**Bottom-up and top-down effects of temperature on body growth, population size spectra and yield in a size-structured food web**

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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 of ‘bottom-up’ and ‘top-down’ effects of temperature: how do temperature effects propagate from individual-level physiology through food webs and alter the size-structure of exploited species in a community? Here we assess how a species-resolved size-based food web is affected by warming through both these pathways, and by exploitation. 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 for temperature-effects on physiology in addition to on basal productivity, projected size-at-age in 2050 increases for all fish species compared to scenarios without warming, whereas size-at-age decreases when temperature affects resource dynamics only. Faster growth rates due to warming, however, do not always translate to larger yields, as lower resource carrying capacities decline with increasing temperature tend to result in declines in the abundance of larger fish and hence spawning stock biomass – the part of the population exposed to fishing. These results show that to understand how global warming impacts the size structure of fish communities, both direct (growth) and indirect (mortality) effects of temperature must be accounted for.

**Introduction**

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% 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 animal biomass for every 1 of warming, especially at higher trophic levels (Lotze *et al.* 2019). Across a range of process-based ecosystem models, declines in productivity of fish stocks and abundance of large fish, have 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, even in areas where warming is predicted to have positive effects on primary production, fish productivity does not appear to increase (Free *et al.* 2019). This suggests that fish population dynamics might be strongly influenced by other factors, such as temperature-driven changes in recruitment, mortality or somatic growth (Free *et al.* 2019), yet the driving mechanisms remain poorly understood.

Global warming is also predicted to cause reductions in the adult body size of organisms, and this is often referred to as the third universal response to warming (Daufresne *et al.* 2009; Sheridan & Bickford 2011; Forster *et al.* 2012). This is expected to be driven by the temperature-size rule (TSR), which is observed in a wide range of ectotherms (Forster *et al.* 2012), and states that individuals reared at warmer temperatures develop faster, mature earlier but reach smaller adult body sizes (Atkinson 1994; Ohlberger 2013). In line with TSR expectations, faster growth rates or larger size-at-age of young life stages are commonly found in both experimental, field data and modelling studies (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Ohlberger *et al.* 2011; Neuheimer & Grønkjaer 2012; Baudron *et al.* 2014; Huss *et al.* 2019; Van Dorst *et al.* 2019). Similarly, declines in maximum or asymptotic body size of fish have been reported to correlate with warming trends for a number of commercially exploited marine fishes (Baudron *et al.* 2014; van Rijn *et al.* 2017; Ikpewe *et al.* 2020). However, in intensively fished stocks, observed adult body sizes can decrease also for other 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). Moreover, decreasing adult fish size in warming waters 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). Similarly, across 335 coastal fish species mean species body size was similarly likely to be larger or smaller in warmer waters (Audzijonyte *et al.* 2020). Also Tu *et al.* (2018) found that temperature had a relatively minor effect on fish size structure, and even when combined with fishing, only 44% of variation in size structure could be explained. Thus, the effects of temperature on body sizes may be more complex than often depicted, and we still do not fully understand the mechanisms by which temperature affects growth and body size over ontogeny (Ohlberger 2013; Audzijonyte *et al.* 2019). Increasing our understanding of these mechanisms is important because 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).

Physiologically structured models can address the complex interplay of direct and indirect temperature impacts on food webs, as they account for the food and size dependence of body growth through ecological interactions using bioenergetic principles. Recent applications have demonstrated decreasing maximum body sizes in fish communities due to changes in plankton abundance or size (Woodworth-Jefcoats *et al.* 2019). Similar body size responses emerge in models that focus on temperature-dependence of physiological processes, such as metabolism and feeding rates (Lefort *et al.* 2015; Woodworth-Jefcoats *et al.* 2019), but it remains unclear to what extent these community body size shifts are driven by declining abundance of large fish versus changes in size-at-age.

To explore how direct and indirect effects of warming impact marine food web size structure and fisheries yields, we evaluate the impacts of temperature-driven changes in resource productivity and individual fish physiology using an example study case of the Baltic Sea. The Baltic Sea constitutes a great example system, 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). By using a temperature-dependent size spectrum model we analyse a set of different scenarios where either fish physiology, basal resources, or both depend on temperature. We investigate the mechanisms underlying the impacts of projected warming on body growth trajectories, average body sizes, population size-structure and fisheries reference points and find that inclusion of temperature-dependent physiological processes in these projections lead to increased fish size-at-age whereas the opposite is true when only resources are temperature-dependent. Nevertheless, increased growth rates do not compensate for changes in size dependent mortality and the overall response to warming is declining mean body sizes of fish populations and lower yields.

**Materials and Methods**

*Food web*

We developed a 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 size structured food web is here characterized by three fish species: Atlantic cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), and two dynamic 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 (ICES 2021). The two background spectra represent 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, gobiidaes 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* (v1.1) (Blanchard *et al.* 2014; Scott *et al.* 2014, 2019; R Core Team 2020), 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 () 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 food) and [] is total mortality. At the boundary weight (, egg size), the flux of individuals is given by recruitment. Total mortality is the sum of the background-, starvation-, fishing-, and predation mortality. The constant species-specific allometric background mortality () depends on the asymptotic weight of a species and is given by:

(2)

where is the mass-exponent of maximum consumption rate (Hartvig *et al.* 2011) 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 (weight, ), and is defined as:

(3)

where , the fraction of energy reserves, is (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 mortality. Predation mortality ( for a prey species (or resource) with weight equals the amount consumed by predator species with weight :

(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 and 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 volume, . Here, available food, , is the integral of the biomass of all prey species () and background resources () that falls within the prey preference () and size-selectivity () of predator 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) 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, , 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. The amount of available prey of suitable sizes (Eq. 7) is multiplied with the allometric function describing the search volume (), where the allometric coefficient is calculated as:

(9)

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

(10)

where is the size-scaling exponent of the search volume. The rate at which food is consumed is given by the product , which is assimilated with efficiency and used to cover basal metabolic costs. Metabolic costs scale allometrically as (subscript denotes standard metabolic rate). The remaining energy, , is thus:

(11)

which 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, ,

(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, , and the factor 2, assuming only females reproduce:

(14)

This total egg production (or physiological recruitment, ) results in recruits via a Beverton-Holt stock recruit relationship, such that recruitment approaches a maximum recruitment for a species (), as the egg production increases,

(15)

where is treated as a free parameter and is estimated in the calibration process by minimizing the residual sum of squares between spawning stock biomass from stock assessments and the MSSM. This calibration also ensures that the species coexist in the model (Jacobsen *et al.* 2017).

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

(16)

where is the population regeneration rate, is the carrying capacity of the background resource and is predation mortality on resource spectrum , and lambda is defined as (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; Thorson *et al.* 2017) We scale rates of individual metabolism (), maximum consumption (), search volume () and background mortality () with temperature using an Arrhenius temperature correction factor:

|  |  |  |
| --- | --- | --- |
|  | , | (17) |

where is the activation energy [] for individual rate , is temperature [], is the reference temperature (here 283.27 , the temperature where the Arrhenius correction factor equals 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 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.* 2004; Dell *et al.* 2011; Englund *et al.* 2011; Thorson *et al.* 2017; Lindmark *et al.* 2021).

Temperature also affects the amount of available background resources, via the same type of individual-level processes. In most 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 abundances-at-size of plankton from either remotely sensed variables such as chlorophyll-a or from output from earth-system models (Blanchard *et al.* 2012; Barange *et al.* 2014; Canales *et al.* 2016; Reum *et al.* 2019; Woodworth-Jefcoats *et al.* 2019). An alternative approach is to force simulation with the growth rate or net primary production (Jennings & Collingridge 2015; Galbraith *et al.* 2017). These differences have been highlighted as a key source of ecosystem model uncertainties observed in global applications of size-structured models (Lotze *et al.* 2019) (Heneghan et al 2020). To more consistently integrate the emergent responses of 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 , where refers to background resource parameter. We assume that 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. scales with temperature in proportion to . This is based on the metabolic theory of ecology (MTE), which predicts that if nutrient levels are constant, higher respiration rates lead to lower biomasses at carrying capacity.

As activation energies vary substantially between processes, species and taxonomic groups, resulting in large uncertainty in these parameters, we parameterized 200 projections of the food web model using randomly sampled activation energies. These were sampled from normal distributions with rate-specific means and standard deviations. For metabolism and maximum consumption, we acquired means and standard deviations from the posterior distributions in (Lindmark *et al.* 2021) (note we assume search volume scales identically as maximum consumption and mortality as metabolism). The normal distributions describing activation energies for resource parameters were defined by a mean equal to the point estimate from 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 and zooplankton) (extracted using the software WebPlotDigitizer v. 4.1 (Rohatgi 2012)). We approximated a standard deviation by finding the value that resulted 95% of the normal distribution being within the confidence interval of the linear regression. 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 the overall mean response and the ranges of predictions resulting from the random draws and visualized it for the analysis of growth and mean size.

We acknowledge that these scenarios are very simplified for evaluating changes in resource productivity versus physiology with warming, and that they 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 versus individual physiology.

*Analysis of responses to warming*

Models were projected with historical fishing mortalities (1974-2014) (ICES 2013, 2015) 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 fishing mortality and temperature was introduced (1974 and 1970, respectively), we applied a 100-year burn-in period using the first fishing mortality and temperature value in the respective time series (Fig. S12). For each species, we used the 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 ) (Fig. S12). To contrast the effects of temperature affecting fish physiology, their resources or both, we considered three different scenarios.

To further explore the effect of temperature on fisheries yield and 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, expressed as fractions of and at ().

*Model calibration*

The MSSM was parameterized to represent the Baltic Sea offshore food web. We estimated species-specific von Bertalanffy growth and length-weight parameters from scientific trawl survey data (for details, see Appendix S1, Table S1). Next, the model was calibrated to average spawning stock biomasses ( from stock assessment data for cod, herring and sprat (ICES 2013, 2015) in 1992-2002, using average fishing mortalities () in the same time frame. 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. S4). The cut-off at 2002 also ensured that we did 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, 2021; Neuenfeldt *et al.* 2020).

Model calibration was done by adjusting the maximum recruitment values () for the three fish species to minimize the residual sum of squares between the natural log of spawning stock biomass estimated in stock assessment output (ICES 2013, 2015) and those emergent in the model for the years 1992-2002, while holding temperature constant at . We used the "L-BFGS-B" algorithm (Byrd *et al.* 1995) in the ‘R’-optimization function ‘*optim’.* We ensured that individual growth rates were close to observed by comparing the growth curves emerging in the model to the von Bertalanffy curves fitted to trawl survey data (Fig. S6), which they were after a stepwise manual increase of the constant in the allometric maximum-consumption rate () (Appendix S1). The level of density dependence imposed by the stock-recruit function (see Eq. 14-15) was also evaluated by assessing the ratio of the physiological recruitment, , to the recruitment (Jacobsen *et al.* 2017) (Appendix S1). 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). A detailed description of the step-by-step calibration protocol used in this study can be found in Appendix S1 and Fig. S4-S9.

**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) 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. 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 (Fig. 1). In contrast, the scenario without temperature-dependent physiological processes all lead to size-at-age decreasing with warming (Fig. 1). In scenarios with temperature-dependent physiological processes, the effects on size-at-age are positive and declines with age. 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. 1).

Chart, diagram

Description automatically generated

*Figure 1. 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 FMSY levels from the size spectrum model. 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 temperature-scaling scenarios. Shaded areas encompass the 2.5 and 97.5 percentiles from the set of 200 simulations with randomly assigned activation energies.*

Chart, diagram

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*Figure 2. 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 FMSY 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.*

Despite the relatively narrow range of activation energies for physiological rates considered here (Fig. S3; Table S3), the uncertainty in projected size-at-age associated with variation in the activation energies is large (Fig. 1). In the scenario where both physiology and resources are affected by temperature, the range of predicted changes in size-at-age vary at approximately % to 40% (Fig. 1). 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 (Eq. 6; Fig. S13).

***Fewer large individuals cause reductions in mean population body size***

Increases in size-at-age (Fig. 1) do not always lead to increased mean body size in the populations (Fig. 2), due to changes in relative abundances at weight (Fig. 3). These changes in the size-structure vary between species, and there is no consistent pattern across species for each scenario.

The only scenario where mean body weight on average increases is where temperature only affects physiology and not the resource (Fig. 2), and this occurs only for cod and sprat. For cod this increase is strong and is driven by both faster growth rates and large increases in the abundance of large fish () (Figs. 1, 3). For sprat the mean body weight in the populations increased only marginally and is mostly driven by faster growth rates (Figs. 1, 3), because the abundance-at-weight for sprat above maturation size is approximately 60-70% of the no-warming scenario (for all sizes) at the end of the warming projections. In contrast, scenarios where only resource is affected by temperature (increased regeneration rate but lower carrying capacity), relative numbers of large individuals and therefore mean body size of all species goes down. 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 size range, with increases only in the very smallest size classes (< 1; Fig. 3).

*Diagram

Description automatically generated with low confidence*

*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 FMSY 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. 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.*

***Temperature and fishing: higher sustained exploitation rates but reduced yields in warmer environments***

Our simulations show that warming led to lower (i.e., the fishing mortality leading to maximum sustainable yield) for all species (Fig. 4). The highest relative yield is found at the coolest temperatures and slightly lower than at the reference temperature. The decline in relative yields 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. In addition, the warming-induced shifts in size-distributions further decreasing the relative abundance of large and, hence, fishable individuals (Fig. 3) likely contribute to the decline in yields.

A picture containing graphical user interface

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*Figure 4. Example of fisheries yield at steady state relative to MSY at (no effect of temperature) in scenario where both physiological processes and resources depend on temperature) relative to projections with constant temperature () and baseline using simulations with constant (not time-varying) temperatures. The x-axis shows fishing mortality, , as a proportion to (as estimated from the size spectrum model) at and the y-axis shows temperature as a proportion of . The other two species are held at their when one species’ F is varied. Note the different scales on the legends. Only mean activation energies are used.*

Yields are highest in cold temperatures with lower than (Fig. 4) because increases with warming (except for the scenario where only resources are temperature dependent, in which case and for sprat and herring declines with warming) (Fig. 5). This increase in 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 scenarios declines with warming (Fig. 5), except for cod when temperature affects only physiological processes (Fig. 5), likely because that is the only scenario leading to higher abundance of fish above maturation sizes, which the fishery targets (Fig. 3).

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*Figure 5. Steady state biomass yield assuming knife edge selectivity at maturation size under two constant temperature simulations and three scenarios for temperature dependence. Colours indicate 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 being temperature dependent and solid lines depicts only physiological temperature scaling. Arrows indicate fishing mortality (F) that leads to maximum sustainable yield (. 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.*

**Discussion**

Using a size-structured and species-resolved food web model, we demonstrate how climate warming affects 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 size-at-age of fishes with warming, whereas only considering invertebrate resources being temperature dependent led to declines in size-at-age for all sizes. The increase in 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 despite increased juvenile size-at-age, warming in most cases leads to smaller mean body size in the population, spawning stock biomass and yields. This is because the carrying capacity of lower trophic level resources declines and fish mortality (background and to some extent predation mortality, see Fig. S14) increases with warming, which shifts the population size structure towards more small individuals.

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). This leads to a community wide decline in mean size of fish (large bodied species becoming relatively fewer). By contrast, the TSR makes predictions about changes in size-at-age over ontogeny, predicting increasing growth and size-at-age of small but decreasing that of large individuals (Atkinson 1994). However, it is not well understood how the size-structure of single fish populations changes due to lower food abundances causing shifts in individual growth rates (i.e., in line with TSR). In our model, we include scenarios that reflect how warmer temperatures change food abundance as well as affect metabolism and food intake rates. 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), and is not in accordance with the TSR. 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). This 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, because this causes declines in the relative abundance of large fish. Therefore, in the scenario with temperature dependence of both resource dynamics and physiology, the predictions on the net effect of warming, resulting in declining mean population body size (and yields), are in line with similar models using empirically derived static plankton spectra (Blanchard *et al.* 2012; Canales *et al.* 2016; Woodworth-Jefcoats *et al.* 2019). If, however, resource carrying capacity 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, as also found in (Ohlberger *et al.* 2011; Ohlberger 2013; Neubauer & Andersen 2019; Gårdmark & Huss 2020). Focusing on changes only in bottom-up processes can therefore 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 (Hilborn & Walters 1992; Lorenzen 2016). Due to the accumulating evidence of time-varying and climate-driven changes in vital rates (survival, growth and reproduction), their relative importance for fisheries reference points and targets are, however, increasingly acknowledged (Thorson *et al.* 2015; Lorenzen 2016). In our modelling system, we find that maximum sustainable yields () and the fishing mortality leading to () vary with both temperature and between modelling scenarios and that the effect can largely be predicted from changes in growth and abundance-at-size. When temperature affects both invertebrate resources (mainly declines in carrying capacity) and fish physiology, warming leads to increased , but in general decreased . The decline in yields with warming is due to reduced resource availability, lowering overall fish abundance, and is in line with earlier studies (Blanchard *et al.* 2012; Lotze *et al.* 2019). In addition, the warming-induced decline in relative abundance of fish above minimum size caught in fisheries further decreases yields in our model. At the same time, faster growth rates (size-at-age), occurring when temperature affect vital rates in fish, can cause to increase with warming in our model. These reference levels should not be viewed as absolute reference points, and the specific results may depend on the model calibration procedure. However, this does suggest that it is important to understand climate-driven changes in vital rates, in particular body growth, as well as bottom-up effects, and how they affect both overall abundance and size-structure when making predictions of climate effects on fisheries productivity. It also indicates that reduced fisheries yields may be common in a warming world, given that productivity may decline in large parts of the oceans (Lotze *et al.* 2019), although there is large variation in these predictions across ecosystems (Steinacher *et al.* 2010).

Including physiological temperature-dependence can strongly influence predictions of warming-effects and it allows for detailed understanding of temperature effects on populations and food webs via both individual bioenergetics and the emerging responses in fish body growth rates. However, it also requires more parameters, which in turn may vary across species. This could reduce generality of predictions and increased challenges in parameterizing models of data poor systems. We approached this by applying random parameterization, rather than fixed values of temperature dependence, by sampling parameters from distributions based on estimates of activation energies of physiological rates in the literature (Lindmark *et al.* 2021), which captures the uncertainty in these parameters. This approach revealed that in terms of body growth and mean body size in populations, the combination of activation energies can determine whether the mean size increases or decreases with warming, and at what age body sizes decline relative to the current temperatures (degree of decline in size-at-age). Hence, better knowledge on the temperature-dependence of rates of biological processes is needed and these parameters should be chosen carefully in future modelling studies.

To disentangle temperature effects on background resources and physiological processes, we modelled temperature dependence of resources by scaling their parameters with the same general Arrhenius equation (Gillooly *et al.* 2001) that we used to scale the physiological processes in fish. Other similar studies using size spectrum models with physiological temperature-dependence instead import 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 and therefore cannot respond to changes in the modelled food web. Moreover, populating a resource size spectrum from observed data can be difficult as observed spectra result from both predation and bottom-up processes. As an alternative, our approach of directly scaling the carrying capacity or turnover rates of background resources with temperature provides a coherent way to model temperature-dependencies across trophic levels. 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 better 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)), which has 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)).

Ecological forecasting is inherently difficult, and climate change alters the already complex causal pathways that drive ecosystem dynamics. Size spectrum models, which are useful for evaluating mechanisms and structuring forces in ecosystems (Andersen & Pedersen 2009; Szuwalski *et al.* 2017; Reum *et al.* 2019), are more appropriate for strategic rather than tactical use for management (Blanchard *et al.* 2014). One example of such a “big-picture” mechanism is the important role of explicitly modelling temperature effects on individual-level metabolism and feeding rates that we identify herein. This not only makes predictions about temperature effects on size-at-age more in line with general observations and predictions (e.g., with the TSR), but also affects the levels of exploitation that leads to maximum sustainable yields, and the corresponding yields. Hence, mechanistic models are important components for increasing our understanding of how and by which processes climate change affects individuals in food webs and resulting effects on fisheries yields, which is needed to generalize across systems and into novel conditions.

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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 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.

**Data availability**

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

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