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

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**Abstract**

Resolving the combined effect of climate warming and exploitation in a food web context is key for predicting future biomass production, size-structure and potential yields of marine fishes. Previous studies based on mechanistic size-based food web models have found that bottom-up processes are important drivers of size-structure and fisheries yield in changing climates. However, we know less about the joint effects of bottom up and ‘top down’ effects (direct effects of warming on individual-level physiology) on the intraspecific size-structure of exploited food webs. Here we assess how various food web metrics are affected by warming through both these pathways, and by exploitation, in a species-resolved size-based food web. We parameterize a dynamic size spectrum model inspired by the offshore Baltic Sea food web, and investigate how individual growth rates, size-structure, relative abundances of species and yields are affected by warming. Warming in based on projections by the regional coupled model system RCA4-NEMO and the RCP 8.5 emission, and we evaluate different scenarios of temperature on physiology and resource productivity. When accounting also for temperature-effects on physiology, projected size-at-age in 2050 increases for all species, whereas size-at-age decreases when temperature only affects resource dynamics, compared 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 declines due to increased lower resource carrying capacity and increased predation mortality rates. These results show that it is important account for both direct and indirect effects of temperature in order to explain results such as increased growth rates and size-at-age within species but overall smaller populations due to reductions of large fish.

**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 4.1% between 1930-2010 due to climate change (Free *et al.* 2019). These results are also matched in magnitude and direction by projections from an ensemble of mechanistic ecosystem models, which predicts ~5% decline in biomass for every 1 of warming, especially at higher trophic levels (Lotze *et al.* 2019). The causes of declines in productivity of fish stocks, and abundance of large fish, have in process-based ecosystem models mainly been linked to changes in primary production or zooplankton abundance (Blanchard *et al.* 2012; Woodworth-Jefcoats *et al.* 2013, 2015; Barange *et al.* 2014; Lotze *et al.* 2019). However, stock assessment models found no clear increase in fish productivity in areas where warming is predicted to have positive effects on primary production (Free *et al.* 2019). Instead, other factors may be more important for population dynamics and productivity, including temperature-driven changes in individual- and population level processes such as recruitment, mortality and somatic growth (Free *et al.* 2019). This demonstrates that the driving mechanisms of changes in fish productivity and biomass with warming are poorly understood.

Moreover, global warming is also predicted to cause reductions in the adult body size of organisms, which is often referred to as the third universal response to warming (Daufresne *et al.* 2009; Sheridan & Bickford 2011; Forster *et al.* 2012). In fish, adult body sizes can decrease for many reasons, including direct removals of old or large fish, or selecting for early maturing and fast growing individuals (Jorgensen *et al.* 2007; Audzijonyte *et al.* 2013). It could also be a plastic adaptive intraspecific response. The temperature-size rule (TSR) (Atkinson 1994) states that individuals reared at warmer temperatures develop faster and thus acquire larger size-at-age or life stage, but reach smaller adult body sizes (Ohlberger 2013). Studies have reported declines in the maximum body size (van Rijn *et al.* 2017), and synchronous declines in asymptotic body size across species in the North Sea (Baudron *et al.* 2014) as indications of a body size response to concurrent warming. However, 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, without potentially confounding effects of fishing were absent. By contrast, faster growth rates or larger size-at-age of young life stages are commonly found in both experimental and field data (Thresher *et al.* 2007; Neuheimer *et al.* 2011; Neuheimer & Grønkjaer 2012; Baudron *et al.* 2014; Huss *et al.* 2019), in line with the TSR. This is likely because most fish species live in thermal environments where growth is still positively related to temperature (Neuheimer *et al.* 2011; Lindmark 2020). Thus, the ecological rule of shrinking body sizes may be more complex than often depicted, as the effects of temperature on growth and body size relationships tend to vary over ontogeny. As body size is a key trait in aquatic ecosystems (Andersen *et al.* 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.

Mechanistic models can be useful for evaluating the implications of temperature-size responses in food webs because these responses emerge from individual-level processes. Using an eco-physiological growth model (generalized von Bertalanffy growth model), Cheung et al. (2013) predicted 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 transfer to the top of food webs (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 reduced abundance of large fish versus changes in size-at-age of large fish.

In this study, we evaluate the separate and combined impacts of temperature-driven changes in resource productivity and individual physiology on individuals and 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 inspired by a simplified Baltic Sea food web, and analyze a set of different scenarios with either fish physiology, their 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 yield in a fished ecosystem. With this setup, we address the questions about how warming affects individual growth in a food web context, how population size-structure is shaped by changes in size-at-age and by changes in relative abundance of differently sized individuals, and lastly how that influences fisheries reference points. Temperature change is based on the regional coupled model system RCA4-NEMO and the RCP 8.5 emission scenario (Dieterich *et al.* 2019; Gröger *et al.* 2019). Uncertainty in the effect of warming on physiology is incorporated by randomly parameterizing these rates using probability distributions from meta-analyses (Lindmark 2020). We find that inclusion of temperature-dependent physiological processes leads to increased size-at-age, especially for smaller individuals and in line with observations, whereas the opposite is observed when only resources are temperature-dependent. However, overall, we find warming leads to declines in mean body size in the population due to shifting size distributions, resulting in lower yields in warmer environments.

**Materials and Methods**

*Food web*

The Baltic Sea is semi-enclosed brackish sea with a relatively species-poor food web. We developed a Multi-species size spectrum model (MSSM) (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: 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 species are dominant fish species 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 background spectra represent groups of species that are food for fish but are not explicitly modelled (Andersen *et al.* 2016b). We assume the pelagic spectra represents mainly phyto- and zooplankton while the benthic background resource spectrum benthic invertebrates, gobiidaes, small flatfish etc.

*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. The total mortality, , is the sum of the background-, starvation-, fishing-, and predation mortality. The constant size-independent species-specific allometric background mortality () depends on the 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 (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 that term 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 rate, . 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 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 rate, 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) |

Here is the size-scaling exponent of the search rate. The rate at which food is consumed is given by the product , and is assimilated with efficiency and used to cover basal metabolic costs. Metabolic costs (, where is for standard) scale allometrically as , where and is the allometric constant and exponent, respectively. 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, i.e.,

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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 production of recruits via a Beverton-Holt stock recruit relationship, such that recruitment reaches a maximum as the egg production increases,

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|  | , | (15) |

where is the maximum recruitment of species . 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 (Hartvig *et al.* 2011).

The temporal dynamics of the background resource () spectra (benthic and pelagic) is 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 () 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 283.15 , where the correction factor=1), and is Boltzmann’s constant in (). We chose an exponential temperature dependence as it provides a good statistical fit to data, is widely adopted, and because we assume that the projected change in ocean temperature in the studied time range does not lead to temperatures above physiological optimum, where physiological rates might be expected to decline (e.g. (Righton *et al.* 2010) as an example for cod). While temperature likely affects other physiological processes as well (e.g. cost of growth (Barneche *et al.* 2019), food conversion efficiency (Handeland *et al.* 2008)), we focus on metabolism, maximum consumption and mortality as their temperature dependence is relatively well documented (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 the 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 , if assuming a fixed supply of limiting resources (e.g. nutrients) for the resource populations. This theoretical prediction has been verified experimentally for phytoplankton (Bernhardt *et al.* 2018). This scenario is referred to as ”exp” for experimental to reflect where data stem from.

**(2)** Empirical scenario: The carrying capacity declines with temperature proportionally to , based on the observed relationship between temperature and the intercept of marine phytoplankton size spectra (Barnes *et al.* 2011). This scenario is referred to as “obs” as data come from remote sensing of chlorophyll-a.

Activation energies (, ), which dictate the temperature sensitivity of a rate, typically vary substantially between processes, species, taxonomic groups, and whether or not intra- or interspecific data are used for estimation (Savage *et al.* 2004; Downs *et al.* 2008; Englund *et al.* 2011; Rall *et al.* 2012). To overcome this, we assigned activation energies by drawing 200 random combinations of activation energies for each temperature-dependent rate from probability distributions (Table 1; Fig S11). The model is then projected to forward to 2050. This is repeated 200 times, each time with another set of parameters. We then quantify the overall mean response and the ranges of predictions resulting from the random draws. The probability distributions for the temperature-dependencies of maximum consumption rate and metabolic rate are taken from a systematic literature review on the intraspecific size- and temperature dependent scaling (Lindmark et al, in prep). Mortality is assumed to scale in proportion to metabolic rate with temperature (Brown *et al.* 2004a; Blanchard *et al.* 2012), and therefore the random draws are taken from the same distribution as metabolic rate. For simplicity, we assumed the distributions of each rate from which the draws are taken are independent. Activation energies for resource parameters were acquired by fitting a linear regression of natural log of growth rate as a function of Arrhenius temperature () from experimental data in (Savage *et al.* 2004) (pooling protists, algae and zooplankton) for the exp-scenario, and fitting 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 to evaluate changes in 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.

*Model calibration*

The MSSM is parameterized to represent the Baltic Sea offshore food web by estimating life history parameters from scientific trawl survey data (for details, see Appendix S1, Table S1-S2). Next, the model is calibrated to averaged stock assessment data for cod, herring and sprat (fishing mortality, F and spawning stock biomass, SSB) (ICES 2013, 2015) in a specific time window to tune the system to get realistic biomass ratios. Ideally, the period for calibration should exhibit relative stability, but such periods do not exist in the Baltic Sea, which is 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 (F) on cod, low cod and herring abundance and high sprat abundance (Gårdmark *et al.* 2015) (Fig. 1, Fig.S2). 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).

Maximum recruitment values () for the three model species were calibrated by minimizing the residual sum of squares between the natural log of spawning stock biomass (SSB) estimated in stock assessment output and those emergent in the model for the years 1992-2002, while holding 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. S4), which they were after a stepwise manual increase of the constant in the allometric maximum-consumption rate () (Appendix S1). We also evaluated the level 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, recruitment is largely controlled by rather than processes emerging from e.g. feeding and food-dependent growth. After calibrating the model, we acquired ratios of 9.8, 9.5 and 9.4 and ratios of 8.8, 8.5 and 8.4 for cod, sprat and herring, respectively, which is largely in line with (Andersen & Beyer 2015) and indicates there is some density dependence in early life stages in the model. A detailed description of the step-by-step calibration protocol used in this study can be found in Appendix S1 and Fig. S3-S9.

*Analysis of responses to warming*

Models where projected with historical fishing efforts (1974-2014) and relative sea surface temperature (1970-2050, acquired from the regional coupled model system RCA4-NEMO under the RCP 8.5 scenario) (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 60-year burn-in period using the first fishing effort and temperature values in the respective time series (Fig. S8, S11). For each species, we used the mean of the FMSY from stock assessment model (to which the model was calibrated) and the FMSY from the size spectrum model as fishing mortality in the years 2014-2050 (Fig. S3, S12).

We evaluated the effects of warming on weight-at-age, population mean weight, abundance-at-weight and fisheries yield by species. This was done for both absolute values, and by comparing warming food webs to a baseline scenario where no warming occurred post 1997 (the mid-point of calibration time window, where temperature averages ) (Fig. S11, S8). To contrast the effects of temperature affecting fish physiology, their resources or both, we considered 5 different scenarios (Table 1) and evaluated the food web metrics for each.

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

Table 1 Temperature-scaling scenarios (columns) and which rates or parameters are temperature dependent (rows) in the time-varying projections. Green/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”, in addition to temperature-dependence of their background resources, the “bottom-up”) has a strong influence on the projected size-at-age in 2050 under the RCP 8.5 emission scenario, relative to the baseline projection (no warming) (Fig. 1). Including empirical temperature dependence of maximum consumption, mortality and metabolism, 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 individuals. In scenarios with temperature-dependent physiological processes, the positive effect of warming on size-at-age is largest for small and young individuals and declines with age. In contrast, when only resource dynamics scale with temperature, small individuals have the largest relative change (negative), and this negative effect of warming declines with age (Fig. 2).

Despite the relatively narrow range of activation energies for physiological rates considered here (Fig. S11; Table S4), the uncertainty in projected size-at-age associated with variation in the activation energies are large. In scenarios where both physiology and resources depend on temperature, the range of predicted changes in size-at-age vary at approximately % to 40% for both scenarios (Fig. 1). Cod, followed by herring and sprat, shows the largest uncertainty in the projected size-at-age (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). Moreover, the consumption rate is slightly more sensitive than the metabolic losses for the energy acquisition (Table S4). This also leads to increases in the size-dependent predation mortality of fish above 1g for all scenarios, and for all body weights in the scenarios where only resources are temperature-dependent (Fig. S14).

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

While there is a positive relationship between the relative change in size-at-age due to warming (Fig. 1) and that of the mean population body weight (Fig. 2), increases in size-at-age do not always lead to increased mean body size in the populations. This reflects a change in the size composition of the populations with warming (Fig. 3). For sprat and herring, the only scenario that has a median increase in mean body weight includes only temperature-dependent physiological processes and no temperature dependence of resources (Fig. 2). The abundance-at-weight for fish above maturation size decreases by 10% at the end of the projection for sprat and herring unless temperature only affects physiology. The increase in predation and background mortality with warming likely contribute to this (Fig. S14). For cod, the abundance of the largest fish (>) increases in all scenarios with physiological temperature dependence (Fig 3), which likely drives the corresponding increase in the mean body weight of the cod population (Fig. 2). This could be an effect of the projections using lower fishing mortalities than observed in the calibration window, as fishing removes the largest individuals disproportionally. By contrast, the abundance of sprat and herring individuals above maturation size only increases with warming if the dynamics of the background resources are not temperature dependent (Fig. 3).

*Warming and fishing: higher sustained exploitation rates but reduced yields*

Fishing removes the largest fish in the populations, but this loss can be counteracted by the increases in growth rates and size-at-age due to temperature effects on physiology (Fig. S15). That is, faster growth due to warming can lead to higher abundance of large fish also when fishing mortality is higher. However, the only case when fisheries yield increases with the projected warming is for cod when temperature only affects physiological rates (Fig. 4). For sprat and herring, and for cod in all other scenarios, yields decline, or are more or less unaffected by warming (Fig. 4). This is 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. While the largest fish can in some cases increase in abundance, especially in cod, they are also rarer in the population and hence this does not counteract the decline in fish that constitute the main catches (Fig. 4).

Warming also influences the fishing effort leading to maximum sustainable yield (FMSY) and the corresponding spawning stock biomass (SSB) (Fig. 5). Based on non-time varying simulations (constant F and temperature until steady state), the fishing mortality corresponding to FMSY increases when the temperature is +2 compared to the reference temperature for cod, and for sprat and herring (except for when temperature only affects basal resources). This is likely due to the enhanced growth rates (size-at-age), which allows higher fishing mortalities without impairing population growth (Fig. S5). However, the fishery yield at FMSY increases relative to non-warming only if temperature acts on physiology alone (Fig. 5; Fig. S16), as 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).

A close up of a map

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 average FMSY levels. Top row shows size-at-age and bottom row shows size-at-age relative to a non-warming scenario. The dashed line in the top row depicts projections assuming a non-warming scenario and thus constitutes a baseline prediction. Colors indicate different temperature-scaling scenarios. Shaded areas encompass the 2.5 and 97.5 percentiles from the set of 200 simulations with randomly assigned activation energies.*

A screenshot of a cell phone

Description automatically generated

*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 average FMSY levels. The dashed horizontal line depicts projections assuming no temperature increase and thus constitutes a baseline prediction. Each dot represents one of the 200 simulations, each with randomly assigned activation energies. Boxplots depict 25%, 50% and 75% quantiles of the 200 simulations in each scenario.*

*A close up of a map

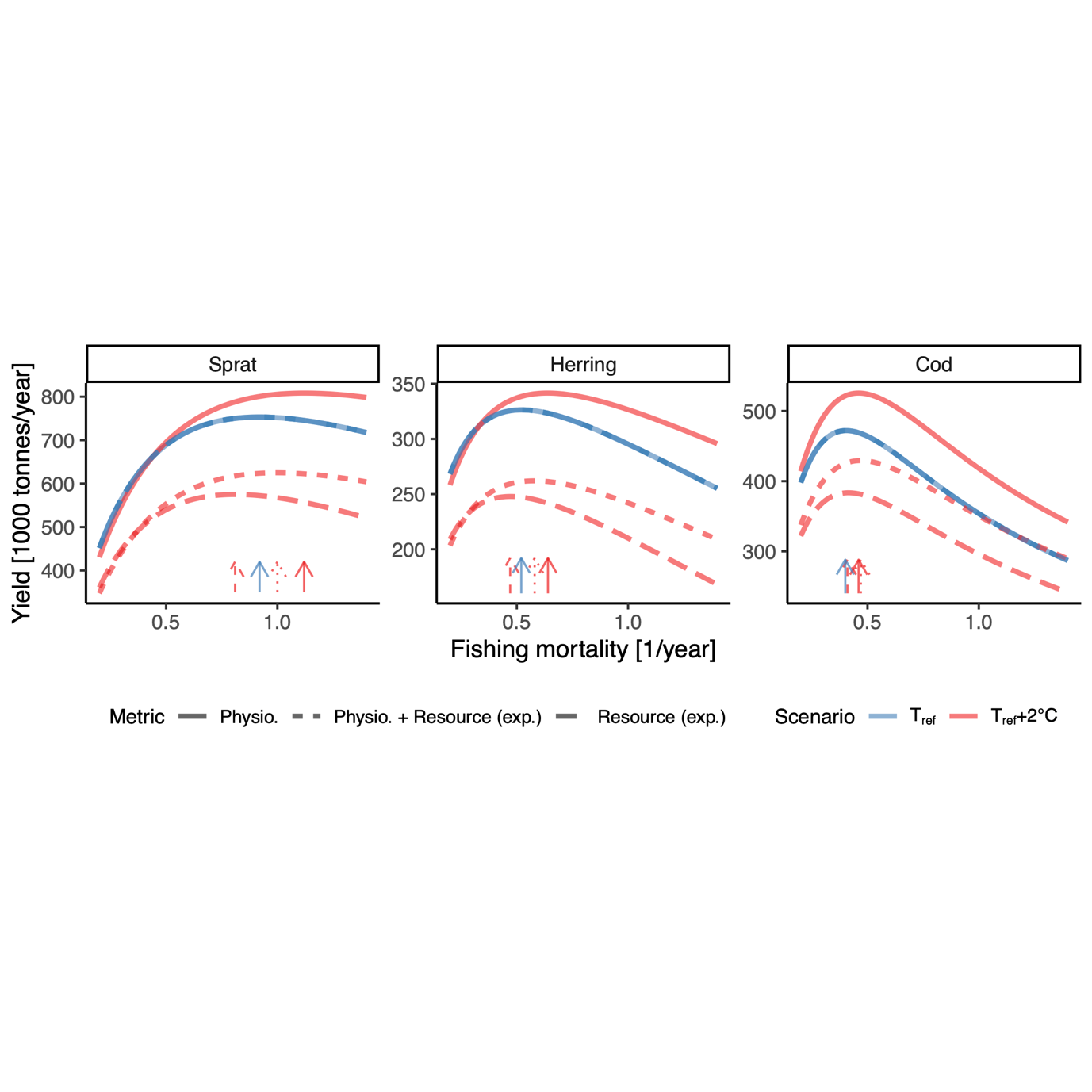
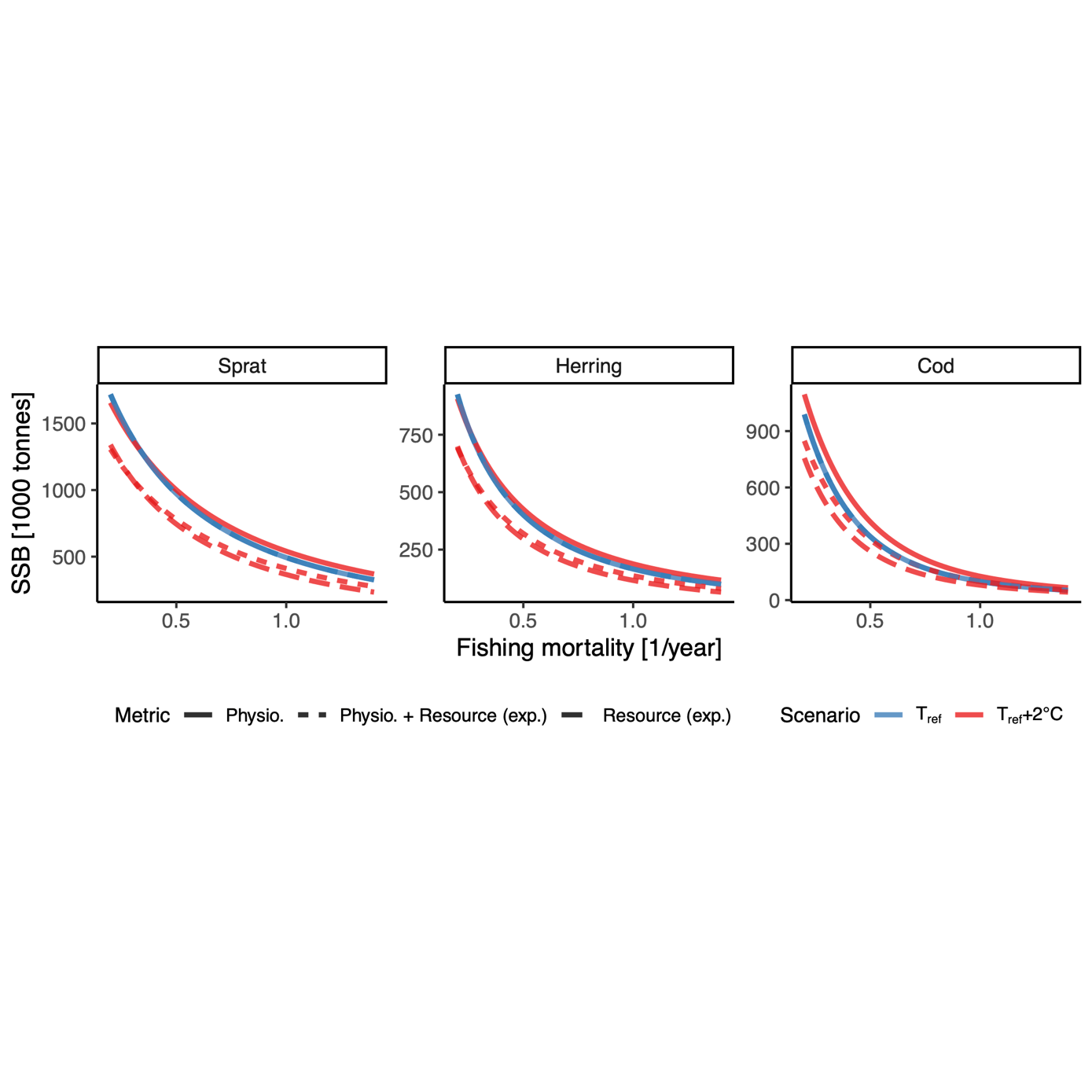
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*Figure 3. Projected abundance-at-weight by species for different scenarios of temperature scaling (indicated by colors, and linetypes in the right column due to overplotting) at 2050 assuming fishing mortality held at average FMSY levels. The left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

A picture containing map, text

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*Figure 4. Time series of projected yield under different temperature scaling scenarios (indicated by colors) and temperature projections according to RCP 8.5 emission scenarios, assuming fishing mortality held at average FMSY levels (after 2014). The horizontal black line corresponds to no temperature increase after 1997. Only mean activation energies are used.*



*Figure 5. Steady state spawning stock biomass yield (top) and fishery yield (bottom) assuming knife edge selectivity at maturation size under constant temperature simulations. Colors indicate the temperature, where blue means (all scaling factors = 1, i.e. no temperature effects), and red depicts warm temperature, here +2. Dashed lines correspond to resource dynamics being temperature dependent, dotted lines correspond to physiological rates and resource dynamics 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 it 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, consumption, background mortality) of fish, and found that including temperature-dependence of physiological rates generally lead to increased size-at-age with warming, whereas only considering resources being temperature dependent leads to declines in size-at-age for all sizes. The increase in size-at-age when including physiological temperature scaling 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 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 and growth theories (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 the population. 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 can vary over ontogeny.

Plastic body growth is generally thought to be less important than environmentally driven recruitment variation, density dependence at early life stages and mortality from fisheries for stock dynamics, in fisheries stock assessment (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 (MSY), FMSY and SSBMSY (the fishing effort leading to MSY and the spawning stock biomass at MSY, respectively) varies 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 MSY, FMSY and BMSY are lower in simulations with +2 warming relative to . By contrast, when temperature affects both physiology and resources, FMSY is higher with warming but BMSY is lower, likely due to due declines in abundance-at-size, and this is true also for cod. When resources do not decline with temperature and only physiology is temperature dependent, all these reference points are higher when temperature is increased by +2. 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, where probability distributions of parameters were derived from meta-analyses based on mainly fish (Lindmark 2020) to capture 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 (and feedbacks from these) 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 is straightforward to model increases in productivity (such 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 ((Morán *et al.* 2010; Yvon‐Durocher *et al.* 2011; Canales *et al.* 2016; Woodworth-Jefcoats *et al.* 2019), but 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; 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. 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 since lacking mechanistic processes are poorer in projecting outside observed conditions (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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