

Bottom up and top down effects of temperature on body growth, population size spectra and yield

Kommenterad [AG1]: just come to think of that the title does not indicate anything about that its done on interacting species – maybe it should?

Max Lindmark^{a,1}, Asta Audzijonyte^b, Julia Blanchard^c, Anna Gårdmark^d

^aSwedish University of Agricultural Sciences, Department of Aquatic Resources, Institute of Coastal Research, Skolgatan 6, Öregrund 742 42, Sweden

^bInstitute for Marine and Antarctic Studies, University of Tasmania, Battery Point, TAS 7001, Australia

^cInstitute for Marine and Antarctic Studies and Centre for Marine Socioecology, University of Tasmania, 20 Castray Esplanade, Battery Point, Hobart, TAS 7000, Australia

^dSwedish University of Agricultural Sciences, Department of Aquatic Resources, Skolgatan 6, SE-742 42 Öregrund, Sweden

Word count

Abstract: 272

Introduction: 1121

Methods: 2744

Results: 685

Discussion: 1777

Abstract

Resolving the combined effect of climate warming and exploitation in a food web context is key for predicting future biomass production, size-structure and potential yields of marine fishes. Previous studies based on mechanistic size-based food web models have found that bottom-up processes are important drivers of size-structure and fisheries yield in changing climates. However, we know less about the joint effects of bottom up and ‘top down’ effects of temperature (~~temperature~~-affecting food availability vs individual-level physiology) on the size-structure of exploited species in food webs. Here we assess how fish individual- versus population mean size ~~various food web metrics~~ are affected by warming through both these pathways, and by exploitation, in a species-resolved size-based food web. We parameterize a dynamic size spectrum food web model inspired by the offshore Baltic Sea food web, and investigate how individual growth rates, size-structure, relative abundances of species and yields are affected by warming. Warming ~~is~~ based on projections by the regional coupled model system RCA4-NEMO and the RCP 8.5 emission scenario, and we evaluate different scenarios of temperature on fish physiology and resource productivity. When accounting also for temperature-effects on physiology, projected size-at-age in 2050 increases for all fish species compared to without warming, whereas size-at-age decreases when temperature only affects resource dynamics, ~~both relative to non-warming scenarios. However, the faster growth rates due to warming in the fully temperature-dependent models however,~~ do not always translate to larger yields, as mean body size and spawning stock biomass declines due to ~~declines-temperature-driven reductions~~ in resource carrying capacity. These results show that it is important account for both direct and indirect effects of temperature ~~in order~~ to explain ~~results such as~~ increased growth rates and size-at-age within species but overall smaller populations and lower yields due to ~~reductions declines~~ of large fish.

Kommenterad [AG2]: wondering whether we can come up with something clearer here? (Also, the processes we go for are not only ‘physiological’ but also ecological, like feeding rates). No good suggestion for an alternative yet though... maybe ‘direct effects on individuals’ is more encompassing, also less specific on the other hand

Kommenterad [AG3]: food web metrics are usually measurements on the web itself, such as connectivity, compartmentness, nestedness etc; better change term (and be more specific, if there’s space)

Kommenterad [AG4]: since it’s a food web model, it’s probably good to specify that your focal species are fish (above you only say ‘exploited species’)

Kommenterad [AG5]: to avoid repetition perhaps?

Kommenterad [AG6]: your last results (fisheries related) on FMSY and yields aren’t visible in the abstract. Shouldn’t they be?

Kommenterad [AG7]: any slightly wider implications (from your discussion)?

Introduction

Climate change is causing shifts in productivity

Kommenterad [AA8]: These are just guiding titles or key points

Climate change affects aquatic food webs directly by affecting species' distribution (Pinsky *et al.* 2013), abundance (McCauley *et al.* 2015), body size (Daufresne *et al.* 2009; Baudron *et al.* 2014), and ecosystem function (Pontavice *et al.* 2019). Global retrospective analysis of warming and fish population dynamics has revealed that productivity (population growth at a given biomass) of scientifically assessed fish populations across ecoregions has already declined by on average 4.1% between 1930-2010 due to climate change (Free *et al.* 2019). These results are also matched in magnitude and direction by projections from an ensemble of mechanistic ecosystem models, which predicts ~5% decline in biomass for every 1 °C of warming, especially at higher trophic levels (Lotze *et al.* 2019). Across a range of process-based ecosystem models, the causes of declines in productivity of fish stocks, and abundance of large fish, have in process-based ecosystem models mainly been mostly linked to changes in primary production or zooplankton abundance (Blanchard *et al.* 2012; Woodworth-Jefcoats *et al.* 2013, 2015; Barange *et al.* 2014; Lotze *et al.* 2019). However, stock assessments models have found no clear increase in fish productivity in areas where warming is predicted to have positive effects on primary production (Free *et al.* 2019). Instead, this suggests that fish population dynamics and productivity might be strongly influenced by other factors, other factors may be more important for population dynamics and productivity, including such as temperature-driven changes in individual and population-level processes such as recruitment, mortality and/or somatic growth (Free *et al.* 2019). (Tu, 2018 #823) This demonstrates that the driving mechanisms of changes in fish productivity and biomass with warming are still poorly understood.

Climate change is also affecting fish sizes, but there is a debate about it

Moreover, global warming is also predicted to cause reductions in the adult body size of organisms, which is often referred to as the third universal response to warming (Daufresne *et al.* 2009; Sheridan & Bickford 2011; Forster *et al.* 2012). Of course, in intensively fished stocks, observed adult body sizes can decrease for many reasons, including direct removals of large fish, or evolution towards earlier maturing and fast growth in response to fishing (Jorgensen *et al.* 2007; Audzijonyte *et al.* 2013). Yet, decreasing fish body sizes could also represent a plastic response to temperature, as predicted by the temperature-size rule (TSR) (Atkinson 1994). TSR, has been observed in a wide range of ectotherms.

Ändrad fältkod

Kommenterad [AG9]: could remove the decimal and just go for 4%

Kommenterad [AG10]: biomass of what? fish/animals/total food web biomass?

Kommenterad [AA11]: I would not necessarily say adaptive, because the whole adaptive significance of TSR is debated and has never been proven to my knowledge

and states that individuals reared at warmer temperatures develop faster, mature earlier but reach smaller adult body sizes (Ohlberger 2013). Studies indeed, declines in fish maximum or asymptotic body size are commonly reported for a number of fished species, e.g. in the Mediterranean have reported declines in the maximum body size (van Rijn *et al.* 2017) or the North Sea, and synchronous declines in asymptotic body size across species in the North Sea (Baudron *et al.* 2014), and appear to be explained by the warming trends. In line with TSR expectations, faster growth rates or larger size-at-age of young life stages are also commonly found in both experimental and field data (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Neuheimer & Grønkaer 2012; Baudron *et al.* 2014; Huss *et al.* 2019), as indications of a body size response to concurrent warming. In fish, adult body sizes can decrease for many reasons, including direct removals of old or large fish, or selecting for early maturing and fast growing individuals (Jørgensen *et al.* 2007; Audzijonyte *et al.* 2013). It could also be a plastic adaptive intraspecific response. The temperature-size rule (TSR) (Atkinson 1994) states that individuals reared at warmer temperatures develop faster and thus acquire larger size-at-age or life stage, but reach smaller adult body sizes (Ohlberger 2013). Studies have reported declines in the maximum body size (van Rijn *et al.* 2017), and synchronous declines in asymptotic body size across species in the North Sea (Baudron *et al.* 2014) as indications of a body size response to concurrent warming. However, Yet, decreasing adult fish size in response to temperature is by far not universal. For example, no clear negative effects of warming on the body size or growth of large fish could be found in a recent experimental study (Barneche *et al.* 2019), or in a semi-controlled lake heating experiment (Huss *et al.* 2019). In both cases, there was no fishing, which can without potentially confound any effects of temperature in exploited populations fishing were absent. By contrast, faster growth rates or larger size-at-age of young life stages are commonly found in both experimental and field data (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Neuheimer & Grønkaer 2012; Baudron *et al.* 2014; Huss *et al.* 2019), in line with the TSR. This is likely because most fish species live in thermal environments where growth is still positively related to temperature (Neuheimer *et al.* 2011; Lindmark 2020). Similarly, across 335 coastal fish species mean body size was similarly equally likely to increase or decrease in response to warming (Audzijonyte, 2020 #833}. Also (Tu, 2018 #823} found that temperature had a relatively minor effect on fish size structure, and even when combined with fishing effects, only 44% of variation in size structure could

Kommenterad [AA12]: I think it makes sense to cite earlier references here, not the review by Jan

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Kommenterad [AA13]: I would not necessarily say adaptive, because the whole adaptive significance of TSR is debated and has never been proven to my knowledge

Ändrad fältkod

Kommenterad [AA14]: I am not sure I understand this sentence. Do you mean, "in both cases the potentially confounding effect of fishing was absent"

Kommenterad [AA15]: This sentence was after the juvenile growth sentence (which I moved) but I am not sure it makes sense. Faster juvenile growth is expected in TSR, so I am not sure what this sentence is trying to justify or add. I would remove it

Kommenterad [AG16]: is it ok to change to "equally likely" here Asta? to avoid repetition

Kommenterad [AA17]: Need to check the actual number

be explained. Thus, the effects of ecological rule of shrinking temperature and climate change effects on body sizes may be more complex than often depicted, but and we still do not fully understand the underlying mechanisms underlying how the effects of temperature on growth and body size relationships tend to vary over ontogeny, or affect population mean body sizes. As body size is a key trait in aquatic ecosystems (Andersen *et al.* 2016a), warming-induced changes in growth and size-at-age of fish populations could have implications not only for biomass and productivity but also ecosystem structure and stability (Audzijonyte *et al.* 2013). It is therefore important to evaluate the impacts of warming on body size and size-based interactions, using e.g. mechanistic size-based food web models.

To study mechanisms we need physiologically structured models that account for size and species interactions

Mechanistic models can be useful for evaluating the implications of temperature-size responses in food webs because they emerge from individual-level processes (references to Angilleta, Atkinson and others?). Using an eco-physiological growth model (generalized von Bertalanffy growth model), Cheung *et al.* (2013) predicted on average declines in community-average maximum body mass by 14-24% by 2050 under high-emission scenarios, due to changes both in distribution and warming-induced constraints on asymptotic mass. While these declines in maximum body size are in line with the “universal” relationship between smaller adult or asymptotic body sizes and warming, both the physiological basis and the magnitude of the reductions have been questioned, in particular for fish (Lefevre *et al.* 2018; Pauly & Cheung 2018). In addition, body growth and resulting size-at-age depends on an interplay between body size, temperature and food availability (Brett *et al.* 1969). This is for instance exemplified in the within-species observation that the optimum temperature for individual growth declines with both body size (Björnsson 2001; García García *et al.* 2011; Lindmark 2020) and reduced food rations (Huey & Kingsolver 2019). Therefore, mechanistic models aiming to predict climate change responses should also account for the food dependence of growth through ecological interactions, e.g. in a bioenergetic framework. Such ecosystem models have predicted declines in the maximum body size in communities, driven by reduced plankton abundance or shifts towards smaller

Kommenterad [AA18]: But this is predicted by the TSR, so not really different from the expectation

Kommenterad [AG19]: or somehow signal that you'll be looking at this

Kommenterad [AG20]: isn't the key conclusion that we need to understand the mechanisms? (not necessarily which tools that should be used to do so – you haven't discussed tools yet). Suggest you change to that

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Kommenterad [AG21]: As the paragraph is written now it seems to focus on the tools rather than on the findings. I would instead focus on the findings (which mechanisms have been identified and how can they help explain the temperature effects on food webs?), and gaps in these findings (what haven't the models been able to explain), and reasons for this (model assumptions made, fundamental processes overlooked). That opens up for a conclusion on that we need another modelling approach to study the question you've identified. Which leads nicely over to 'in this paper we...' -paragraph.

Kommenterad [AA22]: To be honest this model has so many problems but keeps getting cited all the time. It gives a bad name to mechanistic models. The main problem is that the 14-24% includes both intra and interspecific responses, yet it so often gets compared with TSR expectations. Like in the two sentences below ☹️ What proportion of this change is due to predicting TSR response alone? Second, if you want to refer to VB type models that were used to study TSR effects, perhaps it is better to start with Angilleta, Atkinson and others who explored how this simple model could explain TSR. Why refer to the problematic Cheung paper?

Kommenterad [AA23]: Which part of the decline? 14-24%?? Which part of it is intraspecific?

Kommenterad [AA24]: And it also depends on including minor physiological mechanisms, such as the reason we live – reproduction! ☹️

Kommenterad [AA25]: A population model could account for food dependent growth, you don't necessarily need a food web model for that. However, it would be interesting to know how responses in different interacting species play out.

I would suggest to start this paragraph with Angilleta's and other VB type models, then bring in the importance of food dependent growth, as well as dynamic mortality and competition within and across species. And then transition to food web models with temperature effects

Kommenterad [AA26]: Perhaps we need to elaborate a bit more here on what kind of ecosystem models, because EwE also are ecosystem models, but we would not call them physiologically structured. This transition is a bit abrupt. And there are dozens of ecosystem models of all sorts that looked at climate change effects. Some people call NPZ models ecosystem models

Kommenterad [AA27]: Because it is not clear what kind of ecosystem models we are talking about, it is also not clear whether we are talking about plankton or fish communities, or everything.

Also because you are talking about size spectrum model of the Baltic Sea below it is good to introduce size based models and what has been found with the already

plankton, which reduces energy transferred to higher trophic levels (Woodworth-Jefcoats *et al.* 2015). Models that include temperature-dependence of physiological processes (such as metabolism and feeding rates) in species-resolved and size-based food webs in general also find these results (Lefort *et al.* 2015; Woodworth-Jefcoats *et al.* 2019). However, it is unclear to what extent this is driven by declines abundance of large fish versus changes in size-at-age.

In this study, we evaluate the impacts of temperature-driven changes in resource productivity and individual physiology on ~~individuals fish size, fishs and growth and~~ and the ~~structure?~~ ~~oO~~ of the food web. The Baltic Sea constitutes a great example system to explore such impacts of warming, as it is a relatively well understood and species poor system (Mackenzie *et al.* 2007; Casini *et al.* 2009) that in addition experiences rapid warming (Belkin 2009). Here we introduce a temperature-dependent size spectrum model and analyze a set of different scenarios with either fish physiology, basal resources, or both being temperature dependent. We specifically investigate the mechanisms underlying the impacts of projected warming on body growth trajectories, average body sizes, population size-structure and fisheries reference points. We are interested to understand the relative importance of productivity changes versus physiological effects of temperature in climate change responses. Temperature change is based on the regional coupled model system RCA4-NEMO and the RCP 8.5 emission scenario (Dieterich *et al.* 2019; Gröger *et al.* 2019). Uncertainty in the effect of warming on physiology is incorporated by ~~randomly parameterizing these rates~~ running multiple simulations where temperature responses are sampled from using previously established probability distributions from meta-analyses (Lindmark 2020). We find that inclusion of temperature-dependent physiological processes leads to increased size-at-age in fish, especially for ~~smaller individuals~~ juvenile fish ~~and in line with observations~~, whereas the opposite is observed when only resources are temperature-dependent. However, overall, we find that warming leads to declines in mean body size in the fish populations due to shifting size distributions, resulting in lower yields in warmer environments.

Kommenterad [AG28]: not really, do you?

Kommenterad [AG29]: or "focus especially on understanding"

Kommenterad [AA30]: Or are you talking about small sized species like spratt

Kommenterad [AA31]: Under which scenario?

Kommenterad [AA32]: What does it mean? Changes in mortality or changes in growth?

Materials and Methods

Food web

We developed a [m](#)Multi-species size spectrum model (MSSM) (Scott *et al.* 2014) parameterized to represent a simplified version of the food web in the offshore pelagic south-central Baltic Sea ecosystem (Baltic proper) (ICES sub divisions 25-29+32, Appendix Fig S2). This food web is here characterized by three fish species: Atlantic cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), and two dynamic [size structured](#) background resource spectra constituting food for small fish (pelagic and benthic resources). These fish species are dominant in terms of biomass, they are the most important species commercially in this part of the Baltic and they all have analytical stock assessments. The [two](#) background spectra represent [groups of](#) species that are food for fish but are not explicitly modelled (Andersen *et al.* 2016b). The pelagic spectrum represents mainly phyto- and zooplankton while the benthic background resource spectrum [represents](#) benthic invertebrates, gobiidae and small flatfish.

Size spectrum model

The model is based on source code for the multi-species implementation of size spectrum models in the ‘R’-package [mizer](#) (Blanchard *et al.* 2014; Scott *et al.* 2014, 2019; R Core Team 2018), which has been extended to include [multiple background resources](#) and temperature-scaling of key physiological processes. In this section we describe the key elements of the MSSM using the [same notation](#) when possible as in previous multispecies mizer models for consistency (Blanchard *et al.* 2014; Scott *et al.* 2014, 2018).

In MSSMs, individuals are characterized by their weight (w) and species identity (i). The core equation is the McKendrick-von Foerster equation, which here describes the change in abundance at size through time, from food dependent somatic growth and mortality, based on bioenergetic principles:

$$\frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w)N_i(w)}{\partial w} = -\mu_i(w)N_i(w) \quad (1)$$

where $g_i(w)$ [g year⁻¹] is somatic growth (dependent on the availability of food) and $\mu_i(w)$ [year⁻¹] is total mortality. At the boundary weight (w_0 , egg size), the flux of individuals is given by recruitment. Total mortality is the sum of the background-, starvation-, fishing-, and predation mortality. The

Kommenterad [AG33]: reads a bit strange that we explicitly state that the resources have spectra and are size-structured, but not say anything about the size structure of the fish. Reword?

Kommenterad [AG34]:

Kommenterad [AG35]: since there is a new version now, we should probably say which version too, shouldn't we?

Kommenterad [ML36]: Audzijonyte et al. ☺

Kommenterad [AG37]: some of these are truly confusing, like having several different indices for the same thing (like p , j , and i all indexes meaning prey species...). I would consider readability over consistency with the vignette here (ensuring that your readers comprehend your manuscript on its own, without having to read the vignette!). The consistency with the vignette they can get from your code.

Kommenterad [ML38R37]: I landed on a mix between your suggestion for clarification and keeping as is. Thanks for checking carefully!

constant size-independent species-specific allometric background mortality ($\mu_{b,i}$) depends on the asymptotic weight of a species W_i^{n-1} and is given by:

$$\mu_{b,i} = \mu_0 W_i^{n-1} \quad (2)$$

where n is the mass-exponent of maximum consumption rate and μ_0 is an allometric constant. Starvation mortality ($\mu_{s,i}$) is assumed to be proportional to energy deficiency (defined in Eq. 11) and inversely proportional to body mass (weight, w), and is defined as:

$$\mu_{s,i}(w) = \begin{cases} 0 & \alpha f_i(w) h_i w^n > k_{s,i} w^p \\ \frac{k_{s,i} w^p - \alpha f_i(w) h_i w^n}{\xi w} & \text{otherwise} \end{cases} \quad (3)$$

where ξ , the fraction of energy reserves, is 0.1 (Hartvig *et al.* 2011). Instantaneous fishing mortality ($\mu_{f,i}$) (1/year) is defined as:

$$\mu_{f,i}(w_i) = S_i(w) E_i \quad (4)$$

where S_i is the selectivity (by default knife-edge selectivity is assumed with a weight at first catch corresponding to weight at maturation), and E_i is **fishing effort**. E_i is thus fishing mortality, and the terms fishing mortality and effort are used interchangeably henceforth. Predation mortality ($\mu_{p,j}$) for a prey species (or resource) j with weight w_j equals the amount consumed by predator species i with weight w_i :

$$\mu_{p,j}(w_j) = \sum_i \int \phi_j \left(\frac{w_j}{w_i} \right) (1 - f_i(w_i)) \gamma_i w_i^q \theta_{i,j} N_i(w_i) dw \quad (5)$$

where $\theta_{i,j}$ is the non-size based preference of species i on species j , and ϕ_j describes the weight-based preference from the log-normal selection model (see below) (Ursin 1973). The proportions of encountered food that are consumed by a species i follows a Holling functional response type II:

$$f_i(w) = \frac{E_{e,i}(w)}{E_{e,i}(w) + h_i w^{n-1}} \quad (6)$$

where $f_i(w)$ is the feeding level (which describes the level of satiation and varies between 0 and 1), $h_i w^n$ is the allometric maximum consumption rate and $E_{e,i}(w)$ is the encountered food (mass per time). The amount of encountered food for a predator of body weight w is given by the available food in the system multiplied with the **search volume**, γ_i . Here, available food, $E_{a,i}$, is the integral of the biomass

Kommenterad [AG39]: generally it becomes tricky to follow when you as subscripts mix things that are the parameter names (here s for starvation, I guess?) and that are indices (i for species i)

Kommenterad [ML40R39]: Yes, that's not nice but hard to avoid also! Edwards & Auger-Méthé (2019, MEE, "Some guidance on using mathematical notation in ecology"), suggest abbreviating the name part, i.e. $\mu_{sta,i}$ in this case, which is similar to how it's done with $R_{max,i}$

I could consider doing that, but for now I've just defined the symbol directly after the sentence, as in the vignette.

Kommenterad [AG41R39]: yes, could be a solution for later

Kommenterad [AA42]: I think this is the instantaneous fishing mortality with the units (1/year) for the fully recruited individuals. Effort refers to something like nets/day and could lead to different mortality values depending on the stock abundance.

Kommenterad [ML43R42]: Hmm, yes I agree with that definition of effort in general, but in mizer, if catchability is set to 1, the effort corresponds to the instantaneous fishing mortality (1/year), right? (including also selectivity by size, so F is a function of w). Anyway tried to clarify the terms here!

Kommenterad [AA44R42]: I think this is still confusing. Do we need to use same terms as in mizer? Especially because we are not talking about catchability here. What about you say that E_i is the instantaneous mortality (1/year) of fully selected individuals? Would that be correct?

Kommenterad [ML45]: Calling this search volume rather than rate now

of all prey species (j) and background resources (R) that falls within the prey preference ($\theta_{i,j}, \theta_{i,R}$) and size-selectivity (ϕ_i) of **predator** species i :

$$E_{a,i}(w) = \int \left(\sum_R \theta_{i,R} N_R(w_R) + \sum_j \theta_{i,j} N_j(w_j) \right) \phi_i \left(\frac{w_j}{w_i} \right) w_j dw_p \quad (7)$$

where w_j is the weight of prey, $\theta_{i,R}$ is the preference of species i for resource R , and j indicates prey species. Note that in contrast to other MSSMs (Blanchard *et al.* 2014) we have a species-preference for the background resources to account for species feeding differently on benthic and pelagic resources, but assume no preference in terms of the interactions among the size-structured fish species (all terms in the interaction matrix are identical and equal to 1). This is for simplicity, as the body size-only prey selection and encounter rate capture the important predation interactions in this system (as inferred from independent stomach data, see model calibration, Appendix S1) and the species largely occupy similar spatial areas within the study area during the time period of the model calibration (Fig S2). The size-selectivity of feeding, $\phi_i \left(\frac{w_j}{w_i} \right)$, is given by a log-normal selection function (Ursin 1967):

$$\phi_i \left(\frac{w_j}{w_i} \right) = \exp \left[\frac{- \left(\ln \left(w_i / (w_j \beta_i) \right) \right)^2}{2 \sigma_i^2} \right] \quad (8)$$

where parameters β_i and σ_i are the preferred predator-prey mass ratio and the standard deviation of the log-normal distribution, respectively. The amount of available prey of suitable sizes (Eq. 7) is multiplied with the allometric function describing the search volume ($\gamma_i w^q$), where the allometric coefficient is calculated as:

$$\gamma_i(f_0) = \frac{f_0 h_i \beta_i^{2-\lambda} \exp(-(\lambda-2)^2 \sigma_i^2 / 2)}{(1-f_0) \sqrt{2\pi} \kappa \sigma_i} \quad (9)$$

(Andersen & Beyer 2006; Scott *et al.* 2018), to give the actual biomass of food encountered, $E_{e,i}(w)$:

$$E_{e,i}(w) = \gamma_i w^q E_{a,i}(w) \quad (10)$$

where q is the size-scaling exponent of the search volume. The rate at which food is consumed is given by the product $f_i(w) h_i w^n$, which is assimilated with efficiency α and used to cover basal metabolic

Kommenterad [ML46]: We should maybe think about how this should be calculated when there are multiple resources. In the code, it uses one of the kappas... but which one should it be? Sum of all?

Kommenterad [AG47R46]: most likely sum of both (...on the top of my head – inferred from how we define functional responses for multiple resources) – but then the code needs to be corrected as well (later on...); **worth discussing also with Ken**

Kommenterad [ML48R46]: Yes, very important!

Asta, when you introduced the multiple background resources, did you make a choice on how to deal with this? I currently see only "kappa" being used to calculate gamma, which is the plankton resource.

It may also matter that I set the between each species and it's basal resource encounters to sum to 1, and that the kappas as the same for both resources in this model.

Kommenterad [A49R46]: I think with multiple resources it is problematic to use this equation not only because we are not sure which one to use but also because species have different access to these resources. In my model I got a very approximate estimation of gammas using the mean kappa for the three resources, but these gammas seemed quite low, when considering for example search area per day
(`mariaParams$gamma*mariaParams$w_mat^params@q/365`)

I then increased all gammas three times and then again for predators increased gamma three times again, otherwise predators would always starve (since they did not have so much access to the abundant background resource and had to have sufficient intake rates to get enough food on less abundant fish). However, I was quite suspicious with these rates so I used uncertainty evaluation to explore model outcomes to different values

costs. Metabolic costs scale allometrically as $k_{s,i}w^p$ (subscript s denotes standard metabolic rate). The remaining energy, $E_{r,i}$, is thus:

$$E_{r,i}(w) = \max(0, \alpha f_i(w) h_i w^n - k_{s,i} w^p) \quad (11)$$

which is allocated to growth or reproduction. The allocation to reproduction (ψ_i) increases smoothly from 0 around the weight maturation, $w_{mat,i}$, to 1 at the asymptotic weight, W_i , according to the function:

$$\psi_i = \left[1 + \left(\frac{w}{w_{mat,i}} \right)^{-5} \right]^{-1} \left(\frac{w}{W_i} \right)^{1-n} \quad (12)$$

Kommenterad [AA50]: We had a picky reviewer who demanded this to be indicated as a symbol and the number to be included in a parameter list

(Andersen 2019). This function results in that the growth rate, $g_i(w)$,

$$g_i(w) = E_{r,i}(w)(1 - \psi_i(w)) \quad (13)$$

approximates a von Bertalanffy growth curve when the feeding level is constant (Hartvig *et al.* 2011; Andersen 2019). Reproduction is given by the total egg production in numbers, which is the integral of the energy allocated to reproduction multiplied by a reproduction efficiency factor (ϵ , *erepro*) divided by the egg weight, w_0 , and the factor 2, assuming only females reproduce:

$$R_{p,i} = \frac{\epsilon}{2w_0} \int N_{i(w)} E_{r,i}(w) \psi_i(w) dw \quad (14)$$

This total egg production (or physiological recruitment, R_p) results in recruits via a Beverton-Holt stock recruit relationship, such that recruitment ~~reaches approaches~~ a maximum recruitment for a species i ($R_{max,i}$), as the egg production increases,

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$$R_i = R_{max,i} \frac{R_{p,i}}{R_{p,i} + R_{max,i}} \quad (15)$$

~~where $R_{max,i}$ is the maximum recruitment of species i~~ . $R_{max,i}$ is here treated as a free parameter that is estimated in the calibration process by minimizing the residual sum of squares between spawning stock biomass from stock assessments and the MSSM. In doing so, it also ensures that the species coexist in the model (Jacobsen *et al.* 2017).

The temporal dynamics of the background resource (N_R) spectra (benthic and pelagic) are defined as:

$$\frac{\partial N_R(w, t)}{\partial t} = r_o w^{p-1} [\kappa w^{-\lambda}(w) - N_R(w, t)] - \mu_{p,R}(w) N_R(w, t) \quad (16)$$

where $r_o w^{p-1}$ is the population regeneration rate, $\kappa w^{-\lambda}$ is the carrying capacity of the background resource and $\mu_{p,R}$ is predation mortality on resource spectrum R , and λ is defined as $-2 - q + n$ (Andersen 2019).

Temperature dependence

Temperature affects the rate of metabolism (Clarke & Johnston 1999; Gillooly *et al.* 2001), and thus also other biological rates (Englund *et al.* 2011; Rall *et al.* 2012) (Pauly 1980; Thorson *et al.* 2017). We scale rates of individual metabolism ($k_{s,i} w^p$), maximum consumption ($h_i w^n$), search volume ($\gamma_i w^q$) and background mortality ($\mu_o W_i^{n-1}$) with temperature using an Arrhenius temperature correction factor:

$$r(T) = e^{\frac{A_v(T-T_{ref})}{kTT_{ref}}}, \quad (17)$$

where A_v is the activation energy [eV] for individual rate v , T is temperature [K], T_{ref} is the reference temperature (here 283.27 K, the temperature where the Arrhenius correction factor equals 1, see Fig. S12), and k is Boltzmann's constant in eV K^{-1} ($= 8.617 \times 10^{-5} \text{ eV K}^{-1}$). We chose an exponential temperature dependence as it provides a good statistical fit to data, is widely adopted, and because we assume that the projected change in ocean temperature in the studied time range does not lead to temperatures above physiological optima (e.g. (Righton *et al.* 2010) as an example for cod), where physiological rates might be expected to decline. While temperature likely affects other physiological processes as well (such as cost of growth (Barneche *et al.* 2019) or food conversion efficiency (Handeland *et al.* 2008)), we focus on metabolism, maximum consumption, search volume and mortality, as their temperature dependence is relatively well documented (Pauly 1980; Brown *et al.* 2004a; Dell *et al.* 2011; Englund *et al.* 2011; Thorson *et al.* 2017; Lindmark 2020).

Temperature also affects the amount of available background resources, via the same type of individual-level processes. In many size spectrum models to date, climate affects primary production (and in some cases zooplankton), and this is modelled by forcing the background spectra to observed

Ändrad fältkod



abundances-at-size of plankton from either remotely sensed variables such as chlorophyll-a or from output from earth-system models (Canales *et al.* 2016; Woodworth-Jefcoats *et al.* 2019). This allows for predictions tuned to specific systems. However, since we want to study emergent responses and contrast climate warming effects on “bottom up” (e.g. background spectra) to “top down” (physiology), we instead implement temperature scaling to the population biomass regeneration rate and carrying capacity (in the semi-chemostat equation, Eq. 16) with the Arrhenius correction factor with activation energy A_r , where r refers to background resource parameter. We contrasted two scenarios for temperature-dependence of background resources, based on predictions from metabolic scaling theory and observational data:

(1) Metabolic Theory of Ecology (MTE) scenario: The regeneration rate ($r_0 w^{p-1}$) of resources

increases in proportion to $e^{\frac{A_r(T-T_{ref})}{kTT_{ref}}}$ due to elevated metabolic rates in resource organisms, which increases the r rates of energy acquisition, growth, maintenance and reproduction (Savage *et al.* 2004) (but note that these individual-level rates of resources are not explicitly modelled). We implement this by making the parameter r_0 temperature dependent. The carrying capacity (κw^λ) declines at the same rate as population regeneration rate increases with temperature (Savage *et al.* 2004; Gilbert *et al.* 2014),

i.e. κ scales with temperature in proportion to $e^{\frac{-A_r(T-T_{ref})}{kTT_{ref}}}$. This is based on the assumption that a fixed supply of limiting resources (e.g. nutrients) leads to declining abundance or biomass at equilibrium if metabolic rates increase. This theoretical prediction has been verified experimentally for phytoplankton (Bernhardt *et al.* 2018). We refer to this scenario **is referred to** as “exp” for experimental to reflect where data stem from.

(2) Empirical scenario: The carrying capacity declines with temperature proportionally to


$e^{\frac{-A_r(T-T_{ref})}{kTT_{ref}}}$, based on the observed relationship between temperature and the intercept of marine phytoplankton size spectra (Barnes *et al.* 2011). This scenario is referred to as “obs” as data come from remote sensing of chlorophyll-a.



Kommenterad [A51]: I am not sure this explanation is necessarily convincing since you can study emergent responses anyway. I think it is more that you are less interested in specific predictions of primary production but want to understand mechanistically how specific changes in resource will affect your ecosystem

Kommenterad [A52]: I know this is not the time to ask, but did you check whether your r_0 value of 4 actually led to resource depletion at all? The regeneration of resource is very fast and you need massive mortality to have any effect on it to be seen in the next time step. So I am just curious whether temp changes in r_0 in itself had any effect

Kommenterad [A53]: I am not sure I understand the difference between these two scenarios. I thought I did but now that I am reading this I don't get it. Here kappa decreases proportionally based on Arrhenius equation and above is the same. How is this one related to observations?

Activation energies (A_p , A_r), which dictate the temperature sensitivity of a rate, typically vary substantially between processes, species, taxonomic groups, and whether or not intra- or interspecific data are used for estimation (Savage *et al.* 2004; Downs *et al.* 2008; Englund *et al.* 2011; Rall *et al.* 2012). ~~To overcome this, we explored uncertainty around the activation rates by we assigned activation energies by~~ drawing 200 random samples of activation energies for each temperature-dependent rate from ~~distributions~~, either posterior distributions ~~from~~ based meta analyses for specific rates (reference) or, if metaanalyses were not available, from normal distributions based on means and confidence intervals ~~from in~~ literature sources (Table ~~4~~S4 Fig S11). 

Kommenterad [A54]: I expected this table will show parameters of the distributions used to explore uncertainty. I think you meant TableS4

For each of the 200 parameter combinations, each of the six rate activation energy parameters was sampled independently from their respective distribution and the model was projected to 2050. We then quantified~~y~~ the overall mean response and the ranges of predictions resulting from the random draws and visualized~~d~~ it for the analysis of growth and mean size.

Kommenterad [A55]: Just clarifying that for each run ALL rates were sampled independently, not one varied, for example, and others kept same

The posterior distributions for the temperature-dependencies of maximum consumption rate and metabolic rate ~~are were~~ taken from a systematic literature review on the intraspecific size- and temperature dependent scaling (Lindmark 2020). Mortality is assumed to scale in proportion to metabolic rate with temperature (Brown *et al.* 2004a; Blanchard *et al.* 2012), and therefore the random draws are taken from the same distribution as metabolic rate. Activation energies for resource parameters were acquired by fitting a linear regression of natural log of growth rate as a function of Arrhenius temperature ($1/kT$ [eV⁻¹]) from experimental data in (Savage *et al.* 2004) (pooling protists, algae and zooplankton) for the “exp”-scenario. For the “obs” scenarios, we fit a linear regression of natural log of κ as a function of Arrhenius temperature ($1/kT$) from data provided in (Barnes *et al.* 2011). In both cases data were extracted using the software WebPlotDigitizer v. 4.1 (Rohatgi 2012).

Kommenterad [A56]: You might want to put this text into supplements, because the detail is a bit overwhelming by this stage. The main idea you sampled from a distribution.

Kommenterad [ML57]: Hopefully we can cite at least a preprint here. Otherwise we can continue citing the thesis...

We acknowledge that these scenarios are very simplified for evaluating changes in resource productivity versus physiology with warming, and do not necessarily reflect the predicted conditions in the Baltic Sea, nor all the potential pathways by which climate changes affects the environmental conditions in the Baltic Sea. However, the simplicity allows us to contrast effects of warming on basal food resources vs individual physiology.

Kommenterad [A58]: And actually I do not really understand this ... at all...

Model calibration

The MSSM is parameterized to represent the Baltic Sea offshore food web by estimating life history parameters from scientific trawl survey data (for details, see Appendix S1, Table S1). Next, the model was calibrated—run using average fishing mortalities (F) and calibrated to spawning stock biomass (SSB) from stock assessment data for cod, herring and sprat (ICES 2013, 2015) in a specific time window. Ideally, the period for calibration should exhibit relative stability, but such periods do not exist in the Baltic Sea, which is greatly influenced by anthropogenic activities and has experienced dramatic structural changes over the last four decades (Möllmann *et al.* 2009). We chose to calibrate our model to the time period 1992–2002 as in Jacobsen *et al.* (2017), which is a post-regime shift period characterized by high fishing mortality on cod, low cod and herring abundance and high sprat abundance (Gårdmark *et al.* 2015) (Fig. S3). The cut-off at 2002 also ensures that we do not calibrate the model to the period starting from mid 2000's when the growth capacity, condition, proportion of large fish in the population, and reproductive capacity of cod started to decline rapidly (Svedäng & Hornborg 2014; Casini *et al.* 2016; Mion *et al.* 2018; Neuenfeldt *et al.* 2019).

Model calibration was done by adjusting the maximum recruitment values (R_{max}) for the three model species were calibrated by to minimizing the residual sum of squares between the natural log of spawning stock biomass estimated in stock assessment output and those emergent in the model for the years 1992–2002, while holding temperature constant at T_{ref} . Calibration was done using the "L-BFGS-B" algorithm (Byrd *et al.* 1995) in the 'R'-optimization function 'optim'. We ensured that also individual growth rates were close to observed by comparing the growth curves emerging in the model to von Bertalanffy curves fitted to trawl survey data (Fig. S5), which they were after a stepwise manual increase of the constant in the allometric maximum-consumption rate (h_i) (Appendix S1). We also evaluated the level of density dependence imposed by the stock-recruit function (see Eq. 14–15). This was assessed from the ratio of recruitment before and after stock-recruitment density dependence was applied (i.e. $R_{p,i}/R_i$) (Jacobsen *et al.* 2017) (Appendix S1). If this ratio is small (close to 1), there is no additional density dependence from the stock-recruitment function and if it is very high, most spawn

Kommenterad [A59]: I think the convention is to use past tense in methods and results

Kommenterad [A60]: Which ones? Maximum size, maturation size?

Kommenterad [A61]: I think you don't calibrate to fishing mortality but to the biomass

produced by the fish does not recruit, and recruitment is largely controlled by the maximum recruitment parameter ($R_{max,i}$) rather than processes emerging from e.g. feeding and food-dependent growth. After calibrating the model, we acquired $R_{p,i}/R_{max,i}$ ratios of 2.73, 7.2 and 3.19, and R_i/R_{max} ratios of 0.63, 0.86 and 0.68 for cod, herring and sprat, respectively. These values mean that stock recruitment is sensitive to the stock biomass, but there is some density dependence limiting recruitment (i.e. not all spawn produced become recruits), which indicates there is some density dependence in early life stages in the model. A detailed description of the step-by-step calibration protocol used in this study can be found in Appendix S1 and Fig. S3-S9.

Analysis of responses to warming

Models were projected with historical fishing efforts (1974-2014) and relative sea surface temperature (1970-2050, acquired from the regional coupled model system RCA4-NEMO under the RCP 8.5 scenario) (Dieterich *et al.* 2019; Gröger *et al.* 2019). To ensure steady state was reached before time-varying effort and temperature was introduced (1974 and 1970, respectively), we applied a 100-year burn-in period using the first fishing effort and temperature values in the respective time series (Fig. S12). For each species, we used the F_{MSY} from the size spectrum model as fishing mortality in the years 2014-2050 (Fig. S12).

We evaluated the effects of warming on weight-at-age, population mean weight and abundance-at-weight by species. This was done for both absolute values, and by comparing warming food webs to a baseline scenario where no warming occurred post 1997 (the mid-point of calibration time window, where temperature averages T_{ref}) (Fig. S12). To contrast the effects of temperature affecting fish physiology, their resources or both, we considered 5-five different scenarios (Table 1).

To evaluate the effect of temperature on fishing mortality and F_{MSY} (fishing mortality leading to maximized long-term yield), we projected the models to steady state (200 years) under different constant (not time-varying) temperatures and fishing mortalities.

Kommenterad [ML62]: I added a few sentences here. I give more details about the targets in the appendix, so I don't think I need to be more specific here.


This is also not something we calibrate (just like the feeding level, for instance), but something that we check in the model to see it's "appropriate". As with the feeding level, we know what happens at the extremes, and we know roughly where we want it to be, but not more than that...

Kommenterad [AG63]: you applied one value (only the first) from each series, right? just so I get it...

Table 1 Temperature-scaling scenarios (columns) and which rates or parameters are temperature dependent (rows) in the time-varying projections. Green/Yes = temperature dependence included, red/No = not included. See methods for the two alternative approaches to scaling background resources with temperature (experimental or observational).

Temperature dependence

Temperature scenario


	Physio.	Physio. + Resource (obs.)	Physio. + Resource (exp.)	Resource (obs.)	Resource (exp.)
Physiological rates (metabolism, mortality, max. consumption)	Yes	Yes	Yes	No	No
Resource carrying capacity (κ) 	No	Yes	Yes	Yes	Yes
Resource regeneration rate (r_0)	No	No	Yes	No	Yes

Results

Effects of warming on size-at-age depend on physiological temperature-dependence

The inclusion of temperature effects on fish physiological processes (“top-down” effects of warming) is a strong influence on the projected size-at-age in 2050 under the RCP 8.5 emission scenario, relative to the baseline projection (no warming) (Fig. 1). Including temperature dependence of metabolism, maximum consumption, search volume and mortality, with or without temperature-dependent background resource dynamics, leads to warming having positive effects on size-at-age, whereas scenarios without temperature-dependent physiological processes all lead to size-at-age decreasing with warming (Fig. 1). Responses to temperature are strongest in small (young) individuals (Fig. 1).

Kommentarad [AG64]: we don't really see this in fig 1, do we? (we don't have size-specific changes in size), we see strongest effects of temp-scenario on size of young individuals

scenarios with temperature-dependent physiological processes, the effects on size at age are positive and declines with age. In contrast, when only resources are affected by temperature, small individuals have the largest relative decrease in size-at-age, and this negative effect of warming declines with age (Fig. 2) 

Despite the relatively narrow range of activation energies for physiological rates considered here (Fig. S11; Table S4), the uncertainty in projected size-at-age associated with variation in the activation energies are-is large. In scenarios where both physiology and resources are affected by temperature, the range of predicted changes in size-at-age vary at approximately 10% to +40% for both scenarios (Fig. 1). Changes in size-at-age seem to be driven by the temperature-dependence of maximum consumption rate increasing the actual consumption rates ($f_i(w)h_iw^n(T)$), and not due to increased feeding levels ($\frac{E_{e,i}(w)}{E_{e,i}(w)+h_iw^n}$) (Fig. S13).

Fewer large individuals causes reductions in mean population body size

Increases in size-at-age do not always lead to increased mean body size in the populations (Fig. 1-2), due to changes in the size composition with warming (Fig. 3). For cod and sprat, the only scenario that has a median increase in mean body weight includes only temperature-dependent physiological processes and no temperature dependence of resources (Fig. 2). For cod, the abundance of large fish (approximately ~10 kg) increases in the scenario with physiological temperature dependence (Fig 3), which likely drives the corresponding increase in ~~the~~ mean body weight of the cod population in that scenario (Fig. 2), whereas abundance of large cod decreases in all other scenarios (Fig. 3). The abundance-at-weight for sprat above maturation size is approximately 60-70% of the no-warming scenario at the end of the warming projections, unless temperature only affects physiology (in which case it is approximately 90%). In the latter scenario, the median of all simulations shows an increase in the mean size in the population, which is linked to a slightly positive curve of the relative abundance-at-weight (Fig. 3) (but note the absolute abundance is lower for all sizes in the warming scenarios compared to no warming). For herring, all scenarios lead to smaller mean body sizes in the population, and the relative (to non-warming simulation) abundance-at-weight declines with mass in most of the

Kommenterad [AG65]: add a + or – sign, to correspond to your +40%

Kommenterad [AG66]: so the increase needs to come from a temperature-driven increase in maximum consumption rate ($h_iw^n(T)$) then?
(as $\left(\frac{E_{e,i}(w)}{E_{e,i}(w)+h_iw^n}\right) == f_i(w)$). Should that be specified perhaps? And should that also be plotted in the appendix? (I could only see fi in Fig S13)

Kommenterad [AG67]: You present well the size distribution changes, and corresponding changes in median size, but the effects on abundance per se are less apparent in the text. Yet they are important to be able to understand the yield results in the next section. You do have a nice flow in these two first sections, however, so I think it is enough to ensure that you are explicit about abundance results in this section (not only emphasizing median size responses). I've made a few suggestions to that end.

Kommenterad [AG68]: or something similar – else the yield results in the next section become harder to understand

size range, with increases only in the very smallest size-classes (< 1g; Fig. 3). The change in size-structure overall varies between species, and there is no consistent pattern across species for each scenario. This likely reflects that species feed on different resources and that the responses are mediated by food web interactions (e.g. changes in diet and predation and competition).



Warming and fishing: higher sustained exploitation rates but reduced yields

If fishing at the reference fishing mortality that leads to maximum sustainable yield at the reference temperature, $F_{MSY, T_{ref}}$, warming leads to reduced yield for all species (Fig. 4). The highest relative yield is found at the coolest temperatures and F slightly lower than F_{MSY} at the reference temperature. The decline in relative yields are-is likely driven by the warming-induced decline in abundance (due to resource limitation) of all (herring and sprat) or most (cod) size-classes above maturation size (Fig. 3), which is the minimum size targeted by the fishery in the model.

That-y Yields are highest in cold temperatures with F lower than $F_{MSY, T_{ref}}$ is due to because F_{MSY} being larger at higher F increases with warming (except for scenarios where only resources are temperature dependent, in which case F_{MSY} for sprat and herring declines with warming). This is likely due to the enhanced growth rates (size-at-age), which allows higher fishing mortalities without impairing population growth (Fig. 5). However, in all (or, for cod, almost all) scenarios MSY declines with warming, as the targeted fish sizes (above maturation size) decline in abundance (Fig. 3), due to resource limitation. The exception is for cod when temperature affects only physiological processes, because that is the only scenario leading to higher abundance of fish above maturation sizes, which the fishery targets (but note not all mature sizes of cod increase in abundance) (Fig. 3).

Kommenterad [AG69]: should we go into why this occurs for herring, but not for sprat? (more than the somewhat vague, albeit true, statement at the end of the paragraph)

Kommenterad [AG70]: again to help reader understand effects on abundance, and hence yields (in next section)

Kommenterad [AG71]: so which F_{MSY} is this – an F that leads to MSY in no-warming scenarios, or the F that leads to MSY at each respective temperature? (seems from fig 4 that it is the former) Probably good to remind the reader here.

Kommenterad [AG72]: how does this vary across scenarios? Is there any scenario where yields increase with warming above T_{ref} ? (thinking it's important to know, as you discuss importance of not overlooking physiological temp-dep for understanding fish growth responses [based on a comparison across scenarios]; so is knowing the form of temp-dep important also for understanding warming effects on yields?)

Kommenterad [AG73]: is this shown somewhere? if not, should it be?

Kommenterad [AG74]: because it doesn't look as it does for cod; hard to see in the figure so need to be double checked

Kommenterad [AG75]: be nice to include a reference to a figure here. Is this shown anywhere?

Kommenterad [AG76]: Long and needs to be split in two. See a suggestion.

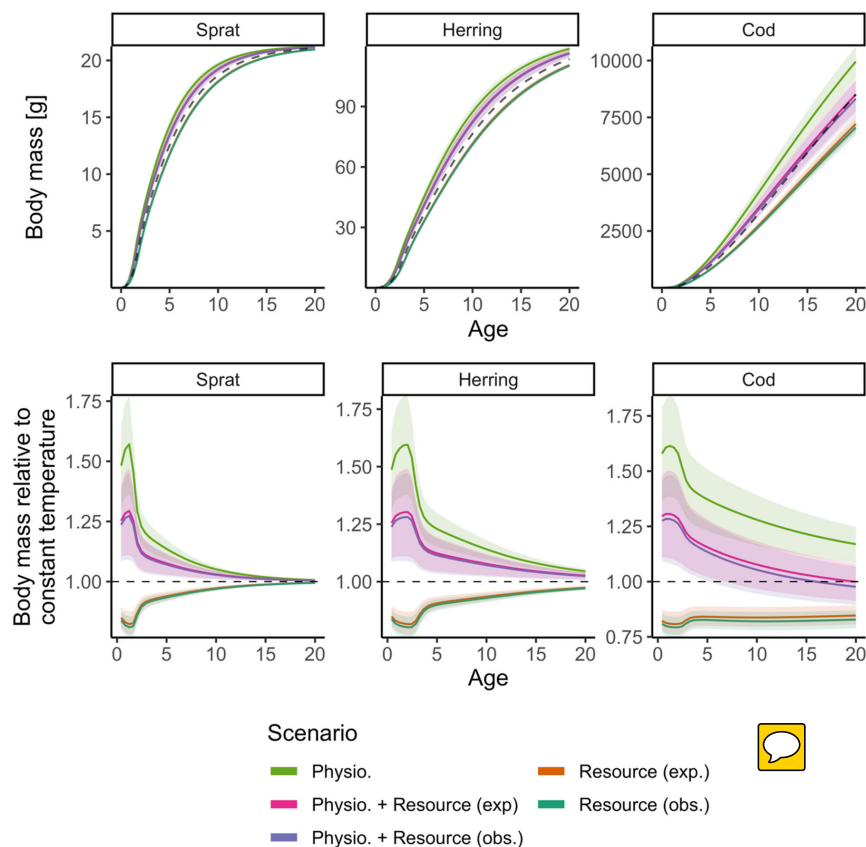


Figure 1. Individual growth trajectories of sprat, herring and *their predator* cod from model projections to year 2050 assuming warming according to RCP 8.5 while keeping fishing mortality at F_{MSY} levels from the size spectrum model (Fig. 5). Top row shows size-at-age and bottom row shows size-at-age relative to a non-warming scenario. The dashed line in the top row depicts projections assuming a non-warming scenario and thus constitutes a baseline prediction. Colours indicate different *scenarios of temperature-scaling scenarios of biological processes* (see Table 1). Shaded areas encompass the 2.5 and 97.5 percentiles from the set of 200 simulations with randomly assigned activation energies.

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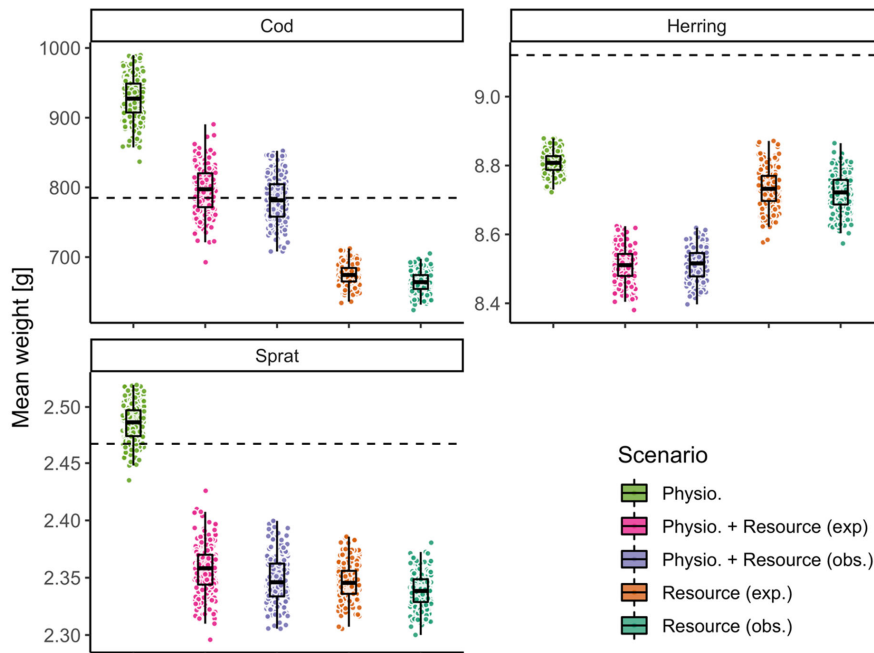


Figure 2. Mean weight across all individuals in the populations of ~~sprat~~cod, herring and ~~cod~~sprat from model projections to year 2050 assuming warming according to RCP 8.5 under different scenarios of temperature dependence of biological processes (see Table 1), while keeping fishing mortality at F_{MSY} levels from the size spectrum model. The dashed horizontal line depicts projections assuming no temperature increase and thus constitutes a baseline prediction. Each dot represents one of the 200 simulations, each with randomly assigned activation energies. Boxplots depict 25%, 50% and 75% quantiles of the 200 simulations in each scenario.

Kommenterad [AG77]: (reading order they appear in figure, if you choose to keep the order in the figure) suggest you re-order in the figure so they always come in the same order across plots (in fig 1 you have sprat, herring, cod all others have cod, herring, sprat, so perhaps change fig 1 instead?)

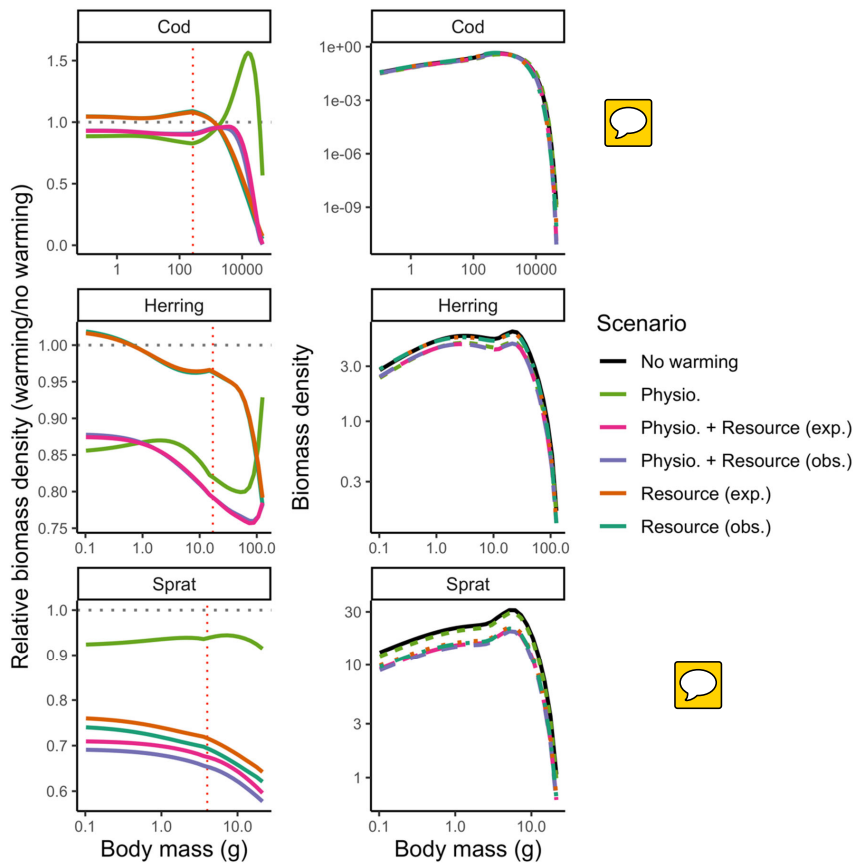


Figure 3. Projected abundance-at-weight by species for different scenarios of temperature scaling indicated by colours (and line types in the right column *due to overplotting*) in 2050 assuming fishing mortality held at F_{MSY} levels from the size spectrum model. The left column shows abundance-at-weight relative to a non-warming scenario and the right column shows absolute abundance-at-weight, with the non-warming scenario shown in black. Vertical red dotted line indicates weight-at-maturation and horizontal black dotted lines indicate the baseline projection (no warming). The right column shows the absolute abundance at weight with the non warming scenario shown in black. Only mean activation energies are used.

Kommenterad [AG78]: would be good if legend in the plot shows the line types as well then

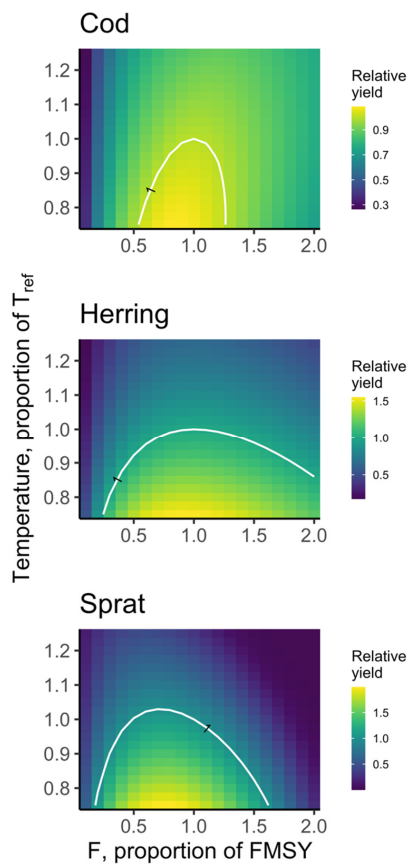


Figure 4. Example of fisheries yield at steady state relative to MSY at T_{ref} (assuming physiological processes and resources depend on temperature according to the “Physio.+Resource (exp).” scenario) relative to projections with ~~no warming~~ constant (temperature ~~at~~ T_{ref}) and baseline $F_{MSY,T_{ref}}$ using simulations with constant (not time-varying) temperatures. The x-axis shows fishing mortality, F , as a ~~proportion to of~~ $F_{MSY,T_{ref}}$ (as estimated from the size spectrum model) at T_{ref} and the y-axis shows temperature as a proportion of T_{ref} . The other two species are held at their $F_{MSY,T_{ref}}$ (estimated at T_{ref}) when one species’ F is varied. Note the different scales on the legends. Only mean activation energies are used.

Kommenterad [AG79]: include here the name you used for this scenario in the previous figure legends

Kommenterad [AG80]: you called this “no warming” earlier, so better use that again

Kommenterad [AG81]: should perhaps call this $F_{MSY@T_{ref}}$ or something similar to indicate that it isn’t F_{MSY} at the respective temperature? both here in the figure text and in the axis label. Especially since you depict the latter, true F_{MSY} at higher/lower temps, in fig 5. (Noted now that you in the result section actually call this $F_{MSY,T_{ref}}$. So better use it here as well then!)

Kommenterad [AG82]: I presume?

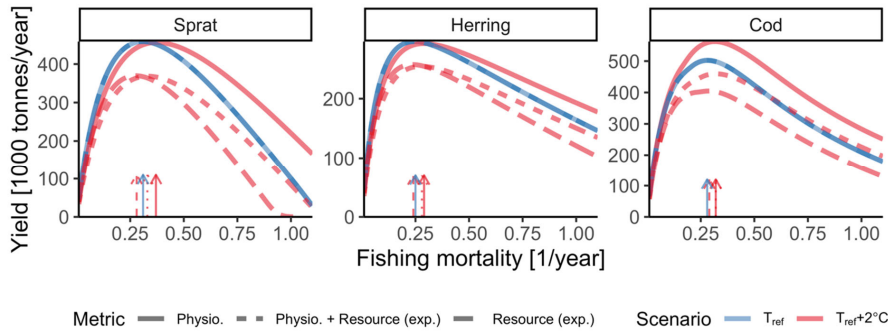


Figure 5. Steady state biomass yield assuming ~~knife-knife~~ edge selectivity at maturation size under two constant temperature simulations and 3 scenarios for temperature dependence (see Table 1). Colours indicate temperature, where blue means $T = T_{ref}$ (all scaling factors = 1, i.e. no temperature effects), and red depicts warm temperature, here $T = T_{ref} + 2^{\circ}\text{C}$. Dashed lines correspond to resource dynamics being temperature dependent, dotted lines correspond to physiological rates and resource dynamics being temperature dependent and solid lines depicts only physiological temperature scaling. Arrows indicate fishing mortality (F) that leads to maximum sustainable yield (i.e. F_{MSY}). F is held constant at the mean F during calibration (mean 1992-2002) for the two other species while estimating yield curves for one species. Note the different scales between species. Only mean activation energies are used.

Kommenterad [AG83]: can't see in legend in the plot that resource only scenario is dashed (Phys+Res looks dashed and Res looks full)

could arrows be made in same style as the lines? don't correspond easily by eye to their respective yield curve

Discussion

Using a size-structured and species-resolved food web model, we ~~assessed~~ demonstrate how the impacts of climate warming on ~~affects~~ individual growth rates, population mean size and size-structure of exploited fish species, and its implications for fisheries yield. We contrasted the effects of warming on resource productivity and individual level physiology (metabolism, feeding and background mortality) of fish, and found that including temperature-dependence of physiological rates generally led to increased fish size-at-age with warming, whereas only considering invertebrate resources being temperature dependent led to declines in size-at-age for all sizes of fish. The increase in fish size-at-age when including temperature dependence of physiological processes is a robust result in this study and occurs in particular for smaller individuals, which is consistent with empirical findings (Thresher *et al.* 2007; Baudron *et al.* 2014; Huss *et al.* 2019). However, our results also show that increased juvenile size-at-age does not necessarily lead to larger population mean body size, spawning stock biomass or yields, as the carrying capacity of background-lower trophic level resources declines and fish mortality (both predation and background) increases with warming, which shifts the population size structure towards more small individuals.

Kommentar AG84: you don't mention this in the results?
only the decline in resource levels

Most results on warming-driven declines in community-wide average body size from mechanistic models find it to be driven by lower food abundance or less energy transferred up in the food web, due to a combination of declines in plankton density and shifts towards smaller plankton at higher temperatures (Lefort *et al.* 2015; Woodworth-Jefcoats *et al.* 2015, 2019). ~~However, it is~~ however unclear how the size-structure of single fish populations change, and how emergent temperature-dependent body growth modifies this. In our model, scenarios with only temperature dependence of resource dynamics lead to declines in size-at-age (that in addition are strongest in young fish), which does not match general observations of how body growth is affected by warming (Morita *et al.* 2010; García García *et al.* 2011). ~~However, in contrast,~~ inclusion of physiological temperature dependence leads to projections more in line with general observations from field data, which often find increased size-at-age that is strongest for small individuals (Thresher *et al.* 2007; Baudron *et al.* 2014; Huss *et al.* 2019). ~~However, this, the increase in body growth is,~~ however, in general not sufficient for maintaining similar mean population body sizes and size-structure if resource carrying capacities decline with warming, which causes declines in the relative abundance of large fish. Therefore, in scenarios with

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temperature dependence of both resource dynamics and physiology, the predictions on the net effect of warming on mean population body size and yields are in line with similar models with empirically derived static plankton spectra (i.e., they decline) (Blanchard *et al.* 2012; Canales *et al.* 2016; Woodworth-Jefcoats *et al.* 2019). If, however resource carrying capacity ~~does-would~~ not decline with temperature, our results show that the increased body growth potential in fish due to faster metabolic and feeding rates can lead to changes towards dominance of larger fish in some populations. This is important to consider, given that predictions about effects of climate change on primary production are uncertain and show large regional variability (Steinacher *et al.* 2010). These results show that it is important account for both direct and indirect effects of temperature in order to explain results such as increased growth rates and size-at-age but overall smaller-bodied populations (Ohlberger 2013; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019). Our findings show that focusing on changes in bottom-up processes can risk missing the potential for fish to increase their growth rates with initial warming, and how that response varies over ontogeny.

In fisheries stock assessment, plastic body growth is generally thought to be less important for stock dynamics than environmentally driven recruitment variation, density dependence at early life stages and mortality ~~for stock dynamics~~ (Hilborn & Walters 1992; Lorenzen 2016). ~~However, d~~Due to the accumulating evidence of time-varying and climate-driven changes in vital rates (survival, growth and reproduction), however, their relative importance for fisheries reference points and targets are increasingly acknowledged (Thorson *et al.* 2015; Lorenzen 2016). In our modelling system, we find that maximum sustainable yields (MSY) and the fishing effort leading to MSY (F_{MSY}) vary with both temperature and between modelling scenarios, and that the effect can largely be predicted from changes in fish body growth and size-structure abundance-at-size. Specifically, for sprat and herring, when temperature affects invertebrate resources only, size-at-age declines and MSY and F_{MSY} are lower in simulations with $+2^{\circ}\text{C}$ warming relative to T_{ref} . By contrast, when temperature affects both physiology and resources, F_{MSY} is higher with warming but the yield is lower, ~~as likely due to due declines in~~ abundance-at-size declines due to resource limitation at higher temperatures. When resources are unaffected by ~~do not decline with~~ temperature and only physiology is depend on ~~temperature dependent~~,

Kommenterad [AG85]: because you don't talk about abundance here, do you? ("smaller populations" = fewer individuals, not smaller individuals)

Kommenterad [AG86]: could also cite Gårdmark & Huss (2020) here if you like, where we also illustrate and discuss this (if it ever comes out; has been accepted for ages...; Gårdmark, A. & M. Huss. Individual variation and interactions explain food web responses to global warming. Philosophical Transactions of the Royal Society London Series B, accepted)

Kommenterad [AG87]: I like these two first paragraphs. The intro, however, contains a lot of text on TSR, which isn't brought up at all in the discussion. Should be, I think, or be toned down in the intro.

Kommenterad [AG88]: not really size-structure (as in proportions), but from abundance-at-size. Else you cannot explain why yields decline with warming

Kommenterad [AG89]: you go further in the results section in explaining this; then you say it is likely due to resource limitation

F_{MSY} is higher when temperature is increased by +2°C, and for cod also the yield is higher. These references should not be viewed as absolute reference points, and the specific results may depend on the model calibration procedure where maximum recruitment. However, this does suggest that it is important to understand climate-driven changes in vital rates, in particular body growth, when making predictions of climate effects on fisheries productivity.

Including physiological temperature-dependence can strongly influence predictions of warming effects and it increases realism, in terms of both individual bioenergetics and the emerging responses in body growth rates. However, it also requires more parameters, which in turn may vary across species. This could lead to reduced generality of predictions and challenges in parameterizing data poor systems. We approached this by applying random parameterization rather than fixed values of temperature dependence by sampling parameters from distributions based on parameter estimates of physiological temperature-dependencies in the literature (Lindmark et al. 2020), which captures the uncertainty in these parameters. Despite being intraspecific parameter estimates (for maximum consumption and metabolic rate; Lindmark et al. 2020), they do not differ much from average, across-taxa estimates (Brown et al. 2004b) and therefore likely represent general scenarios for temperature scaling at temperatures below physiological optimum for species.

In order to disentangle temperature effects on background resources and physiological processes temperature-dependence of individuals feeding on those resources, we modelled temperature dependence of resources by scaling their parameters with the same general Arrhenius equation that we used to scale the physiological processes. Other similar studies using size spectrum models with physiological temperature-dependence instead specify the plankton spectra from climate and earth systems models (Woodworth-Jefcoats et al. 2019) or from satellite data (Canales et al. 2016). Such approaches may lead to predictions that are more relevant for a specific system. However, it also becomes more difficult to separate the mechanisms behind the observed changes, as the resource dynamics then are externally forced rather than emerging from the interplay of temperature- and size-dependent ecological processes. Moreover, populating a resource size spectrum from observed data can be difficult as observed spectra is the result of both predation and bottom up processes. As an alternative,

Kommenterad [AG90]: a bit too long repetition of your results here, I think. In short, temperature-dependence of invertebrate resources reduces both yields and F_{MSY} whereas temperature-dependence of physiology seems to do the opposite. Is such a summary correct?

Kommenterad [AG91]: Very important point, as we've discussed earlier (e.g. in the Lysekil WK). Should this be given more space – a paragraph of its own perhaps?

Kommenterad [AG92]: sentence not complete?

Kommenterad [AG93]: doesn't it also suggest that given that temperature is likely to reduce basal productivity in many parts of the world (e.g. Steinacher et al 2010), yields are likely to decrease even if temperature-driven increases in fish physiological rates will occur?

Kommenterad [AG94]: or? you mean the metaanalysis, right?

Kommenterad [AG95]: some conclusion relating to the approach of drawing from these distributions is needed here. The current conclusion more relates to your other paper, than to what you did herein.

our simpler and more conceptual approach can be used to directly scale the carrying capacity or turnover rates of background resources ~~directly~~. The resource dynamics are then impacted by any warming-driven changes in predators as well as inherent temperature-dependent dynamics, rather than driven by external data (Canales *et al.* 2016) or models (e.g., (Woodworth-Jefcoats *et al.* 2019)). On the downside, this approach means relying on many major simplifications with respect to resource dynamics. In addition, our scenarios only include identical temperature dependencies and baseline carrying capacity of pelagic and benthic resources, and only negative effects of temperature on resource carrying capacity. These may not reflect the actual situation in our case study. Instead, our scenarios reflect the global decline in primary production (Steinacher *et al.* 2010) commonly predicted by coupled climate models (but see e.g. Flombaum *et al.* (2020)). We chose these to contrast reductions in food availability with changes in individual physiology as the former have been linked to declines in community-level body sizes (Woodworth-Jefcoats *et al.* 2019). It would be straightforward to model increases in productivity, as predicted on average by Sarmiento *et al.* (2004), with our approach by using positive activation energies. It is also possible to include temperature-effects of the slope of the size spectrum, as this is often found to be negatively related to temperature (e.g. (Morán *et al.* 2010; Yvon-Durocher *et al.* 2011; Canales *et al.* 2016; Woodworth-Jefcoats *et al.* 2019), but see also Barnes *et al.* (2011)).

Kommenterad [AG96]: or smth similar to link to your previous sentence where you argue for explicit temp-dep of resource dynamics

Ecological forecasting is inherently difficult (~~Lindgren *et al.* 2010~~), and climate change alters the already complex causal pathways that drive ecosystem dynamics. Our example system, the Baltic Sea food web, is influenced greatly by anthropogenic factors, such as overfishing, climate change and deoxygenation. These factors, directly and indirectly, affect the ecology and biology of species, manifested as changes in growth, fecundity, recruitment and spatial distribution (Möllmann *et al.* 2009; Svedäng & Hornborg 2014; Casini *et al.* 2016; Mion *et al.* 2018; Orio *et al.* 2019). Thus, despite being a relatively well studied and species poor ecosystem, understanding the driving mechanisms is not trivial. Size spectrum models are important for evaluating mechanisms and structuring forces in ecosystems (Andersen & Pedersen 2009; Szuwalski *et al.* 2017; Reum *et al.* 2019). However, modelling multiple stressor and interacting non-linear drivers constitutes a particular challenge for these process-based models (Blanchard *et al.* 2017), and predicting the dynamics of species on novel data is often a

Kommenterad [AG97]: this paragraph is quite long, and covers several things (particularities about Baltic foodweb, acknowledging poor fit, issues about forecasting). Split? Focus?

major challenge (Blanchard *et al.* 2014; Spence *et al.* 2016; Andersen 2019). This is also the case here. Overall, we acquire poor fits to data in novel conditions, especially for sprat. This suggests that key processes for their dynamics in this system are unaccounted for, which is also corroborated by a study finding sprat recruitment to be driven mainly by seasonal temperatures rather than spawning stock biomass (MacKenzie & Köster 2004). Although that demonstrates the importance of investigating other aspects of temperature than mean increases, it does not affect our conclusions about the relative impacts of temperature-driven changes in resources and physiology. By contrast, statistical approaches, such as multivariate autoregressive (linear) models fitted to population time series, can reveal good fit to data and be used for short term predictions (Lindegren *et al.* 2010), but projections outside observed conditions remain difficult since they lack descriptions of underlying certain mechanistic processes (Gårdmark *et al.* 2013; Certain *et al.* 2018). Such models have predicted a decline in cod productivity (correlated with reduced salinity) (Lindegren *et al.* 2010), and increased spawning stock biomass of herring and sprat with warming, driven mainly by increased recruitment potential (Bartolino *et al.* 2014). However, ~~since they do not these models the underlying physiological processes they~~ cannot capture changes in body growth and maximum body size with warming, which could be a strong limitation given the observed effects of warming on these traits (Neuheimer *et al.* 2011; Baudron *et al.* 2014; Huss *et al.* 2019) and their impacts on population and community dynamics (De Roos & Persson 2013; Andersen 2019). Here we show that temperature-driven changes in size-at-age vary across ontogeny (in line with observations in other species, e.g. Huss *et al.* 2019) and species, and commonly lead to reduced biomass-at-size of mature size classes. It is important to overcome the challenges associated with forecasting, because of the need for understanding food web and fisheries yield responses to warming. To that end, it is important to evaluate projections from an ensemble of structurally different models in order to resolve underlying mechanisms and thereby guide management of exploitation of fish communities under climate change (Gårdmark *et al.* 2013). These ensembles should include mechanistic and size-based food web models, that are species or trait-resolved and where the interplay of food-dependence and physiological processes and their temperature-dependencies are explicitly modelled.

Formaterat: Teckensnitt: Kursiv

Kommenterad [AG98]: or something that relates back to the findings of Lindegren & Bartolino that you have brought up

Kommenterad [AG99]: the current model isn't a really strong ensemble of structurally different models (e.g. it's much more narrow of an ensemble than what we did in our 2013 paper). Think it would be good if we rather zoom in on an important implication more closely related to your findings. Also check that your overall conclusion here and in the abstract match

Acknowledgements

Thanks to Romain Forestier and Jonatan Reum for contributing to developing code on temperature-dependence in mizer during a workshop, Ken Haste Andersen for helpful discussion on model calibration, Christian Dietrich for providing temperature data, ICES staff, and ~~all people~~ involved in all stages of data collections, the helpful mizer community, and Magnus Huss for providing useful input. This study was supported by grants from the Swedish Research Council FORMAS (no. 217 - 2013 - 1315) and the Swedish Research Council (no. 2015 - 03752) (both to AG).

Kommenterad [AG100]: ??

Author contributions

The code was first developed from mizer (Scott *et al.* 2019) by AA to include multiple background resources, all authors contributed to developing the code to include temperature. ML conceived the idea. All authors contributed to study design. ML parameterized the model with input from AG. ML performed analysis and wrote the first draft. All authors contributed to writing the paper and to revisions.

Kommenterad [ML101]: Does this sound OK to everyone?

Data availability

All model code (parameterization, calibration and analysis) and data is available on GitHub (<https://github.com/maxlindmark/mizer-rewiring/tree/rewire-temp/baltic>), and will be deposited on Zenodo upon publication.

Formaterat: Engelska (Storbritannien)

Ändrad fältkod

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