**Bottom up and top down effects of temperature on body growth, population size spectra and yield – an application of a multi-species size spectrum model**

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**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 bottom up and ‘top down’ effects (direct effects of warming on individual-level physiology) on exploited food webs. Here we assess how 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 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 under different scenarios of fishing mortality and effects of temperature on physiology. When accounting also for how temperature affects physiology compared to the baseline levels, projected size-at-age increases for all species in 2050 based on temperature projections according to the RCP 8.5 scenario, whereas size-at-age decreases when temperature only affects resource dynamics. However, the faster growth rates in the fully temperature-dependent models do not to the same extent translate to larger yields, as spawning stock biomass declines due to increased predation mortality rates. Results from our model suggest that reduced fishing mortality can counteract the potentially negative effects of warming on the abundance of fish above maturation size.

**Introduction**

Climate change affects aquatic food webs directly by shifting 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 (maximum sustainable yield, MSY) 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 of warming, especially at higher trophic levels (Lotze *et al.* 2019). The causes of declines in productivity of fish stocks, and abundance of large fish, have in process-based ecosystem models mainly been linked to changes in primary production or zooplankton (Blanchard *et al.* 2012; Woodworth-Jefcoats *et al.* 2013, 2015; Barange *et al.* 2014; Lotze *et al.* 2019). However, stock assessment models 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, other factors may be more important for population dynamics, including temperature-driven changes in individual- and population level processes such as recruitment, morality and somatic growth (Free *et al.* 2019). Therefore, the driving mechanism of changes in productivity and biomass of higher trophic levels, e.g. fish, with warming is uncertain.

Moreover, global warming is also predicted to cause reductions in the adult body size of organism, and this is often referred to as the third universal response to warming (Daufresne *et al.* 2009; Sheridan & Bickford 2011; Forster *et al.* 2012). Adult body sizes can decrease due to many reasons, including fishing removing old or large fish, or selecting for early maturing and fast growing individuals (Audzijonyte *et al.* 2013). It could also be an adaptive intraspecific response, as the temperature-size rule (TSR) (Atkinson 1994) states that individuals reared at warmer temperatures develop faster and thus acquiring larger size-at-age or life stage, but reach smaller adult body sizes (Ohlberger 2013). Empirical support for this rule in fishes stem mainly for time series data of reconstructed growth trajectories. Studies have also 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). By contrast, no clear negative effects of warming on the body size or growth of large fish could be found in more controlled experiments (i.e. in the absence of potentially confounding factors such as fisheries exploitation) (Barneche *et al.* 2019; Huss *et al.* 2019). However, in line with the TSR, faster growth rates or larger size-at-age of young life stages is commonly found in both experimental and field data (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Neuheimer & Grønkjaer 2012; Baudron *et al.* 2014; Huss *et al.* 2019), as most fish species live in thermal environments where growth is still positively related to temperature. Thus, the ecological rule of shrinking body sizes may be more complex than often depicted, as the effects of temperature on growth and body size relationships tend to vary over ontogeny. As body size is a key trait in aquatic ecosystems (Andersen *et al.* 2016), warming-induced changes in growth and size-at-age of fish populations could have implications not only for biomass and productivity but also their structure and stability (Audzijonyte *et al.* 2013). It is therefore important to develop mechanistic size-based food web models where the impacts of warming on body size and size-based interactions can be evaluated.

Mechanistic models are useful for evaluating the implications of temperature-size responses in food webs, as results emerge from key individual-level processes. Using an eco-physiological growth model (generalized von Bertalanffy growth model), Cheung et al. (2013) predicted a 14-24% decline in community-average maximum body mass by 2050 under high-emission scenarios, due to both changes in distribution and warming-induced constraints asymptotic mass. While these declines in maximum body size are in line with the “universal” relationship between smaller adult or asymptotic body sizes with warming, both the physiological basis and the magnitude of the reductions have been questioned (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 within-species observation that temperature-optimum for growth declines with body size (Björnsson 2001; García García *et al.* 2011) and that the optimum temperature for growth declines with 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 of communities, driven by reduced plankton abundance or shifts towards smaller plankton, which reduces energy transfer to the top of food webs (Woodworth-Jefcoats *et al.* 2015). Models including also physiological scaling in a species-and size-based resolved food web in general also find these results (Lefort *et al.* 2015; Woodworth-Jefcoats *et al.* 2019). It is unclear however how much this is driven by reduced abundance of large fish versus changes in size-at-age of large fish, or if mean size declines but individuals of different size respond positively or negatively. It also remains open as to whether climate warming in such models offer any possibility for individuals (in particular small individuals) to benefit from warming in terms of somatic growth, as is commonly observed (Thresher *et al.* 2007; Baudron *et al.* 2014; Huss *et al.* 2019).

The Baltic Sea constitutes a great example system to explore the impacts of warming, as it is a relatively well understood and species poor system (Casini *et al.* 2009) that in addition experiences rapid warming (Belkin 2009). Here we introduce a temperature-dependent size-spectrum inspired by a simplified the Baltic Sea food web with which we assess the joint impacts of both temperature driven changes in productivity and physiology and its effects on the emergent food web structure. We specifically investigate the impacts of projected warming (using the regional coupled model system RCA4-NEMO and the RCP 8.5 emission scenario) on growth trajectories, average body sizes, population size-structure and yield in a fished ecosystem. Uncertainty in the effect of warming on physiology is incorporated by drawing samples from known distributions, based on meta-analysis. We find that inclusion of temperature-dependent physiological processes in the model leads increased size-at-age, especially for smaller individuals. This is in contrast to models where only the resource dynamics are temperature dependent, in which size-at-age declines with warming.

**Materials and Methods**

*Food web*

The Baltic Sea is semi-enclosed brackish sea with a relatively species-poor food web. We developed a Multi-species size spectrum model (MSSM) parameterized to represent a simplified version of the food web in the 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: cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), and their prey. These species are dominant species in terms of biomass, they are the most important species commercially in this southern sub-region of the Baltic and they all have analytical stock assessments. We also model one pelagic (such as phyto- and zooplankton, mysids) and one benthic background resource spectrum (benthic invertebrates, gobiidaes, small flatfish etc.), which constitute dynamic food sources for the smallest individuals of each of the three fish species.

*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 size-dependent temperature-scaling of key physiological processes. All model code (parameterization, calibration and analysis), together with necessary data is available on GitHub (<https://github.com/maxlindmark/mizer-rewiring/tree/rewire-temp/baltic>), and will be deposited on Zenodo (<http://doi.org/>) upon publication. In this section we describe the key elements of the MSSM using the same notation when possible as in the multispecies mizer model R-vignette for consistencey (Scott *et al.* 2014, 2018).

In MSSMs, individuals are characterized by their weight () and species identity (). The core equation is the McKendrik-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:

(1)

where [] is somatic growth (dependent on the availability of background resources or prey) and [] is total mortality. At the boundary weight (), the flux of individuals is given by recruitment. The total mortality, , is the sum of the background-, starvation-, fishing-, and predation mortality. The constant size-independent species-specific allometric background mortality depends on the maximum body size of a species and is given by:

, (2)

where is the mass-exponent of maximum consumption rate and is an allometric constant. Starvation mortality is assumed to be proportional to energy deficiency (defined in Eq. 11), and inversely proportional to body mass, and is defined as:

, (3)

where (Hartvig *et al.* 2011), Instantaneous fishing mortality (1/year) is defined as:

(4)

where is the selectivity (by default knife-edge selectivity is assumed with a weight at first catch corresponding to weight at maturation), and is fishing effort. is thus fishing mortality and effort is used henceforth. Predation mortality for a prey species () equals the amount consumed by predator species (indexed with mass ):

, (5)

where is the non-size based preference of species on species , and 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 follows a Holling functional response type II:

(6)

where is the feeding level (which describes the level of satiation and varies between 0:1), is the allometric maximum consumption rate and is the encountered food (mass per time). The amount of encountered food for a predator of body weight is given by the available food in the system multiplied with the search rate, . Here, available food, , is the integral of the biomass of all species and background resource that falls within the prey preference () and size-selectivity () of species :

(7)

where is the weight of prey, is the preference of species for resource , and indicates prey species. Note that in contrast to other MSSMs (Blanchard *et al.* 2014; Reum *et al.* 2019) 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 other species interactions (all terms in the species interaction matrix are identical and equal to 1). This is for simplicity, as the body size-only prey selection and encounter captures 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 in the time period of the model calibration (Fig S2). The size-selectivity of feeding, , is given by a log-normal selection function (Ursin 1967):

(8)

where parameters and are the preferred predator-prey mass ratio and the standard deviation of the log-normal distribution, respectively. Together, the size-based selection function and the amount of available prey is multiplied with the allometric function describing the allometric coefficient of search rate, which is calculated as:

(9)

(Andersen & Beyer 2006; Scott *et al.* 2018), to get the actual biomass of food encountered, :

. (10)

Here is the size scaling exponent of the search rate. The rate at which food is consumed is given by the product , and is assimilated with efficiency and used to cover basal metabolic costs. Metabolic costs scale allometrically as , where and is the allometric constant and exponent. The remaining energy, , is thus:

(11)

and is allocated to growth or reproduction. The allocation to reproduction () increases smoothly from 0 around the weight maturation, , to 1 at the asymptotic weight, , according to the function:

(12)

(Andersen 2019). This function results in that the growth rate, i.e.

(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 () divided by the egg weight, :

(14)

This “physiological” recruitment (indexed ) of offspring to each species relates to the total egg production via a Beverton-Holt stock recruit relationship, such that recruitment reaches a maximum as the egg production increases,

, (15)

where is the maximum recruitment of each species. is here treated as a free parameter that is found in the calibration process by minimizing the residual sum of squares between spawning stock biomass from stock assessment and the MSSM. In doing so, it also ensures that the species coexist in the model (Hartvig *et al.* 2011).

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

(16)

where is the population regeneration rate, is the population carrying capacity and is predation mortality and lambda is defined as (Andersen 2019).

*Temperature dependence*

Temperature affects the rate of metabolism (Clarke & Johnston 1999; Gillooly *et al.* 2001), which also affects e.g. maximum consumption rates (Englund *et al.* 2011; Rall *et al.* 2012), and mortality (Pauly 1980; Thorson *et al.* 2017). We scale rates of individual metabolism (), maximum consumption () and background mortality () with temperature using an Arrhenius temperature correction factor:

where is the activation energy for individual rate [], is temperature [], is the reference temperature (here 283.15 , where the correction factor=1), and is Boltzmann’s constant in (). 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 our time-range does not lead to temperatures above physiological optimum, where physiological rates might be expected to decline (e.g. (Righton *et al.* 2010) as an example for cod). While temperature likely affects other physiological processes as well (e.g. cost of growth (Barneche *et al.* 2019), food conversion efficiency (Handeland *et al.* 2008)), we focus on metabolism, maximum consumption and mortality as their temperature dependence is relatively well documented.

Temperature also affects the amount of available background resources, via the same type of individual-level processes. In many size-spectrum model to date, climate impacts primary production (and in some cases zooplankton), and this is modelled by forcing the background spectra to observed abundances-at-size of plankton from either remotely sensed variables such as chlorophyll-a or from output from earth-system model (Canales *et al.* 2016; Woodworth-Jefcoats *et al.* 2019). This allows for predictions tuned to specific systems. However, since we want to contrast climate 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) with the Arrhenius correction factor with activation energy , where refers to background resource parameter. In this approach, we contrasted two scenarios for temperature-dependence based on predictions from metabolic scaling theory and observational data:

1. Metabolic Theory of Ecology (MTE) scenario: The regeneration rate () increases in proportion to due to elevated metabolic rates in resource organisms, which increases the rates of energy acquisition, growth, maintenance and reproduction (Savage *et al.* 2004) (but note these individual-level rates of resources are not explicitly modelled). We implement this by making the parameter temperature dependent. The carrying capacity () declines at the same rate as population regeneration rate increases with temperature (Savage *et al.* 2004; Gilbert *et al.* 2014), i.e. in scales with temperature in proportion to , if assuming a fixed supply of limiting resources (e.g. nutrients) for the resource populations. This theoretical prediction has been verified experimentally (Bernhardt *et al.* 2018). 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 , 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.

Activation energies (), 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 assigned activation energies by drawing 200 random combinations of activation energies for each temperature-dependent rate from probability distributions (Table 1; Fig S11). The model is then projected to either forward to 2050, in total 200 times, each time with another set of parameters. We then quantify the overall mean response and the ranges of predictions from the random draws. The probability distributions for the temperature-dependencies of maximum consumption rate and metabolic rate are taken from a systematic literature review on the intraspecific size- and temperature dependent scaling (Lindmark et al, in prep). Mortality is assumed to scale in proportion to metabolic rate with temperature, and therefore the random draws are take from the same distribution as metabolic rate (Brown *et al.* 2004; Blanchard *et al.* 2012). For simplicity, we assumed the distributions of each rate from which the draws are taken are independent. Activation energies for resource parameters were acquired by fitting a linear regression of natural log of growth rate as a function of Arrhenius temperature () from experimental data in (Savage *et al.* 2004) (pooling protists, algae, zooplankton) for the MTE-scenario, and fitting a linear regression of natural log of as a function of Arrhenius temperature () from data provided in (Barnes *et al.* 2011).

*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-S2). Next, the model is calibrated to averaged stock assessment data (fishing mortality, F and spawning stock biomass, SSB) (ICES 2013, 2015) in a specific time window to tune the system to get realistic biomass ratios. Ideally the period for calibration should exhibit relative stability, but such periods do not exist in the Baltic Sea, which is largely 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 (F) on cod, low cod and herring abundance and high sprat abundance (Gårdmark *et al.* 2015) (Fig. 1, Fig.S2). The cutoff 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; Mion *et al.* 2018; Neuenfeldt *et al.* 2019).

Maximum recruitment values () for the three model species were calibrated by minimizing the residual sum of squares between the natural log of spawning stock biomass (SSB) estimated in stock assessment output and those emergent in the model for the years 1992-2002, while holding the temperature constant at . Calibration was done using the "L-BFGS-B" algorithm (Byrd *et al.* 1995) in the ‘R’-optimization function ‘*optim’*

We ensured that also 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. S4), which they were after a stepwise manual increase of the constant in the allometric maximum-consumption rate () (Appendix S1). We also evaluated the level density dependence due to the stock-recruit function and the reproductive efficiency, . This was assessed from the ratio of recruitment before and after stock-recruitment density dependence was applied (i.e. ) (Jacobsen *et al.* 2017) (Appendix S1). If the ratio is close to 1, there is no additional density dependence from the stock-recruitment function and if it is very high recruitment is largely controlled by rather than emergent processes. After calibrating the model, we acquired ratios of 2.1, 2.1 and 7.6, which is largely in line with (Andersen & Beyer 2015) and indicates there is some density dependence in early life stages in the model. Time series of modelled SSB simulated together with historical temperature and fishing effort data with stock assessment output. 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 where 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). To ensure steady state was reached before time varying effort and mortality was introduced (1974 and 1970, respectively, we applied a 60-year burn-in period using the first fishing effort and temperature values in the respective (Fig. S8, S11). We used the mean of FMSY from stock assessment models (to which the model was calibrated) and FMSY from the size spectrum model as fishing mortalities in the years 2014-2050 (Fig. SX).

We evaluated the effects of warming on weight-at-age, mean population weight, abundance-at-weight and fisheries yield 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 ) (Fig. S11, S8). To contrast the effects of temperature affecting fish physiology, their resources or both, we considered 5 different scenarios and evaluated the food web metrics for each (see Table 1).

To evaluate the effect of temperature on fishing mortality on spawning stock biomass (SSB) and fishing mortality leading to maximized long-term yield (FMSY), we projected the models to steady state under different constant (not time-varying) temperatures and fishing mortalities. In these simulations, fishing mortalities were varied with a factor in relation to FMSY-levels based on either FMSY from the size spectrum model or an average between the size spectrum model and stock assessment FMSY (as the model is calibrated to stock assessment outputs) (Fig. 6).

Table 1 Temperature-scaling scenarios (columns) and which rates or parameters are temperature dependent (rows) in the time-varying projections. Green = temperature dependence included, red = not included. See methods for the two alternative approaches to scaling background resources with temperature (empirical or MTE).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | 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 ( | No | Yes | Yes | Yes | Yes |
| Resource regeneration rate ( | No | No | Yes | No | Yes |

**Results**

The inclusion of temperature effects on fish physiological processes (“top-down”, in addition to temperature-dependence of their background resources, the “bottom-up”) has 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. 2). Including empirical temperature dependence of maximum consumption, mortality and metabolism, with or without temperature-dependence of background resources, 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. 2). Specifically, in scenarios with temperature-dependent physiological processes, the positive effect of warming is largest for small individuals and declines with size. However, when only resource dynamics scale with temperature, small individuals have the largest relative change (negative), and this negative effect of warming declines with body size (Fig. 2).

Despite the relatively narrow range of activation energies for physiological rates considered here (Fig. S10), the uncertainty associated with variation in the activation energies are large. In scenarios where both physiology and resources depend on temperature, the range of predicted changes in size-at-age vary at approximately 5% to 40% for the MTE scenario and approximately 15% to 60% for the empirical scenario for a 3-year-old cod (Fig. 2). The relative difference in size-at-age of a 3-year-old fish in the warming versus the constant temperature scenarios across scaling scenarios vary between approximately 20% to 50% for cod, 15% to 25% for herring and 12% to 15% for sprat (Fig. 2). These changes in size-at-age seem to be driven by the temperature-dependence of maximum consumption rate increasing the actual consumption rates , and not due to increased feeding levels (Fig. S12). Moreover, the consumption rate is slightly more sensitive than the metabolic losses for the energy acquisition (Table SX). This also leads to increases in the size-dependent predation mortality of fish above 1g for all scenarios, and for all body weights in the scenarios where only resources are temperature-dependent (Fig. S13).

There is a positive relationship between the relative change in growth due to warming (Fig. 2) and that of the mean population body weight (Fig. 3). However, the mean body weight does not always increase with warming when the size-at-age does so, except for cod to some degree (Figs. 2-3), reflecting a change in the size composition of the populations (Fig. 4). For sprat and herring, 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. 3). The abundance-at-weight for fish below maturation size decreases by 10% at the end of the projection for all species. The increase in predation and background mortality with warming likely contribute to this (Fig. S13). For cod, the abundance of the largest fish (>500g) increases in all scenarios with physiological temperature dependence (Fig 4-subplot), which drives the corresponding increase in their mean body weight (Fig. 3). By contrast, the abundance of sprat and herring individuals above maturation size only increase with warming if the background resources are independent of temperature (Fig. 4).

Fishing removes the largest fish in the populations, but this can be counteracted by the changes in growth rates and size-from the scaling scenarios accounting for physiology (Fig. S14). Fisheries yield increases with the projected warming for cod if temperature only affects physiological rates (Fig. 5). For sprat and herring, and for cod in all other scenarios, yields decline, or are more or less unaffected by warming (Fig. 5). This is likely driven by the warming-induced decline in abundance of most size-classes above maturation size (Fig. 4), which is the minimum size targeted by the fishery. While the largest fish can in some cases increase in abundance, especially for cod, they are also rarer in the population and hence this does not counteract the decline in fish that constitute the main catches (Fig. 4).

Warming, and whether it acts on background resources or also physiological rates, also influences the fishing effort leading to maximum sustainable yield (FMSY) and the corresponding spawning stock biomass (SSB) (Fig. 6). In the non-time varying simulation, the fishing effort corresponding to FMSY increases when the temperature is +2 compared to the reference temperature (where scaling factors = 1) at steady state, due to the enhanced growth rates (size-at-age) (Fig. S6). However, the fishery yield increases only if temperature acts on physiology alone. Thus, when temperature affects physiological scaling and resource dynamics, the largest relative increases in fisheries yield are acquired in colder temperatures and higher fishing efforts (Fig. S15).

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*Figure 2. Individual growth trajectories of sprat, herring and cod from model projections to year 2050 assuming warming according to RCP 8.5 while keeping fishing mortality at average FMSY levels. 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. Colors indicate different temperature-scaling scenarios. 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 3. Mean weight across all individuals in the populations of sprat, herring and cod from model projections to year 2050 assuming warming according to RCP 8.5 while keeping fishing mortality at average FMSY levels. 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.*

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*Figure 4. Projected abundance-at-weight by species for different scenarios of temperature scaling (indicated by colors) at 2050 assuming fishing mortality held at average FMSY levels (Figure 1A) from different stock assessment estimates and this model. The left column shows size at age relative to a non-warming scenario. 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. Activation energies are the means of their respective distributions (no uncertainty).*

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*Figure 5. Time series of projected yield under different temperature scaling scenarios (indicated by colors) and temperature projections according to RCP 8.5 emission scenarios, assuming fishing mortality held at average FMSY levels (after 2014) from different stock assessment estimates and this model. The horizontal black line corresponds to no temperature increase after 1997. Activation energies are the means of their respective distributions (no uncertainty).*

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*Figure 6. Steady state fishery yield (top) assuming knife edge selectivity at maturation size and spawning stock biomass (SSB) (bottom) under constant temperature simulations. Colors indicate the temperature, where blue means (all scaling factors = 1, i.e. no temperature effects), and red depicts warm temperature, here +2. Dashed lines correspond to resource dynamics being temperature dependent, dotted lines correspond to physiological rates and resource dynamics and solid lines depicts only physiological temperature scaling. Arrows indicate fishing mortality (F) that lead to maximum sustainable yield. F is held constant at the mean F during calibration (mean 1992-2002) for the two other species while estimating it for one species. Note the different scales between species.*

*Main conclusions*

1. The inclusion of temperature-dependent physiological processes can turn around the predicted effect of warming on size-at-age (from declining to increasing), and this happens for most of the random combinations of activation energies (based on meta-analysis).
2. The increased growth rates do not always lead to increased yields in warming scenarios. My interpretation (could be wrong) is that it’s because of changes in the size spectra. Specifically, declines in abundance of most sizes below and slightly above w\_mat, possibly from higher predation mortality rates. The only sizes that increase is the really large fish which do not contribute that much to yield)

**Discussion**

**(Just suggestions for topics at this point)**

* Discuss the main results: large differences in predictions when including physiological scaling, e.g. increased growth rates. Link this to empirical findings (this is often found, especially for young fish).
  + Also, model is relatively sensitive to physiological scaling, as previously found. This is based on that we see large effects even though activation energies are very similar compared to other literature estimates (e.g. Rall et al. 2010 ~ vs Englund et al 2011 ~ for ).
* Compare predictions that match and don’t match to Woodworth-Jefcoats (quite similar model) and Maury & Poggiale.
  + Here I also want to discuss different ways of adding background spectra changes: “Changes in abundance and size-structure of background resources can directly inferred from e.g. climate and earth systems models (Woodworth-Jefcoats et al. 2019)”. However, the simple metabolic approach provides a baseline model for temperature-dependence on population dynamics and allows for an easier interpretation of the relative effects of direct physiological effects (“top down”) vs changes in background productivity (“bottom up”). There are indications that also the slope of the size spectrum ( in the term for carrying capacity), declines with temperature (Yvon‐Durocher *et al.* 2011), however on a global scale this effect is less clear statistically (Barnes *et al.* 2011).
* Limitations and strengths of this type of modelling approach (size spectrum vs other)
* Talk about other temperature effects we do not account for (range shifts, physiological parameters etc etc.)
  + “Our approach categorized one source of uncertainty as environmental variability, but the size spectrum model does not explicitly include environmental variables such as temperature, salinity, and dissolved oxygen into modelling (Andersen and Beyer, 2006; Scott et al., 2014). It is worth noting that incorporating multiple environmental variables into mechanistic modelling is exceedingly difficult as environmental effects on ecosystems are often non-linear and mixed, and it is impossible to include all environmental variables (Pauly, 1980; Pepin, 1991; Charnov and Gillooly, 2004; Pörtner and Knust, 2007). But see Woodwarth.-Jefcoats and Blanchard 2017”
* Need to talk about the state of the Baltic and how that limits our relatively simple model to predict the things that are actually happening there (range shifts of the pelagic, spatial contraction of cod, earlier maturation and poor growth of cod, vitamin deficiency etc etc)
* Large scale models are crucial for informing global assessments about the implications of climate change (Lotze *et al.* 2019), but (by necessity) rely on simplifying assumption and tend to not include species-resolved food webs and the effects of temperature on individual-level physiology (but see (Woodworth-Jefcoats *et al.* 2019)). Instead, temperature is often assumed to act mainly on ecosystem productivity (“bottom up”) rather than on both individual physiology (“top down”) and productivity. This may represent an important knowledge gap, given that warming is generally predicted to affect adult body sizes negatively

Thus, the underlying mechanisms of body size reductions are likely due to an interplay between physiology and ecology (Ohlberger 2013; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019), and not only driven by changes in food web productivity. It is therefore important to also account for warming on individual-level physiology in order to evaluate the effects of warming of population productivity and size-structure.

Thus, there is a need to increase our mechanistic understanding of climate change impacts on the individual-level and how that affects size-based food webs and regional dynamics (Blanchard *et al.* 2012).

s

**Woodworth 2015: (for discussing resources and such…)**

In this study, climate change impacts are represented by a decrease in both small and large phytoplankton density due to increased vertical stratification and subsequent nutrient limitation. While similar trends in phytoplankton biomass are projected for North Atlantic ([Morán et al., 2010](https://www.sciencedirect.com/science/article/pii/S0079661115000646?via%3Dihub" \l "b0190)) and freshwater ([Yvon-Durocher et al., 2011](https://www.sciencedirect.com/science/article/pii/S0079661115000646?via%3Dihub" \l "b0345)) ecosystems, there are regions such as the California Current that are projected to see increasing phytoplankton densities ([Rykaczewski and Dunne, 2010](https://www.sciencedirect.com/science/article/pii/S0079661115000646?via%3Dihub" \l "b0250)). Not only does phytoplankton biomass decrease in our study, the phytoplankton community undergoes a shift towards a greater abundance of small phytoplankton (+1.3%, p < 0.001). A growing number of studies project that climate change will result in reduced organism size (e.g., [Daufresne et al., 2009](https://www.sciencedirect.com/science/article/pii/S0079661115000646?via%3Dihub" \l "b0080), [Morán et al., 2010](https://www.sciencedirect.com/science/article/pii/S0079661115000646?via%3Dihub#b0190), [Sheridan and Bickford, 2011](https://www.sciencedirect.com/science/article/pii/S0079661115000646?via%3Dihub" \l "b0260), [Yvon-Durocher et al., 2011](https://www.sciencedirect.com/science/article/pii/S0079661115000646?via%3Dihub#b0345)). This shift towards smaller phytoplankton, coupled with overall density declines, reduces the energy available to consumers of all sizes. Across both models and all scenarios, including the negative bottom-up impacts of climate change led to declines in biomass and catch at all sizes. Additionally, both models project large fish biomass and catch to decline when fishing is paired with climate change. That two fundamentally different modeling approaches project similar impacts is encouraging about our ability to project climate impacts on the ecosystem, and underscores the importance of including climate change as a component of ecosystem-based fisheries management.

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**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 performed analysis and wrote the first draft. All authors contributed to writing the paper and to revisions.

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