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Lunar rhythms in growth of larval fish

Jeffrey S. Shima, Craig W. Osenberg, Erik G. Noonburg, Suzanne H. Alonzo and Stephen E. Swearer

Article citation details
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Review timeline
Original submission: 19 October 2020
Revised submission: 3 December 2020
Final acceptance: 11 December 2020

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

Review History

RSPB-2020-2609.R0 (Original submission)

Review form: Reviewer 1 (John Christy)

Recommendation
Accept with minor revision (please list 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
I am not a larval fish ecologist nor am I particularly talented at analysis and modeling in R, but I have spent a few decades working on reproductive timing and larval dispersal in the coastal ocean and I have a close colleague who did some of the seminal work in this field with tropical fish, so the topic is not unfamiliar to me.
Given that perspective, I found this to be a simply wonderful study and an excellent paper (I have a very few minor quibbles – see below). I am at a loss to find a single error or lapse in logic or rigor. Rarely am I unable to find at least some fault with a study or paper but this is one such time.
The general problem, how to explain the causes of notoriously large variation in larval fish growth and survival, has vexed marine ecologists for decades. The story told here is fascinating: it connects the timing of reproduction of the sixbar wrasse with lunar cycles of variation in moonlight that affect the abundance in surface waters of both the prey of sixbar larvae (copepods), and, hence, larval growth (featured here), and an important predator (lantern fish), and, hence, larval survival (covered in a previous paper). Modulation of lunar cycle variation in moonlight caused by cloudy conditions provided a natural test of the effects of moonlight across the lunar cycle on growth rate (e.g., relaxation of inhibition of growth by moonlight in the early night).
The sampling program is based on an exceptionally good understanding of the reproductive ecology and behavior of this fish (e.g., solid natural history), and the analysis appears to be thorough and correct. The figures are excellent though I had to work a bit to understand the relatively complex patterns shown in Fig 1b. The hypothesis illustrated in Fig 4 is imaginative, convincing, and intellectually exciting. It prompted me to say "yes!" to myself when I reached that section of the paper.
I look forward to seeing this enjoyable and stimulating paper in print.
Minor points by line
5 "…larval fish growth" Adjectival strings can be misunderstood. Perhaps "growth of larval fish" would be better.
35 moonlight is not a mechanism. Perhaps "…and confirmed the effect of moonlight on growth."
45 "baby" is appropriate for the press release that is sure to come but perhaps "larval fish" or "larval and juvenile fish" would be better here.
58 "…that affect variation in…" may be better.
61-62 "Most ecological studies ignore the night." This seems a bit overstated. Nocturnal studies have a long tradition in many subfields of ecology (especially behavioral ecology, e.g., bats, frogs, orthopterans), including studies of reproductive timing and larval dispersal in estuarine and coastal systems. Perhaps "Nocturnal ecological studies are underappreciated" might be better?

81 "…the growth of larval fish…" and throughout if you agree that removing the adjectival string is helpful.
201 FishID? Please define/explain, or did I miss this above?
220 But isn't variation in food availability the driver and variation in moonlight the correlate of that driver? Perhaps recast
322 Is moonlight the mechanism, or a factor that varies with variation in operation of the mechanism (variation in food due to variation in vertical migration of copepods) ?
352 – 357 This is paradoxical, and I am not sure the paradox is entirely resolved. Settling on the reef large is good but only if you survive to enjoy the benefits of enhanced competitiveness due to large body size.

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list 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

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Is it accessible?
Yes

Is it clear?
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Is it adequate?
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Do you have any ethical concerns with this paper?
No

Comments to the Author
This is a very interesting and well written/executed manuscript. My suggestions in the attached document are mainly to expand the discussion to be a bit more even handed and comprehensive. (See Appendix A)

Decision letter (RSPB-2020-2609.R0)

27-Nov-2020

Dear Dr Shima:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://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.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the 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.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

Research ethics:
If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:

It is a condition of publication that you make available the data and research materials supporting the results in the article. Please see our Data Sharing Policies (https://royalsociety.org/journals/authors/author-guidelines/#data). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

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), 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.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

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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. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr Sasha Dall
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
This paper has now been reviewed by two experts in the field and I have also read the manuscript. As the Referees attest, the central issue of understanding the suite of processes that control growth and survival of larval/juvenile fishes, leading to variability in recruitment, is at the core of many issues in both basic and applied fisheries population biology and continues to vex marine ecologists. I agree with both Referees that this “natural experimental approach” showing that daily growth rates of a coral reef fish are strongly lunar-periodic and predicted by the timing of nocturnal brightness contributes important and interesting data towards understanding the factors that influence growth and survival of larval fishes. It is a very

interesting study that will be of broad interest to the readers of PRSB. Nonetheless, given the apparent strong interest from the Referees, they have also provided several useful comments and suggestions to improve the paper. In particular, I agree with Referee 2 that additional discussion about the factors potentially impacting residual growth variability will lend more strength to the final conclusion of the study. Implementation of the other suggested revisions should further improve the paper as well.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
I am not a larval fish ecologist nor am I particularly talented at analysis and modeling in R, but I have spent a few decades working on reproductive timing and larval dispersal in the coastal ocean and I have a close colleague who did some of the seminal work in this field with tropical fish, so the topic is not unfamiliar to me.
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352 – 357 This is paradoxical, and I am not sure the paradox is entirely resolved. Settling on the reef large is good but only if you survive to enjoy the benefits of enhanced competitiveness due to large body size.

Referee: 2

Comments to the Author(s)
This is a very interesting and well written/executed manuscript. My suggestions in the attached document are mainly to expand the discussion to be a bit more even handed and comprehensive.

Author's Response to Decision Letter for (RSPB-2020-2609.R0)

See Appendix B.

Decision letter (RSPB-2020-2609.R1)

11-Dec-2020

Dear Dr Shima

I am pleased to inform you that your manuscript entitled "Lunar rhythms in growth of larval fish" 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.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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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.

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,
Dr Sasha Dall
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
The authors have done a very thorough job addressing the suggested changes in this revision. I am pleased to recommend acceptance.

Appendix A

Review of RSPB-2020-2609

This study was well written and executed, all statistical methods and conclusions appear to be appropriate and sound, and the manuscript is well written and compelling. It provides a somewhat novel variable (at least one we have not looked at in this way) to investigate with respect to larval fish dynamics and even recruitment variability. And the theory on DVM will certainly raise some eyebrows and have many members of the community designing experiments to test it.

In general, however, I would have liked to see a bit more discussion of other factors that could have contributed to or caused the lunar pattern in residual growth variability. While I am intrigued and even in agreement with the compelling hypothesis presented, a bit more discussion of such factors may even lend more strength to this final conclusion. For example, 1) changing patterns of selective predation across the lunar cycle based on illumination (different predator communities) would certainly have an effect on the composition of survivors. Because all of the fish in this study were already settled to the reef and survived the PLD, this could be important to mention or discuss. 2) Behavior of larvae themselves (not necessarily the community surrounding them) may be mediated by lunar illumination as well, and contribute to the patterns observed. 3) Spawning of other reef associated organisms, if evidence exists for proper lunar timing, could cause an elevated prey field and thus growth rates. And lastly, 4) the fact that the first 20 days of larval growth are relatively invariant deserves discussion. Why would this be? Certainly most of that time is no longer being influenced by endogenous energy sources. So why are small prey items, or predators after smaller larvae, not influenced by lunar illumination (or presumably much else). Are these younger larvae experiencing a more homogenous and ubiquitous prey and predator field? I find this intriguing and I feel it deserves a bit of discussion.

So at the expense of brevity (and if the journal allows) the manuscript would benefit from including some of these points.

353-357 – This could be supported by a high proportion of surviving recruits being back-dated to spawning on the new moon. Do you have such evidence? If not, then this 2 advantageous growth period hypothesis may not be correct, as its advantage should translate to increased survival to settlement.

Figure S4 – I think this is of value and general interest to the manuscript and may be better included in the main body.

Appendix B

Dear Dr Dall,

We wish to express our gratitude to you, the associate editor, and the two external reviewers for your time and constructive feedback on our manuscript.

We append editor/reviewer comments below, and our specific responses to each is indicated in **blue/bold text.** This is followed by a version of our resubmission that includes all tracked changes.

We have added a reference to our published data in dryad, and we have included details of animal ethics/research permit approvals in our Methods. We have uploaded the final version of our manuscript (without tracked changes), separate files for each figure (in .pdf format) and a single file for our electronic supplement (formatted for publication on Figshare).

Best wishes,

Jeff Shima

Associate Editor

Comments to Author:

This paper has now been reviewed by two experts in the field and I have also read the manuscript. As the Referees attest, the central issue of understanding the suite of processes that control growth and survival of larval/juvenile fishes, leading to variability in recruitment, is at the core of many issues in both basic and applied fisheries population biology and continues to vex marine ecologists. I agree with both Referees that this "natural experimental approach" showing that daily growth rates of a coral reef fish are strongly lunar-periodic and predicted by the timing of nocturnal brightness contributes important and interesting data towards understanding the factors that influence growth and survival of larval fishes. It is a very interesting study that will be of broad interest to the readers of PRSB. Nonetheless, given the apparent strong interest from the Referees, they have also provided several useful comments and suggestions to improve the paper. In particular, I agree with Referee 2 that additional discussion about the factors potentially impacting residual growth variability will lend more strength to the final conclusion of the study. Implementation of the other suggested revisions should further improve the paper as well.

RESPONSE: We wish to thank you and your reviewers your time on this. We found all of the reviewers' comments to be helpful. Addressing them has enabled us to strengthen our manuscript.

We detail our specific responses to each comment below. Briefly, we have provided additional discussion of other factors that potentially contribute to variation in residual growth. We have also accepted all but 2 of the (word choice) suggestions of the two reviewers (in two instances, we have opted to retain our original wording, for reasons indicated in those specific responses).

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

I am not a larval fish ecologist nor am I particularly talented at analysis and modeling in R, but I have spent a few decades working on reproductive timing and larval dispersal in the coastal ocean and I have a close colleague who did some of the seminal work in this field with tropical fish, so the topic is not unfamiliar to me.

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I look forward to seeing this enjoyable and stimulating paper in print.

RESPONSE: We are very appreciative of this review, and pleased to learn that the reviewer appears to be as excited by the patterns as we are.

Minor points by line

5 "…larval fish growth" Adjectival strings can be misunderstood. Perhaps "growth of larval fish" would be better.

RESPONSE: We have made this change throughout the manuscript

35 moonlight is not a mechanism. Perhaps "…and confirmed the effect of moonlight on growth."

RESPONSE: We have made this change.

45 "baby" is appropriate for the press release that is sure to come but perhaps "larval fish" or "larval and juvenile fish" would be better here.

RESPONSE: We have made this change.

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RESPONSE: We have made this change.

61-62 "Most ecological studies ignore the night." This seems a bit overstated. Nocturnal studies have a long tradition in many subfields of ecology (especially behavioral ecology, e.g., bats, frogs, orthopterans), including studies of reproductive timing and larval dispersal in estuarine and coastal systems. Perhaps "Nocturnal ecological studies are underappreciated" might be better?

RESPONSE: We have chosen to retain this wording because (1) we believe it to be true (and it implicitly recognises that there are exceptions); (2) the strong wording draws attention to the central issue.

81 "…the growth of larval fish…" and throughout if you agree that removing the adjectival string is helpful.

RESPONSE: We have made this change.

201 FishID? Please define/explain, or did I miss this above?

RESPONSE: We have edited the text to clarify this variable.

220 But isn't variation in food availability the driver and variation in moonlight the correlate of that driver? Perhaps recast

RESPONSE: We have edited the text to read "…was causally linked to variation in growth.")

322 Is moonlight the mechanism, or a factor that varies with variation in operation of the mechanism (variation in food due to variation in vertical migration of copepods) ?

RESPONSE: We have chosen to retain the original wording in this instance: The natural experiment indicates a causal linkage between moonlight and growth of larval fish, although it does not clarify the exact pathway by which nocturnal illumination mediates growth (i.e., we propose that it's effect is mediated through changes in the vertical migration of prey and predators, so in this sense, its effect is indirect).

352 – 357 This is paradoxical, and I am not sure the paradox is entirely resolved. Settling on the reef large is good but only if you survive to enjoy the benefits of enhanced competitiveness due to large body size.

RESPONSE: As reviewer 2 notes, the relative strength of post-settlement selection is a crucial piece of this puzzle. We have expanded this discussion to clarify this, and to indicate where our evidence presented in another paper appears to support it.

Referee: 2

Comments to the Author(s)

This is a very interesting and well written/executed manuscript. My suggestions in the attached document are mainly to expand the discussion to be a bit more even handed and comprehensive. [contents of attached document pasted below]

Review of RSPB-2020-2609

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experiencing a more homogenous and ubiquitous prey and predator field? I find this intriguing and I feel it deserves a bit of discussion.

So at the expense of brevity (and if the journal allows) the manuscript would benefit from including some of these points.

RESPONSE: We have expanded our discussion (with the addition of two new paragraphs; lines 346-365) to address these excellent points.

353-357 – This could be supported by a high proportion of surviving recruits being back-dated to spawning on the new moon. Do you have such evidence? If not, then this 2 advantageous growth period hypothesis may not be correct, as its advantage should translate to increased survival to settlement.

RESPONSE: Reviewer 1 had a related comment. We have expanded this discussion to clarify how benefits to future life stages may outweigh the fitness costs through the pelagic period.

We acknowledge reviewer 2's point, that this is potentially testable. We now clearly indicate where evidence presented in another paper provides indirect support for this hypothesis. A definitive test requires estimating lunar birthdates of adults; however, we are unable to resolve these dates directly (and with certainty) from otoliths of adults because lifetime records of daily growth increments are difficult to distinguish in older individuals.

In a future paper we hope to infer lunar birthdates of adults (based upon characteristic patterns of growth across the larval stage, e.g., Fig 1b), and address this question more directly.

Figure S4 – I think this is of value and general interest to the manuscript and may be better included in the main body.

RESPONSE: While we agree that this supplemental figure is potentially useful for some readers, it is large, and we feel that is not central to our story. Our paper length has also been estimated a 10p (i.e., it already exceeds to desired 6 printed pages for the journal). We hope that those readers with keen interest will access the supplement. We have included an additional citation to Fig S4 in our expanded discussion to better draw attention to this presentation).