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

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**Abstract**

Resolving the combined effect of climate warming and exploitation in a food web context is key for predicting future biomass production, size-structure and potential yields of marine fishes. Previous studies based on mechanistic size-based food web models have found that bottom-up processes are important drivers of size-structure and fisheries yield in changing climates. However, we know less about the joint effects bottom up and ‘top down’ effects (direct effects of warming on individual-level physiology) on the intraspecific size-structure in exploited food webs. Here we assess how various food web metrics are affected by warming through both these pathways and by exploitation in a species-resolved size-based food web. We parameterize a dynamic size spectrum model inspired by the offshore Baltic Sea food web, and investigate how individual growth rates, size-structure, relative abundances of species and yields are affected by warming under different scenarios of fishing mortality and effects of temperature on physiology. When accounting also for how temperature affects physiology compared to the baseline levels, projected size-at-age increases for all species in 2050 based on temperature projections according to the RCP 8.5 scenario, whereas size-at-age decreases when temperature only affects resource dynamics. However, the faster growth rates in the fully temperature-dependent models do not to the same extent translate to larger yields, as mean body size and spawning stock biomass declines due to increased predation mortality rates. Results from our model suggest that reduced fishing mortality can counteract the potentially negative effects of warming on the abundance of fish above maturation size.

**Introduction**

Climate change affects aquatic food webs directly by shifting species’ distribution (Pinsky *et al.* 2013), abundance (McCauley *et al.* 2015), body size (Daufresne *et al.* 2009; Baudron *et al.* 2014), and ecosystem function (Pontavice *et al.* 2019). Global retrospective analysis of warming and fish population dynamics has revealed that productivity (maximum sustainable yield, MSY) of scientifically assessed fish populations across ecoregions has already declined by on average 4.1% between 1930-2010 due to climate change (Free *et al.* 2019). These results are also matched in magnitude and direction by projections from an ensemble of mechanistic ecosystem models, which predicts ~5% decline in biomass for every 1 of warming, especially at higher trophic levels (Lotze *et al.* 2019). The causes of declines in productivity of fish stocks, and abundance of large fish, have in process-based ecosystem models mainly been linked to changes in primary production or zooplankton (Blanchard *et al.* 2012; Woodworth-Jefcoats *et al.* 2013, 2015; Barange *et al.* 2014; Lotze *et al.* 2019). However, stock assessment models found no clear increase in fish productivity in areas where warming is predicted to have positive effects on primary production (Free *et al.* 2019). Instead, other factors may be more important for population dynamics, including temperature-driven changes in individual- and population level processes such as recruitment, morality and somatic growth (Free *et al.* 2019). Therefore, the driving mechanisms of changes in fish productivity and biomass with warming is uncertain.

Moreover, global warming is also predicted to cause reductions in the adult body size of organism, and this is often referred to as the third universal response to warming (Daufresne *et al.* 2009; Sheridan & Bickford 2011; Forster *et al.* 2012). In fish, adult body sizes can decrease due to many reasons, including direct removals of old or large fish, or selecting for early maturing and fast growing individuals (Audzijonyte *et al.* 2013). It could also be an adaptive intraspecific response. The temperature-size rule (TSR) (Atkinson 1994) states that individuals reared at warmer temperatures develop faster and thus acquiring larger size-at-age or life stage, but reach smaller adult body sizes (Ohlberger 2013). 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). However, no clear negative effects of warming on the body size or growth of large fish could be found in two recent studies form more controlled experiments (i.e. in the absence of potentially confounding factors such as fisheries exploitation) (Barneche *et al.* 2019; Huss *et al.* 2019). By contrast, faster growth rates or larger size-at-age of young life stages was 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. Thus, the ecological rule of shrinking body sizes may be more complex than often depicted, as the effects of temperature on growth and body size relationships tend to vary over ontogeny. As body size is a key trait in aquatic ecosystems (Andersen *et al.* 2016), warming-induced changes in growth and size-at-age of fish populations could have implications not only for biomass and productivity but also their structure and stability (Audzijonyte *et al.* 2013). It is therefore important to develop mechanistic size-based food web models where the impacts of warming on body size and size-based interactions can be evaluated.

Mechanistic models are useful for evaluating the implications of temperature-size responses in food webs because results emerge from individual-level processes. Using an eco-physiological growth model (generalized von Bertalanffy growth model), Cheung et al. (2013) predicted a 14-24% decline in community-average maximum body mass by 2050 under high-emission scenarios, due to both changes in distribution and warming-induced constraints asymptotic mass. While these declines in maximum body size are in line with the “universal” relationship between smaller adult or asymptotic body sizes with warming, both the physiological basis and the magnitude of the reductions have been questioned (Lefevre *et al.* 2018; Pauly & Cheung 2018). In addition, body growth and resulting size-at-age depends on an interplay between body size, temperature and food availability (Brett *et al.* 1969). This is for instance exemplified in the within-species observation that the optimum temperature for individuals growth declines with both body size (Björnsson 2001; García García *et al.* 2011) 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 of communities, driven by reduced plankton abundance or shifts towards smaller plankton, which reduces energy transfer to the top of food webs (Woodworth-Jefcoats *et al.* 2015). Models including physiological scaling in a species-and size-based resolved food web in general also find these results (Lefort *et al.* 2015; Woodworth-Jefcoats *et al.* 2019). It is unclear however how much this is driven by reduced abundance of large fish versus changes in size-at-age of large fish. It also remains open as to whether climate warming in such models offer any possibility for individuals (in particular small individuals) to benefit from warming in terms of somatic growth, as is commonly observed (Thresher *et al.* 2007; Baudron *et al.* 2014; Huss *et al.* 2019).

The Baltic Sea constitutes a great example system to explore the impacts of warming, as it is a relatively well understood and species poor system (Mackenzie *et al.* 2007; Casini *et al.* 2009) that in addition experiences rapid warming (Belkin 2009). Here we introduce a temperature-dependent size-spectrum inspired by a simplified the Baltic Sea food web with which we assess the joint impacts of both temperature driven changes in productivity and physiology and its effects on the emergent food web structure. We specifically investigate the impacts of projected warming (using the regional coupled model system RCA4-NEMO and the RCP 8.5 emission scenario) on growth trajectories, average body sizes, population size-structure and yield in a fished ecosystem. Uncertainty in the effect of warming on physiology is incorporated by randomly parameterizing these rates using probability distributions from meta-analyses. We find that inclusion of temperature-dependent physiological processes leads increased size-at-age, especially for smaller individuals and in line with general observations, whereas the opposite is observed when only the resource dynamics are temperature dependent. However, overall we find declines in mean body size in the population, 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) parameterized to represent a simplified version of the food web in the pelagic south-central Baltic Sea ecosystem (Baltic proper) (ICES sub divisions 25-29+32, Appendix Fig S2). This food web is here characterized by three fish species: cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), and their prey. These species are dominant species in terms of biomass, they are the most important species commercially in this southern sub-region of the Baltic and they all have analytical stock assessments. We also model one pelagic (such as phyto- and zooplankton, mysids) and one benthic background resource spectrum (benthic invertebrates, gobiidaes, small flatfish etc.), which constitute dynamic food sources for the smallest individuals of each of the three fish species.

*Size spectrum model*

The model is based on source code for the multi-species implementation of size spectrum models in the ‘R’-package *mizer* (Blanchard *et al.* 2014; Scott *et al.* 2014, 2019; R Core Team 2018), which has been extended to include multiple background resources and 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 the multispecies mizer model R-vignette for consistencey (Scott *et al.* 2014, 2018).

In MSSMs, individuals are characterized by their weight () and species identity (). The core equation is the McKendrik-von Foerster equation, which here describes the change in abundance at size through time from food dependent somatic growth and mortality, based on bioenergetic principles:

(1)

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

, (2)

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

, (3)

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

(4)

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

, (5)

where is the non-size based preference of species on species , and describes the weight-based preference from the log-normal selection model (see below) (Ursin 1973). The proportions of encountered food that are consumed by a species follows a Holling functional response type II:

(6)

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

(7)

where is the weight of prey, is the preference of species for resource , and indicates prey species. Note that in contrast to other MSSMs (Blanchard *et al.* 2014; Reum *et al.* 2019) we have a species-preference for the background resources to account for species feeding differently on benthic and pelagic resources but assume no preference in terms of the other species interactions (all terms in the species interaction matrix are identical and equal to 1). This is for simplicity, as the body size-only prey selection and encounter captures the important predation interactions in this system (as inferred from independent stomach data, see model calibration, Appendix S1) and the species largely occupy similar spatial areas in the time period of the model calibration (Fig S2). The size-selectivity of feeding, , is given by a log-normal selection function (Ursin 1967):

(8)

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

(9)

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

. (10)

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

(11)

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

(12)

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

(13)

approximates a von Bertalanffy growth curve when the feeding level is constant (Hartvig *et al.* 2011; Andersen 2019). Reproduction is given by the total egg production in numbers, which is the integral of the energy allocated to reproduction multiplied by a reproduction efficiency factor () divided by the egg weight, :

(14)

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

, (15)

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

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

(16)

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

*Temperature dependence*

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

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

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

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

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

Activation energies (), which dictate the temperature sensitivity of a rate, typically vary substantially between processes, species, taxonomic groups and whether or not intra- or interspecific data are used for estimation (Savage *et al.* 2004; Downs *et al.* 2008; Englund *et al.* 2011; Rall *et al.* 2012). To overcome this, we assigned activation energies by drawing 200 random combinations of activation energies for each temperature-dependent rate from probability distributions (Table 1; Fig S11). The model is then projected to 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 from the random draws. The probability distributions for the temperature-dependencies of maximum consumption rate and metabolic rate are taken from a systematic literature review on the intraspecific size- and temperature dependent scaling (Lindmark et al, in prep). Mortality is assumed to scale in proportion to metabolic rate with temperature, and therefore the random draws are take from the same distribution as metabolic rate (Brown *et al.* 2004a; Blanchard *et al.* 2012). For simplicity, we assumed the distributions of each rate from which the draws are taken are independent. Activation energies for resource parameters were acquired by fitting a linear regression of natural log of growth rate as a function of Arrhenius temperature () from experimental data in (Savage *et al.* 2004) (pooling protists, algae, zooplankton) for the MTE-scenario, and fitting a linear regression of natural log of as a function of Arrhenius temperature () from data provided in (Barnes *et al.* 2011). In both cases data were extracted using the software WebPlotDigitizer (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 (fishing mortality, F and spawning stock biomass, SSB) (ICES 2013, 2015) in a specific time window to tune the system to get realistic biomass ratios. Ideally the period for calibration should exhibit relative stability, but such periods do not exist in the Baltic Sea, which is largely influenced by anthropogenic activities and has experienced dramatic structural changes over the last four decades (Möllmann *et al.* 2009). We chose to calibrate our model to the time period 1992-2002 as in (Jacobsen *et al.* 2017), which is a post-regime shift period characterized by high fishing mortality (F) on cod, low cod and herring abundance and high sprat abundance (Gårdmark *et al.* 2015) (Fig. 1, Fig.S2). The cutoff at 2002 also ensures that we do not calibrate the model to the period starting from mid 2000’s when the growth capacity, condition, proportion of large fish in the population and reproductive capacity of cod started to decline rapidly (Svedäng & Hornborg 2014; Mion *et al.* 2018; Neuenfeldt *et al.* 2019).

Maximum recruitment values () for the three model species were calibrated by minimizing the residual sum of squares between the natural log of spawning stock biomass (SSB) estimated in stock assessment output and those emergent in the model for the years 1992-2002, while holding the temperature constant at . Calibration was done using the "L-BFGS-B" algorithm (Byrd *et al.* 1995) in the ‘R’-optimization function ‘*optim’.* We ensured that also growth-rates were close to observed by comparing the growth curves emerging in the model to von Bertalanffy curves fitted to trawl survey data (Fig. S4), which they were after a stepwise manual increase of the constant in the allometric maximum-consumption rate () (Appendix S1). We also evaluated the levelof density dependence due to the stock-recruit function. 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 close to 1, there is no additional density dependence from the stock-recruitment function and if it is very high recruitment is largely controlled by rather than emergent processes. After calibrating the model, we acquired ratios of 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. Time series of modelled SSB simulated together with historical temperature and fishing effort data with stock assessment output. A detailed description of the step-by-step calibration protocol used in this study can be found in Appendix S1 and Fig. S3-S9.

*Analysis of responses to warming*

Models where projected with historical fishing efforts (1974-2014) and relative sea surface temperature (1970-2050, acquired from the regional coupled model system RCA4-NEMO under the RCP 8.5 scenario). To ensure steady state was reached before time varying effort and mortality was introduced (1974 and 1970, respectively, we applied a 60-year burn-in period using the first fishing effort and temperature values in the respective (Fig. S8, S11). We used the mean of FMSY from stock assessment models (to which the model was calibrated) and FMSY from the size spectrum model as fishing mortalities in the years 2014-2050 (Fig. S3, S12).

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

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

Table 1 Temperature-scaling scenarios (columns) and which rates or parameters are temperature dependent (rows) in the time-varying projections. Green/Yes = temperature dependence included, red/No = not included. See methods for the two alternative approaches to scaling background resources with temperature (experimental of observational).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Physio. | Physio. + Resource (obs.) | Physio. + Resource (exp.) | Resource (obs.) | Resource (exp.) |
| Physiological rates (metabolism, mortality, max. consumption) | Yes | Yes | Yes | No | No |
| Resource carrying capacity ( | No | Yes | Yes | Yes | Yes |
| Resource regeneration rate ( | No | No | Yes | No | Yes |

**Results**

The inclusion of temperature effects on fish physiological processes (“top-down”, in addition to temperature-dependence of their background resources, the “bottom-up”) has a strong influence on the projected size-at-age in 2050 under the RCP 8.5 emission scenario relative to the baseline projection (no warming) (Fig. 1). Including empirical temperature dependence of maximum consumption, mortality and metabolism, with or without temperature-dependence of background resources, leads to warming having positive effects on size-at-age, whereas scenarios without temperature-dependent physiological processes all lead to size-at-age decreasing with warming (Fig. 1). Specifically, in scenarios with temperature-dependent physiological processes, the positive effect of warming is largest for small individuals and declines with size. However, when only resource dynamics scale with temperature, small individuals have the largest relative change (negative), and this negative effect of warming declines with body size (Fig. 2).

Despite the relatively narrow range of activation energies for physiological rates considered here (Fig. S11; Table S4), the uncertainty associated with variation in the activation energies are large. In scenarios where both physiology and resources depend on temperature, the range of predicted changes in size-at-age vary at approximately % 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).

There is a positive relationship between the relative change in growth due to warming (Fig. 1) and that of the mean population body weight (Fig. 2). However, the mean body weight does not increase with warming when the size-at-age does so, except for cod to some degree (Figs. 1-2), reflecting a change in the size composition of the populations (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 below maturation size decreases by 10% at the end of the projection for all species. The increase in predation and background mortality with warming likely contribute to this (Fig. 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 their mean body weight (Fig. 3). 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 increase with warming if the background resources are independent of temperature (Fig. 3).

Fishing removes the largest fish in the populations, but this can be counteracted by the changes in growth rates and size-at-age due to physiology physiological temperature dependence (Fig. S15). I.e., increased growth rates can lead to higher abundance of large fish when fishing mortality is higher. Fisheries yield increases with the projected warming only 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 of most size-classes above maturation size (Fig. 3), which is the minimum size targeted by the fishery. While the largest fish can in some cases increase in abundance, especially for cod, they are also rarer in the population and hence this does not counteract the decline in fish that constitute the main catches (Fig. 4).

Warming 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 effort 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), sustaining higher fishing mortalities (Fig. S5). However, the fishery yield at FMSY increases only if temperature acts on physiology alone. Thus, when temperature affects physiological scaling and resource dynamics, the largest relative increases in fisheries yield are acquired in colder temperatures and higher fishing efforts (Fig. S16).

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

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*Figure 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 all simulations.*

*A close up of a map

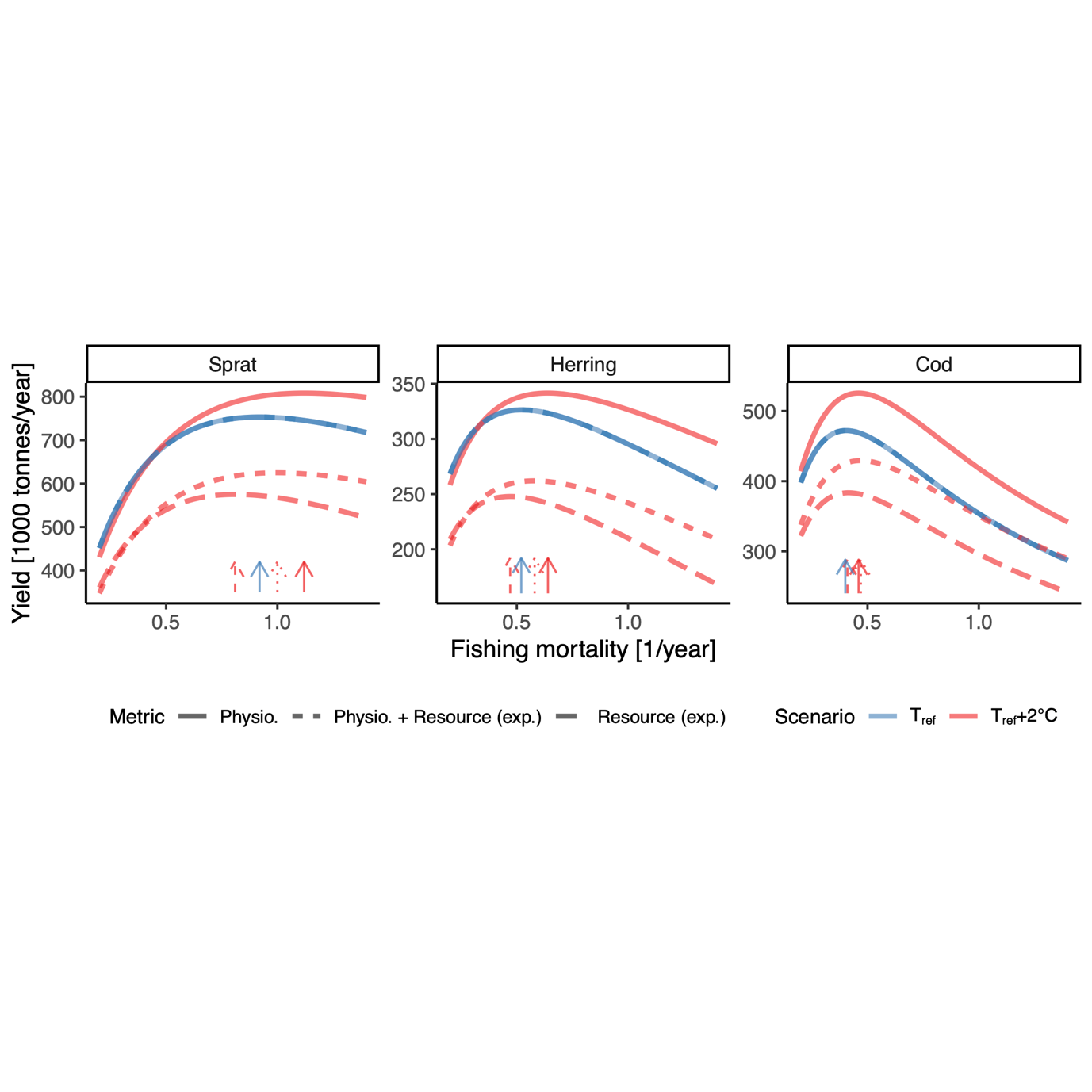
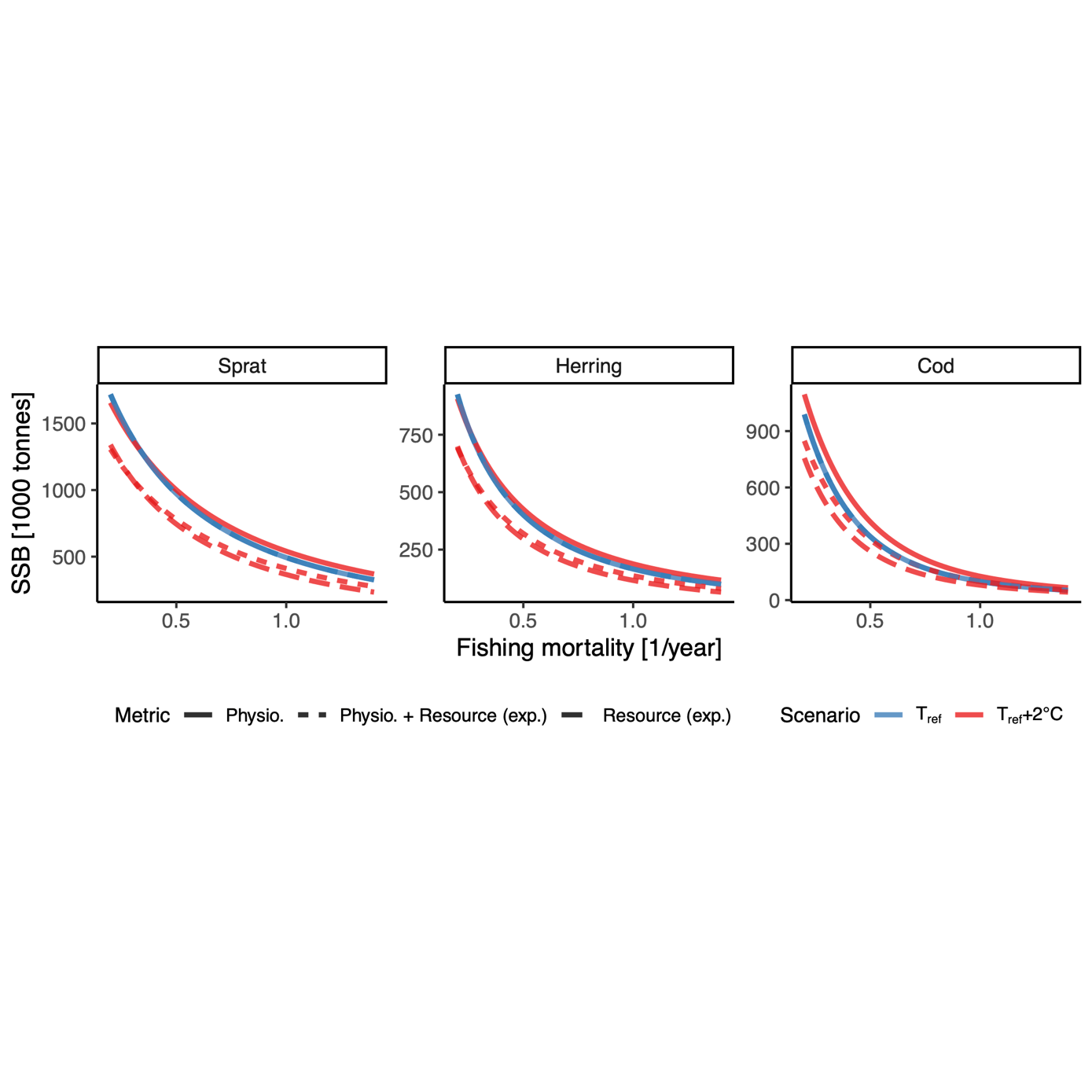
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*Figure 3. Projected abundance-at-weight by species for different scenarios of temperature scaling (indicated by colors) at 2050 assuming fishing mortality held at average FMSY levels (Figure 1A) from different stock assessment estimates and this model. The left column shows size at age relative to a non-warming scenario. Vertical red dotted line indicates weight-at-maturation and horizontal black dotted lines indicate the baseline projection (no warming). The right column shows the absolute abundance-at-weight with the non-warming scenario shown in black. Activation energies are the means of their respective distributions (no uncertainty).*

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*Figure 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) from different stock assessment estimates and this model. The horizontal black line corresponds to no temperature increase after 1997. Activation energies are the means of their respective distributions (no uncertainty).*



*Figure 5. Steady state spawning stock biomass yield (top) and fishery yield 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 and solid lines depicts only physiological temperature scaling. Arrows indicate fishing mortality (F) that lead to maximum sustainable yield. F is held constant at the mean F during calibration (mean 1992-2002) for the two other species while estimating it for one species. Note the different scales between species. Activation energies are the means of their respective distributions (no uncertainty).*

**Discussion**

Using a size-structured and species-resolved food web model, we assessed the impacts of climate warming on individual growth rates, mean population 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), and found that including temperature-dependence of physiological rates lead to increased size-at-age with warming on average, 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, increased juvenile growth and size-at-age does not necessarily lead to larger mean population body size, spawning stock biomass or yields, as mortality (both predation and background) increases.

A strength of mechanistic models is that the underlying causes behind emergent phenomena can be analyzed. Most predictions about declines in body size from mechanistic models find it to be driven by lower food abundance or energy transferred up in the food change, due to a combination of declines in plankton density and shifts towards smaller plankton (Lefort *et al.* 2015; Woodworth-Jefcoats *et al.* 2015, 2019). We also find that these bottom-up driven changes lead to reduction in size-at-age (in particular in smaller individuals) and corresponding changes in mean population body size and abundance of large fish. However, the temperature-size rule (TSR) (Atkinson 1994; Ohlberger 2013), one of several empirical “rules” about the effect of warming in body size, describes an intraspecific response, over ontogeny. In addition to community-wide changes, it is therefore important to also resolve the effects of warming by species as intraspecific responses, which matters for fisheries management. Moreover, the TSR also suggests that development and growth of young individuals is faster with warming if temperatures are not too close to maximum tolerance temperatures (Ohlberger 2013). This can also be predicted form thermal performance curves of body growth, which are unimodal and therefore initial warming is likely beneficial for growth unless e.g. food levels change simultaneously (Jobling 1997; Neuheimer & Grønkjaer 2012). In addition, TSR can also be observed in experiments where food levels are controlled for (but see (Barneche *et al.* 2019)). This implies that the TSR is likely not driven only by lower food availability, as that would not allow smaller individuals to reach larger size-at-age. Inclusion of physiological temperature dependence can be one important factor to consider. This includes mainly higher metabolic costs and also higher feeding rates. In our model, inclusion of physiological temperature dependence leads to projections more in line with general observations, i.e. an in increase in size-at-age that is strongest for small individuals. Increased potential of small individuals to increase their growth rates with warming is not only observed in field data, but can also be predicted from the observation that optimum temperature for growth declines with body size (Morita *et al.* 2010; García García *et al.* 2011; Huss *et al.* 2019). As body size reductions are likely due to an interplay between physiology and ecology (Ohlberger 2013; Audzijonyte *et al.* 2018; Neubauer & Andersen 2019), it is important to consider also physiological responds to temperature, in addition to changing primary production. It is also important to distinguish between body size response at the community level and aggregated intraspecific responses when making predictions at higher levels of biological organization, e.g. mean population or community body size and fisheries yield.

Including physiological temperature-dependence increases realism, both in terms of 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, derived from meta-analyses based on mainly fish 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 temperature 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 we scale physiological processes with. 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 the specific system. However, it becomes 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 the observed spectra is the result of both predation and bottom up processes. As an alternative, the simpler and more conceptual approach used here can be used to scale the carrying capacity or turnover rates of background resources directly and maintain their dynamics. On the downside, this means relying on many major simplifications with respect to resource-dynamics. These may not always be warranted, especially when more detailed predictions are available, but this again depends on the specific aim of the model. 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 again not reflect the actual situation in our case study. We chose these scenarios instead to reflect the often predicted global decline in primary production (Steinacher *et al.* 2010) from coupled climate models, and to contrast reductions in food availability with changes in individual physiology as these former has been linked to declines in community-level body sizes. However also these projections are uncertain, and other studies predict average increases on a global scale, with large regional variations (Sarmiento *et al.* 2004). It is however straightforward to model increases in productivity with our approach by using positive activation energies, if that seems like a more probable scenario in the specific system. 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, see e.g. (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 largely influenced 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 and 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 for sprat in particular. This suggests key processes for their dynamics 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). By contrast, statistical approaches, such as MAR(1) models, can reveal good fit to data and be used for short term predictions (Lindegren *et al.* 2010). Such models have predicted decline in cod productivity (mainly via reduced salinity and offspring survival) (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, 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 and their impacts on population dynamics. Given these difficulties associated with forecasting, it is important to evaluate projections from an ensemble of structurally different models and take advantage of their individual strengths when managing fish communities under climate change.

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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.

**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.

**References**

Andersen, K.H. (2019). *Fish Ecology, Evolution, and Exploitation: A New Theoretical Synthesis*. Princeton University Press.

Andersen, K.H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., *et al.* (2016). Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. *Ann Rev Mar Sci*, 8, 217–241.

Andersen, K.H. & Beyer, J.E. (2006). Asymptotic Size Determines Species Abundance in the Marine Size Spectrum. *The American Naturalist*, 168, 8.

Andersen, K.H. & Beyer, J.E. (2015). Size structure, not metabolic scaling rules, determines fisheries reference points. *Fish Fish*, 16, 1–22.

Andersen, K.Haste. & Pedersen, M. (2009). Damped trophic cascades driven by fishing in model marine ecosystems. *Proceedings of the Royal Society of London B: Biological Sciences*, 277, 795–802.

Atkinson, D. (1994). Temperature and Organism Size—A Biological Law for Ectotherms? In: *Advances in Ecological Research*. Elsevier, pp. 1–58.

Audzijonyte, A., Barneche, D.R., Baudron, A.R., Belmaker, J., Clark, T.D., Marshall, C.T., *et al.* (2018). Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? *Global Ecology and Biogeography*.

Audzijonyte, A., Kuparinen, A., Gorton, R. & Fulton, E.A. (2013). Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. *Biology Letters*, 9, 20121103.

Barange, M., Merino, G., Blanchard, J.L., Scholtens, J., Harle, J., Allison, E.H., *et al.* (2014). Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Clim Change*, 4, 211–216.

Barneche, D.R., Jahn, M. & Seebacher, F. (2019). Warming increases the cost of growth in a model vertebrate. *Functional Ecology*, 33, 1256–1266.

Barnes, C., Irigoien, X., De Oliveira, J.A.A., Maxwell, D. & Jennings, S. (2011). Predicting marine phytoplankton community size structure from empirical relationships with remotely sensed variables. *J Plankton Res*, 33, 13–24.

Bartolino, V., Margonski, P., Lindegren, M., Linderholm, H.W., Cardinale, M., Rayner, D., *et al.* (2014). Forecasting fish stock dynamics under climate change: Baltic herring (Clupea harengus) as a case study. *Fisheries Oceanography*, 23, 258–269.

Baudron, A.R., Needle, C.L., Rijnsdorp, A.D. & Marshall, C.T. (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20, 1023–1031.

Belkin, I.M. (2009). Rapid warming of large marine ecosystems. *Progress in Oceanography*, 81, 207–213.

Bernhardt, J.R., Sunday, J.M. & O’Connor, M.I. (2018). Metabolic Theory and the Temperature-Size Rule Explain the Temperature Dependence of Population Carrying Capacity. *The American Naturalist*, 192, 687–697.

Björnsson, B. (2001). Optimal temperature for growth and feed conversion of immature cod (Gadus morhua L.). *ICES Journal of Marine Science*, 58, 29–38.

Blanchard, J.L., Andersen, K.H., Scott, F., Hintzen, N.T., Piet, G. & Jennings, S. (2014). Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model. *Journal of Applied Ecology*, 51, 612–622.

Blanchard, J.L., Heneghan, R.F., Everett, J.D., Trebilco, R. & Richardson, A.J. (2017). From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems. *Trends in Ecology & Evolution*, 32, 174–186.

Blanchard, J.L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J.I., *et al.* (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 367, 2979–2989.

Brett, J.R., Shelbourn, J.E. & Shoop, C.T. (1969). Growth Rate and Body Composition of Fingerling Sockeye Salmon, Oncorhynchus nerka, in relation to Temperature and Ration Size. *J. Fish. Res. Bd. Can.*, 26, 2363–2394.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004a). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004b). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Byrd, R.H., Lu, Peihuang., Nocedal, Jorge. & Zhu, Ciyou. (1995). A Limited Memory Algorithm for Bound Constrained Optimization. *SIAM J. Sci. Comput.*, 16, 1190–1208.

Canales, T.M., Law, R. & Blanchard, J.L. (2016). Shifts in plankton size spectra modulate growth and coexistence of anchovy and sardine in upwelling systems. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 611–621.

Casini, M., Hjelm, J., Molinero, J.-C., Lövgren, J., Cardinale, M., Bartolino, V., *et al.* (2009). Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences, USA*, 106, 197–202.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Deng Palomares, M.L., *et al.* (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3, 254–258.

Clarke, A. & Johnston, N.M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68, 893–905.

Daufresne, M., Lengfellner, K. & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences, USA*, 106, 12788–12793.

Downs, C.J., Hayes, J.P. & Tracy, C.R. (2008). Scaling metabolic rate with body mass and inverse body temperature: A test of the Arrhenius fractal supply model. *Functional Ecology*, 22, 239–244.

Englund, G., Öhlund, G., Hein, C.L. & Diehl, S. (2011). Temperature dependence of the functional response. *Ecology Letters*, 14, 914–921.

Forster, J., Hirst, A.G. & Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *PNAS*, 109, 19310–19314.

Free, C.M., Thorson, J.T., Pinsky, M.L., Oken, K.L., Wiedenmann, J. & Jensen, O.P. (2019). Impacts of historical warming on marine fisheries production. *Science*, 363, 979–983.

García García, B., Cerezo Valverde, J., Aguado-Giménez, F., García García, J. & Hernández, M.D. (2011). Effect of the interaction between body weight and temperature on growth and maximum daily food intake in sharpsnout sea bream (Diplodus puntazzo). *Aquaculture International*, 19, 131–141.

Gårdmark, A., Casini, M., Huss, M., van Leeuwen, A., Hjelm, J., Persson, L., *et al.* (2015). Regime shifts in exploited marine food webs: detecting mechanisms underlying alternative stable states using size-structured community dynamics theory. *Phil. Trans. R. Soc. B*, 370, 20130262.

Gilbert, B., Tunney, T.D., McCann, K.S., DeLong, J.P., Vasseur, D.A., Savage, V.M., *et al.* (2014). A bioenergetic framework for the temperature dependence of trophic interactions. *Ecology Letters*, 17, 902–914.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001). Effects of size and temperature on metabolic rate. *Science*, 2248–2251.

Handeland, S.O., Imsland, A.K. & Stefansson, S.O. (2008). The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. *Aquaculture*, 283, 36–42.

Hartvig, M., Andersen, K.H. & Beyer, J.E. (2011). Food web framework for size-structured populations. *Journal of Theoretical Biology*, 272, 113–122.

Huey, R.B. & Kingsolver, J.G. (2019). Climate Warming, Resource Availability, and the Metabolic Meltdown of Ectotherms. *The American Naturalist*, 194, E140–E150.

Huss, M., Lindmark, M., Jacobson, P., van Dorst, R.M. & Gårdmark, A. (2019). Experimental evidence of gradual size‐dependent shifts in body size and growth of fish in response to warming. *Glob Change Biol*, gcb.14637.

ICES. (2013). *Report of the Baltic Fisheries Assessment Working Group (WGBFAS)* ( No. ICES CM 2013/ACOM:10.). 10-17 April 2013 ICES Headquarters, Copenhagen.

ICES. (2015). *Report of the Baltic Fisheries Assessment Working Group (WGBFAS)* ( No. ICES CM 2015/ACOM:10). 14-21 April 2015 ICES Headquarters, Copenhagen.

Jacobsen, N.S., Burgess, M.G. & Andersen, K.H. (2017). Efficiency of fisheries is increasing at the ecosystem level. *Fish and Fisheries*, 18, 199–211.

Jobling, M. (1997). Temperature and growth: modulation of growth rate via temperature change. In: *Global Warming: Implications for Freshwater and Marine Fish* (eds. Wood, C.M. & McDonald, D.G.). Cambridge University Press, Cambridge, pp. 225–254.

Lefevre, S., McKenzie, D.J. & Nilsson, G.E. (2018). In modelling effects of global warming, invalid assumptions lead to unrealistic projections. *Global Change Biology*, 24, 553–556.

Lefort, S., Aumont, O., Bopp, L., Arsouze, T., Gehlen, M. & Maury, O. (2015). Spatial and body-size dependent response of marine pelagic communities to projected global climate change. *Global Change Biology*, 21, 154–164.

Lindegren, M., Möllmann, C., Nielsen, A., Brander, K., MacKenzie, B.R. & Stenseth, N.Chr. (2010). Ecological forecasting under climate change: the case of Baltic cod. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2121–2130.

Lotze, H.K., Tittensor, D.P., Bryndum-Buchholz, A., Eddy, T.D., Cheung, W.W.L., Galbraith, E.D., *et al.* (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences*, 116, 12907–12912.

Mackenzie, B.R., Gislason, H., Möllmann, C. & Köster, F.W. (2007). Impact of 21st century climate change on the Baltic Sea fish community and fisheries. *Global Change Biology*, 13, 1348–1367.

MacKenzie, B.R. & Köster, F.W. (2004). Fish Production and Climate: Sprat in the Baltic Sea. *Ecology*, 85, 784–794.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H. & Warner, R.R. (2015). Marine defaunation: Animal loss in the global ocean. *Science*, 347.

Mion, M., Thorsen, A., Vitale, F., Dierking, J., Herrmann, J.P., Huwer, B., *et al.* (2018). Effect of fish length and nutritional condition on the fecundity of distressed Atlantic cod *Gadus morhua* from the Baltic Sea: POTENTIAL FECUNDITY OF BALTIC *G. MORHUA*. *Journal of Fish Biology*, 92, 1016–1034.

Möllmann, C., Diekmann, R., Müller‐Karulis, B., Kornilovs, G., Plikshs, M. & Axe, P. (2009). Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Global Change Biology*, 15, 1377–1393.

Morán, X.A.G., López‐Urrutia, Á., Calvo‐Díaz, A. & Li, W.K.W. (2010). Increasing importance of small phytoplankton in a warmer ocean. *Global Change Biology*, 16, 1137–1144.

Morita, K., Fukuwaka, M., Tanimata, N. & Yamamura, O. (2010). Size-dependent thermal preferences in a pelagic fish. *Oikos*, 119, 1265–1272.

Neubauer, P. & Andersen, K.H. (2019). Thermal performance of fish is explained by an interplay between physiology, behaviour and ecology. *Conserv Physiol*, 7.

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K.H., Andersen, N.G., Niiranen, S., *et al.* (2019). Feeding and growth of Atlantic cod (Gadus morhua L.) in the eastern Baltic Sea under environmental change. *ICES Journal of Marine Science*, fsz224.

Neuheimer, A.B. & Grønkjaer, P. (2012). Climate effects on size-at-age: growth in warming waters compensates for earlier maturity in an exploited marine fish. *Global Change Biology*, 18, 1812–1822.

Neuheimer, A.B., Thresher, R.E., Lyle, J.M. & Semmens, J.M. (2011). Tolerance limit for fish growth exceeded by warming waters. *Nature Climate Change*, 1, 110–113.

Ohlberger, J. (2013). Climate warming and ectotherm body size – from individual physiology to community ecology. *Functional Ecology*, 27, 991–1001.

Orio, A., Bergström, U., Florin, A.-B., Lehmann, A., Šics, I. & Casini, M. (2019). Spatial contraction of demersal fish populations in a large marine ecosystem. *Journal of Biogeography*, 46, 633–645.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, 39, 175–192.

Pauly, D. & Cheung, W.W.L. (2018). Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. *Global Change Biology*, 24, e15–e26.

Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L. & Levin, S.A. (2013). Marine Taxa Track Local Climate Velocities. *Science*, 341, 1239–1242.

Pontavice, H. du, Gascuel, D., Reygondeau, G., Maureaud, A. & Cheung, W.W.L. (2019). Climate change undermines the global functioning of marine food webs. *Global Change Biology*.

R Core Team. (2018). *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing*. Vienna, Austria.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmuller, F., Vucic-Pestic, O., *et al.* (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 367, 2923–2934.

Reum, J.C.P., Blanchard, J.L., Holsman, K.K., Aydin, K. & Punt, A.E. (2019). Species‐specific ontogenetic diet shifts attenuate trophic cascades and lengthen food chains in exploited ecosystems. *Oikos*, 128, 1051–1064.

Righton, D.A., Andersen, K.Haste., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., *et al.* (2010). Thermal niche of Atlantic cod Gadus morhua: limits, tolerance and optima. *Marine Ecology Progress Series*, 420, 1–13.

van Rijn, I., Buba, Y., DeLong, J., Kiflawi, M. & Belmaker, J. (2017). Large but uneven reduction in fish size across species in relation to changing sea temperatures. *Global Change Biology*, 23, 3667–3674.

Rohatgi, A. (2012). *WebPlotDigitalizer: HTML5 based online tool to extract numerical data from plot images. Version 4.1. [WWW document] URL https://automeris.io/WebPlotDigitizer (accessed on January 2019).*

Sarmiento, J.L., Slater, R., Barber, R., Bopp, L., Doney, S.C., Hirst, A.C., *et al.* (2004). Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles*, 18, n/a–n/a.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004). Effects of body size and temperature on population growth. *The American Naturalist*, 163, 429–441.

Scott, F., Blanchard, J. & Andersen, K. (2019). *mizer: Multi-Species sIZE Spectrum Modelling in R*. R. .

Scott, F., Blanchard, J.L. & Andersen, K.Haste. (2014). mizer: An R package for multispecies, trait-based and community size spectrum ecological modelling. *Methods in Ecology and Evolution*, 5, 1121–1125.

Scott, F., Blanchard, J.L. & Andersen, K.Haste. (2018). Multispecies, trait and community size spectrum ecological modelling in R ( mizer ), 1–87.

Sheridan, J.A. & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1, 401–406.

Spence, M.A., Blackwell, P.G., Blanchard, J.L. & Shuter, B. (2016). Parameter uncertainty of a dynamic multispecies size spectrum model \textlesssup\textgreater1\textless/sup\textgreater. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 589–597.

Steinacher, M., Joos, F., Frolicher, T.L., Bopp, L., Cadule, P., Cocco, V., *et al.* (2010). Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences*, 7.

Svedäng, H. & Hornborg, S. (2014). Selective fishing induces density-dependent growth. *Nature Communications*, 5, 4152.

Szuwalski, C.S., Burgess, M.G., Costello, C. & Gaines, S.D. (2017). High fishery catches through trophic cascades in China. *Proceedings of the National Academy of Sciences*, 114, 717–721.

Thorson, J.T., Munch, S.B., Cope, J.M. & Gao, J. (2017). Predicting life history parameters for all fishes worldwide. *Ecological Applications*, 27, 2262–2276.

Thresher, R.E., Koslow, J.A., Morison, A.K. & Smith, D.C. (2007). Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proceedings of the National Academy of Sciences, USA*, 104, 7461–7465.

Ursin, E. (1967). A Mathematical Model of Some Aspects of Fish Growth, Respiration, and Mortality. *Journal of the Fisheries Research Board of Canada*, 24, 2355–2453.

Ursin, E. (1973). On the prey size preferences of cod and dab. *Meddelelser fra Danmarks Fiskeri-og Havun- dersgelser*, 7:8598.

Woodworth-Jefcoats, P.A., Blanchard, J.L. & Drazen, J.C. (2019). Relative Impacts of Simultaneous Stressors on a Pelagic Marine Ecosystem. *Frontiers in Marine Science*, 6.

Woodworth-Jefcoats, P.A., Polovina, J.J., Dunne, J.P. & Blanchard, J.L. (2013). Ecosystem size structure response to 21st century climate projection: large fish abundance decreases in the central North Pacific and increases in the California Current. *Global Change Biology*, 19, 724–733.

Woodworth-Jefcoats, P.A., Polovina, J.J., Howell, E.A. & Blanchard, J.L. (2015). Two takes on the ecosystem impacts of climate change and fishing: Comparing a size-based and a species-based ecosystem model in the central North Pacific. *Progress in Oceanography*, 138, 533–545.

Yvon‐Durocher, G., Montoya, J.M., Trimmer, M. & Woodward, G. (2011). Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Global Change Biology*, 17, 1681–1694.