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

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) and Dr. Easton White (Easton.White@unh.edu)

1  **1 ABSTRACT**

2 Mechanistic models are particularly useful for understanding life history metrics and population dynamics in

3 data deficient species. Data deficiency is a relevant issue in small scale fisheries as they are generally under

4 studied and underrepresented in global fishing datasets. As overfishing remains a global issue, especially in

5 small-scale fisheries, one commonly utilized conservation method is temporary closures. The blue octopus

6 (*Octopus cyanea*) fishery off the southwest coast of Madagascar is one such system that uses temporary

7 closures to conserve an understudied species. This fishery is a key economic resource for the local community

8 as blue octopus catch is sold by local fishers to international and local export markets and is a major

9 component of fisher income. To better understand the biology and assess the sustainability of blue octopus,

10 we parameterize a Levkovitch population matrix model using existing catch data. In this study, we calculate

11 various life history metrics such as time in each stage, stable stage distribution, reproductive value, per

12 stage survivability, and show that this population was in a decline of 1.8% per month at the time of data

13 collection. To sustain the existing population of blue octopus, our model indicates that the fishery would

14 need to close for at least three months annually. Increasing the length of closure is predicted to significantly

15 increase the octopus population at these sites. We show that if implemented correctly, temporary closures

16 could be used to restore this population. The local communities of Madagascar have implemented various

17 fishing restrictions to ensure sustainable fishing since the time of data collection, indicating a need for further

18 research into the effectiveness of these fishing closures. Therefore, our study provides insight into the biology

19 of blue octopus as well as demonstrate how temporary closures can be an effective conservation strategy due

20 to the wide range of implementation options.

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

22  **2 INTRODUCTION**

23 Mechanistic models in ecology explicitly account for species life histories, behavioral, or other mechanisms

24 to describe how a population or community may change over time (André et al., 2010; Briggs-Gonzalez

25 et al., 2016). Biological processes are therefore hypothesized in the model, and each parameter represents

26 these mechanisms and can be measured independently of the data collected. This differs from statistical or

27 phenomenological models, which instead use estimations of relevant parameters to explain the data itself.

28 Mechanistic models can be important in situations without existing long-term data, when future conditions

29 may not be similar to the past, and when different scenarios or actions need to be assessed (Crouse et

30 al., 1987; Nowlis, 2000; Gharouni et al., 2015). Thus, mechanistic models play a critical role in studying

31 the biology of cryptic species, and making informed conservation decisions, such as the management of

32 small-scale fisheries.

33 Worldwide, 32 million fishers make their livelihood in small-scale fisheries, a subsector in which 90 to 95%

34 of fish is distributed for local consumption. These marine products are a vital source of nutrition for

35 these communities (The World Bank, 2012). The southwest region of Madagascar is one such area where

36 subsistence fishing is an essential component to the diet and income of the local community. The ocean

37 environment off the southwest coast of Madagascar is home to a wide variety of marine life, as extensive

38 tidal flats, seagrass beds, and coral reefs are all prominent biomes in the area. In fact, Madagascar has been

39 calculated as a country that would benefit greatly from marine conservation given its economic reliance on

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

41 2000’s, however, Madagascar’s octopus fishery began to move from local, subsistence fishing to also selling

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

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

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

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

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

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

48 2010). LMMAs have grown in popularity among conservationists in small scale fisheries due to this empower-

49 ment of local fishers. Because of this, LMMAs tend to have greater local participation and compliance from

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

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

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

53 significantly since 2004, and fishers in the country have seen significant improvements to fish stocks as well as

54 have experienced economic benefits since (Benbow & Harris, 2011; Gilchrist et al., 2020). In order to protect

55 fishing resources, Madagascar has instituted various conservation programs such as bans on certain types of

56 fishing gear, implemented seasonal fishing regulations, and criminalized the harvest of endangered species.

57 However, these strategies proved ineffective in execution and in their conservation goals (Humber et al.,

58 2006). Both the government and nongovernmental organizations have since pledged to drastically increase

59 the number of regions dedicated as Marine Protected Areas through temporary fishing closures (Cinner et

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

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

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

63 2015; Gnanalingam & Hepburn, 2015). For example, seasonal closures have been shown to be an effective

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

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

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

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

68 and mitigates the financial loss from the fishery that can be seen with permanent closures (Nowlis, 2000;

69 Humber et al., 2006; Cohen & Foale, 2013; Camp et al., 2015; Gnanalingam & Hepburn, 2015; Oliver et al.,

70 2015). However, seasonal closures are not always effective in their goal of replenishing stocks and this can

71 depend on a wide range of factors. Ecological considerations about the life history of the target species, Allee

72 effects, and changes to community structure and species interactions all play a role in how well the seasonal

73 closure will protect the fishery (Russ & Alcala, 1998; Cohen & Foale, 2013; Gnanalingam & Hepburn, 2015;

74 Gilchrist et al., 2020; Grorud-Colvert et al., 2021). Further, the characteristics of the fishery itself has been

75 seen to influence fishery recovery. Fishing method, where the effort will be redistributed to, and fishing

76 activity upon reopening have all been factors in negating the recovery made during the closure (Hiddink

77 et al., 2006; Humber et al., 2006; Cohen & Foale, 2013). Therefore, assessments of each seasonal closure

78 is essential to insuring that they are effective in replenishing fish stocks. Mechanistic modeling allows us

79 to simulate different fishery scenarios and assess how populations will respond to these changes in fishing

80 pressure.

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

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

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

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

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

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

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

88 extremely sensitive to changes in fishing pressure as seen in 2003, when marine resources in Madagascar first

89 began to globalize and octopus became the most economically important fishery in Andavadoaka (Langley,

90 2005; Humber et al., 2006). This has since added significant fishing pressure to Madagascar’s blue octopus

91 populations and yield from this fishery subsequently decreased in regions of this island such as the southwest

92 Andavadoaka region (Humber et al., 2006). However, this population has the ability to quickly bounce back

93 when temporary are introduced into their habitat (Humber et al., 2006; Katsanevakis & Verriopoulos, 2006;

94 Benbow et al., 2014). But, once fishing resumes, populations can suddenly and rapidly decline which has

95 been attributed to heavy fishing pressure in the area right after reopening (Humber et al., 2006; Benbow et

96 al., 2014). Octopus are therefore extremely sensitive to both protection and harvest levels, and understanding

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

98 component to effective conservation of this resource.

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

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

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

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

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

104 1976; Herwig et al., 2012; Raberinary & Benbow, 2012). The *O. cyanea* that live in the southwest region of

105 Madagascar have been shown to be genetically distinct from those outside of the Mozambique Channel (Van

106 Nieuwenhove et al., 2019). This is because the ocean currents in the Channel are comprised primarily of

107 eddies with very little through-flow across the Channel (Schott & McCreary, 2001; Lutjeharms et al., 2012;

108 Hancke et al., 2014). As larval dispersion is primarily controlled by ocean currents, and *O. cyanea* does not

109 migrate across long distances, this shows that the *O. cyanea* in the Mozambique Channel where the data

110 was collected can be considered a distinct population (Van Nieuwenhove et al., 2019).

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

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

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

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

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

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

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

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

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

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

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

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

123 closures have been shown to be a more practical method of octopus conservation in that they can replenish

124 stocks while maintaining fisher income (Benbow et al., 2014). However, this requires a deeper understanding

125 of the biology and population characteristics of *O. cyanea* in this fishery in order to be properly instituted.

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Instituting effective 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 et al., 2016; Ibáñez et al., 2019; Van Nieuwenhove et al., 2019). Lack of field data and difficulty of enforcement has also been a challenge in octopus fisheries, especially in Madagascar (Emery et al., 2016; 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. Following dozens of experimental closures in the region ranging from six weeks to 7 months, the western Madagascar region currently institutes a yearly closure of six weeks from December 15 to January 31. These closures do not completely restrict octopus fishing, but instead institute an area where fishing is not allowed which takes up about 25% of the fishery’s spatial extent. Therefore, some octopus harvest does occur even during a closure (Aina, 2009; Langley, 2005; Humber et al., 2006; Benbow & Harris, 2011; Westerman & Benbow, 2014; Oliver et al., 2015; Rocliffe & Harris, 2015, 2016).

In this paper, we have three 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, and show how these closures can be an effective conservation strategy.

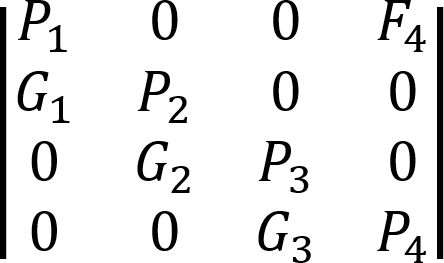
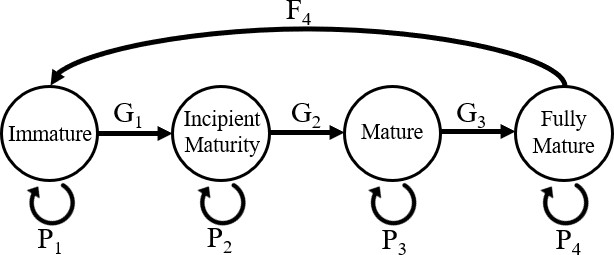


Figure 1: A graph representing the life history of *O. Cyanea* and the subsequent Lefkovitch Matrix where i corresponds with each of the stages of maturity (Immature, Incipient Mature, Mature, and Fully Mature individuals, respectively). *Pi* corresponds to probability of surviving and staying within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

# 3 METHODS

144 As *Octopus cyanea* has an extended larval phase and there is no existing data on the age structure of this

145 population of octopus, we use a stage-based population matrix, otherwise known as a Lefkovitch matrix

146 (Caswell, 2001). Here, the life history of the study organism is grouped by stages (Figure [1),](#_bookmark0) where each unit

147 of the matrix represents a distinct period of the organism’s life where it is subject to different environments,

148 pressures, or physical attributes that would alter the survival and reproductive output at that phase, but the

149 amount of time between each stage is variable. This would simply create different inputs for the probability of

150 remaining in the same stage, and the growth and fecundity inputs can be based on available data. Lefkovitch

151 matrices have not yet been applied to *O. cyanea* populations and therefore could be a useful methodology

152 to understand the dynamics of this population in the western Indian Ocean to better inform management

153 strategies.

154  **3.1 Data**

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

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

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

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

159 2019). In these villages, fishers usually fish along both reef flats and deeper barrier reefs. Fishers bring catch

160 onshore either for household consumption or to sell to buyers for international export. This study collected

161 landing data from February 2005 to February 2006 through daily surveying fishers as they landed onshore

162 within a two hour window. They separated each octopus into five age classes: immature, incipient maturity,

163 maturity, full maturity, and post laying. In this paper we omit stage five, post laying, from this model as

164 blue octopus only brood once, and stage five individuals therefore do not contribute to population growth.

165 They recorded octopus weight, weight and length of gonads, sex, and a visual assessment of maturity class.

166 A subsample of octopus were also collected for octopus length, and laboratory assessment of gonads for a

167 confirmation of maturity class. They gathered this data on a total of 3,253 octopuses, and for the purposes

168 of this study, we model from the 1,578 females collected. Despite there being no standardization for catch

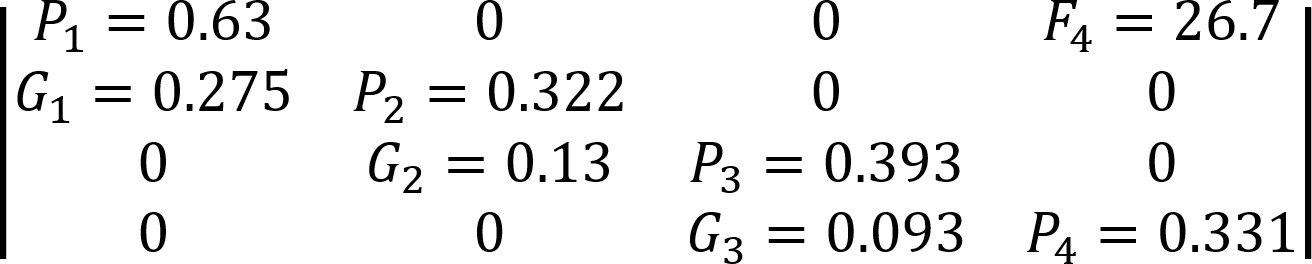
169 effort being available for this dataset, no other maturity stage study has been conducted on this population

170 of *O. cyanea* and is therefore the best available data to fit a Lefkovitch matrix. As there is no previous

171 estimate of the natural death rate of this population, the Lefkovitch matrix, survivability estimates and

172 growth rate calculations for this model also includes the influence of fishing pressure. This data is reported

173 in the appendix.



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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**

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

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

177 data, or simply resulted in matrices that had no reasonable biological interpretation (Caswell, 2001). We

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

179 and calculated using the quadprog package in R (Turlach & Weingessel, 2019). Model accuracy is assessed

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

181 (Table [1).](#_bookmark2) As all of our values calculated from the matrix fall within the known attributes of this species,

182 we are confident that this model gave an accurate mechanistic description for this population’s underlying

183 dynamics.

184  **3.3 Model Analysis**

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

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

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

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

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

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

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

192 0 and 1 except *F*4, the different order of magnitude of these parameters have a lower proportional effect

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

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

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

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 |

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

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

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

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

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

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

202 Finally, we calculate the minimum survivability increase necessary per stage to result in an increase of the

203 overall population. We do this by increasing the *Pi* and *Gi* parameters by increasing percentages in each

204 stage i until the overall eigenvalue (*λ*) became greater than one.

205  **3.4 Management Scenarios**

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

207 rates from 0-10% survival increase of the species. Then, we simulate different closure scenarios for each

208 survival increase by altering the length of annual closures by month using the final month of data collected

209 by Raberinary & Benbow (2012) as the initial population vector, this is multiplied to higher powers of the

210 original matrix during months that are simulated to be “open fishing” and then when a closure was simulated,

211 the matrix with increased survival was multiplied to the population for that month. We simulated these

212 different scenarios in order to analyze all combinations of conservation strategies that result in stable *O.*

213 *cyanea* populations.

214  **4 RESULTS**

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

216 fishing pressure included (Figure [3).](#_bookmark3) The stable stage distribution (Table [2)](#_bookmark4) shows that 65% of the makeup

217 of this population is immature individuals, while actively breeding individuals (fully mature) only make up

218 less than 1% of the naturally occurring population. However, the reproductive output per stage (Table [2)](#_bookmark4)

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

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

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

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

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

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

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

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

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

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

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

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

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

232 7.5% increase in the survivability of the population to ensure a sustainable population when utilizing three

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

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

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

236 once every three months.

237  **5 DISCUSSION**

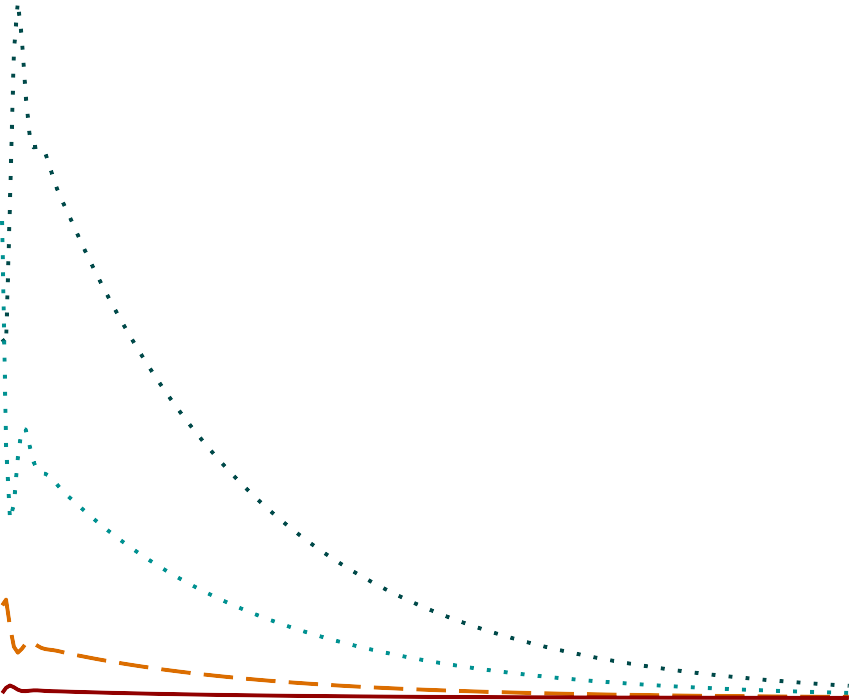
238 Our calculated growth rate of -0.0184 and resulting population projection supports previous reports of

239 overfishing at the time of data collection (Humber et al., 2006; Benbow et al., 2014). Matrix population

240 models will converge or diverge based on their dominant eigenvalue, regardless of the initial population

241 inputted in the model. Therefore, we can still conclude that the population at this time was in an overall

242 decline, despite not knowing the exact number of individuals in this population. Decline in population

150

100

No. Individuals

Stage 1

Stage 2

Stage 3

Stage 4

50

0

2006 2008 2010 2012 2014 2016 2018 2020 2022 2024

## Year

Figure 3: Projection of *O. cyanea* population based off of our calculated Lefkovitch matrix through the present.

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)

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

Pop

ulation Decreasing

**Population Increasing**

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.

243 presents an economic issue for individual fishers as their catch will become less lucrative and a recovery of

244 this population has been shown result in economic gains from fishers in this community (Humber et al.,

245 2006; Benbow et al., 2014; Oliver et al., 2015).

246 Our model provides other information about the life history of this population as well, beyond its overall

247 growth rate. As each column in the matrix represents a proportion of individuals within a stage either growing

248 or staying within a stage (with the exception of the *F*4 parameter), it also shows a per-stage survivability

249 estimate (Table [2)](#_bookmark4) and stage duration (Table [1),](#_bookmark2) life history parameters on which there has been no previous

250 research. However, as the immature stage has a high survivability of 90.4% and a longer duration than the

251 other stages of 2.7 months, this could indicate that although the fishing method employed in this region

252 does not distinguish by octopus size, fishers may not be bringing this smaller catch to landing due to size

253 limits preventing them from selling immature individuals (Humber et al., 2006). Therefore, this challenges

254 our assumption of the data being properly stratified by size. Further, as *O. Cyanea* have an approximately

255 one to two month larval stage (Guard & Mgaya, 2003), the fecundity parameter does not indicate the overall

256 reproductive output of mature individuals, but the number of hatched offspring that will survive its larval

257 stage and back the immature stage. This gives an estimation for larval survivability as female octopus have a

258 fecundity ranging between 27,000 and 375,000 eggs (Guard, 2009), our model indicates that only an average

259 of 26.7 individuals will survive back into immaturity, which indicates a survivability of 0.0001328. There

260 is no other larval survivability estimation that currently exists for this species, which would be a useful

261 further study as this could indicate a recruitment rate for this population. Further, an average lifespan of

262 4.06 months and an age of maturation of 6.82 months indicates that most individuals die before reaching

263 maturation.

264 According to our model, any closure less than three months will not be effective in conserving blue octopus

265 stocks, but the strictness of the closure (i.e. allowing some limited fishing) can be altered depending on how

266 frequently these restricted fishing periods are implemented. This is similar to other studies on temporary

267 closures in this fishery as Oliver et al. (2015) showed that extending the regional closure beyond the

268 conventional six weeks increased octopus catch. Further, a 2-3 month closure was suggested for this area in

269 2011 in order to maximize catch-per unit effort (Benbow & Harris, 2011). Benbow et al. (2014) demonstrated

270 that a 20 week closure had similar positive effects on octopus catch to a seven month closure, yet resulted in

271 less strain on fisheries management investment than the longer seven month closure. There is no previous

272 literature on the per-stage survivability of *Octopus cyanea*, particularly in this region. The overall natural

273 mortality rate of this population has been estimated to range between from 0.0127 per week (0.0552 per

274 month) to 0.0498 per week (0.2164 per month) (Roa-Ureta, 2022). However, this was not included in our

275 model of fishery closures as these closures do not cover the full spatial extent of the fishery (Oliver et al.,

276 2015), and some fishing continues during this time, meaning some fishing mortality exists during closures.

277 Instead, we compared closures to their overall effect on the *O. cyanea* mortality rate. Therefore, the changes

278 to survivability suggested by our analysis is in relation to their overall death rate not fishing rate, indicating a

279 need for further research on the spatial structure of this population. Our analysis of different closure scenarios

280 suggests a range of the simplest actions needed in order to ensure stability of this population, and show how

281 the relationship between closure lengths and their effect on mortality rates can result in multiple different

282 temporary closures that can successfully conserve a fishery. As there are many combinations of survivability

283 increase and frequency of closure suggested by the analysis will result in stable *O. cyanea* populations, the

284 specific strategy chosen should be decided based on which is most convenient and economically feasible to the

285 local fisher community of southwest Madagascar. Among conservationists, there is a growing understanding

286 that decision making is best left to those directly involved with resource extraction and implementing fishing

287 restrictions upon a community without understanding their cultural practices can have detrimental effects

288 upon the community, as well as be less effective in actually protecting natural resources (Humber et al.,

289 2006; Baker-Médard, 2017).

290 When implemented deliberately, establishing periodic closures is an effective and commonly-used strategy in

291 sustainable fishing practices (Humber et al., 2006; Oliver et al., 2015). As Madagascar has been committed

292 to protecting its marine natural resources through increasing the number of marine parks, this study serves

293 to highlight some of the available strategies to make population predictions and conservation strategies with

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

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

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

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

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

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

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

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

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

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

304 Although this is not enough data to conduct a full stock assessment, this speaks to the utility of mechanistic

305 modeling, where we are able to estimate population patterns and other life history traits despite this lack

306 of data. A future study that repeats this method of data collection could rerun this same model with

307 the updated data, and make further conclusions about the status of this fishery today. Even though data

308 collections occurred daily within a two-hour window, catch was not standardized by effort and therefore

309 there could be catch fluctuations between months that are not captured in the data. Further, as stage 1 had

310 a high survival rate yet low duration, this challenges the assumption that the octopus caught are an accurate

311 ratio of the octopus at each stage in the wild. Another shortcoming of this study is that the only available

312 stage data for this species and region was collected in 2006, and the community of southwest Madagascar

313 has implemented several strategies since that time to improve the sustainability of their fish stocks in the

314 region (Humber et al., 2006; Raberinary & Benbow, 2012). Due to the time of data collection, this study

315 does not reflect the current status of *Octopus cyanea*, nor should the findings of this study be implemented

316 in current management decisions. Instead, this study outlines what biological parameters can be estimated

317 from limited data using mechanistic modeling and show how temporary closures are not only an effective

318 method of conservation, but also provide communities with options for effective management and these

319 should be selected based off of the needs of stakeholders. As the community of southwest Madagascar has

320 been involved in deciding when closures should occur and their lengths, this study serves to show the various

321 options available (Benbow & Harris, 2011).

322 Finally, as we are using a Lefkovitch matrix to simulate population fluctuations, these models inherently

323 make simplifying assumptions about the biology of the study species. For example, these models assume

324 that all individuals within a stage are subject to the same growth and mortality rates. As this study uses

325 data collected from a large geographic range (Raberinary & Benbow, 2012), different individuals nesting in

326 different regions may be subject to different selective pressures. Studies on the spatial variability of this

327 population could better inform both our model and the greater understanding of how fishing mortality of

328 this population compares to its natural mortality. Further, this population of blue octopus has been shown

329 to exhibit spatial variability depending on their life stage. Younger individuals tend to live in the shallow

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

331 deeper waters for more suitable habitats for nesting (Raberinary, 2007). Parameters were not extracted from

332 a distribution curve, so adding this to future research could further help explain the uncertainty in octopus

333 dynamics and better model the high variability in populations. Despite these limitations, the data provided

334 is the best data available for fitting a Lefkovitch matrix to this species. Future extensions of this work could

335 include exploring the dynamics of both sexes in the population (Gerber & White, 2014) as male octopus

336 have different growth rates and spatial dynamics (Heukelem, 1976). Further, a better understanding of the

337 seasonal breeding dynamics of this population of blue octopus could give better insight into the health of this

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

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

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

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

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

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

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

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

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

347 more contemporary study on the status of the octopus fishery of southwest Madagascar will paint a more

348 accurate picture of how this population is faring under the current fishing pressure. As a population with

349 highly variable population dynamics, continuous monitoring of landings, fishing effort, and where catch is

350 found is extremely valuable in understanding the status of *Octopus cyanea* in Madagascar, as well as to

351 provide a more informed stock assessment on which to base management decisions. Similar data has been

352 collected by Blue Ventures on this fishery since 2015 and shows there has been an improvement to this

353 fishery since 2006, however there are still indication so that overfishing is occurring. Further, the addition

354 of collecting maturity data on blue octopus would allow for a study of Lefkovitch matrices applied to this

355 population informed by multiple years of data (Roa-Ureta, 2022). Finally, as the people of southwestern

356 Madagascar are actively taking steps to conserve the health of their fisheries, we hope that studies such as

357 these can serve to facilitate the understanding of what options are available when choosing how and when

358 to impose fishing restrictions.

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

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

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