**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 models have found that bottom-up processes are important drivers of size-structure and fisheries yield at the ecosystem level in changing climates. However, we know less about the joint effects bottom up and top down effects (direct of warming on individual-level physiology) on exploited food webs. Using the Baltic Sea as a case study, we assess how various food web metrics are affected by warming and exploitation in a species-resolved size-based food web. We parameterize a dynamic size-spectrum model representing the offshore Baltic Sea food web, and investigate how individual growth rates, size-structure, relative abundances of species and yields are affected by warming under different scenarios of fishing mortality and physiological scaling. We find that the model is able to reproduce realistic biomass densities in the relatively stable time period (1992-2002). Evaluation of steady-state properties at simulated higher temperatures suggests that both warming leads to positive impacts on growth of younger fish within species, but the positive effect levels off and becomes negative for older fish within projected warming scenarios. Any key explanation why? The effect of warming on the abundance size-spectrum, spawning stock biomass and yields of the fisheries depend more strongly on the effect of temperature on basal resources than on individual physiology. Results from our model can be used to qualitatively evaluate how warming and exploitation interactively affect the Baltic Sea fish community, which can inform about potential future yields in a multispecies scenario and thus support strategic management decisions.

**Introduction**

Climate change affects aquatic food webs directly by shifting the distribution of species (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), which can lead to indirect effects through the rewiring of food webs (Frainer *et al.* 2017). Global retrospective analysis of warming and fish population dynamics has revealed that declines in productivity of scientifically assessed fish populations across ecoregions has already declined 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 further declines in biomass by 2100, especially at higher trophic levels (Lotze *et al.* 2019). Large scale models are crucial for informing global assessments about the implications of climate change (Lotze *et al.* 2019). However, by necessity, these models rely on simplifying assumptions (Fulton *et al.* 2019), including species-resolved food webs and the effects of temperature on individual-level physiology (but see (Woodworth-Jefcoats *et al.* 2019)). Instead, temperature is often assumed to act mainly on ecosystem productivity (“bottom up”) rather than both individual physiology (“top down”) and productivity. Thus, there is a need to increase our mechanistic understanding of climate change impacts on individuals and how that affects regional dynamics (Blanchard *et al.* 2012).

The primary effect of temperature is on individual physiology, and individual-level processes such as metabolism, growth and mortality govern ecosystem properties such as biomass production rates, abundance and size spectra (Andersen & Beyer 2006; Jennings & Collingridge 2015; Blanchard *et al.* 2017). However, there is still uncertainty in both the scaling of physiological rates, such as metabolism and ecological rates with body mass and temperature (Brown *et al.* 2004; Dell *et al.* 2011; Englund *et al.* 2011), and there is no consensus or a single framework for implementing this into e.g. models of individual growth. This limits our ability to predict and understand “universal” responses to global warming, such as the shrinking of organisms with warming (Daufresne *et al.* 2009) and the temperature size rule, predicting faster growth rates but smaller asymptotic body sizes with warming (Atkinson 1994). One example of a mechanistic approach to predict changes in physiology to population dynamics and size structure is the model by (Cheung *et al.* 2013). Based on a generalization of the von Bertalanffy growth equation (VBGE), this model predicted a 14-24% reduction in average maximum body mass driven by changes in distribution and physiology. The underlying mechanism here is the assumption that increasing oxygen limitation with warming due to elevated metabolic demands impose growth constraints that lead to smaller asymptotic body masses. This model has however been criticized for not representing the underlying physiological processes accurately – both in what they represent and their parameters (Jutfelt *et al.* 2018; Lefevre *et al.* 2018). In addition, evaluating changes in food web size-structure based on static growth models (as in no food-dependence) is in conflict with the well-known observation that body growth depends on an interplay between body size, temperature and food availability (Brett *et al.* 1969). For instance, the optimum temperature for growth declines with reduced food rations (Huey & Kingsolver 2019), which means that the effects of temperature are mediated by changes in resources levels. It is therefore important to work on developing mechanistic models that are founded on an accurate description of size and temperature-dependence of key physiological processes, and to evaluate them in an ecological context to account for the food dependence of growth (Neubauer & Andersen 2019).

Process-based (or mechanistic) food web models aim represent the dynamics or structure of ecosystems based on an understanding of the key mechanisms behind the phenomena considered, considering both metabolic scaling and feeding interactions e.g. (Brose 2010; Persson & De Roos 2013). This means models can vary in their performance depending on the process they are tailored for (Spence *et al.* 2018), and it is therefore important to both identify and capture the dominant mechanisms in the model (Curtsdotter *et al.* 2019). Traditional Lotka-Volterra-type models describing pairwise species interactions often fail to accurately represent the life history of fish, which in general grow several orders of magnitude in body size and change feeding niches and trophic levels during ontogeny (Werner & Gilliam 1984). Hence, it is often necessary to account for intraspecific variation in body size to capture the ecological function of a typical fish (Hartvig *et al.* 2011). Not surprisingly, work in fish and fisheries ecology have pioneered to capture these processes, for example in physiologically structured models (PSPM) (Metz & Diekmann 1986; De Roos & Persson 2001). Later, the development of trait based size spectrum models allowed for more generic formulations of physiologically based life history description and using body weight at maturation as a distinguishing trait (Hartvig *et al.* 2011), which has provided general insights and mechanisms on e.g. trophic cascades (Andersen & Pedersen 2009). More recently, extensions of the size spectrum framework for modelling size-based food webs include more precise characterization of species, e.g. by defining species feeding preference and life history characteristics – so called multi-species size spectrum models (MSSMs) (Blanchard *et al.* 2014; Scott *et al.* 2014). Such species- and trait-based models have led to a closer connection to observational data, by e.g. both informing and validating model predictions. For instance, (Reum *et al.* 2019), by characterizing species predation preference by both species- and body size, were able to more accurately describe the true feeding links, which in addition weakened the effects of fishing on trophic cascades compared to strictly size-based models. These have also recently been applied to examine the effects of warming and fishing (Woodworth-Jefcoats *et al.* 2019), and a case study on the Hawaiian long line fishery suggest that fishing in general causes declines in mean size and yield, and that climate may enhance this. It is important however to acknowledge that all models come with different sources of uncertainty. In MSSMs, metabolic scaling parameters have a major impact on the uncertainty around model predictions (Zhang *et al.* 2015). This suggests also their temperature dependence is an important source of uncertainty, yet this is rarely quantified in mechanistic models (but see (Fussmann *et al.* 2014)).

Here we use a food web model representing the Baltic Sea as a case study to examine the relative and combined effects of warming on background resources and individual-level physiology affects individual growth trajectories, average body sizes, size-structure and yield in a fished ecosystem. The Baltic Sea is a semi-enclosed regional sea that is experiencing warming with a rate three times the global average (Belkin 2009). By 2050, the regional coupled model system RCA4-NEMO and the RCP 8.5 emission scenario predicts the surface temperature to have increased by 2 compared to the mean in 1970-1999 (Dieterich *et al.* 2019; Gröger *et al.* 2019). The food web model is a multi-species size spectrum model (Blanchard *et al.* 2014; Scott *et al.* 2014), modified to account for temperature dependence of metabolism, maximum consumption rate and background mortality, as well as resource turnover rate and carrying capacity. Uncertainty in the thermal dependence of these rates is incorporated by drawing samples from known distributions, based on meta-analysis and the metabolic theory of ecology. The temperature-dependent model is then projected forward with a time-varying ocean temperature based on the regional coupled model system RCA4-NEMO using the RCP 8.5 scenario. Brief summary of paper and findings. Relate to similar/large scale/ensemble models, e.g. 5%, both growth and yield? And spectera?. Intro to Baltic ecosystem (ecology, development, fishing and climate effects) + motivation for using the Baltic as case study. Cite Andersen food dependence, the size-aspect of interactions, the rate of warming, etc etc, the fishery.

**Materials and Methods**

*Food web*

In this study we develop a Multi-species size spectrum model (MSSM) inspired by a simplified version of the food web in the Baltic proper (ICES sub divisions 25-29+32, Appendix Fig SX). This food web is here characterized by three fish species: cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*). These species all have analytical stock assessments, they are the most important species commercially in this southern sub-region of the Baltic and they constitute the main species in terms of biomass. We also model one pelagic and one benthic background resource spectra, which constitute dynamic food sources for the smallest individuals in each species (such as phyto- and zooplankton, gobiidaes and other small fish).

*Size-spectrum model*

Our 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 we extend by adding multiple background resources and temperature-scaling of key physiological processes and background resource levels. All model code (parameterization, calibration and analysis), together with necessary data is available on GitHub (<https://github.com/maxlindmark/mizer-rewiring/tree/rewire-temp/baltic>), and will be deposited on Zenodo (<http://doi.org/>) upon publication. In this section we describe the key elements of the MSSM, which mostly follow the standard multispecies mizer model (Scott *et al.* 2014).

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:

where [] is somatic growth (dependent on the availability of background resources or prey) and [] is total mortality. The total mortality, , consists of three components: constant allometric background mortality:

fishing mortality:

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. The predation mortality for species equals the amount consumed by species :

The proportion of encountered food that is consumed follows a Holling functional response type II:

where is the *feeding level* (0:1), is the allometric maximum consumption rate and is the encountered food. The amount of encountered food for a predator of body weight is given by the available food in the system, scaled by a size-selection function and the search rate of the predator. Here, available food, , is the integral of all species and background resource

where is the weight of prey, is the preference of species on resource , and indicates species. Note that in contrast to other MSSMs (Blanchard *et al.* 2014; Reum *et al.* 2019) we have a species-preference for the background resources to account for species feeding differently on benthic and pelagic resource, but assume no preference in terms of the species interactions. This is for simplicity, as the body size-only prey selection and encounter captures the important predation interactions in this system (as inferred from independent stomach data, see model calibration, Appendix S1) and the species largely occupy similar spatial areas in the time period considered here. The body size-based selection function, , is given by a log-normal selection function (Ursin 1967):

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

to get the actual encountered food.

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Encountered food is given by the product , and is assimilated with efficiency and used to cover basal metabolic costs, which scale allometrically as . The remaining energy, , is thus:

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

which has the property that the growth rate, i.e.

approximates a von Bertalanffy growth curve when the feeding level is constant (Hartvig *et al.* 2011). Reproduction is given by the total egg-production in numbers, which is the integral of the energy allocated to reproduction multiplied by an efficiency factor () divided by the egg weight, :

The recruitment of offspring to each species relates to the total egg production via a Beverton-Holt stock recruit relationship, such that recruitment reaches a maximum as the egg production increases:

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

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

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

*Temperature dependence*

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

where is the activation energy for individual rate [], is temperature [], is the reference temperature (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 data, is widely adopted and because we assume that the projected change in ocean temperature in our time-range does not lead to temperature above physiological optimum (e.g. (Righton *et al.* 2010) as an example for cod). While temperature likely affects other individual-level processes as well (e.g. cost of growth (Barneche *et al.* 2019), food conversion efficiency (Handeland *et al.* 2008)), we focus on metabolism, maximum consumption and mortality as their temperature dependence is relatively well documented.

Temperature also affects the amount of available background resources. As background resources are not resolved by species or taxonomic group, but simply represent food items for the smallest individuals of each species through a semi-chemostat equation, we implement temperature dependence on background resources by scaling the regeneration rate () and carrying capacity () with the Arrhenius correction factor, with activation energy , where refers to resource parameter. We consider two scenarios based on the metabolic arguments and empirical patterns:

1. The regeneration rate increases due to elevated metabolic rates, which increases the rates of energy acquisition, growth, maintenance and reproduction (Savage *et al.* 2004). Note this is not explicitly modelled. The carrying capacity declines at the same rate as population regeneration rate increase with temperature (Savage *et al.* 2004; Gilbert *et al.* 2014), i.e. , if assuming a fixed supply of resources. This theoretical prediction has been verified experimentally (Bernhardt *et al.* 2018).

Time series of satellite data indicate a decline in primary production with climate change, potentially due to increased stratification and reduced resource levels (Gregg *et al.* 2003). Therefore, we also consider a scenario where the temperature effect is based on observed relationship between temperature and marine phytoplankton size-spectra (Barnes *et al.* 2011).

1. The carrying capacity declines with temperature , where

Activation energies, which dictate the temperature sensitivity of a rate, typically vary substantially between species, taxonomic groups and whether or not intra- or interspecific data are used (Savage *et al.* 2004; Downs *et al.* 2008; Englund *et al.* 2011; Rall *et al.* 2012). Moreover, MSSMs have been shown to be sensitive to metabolic scaling parameters (Zhang *et al.* 2015). To overcome this, we drew 200 combinations of activation energies for each temperature-dependent rate from probability distributions (Table 1; Fig SX). The model is then projected forward 200 times, each time with another set of parameters and quantify the overall mean response as well as individuals draws. The distributions for maximum consumption rate and metabolic rate stem from a dataset from a systematic literature review on the intraspecific size- and temperature dependent scaling (Lindmark et al, in prep) and mortality is assumed to scale in proportion to metabolic rate (Brown *et al.* 2004; Blanchard *et al.* 2012). Activation energies for resource parameters were acquired by fitting linear regression of natural log of growth rate as a function of Arrhenius temperature () from experimental data in (Savage *et al.* 2004) (pooling protists, algae, zooplankton) for the MTE-scenario. For the empirical scenario, we used an activation energy that best fit the decline in phytoplankton size-spectra intercept presented in (Barnes *et al.* 2011) (-0.045 ). We further assume the distributions from which the draws are taken are independent.

*Model calibration*

The Baltic Sea offshore food web has experienced dramatic structure changes over the last decades, which makes it difficult to identify a period of relative stability for model calibration. 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). The cutoff at 2002 also ensures that we do not calibrate the model to years when the physiological state of cod started to drastically deteriorate, i.e. mid 2000’s and onwards when the growth capacity, condition, proportion of large fish in the population and reproductive capacity started to decline (Svedäng & Hornborg 2014; Mion *et al.* 2018; Neuenfeldt *et al.* 2019).

We calibrated the system to the Baltic Sea by finding the vector of -values that minimize the residual sum of square between the natural log of spawning stock biomass (SSB) from stock assessment output and modelled SSB, using the "L-BFGS-B" algorithm in the ‘R’-optimization function ‘*optim’*. During this time period we held the temperature constant at . Mean SSB and F during the calibration time period (1992-2002) from stock assessment were acquired from ICES Working Group Reports (ICES 2013, 2015), and are in unit 106 kg/area. This area corresponds to ICES subdivisions 25-29+32, which equals approximately 2.49E+11 m2 (estimated using ICES shapefiles in ArcGIS). To express the modelled SSB in the same scale, we first defined it in the units g/m2 and then used the converting factor 240.342. Given that the North Sea is approximately 1E11 m2, we used the and divided by 1E11 as starting values, before calibrating the model. This resulted in a starting value for and of 1. We also ensured that also growth-rates were realistic by comparing them to VBGE curves fitted to trawl survey data, and that the density dependence due to the stock-recruit function was appropriate. This was assessed from the ratio of recruitment before and after stock-recruitment density dependence was applied (Jacobsen *et al.* 2017). Lastly, we compared time series of model output simulated together with historical temperature and fishing effort data with stock assessment output. A detailed description of the step-by-step calibration protocol used in this study, inspired by (Jacobsen *et al.* 2017), can be found in Appendix S1.

*Model analyses*

The model was evaluated

Table 1 Parameters of distributions describing activation energies of temperature-dependent rates in the size-spectrum model. See figure 2 for 200 random draws from these distributions which were used as input in projections.

|  |  |  |  |
| --- | --- | --- | --- |
| Symbol | Rate | Distribution | Source |
|  | Metabolism |  | Lindmark *et al.* (*in prep*) |
|  | Background mortality |  | (Brown *et al.* 2004); Lindmark *et al.* (*in prep*) |
|  | Maximum consumption |  | Lindmark *et al.* (*in prep*) |
|  | Background resources carrying capacity |  | Data from Savage *et al.* (2004) for algae, phyto- and zooplankton. |
|  | Background resources growth rate |  | (Gilbert *et al.* 2014); (Savage *et al.* 2004) |

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Figure 1. Time series of (A) effort by species and (B) temperature from the regional coupled model system RCA4-NEMO using the RCP 8.5 scenario. In panel A, the light grey area corresponds to years with from stock assessment. The dark grey area is the calibration time period. We treat the 60 years prior to the start of the F-time series as burn-in and keep the constant and equal to the first time series (in year 1974). The future projections correspond to the mean FMSY from the multispecies stock assessments’ estimates and the size-spectrum model (estimated by keeping each species at their mean assessment FMSY). In panel B, temperature is shown as deviations from the average in 1970-1999. Note the different x-axis of the figures.

**Results**

* With the random combinations activation energies that we believe are more of less realistic, and for scenarios with/without effects of temperature on the background resources, body growth rates increase with warming.
* The positive effect of warming diminishes with age.
* For herring and sprat, warming always has a positive effect on growth given the temperature increase we model (which is about +1.5C, see Figure S11 for the scenario here) – even in the most “unfortunate” parameter combination.
* For cod, the “confidence bands” go below 1 in some combinations of parameters, with and without resource temperature-dependence, suggesting warming has a negative effect on size at age even with a 1.5C increase in temperature.
* These results show that the effect of warming on growth rates does not depend that much on how growth of background resources vary with temperature, as the two lines follow each other and largely overlap.
* I also note that the distributions of activation energies are relatively tight, which makes the “confidence bands” pretty tight. This is because it’s not very likely that we draw one really good activation energy for intake and one really bad for metabolic rate at the same time. This is also why I plot the minimum and maximum rather than some quantile.
* (Suggested sensitivity analysis: redo this analysis in a constant temperature and effort setting (not time-varying), and explore extremes of activation energies to get a better feeling for what the effects are. Will also show which the actual activation energies are that give the min, max and mean response that correspond to the ribbons.)

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*Figure 2. Individual growth trajectories of sprat, herring and cod from model projections. Top row shows size-at-age in 2050 assuming fishing mortality held at average FMSY levels (Figure 1A) from different stock assessment estimates and this model (Fig. S7) and a temperature increase in the Baltic Sea in line with the projection from the RCA4-NEMO assuming the RCP 8.5 emission scenario (Figure 1B). The dashed line in the top row depicts projections assuming no temperature increase (Fig. SX) and thus constitutes a baseline prediction. In both the green and pink projections physiological rates are temperature dependent. In the pink projections also background resources are temperature-dependent via their growth rates and carrying capacities, and in the blue scenario only resource parameters are temperature-dependent. Each line corresponds to a unique parameterization from a random draw of activation energies. For fit of size-at-age to data, see Figure S4.*

This shows that accounting for physiological scaling is important as it captures enhances growth rates, which is widely observed in times series data, and both large and small scale experiments.

A screenshot of a cell phone

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*Figure 3. Projected mean weight by species for different scenarios of temperature scaling in 2050 assuming fishing mortality held at average FMSY levels (Figure 1A) from different stock assessment estimates and this model (Fig. S7) and a temperature increase in the Baltic Sea in line with the projection from the RCA4-NEMO assuming the RCP 8.5 emission scenario (Figure 1B). The dashed horizontal line depicts projections assuming no temperature increase (Fig. SX) and thus constitutes a baseline prediction. In both the green and pink projections physiological rates are temperature dependent. In the pink projections also background resources are temperature-dependent via their growth rates and carrying capacities, and in the blue scenario only resource parameters are temperature-dependent. Each line corresponds to a unique parameterization from a random draw of activation energies.*

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*Figure 4. Left column: Projected abundance-at-weight by species for different scenarios of temperature scaling (indicated by colors) at 2050 assuming fishing mortality held at average FMSY levels (Figure 1A) from different stock assessment estimates and this model. Right column: abundance-at-weight relative to projections with no temperature increase past the calibration period.*

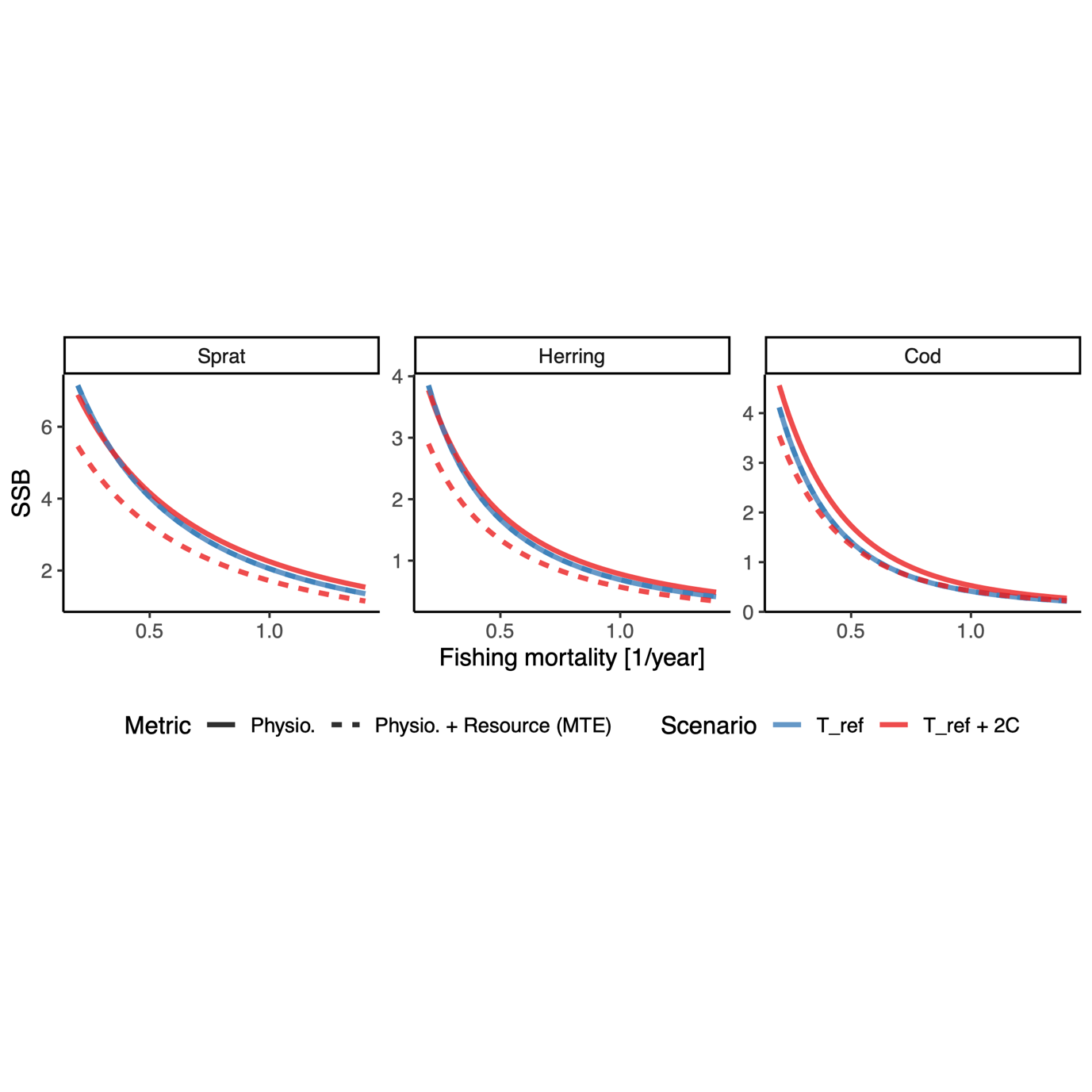
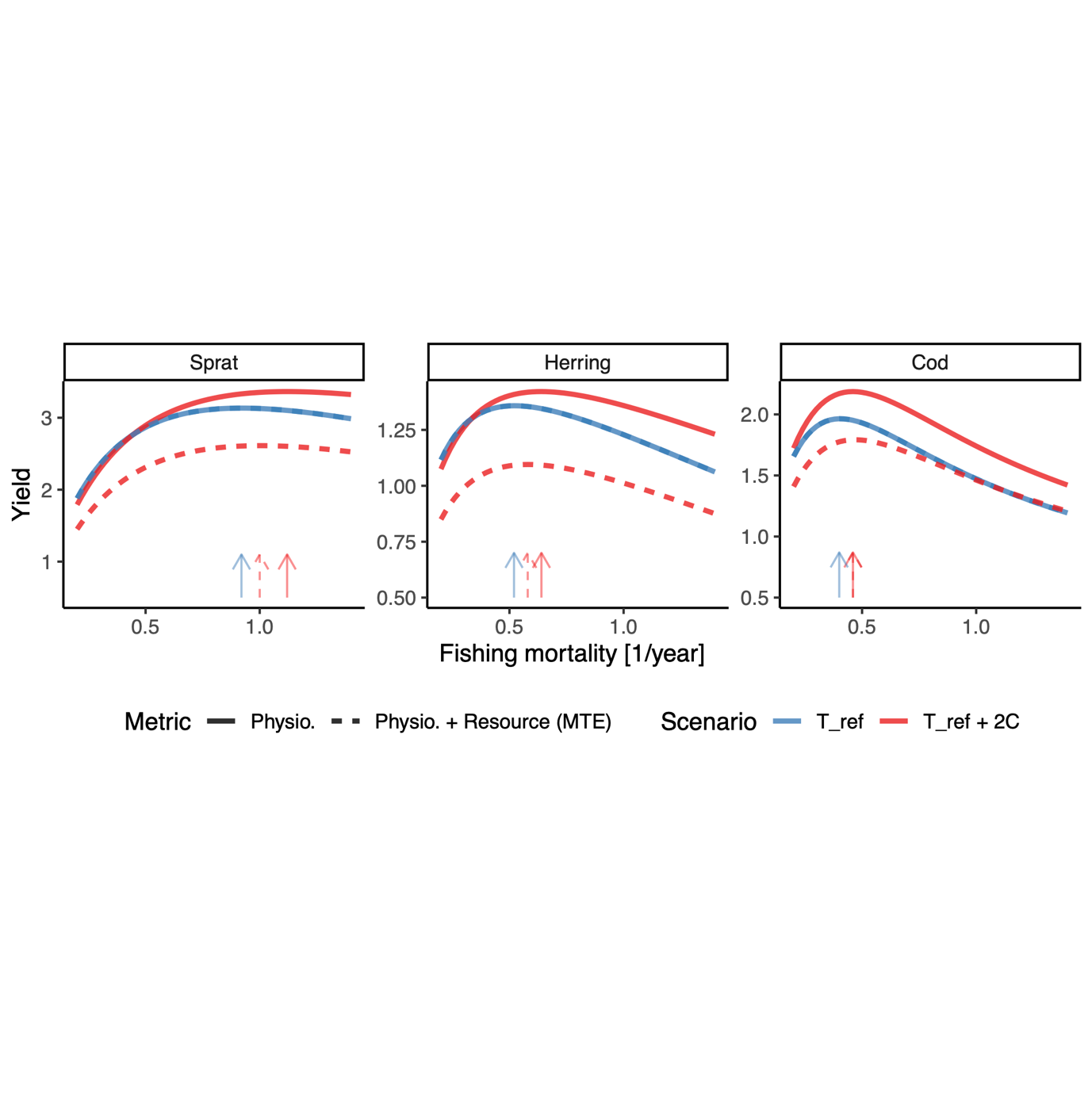
A close up of a map

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Figure 5. Example of projected yield in the time-varying effort and temperature model projection assuming 3 different scenarios (no temperature increase after 1997, without resource temperature-dependence but with effects on individual physiology and with resource temperature dependence and physiological scaling.

Effect of physio is interesting. Without it you would expect declines in yield… (but here I really need the no physio effect, and then both resource scenarios…)

*Figure 6. Steady state fishery yield (top) (assuming knife edge selectivity at maturation size) and spawning stock biomass (SSB) under constant temperatures. Cold = , i.e. no temperature effects, and warm is +2. Arrows indicate 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. Dashed lines correspond to resource dynamics being temperature dependent in addition to physiological rates, solid lines correspond to simulations with only physiological rates being temperature dependent.*



*Preliminary conclusions*

* Top down and bottom up effects of warming both shape food webs.
* An increase in temperature with 1.5C positively affects size-at-age for all species, but the positive effect diminishes with age and often becomes negative for cod aged 5+. This result is not very sensitive to temperature-driven changes in background resources.
* The effect of temperature on resources (bottom up) partly determines whether or not abundance-at-size increases or decreases with warming

**Discussion**

* Compare predictions that match and don’t match to Woodworth-Jefcoats and Olivier
  + (also discuss different ways of adding background spectra changes: “Changes in abundance and size-structure of background resources can directly inferred from e.g. climate and earth systems models (Woodworth-Jefcoats et al. 2019). However, the simple metabolic approach provides a baseline model for temperature-dependence on population dynamics and allows for an easier interpretation of the relative effects of direct physiological effects (“top down”) vs changes in background productivity (“bottom up”)”)
  + There are indications that also the slope of the size-spectrum ( in the term for carrying capacity), declines with temperature (Yvon‐Durocher *et al.* 2011), however on a global scale this effect is less clear statistically (Barnes *et al.* 2011).
* Talk about growth and uncertainty in scaling parameters
* Need to talk about the state of the Baltic and how that limits our relatively simple model to predict the things that are happening there (range shifts of the pelagic, spatial contraction of cod, earlier maturation and poor growth of cod)
* Our approach categorized one source of uncertainty as environmental variability, but the size-spectrum model does not explicitly include environmental variables such as temperature, salinity, and dissolved oxygen into modelling (Andersen and Beyer, 2006; Scott et al., 2014). It is worth noting that incorporating multiple environmental variables into mechanistic modelling is exceedingly difficult as environmental effects on ecosystems are often non-linear and mixed, and it is impossible to include all environmental variables (Pauly, 1980; Pepin, 1991; Charnov and Gillooly, 2004; Po¨rtner and Knust, 2007). But see Woodwarth.-Jefcoats and Blanchard 2017

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**Author contributions**

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

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