Peer Community In Ecology

Habitat complexity reduces cannibalism, enhancing population-level diversity and productivity in a freshwater fish

Matthew Bracken *based on peer reviews by* **Joacim Näslund, Thomas Guillemaud** *and 2 anonymous reviewers*

Eric Edeline, Yoann Bennevault, David Rozen-Rechels (2023) Habitat structural complexity increases age-class coexistence and population growth rate through relaxed cannibalism in a freshwater fish. bioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Ecology. https://www.biorxiv.org/content/10.1101/2023.07.18.549540v4

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Habitat complexity is an important mediator of processes spanning levels of biological organization from organisms to ecosystems (Shumway et al. 2007, Soukup et al. 2022). This complexity, which can be biogenic (e.g., foundation species; Bracken et al. 2007, Ellison 2019) or abiotic (e.g., substrate rugosity; Kovalenko et al. 2012), shapes processes ranging from individual foraging behavior (Michel and Adams 2009) to species' interactions to food-web structure and biogeochemical rates (Langellotto and Denno 2006, Larsen et al. 2021, Soukup et al. 2022). For example, in the presence of simulated aquatic vegetation, predatory diving beetle larvae shift from active foraging to sit-and-wait predation, reducing activity and prey encounter rates (Michel and Adams 2009).

In this contribution, Edeline et al. (2023) present a detailed perspective on the role of habitat complexity in shaping populations of a freshwater fish (medaka, *Oryzias latipes*, Adrianichthyidae), including survival, age-class diversity, population growth rate, and density-dependence in the stock-recruitment relationship associated with changes in carrying capacity. Importantly, changes in these population demographic attributes and rates were associated with the role of habitat complexity in mitigating cannibalism – consumption of juvenile *O. latipes* by conspecific adults. Whereas this is not unexpected – Langelotto and Denno (2006) showed that habitat complexity reduces cannibalism in wolf spiders – the careful work of Edeline et al. (2023) to link changes in habitat complexity to multiple population-level attributes provides a uniquely detailed description of the role of submerged aquatic vegetation in mediating population diversity (e.g., higher age-class diversity) and productivity (e.g., population growth rate).

In many ways, this work by Edeline et al. (2023) provides population-level parallels to perspectives on the role of habitat complexity in determining community-level diversity and productivity. Structurally complex habitats, such as those provided by foundation species (Bracken et al. 2007, Ellison 2019) and substrate heterogeneity (Fairchild et al. 2024), are associated with higher species diversity and abundance at the community level. Edeline et al. (2023) extend these perspectives to the population level, highlighting the importance of habitat complexity across levels of biological organization. Their work highlights within-population diversity and interactions, including cannibalism and competition, illustrating often-neglected aspects of food-web complexity (Polis and Strong 1996).

References:

Matthew E. S. Bracken, Barry E. Bracken, Laura Rogers-Bennett (2007) Species diversity and foundation species: potential indicators of fisheries yields and marine ecosystem functioning. California Cooperative Oceanic Fisheries Investigations Reports 48: 82-91. https://calcofi.org/downloads/publications/calcofireports/v48/Vol_48_Bracken.pdf

Eric Edeline, Yoann Bennevault, David Rozen-Rechels (2023) Habitat structural complexity increases age-class coexistence and population growth rate through relaxed cannibalism in a freshwater fish. bioRxiv, ver.4 peer-reviewed and recommended by PCI Ecology https://www.biorxiv.org/content/10.1101/2023.07.18.549540v4

Aaron M. Ellison (2019) Foundation species, non-trophic interactions, and the value of being common. iScience 13: 254-68. https://doi.org/10.1016/j.isci.2019.02.020

Tom P. Fairchild, Bettina Walter, Joshua J. Mutter, John N. Griffin. (2024) Topographic heterogeneity triggers complementary cascades that enhance ecosystem multifunctionality. Ecology 105: e4434. https://doi.org/10.1002/ecy.4434

Katya E. Kovalenko, Sidinei M. Thomaz, Danielle M. Warfe (2012) Habitat complexity: approaches and future directions. Hydrobiologia 685: 1-17. https://doi.org/10.1007/s10750-011-0974-z

Gail A. Langellotto, Robert F. Denno. (2006) Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrate predators. Ecological Entomology 31: 575-81. https://doi.org/10.1111/j.1365-2311.2006.00816.x

Annegret Larsen, Joshua R. Larsen, Stuart N. Lane (2021) Dam builders and their works: beaver influences on the structure and Function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems. Earth-Science Reviews 218: 103623. https://doi.org/10.1016/j.earscirev.2021.103623

Matt J. Michel, Melinda M. Adams. (2009) Differential effects of structural complexity on predator foraging behavior. Behavioral Ecology: 313-17. https://doi.org/10.1093/beheco/arp005

Gary A. Polis, Donald R. Strong (1996) Food web complexity and community dynamics. American Naturalist 147: 813-46. https://doi.org/10.1086/285880

Caroly A. Shumway, Hans A. Hofmann, Adam P. Dobberfuhl (2007) Quantifying habitat complexity in aquatic ecosystems. Freshwater Biology 52: 1065-76. https://doi.org/10.1111/j.1365-2427.2007.01754.x.

Pavel R. Soukup, Joacim Näslund, Johan Höjesjö, David S. Boukal (2022) From individuals to communities: habitat complexity affects all levels of organization in aquatic environments. Wiley Interdisciplinary Reviews: Water 9: e1575. https://doi.org/10.1002/wat2.1575

Reviews

Evaluation round #2

DOI or URL of the preprint: https://www.biorxiv.org/content/10.1101/2023.07.18.549540v3
Version of the preprint: 3

Authors' reply, 06 March 2025

Download author's reply

Decision by Matthew Bracken, posted 25 February 2025, validated 26 February 2025

Download recommender's annotations

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2023.07.18.549540
Version of the preprint: 2

Authors' reply, 08 November 2024

Download author's reply

Decision by Matthew Bracken, posted 27 March 2024, validated 28 March 2024

Habitat complexity reduces consumption of conspecific juveniles by adult fish

This manuscript has the potential to be an important contribution to our understanding of the role of habitat complexity in facilitating associated organisms. In particular, whereas it is well-known that submerged aquatic vegetation enhances the survival of juvenile fishes and other organisms (e.g., Lazzari 2012 Journal of Applied Icthyology; https://doi.org/10.1111/jai.12048), the study reported here extends that concept to highlight the role of complex submerged habitats in protecting juvenile fish (medaka, *Oryzias latipes*) from cannibalistic consumption by conspecific adults. This is an interesting wrinkle, as it merges concepts of foundation species (sensu Dayton 1972; see Bracken et al. 2007 CalCOFI Reports; https://escholarship.org/content/qt1wk4k66d/qt1wk4k66d.pdf) with those of intraguild predation (e.g., Polis & Holt 1992 Trends Ecol Evol; https://doi.org/10.1016/0169-5347(92)90208-S). The reviewers have made a number of suggestions aimed at improving the manuscript, and I look forward to a revised version of the manuscript that incorporates their suggestions. In addition, I would like to see some discussion that links your findings to real-world phenomena. Southeast Asian fish in experimental ponds in Europe that lack any other fish or predator species are interesting from a modeling perspective, but I would like to see some evidence (e.g., from the literature) that similar phenomena could be important in natural systems. Please provide a point-by-point and line-by-line accounting of your revisions.

Reviewed by anonymous reviewer 1, 17 January 2024

I enjoyed reading this manuscript and the study's objectives, results, and implications are interesting. I hope the authors find my comments helpful.

Summary of strengths of the ms:

- The ms is well-written and clear, and tests an important ecological concept.

· The authors effectively apply a variety of models to their experimental results to help explain mechanisms behind the results.

· The figures are nicely done and clearly display the results.

Summary of weaknesses of the ms:

· The authors say little about how relevant their experimental design is to natural ponds and naturally occurring populations of pond fish.

· The authors do not describe or justify their choices for the material used to manipulate structural complexity and for the different treatments. It is not clear how relevant the manipulation of structural complexity is to real systems, and therefore how applicable the results are to real systems.

Section-by-section comments:

Title

The title is descriptive and concise. My only small note about the title (which admittedly is a bit nitpicky) is the use of the word "fish", which implies that the authors evaluated age-class coexistence and population growth in multiple species of fish. They could consider replacing fish with "medaka" (given how common the species is in experimentation) or "a small pond fish" or "a small freshwater fish", etc.

Abstract

The abstract does a nice job of concisely describing the study's objective and primary results. The sentence on lines 20 – 25 is awkward and the authors could consider making the four results they list here into a numbered list.

Introduction

The introduction is well-written and the study's focus and objectives are articulated effectively. I agree with the authors that intraspecific interactions, and specifically the effects of habitat structural complexity on those interactions, are not as well studied as relationships among predator and prey organisms of different species. The objectives are clear and logical and flow from the introduction.

In the introduction, the authors discuss the idea that large-bodied predators may have limited mobility within structurally complex habitats, leading to lower predator-prey encounter rates and higher prey survival rates. This certainly is a primary way in which habitat structure can dictate the outcomes of predator-prey relationships. They may wish to note that encounter rates also may be reduced via the reduced detection of prey due to the obstruction of vision that structure causes for visually-oriented predators, as described nicely in (e.g.) studies by Bartholomew (such as Bartholomew et al. 2000: MEPS 206: 45-58).

Materials and methods

Cannibalistic assays: this assay is a good idea, and does a nice job of establishing the bounds of cannibalism for adult medaka. But there are a few things that could use clarification for these assays. First, how were the two larvae chosen for each aquarium? Were they purposely of two different sizes/ages, or purposely the same size or age, or randomly selected? It's not clear from the description whether the idea here is to see which of the two larvae (of which one may be larger and one smaller) are selected by the adult (i.e. a prey selection experiment), or whether what is recorded is whether any predation occurred at all (this may be the case, as the authors state that they are using the mean size of the two larvae). If they were recording whether any predation occurred, was it necessary for both larvae to be consumed? If not, how did they account for the fact that the two larvae may have been of different sizes and only the smaller or larger was consumed?

I have no objection to the use of artificial structures to manipulate structural complexity, having done this myself in predation experiments. However, some discussion of the realism and relevance of the geomaterial would be helpful in the ms. Why was this material chosen, and how closely does it simulate any real natural vegetative structure? From figure 1, it is apparent that the geomaterial is a floating mat, perhaps unlike naturally occurring structure that may be much more three dimensional. If this is an accurate observation, how may restricting predation to the very top of the water (presumably where larvae are hiding) affect the relevance of the results to natural ponds? Is there a potential shading effect that may be occurring here, that interferes with visual detection of small larvae? Without this information and insight, it is hard to relate the strong results obtained by the authors to natural systems and natural populations. Additionally, can the authors comment on how characteristics of the artificial structure relate to the mechanisms they introduce in the introduction section? In other words, how effectively does the structure inhibit movement of the adult medaka relative to the juveniles? Is it likely that inhibition of movement is the primary mechanism reducing predation risk, as opposed to impairing visual detection of juvenile prey by adults? Finally, how does their manipulation of habitat structure correspond to what is found in nature? Here what I mean is, the authors created their treatments by using different amounts of the same material, whereas in natural ponds, habitat structure can perhaps differ based on the interstitial spacing between structural elements. In nature this would refer to the spacing between (e.g.) plant shoots or roots, and in the experiment this would refer to the spacing between the strands that make up the material.

Line 193: I was confused about how the geomaterial could have a surface area greater than that of the experimental pond, until I re-read and realized that there were 5 layers of geomaterial used in this complexity treatment. Referring to my comment above about 3 dimensional structure, this treatment seems to be fundamentally different than the others not only in terms of the amount of area covered by the material, but due to the layering which presumably resulted in a thicker layer of habitat structure, creating more of a 3 dimensional "arena" in which the fish could interact.

Results

The results are summarized very nicely, and the authors effectively answer many relevant questions about the outcomes of the two experiments. The authors' interpretations of their results seem reasonable and I am impressed by the use of different types of statistical models to sort through the potential mechanisms that cause their results (in figures 2 – 4). One thing that comes to mind, however, is (again) relevance to naturally occurring populations. While the coexistence of juvenile and adult fish within individual ponds occurs in nature (obviously, because adults reproduce), I wonder whether there are potential roles of habitat diversity and habitat selection that are present in real ponds but not available to these experimental fish. For instance, in the pond experiment the adult fish seem to be forced to forage within the complex structures provided, whereas in real ponds, they may select to hunt plankton in less complex areas. Can the authors comment (perhaps in the discussion) on whether things like habitat diversity and selection may be an important difference between experimental and real ponds?

For table 1, it would be helpful to include some brief text (perhaps in the leftmost column) that reminds the reader what is being modeled, for each model 2 – 5.

Tables and figures

The figures are very nicely done, and the captions explain them sufficiently. One small thing, it is hard to see all 8 lines in figure 3 (maybe some of them strongly overlap?).

Discussion

On lines 466-468, the authors state (for the second time) that newly hatched larvae are very vulnerable to cannibalism in unstructured habitats. I agree that their results suggest that a wide range of fish sizes can consume newly-hatched larvae (particularly with male fish), but their assays were conducted in half-liter containers where fish were forced to exist in the same small space. I suggest making clear the distinction between vulnerability as a function of size (in the assays) vs. vulnerability that may be a function of many other things (e.g. habitat selection) in nature.

Lines 481-490: this is interesting speculation (that an optimal, intermediate level of habitat complexity exists for coexistence of multiple age classes), however it is based on assumptions that may or may not be true (e.g. whether complexity created in this experiment using artificial structure is lower than that found in many natural ponds). This again comes back to the relevance of the chosen artificial structures for the experiments, which is not discussed in the ms.

Specific comments

1. Line 113: tell the reader what CEREEP stands for and where the research was performed.
2. Line 132: The word "then" should be "than". It took me a minute to figure out that this function is

parabolic in shape, and the authors may want to mention that.

3. Line 191: “in” should be “of”.
4. Line 468: “allow” should be “allows”.

Reviewed by anonymous reviewer 2, 02 March 2024

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Reviewed by Joacim Näslund, 05 March 2024

Title and abstract

Does the title clearly reflect the content of the article? [x] Yes, [ ] No (please explain), [ ] I don’t know
Does the abstract present the main findings of the study? [x] Yes, [ ] No (please explain), [ ] I don’t know

Introduction

Are the research questions/hypotheses/predictions clearly presented? [x] Yes, [ ] No (please explain), [ ] I don’t know
Does the introduction build on relevant research in the field? [x] Yes, [ ] No (please explain), [ ] I don’t know

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers? [x] Yes, [ ] No (please explain), [ ] I don’t know
Are the methods and statistical analyses appropriate and well described? [x] Yes, [ ] No (please explain), [ ] I don’t know

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? [x] Yes, [ ] No (please explain), [ ] I don’t know
Are the results described and interpreted correctly? [x] Yes, [ ] No (please explain), [ ] I don’t know

Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [x] Yes, [ ] No (please explain), [ ] I don’t know
Are the conclusions adequately supported by the results (without overstating the implications of the findings)? [x] Yes, [ ] No (please explain), [ ] I don’t know

Detailed comments

The reviewed preprint is a neat study on environmental complexity, combining mesocosm and lab experiments.

The investigators find that structural complexity is important to limit cannibalism, which leads to higher population densities and a higher competition pressure (fish consequently grow slower).

I think the majority of the presentation is good, and I have only a few comments to make - none being particularly severe in nature.

In the introduction, something about rivers could be mentioned when introducing habitat simplification - rivers are important freshwater habitats and are very often heavily modified (channelized), leading to lowered complexity. Channelization could be due to hydropower (rapid removal of water downstream; relating to both modern and old hydropower systems, electricity production, mills, saw mills etc.), shipping, urban development or log-driving (N. Europe and northern N. America). A brief mention of rivers is warranted, in my opinion.

In-text references need to be polished since some initials still remain (e.g. line 52 ”F. E. Smith”).

L 56 and forward: The essence of structural complexity effects on biota is presented as complexity facilitating predator avoidance. This is only true if the main predator itself is not benefited by the complexity, which would be the case for e.g. predatory dragonflies (drawing upon my own work, an example can be found in Mocq et al. 2021 (https://doi.org/10.1111/1365-2656.13473), but there are other examples as well. Furthermore, complexity is also likely increasing substrate area, leading to potentially higher production of primary producers and sessile animals, and in addition the niche diversity could possibly also be increased by addition of complexity (especially when previously absent). We discuss these things in our work Soukup et al. 2022 (https://doi.org/10.1002/wat2.1575). The latter paper may be interesting from the perspective of the reviewed manuscript, but I would in no way want to force the authors to cite it (and neither the previously mentioned paper). I simply relate to these papers because I know them well.

Relating to Figure 4A, I would suggest to expand the axes to 0. For this panel, 0 is a relatively important location in relation to the data plotted. I'd also suggest to extend the predicted line (but not the credibility intervals) so that they reach N(t) = 0 - for clarity about what the regressions look like outside of the data. For panel B, 0 is irrelevant, since no fishes have a length of 0 mm - hence, no changes are suggested for this panel.

Other than that, I do not have any issues to raise. I think this is a very good pre-print.

Sincerely,
Joacim Näslund, Swedish University of Agricultural Sciences

Reviewed by Thomas Guillemaud, 09 February 2024

It's all perfect. The authors solved all the issues I raised in my previous comments (see attached pdf file). Consequently, every question on the checklist below has a "yes" as a reply.

1- Can we get the data and script from the links indicated in the submission form or from the article itself? ==> YES

2- Is there a readme file? ==> YES

3- Are there metadata for the data and comments for the scripts? ==> YES

4- Are the readme, and data files understandable by a normal reader? ==>YES

5- Do the scripts run on the data? ==> YES

6- Are the results the same as in the paper? ==> YES

In summary, data and scripts are available, clear, and understandable. Scripts properly run on data. The results obtained from the scripts are the same as in the article.

I thank the authors for their very clear, detailed, and precise work.

Download the review