Basille, Michael Cherkiss, Jeff Beauchamp, and
- Frank Mazzotti. 2016. "Life Histories and Conservation of Long-lived Reptiles, an Illustration with the
- American Crocodile (Crocodylus Acutus)." Journal of Animal Ecology 1365 (2656.12723): 12.
- ³²² Camp, Edward V., Brett T. van Poorten, and Carl J. Walters. 2015. "Evaluating Short Openings as a
- Management Tool to Maximize Catch-Related Utility in Catch-and-Release Fisheries." North American
- Journal of Fisheries Management 35 (6): 1106–20. https://doi.org/10.1080/02755947.2015.1083495.
- ⁶²⁵ Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Matrix Population
- Models: Construction, Analysis, and Interpretation. Sinauer Associates. https://books.google.com/
- books?id=CPsTAQAAIAAJ.

- Catalán, I. A., M. T. Jiménez, J. I. Alconchel, L. Prieto, and J. L. Muñoz. 2006. "Spatial and Temporal
- Changes of Coastal Demersal Assemblages in the Gulf of Cadiz (SW Spain) in Relation to Environmental
- Conditions." Deep Sea Research Part II: Topical Studies in Oceanography 53 (11-13): 1402–19. https:
- //doi.org/10.1016/j.dsr2.2006.04.005.
- ³³² Cinner, Joshua E., Andrew Wamukota, Herilala Randriamahazo, and Ando Rabearisoa. 2009. "Toward In-
- stitutions for Community-Based Management of Inshore Marine Resources in the Western Indian Ocean."
- Marine Policy 33 (3): 489–96. https://doi.org/10.1016/j.marpol.2008.11.001.
- cohen, Philippa J., and Simon J. Foale. 2013. "Sustaining Small-Scale Fisheries with Periodically Harvested
- Marine Reserves." *Marine Policy* 37 (January): 278–87. https://doi.org/10.1016/j.marpol.2012.05.010.
- ³³⁷ Crouse, Deborah T., Larry B. Crowder, and Hal Caswell. 1987. "A Stage-Based Population Model for
- Loggerhead Sea Turtles and Implications for Conservation." Ecology 68 (5): 1412–23. https://doi.org/
- 10.2307/1939225.
- Emery, Timothy J., Klaas Hartmann, and Caleb Gardner. 2016. "Management Issues and Options for
- Small Scale Holobenthic Octopus Fisheries." Ocean & Coastal Management 120 (February): 180–88.
- https://doi.org/10.1016/j.ocecoaman.2015.12.004.
- Fitahia, Edda Miray, Mikael Croyal, Christian E. Raheriniaina, Véronique Ferchaud-Roucher, and Hassan
- Nazih. 2018. "High-Resolution Mass Spectrometry Unravels a Broad Range of Bioactive Lipid Species
- in Octopus Cyanea and Loligo Sp. By-Products from Southwestern Madagascar." Waste and Biomass
- Valorization 9 (10): 1787–93. https://doi.org/10.1007/s12649-017-9933-x.
- Gharouni, A, Ma Barbeau, A Locke, L Wang, and J Watmough. 2015. "Sensitivity of Invasion Speed to
- Dispersal and Demography: An Application of Spreading Speed Theory to the Green Crab Invasion
- on the Northwest Atlantic Coast." Marine Ecology Progress Series 541 (December): 135–50. https:
- //doi.org/10.3354/meps11508.
- 351 Gilchrist, Hannah, Steve Rocliffe, Lucy G. Anderson, and Charlotte L. A. Gough. 2020. "Reef Fish Biomass
- Recovery Within Community-Managed No Take Zones." Ocean & Coastal Management 192 (July):
- ³⁵³ 105210. https://doi.org/10.1016/j.ocecoaman.2020.105210.
- grammalingam, Gaya, and Chris Hepburn. 2015. "Flexibility in Temporary Fisheries Closure Legislation
- Is Required to Maximise Success." Marine Policy 61 (November): 39–45. https://doi.org/10.1016/j.
- marpol.2015.06.033.
- ³⁵⁷ Grorud-Colvert, Kirsten, Jenna Sullivan-Stack, Callum Roberts, Vanessa Constant, Barbara Horta e Costa.
- Elizabeth P. Pike, Naomi Kingston, et al. 2021. "The MPA Guide: A Framework to Achieve Global
- Goals for the Ocean." Science (New York, N.Y.) 373 (6560): eabf0861. https://doi.org/10.1126/science.
- abf0861.

- Guard, Martin. 2009. "Biology and Fisheries Status of Octopus in the Western Indian Ocean and the
- Suitability for Marine Stewardship Council Certification." e United Nations Environment Programme.
- ₃₆₃ Guard, Martin, and Yunus D. Mgaya. 2003. "The Artisanal Fishery for Octopus Cyanea Gray in Tanzania."
- 364 AMBIO: A Journal of the Human Environment 31 (7): 528–36. https://doi.org/10.1579/0044-7447-
- 31.7.528.
- Herwig, Jade N., Martial Depczynski, John D. Roberts, Jayson M. Semmens, Monica Gagliano, and Andrew
- J. Heyward. 2012. "Using Age-Based Life History Data to Investigate the Life Cycle and Vulnerability
- of Octopus Cyanea." Edited by Sebastian C. A. Ferse. PLoS ONE 7 (8): e43679. https://doi.org/10.
- 369 1371/journal.pone.0043679.
- Heukelem, William F Van. 1976. "Growth, Bioenergetics, and Life-Span of Octopus Cyanea and Octo-
- pus Maya." A Dissertation Submitted to the Graduate Division of the University of Hawaii in Partial
- Fulfillment of the Requirements for the Degree of Doctor of Philosophy in Zoology, 232.
- . n.d. "A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY
- OF HAWAII IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
- DOCTOR OF PHILOSOPHY IN ZOOLOGY AUGUST 1976," 232.
- ³⁷⁶ "HIDDEN HARVEST-The Global Contribution of Capture Fisheries." 2012. 66469-GLB. The World Bank.
- https://documents1.worldbank.org/curated/en/515701468152718292/pdf/664690ESW0P1210120HiddenHarvest0web.
- 378 pdf.
- Hiddink, J. G., T. Hutton, S. Jennings, and M. J. Kaiser. 2006. "Predicting the Effects of Area Closures and
- Fishing Effort Restrictions on the Production, Biomass, and Species Richness of Benthic Invertebrate
- Communities." ICES Journal of Marine Science 63 (5): 822–30. https://doi.org/10.1016/j.icesjms.2006.
- 02.006.
- Humber, F., A. Harris, D. Raberinary, and M. Nadon. 2006. "Seasonal Closures of No-Take Zones to Promote
- A Sustainable Fishery for Octopus Cyanea (Gray) in South West Madagascar." Blue Ventures Conser-
- vation Report. https://blueventures.org/publications/seasonal-closures-of-no-take-zones-to-promote-a-
- sustainable-fishery-for-octopus-cyanea-gray-in-south-west-madagascar/.
- ³⁸⁷ Ibáñez, Christian M., Heather E. Braid, Sergio A. Carrasco, David A. López-Córdova, Gabriela Torretti, and
- Patricio A. Camus. 2019. "Zoogeographic Patterns of Pelagic Oceanic Cephalopods Along the Eastern
- Pacific Ocean." Journal of Biogeography 46 (6): 1260-73. https://doi.org/10.1111/jbi.13588.
- Jones, Owen R., Patrick Barks, Iain M Stott, Tamora D James, Sam C Levin, William K Petry, Pol
- Capdevila, et al. 2021. "Roompadre and Rage Two R Packages to Facilitate the Use of the COMPADRE
- and COMADRE Databases and Calculation of Life History Traits from Matrix Population Models."
- bioRxiv, 2021.04.26.441330. https://doi.org/10.1101/2021.04.26.441330.

- Katsanevakis, Stelios, and George Verriopoulos. 2006. "Seasonal Population Dynamics of Octopus Vulgaris
- in the Eastern Mediterranean." ICES Journal of Marine Science 63 (1): 151–60. https://doi.org/10.
- ³⁹⁶ 1016/j.icesjms.2005.07.004.
- Laroche, J., J. Razanoelisoa, E. Fauroux, and M. W. Rabenevanana. 1997. "The Reef Fisheries Surrounding
- the South-west Coastal Cities of Madagascar." Fisheries Management and Ecology 4 (4): 285–99. https:
- //doi.org/10.1046/j.1365-2400.1997.00051.x.
- MacNeil, M. Aaron, Demian D. Chapman, Michelle Heupel, Colin A. Simpfendorfer, Michael Heithaus, Mark
- Meekan, Euan Harvey, et al. 2020. "Global Status and Conservation Potential of Reef Sharks." Nature
- 583 (7818): 801–6. https://doi.org/10.1038/s41586-020-2519-y.
- 403 Nowlis, Joshua Sladek. 2000. "Short- and Long-Term Effects of Three Fishery-Management Tools on
- Depleted Fisheries." BULLETIN OF MARINE SCIENCE 66 (3): 12.
- Okafor-Yarwood, Ifesinachi, Nelly I. Kadagi, Dyhia Belhabib, and Edward H. Allison. 2022. "Survival of
- the Richest, Not the Fittest: How Attempts to Improve Governance Impact African Small-Scale Marine
- Fisheries." Marine Policy 135 (January): 104847. https://doi.org/10.1016/j.marpol.2021.104847.
- Oliver, Thomas A., Kirsten L. L. Oleson, Hajanaina Ratsimbazafy, Daniel Raberinary, Sophie Benbow, and
- Alasdair Harris. 2015. "Positive Catch & Economic Benefits of Periodic Octopus Fishery Closures: Do
- Effective, Narrowly Targeted Actions 'Catalyze' Broader Management?" Edited by Dennis M. Higgs.
- PLOS ONE 10 (6): e0129075. https://doi.org/10.1371/journal.pone.0129075.
- Raberinary, D., and S. Benbow. 2012. "The Reproductive Cycle of Octopus Cyanea in Southwest Madagascar
- and Implications for Fisheries Management." Fisheries Research 125-126 (August): 190-97. https:
- //doi.org/10.1016/j.fishres.2012.02.025.
- 415 Rodhouse, P. G., and M. Nigmatullin. 1996. "Role as Consumers." Royal Society Publishing, 20.
- https://doi.org/https://doi.org/10.1098/rstb.1996.0090.
- 417 Russ, G. R., and A. C. Alcala. 1998. "Natural Fishing Experiments in Marine Reserves 1983-1993:
- Community and Trophic Responses." Coral Reefs (Online) 17 (4): 383–97. https://doi.org/10.1007/
- s003380050144.
- Santos, M. B, M. R Clarke, and G. J Pierce. 2001. "Assessing the Importance of Cephalopods in the Diets
- of Marine Mammals and Other Top Predators: Problems and Solutions." Fisheries Research 52 (1-2):
- 121-39. https://doi.org/10.1016/S0165-7836(01)00236-3.
- 423 Stubben, Chris J., and Brook G. Milligan. 2007. "Estimating and Analyzing Demographic Models Using
- the Popbio Package in r." Journal of Statistical Software 22 (11).
- ⁴²⁵ Turlach, Berwin A., and Andreas Weingessel. 2019. Quadprog: Functions to Solve Quadratic Programming
- Problems. https://CRAN.R-project.org/package=quadprog.

- ⁴²⁷ Van Nieuwenhove, Annelore Hilde M., Hajaniaina Andrianavalonarivo Ratsimbazafy, and Marc Kochzius.
- 2019. "Cryptic Diversity and Limited Connectivity in Octopuses: Recommendations for Fisheries Man-
- agement." Edited by Giacomo Bernardi. PLOS ONE 14 (5): e0214748. https://doi.org/10.1371/journal.
- pone.0214748.
- Vase, Vinaya Kumar, Mohammed K. Koya, Gyanaranjan Dash, Swatipriyankasen Dash, K. R. Sreenath, D.
- Divu, Rajan Kumar, et al. 2021. "Acetes as a Keystone Species in the Fishery and Trophic Ecosystem
- Along Northeastern Arabian Sea." Thalassas: An International Journal of Marine Sciences 37 (1):
- 367-77. https://doi.org/10.1007/s41208-020-00276-y.
- Wells, M. J., and J. Wells. 1970. "Observations on the Feeding, Growth Rate and Habits of Newly Settled
- 436 Octopus Cyanea." Journal of Zoology 161 (1): 65–74. https://doi.org/
- 10.1111/j.1469-7998.1970.tb02170.x.
- Westerman, Kame, and Sophie Benbow. 2014. "The Role of Women in Community-Based Small-Scale
- Fisheries Management: The Case of the South West Madagascar Octopus Fishery." Western Indian
- Ocean Journal of Marine Science 12 (2): 119–32.
- Westlund, Lena, ed. 2017. Marine Protected Areas: Interactions with Fishery Livelihoods and Food Security.
- Rome: Food; Agriculture Organization of the United Nations.