Peer Community In Ecology

“Hidden” natural selection and the evolution of body size in harvested stocks

Simon Blanchet *based on peer reviews by* ***Jean-François Arnoldi*** *and 1 anonymous reviewer*

Eric Edeline and Nicolas Loeuille (2021) Size-dependent eco-evolutionary feedbacks in fisheries. bioRxiv, ver. 1, peer-reviewed and recommended by Peer Community in Ecology.
https://doi.org/10.1101/2020.04.03.022905

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Humans are exploiting biological resources since thousands of years. Exploitation of biological resources has become particularly intense since the beginning of the 20th century and the steep increase in the worldwide human population size. Marine and freshwater fishes are not exception to that rule, and they have been (and continue to be) strongly harvested as a source of proteins for humans. For some species, fishery has been so intense that natural stocks have virtually collapsed in only a few decades. The worst example begin that of the Northwest Atlantic cod that has declined by more than 95% of its historical biomasses in only 20-30 years of intensive exploitation (Frank et al. 2005). These rapid and steep changes in biomasses have huge impacts on the entire ecosystems since species targeted by fisheries are often at the top of trophic chains (Frank et al. 2005).

Beyond demographic impacts, fisheries also have evolutionary impacts on populations, which can also indirectly alter ecosystems (Uusi-Heikkilä et al. 2015; Palkovacs et al. 2018). Fishermen generally focus on the largest specimens, and hence exert a strong selective pressure against these largest fish (which is called “harvest selection”). There is now ample evidence that harvest selection can lead to rapid evolutionary changes in natural populations toward small individuals (Kuparinen & Festa-Bianchet 2017). These evolutionary changes are of course undesirable from a human perspective, and have attracted many scientific questions. Nonetheless, the consequence of harvest selection is not always observable in natural populations, and there are cases in which no phenotypic change (or on the contrary an increase in mean body size) has been observed after intense harvest pressures. In a conceptual Essay, Edeline and Loeuille (Edeline & Loeuille 2020) propose novel ideas to explain why the evolutionary consequences of harvest selection can be so diverse, and how a cross talk between ecological and evolutionary dynamics can explain patterns observed in natural stocks.

The general and novel concept proposed by Edeline and Loeuille is actually as old as Darwin’s book; The Origin of Species (Darwin 1859). It is based on the simple idea that natural selection acting on harvested

populations can actually be strong, and counter-balance (or on the contrary reinforce) the evolutionary consequence of harvest selection. Although simple, the idea that natural and harvest selection are jointly shaping contemporary evolution of exploited populations lead to various and sometimes complex scenarios that can (i) explain unresolved empirical patterns and (ii) refine predictions regarding the long-term viability of exploited populations.

The Edeline and Loeuille's crafty inspiration is that natural selection acting on exploited populations is itself an indirect consequence of harvest (Edeline & Loeuille 2020). They suggest that, by modifying the size structure of populations (a key parameter for ecological interactions), harvest indirectly alters interactions between populations and their biotic environment through competition and predation, which changes the ecological theatre and hence the selective pressures acting back to populations. They named this process "size-dependent eco-evolutionary feedback loops" and develop several scenarios in which these feedback loops ultimately deviate the evolutionary outcome of harvest selection from expectation. The scenarios they explore are based on strong theoretical knowledge, and range from simple ones in which a single species (the harvest species) is evolving to more complex (and realistic) ones in which multiple (e.g. the harvest species and its prey) species are co-evolving.

I will not come into the details of each scenario here, and I will let the readers (re-)discovering the complex beauty of biological life and natural selection. Nonetheless, I will emphasize the importance of considering these eco-evolutionary processes altogether to fully grasp the response of exploited populations. Edeline and Loeuille convincingly demonstrate that reduced body size due to harvest selection is obviously not the only response of exploited fish populations when natural selection is jointly considered (Edeline & Loeuille 2020). On the contrary, they show that –under some realistic ecological circumstances relaxing exploitative competition due to reduced population densities- natural selection can act antagonistically, and hence favour stable body size in exploited populations. Although this seems further desirable from a human perspective than a downsizing of exploited populations, it is actually mere window dressing as Edeline and Loeuille further showed that this response is accompanied by an erosion of the evolvability –and hence a lowest probability of long-term persistence- of these exploited populations.

Humans, by exploiting biological resources, are breaking the relative equilibrium of complex entities, and the response of populations to this disturbance is itself often complex and heterogeneous. In this Essay, Edeline and Loeuille provide –under simple terms- the theoretical and conceptual bases required to improve predictions regarding the evolutionary responses of natural populations to exploitation by humans (Edeline & Loeuille 2020). An important next step will be to generate data and methods allowing confronting the empirical reality to these novel concepts (e.g. (Monk et al. 2021), so as to identify the most likely evolutionary scenarios sustaining biological responses of exploited populations, and hence to set the best management plans for the long-term sustainability of these populations.

References:

Darwin, C. (1859). On the Origin of Species by Means of Natural Selection. John Murray, London.

Edeline, E. & Loeuille, N. (2021) Size-dependent eco-evolutionary feedbacks in fisheries. bioRxiv, 2020.04.03.022905, ver. 4 peer-reviewed and recommended by PCI Ecology. doi: https://doi.org/10.1101/2020.04.03.022905

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Uusi-Heikkilä, S., Whiteley, A.R., Kuparinen, A., Matsumura, S., Venturelli, P.A., Wolter, C., et al. (2015). The evolutionary legacy of size-selective harvesting extends from genes to populations. Evol. Appl., 8, 597–620. doi: https://doi.org/10.1111/eva.12268

Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.1101/2020.04.03.022905
Version of the preprint: https://www.biorxiv.org/content/10.1101/2020.04.03.022905v2

Authors' reply, 01 March 2021

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Decision by Simon Blanchet, posted 05 February 2021

Minor revisions before recommendation

Dear Authors

Thanks a lot for the thorough revision of you MS entitled "Size-dependent eco-evolutionary feedbacks in fisheries". I have read both the replies to referees' comments and the new version of the MS and I must say that you've done a very good job. The MS is not much more easier to read and the message is flowing very well.

Before I write my recommendation, I have a few more minor comments that you may consider:

-The term "fisheries" appears in the text but there is no argument for targeting this specific type of harvest. I would add a few words by the end of the Introduction to stipulate that most (though not all) examples in the text are from the fishery literature, and why it is important to reply these specific fundamental questions in fishery science (eg because these wild populations are harvested at a worldwide scale and constitute an essential source or proteins).

-L. 79: change "assay" per "essay"

-L. 80: you briefly mention the paper by Kinnison et al. (2015) about cryptic eco-evo: I would provide a few words about this paper and explain why it is a follow-up of this paper.

-L. 96: papers by Hendry and Kinnison (1999, 2000) about fast evolution might also be cited.

-L. 97: I would remove the end of the sentence "...but readers [...] to Section 2".

-L. 160-161: see the recent paper by Kurt Fausch (https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2656.13384). Potentially useful. -L. 171: Change for: "This is true for both aquatic and terrestrial systems (ref)..."

-L 177: Add the latin name for the northen pike.

-L. 197: Check Griffith et al. PNAS 2020 (https://www.pnas.org/content/117/29/17068). Potentially

interesting too.
-L. 250: Add ”effective” before ”population size”. The correlation is generally between genetic diversity and effective population size. Papers by Robin Waples and others might be cited there as this correlation is well known.
-L. 357: Perhaps cite Peralla and Kuparinen 2020 here (already cited after)
-L. 379: You may look at Raffard et al 2020 (https://www.biorxiv.org/content/10.1101/2020.06.10.144337v3) in which we show that change in the variance in the body size of predator populations affect both the brown and green trophic chains through top-down effects. There are probably other experimental papers on the effect of body size on ecosystem functioning.
-L. 452: the negative relationship between body size and genetic diversity is rather well documented, see for instance: De Kort et al. Nat Comm 2020 (https://www.nature.com/articles/s41467-021-20958-2) and Romiguier et al Nature 2014 (https://www.nature.com/articles/nature13685)
-L. 480: Yacine et al is lacking in the reference list.

Good luck

Simon Blanchet

Additional comments from the Managing board

Mandatory modifications

1- Please make sure that:
-Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data. -Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused. -Details on experimental procedures are available to readers in the text or as appendices. Include information about ethical approval for animal experimentation. Provide information about the compliance of their work with ethical standards of their national ethical committees and report the reference number of the ethical committee approval. If the study did not require ethical approval, include some sentences explaining why the approval was not needed.
-Authors have no financial conflict of interest relating to the article. The article must contain a ”Conflict of interest disclosure” paragraph before the reference section containing this sentence: ”The authors of this preprint declare that they have no financial conflict of interest with the content of this article.” If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: ”XXX is one of the PCI Ecology recommenders.”
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3- If not yet done, please send us a picture for which you own the rights that could serve as a thumbnail/illustration for your article on the web site of PCI. It can be a figure of the article.

Optional instructions (we strongly advise you to follow them)

1- We suggest you to remove line numbering from the preprint and put the tables and figures within the text rather than at the end of your MS.
2- Then, we strongly advise you to use the PCI templates (word docx template or latex template) to format your preprint in a PCI style. Here is the links of the templates: https://peercommunityin.org/templates/

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-the text to be replaced by your own text starts with XXX, eg XXXXTitle of the article.
-XXXXthe "cite*as*" *Edeline, E. and Loeuille, N. (2021) Size-dependent eco-evolutionary feedbacks in fisheries. bioRxiv, 2020.04.03.022905, ver. 3 peer-reviewed and recommended by PCI Ecology. doi: https://doi.org/10.1101/2020.04.03.022905*
-XXXXthe date of deposit in the preprint server date of the deposit of the latest version
-XXXXthe surnames and names of the reviewers we sent you Jean-François Arnoldi and an anonymous reviewer
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Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2020.04.03.022905

Authors' reply, 26 January 2021

Dear Simon Blanchet,

We very much appreciated the insightful and constructive comments provided by you, Jean-François Arnoldi and the anonymous reviewer. These comments made us realize that the paper was far too long and complex. In the process of solving this issue, we have profoundly rearranged the whole text. Specifically, in carefully addressing the comments we have: • shortened the whole text from 7721 to less than 6800 words, • reduced the number of figures from six to four, • reworked the whole text so as to provide more explanations or remove unnecessary complexities where needed, • provided the general objectives and overview of the paper in the last paragraph of the introduction, • moved the section describing size-dependent natural selection in the first section, • removed the whole sections dealing with intraguild predation and alternative stable states, • clarified our framework for describing antagonistic and synergistic EEFLs in Fig. 2, • refined the description of EEFLs involved in predator-prey co-evolution (Section 3), including providing a new version of the associated figure (now Fig. 4), • added in Section 4 a Box 2 providing guidance on how to advance our empirical knowledge of EEFLs.

We feel that these changes strongly improved the quality of our manuscript. As requested, we provide a point-by-point response to tour and the reviewers' comments (enclosed).

All persons entitled to authorship have been included and both Nicolas Loeuille and I have read and approved the revised version of this manuscript.

On behalf of Nicolas Loeuille,

Sincerely yours,

Eric Edeline

Download author's reply

Decision by Simon Blanchet, posted 23 May 2020

Revision required

Dear Authors,

Two reviewers have now read the MS, and as you will see both of them found it interesting and timely. I also read it and I also found it very interesting. However, they both raised some concerns that were mostly related to the clarity of the text; one of the referee found it "long" and the other one read it "three times" to fully grasp the story. As a result, they both suggest finding a way to simplify the message and/or re-organize the MS, without providing clear guidance. I must admit that the MS is long and that it needs full concentration to be read at once. I would suggest authors re-working on the introduction (last paragraph at the least) to provide a more thorough plan of the paper with extremely clear objectives. This is important for this type of paper that objectives are clear from the introduction and that a plan is provided (there is currently a plan but it is not elaborated enough). Also, I would suggest synthesizing further section 2 (size-dependent selection) that is important but a bit away from the main objective (perhaps including this information in a box ?). Section 4 (multispecific EEFLS could be reduced in length; it is the most speculative, the less documented and I think there a re few redundancy in the text.

As another note, I what a bit disappointed not to see a section or box about what we must/should do next from an empirical, experimental or theoretical point of view. I think this type of "speculative" paper should provide guidance for future researches as it paves the way toward new research avenues.

Finally, the paper is about harvest (which includes fishery but not only) but almost all examples and all biological foundation (section 2) are fish-based. The paper is actually about fishery and this should make it clear from the beginning. After the introduction I was expecting examples about mammal harvesting or any other types of harvests, but no, it is mainly about fish (which is fine for me!). So if it is about fish, tell it explicitly. Note that I also attached a pdf file with some minor comments.

I hope these comments will be helpful to improve this nice and important piece of work.

Best wishes

Simon Blanchet

Additional requirements of the managing board:

As indicated in the 'How does it work?' section and in the code of conduct, please make sure that:

-Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data.

-Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused.

-Details on experimental procedures are available to readers in the text or as appendices.

-Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is one of the PCI XXX recommenders." **Download recommender's annotations**

Reviewed by anonymous reviewer 1, 06 May 2020

I think the topic of this review was rather interesting and touches upon a timely question. I really enjoyed the idea of integrating natural selection with fisheries selection, and particularly how natural selection could further change due to eco-evolutionary feedback loops.

However, I must say that I read the manuscript three times and was still rather confused how the different mechanisms driving the feedback loops led to changes in natural selection. Exploitative competition and fisheries selection favor small body size. Because of size-selective fisheries, there will be lots of small fish in the population. How does this decrease exploitative competition? If anything, shouldn't it increase that? Therefore, it was not clear to me how these two selection forces together increase the probability of extinction. Interference and cannibalism select for large body size. Removing large, dominant, cannibalistic individuals creates better conditions for small fish and increase their fitness. This idea I get.

As the authors also acknowledge, all of the processes they introduce will likely occur simultaneously and therefore it is difficult to make any clear, realistic predictions. However, it is good to identify these processes although those occurring in the food web likely requires a network model. As I mentioned, I read the manuscript several times, yet I was left rather confused and not super convinced. I think the authors need to clarify the text a lot and perhaps add concrete examples of the processes. It is not easy to explain in a simple way eco-evolutionary processes but there must be a way. If possible, the review could be more focused.

Reviewed by Jean-François Arnoldi, 18 May 2020

This manuscript by Edeline and Loeuille focuses on the role of evolution in shaping the responses of fish populations to harvesting. In particular, they review many plausible scenarios of adaptive responses driven by eco-evolutionary feedbacks (EEFL) where harvesting can alter not only the target population but also the natural selective forces acting upon it.

The paper proceeds as a review, both of empirical evidence (not only in fish) for various mechanisms entering in EEFL and eco-evolutionary models used to describe them. Overall it is quite interesting, well written and extremely well documented. It should be noted, however, that I am not an expert of neither fisheries nor evolutionary dynamics, so I cannot vouch for the relevance of the literature cited. I do have two main points that I believe should be addressed, one conceptual, one presentational.

My conceptual point is about the notion of fitness landscape, as represented in Fig.2 which is at the base of most of the paper.

The way I understand what a fitness landscape is, in relation to adaptive dynamics (Box 1), is that its gradient represents how invadable the resident population is, by closely related phenotypes (here body size). Thus, along evolutionary dynamics, the phenotype climbs the fitness landscape until it reaches an uninvadvable point (or branches out). Fitness is relative to the surrounding phenotypes. But in figure 2, it seems that fitness is an absolute feature of the resident population, related to its persistence, such as its growth rate, or population size (see the line representing an extinction threshold in Fig. 2). I probably misunderstood completely the authors point, but just to be clear, If fitness is resident growth rate, we run into trouble if the resident population is stationary and thus its growth rate is zero, no matter what the fitness landscape may be (in the sense of adaptive dynamics). If we think of fitness as related to population size, it is easy to imagine scenarios in which evolution (which increases fitness by definition) would nonetheless lead to smaller population sizes. Thus, I urge the authors to make crystal clear the assumptions that go into drawing their figure, and lay the basis for their subsequent reasonings.

My presentational point is about the length and structure of the paper.

I find the paper very long, and hard to follow since was not clear to me, at first reading, what the authors contribution was. After a while I understood that they were reviewing many plausible scenarios, without going too much in the details of any, about EEFL. This is fine, but should be announced very clearly. And since one doesn't not need to known one scenario to understand another, the structure of the paper should be designed

so that it becomes easily consulted, depending on what teh reader is interested in. I'm not sure how to do that, since I never wrote a paper of the kind, but I am convinced that giving some serious thoughts into crafting an appropriate reader-friendly structure would greatly benefit the paper.

In hope that these comments will help the authors, Best regards Jean-Francois Arnoldi