

## REVIEW

Habitat structural complexity increases age-class coexistence and population growth rate in fish

Eric Edeline, Yoann Bennevault, David Rozen-Rechels

### General Comments-

Edeline et al. adapt community ecology theories about habitat structure effects on species coexistence to explain habitat structure effects on age-class coexistence within a species. They test their theories with small “medaka” fish in intra-specific predation trials and mesocosms with high or low amounts of structure. The statistical approaches used are rigorous and complex, difficult (for me) to follow, and at times seem to eclipse the rigor of the experiments themselves. However, the approaches taken are effective in evaluating the predictions of the authors’ theories, which are upheld by their results. Importantly, increasing habitat complexity has strong positive effects on juveniles and weak negative effects on adults, such that overall population productivity and carrying capacity are increased by habitat complexity within the range tested experimentally. It is postulated that productivity might decline at very high levels of habitat structural complexity seen in the wild, but this was not seen in the experiments. The quality of the writing is excellent, and while their methods are somewhat clouded in complexity, the authors clearly explain the importance of their findings to the discipline of ecology and to global conservation endeavors. This work merits wide dissemination and should be of broad interest, though it could be improved by some revisions discussed below.

### Specific comments-

Lines 51-62- Some disclaimers to the generality of habitat structure reducing predation should be included. E.g., small bodied prey may avoid macrophyte habitats where such habitats harbor ambush predators (Schultz et al. 2009, <https://doi.org/10.3354/meps07779>).

Line 62- It might be helpful to add a brief explanation of *apparent competition*; negative indirect interactions between victim species that arise because they share a natural enemy. As an alternative reference to Holt’s 1987 paper you could cite the Holt and Bonsall 2017 review of apparent competition. <https://www.annualreviews.org/doi/abs/10.1146/annurev-ecolsys-110316-022628>

Line 67- Citations might be needed after “age classes” to support the statement made in this sentence.

Line 147- Does the term “geomaterial” have a single, accepted and widely understood definition? If not, then just “material” might be more appropriate here.

Line 163- It’s not made clear here why such variable numbers of fish (18-60) fish were introduced to the ponds in experiment 1, despite the later importance of these variable numbers to inferences made about density dependent population growth rates. Was this planned or fortuitous? Why were stocking numbers not varied similarly for experiment 2?

Line 173- I understand that no significant effect of strain was found, but I'm not sure the statistical power to detect a strain effect was high enough to be useful. I.e., it seems like the possibility of a type II error in this test would have been pretty high.

Lines 199-214- The description of Model 1 is hard for this non-statistician to follow and would benefit from additional annotation. For example, a sentence or so with a less technical explanation of the purpose of the model would help.

Line 215-292- Similar issues here: some additional annotation regarding why the particular statistical methods were chosen for models 2-5 could be helpful. It would also be helpful to more fully describe the purpose of each model before describing its structure. An overview of the integrated modeling approach at the beginning of the statistical analyses section (Line 199) would also be helpful; describe the forest before describing each tree.

Table 1- Models are identified by number (2-5) and "Response" (a mathematical term). I think it would be helpful to also have a name for each model, e.g., "Model 2- Population growth" "Model 3- Fish length" etc.

Figure 4- It's unfortunate that the levels of  $N(t)$  for the 2021 experiment are not matched for the low complexity and high complexity treatments in that year. It's also interesting that  $N(t+1)$  seems higher for both complexity treatments in 2021 than 2022.

Line 396- Here an explanation of Model 2 is given, which I think would be more helpful in the methods section.

Line 399- The term "production" is used in this manuscript without clarification as to how it is operationally defined. Secondary production generally refers to change in heterotrophic biomass of a population over a time interval, and therefore accounts for changes in both population numbers and body size distribution over that interval. Here perhaps the term is used to refer just to changes in numbers without incorporation of mass? That should be clarified, or a different term should be used.

Line 474- It's odd that shallow areas are considered "absolute predation refuges." They may be absolute refuges from larger conspecifics, but they are certainly not refuges from wading birds. This could be mentioned.

Line 500- Evidence should be cited at the end of the sentence that begins with "Ample evidence demonstrates..."