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

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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 (affecting food availability vs individual-level physiology) on the size-structure of exploited species in 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 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 in 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, whereas size-at-age decreases when temperature only affects resource dynamics, both relative to non-warming scenarios. However, the faster growth rates in the fully temperature-dependent models do not always translate to larger yields, as mean body size and spawning stock biomass decline due to reductions in resource carrying capacity. These results show that it is important account for both direct and indirect effects of temperature to explain results such as increased growth rates and size-at-age within species but overall smaller populations due to declines of large fish.

**Introduction**

*Climate change is causing shifts in productivity*

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 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, stock assessments have found no increase in fish productivity in areas where warming is predicted to have positive effects on primary production (Free *et al.* 2019). This suggests that fish population dynamics and productivity might be strongly influenced by other factors, such as temperature-driven changes in recruitment, mortality or somatic growth (Free *et al.* 2019). 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*

Global warming is also predicted to cause reductions in the adult body size of organisms, often referred to as the third universal response to warming (Daufresne *et al.* 2009; Sheridan & Bickford 2011; Forster *et al.* 2012). 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, observed in a wide range of ectotherms, states that individuals reared at warmer temperatures develop faster, mature earlier but reach smaller adult body sizes (Ohlberger 2013).Indeed, declines in fish maximum or asymptotic body size are commonly reported for a number of fished species, e.g. in the Mediterranean or the North Sea , 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 & Grønkjaer 2012; Baudron *et al.* 2014; Huss *et al.* 2019). 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 confound any effects of temperature in exploited populations. Similarly, across 335 coastal fish species mean body size was 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, only 44% of variation in size structure could be explained. Thus, the effects of temperature and climate change on body sizes may be more complex than often depicted, and we still do not fully understand the mechanisms underlying how the effects of temperature on growth and body size relationships vary over ontogeny. 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 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 fish size, fish growth and the structure? 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 running multiple simulations where temperature responses are sampled from previously established probability distributions (Lindmark 2020). We find that inclusion of temperature-dependent physiological processes leads to increased size-at-age in fish, especially for juvenile fish , 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.

**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 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 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* (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 () 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:

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|  |  | (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 size-independent species-specific allometric background mortality () depends on the asymptotic weight of a species and is given by:

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|  |  | (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 (weight, ), and is defined as:

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|  |  | (3) |

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

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|  |  | (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 the terms fishing mortality and effort are used interchangeably henceforth. Predation mortality ( for a prey species (or resource) with weight equals the amount consumed by predator species with weight :

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|  |  | (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:

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|  |  | (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 :

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|  |  | (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):

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|  |  | (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:

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|  |  | (9) |

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

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|  |  | (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:

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|  |  | (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:

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|  |  | (12) |

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

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|  |  | (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:

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|  |  | (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 *i* (), as the egg production increases,

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|  |  | (15) |

. 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 () spectra (benthic and pelagic) are defined as:

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|  |  | (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) (Pauly 1980; 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:

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|  | , | (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, see Fig. S12 ), 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.* 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 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 , where 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 () of resources increases in proportion to due to elevated metabolic rates in resource organisms, which increases their 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 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. scales with temperature in proportion to . 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 , 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). We explored uncertainty around the activation rates by drawing 200 random samples of activation energies for each temperature-dependent rate from either posterior distributions based meta analyses for specific rates (reference) or, if metanaalyses were not available, from normal distributions based on means and confidence intervals in literature sources (Table S4 Fig S11).

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.

The posterior distributions for the temperature-dependencies of maximum consumption rate and metabolic rate 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 () 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 as a function of Arrhenius temperature () from data provided in (Barnes *et al.* 2011). In both cases data were extracted using the software WebPlotDigitizer v. 4.1 (Rohatgi 2012). 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.

*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 run using average fishing mortalities () and calibrated to spawning stock biomasses ( 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 () for the three model species to minimize 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 . 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 () (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. ) (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 produced by the fish does not recruit, and recruitment is largely controlled by the maximum recruitment parameter ( ) rather than processes emerging from e.g. feeding and food-dependent growth. After calibrating the model, we acquired ratios of 2.73, 7.2 and 3.19, and 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). 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 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 five different scenarios (Table 1).

To evaluate the effect of temperature on fishing mortality 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.

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).

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| --- | --- | --- | --- | --- | --- | --- |
|  |  | **Temperature scenario** | | | | |
|  |  | Physio. | Physio. + Resource (obs.) | Physio. + Resource (exp.) | Resource (obs.) | Resource (exp.) |
| **Temperature dependence** | 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**

*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, 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. 2). In 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 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 % 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 , and not due to increased feeding levels (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 ) increases in the scenario with physiological temperature dependence (Fig 3), which likely drives the corresponding increase in mean body weight of the cod population in that scenario (Fig. 2). 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). 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. 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 , warming leads to reduced 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 are likely driven by the warming-induced decline in abundance (due to resource limitation) of most size-classes above maturation size (Fig. 3), which is the minimum size targeted by the fishery in the model.

That yields are highest in cold temperatures with lower than is due to being larger at higher with warming (except for scenarios where only resources are temperature dependent, in which case 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 scenarios declines with warming, except 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 increase in abundance) (Fig. 3).

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*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 (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 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 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.*

*A close up of a map

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*Figure 3. Projected abundance-at-weight by species for different scenarios of temperature scaling indicated by colours (and linetypes 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 show 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.*

*A picture containing screenshot

Description automatically generated*

*Figure 4. Example of fisheries yield at steady state relative to MSY at (assuming physiological processes and resources depend on temperature according to the “exp.” scenario) 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.*

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*Figure 5. Steady state biomass yield assuming knife edge selectivity at maturation size under two constant temperature simulations and 3 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 assessed the impacts of climate warming on individual growth rates, population mean size and size-structure, 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 with warming, whereas only considering 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 increased juvenile size-at-age do not necessarily lead to larger population mean body size, spawning stock biomass or yields, as the carrying capacity of background resources decline and mortality (both predation and background) increases, which shifts the population size structure towards more small individuals.

Most results on 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 (Lefort *et al.* 2015; Woodworth-Jefcoats *et al.* 2015, 2019). However, it is unclear how the size-structure of single fish populations change, and how emergent temperature-dependent 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, 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, the increase in body growth is 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 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 not decline, our results show that the increased growth potential due to faster metabolic and feeding rates can lead to changes towards 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 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 than environmentally driven recruitment variation, density dependence at early life stages and mortality for stock dynamics (Hilborn & Walters 1992; Lorenzen 2016). However, 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 increasingly acknowledged (Thorson *et al.* 2015; Lorenzen 2016). In our modelling system, we find that maximum sustainable yields () and the fishing effort leading to () vary between modelling scenarios and that the effect can largely be predicted from changes in growth and size-structure. Specifically, for sprat and herring, when temperature affects resources only, size-at-age declines and and are lower in simulations with +2 warming relative to . By contrast, when temperature affects both physiology and resources, is higher with warming but the yield is lower, likely due to due declines in abundance-at-size. When resources do not decline with temperature and only physiology is temperature dependent, is higher when temperature is increased by +2, 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 increases realism, in terms of both individual bioenergetics and the emerging responses in 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 in the literature (Lindmark 2020), which captures the uncertainty in these parameters. Despite being intraspecific parameter estimates (for maximum consumption and metabolic rate), 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 temperature-dependence, 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. 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, our simpler and more conceptual approach can be used to scale the carrying capacity or turnover rates of background resources directly. The resource dynamics are then impacted by any warming-driven changes in predators, 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 resource, 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)).

Ecological forecasting is inherently difficult (Lindegren *et al.* 2010), and climate change alter the already complex causal pathways that drive ecosystem dynamics. The Baltic Sea 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 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 aspect of temperature than mean increases, it does not affect our conclusions about the relative impacts of changes in resources and physiology. By contrast, statistical approaches, such as multivariate autoregressive (linear) models, can reveal good fit to data and be used for short term predictions (Lindegren *et al.* 2010), but projects outside observed conditions remain difficult since they lack 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 model the underlying physiological processes they cannot capture changes in 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). 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. 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.

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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 is 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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