

ARE SMALLER FISH PRE-ADAPTED TO WARMER OCEANS?*

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Abstract

This contribution suggests that the well-documented genetic selection for smaller fish that is the result of decades of sustained, intensive fishing also selects for “skittish” fish with a relatively high metabolic rate. However, skittish fish are highly susceptible to the higher temperature likely to prevail in the next decades in fresh and marine waters, which should contribute to making fisheries more susceptible to the effects of global warming. We submitted a piece to this effect to a leading fisheries/marine science journal, but for reasons that are mentioned in an appendix, we did not agree to having it published along with a contrarian piece. We present here, instead, the article as originally submitted, along with an appendix with our response to the original reviewers’ comments.

Introduction

There is relatively good evidence that the larger/older fish of various species are more sensitive to higher temperatures than smaller/younger fish (Daufresne et al. 2009; Messmer et al. 2016; Pörtner & Knust 2007). It is also well documented that the intense, sustained exploitation of a given population results in the maximum size and the size at first maturity of the fish in that population to be reduced (Figure 1; Jørgensen et al. 2007; Heino et al. 2015). Combining these two lines of evidence, it could be argued that overfishing leads to fish becoming preadapted to ocean warming. In the following, we suggest that the opposite is the case, given the mechanism that actually causes fishing-induced size reduction.

To live, fish need oxygen, which they obtain through their gills. This organ, having to function as a 2-D surface held against a flow of oxygen-rich water, cannot grow as fast as the volume of the 3-D body that it supplies with oxygen. With isometric growth of head and body observed in most fish (Froese 2006), the O₂ supply per unit weight must therefore decrease as weight increases (G-line in Fig 2A).

As O₂ supply decreases, there will be a weight (W_{max}) beyond which a given fish cannot grow because it uses all the oxygen it gets from its gills for routine activities, with none left for net growth, i.e., the scope for growth has become zero.

From this, it follows that, as shown in Fig. 2B, an individual that has a smaller relative gill size, and/or is more ‘skittish’ (i.e., hyperactive), or inefficient at foraging or that has other reasons to display a high routine O₂ consumption rate, will tend to remain smaller, i.e., its scope for growth will tend to be lower than the individual in Fig. 2A (Pauly 2019).

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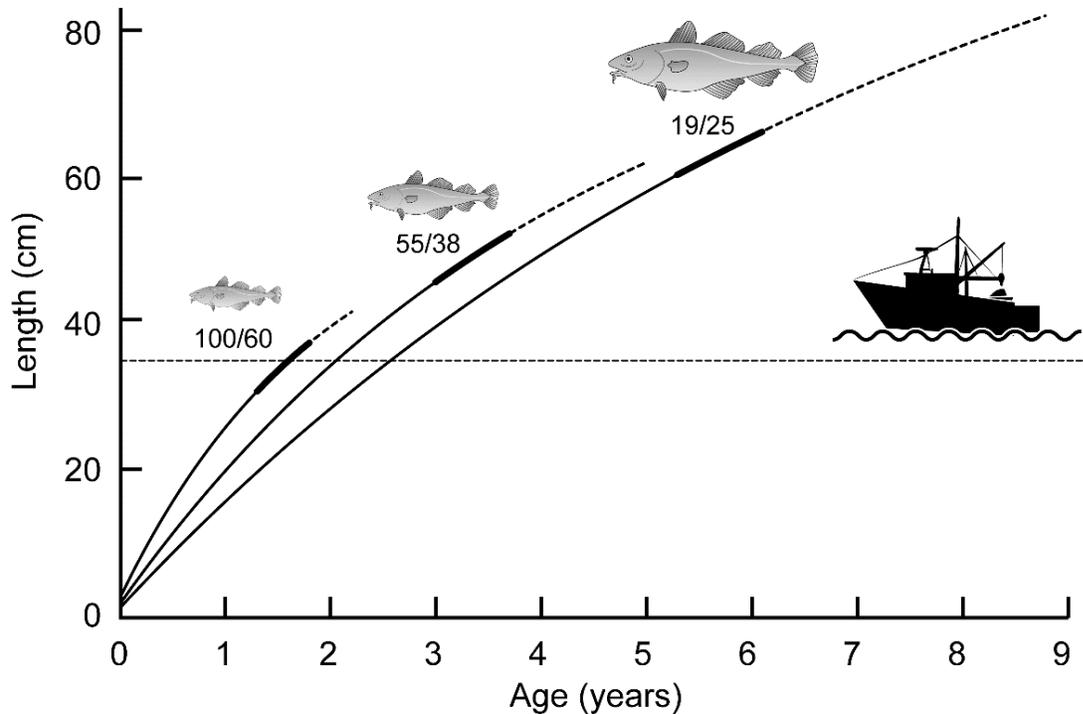


Figure 2. Impact of fishing on the reproduction of cod with small (60 cm), medium (90 cm), and large (120 cm) size growth types. The lower left part of the three growth curves indicates the juvenile phase and the subsequent parts indicate the mean duration of the reproductive phase (i.e. half of the maturing fish are still alive at the end of that phase), with (bold) and without (bold + dashed) fishing. Fish are vulnerable to fishing above 35 cm length (horizontal line), with mortality caused by fishing assumed about twice as high as natural mortality of medium sized cod. Because small cod mature before the onset of fishing, 100% reach maturity compared to no fishing, but their reproductive phase is shortened to 60% of the natural duration (bold section of curve, with indication of these percentages). In contrast, only 19% of large cod reach maturity and their reproductive phase is shortened to 25% of the natural duration. The strong reduction of the participation of large, late maturing cod in reproduction explains the fisheries-induced selection for small size and early maturity.

Fish growth and fisheries

Fish grow throughout their lives and - depending on their reproductive strategy - reach maturity between $1/3$ and $2/3$ of their maximum length (Froese and Binohlan 2000). Returning to Fig. 1, it is evident that the fish of a given population that are eliminated by intense and sustained fishing will tend to be the larger ones which mature at larger sizes, because many of them will be caught before they had a chance to reproduce. Conversely, what is left in that population are the skittish and/or inefficient runts, which managed to reproduce before they could be caught.

This, however, means that these fish do not have scope to accommodate an even higher metabolic rate. Rather, it is the larger fish that could accommodate warming because they could sacrifice some of their remaining scope for growth to accommodate a higher routine metabolism. In other words, you cannot further shrink pre-shrunk fish. This prediction is in line with historical evidence that populations that were subject to intense and prolonged overfishing were more strongly impacted by warming waters (Free et al. 2019).

A fishery that wants to avoid unnatural selection for small size and early maturity would increase the length at first capture close to the natural average length of parents (close to 80 cm in our example), where the catch for the given effort would also be highest (Holt 1958; Froese et al. 2016). Bones and otoliths of cod found in medieval middens suggest indeed a mean length in the catch and the population of about 80 cm at those times of large fish, large stock sizes, and low fishing effort (Barrett et al. 1999).

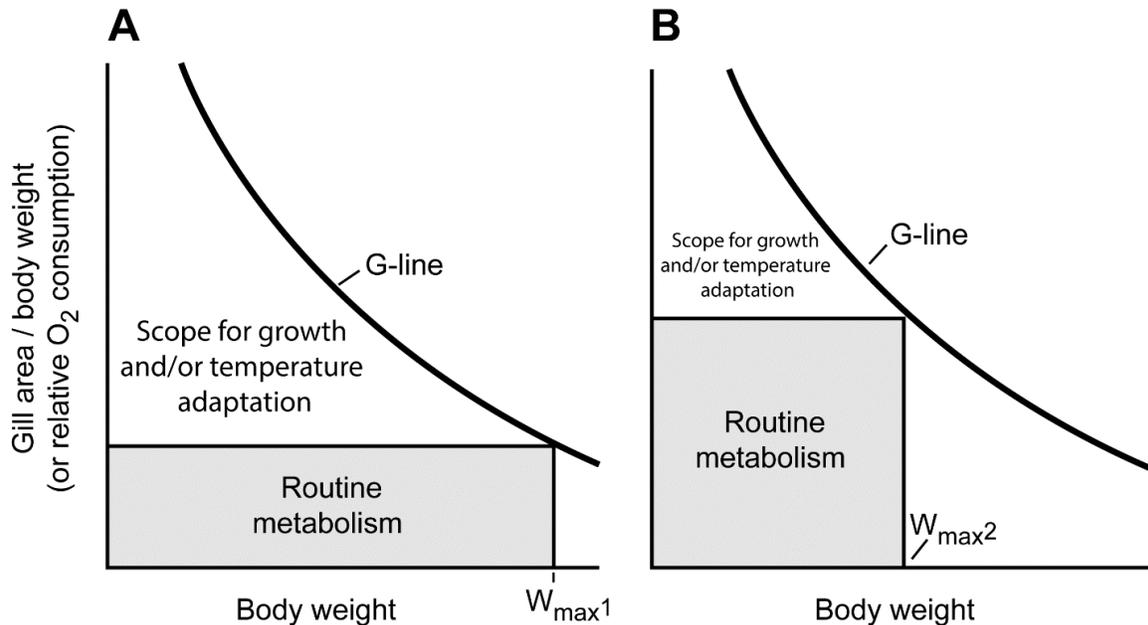


Figure 3. Schematic representation of the mechanism causing fish to remain small when their routine metabolic rate is elevated, featuring gill area per body weight (G-line) decreasing with body weight, due to gill area (a surface) not being able to keep up with body weight (proportional to volume); **A**, Relative O₂ supply (which is proportional to relative gill surface area) drops with increasing weight until a level is reached (at W_{max1}) when O₂ supply is just enough to satisfy routine metabolism. **B**, any factor causing routine metabolism to be elevated (e.g., higher temperature), or which select for fish with a high metabolic rate (size-selective fishing, as in Figure 1) reduces the maximum size that can be reached (hence $W_{max2} < W_{max1}$) and also the scope for adaptation to higher temperature.

Conclusions

In conclusion, overfishing and starting fishing at small body sizes is maladapting exploited fish populations to climate change. To reverse this trend, existing laws (UNCLOS 1982; MSA 2007; CFP 2013; HSP 2018) must finally be implemented, reducing fishing pressure below that which generates maximum sustainable yields and setting length at first capture such that large individuals can reproduce before capture. Such fishing would not only prepare commercial fish and fisheries for warming waters, rebuilding size structure, fecundity, and abundance would also stabilize catches and move exploitation closer to the sustainable maximum, thus mitigating potential future losses (Hixon et al. 2013; Froese et al. 2016, Barneche et al. 2018).

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Appendix

This appendix reproduces the editor’s and reviewers’ comments we received following the submission of the above contribution to a leading fisheries/marine biology journal. We provide here answers to these comments, but did not send them to the editors, because we were offered to resubmit our piece to be published as one side of a ‘pro’ and ‘contra’ pair of opinion pieces, which we didn’t want to do. Thus, these responses are sharper than if we had to placate a journal editor.

The ellipses and words in square brackets are used here to mask the identity of the journal, its handling editor and one reviewer who signed his comment, and whose names would detract from the content of the discussion below.

Editor

I write you in regards to [your submission] entitled “Are smaller fish pre-adapted to warmer oceans?” which you submitted to [our journal]. In view of the criticisms of the reviewers found at the bottom of this letter, as well as my own reading of the manuscript, your manuscript has been denied publication in [our journal]. However, I have also discussed this decision with the Editor-in-Chief, and we do recognize that the argumentation behind the hypothesis you are presenting, and the reviewers’ arguments against it, partly reflect discussions where the scientific community has not yet reached a consensus. In view of this, we see some merit in publishing two articles that would show both sides of the argument. Therefore, we are prepared to

consider a new submission of your manuscript that would be published back-to-back with an invited paper that presents the counterargument.

Please let us know whether this possibility appeals to you. We would then be happy to discuss how to proceed toward the new submission. Thank you for considering [our journal] for the publication of your research. I hope the outcome of this specific submission will not discourage you from the submission of future manuscripts.

Response:

We did not take the offer to present the contribution above “back-to-back with an invited paper that presents the counterargument” because this would have produced what we thought would be an unmerited stage for what arguments without merits. Rather, we are presenting the counterarguments to our submissions here, with what we think are valid counterarguments.

Comments by Reviewer 1

This article is based on the highly contested assumption that fish growth is limited by gill ability to supply oxygen. I will not dwell into multiple papers that have contested this assumption, demonstrating that oxygen supply is driven by demand and can be rapidly modified through multiple mechanisms, so as not to be limited by the gill surface area.

Response:

The vast majority of the “multiple papers” that the reviewer alludes to are contributions claiming *en passant* and without evidence that gills cannot be limiting to growth. The only authors who attempted to show that relative gill surface area can keep up with increasing body weight were Lefevre et al. (2017a, 2017b), and their argument is refuted by geometry and simple arithmetic (Pauly and Cheung 2017a, 2018). Indeed, we have developed this theme in material for a biology class aimed at teenagers (Pauly and Cheung 2017b).

Comment:

However, simply from an evolutionary point of view the idea that fish grow to a size where they become limited by oxygen supply does not make any sense.

Response:

Why not? Life is limited by all kind of factors: light, food, temperature...

Trying to hold one’s breath for a short while suggests that we don’t pay enough attention to oxygen.

Comment:

The basic premise of life-history theory is the trade-off in energy allocation between growth and reproduction (plus associated costs). Skittish individuals mature early not because they cannot get enough oxygen for growth but because they prioritize investment in reproduction versus growth.

Response:

This is demonstrably erroneous, as skittish fish display reduced growth long before they attain sexual maturity (see e.g., Vincent 1960; Bozynski and Pauly 2017). Also, this argument is illogical in that it assumes that the fish which “prioritize investment in reproduction versus growth” would also waste energy in being skittish – as if ‘skittishness’ did not have a cost, and were engaged in a whim.

Comment:

This trade-off has been demonstrated in multiple experiments, is at the core of aquaculture breeding programs (where early maturation and increased investment in reproduction is often not desired) and has been shown in many wild populations. Increased mortality selects for higher investment in reproduction at the cost of growth. There is no need to involve oxygen limitation here at all.

Response:

Breeding programs aiming at increasing meat yields always aim at getting “aggressiveness” out of the genepool (see www.welfarequality.net/media/1050/wq___decreasing_aggression_in_pigs_en.pdf). Similarly, aquaculture breeding programs, which aim for fast growing individual with delayed maturation actually selects for calm (non-skittish) fish; this is the reason with farmed Atlantic salmon (*Salmo salar*) are calm compared with wild conspecifics (Olesen et al. 2011). This also applies to Nile tilapia (*Oreochromis niloticus*), whose fast-growing GIFT strain, as a result of intensive selection for fast growth, consists of individuals that are much calmer than the controls (Bozynski and Pauly 2015).

Comment:

What does this mean for the ability of fisheries to preadapt fish to climate change? Very little is known about the effects of temperature on life-history evolution. How will increased investment in reproduction affect ability to adapt to climate change? It could be argued that earlier maturation correlates to higher metabolism, although again we don't have enough data to show this. If that is the case, then one can imagine that individuals with higher background metabolism might have little room to increase it further with climate warming. Which means that fishing is bad for climate adaptation. But there are many other alternatives. If larger individuals were more sensitive to higher temperatures, it would actually be good to mature earlier when higher temperatures don't damage you too much, so you have at least one chance to reproduce. It is all pure speculation at this stage. Moreover, we also have to consider adaptation. Given large inter-individual variation in standard metabolism level there is good evidence that populations have enough additive genetic variance to adapt. A few generations might be enough to adjust metabolism to new conditions and all this fisheries-driven preadaptation becomes irrelevant.

Response:

Amidst the confusion in this paragraph, there were two points that made sense to us:

- One can imagine that individuals with higher background metabolism might have little room to increase it further with climate warming. Which means that fishing is bad for climate adaptation; and
- If larger individuals were more sensitive to higher temperatures, it would actually be good to mature earlier when higher temperatures don't damage you too much, so you have at least one chance to reproduce.

These are precisely the points that we make, and they are not “pure speculation” (see our other responses).

Comment:

I do agree with the authors that fishing is likely to hinder climate change adaptation. Not because of oxygen limitation, but simply because it is likely to be reducing genetic diversity and a basis upon which selection can work.

Response:

Well, yes. But respiratory performance and the use a fish makes of the oxygen it gets via its gills are also traits “upon which selection can work”.

Comment:

Another thing to add – populations that have been affected by fishing are indeed more vulnerable to climate change, but this can be explained by truncated age and size structure (Seccor et al. 2007 – storage effect; Hsieh et al. 2006, and others). Oxygen limitation is irrelevant here.

Response:

We agree that fisheries, by truncating the natural age and size structure, make fish populations more sensitive to environmental fluctuations, and by extension, to “climate change”. But climate change in the ocean manifests itself as increased water temperature with lower oxygen content, meaning higher metabolic requirements and lower oxygen harvest per breathing effort for the fish. How can oxygen limitation be “irrelevant” in such context?

Comments by Reviewer: 2

This manuscript [...] presents a conceptual idea based in two figures derived from previously published work but is not supported by new analyses of data or models. As such, I find this format to be within the scope of [of an opinion piece in our journal], but that the submission would have been stronger with a more rigorous analysis, and have reviewed the manuscript on this basis.

Response:

We agree that this is an opinion piece, presenting a novel way of thinking about an issue that will soon be on every fishery biologist’s mind, given the simultaneous occurrence of overfishing and ocean warming.

Comment:

The authors start from oxygen uptake as the constraining mechanism for fish metabolism, which in turn sets limits for growth and everything else. This basis is well documented and follows a long tradition in physiology. In general, I am positive to using more physiology in fisheries science and marine ecology.

Response:

We were delighted when we read this sentence, as we also think that “oxygen uptake [i]s the constraining mechanism for fish metabolism, which in turn sets limits for growth and everything else” and that “this basis is well documented and follows a long tradition in physiology”. This, however, is not known to many fishery biologists (notably Reviewer 1), who contest both points.

Comment:

The authors then take as starting point the general observation that larger fish species are most sensitive to climate warming. That is a general observation which could be made more nuanced, but the statement can be accepted for the sake of the general argument. They then combine this with the general trend of fishing to induce evolution towards smaller body sizes, which is supported by models and empirical analysis. They then ask whether fishing, as a long-term effect, would make species more resilient to climate warming. The paper develops this argument, and the details matter.

Response:

This is a fair summary of our argument.

Comment:

The authors rely on two mechanisms, of which one is the different scaling of gill area versus maintenance metabolism. This argument has been published many times before by the same authors, in papers and books, but is flawed. The same assumptions are also used by other authors and modelling tools, and go back to von Bertalanffy’s growth modelling from the 1930s. There are three main problems. First, there is now abundant

evidence that maintenance metabolism scales with weight at exponents well below 1. For life in general it is 0.71 (Brown et al. 2004).

Response:

In both von Bertalanffy's work, and its development by one of us (See Pauly 2019), maintenance metabolism is defined as the oxygen consumption of a fish such that it can generate the ATP to maintain the cellular machinery in its body, with no surplus for growth. This level of oxygen consumption can be estimated from the time-averaged metabolic rate of e.g., the heaviest fish (W_{\max}) of a given species in a given set of environmental conditions (especially temperature). This definition of maintenance makes the way it scales (for weight < W_{\max}) a moot point. In other words, the fact that oxygen consumption relative to body weight in fish scales similar to life in general does not mean that water-breathing animals are not limited by their gills. Rather, it is the intercept or height of the regression line that describes the amount of oxygen available for a given body mass, and that amount is much lower in water-breathers than in animals that breathe air.

Comment:

What matters for the argument here is the intraspecific scaling exponent, which likely is higher than between species but only in some cases as high as 1 (Killen et al. 2010). For most fish the exponent is well below 1. If gill area increases at an exponent with weight slightly higher than 2 (Palzenberger and Pohla 1992 document huge variation), then it is not at all clear that the graphical argument in figure 2 holds.

Response:

Scaling factor differences are of no relevance here. The well-documented scaling factor linking gill respiratory area (or metabolic rate) and body weight in fishes range between 0.6 and 0.9, with the higher values (e.g., in Palzenberger and Pohla 1992) usually referring to juveniles, in which this factor is indeed higher, as it is in teleost larvae (see e.g., Bochdansky and Leggett 2001); this is dealt with at length in Pauly (2010).

Comment:

Second, the authors use the intersection of the two curves as an argument for identifying the adult body size where there will be no more oxygen for growth. From a life history perspective, fish, or any other organism for that matter, don't live to grow but to reproduce. What matters is the size at which the ability to turn resources in the environment into offspring is at maximum. If one accepts that oxygen uptake would be a proxy for this, then it should be actual body mass on the x-axis, and the curves should be drawn not specific to weight but for the total body. That surplus, the difference between the two curves, most certainly peaks at a much smaller body size. Ignoring reproduction as shaping individual growth through adaptation violates the most fundamental insight from Darwin.

Response:

We do not understand this suggestion of reviewer 2, because the X-axis in Figure 2 does show "actual body mass" and the Y-axis shows relative oxygen consumption "for the total body". We do not use the intersection of two curves for anything. Rather, the two panels of Figure 2 display intersections of one curve representing oxygen supply vs body weight with two different thresholds levels, representing maintenance metabolism at W_{\max} (see above for definitions), e.g., in a low and a high temperature environment.

We agree that all living organisms strive to reproduce themselves, but that doesn't mean that, e.g., a fish only has the option of putting all their eggs (so to say) either toward growth or reproduction. A good part of zoology, for example, is devoted to studying strategies and tactics that have evolved to enhance survival of offspring or of close relative.

That local condition should determine growth patterns, which then determine when size at reproduction is reached (Pauly 1984) is indeed a reversal of causal arrow (i.e., growth \rightarrow reproduction) that is usually assumed to run in the opposite direction (i.e., reproduction \rightarrow growth). However, most colleagues who argue for the latter have never examined its implications in depth, and the many logical and empirical problems it causes (e.g., growth in body weight peaks well after onset of reproduction in most highly fecund bony fish; see list of other problems in Pauly (2010)). All they have done is inferring causation from a correlation.

Comment:

Third, it is not only energetics that counts for expected reproduction, but also survival until one can reproduce. Natural mortality usually declines with body size, making the argument above non-linear with size in a non-trivial way. My experience with making models for this is that very few gets it right without doing the actual math. In the argument in this paper mortality is omitted altogether, and any firm conclusions about life history evolution cannot be reached.

Response:

We believe, on the contrary (with Darwin, incidentally) that evolutionary arguments that do not make logical sense, and/or rest on unverified, if widely held assumptions, do not become valid when they are put into mathematical models. For example, a single goldfish can be kept in an aquarium, and its growth, rapid at first, will cease at some point, without that fish have ever spawned or even elaborated gonad tissue. It will also not have been subjected to any mortality, natural or feline-induced. The same is true for most fish in large public aquaria, for which it cannot be argued that their growth stopped because of bad water quality or lack of space. What does this *Gedanken* experiment do? It completely disproves the causal arrow with 'growth \rightarrow mortality'. (This, incidentally, is the kind of thinking that Charles Darwin used to make his points, not math).

Comment:

These three flaws have followed this graphical model and the von Bertalanffy growth curve for life history purposes for a long time. That the model has been published and used widely does not make it right, and I firmly believe it should be abandoned, the sooner the better. If this model, violating known biological observations and mechanisms, happens to make predictions that match observations it is only because there are multiple errors in it that somehow cancel, and any extrapolation or argument about causation would be without mechanistic basis.

Response:

In FishBase (www.fishbase.org), which the authors initiated, there are, as of January 2020, 11,767 sets of von Bertalanffy growth parameters, describing the growth of the Philippine goby *Mistichthys luzonensis*, with reaches 2.5 cm as well as that of the whale shark *Rhincodon typus*, which reaches 14 m. There is hardly any other model in biology that has been fit successfully to so many data sets. We find it extraordinary that the thousands of authors who generated these growth curves have been misled to the extent suggested by this reviewer. As for the sound biological basis of the von Bertalanffy growth equation see Pauly (1981, 2010/2019).

Comment:

The other mechanism the authors draw on is fishing-induced evolution, where it is correct as they state that many fisheries remove late-maturing fish before they reproduce. The consequence, as the authors also state, is that early-maturing fish succeed to reproduce, often at smaller sizes, and that their genes are therefore found in higher proportions in subsequent generations. But selection on maturation age/size does not imply selection for otherwise poor genetic makeup, as the authors describe in imprecise and unprofessional language laden with negative value (lines 50-51). The inference leading up to this statement does not follow logically from the premises stated, which takes away an important basis for their overall conclusion.

Response:

Two points made here are:

- (1) “selection on maturation age/size does not imply selection for otherwise poor genetic makeup”; and
- (2) “the authors [use] imprecise and unprofessional language laden with negative value”.

Re item (1): We agree that being small doesn't necessarily imply being skittish. Thus, just as there are small dogs that are temperamentally skittish (terrier) and others that are calmer (dachshund, or wiener dog), there are small fishes that are small and generally calm (e.g. stonefish), while others are comparatively hyperactive (e.g. anchovies). However, this is not what is meant here. We are referring to individual fish of a given population, which are so skittish that their growth is impaired, so that they it is not caught by a gear that selects larger but calmer fish. Or as stated in our contribution above “what is left in that population are the skittish and /or inefficient runts, which managed to reproduce before they could be caught”. We have never encountered in the literature on genetic selection any arguments to the contrary and the reviewer hasn't either. Instead, he/she complains that our language is imprecise, unprofessional and (negative) value laden.

Yet the survivors (to use a neutral term) are inefficient, at least in terms of food conversion efficiency (Gerking 1971). They are also runts. As defined in Wikipedia, “in a group of animals (usually a litter of animals born in multiple births), a runt is a member which is significantly smaller or weaker than the others.”

Thus, runt is a *precise* term for exactly what we meant, and if it has a negative connotation, it is because, often runts die prematurely. But the runts in our paper don't die. They even reproduce and to increase their share in the population.

We do not respond to the point about “unprofessional language”.

Comment:

I realize that this review is not much of an evaluation of the submitted manuscript but maybe more of a counterargument to the methods and reasoning applied. I am generally reluctant to recommend rejection of a paper only because I disagree. I firmly believe different arguments should be published for everyone to see and judge, and that this is a fundamental strength necessary to ensure scientific progress. I therefore avoid giving a particular recommendation but leave this to the editor(s) to decide.

Response:

Fair enough. However, we decided that we would renounce the editor's offer to present our contribution (above) back-to-back with a contribution that would elaborate on the comments presented in this appendix, which we fear, are only conventional, negative responses to novel thoughts.

Minor comments:

It is unclear how Figure 1 was constructed, why late-maturing fish also grow more slowly during the juvenile phase, and what consequences fisheries selection has for Darwinian selection on life history traits including physiology. The description in the main text is not making use of this figure or explaining it.

Response:

The three hypothetical growth curves for North Sea cod in Figure 1 have the same θ but different L_{∞} values. The corresponding values for K were obtained from $\log_{10}(K) = \theta' - 2 \log_{10}(L_{\infty})$. This empirical model (Pauly 2010/2019) predicts the illustrated growth curves. In other words, it is correct that individuals with a higher K grow faster towards a smaller L_{∞} .