

## Population level effects of acoustic disturbance in Atlantic cod: a size-structured analysis based on energy budgets

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### Article citation details

*Proc. R. Soc. B* **287**: 20200490.

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### Review timeline

Original submission: 19 August 2019

1st revised submission: 2 March 2020

2nd revised submission: 1 May 2020

Final acceptance: 24 May 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

## Review History

### RSPB-2019-1930.R0 (Original submission)

Review form: Reviewer 1

#### Recommendation

Accept with minor revision (please list in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Good

**General interest: Is the paper of sufficient general interest?**

Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**

Good

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

N/A

**Is it clear?**

N/A

**Is it adequate?**

N/A

**Do you have any ethical concerns with this paper?**

No

### **Comments to the Author**

General comments

This is an interesting and important study presenting a modelling approach to assess the consequences of noise disturbance on fish populations. Even though the model is parameterized for a specific cod population, it remains largely theoretical, because there is currently no empirical information on either the exposure rates of individual fish to various noise sources or the actual responses to noise exposure. The authors use the model to investigate the relative importance of different types of effects on long-term population dynamics, and conclude that sub-lethal effects on the energy budget (either via an increased energy expenditure or a decreased energy acquisition) have the potential to cause stronger effects on the population's growth rate than direct effects on survival and reproduction. These results are relevant for designing future experiments as well as effective mitigation measures for the management of noise.

I don't have any major concern with the modelling approach or the main conclusions of the study. However I believe that the presentation of the methods could be improved, to avoid confusion. I detail below the various sections of the manuscript where I think this can be done, but first I have some general points for the authors to consider.

When referring to the effects of noise exposure on reproductive success, I would make sure to mention on all occasions that these are direct effects on reproductive success. There is often confusion between these effects and the indirect decline in reproductive output that is mediated by changes in the energy budget. Generally, it would help if the authors avoided switching among reproductive success, lifetime reproductive output, fecundity, and reproduction. If these terms are meant to represent different vital rates, then they should be defined and used consistently, otherwise I would choose one and use it throughout. An improvement of the terminology would also help in relation to the energetic costs; it might be better to refer to increased energy expenditure, because a reduced energy acquisition via decreased food intake could also be thought of as a net energetic cost of noise exposure. In other words, an increased cost and a decreased food intake ultimately operate via the same pathway, that is, a disruption of the energy budget.

In the Methods, the authors discuss at length the potential responses to noise and the resulting short-term effects. I found several aspects of this confusing: the terminology is not consistent, some of the responses (as well as the short term effects) could be interrelated (e.g. stress can also cause changes in foraging or movement behavior); there is no distinction between acute and

chronic noise, and how these two forms of exposure may follow different response pathways (e.g., the potential but undocumented effects of changed foraging behavior on survival and reproduction in Table 1 are mediated by reduced food intake). Ultimately, I don't think this discussion is relevant to the current study, because of how the effects of noise disturbance are modelled: the exact response is not modelled explicitly; instead, the effects of the various potential responses are simply condensed in a single parameter in each of the formulas for metabolic rate, ingestion, mortality or reproduction. None of these functions is reported in the main text, so the reader is left wondering how these processes are teased apart in the model. I would simplify the presentation of disturbance, describe the direct effects that are modelled, and mention in the Discussion that these can be caused by a variety of responses. In general, there is currently not enough detail in the main text with regard to the simulation of disturbance, so I think those relationships should be brought in from the supplementary material. In contrast, I think Table 1 can be moved to supplementary because it is not relevant to this modelling exercise.

Finally, I would have liked to see a bit more discussion on the way disturbance is modelled and whether this has the potential to affect the results. At the moment, the effects of disturbance are simulated as additive components to the basal rates (be it the basal metabolism, energy intake, mortality or reproductive output). Would a different shape of such functions affect the conclusions on the importance for long-term population dynamics?

From a stylistic perspective, the language could be made more concise and less convoluted. There are a few long sentences where the verb and the direct object (e.g. lines 101-102) or the modal verb and the following verb (e.g. lines 30-31) are separated by a clause, which are difficult to read. Tightening up some of the text and avoiding repetitions could help save space that could then be used to bring in some additional details regarding the model structure from the supplementary material.

Detailed comments:

Line 31: I would change "through... the auditory system" to "through... effects on the auditory system".

Line 33: it is unclear what "these factors" refer to, the effects or the mechanisms; I would change "factors" to "effects".

Line 36: is it worth mentioning the mechanisms by which this might be the case (e.g. lines 226-243 of the Results)?

Lines 44-45: this sentence is out of context in this paragraph; maybe move it below, when introducing the effects of noise on fish.

Line 46: isn't this increase in ambient noise associated with shipping/low frequency noise? Other sources of noise are certainly important, but are not reflected in these long-term trends. I think the sentence needs some rephrasing.

Line 57: this phrasing is misleading. PCAD (now PCoD) has been originally developed for the effects of noise on marine mammals, and is not "generally used"; I would rephrase to something along the lines of "The Population Consequences of Disturbance approach (PCoD) is an effective framework for the analysis of population-level effects of sublethal disturbance, originally developed for marine mammals" and reference both the original National Research Council report (NRC 2005) and the recent PCoD review (Pirodda et al. 2018 Ecology and Evolution).

Line 64: I would change "old" to "pre-exploitation".

Line 71: this is misleading. You do not test for the effects, but for the relative importance of different types of pathways via which noise can impact cod population growth rate.

Lines 72-75: this sentence contains too much detail on the methods for the Introduction. Instead, I would integrate it with the following paragraph (to avoid repetitions and improve conciseness), and expand on these pathways, the associated evidence from the meta-analysis, and why assessing their relative importance is relevant.

Line 89: some of the terminology in Table 1 is confusing (the term "effects" is sometimes used with reference to responses and sometimes to consequences). In the main text and in Table 1 (and its caption), you need to clearly define and distinguish responses (physiological or behavioural; e.g. stress, movement...), from short-term effects on individual-processes, and long-term

population-level consequences, and be consistent throughout. Also, this section needs some tightening to make the message clearer and avoid repetitions.

Line 104: but isn't this an effect on reproductive success, which could have large, direct consequences on this rate and thus increase the relative importance compared to energetic and feeding intake?

Lines 94-109: why is this section included in the methods, considering the actual responses to noise are not modelled explicitly? Disturbance is a unit-less parameter that modifies basal rates, so all this discussion is confusing (as well as slightly contentious). I would remove it and instead describe how disturbance is modelled.

Line 110: This section is vague and does not provide much detail on the actual model. Instead, the reader is repeatedly referred to the supplementary material. I understand that it is impossible, given the length constraints, to bring all those details in the main text, but I think the reader should be able to find, in the main text, some more information about the shape of these functions. I would ask the authors to consider how they could bring in some of those details. As I stated above, I do think that more details are certainly required for the effects of disturbance (lines 131-138).

Line 120: Please clarify what you mean by "partial disturbance".

Line 124: I am unsure about the implications of this assumption. Does that mean that an individual's energy level cannot get so low that it dies? What if disturbance brings the energy level to the minimum: would this not affect an animal's survival?

Line 146: Please define  $L(A_n, r)$ .

Lines 148-150: This sentence is convoluted, please rephrase and simplify.

Line 199: Didn't you say above (line 190) that the intermediate and low feeding level were indeed adjusted to reproduce these growth curves? This is not a validation then, you calibrated the model in this way.

Line 201: this discrepancy between predicted and observed fecundity at larger size is not discussed elsewhere. What does it suggest? Does it matter?

Line 241: I'm not clear on why reproductive failure does not affect fecundity.

Line 246: except for the fecundity of large fish, a discrepancy that is not acknowledged in the discussion.

Line 272: this is an example where specifying that you are referring to direct reproductive success would help. Energetic disruptions will ultimately affect reproductive success, so this sentence could be misleading.

Line 286: there are now several examples in the marine mammal literature that have assessed effects over an individual's lifetime, including using bioenergetic modelling; please rephrase and provide some of these references (e.g. Nabe-Nielsen et al 2018 *Cons Letters*, Pirotta et al 2019 *Oikos*, McHuron et al 2018 *Ecol Modelling*, Villegas-Amtmann et al 2017 *ESR*, Farmer et al 2018 *Biological Conservation*).

Line 299: "probably display some sort of seasonality" is a vague formulation. I would change to "could display seasonal variation".

Line 314: Worth mentioning a couple of examples for the reader to appreciate the difference from the measures listed in association with acute effects.

Line 330: typo "is has".

Figure 1C: This figure is unclear. How is fisheries retention defined? What are the blue and green vertical lines?

## Review form: Reviewer 2

### Recommendation

Reject – article is not of sufficient interest (we will consider a transfer to another journal)

### Scientific importance: Is the manuscript an original and important contribution to its field?

Acceptable

**General interest: Is the paper of sufficient general interest?**

Acceptable

**Quality of the paper: Is the overall quality of the paper suitable?**

Marginal

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

Yes

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

N/A

**Is it clear?**

N/A

**Is it adequate?**

N/A

**Do you have any ethical concerns with this paper?**

No

**Comments to the Author**

Review of RSPB-2019-1930

“Population level effects of acoustic disturbance in North Sea cod: a size-structured analysis based on energy-budgets.” By Soudijn et al.

The paper addresses an important question on how underwater sound may affect North Sea (NS) cod at the population level. Unfortunately, I think that the paper as it stands currently falls short of the goals stated at the onset of the study. My main concern is the weak link between the model and data from the field (figure 2 is a start, but is not sufficient). This leave the paper with a list of theoretical results, that may or may not be relevant for cod in the NS. These results are of course interesting, but it would then demand a major rewrite of the paper to tone down the link to NS cod.

This brings up a second major question, why did the authors choose this framework? In my opinion, the choice of modelling framework seems arbitrary. A full time resolved model seems unnecessary to address the question of sound effects at the population level? A more classical difference equation (matrix model) would suffice and would be much easier to link to data. In addition, I find it peculiar (especially with the detailed modelling of time and pulsed reproduction) that the authors decide to leave out (lines 103-106) the effect of fish leaving the spawning ground (and potentially becoming egg bound, associated with very high mortality) due to acoustic disturbance. This is potentially the most important effect of sound on fish at the population level, and the model is able to account for such effects. By neglecting this process, the authors introduce a potentially serious bias in the model predictions that I believe affect the main conclusions of the paper (lines 33-35):

“Our results show that changes in energetic costs and food intake reduce population growth rates more than changes in mortality and reproduction.”

Moreover, I find the mis-match between investigating sound sources that are mainly point sources of limited duration (e.g. pile driving, seismic surveys etc.) and using a long-term population growth rate metric to evaluate the effects problematic. To me it does not seem like the model account for the fact that the disturbances are intermittent in time.

Despite my major concerns, I think that the work would make a fine contribution to the literature. I encourage the authors to consider my comments and improve the relevance of this modelling exercise.

## Decision letter (RSPB-2019-1930.R0)

11-Nov-2019

Dear Dr Soudijn:

I am writing to inform you that your manuscript RSPB-2019-1930 entitled "Population level effects of acoustic disturbance in North Sea cod: a size-structured analysis based on energy-budgets." has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

- 1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
- 2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
- 3) Line numbers in your main document.

To upload a resubmitted manuscript, log into <http://mc.manuscriptcentral.com/prsb> and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,

Dr The Proceedings B Team  
mailto: [proceedingsb@royalsociety.org](mailto:proceedingsb@royalsociety.org)

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

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Line 330: typo “is has”.

Figure 1C: This figure is unclear. How is fisheries retention defined? What are the blue and green vertical lines?

Referee: 2

Comments to the Author(s)

Review of RSPB-2019-1930

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authors introduce a potentially serious bias in the model predictions that I believe affect the main conclusions of the paper (lines 33-35):

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Moreover, I find the mis-match between investigating sound sources that are mainly point sources of limited duration (e.g. pile driving, seismic surveys etc.) and using a long-term population growth rate metric to evaluate the effects problematic. To me it does not seem like the model account for the fact that the disturbances are intermittent in time.

Despite my major concerns, I think that the work would make a fine contribution to the literature. I encourage the authors to consider my comments and improve the relevance of this modelling exercise.

## Author's Response to Decision Letter for (RSPB-2019-1930.R0)

See Appendix A.

## RSPB-2020-0490.R0

### Review form: Reviewer 1

#### **Recommendation**

Accept with minor revision (please list in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Good

**General interest: Is the paper of sufficient general interest?**

Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**

Good

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

N/A

**Is it clear?**

N/A

**Is it adequate?**

N/A

**Do you have any ethical concerns with this paper?**

No

**Comments to the Author**

I thank the authors for considering my comments and suggestions in detail. I am largely satisfied with the clarifications they have provided and amendments to the text (but see some further comments below), and I believe the message of the manuscript is now clearer and stronger.

I would encourage the authors to carefully proofread the text or possibly ask a native-speaking colleague to do so, particularly for the Introduction and Discussion; the language would benefit from further wordsmithing.

Detailed comments:

Lines 26-27: I think this sentence is still misleading. In this study you do not explicitly assess the effects of noise on cod. Rather, you present an approach to evaluate the population-level consequences of a theoretical source of disturbance. This could indeed correspond to anthropogenic noise in a future application of your model, but, in this paper, you do not include any actual data on the responses of fish to noise or any noise-related input. Also, if I understood correctly, disturbance is modelled as continuous in time, so there is no attempt to simulate realistic noise exposure scenarios. I would thus rephrase this sentence to clarify that you present an approach that could be used to look at the effects of noise and that you used here to assess the relative importance of the four pathways you list below.

Line 36: I am not sure 'population resilience' is the most appropriate term here. Maybe 'population dynamics', instead?

Line 37: I would remove 'the' and change it to 'fish' (i.e. 'fish energy acquisition and expenditure').

Lines 47-55: the syntax and logical flow of this paragraph can be improved (e.g. you use 'further' when discussing the effects of noise exposure, but the previous sentences were discussing the sources and extent of noise disturbance; or you use 'generally' together with 'more often').

Line 58: rather than 'with a "Population Consequences of Disturbance approach" (PCoD) framework' I would say 'using the Population Consequences of Disturbance (PCoD) framework'.

Line 63: 'birds and habitats directive' needs to be written with capital letters. Also, you should report the corresponding numbers/codes for these Directives.

Lines 66-67: the same comments I had on the abstract apply here: you do not assess the effects of noise, but rather present an approach that could be used for these assessments.

Line 70: I would consider changing 'the underlying model assumptions' to something like: "the underlying processes captured in the model equations".

Line 71: I would remove this sentence and leave the references, in support of the previous sentence.

Line 73-74: this is a bit of a tautology, unless you rephrase or clarify why establishing a negative population growth is important (e.g. for management).

Lines 75-87: this paragraph needs to be re-written with a more cohesive structure and a clearer logical flow: describe the potential pathways that have been proposed, how the model was used to assess the relative importance of these pathways, why this is relevant and how it could be used in future assessments.

Line 93: by 'individual food availability', do you mean 'food availability to the individual'? Also, I have read your response to my previous question on starvation; I think that clarification should be included somewhere in the manuscript.

Line 117: 'continuous in time' means that disturbance is constant throughout the life of an individual? Do you think disturbance with different characteristics could affect the conclusions of your study (regarding the relative importance of different pathways)?

Line 139: n is the year, correct?

Line 140: I imagine that the sentence starting with "Here" is meant to go below the equations.

Line 146: the gonadal mass \*just after reproduction\* is set to 0, correct? If so, please clarify.

Lines 198-199 and lines 204-208: I am still confused by these sentences. If I understood correctly, you calibrated the model based on these length-at-age data, so the comparison of your results to these values is not particularly meaningful or surprising (they match because you adjusted the model so that they matched). Instead, I would integrate the whole paragraph 'Data of Atlantic cod' with the previous one, where you describe how feeding level was adjusted to match the observed growth patterns. In the Results, you could then describe how emerging fecundity compares to fecundity data.

Lines 222-225: this probably belongs to the Methods, as a rationale for running a model with disturbance affecting only a portion of the population.

Line 253: same comment as above: "to consider the potential effects of a source of disturbance (e.g. noise pollution)".

Line 255: same comment on the comparison between modelled and observed growth patterns: you calibrated the model in order for these to match, so this sentence is misleading.

Line 265: "how each is related" is unclear. Do you mean: how each of the four components will be affected by noise disturbance?

Line 269: I think that 'dose-response estimates of sound exposure' needs some fleshing out for readers that are unfamiliar with the literature. What about something along the lines of 'estimated dose-response functions relating exposure to noise to the effects on cod'?

Line 272: 'more subtle effects' suggests a subjective judgment on the severity of the responses, which is not what you are trying to say here. I would clarify and say that you are referring to the sub-lethal effects of changes in behavior and physiology.

Line 278: distracts from...the acoustic stimuli of the prey? I am not sure what this means.

Line 295: as I was mentioning in my previous round of comments, I think it is important to always state that you are referring to a direct reduction in reproductive output (to distinguish

from the decrease in reproductive output that results indirectly from an impaired energy budget). This applies throughout.

Line 315: you need to report Latin names when new species are mentioned for the first time.

Line 320: I agree with the statement, but two species hardly constitute a 'wide range of species'. Maybe just state that it is applicable across different taxa?

Line 323: see comments above about matching your results to growth patterns that were used to calibrate the model.

Line 331: 'the timing' is unclear – the timing of what? I think what you mean is temporal variation, i.e. making those components of your model temporally explicit.

Lines 347-351: I am still unconvinced by this statement. It is true that your model suggests that direct effects on reproduction matter less than indirect effects on energetics – however, reproductive periods are also periods where individuals are undergoing greater energetic costs, and are thus more at risk from a reduced energy acquisition or increased energy expenditure resulting from disturbance. More generally, I don't think your results can support any advice on mitigation or management, considering that there is no empirical data informing the effects of noise disturbance on cod. Yours is largely a theoretical exercise and, as such, should not be used to inform management strategies (in my opinion). I would remove this entire section (lines 343-359).

## Review form: Reviewer 3

### **Recommendation**

Reject – article is not of sufficient interest (we will consider a transfer to another journal)

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Marginal

**General interest: Is the paper of sufficient general interest?**

Marginal

**Quality of the paper: Is the overall quality of the paper suitable?**

Acceptable

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

N/A

**Is it clear?**

N/A

**Is it adequate?**

N/A

**Do you have any ethical concerns with this paper?**

No

### **Comments to the Author**

Review Soudijn et al.

The study examines if underwater noise in the marine ecosystem may negatively affect marine fish populations. The strong affirmation that the indirect non-lethal effects are more concern than the direct mortality is the most striking outcome of the text to me (Line 35: “sub-lethal effects of sound exposure may affect populations more than lethal effects.”). First, it is not clear if the text refers to lethal effects created by sound exposure. Instead, does it refer to any other source of mortality? If not, therefore referring to lethal effects of sound only, this statement would really need an amendment to avoid such confusion, as well as avoiding the work to contrast any scenarios against the “direct mortality only” scenario.

If the “lethal effects less impacting than the non-lethal effects” is meant to resulting from other types of pressures than ambient noise, I am not sure it holds most of the time. It is unlikely that a direct effect (removals of fish) would be overruled by an indirect effect (disturbance of fish) unless substantial population compensatory effects apply. The main effect causing the loss seems to result from the reduced individual growth that the acoustic stress might provoke. How to scale this effect up to the population supposes that the sum of effects on individuals could translate into effects on the entire population without any other intermediates. However, one could expect that density-dependence effects, predator-prey trophic interactions or environmental carrying capacity to come into play along the way from individuals to marine communities.

The study might discuss such aspects and tone a little bit down the certainty of the outcomes, provided that, like in any model, the devil is in the details, and what generally matters is scaling relative effects against each other. For example, for a population like the North Sea cod, it is indeed shocking that the fishing pressure or changing climate would not be the most impacting components compared to “changes in foraging and movement behaviour” induced by stress to noise. Why there are not driving the population dynamics here just result from the fact that the model ignored the effect of fishing or climate when being selective in affecting the number of recruits, the growth, or any vital rates. The model does not contrast the stress from changing environmental factors such as temperature with the effect of the noise. However, it seems in the model formulation that some vital rates such as metabolism and digestive time depend on the temperature? The study also assumes that the stress would reduce the number of eggs per individual and therefore would impact the population as a whole for the following year (Line 236: “the reduction in population growth rate results from a decrease of the cumulative lifetime reproductive output”). I, however, think that knowing if the number of recruits actually depends on the number of eggs is still hotly debated in fisheries science (e.g., le Pape et al. 2017 PNAS <https://doi.org/10.1073/pnas.1706893114>). Fish are precisely not marine mammals in that sense (Line 310: “Previous theoretical studies applied a bioenergetics approach to study population

consequences of sound exposure for several species of marine mammals [e.g. 13,40–42]. Our study is the first to develop such methodology for a species of fish”).

Hence, the reader can certainly agree with the text Line 68 “The advantage of using such a mechanistic model is that effects of changes in food intake or energy expenditure are translated to effects on the vital rates through the underlying model assumptions”. This is calling for the underlying model assumptions to be grounded with possible empirical studies (detailing the links between individual animals and vital rates) to avoid firm conclusions to be made from model outcomes only. Line 109: “There is no detailed empirical information available regarding sound exposure levels of cod in the field or the effects of sound exposure on cod.” Nevertheless, in Annex: “The observed effects of anthropogenic noise on fish (row names on the left) were chosen based on a meta-analysis of anthropogenic noise experiments with fish by Cox et al.”. However, it seems none of the Phi parameters ( $\psi_D$  acoustic mortality multiplier,  $\psi_B$  acoustic reproductive failure multiplier,  $\psi_T$  acoustic energy expenditure multiplier,  $\psi_I$  acoustic feeding failure multiplier) are grounded to any previous empirical studies while it is likely they are driving the model outcomes (there are kind of weighting factors). So it might be beneficial to run a row of sensitivity analyses on each of them to study the possible non-linear responses and express and uncertainty ranges. We also have no documentation here that would map where the fish is and where the pressure distributes, and at what intensity; therefore no information is provided to deduce what would be the part of the population exposed to the pressure.

While I should acknowledge the vast amount of work and dedication that is shown here, I am not entirely convinced about the outcomes of the study in its present form. I am not entirely convinced because, by model construction only, one can expect that (Line 248) “changes in food intake simultaneously affect survival, annual reproductive output and the age at maturation. On the other hand, mortality only affects survival. Reproductive failure directly reduces the annual reproductive output”. Along with this, before getting i) empirical pieces of evidence of stress at the individual level, ii) the spatial pressure field described and crossed with where the fish distribute, and iii) the scaling of the acoustic stress compared to other pressures, one could ask if direct or indirect stress to noise on fish matters at all? Hence, it appears premature at this stage to search for acoustic mitigation measures for possible effects on fish (line 343 onwards).

## Decision letter (RSPB-2020-0490.R0)

06-Apr-2020

Dear Dr Soudijn:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers’ comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors still have some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into <http://mc.manuscriptcentral.com/prsb> and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with

Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

In this revision please upload a file under "Response to Referees" in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. This was not provided in your resubmission, so please make sure that you detail how you have addressed the more significant comments of the referees. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (<https://royalsociety.org/journals/ethics-policies/>). You should pay particular attention to the following:

#### Research ethics:

If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

#### Use of animals and field studies:

If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

#### Data accessibility and data citation:

It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (<https://royalsociety.org/journals/ethics-policies/data-sharing-mining/>). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (<http://datadryad.org/>) and have not already done so you can submit your data via this link

[http://datadryad.org/submit?journalID=RSPB&manu=\(Document not available\)](http://datadryad.org/submit?journalID=RSPB&manu=(Document not available)), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy <http://royalsocietypublishing.org/data-sharing>.

#### Electronic supplementary material:

All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the

accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,  
Dr Daniel Costa  
mailto:proceedingsb@royalsociety.org

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).

I thank the authors for considering my comments and suggestions in detail. I am largely satisfied with the clarifications they have provided and amendments to the text (but see some further comments below), and I believe the message of the manuscript is now clearer and stronger.

I would encourage the authors to carefully proofread the text or possibly ask a native-speaking colleague to do so, particularly for the Introduction and Discussion; the language would benefit from further wordsmithing.

Detailed comments:

Lines 26-27: I think this sentence is still misleading. In this study you do not explicitly assess the effects of noise on cod. Rather, you present an approach to evaluate the population-level consequences of a theoretical source of disturbance. This could indeed correspond to anthropogenic noise in a future application of your model, but, in this paper, you do not include any actual data on the responses of fish to noise or any noise-related input. Also, if I understood correctly, disturbance is modelled as continuous in time, so there is no attempt to simulate realistic noise exposure scenarios. I would thus rephrase this sentence to clarify that you present an approach that could be used to look at the effects of noise and that you used here to assess the relative importance of the four pathways you list below.

Line 36: I am not sure 'population resilience' is the most appropriate term here. Maybe 'population dynamics', instead?

Line 37: I would remove 'the' and change it to 'fish' (i.e. 'fish energy acquisition and expenditure').

Lines 47-55: the syntax and logical flow of this paragraph can be improved (e.g. you use 'further'

when discussing the effects of noise exposure, but the previous sentences were discussing the sources and extent of noise disturbance; or you use 'generally' together with 'more often').

Line 58: rather than 'with a "Population Consequences of Disturbance approach" (PCoD) framework' I would say 'using the Population Consequences of Disturbance (PCoD) framework'.

Line 63: 'birds and habitats directive' needs to be written with capital letters. Also, you should report the corresponding numbers/codes for these Directives.

Lines 66-67: the same comments I had on the abstract apply here: you do not assess the effects of noise, but rather present an approach that could be used for these assessments.

Line 70: I would consider changing 'the underlying model assumptions' to something like: "the underlying processes captured in the model equations".

Line 71: I would remove this sentence and leave the references, in support of the previous sentence.

Line 73-74: this is a bit of a tautology, unless you rephrase or clarify why establishing a negative population growth is important (e.g. for management).

Lines 75-87: this paragraph needs to be re-written with a more cohesive structure and a clearer logical flow: describe the potential pathways that have been proposed, how the model was used to assess the relative importance of these pathways, why this is relevant and how it could be used in future assessments.

Line 93: by 'individual food availability', do you mean 'food availability to the individual'? Also, I have read your response to my previous question on starvation; I think that clarification should be included somewhere in the manuscript.

Line 117: 'continuous in time' means that disturbance is constant throughout the life of an individual? Do you think disturbance with different characteristics could affect the conclusions of your study (regarding the relative importance of different pathways)?

Line 139: n is the year, correct?

Line 140: I imagine that the sentence starting with "Here" is meant to go below the equations.

Line 146: the gonadal mass \*just after reproduction\* is set to 0, correct? If so, please clarify.

Lines 198-199 and lines 204-208: I am still confused by these sentences. If I understood correctly, you calibrated the model based on these length-at-age data, so the comparison of your results to these values is not particularly meaningful or surprising (they match because you adjusted the model so that they matched). Instead, I would integrate the whole paragraph 'Data of Atlantic cod' with the previous one, where you describe how feeding level was adjusted to match the observed growth patterns. In the Results, you could then describe how emerging fecundity compares to fecundity data.

Lines 222-225: this probably belongs to the Methods, as a rationale for running a model with disturbance affecting only a portion of the population.

Line 253: same comment as above: "to consider the potential effects of a source of disturbance (e.g. noise pollution)".

Line 255: same comment on the comparison between modelled and observed growth patterns: you calibrated the model in order for these to match, so this sentence is misleading.

Line 265: “how each is related” is unclear. Do you mean: how each of the four components will be affected by noise disturbance?

Line 269: I think that ‘dose-response estimates of sound exposure’ needs some fleshing out for readers that are unfamiliar with the literature. What about something along the lines of ‘estimated dose-response functions relating exposure to noise to the effects on cod’?

Line 272: ‘more subtle effects’ suggests a subjective judgment on the severity of the responses, which is not what you are trying to say here. I would clarify and say that you are referring to the sub-lethal effects of changes in behavior and physiology.

Line 278: distracts from...the acoustic stimuli of the prey? I am not sure what this means.

Line 295: as I was mentioning in my previous round of comments, I think it is important to always state that you are referring to a direct reduction in reproductive output (to distinguish from the decrease in reproductive output that results indirectly from an impaired energy budget). This applies throughout.

Line 315: you need to report Latin names when new species are mentioned for the first time.

Line 320: I agree with the statement, but two species hardly constitute a ‘wide range of species’. Maybe just state that it is applicable across different taxa?

Line 323: see comments above about matching your results to growth patterns that were used to calibrate the model.

Line 331: ‘the timing’ is unclear – the timing of what? I think what you mean is temporal variation, i.e. making those components of your model temporally explicit.

Lines 347-351: I am still unconvinced by this statement. It is true that your model suggests that direct effects on reproduction matter less than indirect effects on energetics – however, reproductive periods are also periods where individuals are undergoing greater energetic costs, and are thus more at risk from a reduced energy acquisition or increased energy expenditure resulting from disturbance. More generally, I don’t think your results can support any advice on mitigation or management, considering that there is no empirical data informing the effects of noise disturbance on cod. Yours is largely a theoretical exercise and, as such, should not be used to inform management strategies (in my opinion). I would remove this entire section (lines 343-359).

Referee: 3

Comments to the Author(s).  
Review Soudijn et al.

The study examines if underwater noise in the marine ecosystem may negatively affect marine fish populations. The strong affirmation that the indirect non-lethal effects are more concern than the direct mortality is the most striking outcome of the text to me (Line 35: “sub-lethal effects of sound exposure may affect populations more than lethal effects.”). First, it is not clear if the text refers to lethal effects created by sound exposure. Instead, does it refer to any other source of mortality? If not, therefore referring to lethal effects of sound only, this statement would really need an amendment to avoid such confusion, as well as avoiding the work to contrast any scenarios against the “direct mortality only” scenario.

If the “lethal effects less impacting than the non-lethal effects” is meant to resulting from other

types of pressures than ambient noise, I am not sure it holds most of the time. It is unlikely that a direct effect (removals of fish) would be overruled by an indirect effect (disturbance of fish) unless substantial population compensatory effects apply. The main effect causing the loss seems to result from the reduced individual growth that the acoustic stress might provoke. How to scale this effect up to the population supposes that the sum of effects on individuals could translate into effects on the entire population without any other intermediates. However, one could expect that density-dependence effects, predator-prey trophic interactions or environmental carrying capacity to come into play along the way from individuals to marine communities.

The study might discuss such aspects and tone a little bit down the certainty of the outcomes, provided that, like in any model, the devil is in the details, and what generally matters is scaling relative effects against each other. For example, for a population like the North Sea cod, it is indeed shocking that the fishing pressure or changing climate would not be the most impacting components compared to “changes in foraging and movement behaviour” induced by stress to noise. Why there are not driving the population dynamics here just result from the fact that the model ignored the effect of fishing or climate when being selective in affecting the number of recruits, the growth, or any vital rates. The model does not contrast the stress from changing environmental factors such as temperature with the effect of the noise. However, it seems in the model formulation that some vital rates such as metabolism and digestive time depend on the temperature? The study also assumes that the stress would reduce the number of eggs per individual and therefore would impact the population as a whole for the following year (Line 236: “the reduction in population growth rate results from a decrease of the cumulative lifetime reproductive output”). I, however, think that knowing if the number of recruits actually depends on the number of eggs is still hotly debated in fisheries science (e.g., le Pape et al. 2017 PNAS <https://doi.org/10.1073/pnas.1706893114>). Fish are precisely not marine mammals in that sense (Line 310: “Previous theoretical studies applied a bioenergetics approach to study population consequences of sound exposure for several species of marine mammals [e.g. 13,40–42]. Our study is the first to develop such methodology for a species of fish”).

Hence, the reader can certainly agree with the text Line 68 “The advantage of using such a mechanistic model is that effects of changes in food intake or energy expenditure are translated to effects on the vital rates through the underlying model assumptions”. This is calling for the underlying model assumptions to be grounded with possible empirical studies (detailing the links between individual animals and vital rates) to avoid firm conclusions to be made from model outcomes only. Line 109: “There is no detailed empirical information available regarding sound exposure levels of cod in the field or the effects of sound exposure on cod.” Nevertheless, in Annex: “The observed effects of anthropogenic noise on fish (row names on the left) were chosen based on a meta-analysis of anthropogenic noise experiments with fish by Cox et al.”. However, it seems none of the Phi parameters ( $\phi\_D$  acoustic mortality multiplier,  $\phi\_B$  acoustic reproductive failure multiplier,  $\phi\_T$  acoustic energy expenditure multiplier,  $\phi\_I$  acoustic feeding failure multiplier) are grounded to any previous empirical studies while it is likely they are driving the model outcomes (there are kind of weighting factors). So it might be beneficial to run a row of sensitivity analyses on each of them to study the possible non-linear responses and express and uncertainty ranges. We also have no documentation here that would map where the fish is and where the pressure distributes, and at what intensity; therefore no information is provided to deduce what would be the part of the population exposed to the pressure.

While I should acknowledge the vast amount of work and dedication that is shown here, I am not entirely convinced about the outcomes of the study in its present form. I am not entirely convinced because, by model construction only, one can expect that (Line 248) “changes in food intake simultaneously affect survival, annual reproductive output and the age at maturation. On the other hand, mortality only affects survival. Reproductive failure directly reduces the annual reproductive output”. Along with this, before getting i) empirical pieces of evidence of stress at the individual level, ii) the spatial pressure field described and crossed with where the fish distribute, and iii) the scaling of the acoustic stress compared to other pressures, one could ask if

direct or indirect stress to noise on fish matters at all? Hence, it appears premature at this stage to search for acoustic mitigation measures for possible effects on fish (line 343 onwards).

## Author's Response to Decision Letter for (RSPB-2020-0490.R0)

See Appendix B.

## RSPB-2020-0490.R1 (Revision)

### Review form: Reviewer 1

#### **Recommendation**

Accept as is

**Scientific importance: Is the manuscript an original and important contribution to its field?**

Good

**General interest: Is the paper of sufficient general interest?**

Good

**Quality of the paper: Is the overall quality of the paper suitable?**

Good

**Is the length of the paper justified?**

Yes

**Should the paper be seen by a specialist statistical reviewer?**

No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**

No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**

Yes

**Is it clear?**

Yes

**Is it adequate?**

Yes

**Do you have any ethical concerns with this paper?**

No

### Comments to the Author

I thank the authors for responding to my remaining comments. I believe the rationale, goals and main conclusions of the manuscript are now clear and supported by the analyses presented. I also think that the issues with the convoluted language have been addressed (on a very minor last note: I would be consistent and use either 'sub-lethal' or 'non-lethal').

## Decision letter (RSPB-2020-0490.R1)

24-May-2020

Dear Dr Soudijn

I am pleased to inform you that your manuscript entitled "Population level effects of acoustic disturbance in Atlantic cod: a size-structured analysis based on energy-budgets." has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact [procb\\_proofs@royalsociety.org](mailto:procb_proofs@royalsociety.org)

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An e-mail request for payment of any related charges will be sent out after proof stage (within approximately 2-6 weeks). The preferred payment method is by credit card; however, other payment options are available

### Electronic supplementary material:

All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,  
Dr Daniel Costa

Editor, Proceedings B  
mailto:proceedingsb@royalsociety.org

Associate Editor:  
Board Member: 1  
Comments to Author:  
(There are no comments.)

Board Member: 2  
Comments to Author:  
(There are no comments.)

# Appendix A

Dear editor and reviewers,

Thank you for your consideration of our manuscript. We have carefully considered all comments and have changed the manuscript accordingly. The manuscript has changed considerably and we believe it has improved substantially due to your reviews.

We reply to each of the comments in detail below (in blue). We have indicated line numbers of changed where possible. The line numbers correspond to the line numbers such as represented in the document without track changes or the document with track changes with the “no markup” setting activated.

We look forward to hearing your opinion about the new version of the manuscript.

Kind regards,

Floor Soudijn on behalf of all authors.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

General comments

This is an interesting and important study presenting a modelling approach to assess the consequences of noise disturbance on fish populations. Even though the model is parameterized for a specific cod population, it remains largely theoretical, because there is currently no empirical information on either the exposure rates of individual fish to various noise sources or the actual responses to noise exposure. The authors use the model to investigate the relative importance of different types of effects on long-term population dynamics, and conclude that sub-lethal effects on the energy budget (either via an increased energy expenditure or a decreased energy acquisition) have the potential to cause stronger effects on the population's growth rate than direct effects on survival and reproduction. These results are relevant for designing future experiments as well as effective mitigation measures for the management of noise.

I don't have any major concern with the modelling approach or the main conclusions of the study. However I believe that the presentation of the methods could be improved, to avoid confusion. I detail below the various sections of the manuscript where I think this can be done, but first I have some general points for the authors to consider.

Dear reviewer 1,

We appreciate your enthusiasm about our study and your elaborate, detailed review. We feel that your input has improved the manuscript significantly and we hope that the issues that you raised have been resolved in the new version.

1. When referring to the effects of noise exposure on reproductive success, I would make sure to mention on all occasions that these are direct effects on reproductive success. There is often confusion between these effects and the indirect decline in reproductive output that is mediated by changes in the energy budget.

Thank you for pointing out that it should be made more clear that we model direct effects of sound exposure. We have added a sentence to the introduction L78-80 and methods L115-116 sections and added a sentence in the discussion (L260-262) to clarify this.

2. Generally, it would help if the authors avoided switching among reproductive success, lifetime reproductive output, fecundity, and reproduction. If these terms are meant to represent different vital rates, then they should be defined and used consistently, otherwise I would choose one and use it throughout.

The lifetime reproductive output is a cumulative quantity that depends on the survival probability as well as the annual reproductive output of the individual. We now explicitly define this term in the methods section, L140-148.

We have changed the term reproductive success to reproductive output throughout the text. We use reproductive output and annual reproductive output interchangeably, but always describe the lifetime reproductive output as "cumulative lifetime reproductive output" to keep a clear distinction.

When explaining indirect effects of the changes in the net energy on the population growth rate we have changed fecundity to "the energy in the gonads" (L250-251).

The word reproduction is still used a few times in the text to refer to the process of reproduction in general.

3. An improvement of the terminology would also help in relation to the energetic costs; it might be better to refer to increased energy expenditure, because a reduced energy acquisition via decreased food intake could also be thought of as a net energetic cost of noise exposure. In other words, an increased cost and a decreased food intake ultimately operate via the same pathway, that is, a disruption of the energy budget.

Thank you for pointing out this potentially confusing term. We have changed the term increased energetic costs to increased energy expenditure throughout the main text and appendix. See for example L29, L78 and L128-130 in the main text.

4. In the Methods, the authors discuss at length the potential responses to noise and the resulting short-term effects. I found several aspects of this confusing: the terminology is not consistent, some of the responses (as well as the short term effects) could be interrelated (e.g. stress can also cause changes in foraging or movement behavior); there is no distinction between acute and chronic noise, and how these two forms of exposure may follow different response pathways (e.g., the potential but undocumented effects of changed foraging behavior on survival and reproduction in Table 1 are mediated by reduced food intake).

We see now that the presentation of the table at the start of the model description was confusing and has led to confusion on how we implemented the potential effects of noise in the model. The table is meant to motivate the choice of potential pathways through which noise may affect individual level processes. We have moved the table to the appendix and have simplified its contents somewhat (appendix A Table A1, and L 3-23 in the appendix). Many acoustic disturbances are of an impulsive nature (seismic surveys, pile driving), our choice of 'potential effects' relate to regular exposure to such pulses, not the effects of individual pulses. In the table we give a broad overview of how acoustic disturbances may affect individual-level processes. We make this explicit in the text of the appendix (Appendix A, L7-11).

5. Ultimately, I don't think this discussion is relevant to the current study, because of how the effects of noise disturbance are modelled: the exact response is not modelled explicitly; instead, the effects of the various potential responses are simply condensed in a single parameter in each of the formulas for metabolic rate, ingestion, mortality or reproduction. None of these functions is reported in the main text, so the reader is left wondering how these processes are teased apart in the model. I would simplify the presentation of disturbance, describe the direct effects that are modelled, and mention in the Discussion that these can be caused by a variety of responses.

In general, there is currently not enough detail in the main text with regard to the simulation of disturbance, so I think those relationships should be brought in from the supplementary material.

Following your suggestions, we have moved part of the equations from the appendix to the main text to explain more clearly how the effects of acoustic disturbance have been implemented in the model (L118-L149). We describe the link to empirical evidence in the introduction (L75-81). The links between sound exposure and individual level processes are covered in the discussion (L277-313).

6. In contrast, I think Table 1 can be moved to supplementary because it is not relevant to this modelling exercise.

Done. See response to comment 4

7. Finally, I would have liked to see a bit more discussion on the way disturbance is modelled and whether this has the potential to affect the results. At the moment, the effects of disturbance are simulated as additive components to the basal rates (be it the basal metabolism, energy intake, mortality or reproductive output). Would a different shape of such functions affect the conclusions on the importance for long-term population dynamics?

Thank you for this suggestion.

A change from, for example, an additive effect to a multiplication of the basal rates would affect how the effect on the population growth rate scales with the factor that is changed (e.g. where you are on the x-axis of Figure 2). This would, as far as we can see, not change the relative sensitivity to absolute changes in the four processes. The question remains how sound exposure actually affects the energy expenditure, food intake, reproduction and mortality in an absolute sense. Even if the population growth rate is less sensitive to changes in mortality, if the increase in mortality due to sound exposure is very large, it would still be more important than a small decrease in food intake. We have added text to the discussion to make this explicit (L269-275). One aspect we discuss in this respect is how the timing of disturbances could potentially affect the population growth rate (L 335-340).

8. From a stylistic perspective, the language could be made more concise and less convoluted. There are a few long sentences where the verb and the direct object (e.g. lines 101-102) or the modal verb and the following verb (e.g. lines 30-31) are separated by a clause, which are difficult to read. Tightening up some of the text and avoiding repetitions could help save space that could then be used to bring in some additional details regarding the model structure from the supplementary material.

Thank you for pointing out these sentences. We have carefully considered the text again and simplified complex sentences throughout the text where we encountered them (e.g. L28-30, L78-81, L159-161).

Detailed comments:

Line 31: I would change "through... the auditory system" to "through... effects on the auditory system".

Changed, see L29.

Line 33: it is unclear what "these factors" refer to, the effects or the mechanisms; I would change "factors" to "effects".

Changed this (L31).

Line 36: is it worth mentioning the mechanisms by which this might be the case (e.g. lines 226-243 of the Results)?

We included the mechanisms in the abstract (L31-33)

Lines 44-45: this sentence is out of context in this paragraph; maybe move it below, when introducing the effects of noise on fish.

Thank you for pointing this out. We have rewritten the introduction and the sentence now fits well in the paragraph (L42-55)

Line 46: isn't this increase in ambient noise associated with shipping/low frequency noise? Other sources of noise are certainly important, but are not reflected in these long-term trends. I think the sentence needs some rephrasing.

We have rephrased this statement (L43-49).

Line 57: this phrasing is misleading. PCAD (now PCoD) has been originally developed for the effects of noise on marine mammals, and is not "generally used"; I would rephrase to something along the lines of "The Population Consequences of Disturbance approach (PCoD) is an effective framework for the analysis of population-level effects of sublethal disturbance, originally developed for marine mammals" and reference both the original National Research Council report (NRC 2005) and the recent PCoD review (Pirodda et al. 2018 Ecology and Evolution).

Thank you for these suggestions. We have rewritten the introduction on this point (L57-61).

Line 64: I would change "old" to "pre-exploitation".

We have rewritten the introduction and these sentences have been removed from the manuscript in response to comments of reviewer 2.

Line 71: this is misleading. You do not test for the effects, but for the relative importance of different types of pathways via which noise can impact cod population growth rate.

We have rephrased this sentence (L75) in accordance with your suggestion.

Lines 72-75: this sentence contains too much detail on the methods for the Introduction. Instead, I would integrate it with the following paragraph (to avoid repetitions and improve conciseness), and expand on these pathways, the associated evidence from the meta-analysis, and why assessing their relative importance is relevant.

We have restructured this section of the introduction, in line with this suggestion. It now reads much better and repetitions are avoided, and we discuss the relationship to empirical evidence and relevance of this approach (L76-87).

Line 89: some of the terminology in Table 1 is confusing (the term "effects" is sometimes used with reference to responses and sometimes to consequences). In the main text and in Table 1 (and its caption), you need to clearly define and distinguish responses (physiological or behavioural; e.g. stress, movement...), from short-term effects on individual-processes, and long-term population-level

consequences, and be consistent throughout. Also, this section needs some tightening to make the message clearer and avoid repetitions.

Thank you for pointing this out. We have moved the table and the corresponding text to the appendix (Table A1 and L2-23 in the appendix). We have changed the text and the table and have made a distinction between primary *effects* as documented in the review of the experimental studies and *consequences* for individual level processes.

Line 104: but isn't this an effect on reproductive success, which could have large, direct consequences on this rate and thus increase the relative importance compared to energetic and feeding intake?

The actual effects of sound exposure are most likely a combination of the effects that we have studied. We have focussed on investigating the relative importance of potential effects of sound exposure through different pathways. We have clarified in the introduction (L75-77 and L84-87) and discussion (L266-276) that we investigate the sensitivity of the population to potential consequences of sound exposure. We have added a sentence to the appendix clarifying that we do consider the effect of a change in reproductive output (which could mimic moving away from the spawning grounds; appendix L21-24).

Lines 94-109: why is this section included in the methods, considering the actual responses to noise are not modelled explicitly? Disturbance is a unit-less parameter that modifies basal rates, so all this discussion is confusing (as well as slightly contentious). I would remove it and instead describe how disturbance is modelled.

[See response to comment 4.](#)

Line 110: This section is vague and does not provide much detail on the actual model. Instead, the reader is repeatedly referred to the supplementary material. I understand that it is impossible, given the length constraints, to bring all those details in the main text, but I think the reader should be able to find, in the main text, some more information about the shape of these functions. I would ask the authors to consider how they could bring in some of those details. As I stated above, I do think that more details are certainly required for the effects of disturbance (lines 131-138).

[See response to comment 5.](#)

Line 120: Please clarify what you mean by "partial disturbance".

[We have rephrased this sentence \(L107-108\).](#)

Line 124: I am unsure about the implications of this assumption. Does that mean that an individual's energy level cannot get so low that it dies? What if disturbance brings the energy level to the minimum: would this not affect an animal's survival?

[Because we assume a time-invariant disturbance in our study, the individuals stop growing as soon as the food intake is equal to the energetic costs. When this occurs, the individual will stop growing. As soon as individuals reach this point before maturation they never reproduce and the population growth rate becomes incalculable, this is where the lines stop in figure 2.](#)

Line 146: Please define  $L(A_n, r)$ .

[We now define this term in L159-161](#)

Lines 148-150: This sentence is convoluted, please rephrase and simplify.

[Thank you for pointing this out. We rephrased the sentence \(L158-161\).](#)

Line 199: Didn't you say above (line 190) that the intermediate and low feeding level were indeed adjusted to reproduce these growth curves? This is not a validation then, you calibrated the model in this way.

Thank you for indicating this is confusing. To avoid confusion we have removed the sentence (L208-212).

Line 201: this discrepancy between predicted and observed fecundity at larger size is not discussed elsewhere. What does it suggest? Does it matter?

This finding suggests that large individuals have more energy available for reproduction than the model predicts. This implies that we probably underestimate the "real" population growth rate somewhat. Most theoretical models underestimate fecundity of large fish. It is not totally clear what is the reason for this. Or, which change of assumptions in the energy budget may fix it. We have added discussion of this topic to the manuscript (L326-334).

Line 241: I'm not clear on why reproductive failure does not affect fecundity.

Thank you for pointing this out. We meant that it does not affect the investment in reproduction. It certainly does affect the reproductive output. We have rephrased this (L250-251).

Line 246: except for the fecundity of large fish, a discrepancy that is not acknowledged in the discussion.

We have added discussion of this topic to the manuscript (L326-334).

Line 272: this is an example where specifying that you are referring to direct reproductive success would help. Energetic disruptions will ultimately affect reproductive success, so this sentence could be misleading.

Thank you for pointing this out. We changed the sentence (L296-299).

Line 286: there are now several examples in the marine mammal literature that have assessed effects over an individual's lifetime, including using bioenergetic modelling; please rephrase and provide some of these references (e.g. Nabe-Nielsen et al 2018 Cons Letters, Pirodda et al 2019 Oikos, McHuron et al 2018 Ecol Modelling, Villegas-Amtmann et al 2017 ESR, Farmer et al 2018 Biological Conservation).

Thank you for the suggested references. We have rewritten this section (L315-317).

Line 299: "probably display some sort of seasonality" is a vague formulation. I would change to "could display seasonal variation".

We have rephrased this (L335-341).

Line 314: Worth mentioning a couple of examples for the reader to appreciate the difference from the measures listed in association with acute effects.

Thank you for pointing this out. We have added some examples of long term non-lethal effects and have moved some text around to link them to different mitigation measures (L356-363).

Line 330: typo "is has".

Thank you, this sentence was removed from the manuscript in response to a comment from reviewer 2.

Figure 1C: This figure is unclear. How is fisheries retention defined? What are the blue and green vertical lines?

We moved the figure to the appendix to create space for additional text in the discussion. We have added the explanation of the vertical lines to the figure legend (appendix, figure A1 )

Referee: 2

Comments to the Author(s)

Review of RSPB-2019-1930

"Population level effects of acoustic disturbance in North Sea cod: a size-structured analysis based on energy-budgets." By Soudijn et al.

The paper addresses an important question on how underwater sound may affect North Sea (NS) cod at the population level. Unfortunately, I think that the paper as it stands currently falls short of the goals stated at the onset of the study.

Dear reviewer 2,

Thank you for your comments on our manuscript. We have carefully considered your critiques and have changed the manuscript accordingly. We hope you will find our adjustments and additional explanations helpful.

1. My main concern is the weak link between the model and data from the field (figure 2 is a start, but is not sufficient). This leave the paper with a list of theoretical results, that may or may not be relevant for cod in the NS. These results are of course interesting, but it would then demand a major rewrite of the paper to tone down the link to NS cod.

Thank you for pointing this out. Our work should not be interpreted as specific for North Sea cod. We aim for a more general study. At the same time, we do need a realistic set of parameter values in order to obtain consistent results. This is always a difficult balance in this type of modelling work, and we see now that the manuscript leaned too far towards the 'North Sea side'. We have changed the manuscript structurally by removing all reference to the North Sea cod population from the introduction and discussion (e.g. L56-76, L364-369). In the methods section and appendix we explain how we parameterize the model for Atlantic cod based on data from the North Sea (e.g. L185-191). We feel this has substantially cleared up the aim and scope of our work.

2. This brings up a second major question, why did the authors choose this framework? In my opinion, the choice of modelling framework seems arbitrary. A full time resolved model seems unnecessary to address the question of sound effects at the population level? A more classical difference equation (matrix model) would suffice and would be much easier to link to data.

Thank you for pointing out that we did not motivate the choice of model structure sufficiently. We have added a paragraph to the introduction where we explain our choice of model (L66-74). While a matrix model is a great tool for studying population level effects of disturbance, it would not be a suitable tool for the current research question because the effects of acoustic disturbance on the vital rates of the fish are not known. The model that we use, allows us to manipulate individual level processes and consider the effect of changes in these processes on the vital rates and subsequently the population growth rate. To achieve the same aim using a matrix model requires linking the entries of the matrix to the underlying energy budget processes and an iterative procedure to solve for the population growth rate while adjusting the matrix entries. See for an example of this more round-about approach Klanjscek et al. (2006).

3. In addition, I find it peculiar (especially with the detailed modelling of time and pulsed reproduction) that the authors decide to leave out (lines 103-106) the effect of fish leaving the spawning ground (and

potentially becoming egg bound, associated with very high mortality) due to acoustic disturbance. This is potentially the most important effect of sound on fish at the population level, and the model is able to account for such effects. By neglecting this process, the authors introduce a potentially serious bias in the model predictions that I believe affect the main conclusions of the paper (lines 33-35):

“Our results show that changes in energetic costs and food intake reduce population growth rates more than changes in mortality and reproduction.”

Thank you for pointing this out. We have realized that the objective of our study was not well enough explained in the introduction. We have added a sentence to the introduction (L75-77) explaining that we are assessing the relative importance of potential pathways through which noise may affect fish. There certainly are realistic situations where combinations of life history and exposure could have much more dramatic consequences than we have studied here, but those are not the focus of our work. This has been more clearly described in the current version of the manuscript. The effect of mortality as well as reproduction are considered in our study. We have actually mimicked the effect of failed spawning events, but it is hard to include this in our table in a consistent way and therefore as somewhat hidden in the manuscript. We have added a sentence to explain this better in the appendix (appendix, L19-24). In addition, we have clarified in the discussion that we are not considering the absolute effects of specific acoustic disturbances but investigate the sensitivity of the population to potential consequences of sound exposure (L266-276).

4. Moreover, I find the mis-match between investigating sound sources that are mainly point sources of limited duration (e.g. pile driving, seismic surveys etc.) and using a long-term population growth rate metric to evaluate the effects problematic.

Thank you for raising this issue.

The population growth rate or life time reproductive output is a generally accepted measure for population performance in conservation biology (e.g. Caswell 2001, Pirotta et al. 2018). The population growth rate gives an indication of how a disturbance (be it pulsed or continuous) affects the population as a whole. Moreover, while each individual disturbance (sonar ping, airgun for seismic exploration, explosion or pile hammer stroke) is pulsed, with a repeated occurrence these disturbances could arguably be viewed as a continuous source of stress. We have added a sentence to the introduction to explain the relevance of considering population consequences of disturbance (L61-63) and the relevance of the use of the population growth rate metric (L72-74).

5. To me it does not seem like the model account for the fact that the disturbances are intermittent in time.

Thank you for raising this issue. Indeed, we do not address the intermittent nature of disturbance. While the model is capable of doing so, we have chosen to limit the current study to continuous disturbances. We realized that this choice needs to be better explained and motivated, and have made adjustments to do so.

We have moved part of the equations from the appendix to the main text to explain how the effects of acoustic disturbance have been implemented in the model (L118-L149). We moved the table with acoustic disturbance effects and corresponding text to the appendix (appendix, L3-23). We mention the link to the experimental evidence now in the introduction (L76-81). We discuss the links between sound exposure and individual level processes extensively in the discussion (L277-313). In addition, we have clarified in the discussion (L266-276) that we are not considering the absolute effects of specific acoustic disturbances. Our study does not aim to unveil the effects of sound exposure on the North Sea cod population in as much realistic detail as possible. We investigate the sensitivity of the population to potential consequences of sound exposure. We hope that the above changes make that clear. We cannot model the actual time-explicit sound exposure of North sea cod, because there are no empirical data available to us that show the sound exposure of the cod population in the North Sea (or another area).

We could have made assumptions about the length and frequencies of sound disturbance or studied a few scenarios. However, this is not the scope we chose for the current work. Instead, we investigate the effect that sound disturbance may have “on average”. In many parts of the world noise pollution has become the rule rather than the exception. Seismic surveys last several months, as does pile driving for offshore wind farms. Shipping noise is a continuous sound source that is present in many seas and oceans also. From this perspective, it is interesting to think about how an increase in sound levels due to all these sources may affect populations in general and over the entire lifetime of the animals. We do this by mimicking changes in energy expenditure, food intake, mortality and reproduction, which are all likely to be affected directly by sound exposure to some extent.

Despite that we focus on continuous disturbances in this ms, we acknowledge that the effect of temporally heterogeneous and/or seasonal disturbances, are of high priority for further research and discuss the potential importance of the timing of a disturbance in relation to temporal variation in the food source and occurrence of the disturbance (L335-340).

Despite my major concerns, I think that the work would make a fine contribution to the literature. I encourage the authors to consider my comments and improve the relevance of this modelling exercise.

We appreciate your thorough review of our work!

#### References

Caswell, H. 2001. Matrix population models. 2nd edition. Sinauer Associates, Inc., Sunderland.

Klanjscek, T., Caswell, H., Neubert, M.G. & Nisbet, R.M. 2006. Integrating dynamic energy budgets into matrix population models. *Ecol. Modell.*, 196, 407–420 .

Pirotta, E., C. G. Booth, D. P. Costa, E. Fleishman, S. D. Kraus, D. Lusseau, D. Moretti, L. F. New, R. S. Schick, L. K. Schwarz, S. E. Simmons, L. Thomas, P. L. Tyack, M. J. Weise, R. S. Wells, and J. Harwood. 2018. Understanding the population consequences of disturbance. *Ecology and Evolution* 8:9934–9946.

## Appendix B

Dear editor and referees,

Thank you for your consideration of our manuscript. We have made adjustments throughout the manuscript in response to your suggestions as indicated below in blue. We have indicated line numbers of changes that correspond to the line numbers such as represented in the document without track changes or the document with track changes with the “no markup” or “simple markup” settings activated.

We believe that the manuscript has been improved by additional clarifications and adjustments and hope that you will find our changes have clarified all uncertainties. As referee 1 suggested, a native English speaking colleague proofread our manuscript before resubmission.

We are looking forward to hear your decision.

Kind regards,  
Floor Soudijn on behalf of all authors.

Referee: 1

Comments to the Author(s).

I thank the authors for considering my comments and suggestions in detail. I am largely satisfied with the clarifications they have provided and amendments to the text (but see some further comments below), and I believe the message of the manuscript is now clearer and stronger.

I would encourage the authors to carefully proofread the text or possibly ask a native-speaking colleague to do so, particularly for the Introduction and Discussion; the language would benefit from further wordsmithing.

Detailed comments:

Lines 26-27: I think this sentence is still misleading. In this study you do not explicitly assess the effects of noise on cod. Rather, you present an approach to evaluate the population-level consequences of a theoretical source of disturbance. This could indeed correspond to anthropogenic noise in a future application of your model, but, in this paper, you do not include any actual data on the responses of fish to noise or any noise-related input. Also, if I understood correctly, disturbance is modelled as continuous in time, so there is no attempt to simulate realistic noise exposure scenarios. I would thus rephrase this sentence to clarify that you present an approach that could be used to look at the effects of noise and that you used here to assess the relative importance of the four pathways you list below.

Thank you for pointing out that the formulation in our abstract is confusing. We have rephrased the indicated sentences (L27-29).

Line 36: I am not sure ‘population resilience’ is the most appropriate term here. Maybe ‘population dynamics’, instead?

We have rephrased the sentence (L36).

Line 37: I would remove ‘the’ and change it to ‘fish’ (i.e. ‘fish energy acquisition and expenditure’). We have removed the word ‘the’ but have not replaced it with fish (L38).

Lines 47-55: the syntax and logical flow of this paragraph can be improved (e.g. you use 'further' when discussing the effects of noise exposure, but the previous sentences were discussing the sources and extent of noise disturbance; or you use 'generally' together with 'more often'). Thank you for spotting the incorrect use of the words "further" and "generally". We have rephrased these sentences (L50-54)

Line 58: rather than 'with a "Population Consequences of Disturbance approach" (PCoD) framework' I would say 'using the Population Consequences of Disturbance (PCoD) framework'. Thank you, we have adjusted this (L59).

Line 63: 'birds and habitats directive' needs to be written with capital letters. Also, you should report the corresponding numbers/codes for these Directives. Thank you, we have adjusted this (L65)

Lines 66-67: the same comments I had on the abstract apply here: you do not assess the effects of noise, but rather present an approach that could be used for these assessments. We have rephrased the sentence (L67-69, L73-75).

Line 70: I would consider changing 'the underlying model assumptions' to something like: "the underlying processes captured in the model equations". We have rephrased this sentence (L70-72).

Line 71: I would remove this sentence and leave the references, in support of the previous sentence. Thank you for your comment. We have kept this sentence because the comments from the previous reviewer 2 made it clear that it is not directly obvious that our methodology is appropriate for the problem that we address.

Line 73-74: this is a bit of a tautology, unless you rephrase or clarify why establishing a negative population growth is important (e.g. for management). Thank you for your comment. We have kept this sentence as the comments from the previous reviewer 2 showed that it is not clear to everyone what a population growth rate implies.

Lines 75-87: this paragraph needs to be re-written with a more cohesive structure and a clearer logical flow: describe the potential pathways that have been proposed, how the model was used to assess the relative importance of these pathways, why this is relevant and how it could be used in future assessments. Thank you for indicating that this section was not clearly structured. We have reorganized the section (L78-90).

Line 93: by 'individual food availability', do you mean 'food availability to the individual'? Also, I have read your response to my previous question on starvation; I think that clarification should be included somewhere in the manuscript. Thank you for indicating this is unclear, we have rephrased to: "the individual-level food availability" (L96). We added an explanation of what happens when the net-energy reaches zero in the methods text (L98-101).

Line 117: 'continuous in time' means that disturbance is constant throughout the life of an individual? Do you think disturbance with different characteristics could affect the conclusions of your study (regarding the relative importance of different pathways)? The complete sentence is: "Due to a lack of detailed information, the effects of sound exposure are assumed continuous through time and independent of age or size." This sentence indeed means that the disturbances are assumed to be present continuously throughout the full life cycle at the same level. We explain in the discussion (L347-349)

that in reality sound effects may differ between life stages. Differences between life stages in sound effects/exposure could lead to different conclusions, but it is impossible to say how. We have added a sentence to the discussion to explain this (L349-351).

Line 139:  $n$  is the year, correct?

Thank you for spotting this omission, we have added the symbol  $n$  to the sentence (L152).

Line 140: I imagine that the sentence starting with "Here" is meant to go below the equations. This sentence is indeed situated below the equations (in our version of the file).

Line 146: the gonadal mass \*just after reproduction\* is set to 0, correct? If so, please clarify.

This is indeed correct. As is described in the equations, the gonadal mass is set to zero at timepoint  $\zeta_n^+$ . Just before that, the gonadal mass at timepoint  $\zeta_n^-$  is used to calculate the number of offspring. We have rephrased the text somewhat to make this more explicit (L153-160).

Lines 198-199 and lines 204-208: I am still confused by these sentences. If I understood correctly, you calibrated the model based on these length-at-age data, so the comparison of your results to these values is not particularly meaningful or surprising (they match because you adjusted the model so that they matched). Instead, I would integrate the whole paragraph 'Data of Atlantic cod' with the previous one, where you describe how feeding level was adjusted to match the observed growth patterns. In the Results, you could then describe how emerging fecundity compares to fecundity data.

Thank you for your comment. We tried to clarify this point in the previous revision, but rereading the text I understand your confusion.

The length at age data was not used to calibrate the model for the maximum feeding level. For a situation of unlimited feeding the food intake is controlled by the metabolic maintenance costs and digestion time parameters, that are derived from different data (laboratory growth experiments and oxygen consumption data). The good match between length at age predicted by the model for the high feeding level and the North Sea field data is thus not due to model calibration.

On the other hand, the values for the intermediate and low feeding levels were derived based on the length-at-age data.

We have adjusted the explanation of the derivation of the feeding level functions (L203-210) and simplified the text about the data that was used (L212-216). In addition, we made it more clear in the results section that we only compare model output for the high feeding level, or "maximum growth" with the field data (L218-221).

Lines 222-225: this probably belongs to the Methods, as a rationale for running a model with disturbance affecting only a portion of the population.

Thank you for your comment. We moved some of these sentences from the results (L236-237) to the methods section (L114-117).

Line 253: same comment as above: "to consider the potential effects of a source of disturbance (e.g. noise pollution)".

We rephrased this (L266-267).

Line 255: same comment on the comparison between modelled and observed growth patterns: you calibrated the model in order for these to match, so this sentence is misleading.

See explanation above.

We have adjusted the explanation of the derivation of the feeding level functions (L203-210) and simplified the text about the data that was used (L212-216). In addition, we made it more clear in the results section that we only compare model output for the high feeding level, or "maximum growth" with the field data (L218-221). In the discussion, we added the word maximum (L269).

Line 265: "how each is related" is unclear. Do you mean: how each of the four components will be affected by noise disturbance?

Thank you for your comment. We have adjusted the sentence (L280-281).

Line 269: I think that 'dose-response estimates of sound exposure' needs some fleshing out for readers that are unfamiliar with the literature. What about something along the lines of 'estimated dose-response functions relating exposure to noise to the effects on cod'?

We rephrased this (L284-286).

Line 272: 'more subtle effects' suggests a subjective judgment on the severity of the responses, which is not what you are trying to say here. I would clarify and say that you are referring to the sub-lethal effects of changes in behavior and physiology.

We have replaced 'more subtle' with 'sub-lethal' (L287-288).

Line 278: distracts from...the acoustic stimuli of the prey? I am not sure what this means.

We have added the word "fish" (L294).

Line 295: as I was mentioning in my previous round of comments, I think it is important to always state that you are referring to a direct reduction in reproductive output (to distinguish from the decrease in reproductive output that results indirectly from an impaired energy budget). This applies throughout.

We have not added the word "direct" because it is already mentioned in the sentence previous to this sentence that we are talking about a direct effect of sound on reproductive output (L308-311). Moreover, in this case it does not matter whether it is direct or indirect. What does matter is whether only the reproduction is affected or multiple factors at the same time (through indirect effects).

Line 315: you need to report Latin names when new species are mentioned for the first time.

We have added latin names for the Ambon damselfish (L306) and the pilot whale (L331).

Line 320: I agree with the statement, but two species hardly constitute a 'wide range of species'.

Maybe just state that it is applicable across different taxa?

We have rephrased the sentence (L336).

Line 323: see comments above about matching your results to growth patterns that were used to calibrate the model.

See explanation above.

We have adjusted the explanation of the derivation of the feeding level functions (L203-210) and simplified the text about the data that was used (L212-216). In addition, we made it more clear in the results section that we only compare model output for the high feeding level, or "maximum growth" with the field data (L218-221).

In the discussion, we added the word maximum (L269, L339).

Line 331: 'the timing' is unclear – the timing of what? I think what you mean is temporal variation, i.e. making those components of your model temporally explicit.

We have replaced 'the timing' with 'temporal variation' (L347).

Lines 347-351: I am still unconvinced by this statement. It is true that your model suggests that direct effects on reproduction matter less than indirect effects on energetics – however, reproductive periods are also periods where individuals are undergoing greater energetic costs, and are thus more at risk from a reduced energy acquisition or increased energy expenditure resulting from disturbance. More generally, I don't think your results can support any advice on mitigation or management, considering that there is no empirical data informing the effects of noise disturbance on cod. Yours is largely a theoretical exercise and, as such, should not be used to inform management strategies (in my opinion). I would remove this entire section (lines 343-359).

Thank you for indicating that the text was perhaps somewhat too speculative. We have partly removed the text in this section from the manuscript and have rewritten the remaining text (L362-372).

Referee: 3

Comments to the Author(s).

Review Soudijn et al.

1. The study examines if underwater noise in the marine ecosystem may negatively affect marine fish populations. The strong affirmation that the indirect non-lethal effects are more concern than the direct mortality is the most striking outcome of the text to me (Line 35: "sub-lethal effects of sound exposure may affect populations more than lethal effects."). First, it is not clear if the text refers to lethal effects created by sound exposure. Instead, does it refer to any other source of mortality? If not, therefore referring to lethal effects of sound only, this statement would really need an amendment to avoid such confusion, as well as avoiding the work to contrast any scenarios against the "direct mortality only" scenario.

If the "lethal effects less impacting than the non-lethal effects" is meant to resulting from other types of pressures than ambient noise, I am not sure it holds most of the time. It is unlikely that a direct effect (removals of fish) would be overruled by an indirect effect (disturbance of fish) unless substantial population compensatory effects apply. The main effect causing the loss seems to result from the reduced individual growth that the acoustic stress might provoke. How to scale this effect up to the population supposes that the sum of effects on individuals could translate into effects on the entire population without any other intermediates. However, one could expect that density-dependence effects, predator-prey trophic interactions or environmental carrying capacity to come into play along the way from individuals to marine communities.

The study might discuss such aspects and tone a little bit down the certainty of the outcomes, provided that, like in any model, the devil is in the details, and what generally matters is scaling relative effects against each other. For example, for a population like the North Sea cod, it is indeed shocking that the fishing pressure or changing climate would not be the most impacting components compared to "changes in foraging and movement behaviour" induced by stress to noise. Why there are not driving the population dynamics here just result from the fact that the model ignored the effect of fishing or climate when being selective in affecting the number of recruits, the growth, or any vital rates. The model does not contrast the stress from changing environmental factors such as temperature with the effect of the noise. However, it seems in the model formulation that some vital rates such as metabolism and digestive time depend on the temperature? The study also assumes that the stress would reduce the number of eggs per individual and therefore would impact

the population as a whole for the following year (Line 236: “the reduction in population growth rate results from a decrease of the cumulative lifetime reproductive output”). I, however, think that knowing if the number of recruits actually depends on the number of eggs is still hotly debated in fisheries science (e.g., le Pape et al. 2017 PNAS <https://doi.org/10.1073/pnas.1706893114>). Fish are precisely not marine mammals in that sense (Line 310: “Previous theoretical studies applied a bioenergetics approach to study population consequences of sound exposure for several species of marine mammals [e.g. 13,40–42]. Our study is the first to develop such methodology for a species of fish”).

Thank you for pointing out that it was not clear that we are speaking about noise related effects in our manuscript. To avoid confusion, we have changed the text to “lethal effects of sound exposure” in the abstract (L35-37). The study was designed with noise related effects in mind. The changes in the processes that we consider are thus implemented as far as the knowledge about effects of sound exposure on fish goes (not very far).

The aim of our study is first, to present a methodology that can be used to assess the effect of sound exposure on cod. And second, we explore the relative importance of changes in four processes that could be affected by noise (reproduction, mortality, food intake, energetic costs). We do the latter by performing a sensitivity analysis on changes in four different processes. To clarify this we have rephrased the description of the aims of our study in the abstract (L27-29) and introduction (L67-69, L73-75).

Our model does not consider effects other than sound on the population. It would be interesting, but the amount of work of a new study, to contrast different potential disturbances against each other. In the discussion, we discuss several possible improvements of the model, such as density dependence (L356-359).

The lifetime reproductive output is a method designed to estimate the number of offspring an individual contributes to the next generation. This quantity takes the survival probability of an individual up to the age of maturation into account (L159, L173-175). Our results show indeed, that a direct reduction of the number of offspring per individual does not have a strong effect on the lifetime reproductive output (Figure 2, L231-232). The model that we use is based on typical life history characteristics of cod (e.g an individual produces many small offspring). On the other hand, the whale model that the reviewer refers to is based on a totally different set of assumptions which will lead to different results.

2. Hence, the reader can certainly agree with the text Line 68 “The advantage of using such a mechanistic model is that effects of changes in food intake or energy expenditure are translated to effects on the vital rates through the underlying model assumptions”. This is calling for the underlying model assumptions to be grounded with possible empirical studies (detailing the links between individual animals and vital rates) to avoid firm conclusions to be made from model outcomes only. Line 109: “There is no detailed empirical information available regarding sound exposure levels of cod in the field or the effects of sound exposure on cod.” Nevertheless, in Annex: “The observed effects of anthropogenic noise on fish (row names on the left) were chosen based on a meta-analysis of anthropogenic noise experiments with fish by Cox et al.”. However, it seems none of the Phi parameters ( $\psi_D$  acoustic mortality multiplier,  $\psi_B$  acoustic reproductive failure multiplier,  $\psi_T$  acoustic energy expenditure multiplier,  $\psi_I$  acoustic feeding failure multiplier) are grounded to any previous empirical studies while it is likely they are driving the model outcomes (there are kind of weighting factors). So it might be beneficial to run a row of sensitivity analyses on each of them to study the possible non-linear responses and express and uncertainty ranges. We also have no documentation here that would map where the fish is and where the pressure distributes, and at what intensity; therefore no information is provided to deduce what would be the part of the population exposed to the pressure.

We fully agree that an actual assessment of noise effects on cod populations requires more empirical work that quantifies the individual level effects of sound for cod or fish in general. There is unfortunately no information available regarding the link between sound exposure and the vital rates for cod or any other marine fish. Based on experimental studies we deducted several processes that are potentially affected by sound exposure. Since we had no quantification of these effects we did exactly as the reviewer suggests, and executed a sensitivity analysis by varying the values of the Phi parameters over their entire domain and assessing the changes (presented in figure 2).

We moved the text that explains that there is no quantification of sound exposure effects available, to the start of the section about the implementation of the sound effects (L119-130). We also added a sentence to make explicit that we considered a broad range of different values for the disturbance parameters (L128-130). Such an analysis is also known as a sensitivity analysis (L113). We added a sentence to the introduction explaining that there are no empirical data that quantify the relationship between sound exposure and vital rates (L78-79) available.

3. While I should acknowledge the vast amount of work and dedication that is shown here, I am not entirely convinced about the outcomes of the study in its present form. I am not entirely convinced because, by model construction only, one can expect that (Line 248) "changes in food intake simultaneously affect survival, annual reproductive output and the age at maturation. On the other hand, mortality only affects survival. Reproductive failure directly reduces the annual reproductive output".

These effects are indirect and emerge from individual level assumptions in the model. These effects were not implemented in the model directly. To clarify this we have added the word "indirectly" to the abstract (L33-35) and discussion (L273-275). We have also rephrased the summarizing sentence in the results section to make this more clear (L258-260).

4. Along with this, before getting i) empirical pieces of evidence of stress at the individual level, ii) the spatial pressure field described and crossed with where the fish distribute, and iii) the scaling of the acoustic stress compared to other pressures, one could ask if direct or indirect stress to noise on fish matters at all? Hence, it appears premature at this stage to search for acoustic mitigation measures for possible effects on fish (line 343 onwards).

We absolutely agree with the reviewer on this point. More empirical work is needed to answer this question. Our study indicates that this empirical work should be focused on non-lethal effects. We have rephrased the section about mitigation measures (L362-372).