# Assessing the need for temporary fishing closures to support sustainability for a small-scale octopus fishery

Sophie Wulfing1*∗*, Ahilya Sudarshan Kadba1, Mez Baker-Médard2, and Easton R. White1 1Department of Biological Sciences, University of New Hampshire, 03824, NH, USA

2Department of Environmental Studies, Middlebury College, Middlebury, VT 05753

\* Corresponding authors: Sophie Wulfing [(SophieWulfing@gmail.com)](mailto:(SophieWulfing@gmail.com) and Dr. Easton White [(Easton.White@unh.edu)](mailto:(Easton.White@unh.edu)

# 1 1 ABSTRACT

2 The blue octopus (*Octopus cyanea*) fishery off the southwest coast of Madagascar is important for coastal

3 communities. This fishery is a key economic resource for the local community as blue octopus catch is sold

4 by local fishers to international and local export markets. Thus, it is important to monitor and evaluate

5 the status of octopus to ensure its sustainability. One common octopus management approach is through

6 the use of temporary spatial closures. Models can be a useful support tool to evaluate the status of a

7 population and assess different possible management strategies. To better understand the biology and assess

8 the sustainability of blue octopus, we parameterize a Levkovitch population matrix model using existing

9 catch data. We found that the octopus population was experiencing a 1.8% decline per month at the time

10 of data collection in 2006. However, since 2006, a number of management practices, including temporary

11 closures lasting several weeks to several months have been implemented successfully. In line with these

12 efforts, our model indicates that the fishery has likely been sustained since 2006 due to these annual closures.

13 Our model provides support to the idea that temporary closures have restored this population and that

14 temporary closures provide flexibility in management strategies that local communities can tailor to their

15 economic and social needs. In addition, we were able to estimate several important life history metrics,

16 such as time in each stage, stable stage distribution, reproductive value, and per stage survivability, that

17 can be used in future work. Collectively, our study provides insight into the biology of blue octopus as well

18 as demonstrate how temporary closures can be an effective conservation strategy due to the wide range of

19 implementation options.

20 Keywords: *Octopus Cyanea*, matrix model, small scale fisheries, Madagascar, temporary closures

# 21 2 INTRODUCTION

22 Worldwide, an estimated 58.5 to 60.2 million people make their livelihood in small-scale fisheries, a subsector

23 in which 90 to 95% of fish is distributed for local consumption, making these marine products a vital source

24 of nutrition for these communities (FAO, 2022; FAO et al., 2023). The southwest region of Madagascar is one

25 such area where subsistence fishing is an essential component to the diet and income of the local community.

26 The ocean environment off the southwest coast of Madagascar is home to a wide variety of marine life, as

27 extensive tidal flats, seagrass beds, and coral reefs are all prominent biomes in the area. In fact, Madagascar

28 has been calculated as a country that would benefit greatly from marine conservation given its economic

29 reliance on marine harvests and the fact that it is a refuge to many marine species (Laroche et al., 1997). In

30 the early 2000’s, however, Madagascar’s octopus fishery began to move from local, subsistence fishing to also

31 selling catch to export markets (Humber et al., 2006). There is evidence that up to 75% of all fish caught in

32 select villages is now sold to outside entities for international export (Baker-Médard, 2017).

33 Locally-Managed Marine Areas (LMMAs) are defined as coastal and near-shore fisheries in which resources

34 are managed almost entirely by local communities and fishery stakeholders that live in the region. Because

35 management is conducted by those directly affected by the fishery, goals typically include maintaining the

36 livelihood and economic and cultural goals of the local community along with environmental goals (Govan,

37 2010). LMMAs have grown in popularity among conservationists in small scale fisheries due to this empow-

38 erment of local fishers. Because of this, LMMAs tend to have greater local participation and compliance

39 from stakeholders when compared to top-down regulation from governing bodies (Katikiro et al., 2015).

40 LMMAs have been shown to improve both fisheries and fisher livelihoods in Kenya (Kawaka et al., 2017),

41 Pacific Islands (Govan, 2010), and in Madagascar (Mayol, 2013). In Madagascar, the use of LMMAs has

42 increased significantly since 2004, which has resulted in increased landings and Catch Per Unit Effort for

43 local fishers (Benbow & Harris, 2011; Gilchrist et al., 2020). In order to protect fishing resources, these

44 LMMAs instituted various conservation programs such as bans on certain types of fishing gear, implemented

45 seasonal fishing regulations, and criminalized the harvest of endangered species.

46 One commonly used conservation strategy in LMMAs in Madagascar are seasonal closures. These types

47 of reserves have a long history of use and have been seen to successfully rehabilitate stocks (Camp et al.,

48 2015; Gnanalingam & Hepburn, 2015). For example, seasonal closures have been shown to be an effective

49 conservation strategy in increasing biomass the Atlantic sea scallop (*Placopecten magellanicus*) fishery in

50 the United States (Bethoney & Cleaver, 2019), restored natural trophic interactions in coral reef fisheries

51 in Kenya (McClanahan, 2008), and successfully restored the striped marlin (*Kajikia audax*) stocks in Baja

52 California (Jensen et al., 2010). This method is flexible, logistically simple for fishers and managers to

53 understand, and mitigates the financial loss from the fishery that can be seen with permanent closures

54 (Nowlis, 2000; Humber et al., 2006; Cohen & Foale, 2013; Camp et al., 2015; Gnanalingam & Hepburn,

55 2015; Oliver et al., 2015).

56 Octopus are a vital part of many ocean ecosystems and, compared to other fisheries, have a unique life

57 history that can lead to distinct and variable population dynamics. Cephalopods act as both predators and

58 prey in an ecosystem (Rodhouse & Nigmatullin, 1996; Santos et al., 2001; Vase et al., 2021), situating them

59 in a key role in food webs. Further, their abundance varies drastically with a wide range of ocean conditions

60 including sea surface and bottom temperature, salinity, currents, and sediment type (Catalán et al., 2006;

61 Ibáñez et al., 2019; Van Nieuwenhove et al., 2019). Compared to other exploited marine organisms, octopus

62 have a short lifespan coupled with a fast reproduction rate and high fecundity which makes their populations

63 more responsive to fishing pressures (Langley, 2005; Humber et al., 2006). Increased fishing pressure due to

64 globalization of the blue octopus in 2003 has since added significant fishing pressure to Madagascar’s blue

65 octopus populations and yield from this fishery subsequently decreased in regions of this island such as the

66 southwest region of Toliara (Langley, 2005; Humber et al., 2006). However, previous temporary closures

67 on the fishery resulted increases in octopus, possibly indicating that this fishery has the ability to recover

68 when fishing pressure is decreased (Humber et al., 2006; Katsanevakis & Verriopoulos, 2006; Benbow et al.,

69 2014). However, right after reopening, catch began to decline again, which has been attributed to heavy

70 fishing pressure right after reopening (Humber et al., 2006; Benbow et al., 2014; Oliver et al., 2015). Octopus

71 populations are therefore sensitive to both the increase and alleviation of fishing pressure and understanding

72 their biology and how these population dynamics will react to changes in fishing pressure is a key component

73 to effective conservation of this resource.

74 *Octopus cyanea*, or blue octopus, is the most abundant cephalopod species in the western Indian Ocean and

75 is caught in about 95% of local landings in Madagascar (Humber et al., 2006; Oliver et al., 2015). Like

76 other cephalopod species, very little is known about their life history including natural death rate, larval

77 survivability, and how much time this species remains in each stage of maturity. Further, age is difficult to

78 determine from size alone as they have variable growth rates up to maturity (Wells & Wells, 1970; Heukelem,

79 1976; Herwig et al., 2012; Raberinary & Benbow, 2012). The *O. cyanea* that live in the southwest region of

80 Madagascar have been shown to be genetically distinct from those outside of Madagascar (Van Nieuwenhove

81 et al., 2019). This is because the ocean currents in the Channel are comprised primarily of eddies with very

82 little through-flow across the Channel (Schott & McCreary, 2001; Lutjeharms et al., 2012; Hancke et al.,

83 2014). As larval dispersion is primarily controlled by ocean currents, and *O. cyanea* does not migrate across

84 long distances, this shows that the *O. cyanea* in Madagascar where the data was collected can be considered

85 a distinct population (Van Nieuwenhove et al., 2019).

86 Size limits have been shown to be effective methods of conservation of species like *Octopus cyanea* that are

87 harvested before maturity, and are restrictions that are easy to understand and implement in small scale

88 fisheries (Nowlis, 2000). However, even though this is a conservation strategy often implemented in octopus

89 fisheries, it has been shown to be less effective than instituting an overall cap on fishing effort, such as effort

90 rotation or limiting the number if fishers (Emery et al., 2016). To protect this species, size limits have been

91 imposed on blue octopus catch in Madagascar, but these regulations are difficult in practice, as the fishing

92 method used to harvest octopus involves spearing the octopus’s den and extracting the octopus from the

93 den. Blue octopus therefore typically die before size can be assessed, so octopus too small for market sale are

94 typically harvested for household consumption (Humber et al., 2006). Further, the relationship between size

95 and maturity stage is not strongly correlated (Raberinary & Benbow, 2012) and as a result, size restrictions

96 wouldn’t necessarily protect the individuals ready to reproduce and would be difficult to implement in the

97 field both due to the biology of *O. cyanea* and the characteristics of this small scale fishery. Therefore,

98 temporary closures have been shown to be a more practical method of octopus conservation in that they

99 can replenish stocks while maintaining fisher income (Benbow et al., 2014). Temporary closures provide

100 many options for their duration and intensity (in other words, how much fishing can occur during a closure).

101 However, this requires a deeper understanding of the biology and population characteristics of *O. cyanea* in

102 this fishery in order to be properly instituted. Instituting effective temporary closures in octopus fisheries can

103 be difficult due to their short lifespan, high mortality, and sensitivity to environmental conditions (Catalán

104 et al., 2006; Emery et al., 2016; Ibáñez et al., 2019; Van Nieuwenhove et al., 2019). Lack of field data and

105 difficulty of enforcement has also been a challenge in octopus fisheries, especially in Madagascar (Emery et

106 al., 2016; Benbow et al., 2014). This indicates that a thorough understanding of the life history of *O. cyanea*

107 and the harvest methods employed by fishers is necessary to enact meaningful fishing restrictions.

108 Ever since 2004, the western Madagascar region currently institutes a yearly closure of six weeks from

109 December 15 to January 31. In addition to the regional closure, individual villages institute their own local

110 closures once a year, typically lasting 2-3 months. These closures do not completely restrict octopus fishing,

111 but instead institute an area where fishing is not allowed which takes up about 25% of the fishery’s spatial

112 extent. Therefore, some octopus harvest does occur even during one of these closures (Aina, 2009; Humber

113 et al., 2006; Benbow & Harris, 2011; Westerman & Benbow, 2014; Oliver et al., 2015; Rocliffe & Harris,

114 2015, 2016).

115 In this paper, we have three goals: 1) we will create a theoretical estimation of the species’ life history

116 traits in different stages of its development, 2) as well as fit a Levkovitch matrix to the data collected in

117 2006 on *Octopus cyanea* populations in southwestern Madagascar, and 3) given this information in 2006, we

118 will determine the frequency and length in which these temporary closures should take place to maximize

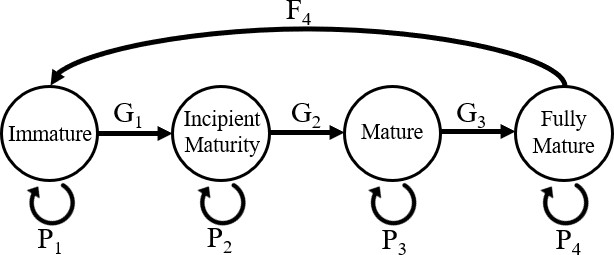
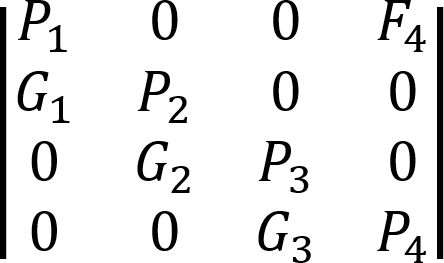
119 population health of the fishery and maximizing catch for the local community, and show how temporary

120 closures can be an effective conservation strategy as well as demonstrate the numerous options available

121 when deciding the length and intensity of closures. This study is not meant to be a current stock assessment

122 of this fishery as local communities have taken numerous steps to conserve blue octopus since the time of

123 data collection.

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

# 3 METHODS

125 Population matrix models are a commonly used mechanistic model to predict future population dynamics

126 by splitting the life history of the study organism up into a Leslie Matrix (Leslie, 1945) where a population is

127 split up into groups of ages, and a transformation matrix is applied to predict what the population makeup

128 will be in future years. As *Octopus cyanea* has an extended larval phase and there is no existing data on

129 the age structure of this population of octopus, we use a stage-based population matrix, otherwise known

130 as a Lefkovitch matrix (Caswell, 2001). Here, the life history of the study organism is grouped by stages

131 (Figure [1),](#_bookmark0) where each unit of the matrix represents a distinct period of the organism’s life where it is subject

132 to different environments, pressures, or physical attributes that would alter the survival and reproductive

133 output at that phase, but the amount of time between each stage is variable. This would simply create

134 different inputs for the probability of remaining in the same stage, and the growth and fecundity inputs can

135 be based on available data. Lefkovitch matrices have not yet been applied to *O. cyanea* populations and

136 therefore could be a useful methodology to understand the dynamics of this population in the western Indian

137 Ocean to better inform management strategies.

138 **3.1 Data**

139 To inform our model, we use data collected by Raberinary & Benbow (2012) from landings ranging from

140 the villages of Ampasilava in the south to Andragnombala in the north which spans about 30 kilometers

141 of coastline. These villages are located along the Mozambique channel, where a lack of through current

142 and prevalence of eddies results in a genetically distinct population of *O. cyanea* (Van Nieuwenhove et al.,

143 2019). In these villages, fishers usually fish along both reef flats and deeper barrier reefs. Fishers bring catch

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onshore either for household consumption or to sell to buyers for international export. 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 separated each octopus into five age classes: immature, incipient maturity, maturity, full maturity, and post laying. In this paper we omit stage five, post laying, from this model as blue octopus only brood once, and stage five individuals therefore do not contribute to population growth. 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 3,253 octopuses, and for the purposes of this study, we model from the 1,578 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.

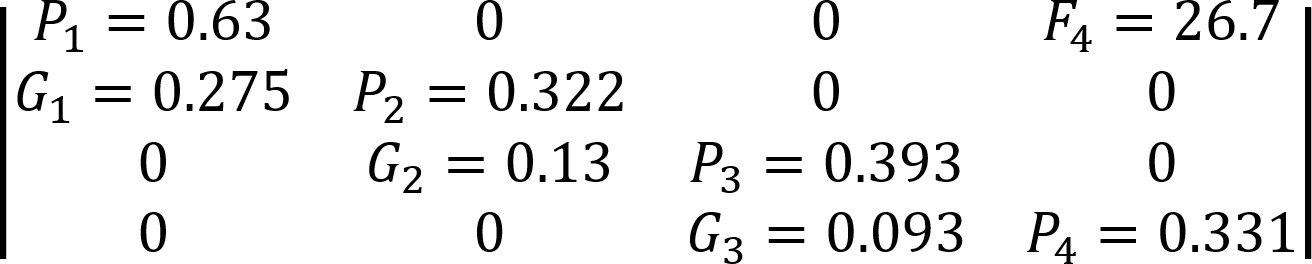


Figure 2: Stage-based population matrix calculated using Wood’s quadratic programming method and pa- rameterized using data from Raberinary and Benbow (2012).

### 3.2 Model Parameterization

156 In order to parameterize this model, we use Wood’s Quadratic Programming method (Caswell, 2001). Other

157 methods required longer time series than were available to us, were extremely sensitive to noise in the data,

158 or simply resulted in matrices that had no reasonable biological interpretation (Caswell, 2001). One strength

159 of Woods Quadratic Programming is it allows for constraining parameters to be within certain ranges. For

160 example, we can constrain all parameters to be greater than zero, place zeros in the solution matrix to reflect

161 *Octopus cyanea* biology, and ensure that all *Pi* and *Gi* parameters don’t add up to more than 1, which would

162 imply that individuals in stage i are somehow multiplying themselves. The matrices then become quadratic

163 equations that are solved through sum of squares minimization while also remaining within these constraints.

164 We estimate a preliminary stage-based matrix model (Figure [2)](#_bookmark1) based on Raberinary and Benbow (2012)

165 data and calculated using the quadprog package in R (Turlach & Weingessel, 2019). We assessed model

166 estimates by comparing life history values inferred from the matrix with existing literature on *O. cyanea*

167 life history (Table [1).](#_bookmark2) As all of our values calculated from the matrix fall within the known attributes of

168 this species, we are confident that this model gave an accurate mechanistic description for this population’s

169 underlying dynamics.

### 170 3.3 Model Analysis

171 Eigenvalues (*λ*) are calculated from the matrix and future populations can be predicted by multiplying

172 an initial population vector to incrementally higher powers of our matrix where the power of the matrix

173 corresponds to the time length of the projection. The initial population vector used is the blue octopus data

174 collected in the final month of data collection from Raberinary & Benbow (2012). This month of data is

175 not included in the parameterization of the model as it occurred after a temporary closure that was being

176 tested at the time. We perform sensitivity analysis on the population matrix and eigenvalues using the r

177 package popbio (Stubben & Milligan, 2007). Further, as all of the parameters are scaled to a value between

178 0 and 1 except *F*4, the different order of magnitude of these parameters have a lower proportional effect

179 on the eigenvalue than *F*4. To address this, we also conduct elasticity analysis using the popbio package

180 (Stubben & Milligan, 2007). This allows us to identify the groups within this octopus population whose

181 protection will most benefit population growth, essentially creating focus points of conservation. The results

182 of sensitivity and elasticity analysis are included in the supplementary material. Other life history traits

183 that can be calculated from this matrix are stable stage distribution, reproductive value of each stage, and

184 per-stage survivability. We also use the R package Rage (Jones et al., 2021) to calculate the age in each

185 stage, life expectancy and longevity, the age and probability of reaching maturity, and generation time of

186 this population. We then used the Rage package in R to analyze various life history traits of this matrix,

187 the output of which is included in the supplementary material.

188 In order to incorporate uncertainty in the model, we use a Monte Carlo simulation to draw 1,000 new matrix

189 entries from a normal distribution centered on our default estimate for that matrix entry. We test different

190 levels of variability by increasing the standard deviation used in the random draws for each entry. The

191 maximum standard deviation tested was 0.03 because higher standard deviations resulted in matrix entries

192 that were too high to have realistic biological interpretations. We then calculate and evaluate the resulting

193 dominant eigenvalues for the new matrices.

194 Finally, we calculate the minimum survivability increase necessary per stage in our default matrix to result

195 in an increase of the overall population. We do this by increasing the *Pi* and *Gi* parameters by increasing

196 percentages in each stage i until the overall eigenvalue (*λ*) became greater than one.

Table 1: Existing research and information on the per-stage duration of *O. cyanea*. All existing estimates are from Heukelem (1973), Heukelem (1976), Guard & Mgaya (2003), Humber et al. (2006), Aina (2009). Note: Heukelem (1976) estimate the time to maturity to be 10-13 months (i.e. stages 1-3 combined). Equations used to estimate metrics from this Lefkovitch Matrix are outlined in Barot et al. (2002).

|  |  |  |  |
| --- | --- | --- | --- |
| Stage | Existing Estimated Duration | Estimate from Lekfovitch  Matrix (Months) | Standard Deviation of Estimate (Months) |
| Egg | 20-35 days | NA | NA |
| Larval | 28-56 days | NA | NA |
| 1: Immature | No existing estimate | 2.699666 | 2.1420858 |
| 2: Incipient Maturity | No existing estimate | 1.474724 | 0.8367118 |
| 3: Mature | No existing estimate | 1.646790 | 1.0320502 |
| 4: Fully Mature | No existing estimate | 1.494651 | 0.8598431 |
| 5: Post Laying | 45-61 days | NA | NA |
| Post Larval Phase (Stage 1-5) | 9-18 months | NA | NA |

### 197 3.4 Management Scenarios

198 In order to determine optimal conservation strategies, we alter the survivability of *O. cyanea* by different

199 rates from 0-10% survival increase of the species. 10% is the maximum survival increase used because

200 increasing the overall survivability of matrix by more than 10% would result in some stages reaching a

201 survivability of more than 1, implying that the stage would somehow be multiplying itself within a month

202 timestep. We therefore limit survival increases to a maximum of 10% to stay within biologically meaningful

203 parameters. Then, we simulate different closure scenarios for each survival increase by altering the length

204 of annual closures by month using the final month of data collected by Raberinary & Benbow (2012) as the

205 initial population vector, this is multiplied to higher powers of the original matrix during months that are

206 simulated to be “open fishing” and then when a closure was simulated, the matrix with increased survival

207 was multiplied to the population for that month. We simulated these different scenarios in order to analyze

208 all combinations of conservation strategies that result in stable *O. cyanea* populations.

209 **4 RESULTS**

210 The resulting eigenvalue of our matrix is 0.982, indicating a population decline of 1.8% per month with

211 fishing pressure included. The stable stage distribution (Table [2)](#_bookmark3) shows that 65% of the makeup of this

212 population is immature individuals, while actively breeding individuals (fully mature) only make up less

213 than 1% of the naturally occurring population. However, the reproductive output per stage (Table [2)](#_bookmark3) shows

214 that on average, an individual in this fully mature population is expected to have 41 times the number

215 of offspring as those in stage 1. Larval survivability of 0.0001328 is calculated by dividing our estimated

216 number of larvae surviving back to stage 1 (*F*4) by 201,000 - the average estimated reproductive output of

Table 2: Stable stage distribution and reproductive value of each stage of this blue octopus population matrix given in Figure [2.](#_bookmark1) The survivability (i.e. the proportion of individuals who survive from stage i to stage i+1) in each stage includes death rate from fishing. Stages 1-4 survivability were calculated by summing up the proportion of individuals surviving and staying within a stage every month (*Pi*) and the proportion of individuals surviving and growing every month (*Gi*). Larval survivability of 0.0001328 was calculated by dividing our estimated number of larvae surviving back to stage 1 (*F*4) by the average estimated reproductive output of *O. cyanea*.

|  |  |  |  |
| --- | --- | --- | --- |
| Stage | Stable Stage Distribution (Dominant Eigenvector) | Reproductive Value (Left | Survivability |
| 1 Immature | 0.657 | 1.000 | 0.9048003 |
| 2 Incipient Maturity | 0.274 | 1.279 | 0.4519657 |
| 3 Mature | 0.061 | 6.491 | 0.4859363 |
| 4 Fully Mature | 0.009 | 41.029 | 0.3309474 |

Eigenvector)

217 *O. cyanea* by (Guard, 2009). The life expectancy of this population is calculated by the Rage package to

218 be 4.06 months with a standard deviation of 2.42 months. The calculated age of maturity is 6.82 months

219 with probability of reaching maturation of 0.022. The longevity of this population (the amount of months

220 for only 1% of the population to remain) is 12 months with a generation time of 7.38 months.

221 The analysis of the Monte Carlo simulation shows that the resulting dominant eigenvalues are still below 1

222 on average, but there is a lot of variability around the mean of 0.98 (Figure [3).](#_bookmark4) As the standard deviation

223 increases in the simulation, the proportion of matrices with dominant eigenvalues above one also increases.

224 Changing the survivability of each stage (Figure [4)](#_bookmark5) shows that immature individuals (Stage 1) would need

225 the smallest amount (5%) of survival increase in order to result in overall population growth. Stage 4, on

226 the other hand, requires a survivability increase of 25% in order to create a viable population.

227 Our analysis of different closure scenarios (Figure [5)](#_bookmark6) indicates closures two months in length or shorter may

228 be ineffective in ensuring a stable population, regardless of how much these closures decreased the death

229 rate of the species. Further, as our baseline growth rate is close to stable (-0.0184), it took a maximum of a

230 7.5% increase in the survivability of the population to ensure a sustainable population when utilizing three

231 month closures. This analysis (Figure [5)](#_bookmark6) provides all the possible combinations of increased survival rates

232 and frequency of closures that will result in a stable population. Suggested changes in overall survivability

233 range from 2-7.5%, and the ranges of frequencies of closures span from permanent closure (every month) to

234 once every three months.

300

sd: 0.01

sd: 0.03

sd: 0.02

200

100

Count

0

0.8 0.9 1.0 1.1 0.8 0.9 1.0 1.1 0.8 0.9 1.0 1.1

## Dominant eigenvalue

Figure 3: Monte Carlo simulation where matrix entries are drawn from a normal distribution centered on the default matrix at standard deviations of 0.01 (left), 0.02 (middle), and 0.03 (right). Eigenvalues are then calculated from each of the resulting matrices and plotted in a histogram after 1,000 simulations. The vertical dashed line indicates *λ* = 1, or where the eigenvalue indicates an increasing octopus population.

30

20 Stage

Percent survival increase

 Larval  1

 2

 3

10 4

0

Larval 1 2 3 4

#### Stage

Figure 4: Minimum percent of per-stage survivability change needed to create population increase. Each stage was increased by higher percentages until the eigenvalue of the overall system became greater than zero.

10.0

**Population Increasing**

Population Decreasing

7.5

Percent change in survival

#### Eigenvalue

1.050



5.0

1.025

1.000

2.5

0.0

1 3 6 9 12

#### Length of closure (months)

Figure 5: 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.

235 **5 DISCUSSION**

236 Our model provides information about the life history of this population of *Octopus cyanea*. As each column

237 in the matrix represents a proportion of individuals within a stage either growing or staying within a stage

238 (with the exception of the *F*4 parameter), it shows a per-stage survivability estimate (Table [2)](#_bookmark3) and stage

239 duration (Table [1),](#_bookmark2) life history parameters on which there has been no previous research. However, as the

240 immature stage has a high survivability of 90.4% and a longer duration than the other stages of 2.7 months,

241 could challenge the assumption made in the model that octopus harvest does not distinguish by size. Further,

242 as *O. Cyanea* have an approximately one to two month larval stage (Guard & Mgaya, 2003), the fecundity

243 parameter does not indicate the overall reproductive output of mature individuals, but the number of hatched

244 offspring that will survive its larval stage and back the immature stage. This gives an estimation for larval

245 survivability as female octopus have a fecundity ranging between 27,000 and 375,000 eggs (Guard, 2009), our

246 model indicates that only an average of 26.7 individuals will survive back into immaturity, which indicates

247 a survivability of 0.0001328. There is no other larval survivability estimation that currently exists for this

248 species, which would be a useful further study as this could indicate a recruitment rate for this population.

249 Further, an average lifespan of 4.06 months and an age of maturation of 6.82 months indicates that most

250 individuals die before reaching maturation. The overall natural mortality rate of this population has been

251 estimated to range from 0.0127 per week (0.0552 per month) to 0.0498 per week (0.2164 per month) (Roa-

252 Ureta, 2022). However, this was not included in our model of fishery closures as the local closures do not

253 cover the full spatial extent of the fishery, have variable spatial extents, and some fishing continues during

254 this time, meaning some fishing mortality exists during closures (Oliver et al., 2015). Instead, we compared

255 closures to their overall effect on the *O. cyanea* mortality rate.

256 Our calculated growth rate of -0.0184 and resulting population projection supports previous reports of

257 overfishing at the time of data collection in 2006 (Humber et al., 2006; Benbow et al., 2014). With this

258 negative growth rate, our models suggest that, without changes to management practices, the octopus

259 population may have continued to decline. According to our model, any closure less than three months,

260 without additional management actions, may not be effective in conserving blue octopus stocks. Uncertainty

261 in model parameters can lead to situations where the the population would be assessed as increasing in

262 2006, as demonstrated by the Monte Carlo simulation (Figure [3),](#_bookmark4) even though the average eigenvalue of

263 these simulations remain below 1. This demonstrates the need for further investigation into this fishery,

264 as octopus population dynamics can be highly variable (Humber et al., 2006), and therefore a Lefkovitch

265 matrix may not be able to capture all of the nuances of blue octopus population dynamics. Thus, given data

266 and model limitations, this study serves mainly to show how temporary closures are an effective tool for

267 conservation, and caution should be taken when considering whether the octopus population was actually in

268 decline or not in 2006. We describe this limitation more below. In general, declines in octopus populations

269 presents an economic issue for individual fishers as their catch will become less lucrative. A successful short

270 term closure management regimes has been shown result in economic gains from fishers in this community

271 (Humber et al., 2006; Benbow et al., 2014; Oliver et al., 2015). Further, sale prices on opening day tend to

272 increase as buyers are typically guaranteed larger catch (Oliver et al., 2015).

273 Since the time of data collection, there have been a number of important changes to fisheries management in

274 the region (Oliver et al., 2015; Roa-Ureta, 2022). For example, temporary closures in this fishery (Oliver et

275 al., 2015) showed that extending the regional closure beyond the conventional six weeks increased octopus

276 catch. Further, a 2-3 month closure was suggested for this area in 2011 in order to maximize catch-per unit

277 effort (Benbow & Harris, 2011). Benbow et al. (2014) demonstrated that a 20-week closure had similar

278 positive effects on octopus catch when compared to a seven month closure, yet resulted in less strain on

279 fisheries management investment than the longer seven month closure. Individual villages also institute their

280 own closures. These closures typically span 2-3 months and restrict fishing in ~20% of the fishery’s spatial

281 extent, so some fishing is still allowed to occur during this time. (Rocliffe & Harris, 2015, 2016; WWF, 2017).

282 Therefore, the changes to survivability suggested by our analysis is in relation to their overall death rate not

283 fishing rate, indicating a need for further research on the spatial structure of this population. Our analysis

284 of different closure scenarios suggests a range of the simplest actions needed in order to ensure sustainability

285 of this population, and how the relationship between closure lengths and their effect on mortality rates can

286 result in multiple different temporary closures that can successfully conserve a fishery. Thus, despite the

287 simplicity of our model, our findings for possible closure lengths is very close to those currently practiced

288 in Madagascar and elsewhere, and therefore suggest that temporary closure efforts in Madagascar are both

289 necessary and have been effective in conserving this fishery. As we describe later, more realistic extensions

290 of this model can be built to guide specific management practices.

291 Our analysis confirms that establishing periodic closures is an effective and commonly-used strategy in

292 sustainable fishing practices when they are implemented deliberately (Humber et al., 2006; Oliver et al.,

293 2015). As Madagascar has been committed to protecting its marine natural resources through increasing

294 the number of marine parks, this study serves to highlight the effectiveness of these temporary closures and

295 explore some of the available strategies to make population predictions and conservation strategies with

296 limited data sources (Westlund, 2017). Implementing fishing restrictions without regard for social norms

297 can undermine cultural practices and in turn be detrimental to both the people and fishery, and halts the

298 dissemination of traditional ecological knowledge (Okafor-Yarwood et al., 2022). For this reason, both the

299 Madagascar government and scientific community has found a new emphasis on studying the complex social

300 structures within the community in question in order to more effectively conserve resources along with

301 peoples’ livelihoods (Billé & Mermet, 2002; Baker-Médard et al., 2021). This has been shown to increase

302 participation in conservation practices, therefore making them more effective.

303 The mechanistic methods used in this study allowed us to gain a baseline understanding of the growth rate

304 and mortality of this population despite the limited data used to parameterize the model. Limitations of

305 this study include the data collection process as this model is only parameterized using one year of data. As

306 octopus population dynamics are extremely variable, one year of data collection may not be sufficient to get

307 a comprehensive understanding of this population’s growth rate, as shown by the uncertainty analysis in this

308 paper, where some simulations of uncertainty resulted in stable populations. Although this is not enough

309 data to conduct a full stock assessment, this speaks to the utility of mechanistic modeling, where we are able

310 to estimate population patterns and other life history traits despite this lack of data. A future study that

311 repeats this method of data collection could rerun this same model with the updated data, and make further

312 conclusions about the status of this fishery today. Even though data collections occurred daily within a two-

313 hour window, catch was not standardized by effort and therefore there could be catch fluctuations between

314 months that are not captured in the data. Further, as stage 1 had a high survival rate yet low duration,

315 this challenges the assumption that the octopus caught are an accurate ratio of the octopus at each stage in

316 the wild. Another shortcoming of this study is that the only available stage data for this species and region

317 was collected in 2006, and the community of southwest Madagascar has implemented several strategies since

318 that time to improve the sustainability of their fish stocks in the region (Humber et al., 2006; Raberinary &

319 Benbow, 2012). Due to the time of data collection, this study does not reflect the current status of *Octopus*

320 *cyanea*, nor should the findings of this study be implemented in current management decisions. In fact,

321 more recent and comprehensive research has shown that this fishery has been fished largely sustainably from

322 2015 to 2017, however since then, the fishery shows evidence of operating at capacity or above (Roa-Ureta,

323 2022). Instead, this study outlines what biological parameters can be estimated from limited data using

324 mechanistic modeling and show how temporary closures are not only an effective method of conservation,

325 but also provide communities with options for effective management and these should be selected based off

326 of the needs of stakeholders. As the community of southwest Madagascar has been involved in deciding when

327 closures should occur and their lengths, this study serves to show the various options available (Benbow &

328 Harris, 2011).

329 We made a number of simplifying assumptions in our models of the biology of the study species. For example,

330 our models assume that all individuals within a stage are subject to the same growth and mortality rates.

331 As this study uses data collected from a large geographic range (Raberinary & Benbow, 2012), different

332 individuals nesting in different regions may be subject to different selective pressures. Studies on the spatial

333 variability of this population could better inform both our model and the greater understanding of how fishing

334 mortality of this population compares to its natural mortality. Further, this population of blue octopus has

335 been shown to exhibit spatial variability depending on their life stage. Younger individuals tend to live in

336 the shallow inner zone of the reef and larger individuals, who are more able to withstand stronger currents,

337 move to deeper waters for more suitable habitats for nesting (Raberinary, 2007). Our management scenario

338 analysis also assumes that each lifestage would be affected equally by a closure, which could be challenged

339 by the previous result that fishers are not bringing smaller catch to landing due to the size limits. Further,

340 explorations into uncertainty analysis of this population would help better understand the sustainability of

341 this fishery. Despite these limitations, the data provided is the best data available for fitting a Lefkovitch

342 matrix to this species. Future extensions of this work could include applying this method to a data rich

343 fishery, where the conclusions of the model can be compared to empirical data. Further, valuable future

344 research could explore the dynamics of both sexes in the population (Gerber & White, 2014) as male octopus

345 have different growth rates and spatial dynamics (Heukelem, 1976). A better understanding of the seasonal

346 breeding dynamics of this population of blue octopus could also give better insight into the health of this

347 fishery (White & Hastings, 2020). Cephalopod juveniles (a key life stage in understanding future population

348 dynamics) often have two seasonal peaks per year, indicating biannual spawning periods (Humber et al., 2006;

349 Katsanevakis & Verriopoulos, 2006). This is related to seasonal fluctuations in temperature, as cephalopod

350 growth is related to environmental temperature (Domain et al., 2000). However, this relationship is subject

351 to a lot of variation (Heukelem, 1976; Herwig et al., 2012). Further, as Madagascar is a tropical climate,

352 this trend may be different in our region of study, as suggested by Raberinary & Benbow (2012), where all

353 life stages of O. cyanea were observed year round, suggesting continuous breeding. A better understanding

354 the seasonality of this population could further inform when closures should take place.

355 **6 CONCLUSIONS**

356 With a short generation time, cephalopod species respond more quickly to new management strategies. As a

357 population with highly variable population dynamics, continuous monitoring of landings, fishing effort, and

358 where catch is found is extremely valuable in understanding the status of *Octopus cyanea* in Madagascar.

359 This research confirms thae need for temporary closures on this fishery. Similar data has been collected by

360 Blue Ventures on this fishery since 2015 and shows there has been an improvement to this fishery since 2006

361 due to local efforts, including temporary closures. Further, this collection effort does not include maturity

362 data which would improve the analysis of this study through incorporation of multiple years of catch data

363 (Roa-Ureta, 2022). However, this study serves to confirm the effectiveness of these closures. Finally, as

364 the people of southwestern Madagascar are actively taking steps to conserve the health of their fisheries,

365 we hope that studies such as these can serve to facilitate the understanding of what options are available

366 when choosing how and when to impose fishing restrictions. We also hope that future work can build on our

367 models to be more realistic for this system and produce specific management guidance.

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371 about data collection.

372 *Data Availability* - All supplemental material and code for this project are available at [https://github.com/](https://github.com/swulfing/OCyanea)

373 [swulfing/OCyanea](https://github.com/swulfing/OCyanea). All data used to parameterize this model was collected in Raberinary & Benbow (2012)

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