Review of the manuscript - Effects of adaptive harvesting on fishing down processes and resilience changes in predator-prey systems (PCI Ecol)

Summary of the study:

In this manuscript, the authors use theoretical ecology to explore the impact of fishing on a prey-predator system and the adaptive behavior of the fishery considering the response of the ecological system in terms of the relative abundance of these compartments. More specifically, the authors use a system of well-known Lotka-Volterra equations to represent the trophic interactions between 2 or 3 fish "functional groups" and the impact of fishing on each of them through additional mortality. By solving this system of equation under the assumption of equilibrium, this study predicts how both the relative proportion of fishing effort allocated to prey and predators and the prey and predator density change in response to an increase in the total fishing effort. Such responses highlight both the existence and succession of stable and unstable states depending on the parameters of the system, including biological (e.g., carrying capacity, energy conversion efficiency), economic (e.g., species price), fisheries-related parameters (e.g., catchability, adaptation speed). Additionally, through the analytic treatment of the system equations, the authors bring to light feedback loops that may stabilize or destabilize the system. In their Discussion, the authors analyze their results in the light of known or assumed responses of marine ecosystems to fishing exploitation, notably referring to the "fishing down the marine food web" phenomenon or fishing-induced trophic cascades.

General comment:

In the present manuscript, the author try to use ecological theory to investigate / reproduce / verify mechanisms of fishing impact on food webs that have been mainly empirically demonstrated, e.g. the fishing down the marine food web phenomenon. This type of exercise is relatively rare and welcome, and provides precious knowledge for fisheries and ecosystem ecology. This is, to me, the main asset of the present manuscript.

I haven't been practicing analytical solving of that type of theoretical equation systems under equilibrium conditions for a while; thus, I don't consider myself as an expert of the methodology applied here and I didn't review finely the mathematical developments presented in the manuscript but I compared them to the cited literature, followed and understood the different steps of the solving and didn't notice any major issue. I appreciate the different levels of complexity investigated to represent the ecological system by the increasing the number of its components or allowing population cycles to occur. They allow the reader to better understand the implications of the different assumptions made here on the final results. What has been conducted in this study and is perceptible in the Methods and Results parts, but also in the Appendices represent a substantial amount of work and should be acknowledged.

The manuscript is well written and, though I recommend a careful reading for removing some typos, I don't see any need of language revision. Once again, the methodology is relatively clear (but see my comments below) and, in relation with my first comment, I do appreciate that the authors try to connect their theoretical findings to empirical observations and concrete applications for fisheries management.

Having said that, I have a couple of reservations that I recommend the author to address. Some of these remarks concern the scientific content but most of them focus on the manuscript structure and the choices that are made regarding what to include or not in the main body.

My major concerns are about the choices that have been made by the authors in terms of manuscript organization.

First, I found that the Material and Methods ("Model" part) was too much diluted. There are some important pieces of the methodological framework description that are present in the Results, making this part very dense and not fluid enough. Additionally some methodological details that should be appearing in the manuscript are only present in the Appendix: I had to regularly go back and forth between the Appendix and the main text to understand some parts of the results.

Moreover, I think that the disproportionate size of the Appendix relative to the main body highlights that some material could be also transferred to the Results. I am notably thinking of transferring some useful summary tables about the model equilibriums into the Results.

Last, and maybe more importantly, I was a bit surprised by the choice of the authors of focusing the manuscript on the 2-component prey-predator system. In the Appendix, the authors also present a big piece of work that they conducted for studying a tri-trophic system. Even if less sensitivity analyses are conducted for this study case, I think it is a key result of the manuscript on which the authors should emphasize. This would be all the more welcome as it would further support the exploration of the fishing down the marine food web, which can't be simply studied based on a simple prey-predator system.

More generally, and it is probably a consequence of what I describe in the paragraph above, I had some difficulties to identify the common thread of the manuscript. To me, the methodological developments and results in the main text don't seem pertinent enough for testing the relevance of the fishing down marine food web while this phenomenon is central in the introduction and the discussion. It may be tackled by giving more importance to the tritrophic chain example.

If it turns out that the authors want to focus a bit more their manuscript on the FDMFW/FTMFW, which would be, to my mind, highly valuable, I suggest they add another component to their main results. Indeed, in most of their figures, the authors represent the response of the TL of catches to increasing fishing effort. This response allows to check that the model is able to reproduce what we are supposed to observe in both FDMFW and FTMFW concepts (i.e., decrease in TL of catch). However, one key point is missing to characterize whether we observe FDMFW and/or FTMFW: do the mean TL of the community (i.e., TL of the biomass or density) decrease?

<u>Conclusion</u>:

Based on my general comments above about the quality of the work and its interest for the community, I consider that this manuscript must be published. However, some easily doable but substantial and

necessary modifications in the manuscript structure would definitely benefit to its clarity. The introduction and discussion would also be easily improved by redefining some key concepts that have are highlighted in my review.

Specific comments:

L21 – "are experiencing" -> "have experienced over the 20th century"?

L23-27 – I think here could be clearly mentioned the opposition between the Fishing Down (e.g., Pauly) and the Fishing Through (e.g., Branch) the marine food web. I think this study has the potential to partially assess the relevance of each hypothesis. The key question is: does the decrease in the TL of catches reflect a change in the ecosystem in response to fishing or a changed in the fishing practices? (…the solution being probably a bit of both)

L23 – I would say "more commercially valuable"

L25 – I would mention "diversification" of fish products

L28-30 – So, in the light of my previous comment about fishing down/through, this "variety of ecological situations" don't match all, *per se*, fishing down the marine food web (FDMFW).

L29-31 – Not sure to understand the use of this information here.

L38 – As -> similar to?

L37-38 – The transition between FDMFW and the adaptive harvesting is not obvious for me. But maybe you chose to work with adaptive harvesting simply because it is a way of testing FDMFW vs FTMFW..? Since it allows you to represent the impact of fishing on the trophic network while representing the response of the fishery itself to such changes..?

L54 – Maybe cite 1 ref for the Lotka-Volterra model (even if it's so popular) + please provide some text making explicit the meaning of each equation (what processes are represented through each term?); this will also highlight the assumptions underlying your equations (e.g., the whole natural mortality of N is the mortality inflected by the predator P)

L56-59 – Even if they can differ according to the model, maybe the authors could provide an expl of units for each variable between brackets..?

L56-59 – eN and eP should be already defined there

L59 – Not sure to understand the "intra-guild predation" term here

L60 – Considering a fleet, the effort integrates the number of vessels but also their relative power (linked to boat size, engine power etc). I would even use the term fishery, which is more generic, hence maybe more appropriate for this study.

Eq(2) – Could the authors justify this formula? …Not only citing the references from the literature but also explaining how it is constructed, what it conceptualizes. Once again, this would be the opportunity to precise the underlying assumptions (e.g., fixed costs, price not depending on the fished quantity etc.)

L63-… please define all the variables under the equations. Then, you can bring some details and explanations about each term. Here G is defined too late in the text.

L65-67 – “These effort shares……..specifically harvest prey or predators”. No specific need to mention it if the notion of effort is correctly defined above in the text.

L70-73 – Ok, I finally got the reference! But, as far as I am concerned, the citation should appear right before writing down the equation. I think mentioning pollinators work here is not useful.

L77-79 – Something about how the equilibriums have been calculated is missing. The authors should at least mention the different steps for calculating them: calculation of N, P and eN when considering null derivatives (+ explain why working with null derivative etc.) etc. I don’t think a huge paragraph is required but the reader should understand the principle even if not used to such analytical solving.

L.77… – It is a bit fuzzy for me whether the different equilibriums are a result or are part of the methodology, since they directly derive from the equation system. I would mainly put the derived graphs and figures in the results. For a greater structure we could imagine having a “model” part and an “analytic solving” part in the Mat&Meth. I let the authors think about how to reorganize the Results and the M&M. This would benefit to the Results by making it more straightforward.

L.77 – The notion of equilibrium and its bases and meaning should be better explained/justified

L77-105 – I find the description of the 3 equilibria is very clear!

L106 – 2 “the” + “patterns depend”?

L106-124 – Here I think we clearly miss details about the stable/unstable equilibria. A few lines from the Appendix should be transferred here to explain what they are (+ a few lines about their determination should be added in the Methods part). If such details are provided, I think the Table A2 could be easily transferred to the Results (or Methods, depending on the restructuration of these two parts).

Figure 1 – Nice figure that well illustrate the results. But it would answer way better to the FDMFW/FTMFW question with the trend observed for the TL of the community.

L125-130 – In my opinion, this should be in the Methods part

L133-146 – well described!

L146 – I would put an upper case to “condition” → “Condition (6)” will be clearer

L156-161 – Once again - In my opinion, this should be in the Methods part

L162-174 – This is not at all a result, but it belongs to the methodology! Moreover the authors pack this part off, preventing the reader to understand the interest of these developments.

L162-178 - This part is really interesting. However, as I am gonna mention in the following paragraph, I think that it is less important than the results about the tritrophic structure, that would definitely be relevant for checking the pertinence of FDMFW/FTMFW.

Fig 3 – never defined in the main text what was a Rosenzweig-MacArthur model

L180-191 – See my comment about much more describing the results of the tritrophic here. It is way more interesting than the simple case. Bu the simple case is still useful for setting the bases of the analysis and have a careful look at some patterns that will also be observed with the tritrophic chain.

L195-208 – Review at the light of the opposite hypotheses of FDMFW & FTMFW

L202 – "(Andersen et al. 2015) also showed" Example of citation with remaining brackets. There are several typos like this in the text

L211- "fishery regime" deosn't look very adapted to the situation. Here we more talk about "ecosystem regime shift". Fishing altered the structure of the ecosystem through a trophic cascade, resulting in totally different relative abundance of its different components. The hypothesis is that fishing reflect such changes.

L214-215 – "precise empirical investigations": do the author means quantitative/mechanistic analyses? (hence not being empirical)

L216-220 – In the model description, Krivan and Smith is already cited as a reference for the model elicitation. So, is it a surprise that the results are coherent if the main equations are the same? Could the authors develop what they mean here?

L231 – "We find that adaptive foraging" – the authors have just said that it was not a "foraging" one, right..?

L232 – "regime shift" in the context of this manuscript. Do the authors mean "ecosystem regime shift"?

L231-233 – Yes. But I am not sure it is specific of adaptive fishing. Here, abrupt regime shifts don't systematically involve that characteristic: the regime shift is the consequence of instability and extreme pressure exerted on predators. In that case, the "adaptive" aspect of fishing appears once the regime shift has occurred, when targeting prey becomes more strategic (relatively more abundant than predators).

L236-237 – I am not sure the terms used here are really adapted. The literature the authors refer to is essentially tackling "ecological regime shifts", i.e. changes that are not (or not systematically) caused by fishing but mainly by environmental changes. Sometimes, fishing is described as a factor favoring these shifts but not their main driver. Thus, we can't say "fisheries-induced". Also, a substantial part of the literature that studied fishing as driver of ecosystem regime shifts mainly refer to "trophic cascades", most of the time showing the positive impact of abrupt reduction in the abundance of targeted predator species on their prey, and potentially the negative impact on the latter's prey - Pershing et al 2015 or Frank et al 2005 already cited, or(https://doi.org/10.1098/rstb.2013.0265), Mollmann et al 2008 (https://doi.org/10.1093/icesjms/fsm197), Pace et al 1999 (https://doi.org/10.1016/S0169-5347(99)01723-1) etc. That said, the present work would be, indeed, an interesting way of exploring such top-down impacts of fishing and their propagation through cascades. More recently, several studies have tried to assess the relevance of exploiting lower trophic levels, small pelagic fish (Soudijn et al 2021, https://doi.org/10.1073/pnas.1917079118 ; Hilborn et al 2017, https://doi.org/10.1016/j.fishres.2017.01.008), and quantify the impact on predator dynamics. This might be a nice resource for the discussion.

L245-246 – Maybe could link relatively easily this high conversion efficiency with the traits of small pelagic fish that are a key food resource for marine predators, since they are abundant and most of all, are highly energetic prey, compared with other organisms as small invertebrates.

L228-246 – I find thrilling that idea that a progressive increase in fishing effort can, depending on the cases, trigger an abrupt regime shift or a more continual change up to a gradual FDMFW; and that the type of response is dependent on the stability or instability of the system, itself influenced by the ecological characteristics of the system (carrying capacity) and the species targeted (growth rate, conversion efficiency…), and the fishery efficiency. Maybe this could be formulated in a clearer way in the discussion. The parameters influencing the stability/instability could even be discussed based on the Pershing et al. 2014.

L254-262 – & L275-279 I appreciate the attempts of the authors of linking their theoretical exercise and examples of true fisheries. However, the present model represent very simple case of predator-prey interactions, i.e. single predator feeding on a single prey, both being potentially targeted. In the real world, mixed fisheries include a much wider diversity of species with more complex relationships. Due to such discrepancies between reality and the model complexity, I have some doubts about directly applying this approach at the scale of individual fishermen. Nonetheless, we could imagine that the insights collected about the trade-offs between different target species and the speed at which they are happen could mobilized in more applied approaches. More generally, I find very useful the present work in a highly aggregated scale, especially in the context of exploring the FDTMFW phenomenon or trophic cascades.

TableA1 – I would maybe merge this one with the Table A2, slightly simplify it, and transfer it to the results..? Just letting the mathematical developments in this Appendix.

Appendix C – I think I've already said several times that this part would be relevant in the main text ;) Even if the authors don't choose to put everything from that section, one pertinent figure, the associated text and the reference to what remains in the Appendix would be great.