Fisheries Research

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

--Manuscript Draft--

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Corresponding Author:	Sophie Wulfing University of New Hampshire Dover, NH UNITED STATES
First Author:	Sophie Wulfing
Order of Authors:	Sophie Wulfing
	Ahilya Sudarshan Kadba
	Merrill Baker-Médard
	Easton R. White
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Abstract:	Mechanistic models are particularly useful for understanding life history metrics and 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. One approach to address sustainability concerns is through the use of temporary spatial closures. The blue octopus (Octopus cyanea) fishery off the southwest coast of Madagascar is one such system that uses temporary closures to conserve an understudied species. As the Mozambique channel consists of strong eddies and little throughflow, the O. cyanea caught in this channel can be considered a distinct population as larval dispersal is largely controlled by ocean currents. This fishery is a key economic resource for the local community as blue octopus catch is sold by local fishers to international and local export markets and is a major component of fisher income. To better understand the biology and assess the sustainability of blue octopus, we parameterize a Levkovitch population matrix 12 model using existing catch data. We found that the octopus population was experiencing a 1.8% decline per month at the time of data collection in 2006. However, since 2006, a number of management practices, including temporary closures lasting several weeks to several months have been implemented successfully. In line with these efforts, our model indicates that the fishery would need to close for two to three months annually for the fishery to be sustainable. Our model provides support to the idea that temporary closures have restored this population and that temporary closures provide flexibilty in management strategies that local communities can tailor to their economic and social needs. In addition, we were able to estimate several important life history metrics, such as time in each stage, stable stage distribution, reproductive value, and per stage survivability, that can be used in future work. Collectively, our study provides insight into the biology of blue octopus as well as demonstrate how temporary closures can be an effective conservation strategy due to the wide range of implementation options.

University of New Hampshire

College of Life Sciences and Agriculture
Department of Biological Sciences
Rudman and Spaulding Halls 46 College Road
Durham, NH 03824-2617 USA

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Dear Editorial Board,

Please find enclosed the revision of the manuscript: "**Using matrix models to assess temporary closure strategies for small scale fisheries**", by Sophie Wulfing, Ahilya Sudarshan Kadba, Merrill Baker-Médard, and Easton R. White for consideration in *Fisheries Research* as a Research Article. All sources of funding are acknowledged in the manuscript. There is no financial interest to report. I certify that the submission is our own original work and is not under review at any other publication, and this publication is available as a preprint on https://www.biorxiv.org/.

We believe this manuscript will be of general interest to the readers of *Fisheries Research* for both the scientific insights and the implications for fisheries management in Madagascar. We fit a Lefkovitch matrix population model to *Octopus cyanea* stocks in southwest Madagascar and found that populations are decreasing according to the model. We calculated estimates for Octopus Cyanea stocks' per-life stage duration, survivability, and reproductive value along with the stable stage distribution. Finally, we simulated various management scenarios and found that temporary closures are an effective and flexible strategy for fishery conservation in fast growing species. These results highlight the importance of understanding life history patterns when instituting conservation initiatives as well as create estimates for the life history traits of *Octopus cyanea*.

We look forward to hearing from you at your earliest convenience.

Sincerely,

Sophie Wulfing
Masters Student
Department of Biological Sciences
University of New Hampshire

Dear Editor,

Thank you for giving us the opportunity to re-submit a revised draft of our manuscript titled, "Using mechanistic models to assess temporary closure strategies for small scale fisheries". We thank the reviewers for their constructive comments on the manuscript. We have now altered our framing, addressed limitations in the data, and clarified other points in the text.

Below we detail the changes we made to our manuscript in response to each reviewer comment. We leave the *original reviewer comments in red, italicized font*. Our responses are in black, Roman font. We have also included line numbers of the revised manuscript for each response.

Reviewer #1 Response to Questions

Big picture: We appreciate the additional feedback from reviewer #1 for this study. We have worked hard in both iterations to improve the overall manuscript. We make clarifications throughout the manuscript, but especially in the introduction and discussion.

We agree that our model provides results that appear to contrast with field data. We don't think we explained this well originally. We appreciate the reviewer pushing us on these points. Now, as we note in two paragraphs of the discussion, our model is, of course, wrong. We make a number of simplifying assumptions. We hope that future work can build on this first paper by addressing some of these assumptions that might be important. That being said, our results don't depart greatly from field data. As the reviewer rightly points out, there are many areas of Madagascar, and elsewhere, where short term closures have been effective at promoting octopus populations. Our models agree with these findings and we have now reworked the discussion to reflect this. The reviewer points out that short closures (on the order of weeks) have helped sustain populations. There is actually a range of closure and management mechanisms in Madagascar. There are short (usually 6 weeks) rotating closures between June-August led by individual communities. In addition, there are regional closures for 6 weeks in December and January that is guided above the village level. It is not clear how enforced these closures are and how this might vary between villages. Either way, there is a history of closures that can be for several months per year depending on the location. Thus, our result of 3 months being necessary to ensure positive population growth is actually remarkably close to what is already being done in the field. We have tried to emphasize this point more clearly. In addition, some communities have implemented additional measures, such as allowing harvesting only by locals, size restrictions, etc. that may also contribute to slight mismatches in our results.

In general, we hope we more clearly explain that we think current management practices are working well. The fishery may have been declining 20 years ago, but a combination of closures and other management practices has increased stocks. Our model results **agree** with this field data and the experimental closures.

We think our revised abstract also makes these points more clearly: "We found that the octopus population was experiencing a 1.8% decline per month at the time of data collection in 2006. However, since 2006, a number of management practices, including temporary closures lasting several weeks to several months have been implemented successfully. In line with these efforts, our model indicates that the fishery would need to close for two to three months annually for the fishery to be sustainable. Our model provides support to the idea that temporary closures have restored this population and that temporary closures provide flexibility in management strategies that local communities can tailor to their economic and social needs."

1. Are the objectives and the rationale of the study clearly stated?

Please provide suggestions to the author(s) on how to improve the clarity of the objectives and rationale of the study. Please number each suggestion so that author(s) can more easily respond.

Reviewer #1: Objectives and rationale are clear yet those objectives and rationale are excessive for the data available for the study.

In the detailed comments below, we tried to address this concern. Generally, we have tried rewriting the text to be clear on our intentions for the manuscript.

3. If applicable, are statistical analyses, controls, sampling mechanism, and statistical reporting (e.g., P-values, CIs, effect sizes) appropriate and well described?

Please clearly indicate if the manuscript requires additional peer review by a statistician. Kindly provide suggestions to the author(s) on how to improve the statistical analyses, controls, sampling mechanism, or statistical reporting. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Mark as appropriate with an X:
Yes [] No [X] N/A []
Provide further comments here:
The method employed did not yield measures of statistical uncertainty such as standard errors, confidence intervals, or Bayesian credible intervals. This is because there was no likelihood function defined as objective function during optimization.

Correct. We think this would be great for future work, especially if our study helps spur additional data collection.

4. Could the manuscript benefit from additional tables or figures, or from improving or removing (some of the) existing ones?

Please provide specific suggestions for improvements, removals, or additions of figures or tables. Please number each suggestion so that author(s) can more easily respond.

Reviewer #1: Yes. The ms. would be complete as a methodological innovation article if it added two more applications: one to a data-rich fishery and another to simulated data where the true values of parameters are known.

We have tried to address these concerns through a different approach outlined below. We think it is outside the scope of the current study to run our models for a whole new fishery or to use simulated data. We agree that both approaches are interesting, but each feel like future work. We already have a lot in this one paper. On lines 348-349 we acknowledge that these are valuable future directions for research.

5. If applicable, are the interpretation of results and study conclusions supported by the data?

Please provide suggestions (if needed) to the author(s) on how to improve, tone down, or expand the study interpretations/conclusions. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: Mark as appropriate with an X:
Yes [] No [X] N/A []
Provide further comments here:
The data are very old and limited in scope yet authors make statements about management measures that they claim need to be implemented.

We appreciate this concern. Below, we indicate specific places (mostly in the abstract, intro, and discussion) where we have reworked the text. The data is old. We now more clearly note that the model only indicates a possible declining octopus population in 2006. The population may have continued to decline **without** management action. We more clearly describe how management actions were taken that generally align with our model outputs.

On Lines 12-22, we reworded the abstract to read: We found that the octopus population was experiencing a 1.8% decline per month at the time of data collection in 2006. However, since 2006, a number of management practices, including temporary closures lasting several weeks to several months have been implemented successfully. In line with these efforts, our model indicates that the fishery would need to close for two to three months annually for the fishery to be sustainable. Our model provides support to the idea that temporary closures have restored this population and that temporary closures provide flexibility in management strategies that local communities can tailor to their economic and social needs. In addition, we were able to estimate several important life history metrics, such as time in each stage, stable stage distribution, reproductive value, and per stage survivability, that can be used in future work. Collectively, our study provides insight into the biology of blue octopus as well as demonstrate how temporary closures can be an effective conservation strategy due to the wide range of implementation options.

On lines 240-241 have specified our results as “closures two months in length or shorter may be ineffective in ensuring a stable population”

We have removed lines 58-61 in the previous manuscript that read “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 Marine Protected Areas through temporary fishing closures (Cinner et al., 2009; Oliver et al., 2015; Baker-Médard, 2017)”

We have removed lines 71-81 in the previous manuscript that read “However, seasonal closures 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 seasonal closure will protect the fishery (Russ & Alcala, 1998; Cohen & Foale, 2013; Gnanalingam & 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 & Foale, 2013). Therefore, assessments of each seasonal closure is essential to insuring that they are effective in replenishing fish stocks. Mechanistic modeling allows us to simulate different fishery scenarios and assess how populations will respond to these changes in fishing pressure.”

We have added on lines 87-99 “Compared to other exploited marine organisms, octopus have a short lifespan coupled with a fast reproduction rate and high fecundity which makes their populations more responsive to fishing pressures (Langley, 2005; Humber et al., 2006). Increased fishing pressure due to globalization of the blue octopus in 2003 has since added significant fishing pressure to Madagascar’s blue octopus populations and yield from this fishery subsequently decreased in regions of this island such as the southwest region of Toliara (Langley, 2005; Humber et al., 2006). However, previous temporary closures on the fishery resulted in population increases, indicating that this fishery has the ability to recover when fishing pressure is decreased (Humber et al., 2006; Katsanevakis & Verriopoulos, 2006; Benbow et al., 2014). However, right after reopening, stocks began to decline again, which has been attributed to heavy fishing pressure right after reopening (Humber et al., 2006; Benbow et al., 2014; Oliver et al., 2015). Octopus populations are therefore sensitive to both the increase and alleviation of fishing pressure and understanding their biology and how these population dynamics will react to changes in fishing pressure is a key component to effective conservation of this resource.”

We have removed lines 244-247 in the previous manuscript that read "Matrix population models will converge or diverge based on their dominant eigenvalue, regardless of the initial population inputted in the model. Therefore, we can still conclude that the population at this time was in an overall decline, despite not knowing the exact number of individuals in this population."

We have added on lines 249-259 "Our calculated growth rate of -0.0184 and resulting population projection supports previous reports of overfishing at the time of data collection in 2006 (Humber et al., 2006; Benbow et al., 2014). With this negative growth rate, our models suggest that, without changes to management practices, the octopus population may have continued to decline. In addition, according to our model, any closure less than three months, without additional management actions, may not be effective in conserving blue octopus stocks. However, given data and model limitations, we do not have a measurement of uncertainty for the growth. Thus, caution should be taken when considering whether the octopus population was actually in decline or not in 2006. We describe this limitation more below. In general, declines in octopus populations presents an economic issue for individual fishers as their catch will become less lucrative. Octopus population recovery has been shown to result in economic gains from fishers in this community (Humber et al., 2006; Benbow et al., 2014; Oliver et al., 2015)."

We have added on lines 273-278 " Our analysis of different closure scenarios suggests a range of the simplest actions needed in order to ensure sustainability of this population, and show how the relationship between closure lengths and their effect on mortality rates can result in multiple different temporary closures that can successfully conserve a fishery. Thus, despite the simplicity of our model, our findings for possible closure lengths is very close to those currently practiced in Madagascar and elsewhere. As we describe later, more realistic extensions of this model can be built to guide specific management practices."

6. Have the authors clearly emphasized the strengths of their study/theory/methods/argument?

Please provide suggestions to the author(s) on how to better emphasize the strengths of their study. Please number each suggestion so that the author(s) can more easily respond.

Reviewer #1: No. Authors need to expand the analysis to more cases to understand the scope and limitations of the method proposed.

As we describe at the beginning of this document, in the abstract and discussion, we have tried to more clearly demonstrate the usefulness of our current work. We found a declining octopus population in 2006, which aligns with field data, show that short (2+ month) closures can be effective, which aligns with field data, and estimate a number of biological parameters (e.g., stage duration, survival) that have not been widely available for this species.

Reviewer #1 Specific Comments

1 Overview

Unfortunately, this is not an improvement over the first version that I reviewed. Authors insist on providing management advice and making statements about the status of the stock based on the smallest of evidence which is in addition very old.

We are disappointed to hear this assessment. We worked hard to rephrase and rework our manuscript. In the manuscript, we specifically wrote, "Due to the time of data collection, this study does not reflect the current status of *Octopus cyanea*, nor should the findings of this study be implemented in current management decisions." We have two paragraphs of study limitations, both in terms of the model and current data collection efforts, clearly laid out in the discussion. We outline our response more in the previous comments.

I think authors need to write a new ms. with more examples of the use of Lefkovitch matrices, a new submission where the Madagascar application would be just one example. A second example from a data-rich fishery that also has open and closed seasons and where the results of Lefkovitch matrices modelling can be compared with results from data-rich applications would be very useful. A further third application of Lefkovitch matrices applied to simulated data from an operating model where the truth is known would make the ms. complete.

We appreciate the detailed comments and we try to address each of them below. We don't think it is a fair ask to request we "write a new ms". Our work provides new information on octopus life history and the effects of potential management strategies. We clearly highlight the limitations of our approach and point out possible future work that might be helpful or interesting. The work the reviewer proposes is interesting, but it would have to be a whole separate manuscript.

2 Specific issues

2.1 Title

Change 'mechanistic models' to 'Lefkovitch Matrix models' because 'mechanistic models' doesn't say anything, it's too general. Actually all stock assessment models (except CPUE standardization) are mechanistic models so saying that in the title is like saying nothing. The novelty of your work is in using those matrices, that should be in the title.

Our title has been changed to "Using matrix models to assess temporary closure strategies for small scale fisheries"

2.2 Abstract

"As overfishing remains a global issue, .."

But does it? Most fisheries in the world have not been assessed so we just don't know whether overfishing is a global issue. Perhaps the global issue is underfishing due to fear of over-

conservative managers facing lack of stock assessment results? I suggest to change the sentence to ”As overfishing remains a concern, ..”.

Overfishing is a global issue. We don’t mean to imply that most fisheries are overfished. We actually don’t think this is true, our intention with that statement was to say it’s an issue that exists in all areas of the globe and is not concentrated in one region. This line has been removed from the abstract.

”To sustain the existing population of blue octopus, our model indicates that the fishery would need to close for at least three months annually.”
The authors continue to present this claim despite the fact that it is known to be a false and alarmist prediction. ***The fishery has evolved for 12 years after the data used to make your prediction with much shorter closures and there has been no collapse. Denying the facts is not a good strategy.*** *You need to face the evidence and explain why despite your prediction the fishery has continued normally. What is so fundamentally wrong in your model or your data or both?*

We think there has been a misunderstanding, because of how we wrote the original manuscript, with what we are claiming in our work. We have now completely reworked our wording, especially in the first paragraph of the discussion. On lines 250-252 we note: “With this negative growth rate, our models suggest that, without changes to management practices, the octopus population may have continued to decline.” Since the data was collected there have been a number of changes to management practices. We actually believe our model strongly supports what has happened in the field. We agree we did not phrase this well in our original manuscript. It is actually remarkable that, despite a very simple model, we find that several months of closures can be used as a strategy to increase harvests—exactly as seen in numerous field experiments.

2.3 Introduction

L. 23-25. Mechanistic models are the bread and butter of stock assessment and fisheries research. Your audience needs no convincing in this respect. Instead, you should be convincing your audience of the advantages of using Leftkovitch Matrices.

First paragraph of the introduction has been changed to focus on the value and function of Lefkovitch matrices on lines 25-46.

L. 86-98. You need to tone down the hype. I counted seven unjustified superlatives in these few paragraphs. Your superlatives make octopus stocks look fragile to fishing while in fact they are *relatively more resilient than long-lived stock on account of their capacity to quickly bounce back from low abundance. They are more variable, not more fragile.*

The paragraph on lines 87-99 has been changed to avoid sensationalizing the variability of octopus stocks. Instead it now reads:

"Compared to other exploited marine organisms, octopus have a short lifespan coupled with a fast reproduction rate and high fecundity which makes their populations more responsive to fishing pressures (Langley, 2005; Humber et al., 2006). Increased fishing pressure due to globalization of the blue octopus in 2003 has since added significant fishing pressure to Madagascar's blue octopus populations and yield from this fishery subsequently decreased in regions of this island such as the southwest region of Toliara (Langley, 2005; Humber et al., 2006). However, previous temporary closures on the fishery resulted in population increases, indicating that this fishery has the ability to recover when fishing pressure is decreased (Humber et al., 2006; Katsanevakis & Verriopoulos, 2006; Benbow et al., 2014). However, right after reopening, stocks began to decline again, which has been attributed to heavy fishing pressure right after reopening (Humber et al., 2006; Benbow et al., 2014; Oliver et al., 2015). Octopus populations are therefore sensitive to both the increase and alleviation of fishing pressure and understanding their biology and how these population dynamics will react to changes in fishing pressure is a key component to effective conservation of this resource."

2.4 Materials and Methods

L. 170-172. "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 also includes the influence of fishing pressure."

This seems to be false. You quote a technical report by Roa-ureta (2022) and in that report there are estimates of natural mortality rate for several years. Later you quote the report and explain why you chose not to use those estimates for natural mortality but still, you should correct this misleading sentence which is contradicted in your Discussion.

This line has been removed.

L. 175-177. "In order to parameterize this model, we use 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)."

You need to explain how Wood's Quadratic Programming work in terms of familiar terminology. It is clear that it is not likelihood maximization so it is not a statistical analysis so I guess it is a linear optimization method. Explain in sufficient detail what is the objective function, make your readers believe you've chosen the correct method for parameterization.

We better explained the utility and purposes of Woods Quadratic Programming method on lines 180-185. We explain that: “One strength of Woods Quadratic Programming is it allows for constraining parameters to be within certain ranges. For example, we can constrain all parameters to be greater than zero, place zeros in the solution matrix to reflect *Octopus cyanea* biology, and ensure that all Pi and Gi parameters don't add up to more than 1, which would imply that individuals in stage i are somehow multiplying themselves. The matrices then become quadratic equations that are solved through sum of squares minimization while also remaining within these constraints.”

L. 181-183. ”As all of our values calculated from the matrix fall within the known attributes of this species, we are confident that this model gave an accurate mechanistic description for this population’s underlying dynamics.”
You cannot determine the underlying dynamics with one year of data. Dynamics means change in time. It is impossible to determine the dynamics of a system with one time step of data. What you can do is to assume stationary behaviour, meaning that the current distribution across stages has reached equilibrium. What you may use instead of ’dynamics’ is ’structure’. You can be confident that your (presumably) linear optimization gave you the true equilibrium stage structure.

We have removed this line from the manuscript.

Management Scenarios. The language here is too terse. E.g.: ”In order to determine optimal conservation strategies, we alter the survivability of O. cyanea by different rates from 0-10% survival increase of the species.” Do you alter the survivavility by steps of 1% to each of the stages, or just two levels, 0 and 10%?
It seems you assume that some background survavility happening during months of fishing get reduced from 0 to 10% in months of closure. In that way you can project the matrices under different scenarios. But why only 10% as maximum increase in survivavility during months of closure? Is fishing mortality so low that only account for up to 10% less survivability?

10% survivability was the maximum only because increasing the survivability by more than 10% would result in parameters being outside of biologically reasonable estimations in this model. Basically, the immature individuals would reach a survivability of over 100%, meaning they are somehow multiplying themselves.

This has been explained on lines 215-219 “10% is the maximum survival increase used because increasing the overall survivability of matrix by more than 10% would result in some stages reaching a survivability of more than 1, implying that the stage would somehow be multiplying itself within a month timestep. We therefore limit survival increases to a maximum of 10% to stay within biologically meaningful parameters."

On lines 342-344 we note that "Our management scenario analysis also assumes that each lifestage would be affected equally by a closure, which could be challenged by the previous result that fishers are not bringing smaller catch to landing due to the size limits."

2.5 Results

"Our analysis of different closure scenarios (Figure 5) indicates closures two months in length or shorter will be ineffective in ensuring a stable population, regardless of how much these closures decreased the death rate of the species."

So the model or the data or both are fundamentally wrong because we know for a fact that the stock has continued yielding not just stable, but growing landings since 2015 and up to 2021, under the same regime of very short (just weeks) closures at the turn of each year.

We have not found any papers that claim that closures of "just weeks" are effective. For some situations in the field, there might be a short two-week closure, but this is coupled by other closures throughout the year. Our work actually doesn't require that the closures are a continuos set of months. However, our model supports the idea that "just weeks" could be effective if other management interventions were also enacted. As we note in the first paragraph of the discussion, "According our model, any closure less than three months, without additional management changes, may not be effective in conserving blue octopus stocks." Since the data was collected there have been numerous interventions, especially spatial closures, for octopus in the region. Our results are actually strongly aligned with field studies that show 6-12 weeks of closures may be effective in promoting harvest.

2.6 Discussion

L. 238-239. "Our calculated growth rate of -0.0184 and resulting population projection supports previous reports of overfishing at the time of data collection (Humber et al., 2006; Benbow et al., 2014)."

Your value of -0.0184 for the population growth rate is awfully close to 0 and no measure of statistical uncertainty is provided. Clearly, taking into account the sparsity of data, the standard error around that estimate must be substantial, so for all we know from you calculations, the stock might actually be increasing (instead of -0,0184 it could be +0.0184) considering statistical

uncertainty. Yet you use your results to say that the stock is declining and that closures of longer than 3 months are necessary, potentially affecting the livelihoods of those fishers with not very solid data and analysis.

We note that our predicted growth rate was negative at the time of data collection. We have now clarified better to note the stock **was possibly declining. However,** with management intervention since data collection, the fishery has been harvested sustainably. We agree with this. Our model agrees with this as well. We say that any closure less than three months, **without additional management changes**, may not be effective in conserving blue octopus stocks. There have been numerous interventions over the past two decades. Our modeling results largely support this.

L. 272-276. "The overall natural mortality rate of this population has been estimated to range between from 0.0127 per week (0.0552 per month) to 0.0498 per week (0.2164 per month) (Roa-Ureta, 2022). However, this was not included in our model of fishery closures as these closures do not cover the full spatial extent of the fishery (Oliver et al.,2015), and some fishing continues during this time, meaning some fishing mortality exists during closures."
I don't understand your explanation of why those estimates are not useful to you. I read the report by Roa-Ureta and it has both natural and fishing mortality estimates per week and it explains that those estimates are valid over the whole of SW Madagascar octopus fishing grounds and that the natural mortality is the average over an annual season while fishing mortality rates are estimated by week, so your closures in time and space obviously fall within the scope of the estimates in Roa-Ureta's report. Probably you need to introduce constrains in your linear optimization method to the effect that the addition of your stagebased survival rates equal a random number that comes from the sum of natural and fishing mortality within a few standard errors of Roa-Ureta's estimates.

It's true that Roa-Ureta's report does estimate a natural survivability for the whole fishery. However, there are also local spatial closures that happen at the same time for 2-7 months and restrict fishing in ~20% of the fishery's spatial extent, (Rocliffe & Harris, 2015, 2016; WWF, 2017). As octopus have also been shown to exhibit spatial variability in their population structure, (Raberinary 2007), we feel we are unable to extrapolate this estimation to the whole population or to every type of spatial closure that occurs here.

We have further clarified this on lines 307-312: "The overall natural mortality rate of this population has been estimated to range from 0.0127 per week (0.0552 per month) to 0.0498 per week (0.2164 per month) (Roa-Ureta, 2022). However, this was not included in our model of fishery closures as the local closures do not cover the full spatial extent of the fishery, have variable spatial extents, and some fishing continues during this time, meaning some fishing mortality exists during closures (Oliver et al., 2015). Instead, we compared closures to their overall effect on the O. cyanea mortality rate"

L. 351-353. "Similar data has been collected by Blue Ventures on this fishery since 2015 and shows there has been an improvement to this fishery since 2006, however there are still indication so that overfishing is occurring."
What are those indications? You need to named them.

This line has been removed

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Reviewer #2 Specific comments

This is a vast improvement on the previous version of this manuscript that I reviewed and presents the available data in a much more useful format.

Please revise the penultimate sentence of the abstract "indicating a need for further research into the effectiveness of these fishing closures" the Oliver et al paper documents the fisheries benefits of the closures quite clearly. Either remove this part of the sentence or revise to focus on the population/stock benefits of the closures needs more research.

The abstract has been changed and no longer includes this line.

e.g. having reviewed the earlier draft of this manuscript I am still struggling with the lack of references to larval dispersal rates/distance in the abstract and claims that closures can restore the local octopus populations. This is well integrated into the body of the article now but warrants a mention in the abstract.

We have added the line "As the Mozambique channel consists of strong eddies and little throughflow, the *O. cyanea* caught in this channel can be considered a distinct population as larval dispersal is largely controlled by ocean currents." in lines 7-8

I actually think the discussion is much stronger than the abstract in highlighting the utility of the research presented here, and the abstract would benefit from further review to make it clear.

Abstract on lines 2-22 was changed to reflect topics brought up in the discussion.

Line 58-60 I appreciate the addition of more information on LMMAs preceding this sentence as that is the common management measure in the southwest but I still question this link to *temporary fishing closures as MPAs. I think this sentence could be deleted as the sentence start on line 61 is much more clearly phrased.*

This line has been deleted.

Line 89 first reference to Andavadoaka. Think this needs more context, eg a small fishing village in southwest Madagascar?

This line was actually deleted in other edits.

Line 92 Andavadoaka is not a region. It is a village. A regional reference would be Morombe, or better Toliara.

This was changed to Toliara on line 92

Line 93 missing the word closures after temporary

This line was deleted in other edits

Line 94. I would prefer stocks instead of populations in this sentence

This was changed to stocks on line 95.

Line 104-110 Great I love this reference and wasn't aware of it and that is super exciting . Please revise your use of beyond Moz channel to beyond Madagascar as that is what the article states, and worth mentioning that genetic studies indicate limited genetic flow beyond southern Madagascar even as you note in line 158.

The words “Mozambique Channel” were changed to “Madagascar” on lines 106 and 110.

Line 114 change institution for instituting.

Institution has been changed to “instituting” on line 115

Line 123 missing a space between be and a

This has been fixed on line 124

Line 131-137 there is still some confusion that I can hopefully clarify and I am sorry that the literature you have found is not clear on this. There are 2 types of temporary closure in sw Madagascar. A regional closure for 6 weeks in December and january which covers the entire southwest fishery, so no octopus is bought at all during this time period (does not necessarily mean it isn't caught but certainly the fishing effort will decrease significantly….). And then the community led rotating closures which is where the 25% of the fishing area figure comes in.

These have varied from 6 weeks to 7 months, and are now usually held between June-August for a period of 2-3 months with exact dates reviewed every year by the CGP (octopus fishery management committee) depending on buyer availability, tides and community choice. Lines 266-271 seem to capture this much better!

Thank you for the additional context! We really appreciate it. We have tried to explain this more clearly now. Lines 134-136 has been changed to "The western Madagascar region currently institutes a yearly closure of six weeks from December 15 to January 31. In addition to the regional closure, individual villages institute their own local closures once a year, lasting from six weeks to seven months."

Line 235 this is super interesting and does add to research around the ideal cadence of closures

Thank you!

Lines 244-245 Oliver et al show the economic benefits to the communities of the closures, and the management regime including the closures includes price negotiations for open day catch where the buyer is guaranteed a large volume of octopus so they are willing to pay more as their costs are lowered because of the scale of the catch. The current phrasing of 'recovery of the population has been shown to result in economic gains from fishers in the community' does not capture all of this nuance I think

On line 259-260 we add "Further, sale prices on opening day tend to increase as buyers are typically guaranteed larger catch".

Line 251-253 this is correct. We assume that they are not selling undersized octopus and would just eat it at home so it does not get recorded in the dataset

Lines 295-297 have been changed to "this indicates that although the fishing method employed in this region does not distinguish by octopus size, fishers are not bringing this smaller catch to landing due to size limits preventing them from selling immature individuals"

Line 274-276 as noted above there is a need for clarity on the closure types. The regional 6 week closure is the whole fishery. The community led 2-3 month closures are approx 25% of a village's fishing grounds.

On lines 268-271 we have added the line "Individual villages also institute their own closures. These closures span 2-7 months and restrict fishing in ~20% of the fishery's spatial extent, so some fishing is still allowed to occur during this time." to distinguish between the two closure types

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

SOPHIE WULFING[1*], AHILYA SUDARSHAN KADBA[1], MEZ BAKER-MÉDARD[2], AND EASTON R. WHITE[1] [1]Department of Biological Sciences, University of New Hampshire, 03824, NH, USA

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

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

1 ABSTRACT

Mechanistic models are particularly useful for understanding life history metrics and 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. One approach to address sustainability concerns is through the use of temporary spatial closures. The blue octopus (*Octopus cyanea*) fishery off the southwest coast of Madagascar is one such system that uses temporary closures to conserve an understudied species. As the Mozambique channel consists of strong eddies and little throughflow, the *O. cyanea* caught in this channel can be considered a distinct population as larval dispersal is largely controlled by ocean currents. This fishery is a key economic resource for the local community as blue octopus catch is sold by local fishers to international and local export markets and is a major component of fisher income. To better understand the biology and assess the sustainability of blue octopus, we parameterize a Levkovitch population matrix model using existing catch data. We found that the octopus population was experiencing a 1.8% decline per month at the time of data collection in 2006. However, since 2006, a number of management practices, including temporary closures lasting several weeks to several months have been implemented successfully. In line with these efforts, our model indicates that the fishery would need to close for two to three months annually for the fishery to be sustainable. Our model provides support to the idea that temporary closures have restored this population and that temporary closures provide flexibilty in management strategies that local communities can tailor to their economic and social needs. In addition, we were able to estimate several important life history metrics, such as time in each stage, stable stage distribution, reproductive value, and per stage survivability, that can be used in future work. Collectively, our study provides insight into the biology of blue octopus as well as demonstrate how temporary closures can be an effective conservation strategy due to the wide range of implementation options.

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

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 (Briggs-Gonzalez et al., 2016). Biological processes are therefore hypothesized in the model, and each parameter represents these mechanisms and can be measured independently of the data collected. Population matrix models are a commonly used mechanistic model to predict future population dynamics by splitting the life history of the study organism up into a Leslie Matrix (Leslie, 1945) where a population is split up into groups of ages, and a transformation matrix is applied to predict what the population makeup will be in future years. However, these models require extremely in-depth data collection to inform each entry of the model, such as yearly survival rate based on age. This is not a reality for many organisms where these kind of data cannot be collected due to the difficulty in monitoring some species in yearly increments (Crouse et al., 1987) and for organisms that have long larval stages, where calculating survival probabilities for this time is nearly impossible (Gharouni et al., 2015).

Instead, Lefkovitch matrices are specialized matrices are used for “structured populations” – populations in which individuals can be categorized based on age, stage, weight or length. Each unit of the matrix represents a distinct period of the organism’s life where it is subject to different environments, pressures, or physical attributes that would alter the survival and reproductive output at that phase, but the amount of time between each stage is now variable. They use demographic rates to create a projection matrix – a square matrix where the number of rows and columns are equivalent to the number of life stages. These models can be 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 simulated and assessed (Crouse et al., 1987; Nowlis, 2000; Gharouni et al., 2015). Thus, Lefkovitch matrix models play a critical role in studying the biology of cryptic species, and 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 (The World Bank, 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 environment off the southwest coast of Madagascar is home to a wide variety of marine life, as extensive tidal flats, seagrass beds, and coral reefs are all prominent biomes in the area. In fact, Madagascar has been calculated as a country that would benefit greatly from marine conservation given its economic reliance on marine harvests and the fact that it is a refuge to many marine species (Laroche et al., 1997). In the early 2000’s, however, Madagascar’s octopus fishery began to move from local, subsistence fishing to also selling catch to export markets (Humber et al., 2006). There is evidence that up to 75% of all fish caught in select villages is now sold to outside entities for international export (Baker-Médard, 2017).

Locally-Managed Marine Areas (LMMAs) are defined as coastal and near-shore fisheries in which resources are managed almost entirely by local communities and fishery stakeholders that live in the region. Because management is conducted by those directly affected by the fishery, goals typically include maintaining the livelihood and economic and cultural goals of the local community along with environmental goals (Govan, 2010). LMMAs have grown in popularity among conservationists in small scale fisheries due to this empowerment of local fishers. Because of this, LMMAs tend to have greater local participation and compliance from stakeholders when compared to top-down regulation from governing bodies (Katikiro et al., 2015). LMMAs have been shown to improve both fisheries and fisher livelihoods in Kenya (Kawaka et al., 2017), Pacific Islands (Govan, 2010), and in Madagascar (Mayol, 2013). In Madagascar, the use of LMMAs has increased significantly since 2004, and fishers in the country have seen significant improvements to fish stocks as well as have experienced economic benefits since (Benbow & Harris, 2011; Gilchrist et al., 2020). In order to protect fishing resources, these LMMAs instituted various conservation programs such as bans on certain types of fishing gear, implemented seasonal fishing regulations, and criminalized the harvest of endangered species.

One commonly used conservation strategy in LMMAs in Madagascar are seasonal closures. These types of reserves have a long history of use and have been seen to successfully rehabilitate stocks (Camp et al., 2015; Gnanalingam & Hepburn, 2015). For example, seasonal closures have been shown to be an effective conservation strategy in increasing biomass the Atlantic sea scallop (*Placopecten magellanicus*) fishery in the United States (Bethoney & Cleaver, 2019), restored natural trophic interactions in coral reef fisheries in Kenya (McClanahan, 2008), and successfully restored the striped marlin (*Kajikia audax*) stocks in Baja California (Jensen et al., 2010). This method is flexible, logistically simple for fishers and managers to understand, and mitigates the financial loss from the fishery that can be seen with permanent closures (Nowlis, 2000; Humber et al., 2006; Cohen & Foale, 2013; Camp et al., 2015; Gnanalingam & Hepburn, 2015; Oliver et al., 2015).

Octopus 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 & Nigmatullin, 1996; Santos et al., 2001; Vase et al., 2021), situating them in a key role in food webs. 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 et al., 2019). Compared to other exploited marine organisms, octopus have a short lifespan coupled with a fast reproduction rate and high fecundity which makes their populations more responsive to fishing pressures (Langley, 2005; Humber et al., 2006). Increased fishing pressure due to globalization of the blue octopus in 2003 has since added significant fishing pressure to Madagascar's blue octopus populations and yield from this fishery subsequently decreased in regions of this island such as the southwest region of Toliara (Langley, 2005; Humber et al., 2006). However, previous temporary closures on the fishery resulted in population increases, indicating that this fishery has the ability to recover when fishing pressure is decreased (Humber et al., 2006; Katsanevakis & Verriopoulos, 2006; Benbow et al., 2014). However, right after reopening, stocks began to decline again, which has been attributed to heavy fishing pressure right after reopening (Humber et al., 2006; Benbow et al., 2014; Oliver et al., 2015). Octopus populations are therefore sensitive to both the increase and alleviation of fishing pressure and understanding their biology and how these population dynamics will react to changes in fishing pressure is a key component to effective conservation of this resource.

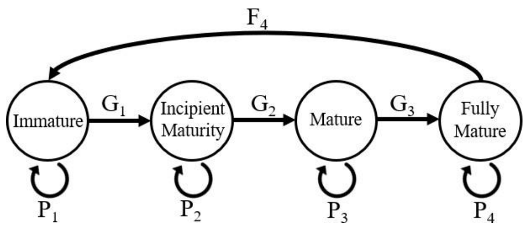
Octopus cyanea, or blue octopus, is the most abundant cephalopod species in the western Indian Ocean and is caught in about 95% of local landings in Madagascar (Humber et al., 2006; Oliver et al., 2015). Like other cephalopod species, very little is known about their life history including natural death 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 & Wells, 1970; Heukelem, 1976; Herwig et al., 2012; Raberinary & Benbow, 2012). The *O. cyanea* that live in the southwest region of Madagascar have been shown to be genetically distinct from those outside of Madagascar (Van Nieuwenhove et al., 2019). This is because the ocean currents in the Channel are comprised primarily of eddies with very little through-flow across the Channel (Schott & McCreary, 2001; Lutjeharms et al., 2012; Hancke et al., 2014). As larval dispersion is primarily controlled by ocean currents, and *O. cyanea* does not migrate across long distances, this shows that the *O. cyanea* in Madagascar where the data was collected can be considered a distinct population (Van Nieuwenhove et al., 2019).

Size limits have been shown to be effective methods of conservation of species like *Octopus cyanea* that are harvested before maturity, and are restrictions that are easy to understand and implement in small scale fisheries (Nowlis, 2000). However, even though this is a conservation strategy often implemented in octopus fisheries, it has been shown to be less effective than instituting an overall cap on fishing effort, such as effort rotation or limiting the number if fishers (Emery et al., 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, so octopus too small for market sale are typically harvested for household consumption (Humber et al., 2006). Further, the relationship between size and maturity stage is not strongly correlated (Raberinary & Benbow, 2012) and as a result, size restrictions wouldn't necessarily protect the individuals ready to reproduce and would be difficult to implement in the field both due to the biology of *O. cyanea* and the characteristics of this small scale fishery. Therefore, temporary closures have been shown to be a more practical method of octopus conservation in that they can replenish stocks while maintaining fisher income (Benbow et al., 2014). Temporary closures provide many options for their duration and intensity (in other words, how much fishing can occur during a closure). However, this requires a deeper understanding of the biology and population characteristics of *O. cyanea* in this fishery in order to be properly instituted. Instituting effective temporary closures in octopus fisheries can be difficult due to their short lifespan, high mortality, and sensitivity to environmental conditions (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. The western Madagascar region currently institutes a yearly closure of six weeks from December 15 to January 31. In addition to the regional closure, individual villages institute their own local closures once a year, lasting from six weeks to seven months. These closures do not completely restrict octopus fishing, but instead institute an area where fishing is not allowed which takes up about 25% ofthe fishery's spatial extent. Therefore, some octopus harvest does occur even during one of these closures (Aina, 2009; Langley, 2005; Humber et al., 2006; Benbow & Harris, 2011; Westerman & Benbow, 2014; Oliver et al., 2015; Rocliffe & Harris, 2015, 2016; WWF, 2017).

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 temporary closures can be an effective conservation strategy as well as demonstrate the numerous options available when deciding the length and intensity of closures. This study is not meant to be a current stock assessment of this fishery as local communities have taken numerous steps to conserve blue octopus since the time of data collection.

3 METHODS

As *Octopus cyanea* has an extended larval phase and there is no existing data on the age structure of this population of octopus, we use a stage-based population matrix, otherwise known as a Lefkovitch matrix (Caswell, 2001). Here, the life history of the study organism is grouped by stages (Figure 1), where each unit of the matrix represents a distinct period of the organism's life where it is subject to different environments, pressures, or physical attributes that would alter the survival and reproductive output at that phase, but the amount of time between each stage is variable. This would simply create different inputs for the probability of



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

Figure 1: A graph representing the life history of *O. Cyanea* and the subsequent Lefkovitch 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.

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 *O. 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.

3.1 Data

To inform our model, we use data collected by Raberinary & Benbow (2012) from landings ranging from the villages of Ampasilava in the south to Andragnombala in the north which spans about 30 kilometers of coastline. These villages are located along the Mozambique channel, where a lack of through current and prevalence of eddies results in a genetically distinct population of *O. cyanea* (Van Nieuwenhove et al., 2019). In these villages, fishers usually fish along both reef flats and deeper barrier reefs. Fishers bring catch 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.

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

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

3.2 Model Parameterization

In order to parameterize this model, we use 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). One strength of Woods Quadratic Programming is it allows for constraining parameters to be within certain ranges. For example, we can constrain all parameters to be greater than zero, place zeros in the solution matrix to reflect *Octopus cyanea* biology, and ensure that all P_i and G_i parameters don't add up to more than 1, which would imply that individuals in stage i are somehow multiplying themselves. The matrices then become quadratic equations that are solved through sum of squares minimization while also remaining within these constraints. We estimate a preliminary stage-based matrix model (Figure 2) based on Raberinary and Benbow (2012) data and calculated using the quadprog package in R (Turlach & Weingessel, 2019). We assessed model estimates 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 fall within the known attributes of this species, we are confident that this model gave an accurate mechanistic description for this population's underlying dynamics.

3.3 Model Analysis

Eigenvalues (λ) are calculated from the matrix and future populations can be predicted by multiplying an initial population vector to incrementally higher powers of our matrix where the power of the matrix corresponds to the time length of the projection. The initial population vector used is the blue octopus data collected in the final month of data collection from Raberinary & Benbow (2012). This month of data is not included in the parameterization of the model as it occurred after a temporary closure that was being tested at the time. We perform sensitivity analysis on the population matrix and eigenvalues using the r package popbio (Stubben & Milligan, 2007). Further, as all of the parameters are scaled to a value between 0 and 1 except F_4, the different order of magnitude of these parameters have a lower proportional effect on the eigenvalue than F_4. To address this, we also conduct elasticity analysis using the popbio package (Stubben & Milligan, 2007). This allows us to identify the groups within this octopus population whose protection will most benefit population growth, essentially creating focus points of conservation. The results of sensitivity and elasticity analysis are included in the supplementary material. Other life history traits that can be calculated from this matrix are stable stage distribution, reproductive value of each stage, and per-stage survivability. We also use the R package Rage (Jones et al., 2021) to calculate the age in each stage, life expectancy and longevity, the age and probability of reaching maturity, and generation time of this population. We then used the Rage package in R to analyze various life history traits of this matrix, the output of which is included in the supplementary material.

Finally, we calculate the minimum survivability increase necessary per stage to result in an increase of the overall population. We do 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 alter the survivability of *O. cyanea* by different rates from 0-10% survival increase of the species. 10% is the maximum survival increase used because increasing the overall survivability of matrix by more than 10% would result in some stages reaching a survivability of more than 1, implying that the stage would somehow be multiplying itself within a month timestep. We therefore limit survival increases to a maximum of 10% to stay within biologically meaningful parameters. Then, we simulate different closure scenarios for each survival increase by altering the length of annual closures by month using the final month of data collected by Raberinary & Benbow (2012) as the initial population vector, this is multiplied to higher powers of the original matrix during months that are 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.

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

4 RESULTS

The resulting eigenvalue of our matrix is 0.982, indicating a population decline of 1.8% per month with fishing pressure included (Figure 3). The stable stage distribution (Table 2) shows that 65% of the makeup of this population is immature individuals, while actively breeding individuals (fully mature) only make up less than 1% of the naturally occurring population. However, the reproductive output per stage (Table 2) shows that on average, an individual in this fully mature population is expected to have 41 times the number of offspring as those in stage 1. Larval survivability of 0.0001328 is calculated by dividing our estimated number of larvae surviving back to stage 1 (F_4) by 201,000 - the average estimated reproductive output of *O. cyanea* by (Guard, 2009). The life expectancy of this population is calculated by the Rage package to be 4.06 months with a standard deviation of 2.42 months. The calculated age of maturity is 6.82 months with probability of reaching maturation of 0.022. The longevity of this population (the amount of months for only 1% of the population to remain) is 12 months with a generation time of 7.38 months.

Changing the survivability of each stage (Figure 4) shows 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, requires a survivability increase of 25% in order to create a viable population.

Our analysis of different closure scenarios (Figure 5) indicates closures two months in length or shorter may be ineffective in ensuring a stable population, regardless of how much these closures decreased the death rate of the species. Further, as our baseline growth rate is 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 5) 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.

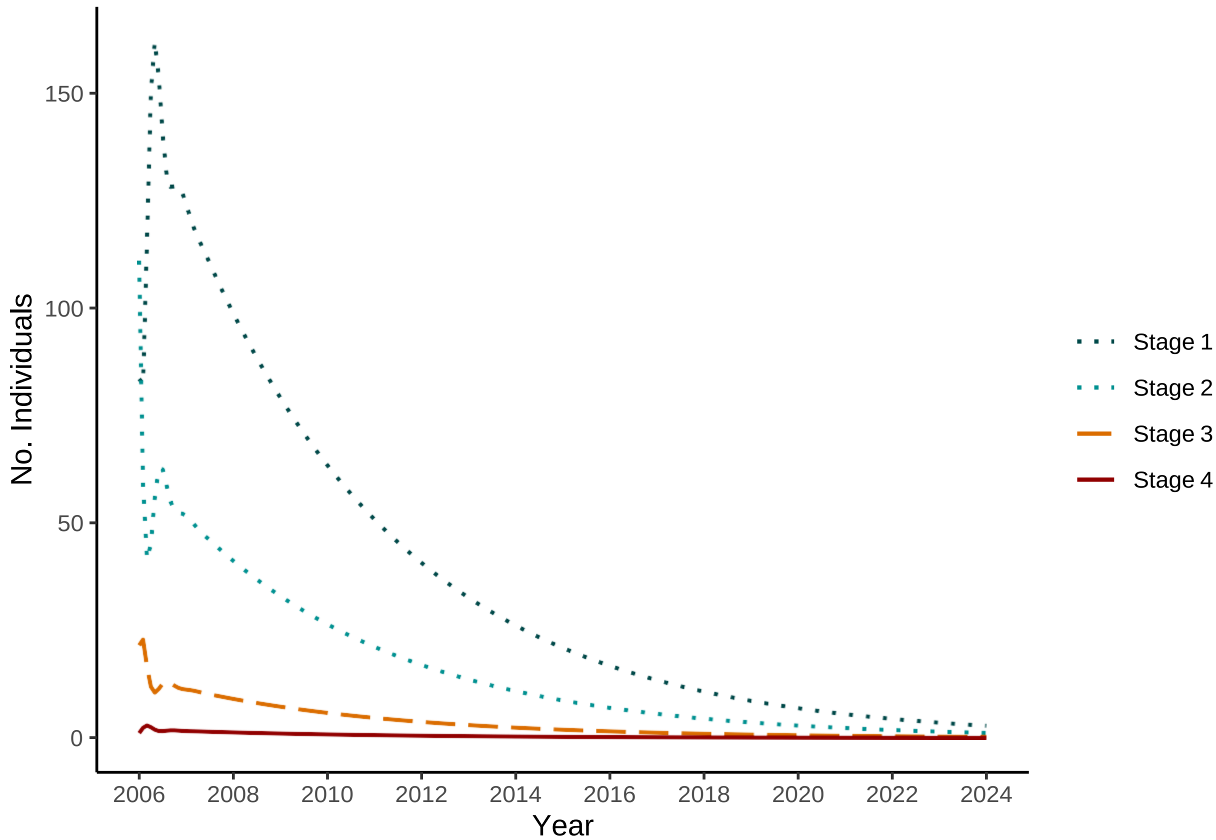


Figure 3: Projection of *O. cyanea* population based off of our calculated Lefkovitch matrix through the present. This does not reflect actual populations of blue octopus over time, but the predictions from our model given no action is taken to relieve fishing pressure.

5 DISCUSSION

Our calculated growth rate of -0.0184 and resulting population projection supports previous reports of overfishing at the time of data collection in 2006 (Humber et al., 2006; Benbow et al., 2014). With this negative growth rate, our models suggest that, without changes to management practices, the octopus population may have continued to decline. In addition, according to our model, any closure less than three months, without additional management actions, may not be effective in conserving blue octopus stocks. However, given data and model limitations, we do not have a measurement of uncertainty for the growth. Thus, caution should be taken when considering whether the octopus population was actually in decline or not in 2006. We describe this limitation more below. In general, declines in octopus populations presents an

Table 2: Stable stage distribution and reproductive value of each stage of this blue octopus population matrix given in Figure 2. 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 (P_i) and the proportion of individuals surviving and growing every month (G_i). 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 Eigenvector)	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

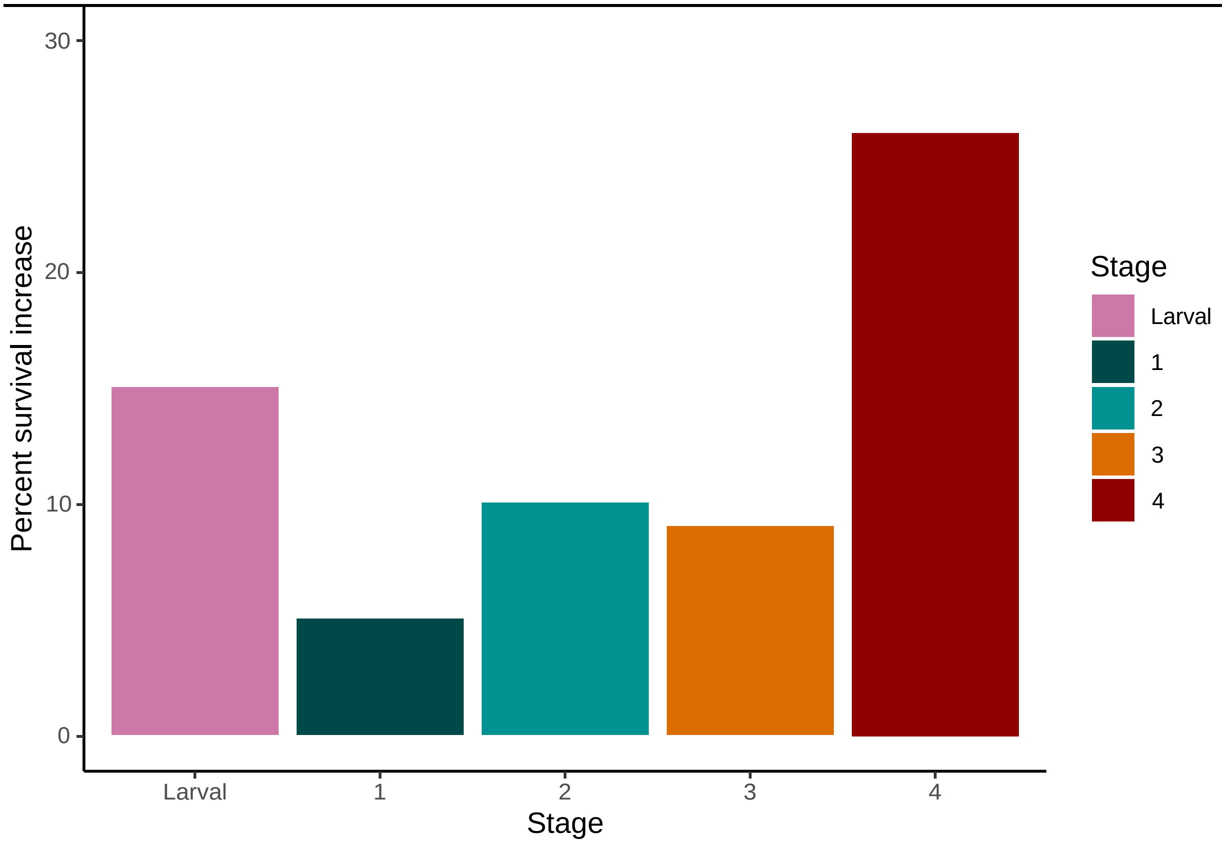


Figure 4: Minimum percent of per-stage survivability change needed to create population increase. Each stage was increased by higher percentages until the eigenvalue of the overall system became greater than zero.

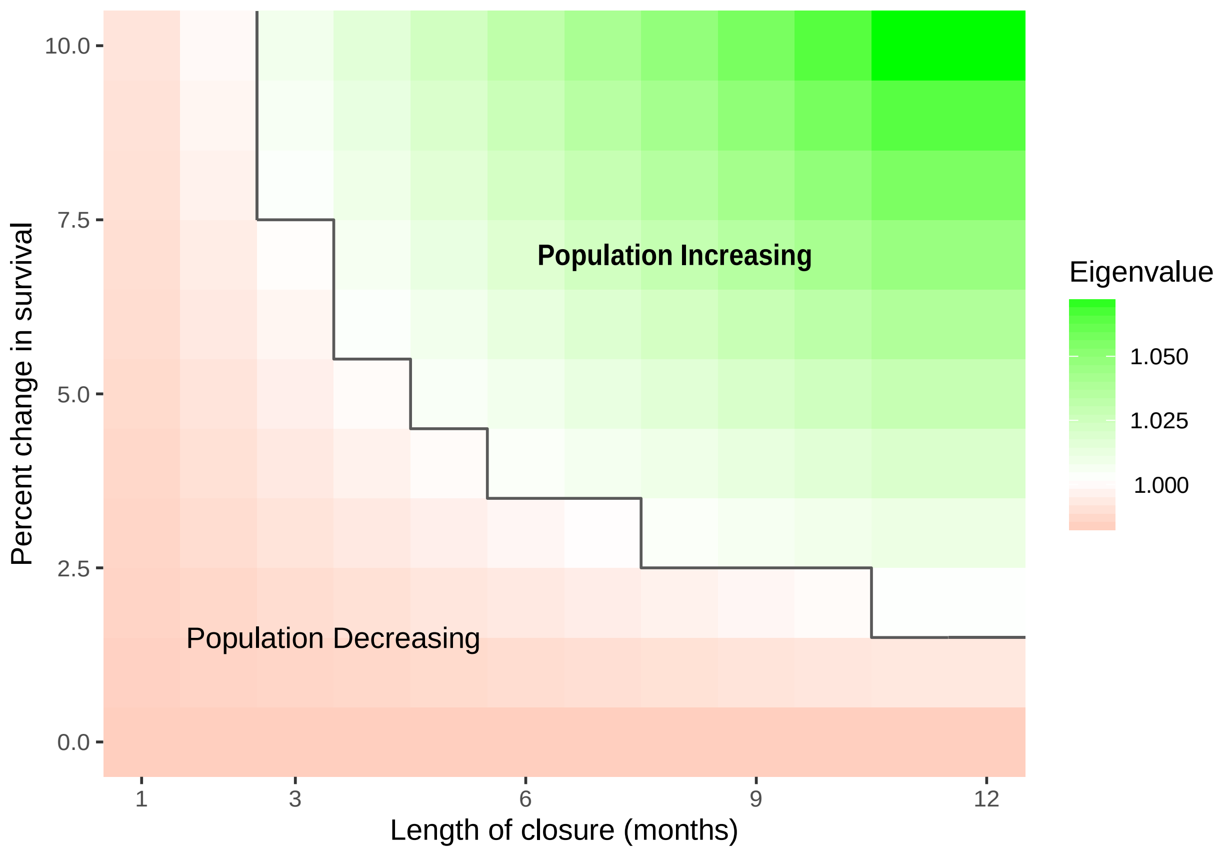


Figure 5: Analysis of different management scenarios. The black line separates the scenarios that succeed in sustaining the population from the scenarios that don't. Green and white squares indicate theoretically successful management scenarios where red refers to the strategies that will not result in overall population growth.

economic issue for individual fishers as their catch will become less lucrative. Octopus population recovery has been shown to result in economic gains from fishers in this community (Humber et al., 2006; Benbow et al., 2014; Oliver et al., 2015). Further, sale prices on opening day tend to increase as buyers are typically guaranteed larger catch (Oliver et al., 2015).

However, since the time of data collection, there have been a number of important changes to fisheries management in the region that explains the discrepancy between our model and robust octopus populations in many areas of Madagascar (Oliver et al., 2015; Roa-Ureta, 2022). For example, temporary closures in this fishery (Oliver et al., 2015) showed that extending the regional closure beyond the conventional six weeks increased octopus catch. Further, a 2-3 month closure was suggested for this area in 2011 in order to maximize catch-per unit effort (Benbow & Harris, 2011). Benbow et al. (2014) demonstrated that a 20-week closure had similar positive effects on octopus catch when compared to a seven month closure, yet resulted in less strain on fisheries management investment than the longer seven month closure. Individual villages also institute their own closures. These closures span 2-7 months and restrict fishing in ~20% of the fishery's spatial extent, so some fishing is still allowed to occur during this time. (Rocliffe & Harris, 2015, 2016; WWF, 2017). Therefore, the changes to survivability suggested by our analysis is in relation to their overall death rate not fishing rate, indicating a need for further research on the spatial structure of this population. Our analysis of different closure scenarios suggests a range of the simplest actions needed in order to ensure sustainability of this population, and show how the relationship between closure lengths and their effect on mortality rates can result in multiple different temporary closures that can successfully conserve a fishery. Thus, despite the simplicity of our model, our findings for possible closure lengths is very close to those currently practiced in Madagascar and elsewhere. As we describe later, more realistic extensions of this model can be built to guide specific management practices.

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

Our model provides other information about the life history of this population as well, beyond its overall growth rate. As each column in the matrix represents a proportion of individuals within a stage either growing or staying within a stage (with the exception of the F_4 parameter), it also shows a per-stage survivability estimate (Table 2) and stage duration (Table 1), life history parameters on which there has been no previous research. However, as the immature stage has a high survivability of 90.4% and a longer duration than the other stages of 2.7 months, this indicates that although the fishing method employed in this region does not distinguish by octopus size, fishers are not bringing this smaller catch to landing due to size limits preventing them from selling immature individuals (Humber et al., 2006). Therefore, this could challenge our assumption of the data being properly stratified by size. Further, as *O. Cyanea* have an approximately one to two month larval stage (Guard & Mgaya, 2003), the fecundity parameter does not indicate the overall reproductive output of mature individuals, but the number of hatched offspring that will survive its larval stage and back the immature stage. This gives an estimation for larval survivability as female octopus have a fecundity ranging between 27,000 and 375,000 eggs (Guard, 2009), our model indicates that only an average of 26.7 individuals will survive back into immaturity, which indicates a survivability of 0.0001328. There is no other larval survivability estimation that currently exists for this species, which would be a useful further study as this could indicate a recruitment rate for this population. Further, an average lifespan of 4.06 months and an age of maturation of 6.82 months indicates that most individuals die before reaching maturation. The overall natural mortality rate of this population has been estimated to range from 0.0127 per week (0.0552 per month) to 0.0498 per week (0.2164 per month) (Roa-Ureta, 2022). However, this was not included in our model of fishery closures as the local closures do not cover the full spatial extent of the fishery, have variable spatial extents, and some fishing continues during this time, meaning some fishing mortality exists during closures (Oliver et al., 2015). Instead, we compared closures to their overall effect on the *O. cyanea* mortality rate.

The mechanistic methods used in this study allowed us to gain a baseline understanding of the growth rate and mortality of this population despite the limited data used to parameterize the model. Limitations of this study include the data collection process as this model is only parameterized using one year of data. Although this is not enough data to conduct a full stock assessment, this speaks to the utility of mechanistic modeling, where we are able to estimate population patterns and other life history traits despite this lack of data. A future study that repeats this method of data collection could rerun this same model with the updated data, and make further conclusions about the status of this fishery today. Even though data collections occurred daily within a two-hour window, catch was not standardized by effort and therefore there could be catch fluctuations between months that are not captured in the data. Further, 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. Another shortcoming of this study is that the only available stage data for this species and region was collected in 2006, and the community of southwest Madagascar has implemented several strategies since that time to improve the sustainability of their fish stocks in the region (Humber et al., 2006; Raberinary & Benbow, 2012). Due to the time of data collection, this study does not reflect the current status of *Octopus cyanea*, nor should the findings of this study be implemented in current management decisions. Instead, this study outlines what biological parameters can be estimated from limited data using mechanistic modeling and show how temporary closures are not only an effective method of conservation, but also provide communities with options for effective management and these should be selected based off of the needs of stakeholders. As the community of southwest Madagascar has been involved in deciding when closures should occur and their lengths, this study serves to show the various options available (Benbow & Harris, 2011).

We made a number of simplifying assumptions in our models of the biology of the study species. For example, our models assume that all individuals within a stage are subject to the same growth and mortality rates. As this study uses data collected from a large geographic range (Raberinary & Benbow, 2012), different individuals nesting in different regions may be subject to different selective pressures. Studies on the spatial variability of this population could better inform both our model and the greater understanding of how fishing mortality of this population compares to its natural mortality. Further, this population of blue octopus has been shown to exhibit spatial variability depending on their life stage. Younger individuals tend to live in the shallow inner zone of the reef and larger individuals, who are more able to withstand stronger currents, move to deeper waters for more suitable habitats for nesting (Raberinary, 2007). Our management scenario analysis also assumes that each lifestage would be affected equally by a closure, which could be challenged by the previous result that fishers are not bringing smaller catch to landing due to the size limits. Parameters were not extracted from a distribution curve, so adding this to future research could further help explain the uncertainty in octopus dynamics and better model the high variability in populations. Despite these limitations, the data provided is the best data available for fitting a Lefkovitch matrix to this species. Future extensions of this work could include applying this method to a data rich fishery, wherethe conclusions of the model can be compared to empirical data. Further, valuable future research could explore the dynamics of both sexes in the population (Gerber & White, 2014) as male octopus have different growth rates and spatial dynamics (Heukelem, 1976). A better understanding of the seasonal breeding dynamics of this population of blue octopus could also give better insight into the health of this fishery (White &

Hastings, 2020). Cephalopod juveniles (a key life stage in understanding future population dynamics) often have two seasonal peaks per year, indicating biannual spawning periods (Humber et al., 2006; Katsanevakis & Verriopoulos, 2006). This is related to seasonal fluctuations in temperature, as cephalopod growth is related to environmental temperature (Domain et al., 2000). However, this relationship is subject to a lot of variation (Heukelem, 1976; Herwig et al., 2012). Further, as Madagascar is a tropical climate, this trend may be different in our region of study, as suggested by Raberinary & Benbow (2012), where all life stages of O. cyanea were observed year round, suggesting continuous breeding. A better understanding the seasonality of this population could further inform when closures should take place.

6 CONCLUSIONS

With a short generation time, cephalopod species respond more quickly to new management strategies. A more contemporary study on the status of the octopus fishery of southwest Madagascar will paint a more complete picture of how this population is faring under the current fishing pressure. As a population with highly variable population dynamics, continuous monitoring of landings, fishing effort, and where catch is found is extremely valuable in understanding the status of *Octopus cyanea* in Madagascar. Similar data has been collected by Blue Ventures on this fishery since 2015 and shows there has been an improvement to this fishery since 2006 due to local efforts, including temporary closures. Further, this collection effort does not include maturity data which would improve the analysis of this study through incorporation of multiple years of catch data (Roa-Ureta, 2022). Finally, as the people of southwestern Madagascar are actively taking steps to conserve the health of their fisheries, we hope that studies such as these can serve to facilitate the understanding of what options are available when choosing how and when to impose fishing restrictions. We also hope that future work can build on our models to be more realistic for this system and produce specific management guidance.

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Data Availability - All supplemental material and code for this project are available at https://github.com/swulfing/OCyanea. All data used to parameterize this model was collected in Raberinary & Benbow (2012)

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University of New Hampshire

College of Life Sciences and Agriculture
Department of Biological Sciences
Rudman and Spaulding Halls 46 College Road
Durham, NH 03824-2617 USA

28-August-2023

Dear Editorial Board,

Please below our CRediT author statement for the manuscript: "**Using mechanistic models to assess temporary closure strategies for small scale fisheries**", by Sophie Wulfing, Ahilya Sudarshan Kadba, Merrill Baker-Médard, and Easton R. White.

Author Contributions:
Sophie Wulfing: Conceptualization, Methodology, Software, Formal Analysis, Writing – Review & Editing
Ahilya Sudarshan Kadba: Data Curation, Writing – Original Draft, Writing – Review & Editing
Mez Baker-Médard: Validation, Writing – Original Draft, Writing – Review & Editing, Funding acquisition, Supervision, Project administration
Easton R. White: Methodology, Validation, Writing – Original Draft, Writing – Review & Editing, Funding acquisition, Supervision, Project administration

Sincerely,

Sophie Wulfing
Masters Student
Department of Biological Sciences
University of New Hampshire

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: