

## After 15 years, no evidence for trophic cascades in marine protected areas

Katrina D. Malakhoff and Robert J. Miller

### Article citation details

*Proc. R. Soc. B* **288**: 20203061.  
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### Review timeline

Original submission: 3 July 2020  
1st revised submission: 8 December 2020  
2nd revised submission: 21 January 2021  
Final acceptance: 22 January 2021

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

## Review History

### RSPB-2020-1601.R0 (Original submission)

#### Review form: Reviewer 1

##### Recommendation

Major revision is needed (please make suggestions in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Excellent

**General interest: Is the paper of sufficient general interest?**

Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**

Excellent

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

### **Comments to the Author**

#### GENERAL COMMENT

This is a paper of general interest that may provoke substantial and much needed discussion. The key point is that indirect effects due to marine reserves do occur in some cases, many of which attract study, but they are not ubiquitous. The importance of documenting direct effects is just as important as documenting indirect effects, but the lack of finding the latter has had major problems for representing marine systems, policy-making and supporting legislation. Each of these 3 points has led to a crisis in marine science, coastal management and public perception of marine reserves in several countries.

This kind of paper has long been needed to fill a critical gap in the literature and start the discussion on just how general trophic cascades are. The data presented are compelling and the evidence for the statements are well supported. This is a strength of the paper - and something that is needed for what is key issue facing the perception of marine ecosystems. That is, trophic cascades are strong and ubiquitous in marine systems, particularly kelp forests.

Because the dogma is sufficiently strong, it is likely that reviewers will struggle with the non-effects. These kinds of reviewers might claim weakness in experimental design, power of statistical analysis and scale of observations. None of these issues apply here, which underpins the value of this study.

#### SPECIFIC COMMENTS

If this paper is to be a landmark paper, it the major themes could be considered from a broader perspective. Currently, the Discussion is strongly tied to locality and species of interest. There does appear to be scope to recognise broader points. For example;

1. The interaction strength is insufficiently strong between each trophic level. The reasons for this a diverse and it is not possible to list them all in this paper. The reader might want to know that this breadth exists.
2. What other kelp-urchin of kelp regions of the world have been characterised as being non-tropically structured systems? There is good literature on this issue. These papers are missing, yet they support key evidence on which the scholarship of this paper is based. Citing those regions would provide this paper with some authority. Parochialism can create a negative impression for reviewers, but this is not an issue on which this paper should be rejected. It can be addressed with the application of scholarship.
3. It is quite clear that the direct effect of protecting fished species in marine reserves over

indirect effects that are often predicted but seldom clearly documented. This has held back policy development in marine reserves internationally and has even resulted in their abolishment by way of rezoning to allow for fishing. Part of the difficulty has been the failure for these kinds of papers to be published.

## Review form: Reviewer 2

### Recommendation

Reject - article is scientifically unsound

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Good

**General interest: Is the paper of sufficient general interest?**

Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**

Marginal

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

Yes

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

Yes

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

Yes

### Comments to the Author

I've now read the paper by Malakhoff and Miller where the study whether the abundance of two sea urchin respond to increased predation by a protected species before and after the establishment of marine reserves. Their results suggest that marine reserves don't have the intended consequences, and actually lead to increases in the intermediate predators. While interesting, issues exist that would need to be addressed. Below I suggest ways in which these could be overcome.

## MAJOR:

1) The introduction does not clearly convey what in this study makes it particularly novel, compared to other existing studies on this same topic and this same study site (E.g. Selden et al 2017, Proc B). The study even states other studies did not consider the two urchin species separately as a selling point. We can discuss whether that in and of itself is a good enough selling point, but it is also not accurate given that Selden's study does consider both species separately and simultaneously.

2) Also, in light of Selden's results showing how sheaphead predation differs among both species of urchins due to size refugia, thus leading to an increase in red urchin populations, it is unclear what exactly the contribution of this paper is. The result "We find that biomass of the fished red urchin has responded positively to reserve protection, while purple urchins have not responded to reserves." is in direct support of Selden's observations that sheaphead have not gotten large enough to effectively consume them, although predation rates are indeed larger outside inside the reserves than outside, suggesting trophic cascades are a matter of time. To be clear, I don't contest the results of this study, I contest the motivations, which come across as if this paper had been the only one to ever look at this problem in this specific way. It would have been much more interesting and informative to draw from what we already know from previous studies (e.g., Selden et al), and use that information to come up with testable hypotheses: e.g., trophic cascades are not \*yet\* expected, given observed predation rates. Which is not to say they won't even happen! And it could set the stage for a "30 years" later paper by the same authors.

3) Time series can't be analyzed as was done, as time series are, by definition, temporally autocorrelated. This autocorrelation needs to be accounted for using ARMA GLMMs (see this site for resources in how to\_ <https://petolau.github.io/Analyzing-double-seasonal-time-series-with-GAM-in-R/>)

It does not mean the results are invalidated, but the authors do not currently provide the correct analyses, so it is impossible to know whether results would or would not hold once analyses are correctly done. The use of ANCOVA would be ok in this case, but the existence of clearly nonlinear patterns suggest ARMA GAMMS to be better suited.

4) Many of the analyses provided (e.g in fig 2) show blatant violations of model assumptions (e.g., fitted linear models through clearly non linear data). It's not clear why this was done since the hypotheses were tested using GAMs.

5) Model statistics (beyond p-values) need to be reported in the results (e.g., effect sizes, estimates, standard errors, degrees of freedom, goodness of fit, etc)- Including model selection.

6) I think the authors make too much of a straw-man of the trophic cascade hypothesis, as given what we currently know about the system (Selden et al) and existing theory (Jiao et al), it is somewhat clear that a trophic cascade was not the baseline expectation for this system. Also, it isn't clear to me that a temporal lag has been successfully disproven by the current data, and if it was I apologize I have missed it, but it does emphasize that more handholding may be needed.

## MINOR:

## INTRODUCTION

L-3 The first sentence of the paper is a bit too colloquial. Consider rephrasing along the following lines: "Fishing often leads to fewer, smaller fish".

L-19-20: Please cite the very extensive literature on the topic by John Bruno and colleagues that show how marine reserves does not aid in coral recovery.

L-25-35: Work by Jing Jiao and colleagues (Jiao et al 2016 *Ecosphere*) show under which conditions trophic cascades are not expected within marine reserves and should be considered not only as relevant literature but as possible hypotheses and expectations for this study.

L-36-38: Colloquial and uninformative. Also, how will an ecologist create a species? Please rephrase along the following lines: "To tease apart the effects of direct vs indirect effects while controlling for species identity and the specifics of predator-prey interactions, considering species of similar ecology and morphology under identical environmental conditions is important. A natural experiment exists in the .... of southern California that mimics those ideal conditions".

L-53: The Selden et al study that you cite here considers the body size of both species separately, correct? Also, why is that important? what does your paper that others have failed to do?

L-54-56: Breaks with the flow of the introduction, consider explaining in your methods under study system instead. You can pose questions and explain what will be done without talking about the Channel Islands at this point.

#### METHODS:

L-285: Please cite the R team when stating R was used. Correct citation can be found on the R forge website.

L-290: The linear mixed model to test what? Please explain what is being tested, then present how you do so.

L-303: just state effect sizes-

#### RESULTS:

FIGURES: the order of the figures don't match appearance in the text. Figure 3 is called before Figure 2 for no apparent reason.

#### DISCUSSION:

L-191:192. Colloquial. Just state your interpretation. A question isn't needed here and is much better suited for an introduction.

## Decision letter (RSPB-2020-1601.R0)

15-Sep-2020

Dear Ms Malakhoff:

I am writing to inform you that your manuscript RSPB-2020-1601 entitled "After 15 years, no evidence for trophic cascades in marine protected areas" has, in its current form, been rejected for publication in *Proceedings B*.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

- 1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
- 2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
- 3) Line numbers in your main document.
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Sincerely,  
Dr Daniel Costa  
mailto:proceedingsb@royalsociety.org

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)  
GENERAL COMMENT

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Referee: 2

Comments to the Author(s)

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#### METHODS:

L-285: Please cite the R team when stating R was used. Correct citation can be found on the R forge website.

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RESULTS:

FIGURES: the order of the figures don't match appearance in the text. Figure 3 is called before Figure 2 for no apparent reason.

DISCUSSION:

L-191:192. Colloquial. Just state your interpretation. A question isn't needed here and is much better suited for an introduction.

## Author's Response to Decision Letter for (RSPB-2020-1601.R0)

See Appendix A.

## RSPB-2020-3061.R0

### Review form: Reviewer 1

#### **Recommendation**

Accept as is

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Excellent

**General interest: Is the paper of sufficient general interest?**

Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**

Excellent

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

**Comments to the Author**

The authors have done a good job with the revisions. The credibility and authority of the manuscript is sufficiently robust to achieve the kind of discussion needed in this discipline.

## Review form: Reviewer 3

**Recommendation**

Accept as is

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Excellent

**General interest: Is the paper of sufficient general interest?**

Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**

Excellent

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

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**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

**Comments to the Author**

I am in complete agreement with Referee 1: this is an excellent paper that rigorously examines indirect effects of a reserve system using multiple reserve vs. non-reserve sites and including

comparisons pre- and post-reserve establishment. It shows the great value of having replicates, and scientifically challenges prior evidence for indirect effects of lobsters and the sheephead wrasse, evidence based largely on the proliferation of the top down paradigm, unreplicated field studies, and speculation from laboratory predation studies. Referee 1 made suggestions for revision and these are well handled in the revised ms.

Referee 2 did not seem to appreciate problems with prior studies that purported to show indirect effects, and quibbled with the statistical analyses. Again and in my opinion, these criticisms were well handled in the revised ms.

This paper should add much needed scientific rigor to important policy decisions concerning the efficacy of marine reserves in kelp systems.

## Decision letter (RSPB-2020-3061.R0)

15-Jan-2021

Dear Ms Malakhoff

I am pleased to inform you that your manuscript RSPB-2020-3061 entitled "After 15 years, no evidence for trophic cascades in marine protected areas" has been accepted for publication in Proceedings B.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into <https://mc.manuscriptcentral.com/prsb> and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Before uploading your revised files please make sure that you have:

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- 2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

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4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation

It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository (<https://royalsociety.org/journals/authors/author-guidelines/#data>).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:

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- Phylogenetic data: TreeBASE accession number S9123
- Final DNA sequence assembly uploaded as online supplemental material
- Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311

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If you wish to submit your data to Dryad (<http://datadryad.org/>) and have not already done so you can submit your data via this link

[http://datadryad.org/submit?journalID=RSPB&manu=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document not available)) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see <https://royalsociety.org/journals/ethics-policies/data-sharing-mining/> for more details.

6) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit <https://royalsociety.org/journals/authors/author-guidelines/>.

Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,

Dr Daniel Costa

<mailto:proceedingsb@royalsociety.org>

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).

The authors have done a good job with the revisions. The credibility and authority of the manuscript is sufficiently robust to achieve the kind of discussion needed in this discipline.

Referee: 3

Comments to the Author(s).

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## Decision letter (RSPB-2020-3061.R1)

22-Jan-2021

Dear Ms Malakhoff

I am pleased to inform you that your manuscript entitled "After 15 years, no evidence for trophic cascades in marine protected areas" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,  
Proceedings B  
<mailto:proceedingsb@royalsociety.org>

## Appendix A

RSPB-2020-1601, Malakhoff and Miller, "After 15 years, no evidence for trophic cascades in marine protected areas"

### Response to reviews

Below we copy the reviewer comments in italics with our responses following in plain text.

#### Referee: 1

*Comments to the Author(s)*

##### GENERAL COMMENT

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*This kind of paper has long been needed to fill a critical gap in the literature and start the discussion on just how general trophic cascades are. The data presented are compelling and the evidence for the statements are well supported. This is a strength of the paper – and something that is needed for what is key issue facing the perception of marine ecosystems. That is, trophic cascades are strong and ubiquitous in marine systems, particularly kelp forests.*

We sincerely thank the reviewer for these comments, which we strongly agree with. If our paper is published in Proc B, we would love it if you wrote a commentary to this effect!

*Because the dogma is sufficiently strong, it is likely that reviewers will struggle with the non-effects. These kinds of reviewers might claim weakness in experimental design, power of statistical analysis and scale of observations. None of these issues apply here, which underpins the value of this study.*

Thank you – we have gotten comments even from colleagues here at UCSB that are knee-jerk reactions to the lack of trophic cascade effects, and searching for reasons why. The patterns in the data, however, are sufficiently strong to overcome these reactions, we think.

##### SPECIFIC COMMENTS

*If this paper is to be a landmark paper, it the major themes could be considered from a broader perspective. Currently, the Discussion is strongly tied to locality and species of interest. There does appear to be scope to recognise broader points. For example;*

*1. The interaction strength is insufficiently strong between each trophic level. The reasons for this are diverse and it is not possible to list them all in this paper. The reader might want to know that this breadth exists.*

This is a good point. We have now briefly introduced this idea in the Introduction (Line 30) and pointed this out in a new paragraph in the Discussion, in which we briefly describe the complexity of the kelp forest food web and the ways that could act to dampen the strength of top-down control (Lines 238-248).

*2. What other kelp-urchin or kelp regions of the world have been characterised as being non-tropically structured systems? There is good literature on this issue. These papers are missing, yet they support key evidence on which the scholarship of this paper is based. Citing those regions would provide this paper with some authority. Parochialism can create a negative impression for reviewers, but this is not an issue on which this paper should be rejected. It can be addressed with the application of scholarship.*

We appreciate this input, and have added context from other regions to a new paragraph in the Discussion (Lines 249-268). If we have missed anything critical, we'd be happy to add it.

*3. It is quite clear that the direct effect of protecting fished species in marine reserves over indirect effects that are often predicted but seldom clearly documented. This has held back policy development in marine reserves internationally and has even resulted in their abolishment by way of rezoning to allow for fishing. Part of the difficulty has been the failure for these kinds of papers to be published.*

We agree!

Referee: 2

*Comments to the Author(s)*

*I've now read the paper by Malakhoff and Miller where the study whether the abundance of two sea urchin respond to increased predation by a protected species before and after the establishment of marine reserves. Their results suggest that marine reserves don't have the intended consequences, and actually lead to increases in the intermediate predators. While interesting, issues exist that would need to be addressed. Below I suggest ways in which these could be overcome.*

**MAJOR:**

*1) The introduction does not clearly convey what in this study makes it particularly novel, compared to other existing studies on this same topic and this same study site (E.g. Selden et al 2017, Proc B). The study even states other studies did not consider*



*the two urchin species separately as a selling point. We can discuss whether that in and of itself is a good enough selling point, but it is also not accurate given that Selden's study does consider both species separately and simultaneously.*

The Selden et al. (2017) study was conducted over a period of two Augusts inside and outside a single marine reserve at Catalina Island, in the southern Channel Islands, which is ~150 km south of our study area, the northern Channel Islands. Selden did predation trials with urchins in the field to examine patterns of sheephead predation on them. She showed that larger sheephead tend to eat urchins more often than smaller individuals, and that sheephead preferentially eat smaller urchins of both species. Selden et al. also did do surveys inside and outside the single reserve, which showed that purple urchin numbers were lower inside the reserve, while red urchins were no different inside and outside. Selden et al attributed this difference in purple urchins to higher predation inside the reserve.

The reviewer is correct, therefore, that Selden et al. do consider both species, but we do not consider that study as a good evaluation of the effect of reserve protection on the populations of urchins and on their effect on kelp. Like many other reserve studies, it has an n of one and is short term. We do, however, consider this study valuable information on the size dependence of sheephead predation on urchins, and it was one of the motivations for our separate analyses of small urchins that might be more sensitive to predation. We cite it in the Discussion in this regard (Lines 203-206).

The strength of our study, we think, is in its examination of both urchin species as a species pair, one fished and one not, but otherwise ecologically comparable and, most importantly, sharing predators. Another significant strength is in its use of the amazing long-term dataset collected by the National Park Service. We have now tried to emphasize these points better in the introduction (Lines 15-18, 52). We also think that it is the first robust analysis of trophic cascades due to reserves in California across this length of time. However, there are studies that have used more limited data to look at this question in the region. We don't think this will significantly dilute the manuscript's impact, especially considering that the message goes so against the grain of the current literature.

*2) Also, in light of Selden's results showing how sheaphead predation differs among both species of urchins due to size refugia, thus leading to an increase in red urchin populations, it is unclear what exactly the contribution of this paper is. The result "We find that biomass of the fished red urchin has responded positively to reserve protection, while purple urchins have not responded to reserves." is in direct support of Selden's observations that sheaphead have not gotten large enough to effectively consume them, although predation rates are indeed larger outside inside the reserves than outside, suggesting trophic cascades are a matter of time. To be clear, I don't contest the results of this study, I contest the motivations, which come across as if this paper had been the only one to ever look at this problem in this specific way. It would have been much more interesting and informative to draw from what we already know form previous studies (e.g., Selden et al), and use that information to come up with testable*

*hypotheses: e.g., trophic cascades are not \*yet\* expected, given observed predation rates. Which is not to say they won't even happen! And it could set the stage for a "30 years" later paper by the same authors.*

Seldon et al. examined sheephead predation rates on urchins inside and outside one reserve outside our study region in August 2010. She did find that larger red urchins were slightly less vulnerable to sheephead predation than larger purple urchins, although the magnitude of this difference was small. Importantly, however, there was no difference between the two species in predation rate of small individuals, which was much higher than predation on larger individuals in both species. Many studies have suggested that urchins attain a size refuge from predation, and we did use this idea to motivate the hypothesis that densities of small urchins, regardless of species, would be lower inside reserves (Lines 91-104, 153-165). We used the same size threshold that Seldon et al. used, 35 mm, to define small urchins (Lines 348-349). Our results, which show that reserve protection did not affect juvenile purple urchin densities, but increased densities of red urchins, do not support Seldon et al.'s conclusions, which clearly predict that small urchins of both species would be reduced in reserves.

We cited results from the literature showing that sheephead in the reserves are in fact abundant and large enough to eat urchins (Lines 201-210). We have now added to this to more explicitly point out the size issue and the fact that average size of sheephead in all the reserves we analyzed was larger than 25 cm, the size at which Seldon et al. observed sheephead to be effective predators on small urchins, and in some reserves was much larger. Moreover, we show, based on previous studies, that numbers and sizes of urchin predators overall, both sheephead and lobster, were higher in the reserves, particularly lobster (Lines 214-218).

Therefore, although Seldon et al.'s results are partially consistent with the difference we saw in larger urchins, the lack of response of purple urchins of any size, and the positive response of small red urchins, to reserve protection, is the opposite of what is predicted by Seldon et al.'s study, strongly suggesting that the mechanism producing more red urchins inside reserves is protection from fishing.

Although we make a case for why we think that trophic cascades should be evident by now if they are ever going to happen in the Channel Islands reserve network (Lines 222-226), we do agree with the reviewer that it's possible they will develop at some point in the future. We have now explicitly acknowledged this (Lines 226-228).

*3) Time series can't be analyzed as was done, as time series are, by definition, temporally autocorrelated. This autocorrelation needs to be accounted for using ARMA GLMMs (see this site for resources in how to\_ <https://petolau.github.io/Analyzing-double-seasonal-time-series-with-GAM-in-R/>) It does not mean the results are invalidated, but the authors do not currently provide the correct analyses, so it is impossible to know whether results would or would not hold once analyses are correctly done. The use of ANCOVA would be ok in this case, but the existence of clearly nonlinear patterns suggest ARMA GAMMS to be better suited.*

BACI analysis using repeated measures as performed here can be done on time series data; in fact having multiple before and after time points is considered an advantage in the analysis (Underwood 1993). The issue of temporal autocorrelation in BACI has been analyzed and discussed extensively by Stewart-Oaten and others (e.g. Stewart-Oaten 1986). Because the measurements of mobile organisms we are studying are annual, they are highly likely to be independent (Underwood 1993), but we have nevertheless taken into account temporal autocorrelation using an AR(1) term in our models after consulting ACF (autocorrelation function) and pACF (partial autocorrelation function) plots to check for lags. Biomass values were log-transformed to account for the right-skewed (non-normal) distribution of values and heteroscedasticity. Standard model-checking procedures were followed and qq-plots and residuals plots do not show a violation of the homogeneity of variance assumption. We have now clarified the fact that these steps were taken in the Methods (Lines 336-342).

We assume the reviewer is suggesting ARMA GLMMs in their final point, not GAMMs. Model assumptions for an ARMA LMM with log transformation of the response variable were met. A similar (although not equivalent) approach would be to use a gaussian ARMA GLMM with a log-link, but this would not affect the variance of the residuals and therefore we would still have an issue of heterogeneous variances.

Stewart-Oaten, A., Murdoch, W.W. and Parker, K.R., 1986. Environmental impact assessment: "Pseudoreplication" in time?. *Ecology*, 67(4), pp.929-940.

*4) Many of the analyses provided (e.g in fig 2) show blatant violations of model assumptions (e.g., fitted linear models through clearly non linear data). It's not clear why this was done since the hypotheses were tested using GAMs.*

We used generalized linear mixed effects models (GLMMs) and linear mixed effects models (LMMs), not GAMs. We can understand why the reviewer may think that these data violate the assumptions of GLMM, but inspection of model diagnostics (residuals plots and QQ plots) did not suggest violation of assumptions of distribution/homoscedasticity. Moreover, Schielzeth et al. (2020) evaluated the consequences of violating such assumptions in GLMM and found that the models were highly robust to violations. In fact, they found that "results show remarkable robustness of mixed-effects models that should allow researchers to use mixed-effects models even if the distributional assumptions are objectively violated." Our data do not objectively violate assumptions, fortunately. Figure 3 is displayed with fitted lines using a linear smoother on untransformed data. The purpose of this figure is to demonstrate the BACI process of comparing slopes before and after an event (the establishment of marine reserves) at control and impact sites - the linear smoothers fit to this figure do not represent the actual model terms. This may give the impression of assumption violations, but we prefer to show the raw data rather than the transformed data for the sake of interpretability.

Schielzeth, H., Dingemanse, N.J., Nakagawa, S., Westneat, D.F., Alaguela, H., Teplitsky, C., Réale, D., Dochtermann, N.A., Garamszegi, L.Z. and Araya-Ajoy, Y.G., 2020. Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods in Ecology and Evolution*, 11(9), pp.1141-1152.

5) *Model statistics (beyond p-values) need to be reported in the results (e.g., effect sizes, estimates, standard errors, degrees of freedom, goodness of fit, etc)- Including model selection.*

We have now added a new table to the Supplementary material with this information to avoid bogging down the text (Table ST2).

6) *I think the authors make too much of a straw-man of the trophic cascade hypothesis, as given what we currently know about the system (Selden et al) and existing theory (Jiao et al), it is somewhat clear that a trophic cascade was not the baseline expectation for this system. Also, it isn't clear to me that a temporal lag has been successfully disproven by the current data, and if it was I apologize I have missed it, but it does emphasize that more handholding may be needed.*

We disagree that this is a straw man argument. First, more generally, the sea otter-sea urchin-kelp trophic cascade paradigm has been the dominant depiction of kelp forest ecology in textbooks for decades. For example, in Ch. 15 of the best-selling Ecology text in America, Elements of Ecology (9<sup>th</sup> ed):

“Predators often function as keystone species within communities.... For example, sea otters (*Enhydra lutris*) are a keystone predator in the kelp bed communities found in the coastal waters of the Pacific Northwest. Sea otters eat urchins, which feed on kelp. The kelp beds provide habitat to a wide diversity of other species. ... With the decline of sea otters, the sea urchin population has increased dramatically (Figure 16.6). The result is overgrazing of the kelp beds and a loss of habitat for the many species inhabiting these communities.”

Although the sea otter situation in the Aleutian islands is the most generally publicized example of a kelp forest trophic cascade, marine ecologists actually recognized the possibility earlier, when North and Pearse (1970) hypothesized that extirpation of sea otters was a potential cause of sea urchin population irruptions in southern California. Tegner (1980) first suggested that sheephead wrasse and spiny lobster were regulating urchin populations, and indirectly kelp, in southern California, playing the same role as otters. Jackson et al (2001) suggested that southern California kelp forests “collapsed” in the 1950s to 1970s due to sea urchin grazing, consequent to overfishing of lobsters, sheephead and abalone. In the Channel Islands, Lafferty (2004) and Lafferty and Behrens (2004) posited that lobster were the key predator regulating urchins, and indirectly kelp. At that time there was only one established marine reserve to work with, at Anacapa Island. In 2006, in a study published in *Science* based on an analysis of satellite-derived chlorophyll as a measure of “bottom-up” factors and the same NPS

kelp forest dataset we used, Halpern et al. concluded that Channel Islands kelp forests had strong top-down control via trophic cascades, and that the strength of cascades would increase in marine reserves over time.

This body of scientific work, moreover, is also reflected in management/policy statements and in popular communication about marine reserves in our region. For example, a report commissioned by the CA Ocean Protection Council and Dept of Fish and Wildlife to provide guidance on issuing scientific research permits inside MPAs identified 10 “strongly interacting” species to focus on when valuating possible impacts of research projects. At the top of the list with the highest “interaction scores” were giant kelp, both species of sea urchin studied here, and sheephead and lobster that prey on them. The report stated:

“Few studies have quantified the strength of interactions among species, especially those interactions that extend through a community (e.g. trophic cascades). Yet, because of the strong roles played by these species in organizing and structuring communities [75], understanding the impacts of research activities on foundation species (*sensu* [33]) is particularly important as reflected in our sensitivity analyses. As more knowledge is accrued, the ability to quantify species interactions will improve and the values needed to populate our model will become more refined. This reinforces the importance of conducting studies in protected ecosystems where natural species interactions can more readily be quantified.”

We think that the results of our study contribute directly to informing on strong interactions, or in this case the lack thereof, per this guidance.

The California Marine Sanctuary Foundation is one of several NGOs that advocate for MPA expansion in California. At the top of their infographic on the benefits of MPAs, under the heading “Ecosystem maintenance and restoration”, juxtaposed photos of an urchin barren and kelp forest are shown, with the explanation: “The top image shows an urchin barren. With the loss of apex predators, like the spiny lobster or southern sea otter, urchin populations take over and consume most of the kelp within an ecosystem. After years of protection (see bottom image) lobster populations are able to rebound and keep urchin populations at bay, allowing kelp forests to thrive- the result of an MPA!”

<https://californiampas.org/wp-content/uploads/2016/08/MPA-Benefits-Infographic.pdf>

These are a couple of examples; there are many more. We realize that oversimplification of ecological relationships is common in the public sphere. However, in this case, the idea of pervasive trophic cascades in kelp forests of California and elsewhere has arisen from the scientific literature.

We didn’t disprove a temporal lag in the paper – that can never be conclusively done. However, we do present evidence that populations of lobster and sheephead, the main urchin predators, have rebounded in the reserves to an extent that they should be impacting urchin populations if they ever will (Lines 207-228). We also summarize

literature results suggesting that indirect effects of reserves should take ~13 years on average to be seen (lines 222-224). We have now more clearly acknowledged, however, that more time could still conceivably result in trophic cascades (Lines 226-228).

Saarman, E.T., Owens, B., Murray, S.N., Weisberg, S.B., Ambrose, R.F., Field, J.C., Nielsen, K.J. and Carr, M.H., 2018. An ecological framework for informing permitting decisions on scientific activities in protected areas. *PloS one*, 13(6), p.e0199126.

Halpern, B.S., Cottenie, K. and Broitman, B.R., 2006. Strong top-down control in southern California kelp forest ecosystems. *Science*, 312(5777), pp.1230-1232.

North WJ, Pearse JS. Sea urchin population explosion in southern California coastal waters. *Science*. 1970 Jan 9;167(3915):209.

MINOR:

## INTRODUCTION

*L-3 The first sentence of the paper is a bit too colloquial. Consider rephrasing along the following lines: "Fishing often leads to fewer, smaller fish".*

We recognize that the current prose is slightly outside the norm of scientific writing, but we don't agree that it is colloquial i.e. imprecise. Also, we prefer not to use the passive voice as it is well known to decrease readability.

*L-19-20: Please cite the very extensive literature on the topic by John Bruno and colleagues that show how marine reserves does not aid in coral recovery.*

Good point. We have added Bruno et al 2019, a review paper which nicely summarizes this work (Line 20).

Bruno, J.F., Côté, I.M. and Toth, L.T., 2019. Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience?. *Annual review of marine science*, 11, pp.307-334.

*L-25-35: Work by Jing Jiao and colleagues (Jiao et al 2016 *Ecoshpere*) show under which conditions trophic cascades are not expected within marine reserves and should be considered not only as relevant literature but as possible hypotheses and expectations for this study.*

Jiao et al (2016) use modeling results to suggest that movements of predators outside reserves might dilute their effect on prey. One strength of our study is that we have a pair of prey species, one fished and the other not. It is certainly true that Jiao et al.'s hypothesis could be one reason (among several) explaining the lack of predation effect on the unfished urchin species. We have now added this to the Discussion, along with

more description of how trophic complexity can weaken possible cascades, as requested by Reviewer 1 (Lines 239-249).

*L-36-38: Colloquial and uninformative. Also, wow will an ecologist create a species? Please rephrase along the following lines: "To tease apart the effects of direct vs indirect effects while controlling for species identity and the specifics of predator-prey interactions, considering species of similar ecology and morphology under identical environmental conditions is important. A natural experiment exists in the .... of southern California that mimics those ideal conditions-".*

We have revised this as suggested (Lines 36-38).

*L-53: The Selden et al study that you cite here considers the body size of both species separately, correct? Also, why is that important? what does your paper that others have failed to do?*

Please see above description of how our study, an examination of long-term responses of urchin populations to marine reserve protection, differs from Selden et al.'s sheephead predation experiments.

*L-54-56: Breaks with the flow of the introduction, consider explaining in your methods under study system instead. You can pose questions and explain what will be done without talking about the Channel Islands at this point.*

We appreciate the reviewer's opinion, and debated whether to omit this in service to increased generality, but after careful consideration have retained it because we think that the exceptional nature of the dataset is one of the significant elements of our study. Also we like to highlight the NPS's Kelp Forest Monitoring program, which is always under the gun of funding cuts.

#### *METHODS:*

*L-285: Please cite the R team when stating R was used. Correct citation can be found on the R forge website.*

This has been done (Line 308).

*L-290: The linear mixed model to test what? Please explain what is being tested, then present how you do so.*

This has been clarified (Lines 326-327).

*L-303: just state effect sizes-*

Corrected (Line 341)

*RESULTS:*

*FIGURES: the order of the figures don't match appearance in the text. Figure 3 is called before Figure 2 for no apparent reason.*

Thank you for catching this; the order of the figures has been corrected.

*DISCUSSION:*

*L-191:192. Colloquial. Just state your interpretation. A question isn't needed here and is much better suited for an introduction.*

The question "Why have increased predator populations inside reserves apparently not affected urchin populations and led to trophic cascades?" is, we think, clear and does not fit the definition of colloquial. Since the question motivates the following Discussion, we have retained it.