

Dear Editor,

We are glad that you found our manuscript of interest. In the revised version, we have followed your guidelines, as detailed below in red. In particular, we added the tritrophic model in the main text, and modified the title and abstract accordingly. We thank you and the referees for their work and useful comments.

Best regards,

Dr. Eric Tromeur

Pr. Nicolas Loeuille

Editor : Merits Revision to Improve Clarity and Thread

This preprint has the potential to provide a clear mathematical representation of how adaptive fishing, depending on fishing effort and the speed at which the fishermen can switch between harvesting predator and prey, can destabilize food webs and lower the mean catch trophic level (i.e. fishing down the food web). The general methods used appear sound and appropriate to tackle the question at hand. There are some issues, however, raised by the reviewers that should be addressed before the pre-print is recommended. The preprint would benefit from some further clarification, and some re-arrangement of the text to increase the readability and to clarify how the models specifically address your question for a wider audience.

Recommendations from reviewers to be included in revision:

1. Clarify the common thread of the manuscript, which should be supported by methods.
2. Plain language summaries and conceptual diagram for what you would expect to see for different model outcomes and what they mean in terms of fishing down the food web, to clarify how the models represent different scenarios for a wider audience.
3. The tri-trophic model best represents the fishing down the food web thread, you should consider including in the main text.
3. More information in the "Material and Methods" section, moving some from the Results and Appendixes, and filling in some missing information, to increase the ability to reproduce the results.

In addition the reviewers provide many useful specific comments that should be addressed to improve the manuscript.

We are glad that you found our manuscript of interest. In the revised version, we have followed your guidelines, as detailed below. We thank you and the referees for their work and useful comments.

Review by anonymous

Broadly the authors set out to do two things. First is to model populations dynamics as a function of different harvesting behaviour (strategies), namely a predator, prey, or mixed fishing approach. The second is to assess the resilliance of these systems based on the different harvesting strategies. And although the objectives are clear I feel that a clear 'take home message' is missing (or I have struggled to grasp it) - but I think the results seem to suggest that an adaptive fishing strategy (that focuses on harvesting a select group of species based on population trends) is more likely to result in a more 'stable'/resilient system. With the caveat that this will also be strongly inflounced/hampered/modified by economic factors (the return on catch).

Actually, the main messages are two fold : (1) adaptive harvesting naturally leads to fishing down the food web patterns, a key message we feel is quite new ; (2) adaptation in the harvesting process is actually here not stabilizing, as it can lead to positive feedback loops (see figure 2). We have tried to highlight better these take home messages in the new version of the manuscript :

« Our results suggest that adaptive harvesting results in the progressive decline in the mean trophic level of catches. Therefore, fishing down the food web naturally emerges from the adaptive harvesting in our model. Interestingly, our results also suggest that such an adaptive behaviour may be harmful for the overall resilience of the system. » (lines 52-55)

My main concern with this manuscript is not very clear/easy to follow which might make it less accessible to more general readers - the paper itself presents a lot of models/conditions that ahve multiple parameters for three different scenarios which means there is a lot of information that needs to be absorbed. I think there would be benefit in potentially trying to phrase some things in 'plain language' alongside the mathematical derivative (particularly the conditions for stability). This could also be aided by linking to supplementary table 2A at the begining of the results section as it was nice to see all the different conditions presented side-by-side.

We have amply rewritten the presentation of the results in the new version of the manuscript. We used plain language as much as possible. We also added a simplified version of Table A2 in the result section.

Building on this a conceptual figure could be particulalry useful. Although figure 1 (particularly b) are helpful I found myself wishing for a figure that sort of showcased the population dynamics of predator and prey over time under different the harvesting strategies - potentially even showcasing some of the 'tipping points' as conditions for equilibrium/stability become violated. I feel like this presents a more intuitive way to think of population dynamics - although I'm uncertain as to how easy it will be to implement since the total effort also paly a role in shaping these dynamics and adds another layer of complexity.

Thank you for this relevant suggestion. Note however that we here assess the sustainability of the fishing activities based on the computations of yield and ecological states in the long run (ie, at equilibrium), not on the population dynamics themselves. We think that presenting population dynamics may actually confuse the readers rather than clarifying our general method.

Is it possible to avoid the use of 'condition 6' in the text? I find that I have to remind myself of this condition constatly and it might be easier to rater use a 'plain language phrasing' and link to eq. 6 is parenthesis

Thank you for the relevant suggestion. We rephrased the text accordingly.

Please define μ (l. 56). It is unclear what predator-to-prey conversion efficiency means.

We now define μ explicitly in the text.

Results: A subheader after l. 155 to designate the resilience section here might be nice to break up this section (the preceding section could also be subheader-ed if so desired)

We agree and we created a subsection dedicated to resilience and stability analysis.

Figure captions/legends. This may be tedious but please rediefine parameters. There are many and it is not always intuitive - this is particulalry the case for figure 2.

We have reworked the captions and now define parameters where needed, paying a particular attention to Figure 2.

Figure 1.b The numbers are discussed in text but I think it would be good to either include a description in the figure caption or to see if these could be inculded on the figure itself.

We have reworked the figure caption to clarify the meaning of (1) to (4).

Review by Pierre-Yves Hervann

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.

We are glad that the reviewer found our analysis of interest and we thank him for his work and comments. We have tried to account for his remarks and we feel the manuscript is greatly improved as a result.

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.

Thank you for this useful comment. We have reworked the method presentation accordingly. We transferred various components in the method section, including the definition of resilience, as well as the presentation of the ecological models (Rosenzweig-MacArthur model and the three-species model).

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.

We have tried to improve the communication between the result part and the appendices and we added a simplified version of the summary table in the main text.

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.

Thank you for your appreciation of these results. We agree. Actually, the mathematical treatment of the three species model is not possible and we can only do simulations there. However, we completely agree that this analysis is important, as it suggests that the pattern we get is not restricted to two species models, but may also happen in more complex systems. We therefore transferred the three-species model description and results in the main text.

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.

We have reworked the presentation of the main results. We hope that the text is now clearer in the revised manuscript. As suggested this includes the analysis of the three-species model in the main text.

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?

Thank you for this relevant suggestion. We now refer to the ecosystem MTL in the Results, and we added a specific paragraph in the Discussion on catch and ecosystem MTL indicators.

Conclusion:

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”?

We rephrased accordingly

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)

Actually, as explained by Branch et al. (2010), "There are at least two ways that fishing down the food web could occur. The first is through the sequential replacement of high-value upper-trophic-level species with less valuable lower-trophic-level species as the former are depleted to economic extinction. The second mechanism is through the sequential addition of lower-trophic-level fisheries within an ecosystem. We refer to the latter mode as “fishing through the food web” to emphasize that fisheries for high-trophic-level species are maintained despite a decline in the overall mean trophic level of landings. "

Our results would be more coherent with the first mechanism. We make it clearer in the revised manuscript.

L23 – I would say “more commercially valuable”

We rephrased accordingly.

L25 – I would mention “diversification” of fish products

We do not mention diversification elsewhere in the paper, so we prefer not to add this term here.

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).

We hope that our clarifications on this (based on the previous concept) will allow the reader to better grasp what we mean here when referring to the fishing down the food web.

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

We agree and we deleted this sentence

L38 – As -> similar to?

We rephrased.

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 FTMFV..? 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..?

We have reworked the text and now propose a little more details to make this link clearer.

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 inflicted by the predator P)

We have paid extra attention to clearly define in plain language the various parameters of equations (1) just below them, so that their biological meaning should be accessible, including for non-theoreticians.

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..?

We have followed your suggestion and now make the dimensions of the various parameters and variables explicit.

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

We have followed your suggestion to define these two parameters earlier.

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

We removed this sentence, as we agree that it may be unclear for some readers and because it is not really necessary or central 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.

We now use the term fishery here.

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.)

We have rewritten the presentation of equation (2) to clarify its components and its implicit assumptions.

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.

We have followed your suggestion and we now define G earlier.

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.

We rephrased accordingly.

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

We now introduce replicator dynamics earlier. And we deleted the reference to work on pollinators.

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.

We have followed this suggestion and now state more explicitly how the mathematical analysis is handled.

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.

We believe that analysis of the different equilibria and their stability condition is very important, and should therefore be in the Result section. Figure 1 is only an illustration of these analytical results. Analytic solving is a result and usually put in result sections in theoretical articles.

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

It is now explained.

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

Thank you!

L106 – 2 “the” + “patterns depend”?

We rephrased accordingly.

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).

We added a section on Local stability analysis and resilience calculation in the Methods part of the paper.

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.

As explained earlier, we now refer to the ecosystem MTL in the decription of the Results, and we added a paragraph in the Discussion on ecosystem and catch MTL indicators.

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

We believe it is useful to have this information here.

L133-146 – well described!
Thank you!

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

As suggested by the other reviewer, we now write it with more explicit terms

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

We put it in the Methods.

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.

We now present this model in the Method part.

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.

We are glad you like this analysis. We have included the tritrophic model in the main text.

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

We now mention it in the main text.

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.

We included the tritrophic model in the main text.

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

These are not opposite hypotheses, according to Branch et al. (2010).

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

Done.

L211- “fishery regime” doesn’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.

Actually, the Frank et al (2005) paper precisely mentions that what shifted was the fishery regime. We feel it is important to include here, as not many instances of shifts are actually clearly documented in the literature.

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

We mean "precise empirical investigations", empirical data that would for instance link changes in catches with changes in fishing practices.

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?

The model is actually quite different as in their model the top predator density is allowed to vary. This difference is highlighted just below. The global idea of our model is similar to adaptive foraging models, so we agree it is somewhat normal that results are similar!

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

We changed to "adaptive harvesting".

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

Actually, it should be called a "socio-ecosystem regime shift", as both ecological (prey and predator densities) and economic (share of effort) parameters here shift abruptly.

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).

We do not refer to adaptive harvesting. We refer to social-ecological feedbacks in general. We rephrased the text for clarification.

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”.

We agree and followed your suggestion, ie, we changed to "ecological regime shift".

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](https://doi.org/10.1016/S0169-5347(99)01723-1)) etc.

We have reworked the text to better acknowledged the role of "trophic cascades" (now explicitly defined) in the main text.

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.

Thank you for these very interesting papers, we included them at the end of the discussion, when discussing the limits of our model.

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.

While we agree in principle, we could not find empirical assessments allowing us to make this link.

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.

Thank you, we also find this idea quite intriguing. We have reworked the texte to make it clearer

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.

We fully agree. Actually, as we stress at the very end of the manuscript, we view this use of simple models as a tool to highlight key feedback processes, not really to guide management for a precise situation.

Table A1 – 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.

We merged Table A1 and Table A2, and we included it in the main text in a simplified version (without the last line of Table A1), as Table 1. Note however that we kept the complete version of Table A1 and Table A2 (with the last line, that displays the relationship between feasibility and stability conditions) in the 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.

We put the three-species model in the main text.