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

3

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26 **Abstract**

27 Resolving the combined effect of climate warming and exploitation in a food web context is
28 key for predicting future biomass production, size-structure, and potential yields of marine
29 fishes. Previous studies based on mechanistic size-based food web models have found that
30 bottom-up processes are important drivers of size-structure and fisheries yield in changing
31 climates. However, we know less about the joint effects of ‘bottom-up’ and ‘top-down’ effects
32 of temperature: how do temperature effects propagate from individual-level physiology
33 through food webs and alter the size-structure of exploited species in a community? Here we
34 assess how a species-resolved size-based food web is affected by warming through both these
35 pathways, and by exploitation. We parameterize a dynamic size spectrum food web model
36 inspired by the offshore Baltic Sea food web, and investigate how individual growth rates, size-
37 structure, relative abundances of species and yields are affected by warming. The magnitude
38 of warming is based on projections by the regional coupled model system RCA4-NEMO and
39 the RCP 8.5 emission scenario, and we evaluate different scenarios of temperature dependence
40 on fish physiology and resource productivity. When accounting for temperature-effects on
41 physiology in addition to on basal productivity, projected size-at-age in 2050 increases on
42 average for all fish species, mainly for young fish, compared to scenarios without warming. In
43 contrast, size-at-age decreases when temperature affects resource dynamics only, and the
44 decline is largest for young fish. Faster growth rates due to warming, however, do not always
45 translate to larger yields, as lower resource carrying capacities with increasing temperature tend
46 to result in declines in the abundance of larger fish and hence spawning stock biomass – the
47 part of the population exposed to fishing. These results show that to understand how global
48 warming impacts the size structure of fish communities, both direct metabolic effects and
49 indirect effects of temperature via basal resources must be accounted for.

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51 **Key words**

52 Body size, climate change, fisheries yield, food web, metabolic theory, multi species, size

53 spectrum

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76 **Introduction**

77 Climate change affects aquatic food webs directly by affecting species' distribution (Pinsky *et al.* 2013), abundance (McCauley *et al.* 2015), body size (Daufresne *et al.* 2009; Baudron *et al.* 2014), and ecosystem function (Pontavice *et al.* 2019). Global retrospective analysis of 80 warming and fish population dynamics has revealed that productivity (population growth at a 81 given biomass) of scientifically assessed fish populations across ecoregions has already 82 declined by ~4% on average between 1930 and 2010 due to climate change (Free *et al.* 2019). 83 These results are also matched in magnitude and direction by projections from an ensemble of 84 mechanistic ecosystem models, which predict ~5% decline in animal biomass for every 1 °C of 85 warming, especially at higher trophic levels (Lotze *et al.* 2019). Across a range of process- 86 based ecosystem models, declines in productivity of fish stocks and abundance of large fish, 87 have been mostly linked to changes in primary production or zooplankton abundance 88 (Blanchard *et al.* 2012; Woodworth-Jefcoats *et al.* 2013, 2015; Barange *et al.* 2014; Lotze *et al.* 2019). However, even in areas where warming is predicted to have positive effects on 89 primary production, fish productivity does not appear to increase (Free *et al.* 2019). This 90 suggests that fish population dynamics might be strongly influenced by other factors, such as 91 temperature-driven changes in recruitment, mortality or somatic growth (Free *et al.* 2019), yet 92 the driving mechanisms remain poorly understood. 93

94 Global warming is also predicted to cause reductions in the adult body size of organisms, 95 and this is often referred to as the third universal response to warming (Daufresne *et al.* 2009; 96 Sheridan & Bickford 2011; Forster *et al.* 2012). It is often attributed to the temperature-size 97 rule (TSR) is observed in a wide range of ectotherms (Forster *et al.* 2012). This is an 98 intraspecific rule stating that individuals reared at warmer temperatures develop faster, mature 99 earlier but reach smaller adult body sizes (Atkinson 1994; Ohlberger 2013). In line with TSR 100 expectations, faster growth rates or larger size-at-age of young life stages are commonly found

101 in both experimental, field data and modelling studies (Thresher *et al.* 2007; Neuheimer *et al.*
102 2011; Ohlberger *et al.* 2011; Neuheimer & GrønkJaer 2012; Baudron *et al.* 2014; Huss *et al.*
103 2019; Van Dorst *et al.* 2019). Similarly, declines in maximum or asymptotic body size of fish
104 have been reported to correlate with warming trends for a number of commercially exploited
105 marine fishes (Baudron *et al.* 2014; van Rijn *et al.* 2017; Ikpewe *et al.* 2020). However, in
106 intensively fished stocks, observed adult body sizes can decrease also for other reasons,
107 including direct removals of large fish, or evolution towards earlier maturing and fast growth
108 in response to fishing (Jorgensen *et al.* 2007; Audzijonyte *et al.* 2013). Moreover, decreasing
109 adult fish size in warming waters is by far not universal. For example, no clear negative effects
110 of warming on the body size or growth of large fish could be found in a recent experimental
111 study (Barneche *et al.* 2019), or in a semi-controlled lake heating experiment (Huss *et al.* 2019).
112 Similarly, across 335 coastal fish species mean species body size was similarly likely to be
113 larger or smaller in warmer waters (Audzijonyte *et al.* 2020). Also Tu *et al.* (2018) found that
114 temperature had a relatively minor effect on fish size structure, and even when combined with
115 fishing, only 44% of variation in size structure could be explained. Thus, the effects of
116 temperature on body sizes may be more complex than often depicted, and we still do not fully
117 understand the mechanisms by which temperature affects growth and body size over ontogeny
118 (Ohlberger 2013; Audzijonyte *et al.* 2019). Increasing our understanding of these mechanisms
119 is important because body size is a key trait in aquatic ecosystems (Andersen *et al.* 2016) and
120 warming-induced changes in growth and size-at-age of fish populations could have
121 implications not only for biomass and productivity, but also ecosystem structure and stability
122 (Audzijonyte *et al.* 2013).

123 Physiologically structured models can address the complex interplay of direct and indirect
124 temperature impacts on food webs, as they account for the food and size dependence of body
125 growth through ecological interactions using bioenergetic principles. Recent applications have

126 demonstrated decreasing maximum body sizes in fish communities due to changes in plankton
127 abundance or size (Woodworth-Jefcoats *et al.* 2019). Similar body size responses emerge in
128 models that focus on temperature-dependence of physiological processes, such as metabolism
129 and feeding rates (Lefort *et al.* 2015; Woodworth-Jefcoats *et al.* 2019), but it remains unclear
130 to what extent these community body size shifts are driven by declining abundance of large
131 fish versus changes in size-at-age across a range of ages.

132 To explore how direct and indirect effects of warming impact marine food web size structure
133 and fisheries yields, we evaluate the impacts of temperature-driven changes in resource
134 productivity and individual fish physiology using an example case of the Baltic Sea. The Baltic
135 Sea constitutes a great example system, as it is a relatively well understood and species poor
136 system (Mackenzie *et al.* 2007; Casini *et al.* 2009) that also is one of the warming hotspots
137 globally (Belkin 2009). By using a temperature-dependent size spectrum model we analyse a
138 set of different scenarios where either fish physiology, basal resources, or both depend on
139 temperature, and contrast these scenarios to one another and to non-warming scenarios. We
140 investigate the mechanisms of warming effects on body growth trajectories, average body
141 sizes, population size-structure and fisheries reference points and find that not only the
142 magnitude of projected fish size-at-age, but also the effect of size, depend on whether
143 temperature-dependence of physiological processes is accounted for or not. Most importantly,
144 increased growth rates (mainly for juveniles) generally do not compensate for lower overall
145 adult biomasses that is due to declining resource levels, such that warming often causes
146 declining mean body sizes of fish populations and lower fisheries yields.

147

148 **Materials and Methods**

149 *Food web*

150 We developed a multi-species size spectrum model (MSSM) (Scott *et al.* 2014), parameterized
151 to represent a simplified version of the food web in the offshore pelagic south-central Baltic
152 Sea ecosystem (Baltic proper) (ICES sub divisions 25-29+32, Fig. S2, *Supporting*
153 *Information*). This size structured food web is here characterized by three fish species: Atlantic
154 cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), and two
155 dynamic background resource spectra constituting food for small fish (pelagic and benthic
156 resources). In this part of the Baltic Sea, these fish species are dominant in terms of biomass,
157 they are the most important species commercially and they all have analytical stock
158 assessments (ICES 2021). The pelagic background resource spectrum represents mainly phyto-
159 and zooplankton while the benthic background resource spectrum represents benthic
160 invertebrates, gobiidae and small flatfish.

161

162 ***Size spectrum model***

163 The model is based on source code for the multi-species implementation of size spectrum
164 models in the ‘R’-package *mizer* (v1.1) (Blanchard *et al.* 2014; Scott *et al.* 2014; R Core Team
165 2020), which has been extended to include multiple background resources (Audzijonyte *et al.*,
166 *unpublished*) and temperature-scaling of key physiological processes. In this section we
167 describe the key elements of the MSSM using the same notation when possible as in previous
168 multispecies *mizer* models for consistency (Blanchard *et al.* 2014; Scott *et al.* 2014, 2018).

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

$$173 \quad \frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w)N_i(w)}{\partial w} = -\mu_i(w)N_i(w) \quad (1)$$

174 where $g_i(w)$ (g year^{-1}) is somatic growth (dependent on the availability of food) and $\mu_i(w)$
 175 (year^{-1}) is total mortality. At the boundary weight (w_0 , egg size), the influx of individuals is
 176 given by recruitment. Total mortality is the sum of the background-, starvation-, fishing-, and
 177 predation mortality. The constant species-specific allometric background mortality ($\mu_{bac,i}$)
 178 depends on the asymptotic weight of a species W_i^{n-1} and is given by:

$$179 \quad \mu_{bac,i} = \mu_0 W_i^{n-1} \quad (2)$$

180 where n is the mass-exponent of maximum consumption rate (Hartvig *et al.* 2011) and μ_0 is an
 181 allometric constant. Starvation mortality ($\mu_{stv,i}$) is assumed to be proportional to energy
 182 deficiency (defined in Eq. 11) and inversely proportional to body mass (weight, w), and is
 183 defined as:

$$184 \quad \mu_{stv,i}(w) = \begin{cases} 0 & \alpha f_i(w) h_i w^n > k_{met,i} w^p \\ \frac{k_{met,i} w^p - \alpha f_i(w) h_i w^n}{\xi w} & otherwise \end{cases} \quad (3)$$

185 where ξ , the fraction of energy reserves, is 0.1 (Hartvig *et al.* 2011). Instantaneous fishing
 186 mortality ($\mu_{fis,i}$) (year^{-1}) is defined as:

$$187 \quad \mu_{fis,i}(w_i) = S_i(w) F_i \quad (4)$$

188 where S_i is the selectivity (by default knife-edge selectivity is assumed with a weight at first
 189 catch corresponding to weight at maturation), and F_i is fishing mortality. Predation mortality
 190 ($\mu_{pre,j}$) for a prey species (or resource) j with weight w_j equals the amount consumed by
 191 predator species i with weight w_i :

$$192 \quad \mu_{pre,j}(w_j) = \sum_i \int \phi_i \left(\frac{w_j}{w_i} \right) (1 - f_i(w_i)) \gamma_i w_i^q \theta_{i,j} N_i(w_i) dw \quad (5)$$

193 where $\theta_{i,j}$ is the non-size based preference of species i on species j , and ϕ_j describes the
 194 weight-based preference from the log-normal selection model (see below) (Ursin 1973).
 195 Satiation is represented in the model with a Holling functional response type II, which
 196 determines the feeding level $f_i(w)$:

197
$$f_i(w) = \frac{E_{enc,i}(w)}{E_{enc,i}(w) + h_i w^n} \quad (6)$$

198 describing the level of satiation (between 0 and 1). $h_i w^n$ is the allometric maximum
 199 consumption rate and $E_{enc,i}(w)$ is the encountered food (mass per time). The amount of
 200 encountered food for a predator of body weight w is given by the available food in the system
 201 multiplied with the search volume, γ_i . Here, available food, $E_{ava,i}$, is the integral of the biomass
 202 of all prey species (j) and background resources (R) that falls within the prey preference
 203 ($\theta_{i,j}, \theta_{i,R}$) and size-selectivity (ϕ_i) of predator species i :

204
$$E_{ava,i}(w) = \int \left(\sum_R \theta_{i,R} N_R(w_R) + \sum_j \theta_{i,j} N_j(w_j) \right) \phi_i \left(\frac{w_j}{w_i} \right) w_j dw_p \quad (7)$$

205 where w_j is the weight of prey, $\theta_{i,R}$ is the preference of species i for resource R , and j indicates
 206 prey (fish) species. Note that in contrast to other MSSMs (Blanchard *et al.* 2014) species have
 207 a preference for the background resources to account for them feeding differently on benthic
 208 and pelagic resources, but assume no preference in terms of the interactions among the size-
 209 structured fish species (all terms in the interaction matrix are identical and equal to 1). This is
 210 for simplicity, as the body size-only prey selection and encounter rate capture the important
 211 predation interactions in this system (as inferred from independent stomach data, see model
 212 calibration, *Supporting Information*), the species largely occupy similar spatial areas within the
 213 study area during the time period of the model calibration (Fig. S2), and we do not explicitly
 214 model any other prey sources these species could select. The size-selectivity of feeding,
 215 $\phi_i \left(\frac{w_j}{w_i} \right)$, is given by a log-normal selection function (Ursin 1967):

216
$$\phi_i \left(\frac{w_j}{w_i} \right) = \exp \left[\frac{- \left(\ln \left(\frac{w_i}{(w_j \beta_i)} \right) \right)^2}{2 \sigma_i^2} \right] \quad (8)$$

217 where parameters β_i and σ_i are the preferred predator-prey mass ratio and the standard
 218 deviation of the log-normal distribution, respectively. The amount of available prey of suitable
 219 sizes (Eq. 7) is multiplied with the allometric function describing the search volume ($\gamma_i w^q$),
 220 where the allometric coefficient is calculated as:

$$221 \quad \gamma_i(f_0) = \frac{f_0 h_i \beta_i^{2-\lambda} \exp\left(-\frac{(\lambda-2)^2 \sigma_i^2}{2}\right)}{(1-f_0) \sqrt{2\pi} \kappa \sigma_i} \quad (9)$$

222 (Andersen & Beyer 2006; Scott *et al.* 2018), to give the actual biomass of food encountered,
 223 $E_{enc,i}(w)$:

$$224 \quad E_{enc,i}(w) = \gamma_i w^q E_{ava,i}(w) \quad (10)$$

225 where q is the size-scaling exponent of the search volume. The rate at which food is consumed
 226 is given by the product $f_i(w) h_i w^n$, which is assimilated with efficiency α and used to cover
 227 metabolic costs. Metabolic costs scale allometrically as $k_{met,i} w^p$. The net energy, $E_{net,i}$, is
 228 thus:

$$229 \quad E_{net,i}(w) = \max(0, \alpha f_i(w) h_i w^n - k_{met,i} w^p) \quad (11)$$

230 which is allocated to growth or reproduction. The allocation to reproduction (ψ_i) increases
 231 smoothly from 0 around the weight maturation, $w_{mat,i}$, to 1 at the asymptotic weight, W_i ,
 232 according to the function:

$$233 \quad \psi_i = \left[1 + \left(\frac{w}{w_{mat,i}}\right)^{-m}\right]^{-1} \left(\frac{w}{W_i}\right)^{1-n} \quad (12)$$

234 (Andersen 2019). This function results in the growth rate, $g_i(w)$,

$$235 \quad g_i(w) = E_{net,i}(w) (1 - \psi_i(w)) \quad (13)$$

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

239 efficiency factor (ϵ , *erepro*) divided by the egg weight, w_0 , and the factor 2, assuming only
 240 females reproduce:

$$241 \quad R_{phy,i} = \frac{\epsilon}{2w_0} \int N_{i(w)} E_{net,i}(w) \psi_i(w) dw \quad (14)$$

242 This total egg production (or physiological recruitment, $R_{phy,i}$) results in recruits via a
 243 Beverton-Holt stock recruit relationship, such that recruitment approaches a maximum
 244 recruitment for a species i ($R_{max,i}$), as the egg production increases,

$$245 \quad R_i = R_{max,i} \frac{R_{P,i}}{R_{P,i} + R_{max,i}} \quad (15)$$

246 where $R_{max,i}$ is treated as a free parameter and is estimated in the calibration process by
 247 minimizing the residual sum of squares between spawning stock biomass from stock
 248 assessments and the MSSM. The calibration also ensures that the species coexist in the model
 249 (Jacobsen *et al.* 2017).

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

$$252 \quad \frac{\partial N_R(w, t)}{\partial t} = r_0 w^{p-1} [\kappa w^{-\lambda}(w) - N_R(w, t)] - \mu_{p,R}(w) N_R(w, t) \quad (16)$$

253 where $r_0 w^{p-1}$ is the population regeneration rate, $\kappa w^{-\lambda}$ is the carrying capacity of the
 254 background resource and $\mu_{pre,R}$ is predation mortality on resource spectrum R , and λ is defined
 255 as $-2 - q + n$ (Andersen 2019).

256

257 **Temperature dependence**

258 Temperature affects the rate of metabolism (Clarke & Johnston 1999; Gillooly *et al.* 2001),
 259 and thus also other biological rates (Englund *et al.* 2011; Rall *et al.* 2012; Thorson *et al.* 2017).

260 We scale rates of individual metabolism ($k_{met,i} w^p$) (in *mizer*, this represents all metabolic
 261 costs, i.e., standard, activity and digestion. Henceforth, we assume $k_{met,i} w^p$ scales as standard

262 metabolic rate and refer to it as metabolism or metabolic rate), maximum consumption ($h_i w^n$),
263 search volume ($\gamma_i w^q$) and background mortality ($\mu_0 W_i^{n-1}$) with temperature using an
264 Arrhenius temperature correction factor:

$$265 \quad r(T) = e^{\frac{A_v(T-T_{ref})}{kTT_{ref}}} \quad (17)$$

266 where A_v is the activation energy (eV) for individual rate v , T is temperature (K), T_{ref} is the
267 reference temperature (here 283.27 K, the temperature where the Arrhenius correction factor
268 equals 1), and k is Boltzmann's constant in eV K^{-1} ($= 8.617 \times 10^{-5} \text{ eV K}^{-1}$). We chose an
269 exponential temperature dependence as it provides a good statistical fit to data, is widely
270 adopted, and because we assume that the projected change in ocean temperature in the studied
271 time range does not lead to temperatures above physiological optima (e.g. (Righton *et al.* 2010)
272 as an example for cod), where physiological rates might be expected to decline. While
273 temperature likely affects other physiological processes as well (such as cost of growth
274 (Barneche *et al.* 2019) or food conversion efficiency (Handeland *et al.* 2008)), we focus on
275 metabolism, maximum consumption, search volume and mortality, as their temperature
276 dependencies are relatively well documented (Pauly 1980; Brown *et al.* 2004; Dell *et al.* 2011;
277 Englund *et al.* 2011; Thorson *et al.* 2017; Lindmark *et al.* 2021).

278 Temperature also affects the amount of available background resources, via the same type
279 of individual-level processes. In most size spectrum models to date, climate affects primary
280 production (and in some cases zooplankton), and this is modelled by forcing the background
281 spectra to observed abundance-at-size of plankton from either remotely sensed variables such
282 as chlorophyll-a or from output from earth-system models (Blanchard *et al.* 2012; Barange *et al.*
283 *et al.* 2014; Canales *et al.* 2016; Reum *et al.* 2019; Woodworth-Jefcoats *et al.* 2019). An
284 alternative approach is to force simulation with the growth rate or net primary production
285 (Jennings & Collingridge 2015; Galbraith *et al.* 2017). These differences have been highlighted

286 as a key source of ecosystem model uncertainties observed in global applications of size-
287 structured models (Lotze *et al.* 2019; Heneghan *et al.* 2021). In order to integrate the emergent
288 responses of climate warming effects on “bottom-up” (e.g., background spectra) and “top-
289 down” (physiology) processes, we apply the temperature scaling to the terms of the background
290 resource’s semi-chemostat growth equation (Eq. 16), i.e., their biomass regeneration rate and
291 carrying capacity. We use the same Arrhenius correction factor with activation energy A_r ,
292 where r refers to background resource parameter. We assume that as temperature goes up, the
293 carrying capacity (κw^λ) declines at the same rate as population regeneration ($r_0 w^{p-1}$) rate
294 increases (Savage *et al.* 2004; Gilbert *et al.* 2014), i.e. κ scales with temperature in proportion
295 to $e^{\frac{-A_r(T-T_{ref})}{kTT_{ref}}}$. This is based on the metabolic theory of ecology (MTE), which predicts that if
296 nutrient levels are constant, higher respiration rates lead to lower biomasses at carrying
297 capacity (Savage *et al.* 2004; Bernhardt *et al.* 2018). Corroborating this assumption is the
298 common prediction that primary production overall declines under global warming (though the
299 trends vary regionally) (Steinacher *et al.* 2010; Heneghan *et al.* 2019; Kwiatkowski *et al.* 2019).
300 Our implementation of temperature impacts on the background spectrum assumes that its size
301 structure is not affected by the temperature (the slope of the spectrum does not change) – only
302 the overall level of background resources, in order to simplify the analyses. As an example,
303 using the average activation energy for resource carrying capacity (see next paragraph), the
304 elevation of our background resource spectra (abundance at the geometric mean weight,
305 (Heneghan *et al.* 2019)), declines with 8.7% with a 1°C increase in temperature, which is line
306 with previous studies (Free *et al.* 2019; Heneghan *et al.* 2019; Lotze *et al.* 2019).

307 As activation energies vary substantially between processes, species and taxonomic groups
308 and are estimated with uncertainty, we parameterized 200 projections of the food web model
309 using randomly sampled activation energies from normal distributions with rate-specific means

310 and standard deviations. For metabolism and maximum consumption, we acquired means and
311 standard deviations from the posterior distributions in (Lindmark *et al.* 2021) (note we assume
312 search volume scales identically as maximum consumption and mortality as metabolism). The
313 normal distributions describing activation energies for background resource parameters were
314 defined by a mean equal to the point estimate from a linear regression of natural log of growth
315 rate as a function of Arrhenius temperature ($1/kT$ [eV^{-1}]) from experimental data in Savage
316 *et al.* (2004) (pooling protists, algae and zooplankton, extracted using the software
317 WebPlotDigitizer v. 4.1 (Rohatgi 2012)). We approximated a standard deviation by finding the
318 value that resulted in 95% of the normal distribution being within the confidence interval of
319 the linear regression. For each of the 200 parameter combinations, each of the six rate activation
320 energy parameters was sampled independently from their respective distribution and the model
321 was projected to 2050. We then quantified the overall mean response and the ranges of
322 predictions resulting from 200 randomly parameterised simulations and visualized it for the
323 analysis of growth and mean size.

324 We acknowledge that these scenarios are very simplified for evaluating changes in resource
325 productivity versus physiology with warming, and that they do not necessarily reflect the
326 predicted conditions in the Baltic Sea, nor all the potential pathways by which climate changes
327 affects the environmental conditions in the Baltic Sea. However, the simplicity allows us to
328 contrast effects of warming on basal food resources versus individual physiology of fish.

329

330 ***Model calibration***

331 We estimated species-specific von Bertalanffy growth and length-weight parameters from
332 scientific trawl survey data (for details, see *Supporting Information*, Table S1). Next, the model
333 was calibrated to average spawning stock biomasses (SSB_i) from stock assessment data for
334 cod, herring and sprat (ICES 2013, 2015) in 1992-2002, using average fishing mortalities (F_i)

335 in the same time frame. Ideally, the period for calibration should exhibit relative stability, but
336 such periods do not exist in the Baltic Sea, which is greatly influenced by anthropogenic
337 activities and has undergone dramatic structural changes over the last four decades (Möllmann
338 *et al.* 2009). We chose to calibrate our model to the time period of 1992-2002 as in Jacobsen
339 *et al.* (2017), which is a post-regime shift period characterized by high fishing mortality on
340 cod, low cod and herring abundance and high sprat abundance (Gårdmark *et al.* 2015) (Fig.
341 S4). The cut-off at 2002 also ensured that we did not calibrate the model to the period starting
342 from mid 2000's when the growth capacity, condition, proportion of large fish in the
343 population, and reproductive capacity of cod started to decline rapidly (Svedäng & Hornborg
344 2014; Casini *et al.* 2016; Mion *et al.* 2018, 2021; Neuenfeldt *et al.* 2020).

345 Model calibration was done by tuning the maximum recruitment parameter (R_{max}) for the
346 three fish species to minimize the residual sum of squares between the natural log of spawning
347 stock biomass estimated in stock assessment output (ICES 2013, 2015) and those emergent in
348 the model for the years 1992-2002, while holding temperature constant at T_{ref} . We used the
349 "L-BFGS-B" algorithm (Byrd *et al.* 1995) in the 'R'-optimization function '*optim*'. We ensured
350 that individual growth rates were close to observed by comparing the growth curves emerging
351 in the model to the von Bertalanffy curves fitted to trawl survey data (Fig. S6), which they were
352 after a stepwise manual increase of the constant in the allometric maximum-consumption rate
353 (h_i) (*Supporting Information*). The level of density dependence imposed by the stock-
354 recruitment function (see Eq. 14-15) was also evaluated by assessing the ratio of the
355 physiological recruitment, $R_{phy,i}$, to the recruitment R_i (Jacobsen *et al.* 2017) (*Supporting*
356 *Information*). These final values mean that stock recruitment is sensitive to the stock biomass,
357 but there is some density dependence limiting recruitment (i.e., not all spawn produced become
358 recruits). A detailed description of the step-by-step calibration protocol used in this study can
359 be found in Fig. S4-S9, *Supporting Information*.

360

361 *Analysis of responses to warming*

362 Models were projected with historical fishing mortalities (1974-2014) (ICES 2013, 2015) and
363 centred sea surface temperature trends (1970-2050, acquired from the regional coupled model
364 system RCA4-NEMO under the RCP 8.5 scenario) (Dieterich *et al.* 2019; Gröger *et al.* 2019).
365 To ensure steady state was reached before time-varying fishing mortality and temperature was
366 introduced (1974 and 1970, respectively), we applied a 100-year burn-in period using the first
367 fishing mortality and temperature value in the respective time series (Fig. S12). For each
368 species, we used the fishing mortality at maximum long-term ('sustainable') yield, F_{MSY} , from
369 the size spectrum model as fishing mortality in the years 2014-2050 (Fig. S12). We evaluated
370 the effects of warming on weight-at-age, population mean weight and abundance-at-weight by
371 species. This was done for both absolute values, and by comparing warming food webs to a
372 baseline scenario where no warming occurred post 1997 (the mid-point of calibration time
373 window, where temperature averages T_{ref}) (Fig. S12). In this way the three scenarios
374 considered contrast the effects of temperature affecting fish physiology, their resources or both.

375 Finally, to explore the effect of temperature on fisheries yield and F_{MSY} , we specified a range
376 of constant (not time-varying) temperatures and fishing mortalities, expressed as proportions
377 of T_{ref} and F_{MSY} at the reference temperature ($F_{MSY,T_{ref}}$), respectively, and projected the
378 models to steady state (200 years).

379

380 **Results**

381 *Effects of warming on size-at-age depend on physiological temperature-dependence*

382 The inclusion of temperature effects on fish physiological processes ("top-down" effects of
383 warming) has a strong influence on the projected size-at-age in 2050 under the RCP 8.5
384 emission scenario, relative to the baseline projection (no warming) (Fig. 1). Including

385 temperature dependence of metabolism, maximum consumption, search volume and mortality,
386 with or without temperature-dependent background resource dynamics, leads to warming
387 having positive effects on size-at-age (Fig. 1). In contrast, the scenarios without temperature-
388 dependent physiological processes all lead to size-at-age decreasing with warming (Fig. 1). In
389 scenarios with temperature-dependent physiological processes, the effects on size-at-age are
390 positive and declines with age. When only resources are affected by temperature, small
391 individuals have the largest relative decrease in size-at-age, and this negative effect of warming
392 declines with age (Fig. 1).

393 Despite the relatively narrow range of activation energies for physiological rates considered
394 here (Fig. S3; Table S3), the uncertainty in projected size-at-age associated with variation in
395 the activation energies is large (Fig. 1). In the scenario where both physiology and resources
396 are affected by temperature, the range of predicted changes in size-at-age vary at approximately
397 +10% to +40% (Fig. 1). Changes in size-at-age seem to be driven by the temperature-
398 dependence of maximum consumption rate ($h_i w^n(T)$) increasing the actual consumption rates
399 ($f_i(w)h_i w^n(T)$), and not due to increased feeding levels (Eq. 6; Fig. S13).

400

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

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

406 The only scenario where mean body weight on average increases is where temperature only
407 affects physiology and not the resource (Fig. 2), and this occurs only for cod and sprat. For cod
408 this increase is strong and is driven by both faster growth rates and large increases in the
409 abundance of large fish (~10 kg) (Figs. 1, 3). For sprat the mean body weight in the populations

410 increased only marginally and is mostly driven by faster growth rates and relative abundance
411 of fish above 10 g (Figs. 1, 3). In contrast, scenarios where only resources are affected by
412 temperature, relative numbers of large individuals and therefore mean body size of all species
413 goes down. For herring, all scenarios lead to smaller mean body sizes in the population, and
414 the relative (to non-warming simulation) abundance-at-weight declines with mass in most of
415 the size range, with increases only in the very smallest size classes (< 1g; Fig. 3).

416

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

419 Our simulations applying a range of stable (not time-varying) temperature and fishing scenarios
420 showed that warming led to higher or equal F_{MSY} (i.e., the fishing mortality leading to
421 maximum sustainable yield) (Fig. 4) in six out of nine species \times scenario combinations. The
422 increase in F_{MSY} is likely due to the enhanced growth rates (size-at-age), which allow higher
423 fishing mortalities without impairing population growth. Cod in the scenario with only
424 physiological scaling is the exemption, with higher yields as temperature increase, due to the
425 increase in growth rate, average size and relative abundance of large individuals in that
426 warming scenario for cod (See Figs. 1-3).

427 While F_{MSY} generally increases, it results in lower yields in eight out of nine
428 species \times scenario combinations (Fig. 5). In general, the highest relative yield is found at the
429 coolest temperatures and F slightly lower than F_{MSY} at the reference temperature (Fig. 5). The
430 decline in relative yields of herring and sprat in all scenarios (Fig. 4) is likely driven by the
431 warming-induced decline in abundance, due to resource limitation (Fig. 3). In all scenarios
432 where only the resource is temperature dependent, the corresponding maximum sustainable
433 yield (MSY) declines with warming (Fig. 4).

434

435 **Discussion**

436 ***Combined temperature impacts on fish growth rates, body size and fisheries yield***

437 Using a size-structured and species-resolved food web model, we demonstrate how climate
438 warming affects growth rates, population mean size and size-structure of interacting exploited
439 fish species and assess its implications for fisheries yield. We contrasted the effects of warming
440 on resource productivity and individual level physiology (metabolism, feeding and background
441 mortality) of fish, and found that including temperature-dependence of physiological rates
442 generally led to increased size-at-age of fishes with warming, whereas when temperature
443 affects only the background resource species, size-at-age declines for fish of all sizes. The
444 increase in size-at-age when including temperature dependence of physiological processes is
445 strongest in juveniles of all three fish species, yet, despite increased growth rates, in most cases
446 warming leads to smaller mean body size in the population, lower spawning stock biomass
447 (biomass of mature fish) and reduced yields. This is because the carrying capacity of lower
448 trophic level resources declines and fish mortality (background and to some extent predation
449 mortality, see Fig. S14) increases with warming, which shifts the population size structure
450 towards smaller individuals.

451 Mechanistic models exploring warming-driven declines in community-wide average body
452 size often find these declines to be driven by lower food abundance or decreased energy transfer
453 efficiency in the food web, due to a combination of declines in plankton density and shifts
454 towards dominance of smaller plankton at higher temperatures (Lefort *et al.* 2015; Woodworth-
455 Jefcoats *et al.* 2015, 2019). This leads to a community wide decline in mean size of fish, where
456 large bodied species become relatively fewer. The cause of these community-level changes are
457 different from those expected at an individual species level, where temperature can either lead
458 to size-at-age changes over ontogeny (in accordance with the temperature-size rule), or a
459 change in the relative abundance of small vs large individuals. TSR predicts higher growth

460 rates and thus size-at-age of juveniles, but smaller adults body sizes (Atkinson 1994), although
461 the physiological processes that lead to these changes remain debated (Audzijonyte *et al.* 2019).
462 In our model, we include scenarios that reflect both warmer temperatures impact on food
463 abundance as well physiological changes in metabolism and food intake rates. Scenarios with
464 only temperature dependence of resource dynamics lead to declines in size-at-age (that in
465 addition are strongest in young fish). This does not match general observations and predictions
466 of how body growth is affected by warming (Thresher *et al.* 2007; Morita *et al.* 2010; Huss *et al.*
467 *et al.* 2019; Lindmark *et al.* 2021), and is not in accordance with the TSR. In contrast, inclusion
468 of physiological temperature dependence leads to projections more in line with general
469 observations from field data, which often find increased size-at-age that is strongest and
470 positive for small individuals, and that this effect diminishes over ontogeny (Thresher *et al.*
471 2007; Huss *et al.* 2019).

472 The general increase in body growth is, however, in general not sufficient for maintaining
473 similar mean population body sizes and size-structure if resource carrying capacities decline
474 with warming, because this causes declines in the relative abundance of large fish. Mean body
475 size in the population and yields therefore decline in the scenario with temperature dependence
476 of both resource dynamics and physiology. These predictions on the net effect of warming are
477 in line with similar models using empirically derived static plankton spectra (Blanchard *et al.*
478 2012; Canales *et al.* 2016; Woodworth-Jefcoats *et al.* 2019), and empirical studies (Van Dorst
479 *et al.* 2019). If, however, resource carrying capacity would not decline with temperature, our
480 results show that the increased body growth potential in fish due to faster metabolic and feeding
481 rates can lead to changes towards dominance of larger fish in some populations. This is
482 important to consider, given that predictions about effects of climate change on primary
483 production are uncertain and show large regional variability (Steinacher *et al.* 2010). These
484 results show that it is important to account for both direct and indirect effects of temperature

485 in order to explain results such as increased growth rates and size-at-age but overall smaller-
486 bodied populations, as also found in (Ohlberger *et al.* 2011; Ohlberger 2013; Neubauer &
487 Andersen 2019; Gårdmark & Huss 2020). Focusing on changes only in bottom-up processes
488 can therefore risk missing the potential for fish to increase their growth rates with initial
489 warming, and how that response varies over ontogeny.

490 In fisheries stock assessment, plastic body growth is generally thought to be less important
491 for stock dynamics than environmentally driven recruitment variation, density dependence at
492 early life stages and mortality (Hilborn & Walters 1992; Lorenzen 2016). Due to the
493 accumulating evidence of time-varying and climate-driven changes in vital rates (survival,
494 growth and reproduction), their relative importance for fisheries reference points and targets
495 are now becoming acknowledged (Thorson *et al.* 2015; Lorenzen 2016). In our modelling
496 system, we find that maximum sustainable yields (*MSY*) and the fishing mortality leading to
497 *MSY*, i.e., F_{MSY} , vary with both temperature and between modelling scenarios and that the
498 effect can largely be predicted from changes in growth and abundance-at-size. When
499 temperature affects both the background resources (mainly declining carrying capacity) and
500 fish physiology, warming tends to increase F_{MSY} , but the yield (*MSY*) derived at this
501 exploitation rate is lower. The decline in yields with warming is due to reduced resource
502 availability, lowering overall fish abundance, and is in line with earlier studies (Blanchard *et*
503 *al.* 2012; Lotze *et al.* 2019). In addition, the warming-induced decline in relative abundance of
504 fish above minimum size caught in fisheries further decreases yields in our model. At the same
505 time, faster growth rates (size-at-age), occurring when temperature affects vital rates in fish,
506 can cause F_{MSY} to increase with warming. These reference levels should not be viewed as
507 absolute reference points, and the specific results may depend on the model calibration
508 procedure. However, our findings suggest that climate change predictions on fisheries
509 productivity must consider both temperature impacts on vital rates, in particular body growth,

510 as well as bottom-up processes and their effects on both the overall abundance and size-
511 structure of the stock. It also indicates that because productivity may decline with warming in
512 large parts of the oceans (Lotze *et al.* 2019; Heneghan *et al.* 2021) (although there is large
513 variation in these predictions across ecosystems (Steinacher *et al.* 2010)), reduced fisheries
514 yields may be common in a warming world.

515

516 ***Parameterizing and modelling temperature effects***

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

532 To disentangle temperature effects on background resources and physiological processes,
533 we modelled temperature dependence of resources by scaling their parameters with the same
534 general Arrhenius equation (Gillooly *et al.* 2001) that we used to scale the physiological

535 processes in fish. Other similar studies using size spectrum models with physiological
536 temperature-dependence instead import the plankton spectra from climate and earth systems
537 models (Woodworth-Jefcoats *et al.* 2019) or from satellite data (Canales *et al.* 2016). Such
538 approaches may lead to predictions that are more relevant for a specific system. However, it
539 also becomes more difficult to separate the mechanisms behind the observed changes, as the
540 resource dynamics then are externally forced and cannot respond to changes in the modelled
541 food web. Moreover, populating a resource size spectrum based on observed data can be
542 difficult as observed spectra result from both predation and bottom-up processes. As an
543 alternative, our approach of directly scaling the carrying capacity or turnover rates of
544 background resources with temperature provides a coherent way to model temperature-
545 dependencies across trophic levels. The resource dynamics are then impacted by any warming-
546 driven changes in predators, as well as inherent temperature-dependent dynamics, rather than
547 driven by external data (Canales *et al.* 2016) or models (e.g., Woodworth-Jefcoats *et al.* 2019).
548 On the downside, this approach means relying on many major simplifications with respect to
549 resource dynamics. In addition, our scenarios only include identical temperature dependencies
550 and baseline carrying capacity of pelagic and benthic resources, and only negative effects of
551 temperature on resource carrying capacity. These may not reflect the actual situation in the
552 Baltic Sea and might better reflect the global decline in primary production (Steinacher *et al.*
553 2010) commonly predicted by coupled climate models (but see e.g. Flombaum *et al.* (2020)),
554 which has been linked to declines in community-level body sizes (Woodworth-Jefcoats *et al.*
555 2019). It would be straightforward to model increases in productivity, as predicted on average
556 by Sarmiento *et al.* (2004), with our approach by using positive activation energies. It is also
557 possible to include temperature-effects of the slope of the size spectrum, as this is often found
558 to be negatively related to temperature (e.g., (Morán *et al.* 2010; Yvon-Durocher *et al.* 2011;
559 Canales *et al.* 2016; Woodworth-Jefcoats *et al.* 2019), but see also Barnes *et al.* (2011)).

560

561 **Conclusion**

562 Ecological forecasting is inherently difficult, and climate change alters the already complex
563 causal pathways that drive ecosystem dynamics. Size spectrum models have successfully been
564 used to evaluate size-based mechanisms and structuring forces in ecosystems (Andersen &
565 Pedersen 2009; Szuwalski *et al.* 2017; Reum *et al.* 2019). In this study, we have highlighted
566 the important role of explicitly modelling temperature effects on individual-level metabolism
567 and feeding rates. This not only makes predictions about temperature effects on size-at-age
568 more in line with general observations and predictions (e.g., with the TSR), but also affects the
569 levels of exploitation that leads to maximum sustainable yields, and the corresponding yields.
570 Hence, accounting for temperature-dependence of both ecological and physiological processes
571 underlying population dynamics is important for increasing our understanding of how and by
572 which processes climate change affects individuals in food webs and resulting effects on
573 fisheries yields, which is needed to generalize across systems and into novel conditions.

574

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583

584 **Author contributions**

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

590

591 **Data availability**

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

595

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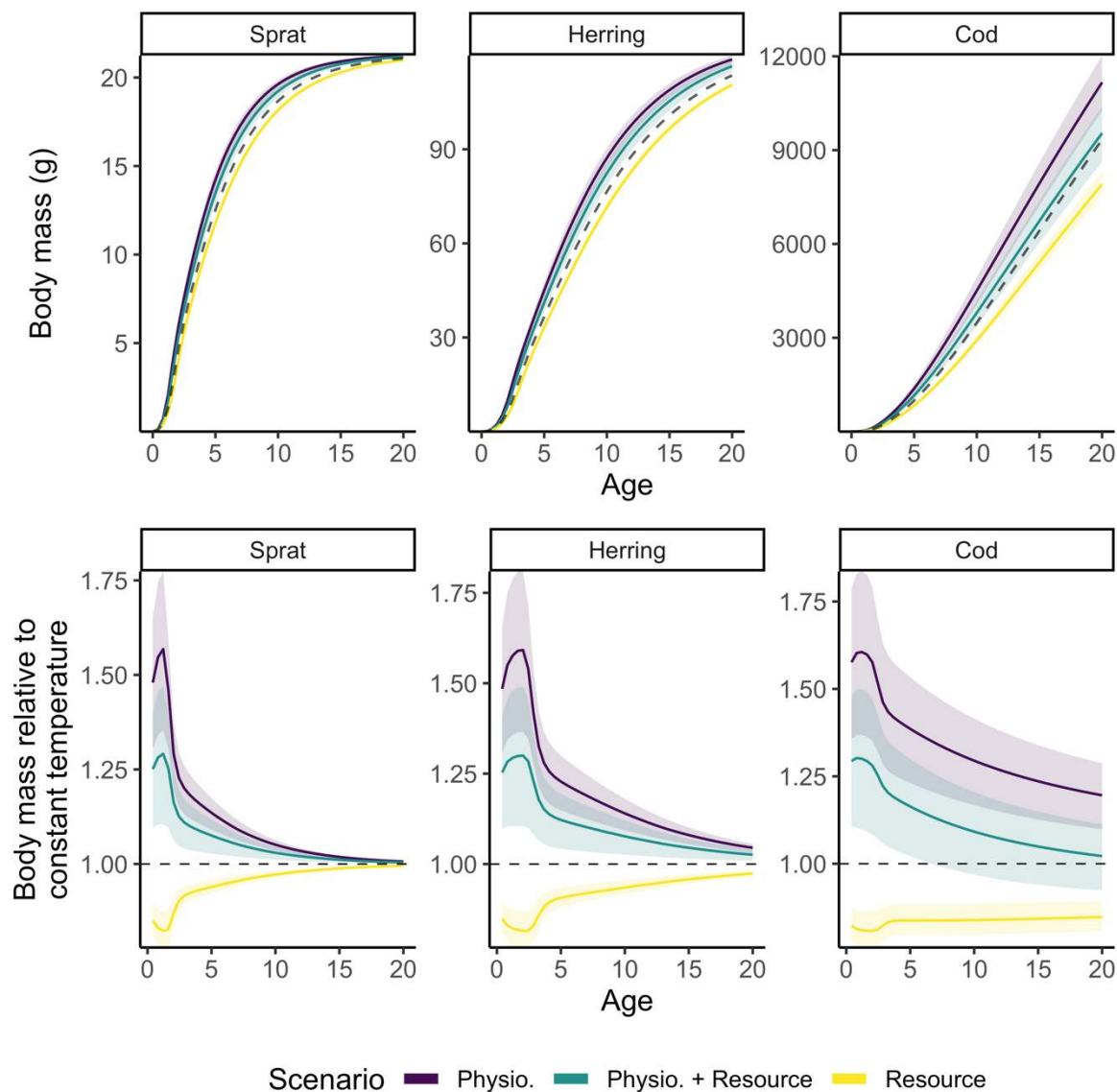
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864 *Figure 1. Individual growth trajectories of sprat, herring, and cod from model projections to year 2050*

865 *assuming warming according to RCP 8.5 while keeping fishing mortality at F_{MSY} levels from the size*

866 *spectrum model. Top row shows size-at-age and bottom row shows size-at-age relative to a non-*

867 *warming scenario. The dashed line in the top row depicts projections assuming a non-warming scenario*

868 *and thus constitutes a baseline prediction. Colours indicate different temperature-scaling scenarios.*

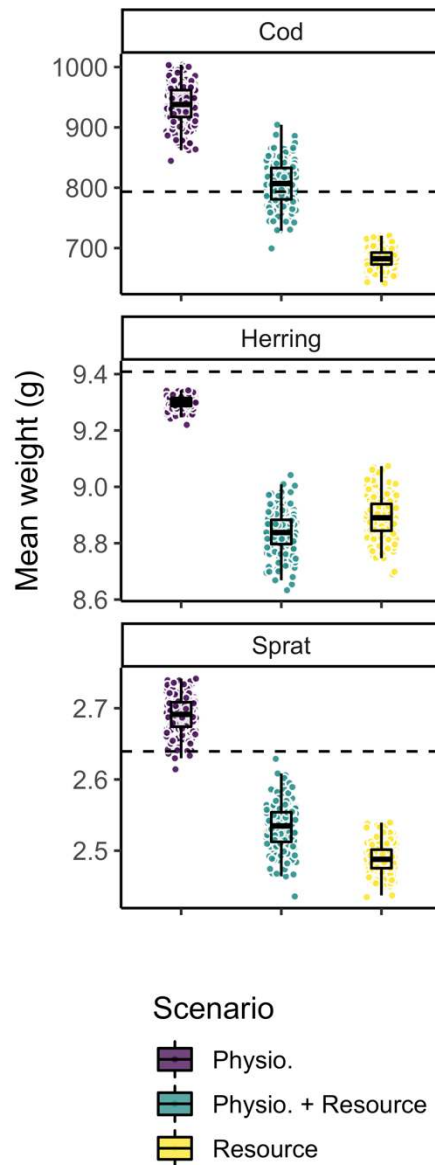
869 *Shaded areas encompass the 2.5 and 97.5 percentiles from the set of 200 simulations with randomly*

870 *assigned activation energies.*

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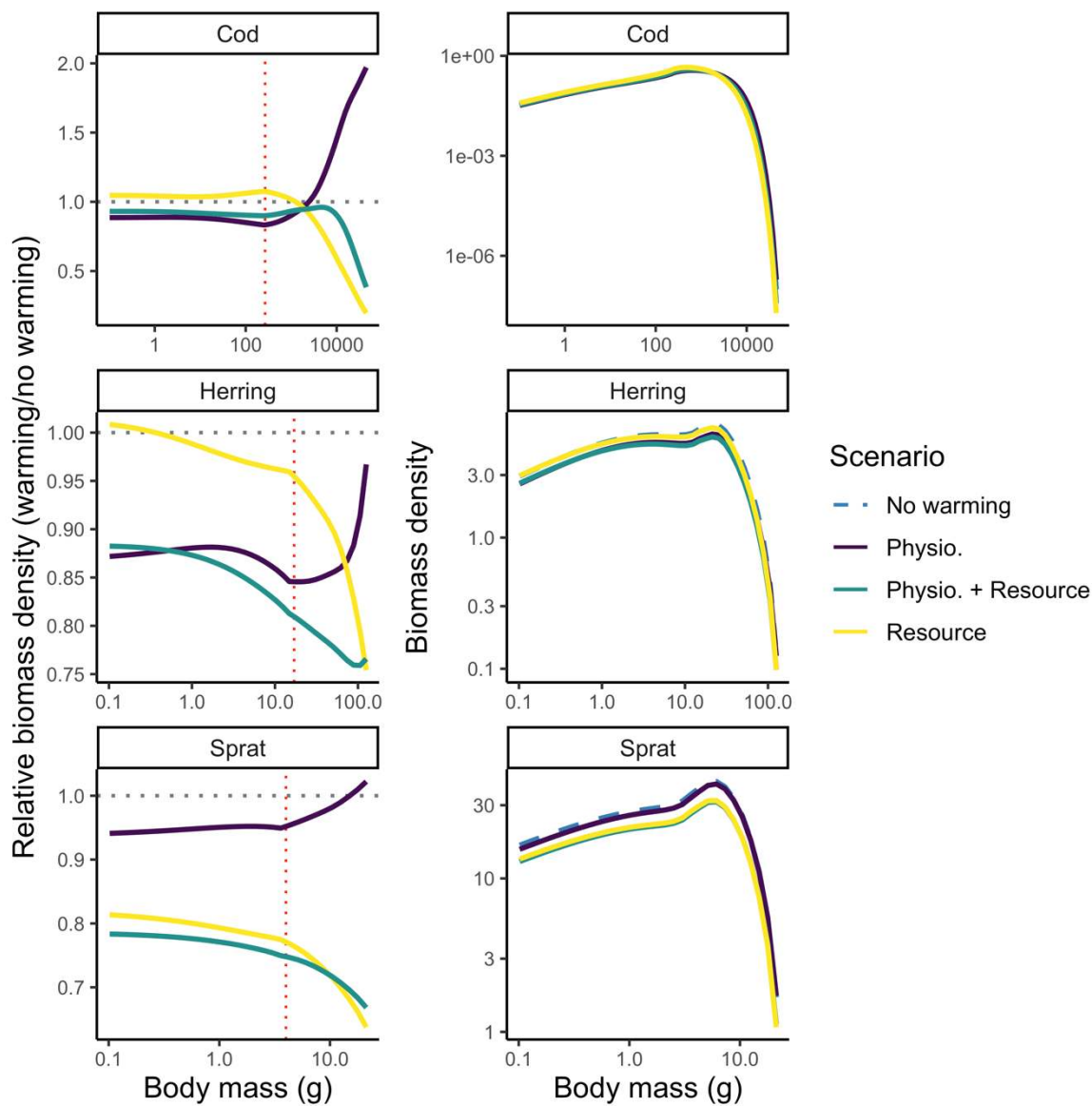
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875 *Figure 2. Mean weight across all individuals in the populations of sprat, herring and cod from model*
876 *projections to year 2050 assuming warming according to RCP 8.5 while keeping fishing mortality at*
877 *F_{MSY} levels from the size spectrum model. The dashed horizontal line depicts projections assuming no*
878 *temperature increase and thus constitutes a baseline prediction. Each dot represents one of the 200*
879 *simulations, each with randomly assigned activation energies. Boxplots depict 25%, 50% and 75%*
880 *quantiles of the 200 simulations in each scenario.*

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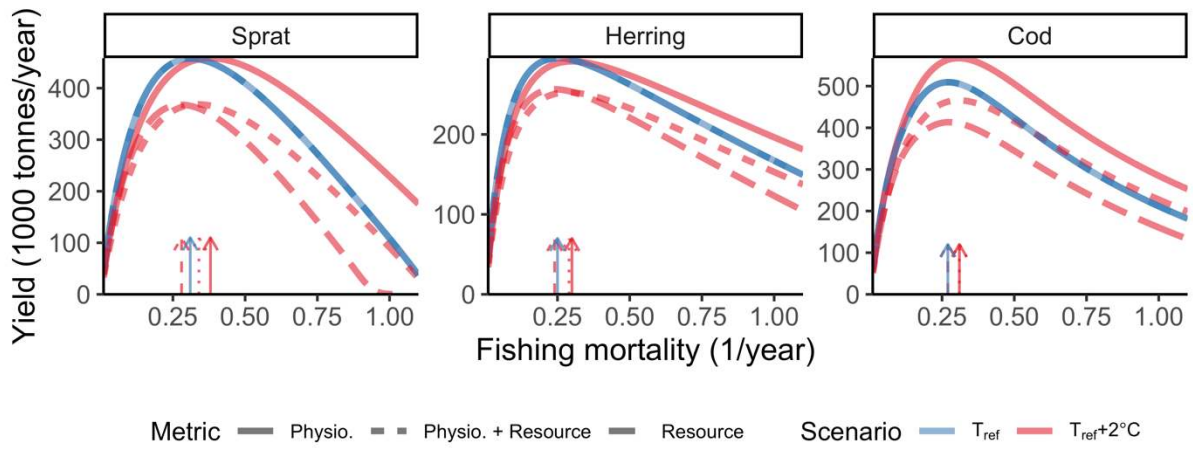


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885 *Figure 3. Projected abundance-at-weight by species for different scenarios of temperature scaling*
 886 *indicated by colours (and line types in the right column due to overplotting) in 2050 assuming fishing*
 887 *mortality held at F_{MSY} levels from the size spectrum model. The left column shows abundance-at-weight*
 888 *relative to a non-warming scenario and the right column shows absolute abundance-at-weight with the*
 889 *non-warming scenario shown in black. Vertical red dotted line indicates weight-at-maturation and*
 890 *horizontal black dotted lines indicate the baseline projection (no warming). Only mean activation*
 891 *energies are used (Table S3, Supporting Information).*

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895 *Figure 4. Steady state biomass yield assuming knife edge selectivity at maturation size under two*
 896 *constant temperature simulations and three scenarios for temperature dependence. Colours indicate*
 897 *temperature, where blue means $T = T_{ref}$ (i.e., no temperature effects), and red depicts warm*
 898 *temperature, here $T = T_{ref}+2^{\circ}C$. Dashed lines correspond to resource dynamics being temperature*
 899 *dependent, dotted lines correspond to physiological rates and resource dynamics being temperature*
 900 *dependent and solid lines depicts only physiological temperature scaling. Arrows indicate fishing*
 901 *mortality (F) that leads to maximum sustainable yield (F_{MSY}). F is held constant at the mean F during*
 902 *calibration (mean 1992-2002) for the two other species while estimating yield curves for one species.*
 903 *Note the different scales between species. Only mean activation energies are used (Table S3, Supporting*
 904 *Information).*

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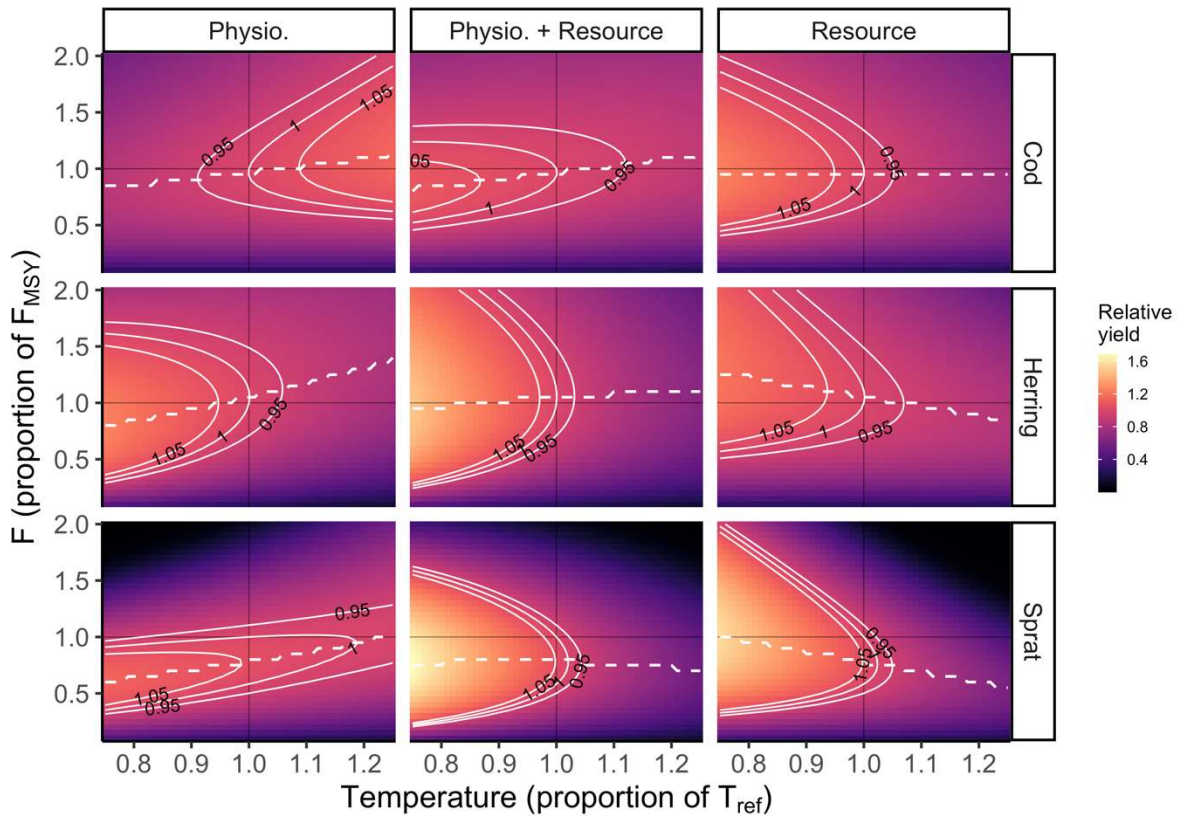
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915 *Figure 5. Example of fisheries yield at steady state relative to MSY at T_{ref} (no effect of temperature)*
 916 *from simulations with constant (not time-varying) temperatures with the three temperature dependence*
 917 *scenarios (columns). The y-axis shows fishing mortality, F , as a proportion to F_{MSY} (as estimated from*
 918 *the size spectrum model) at T_{ref} and the x-axis shows temperature as a proportion of T_{ref} . The other*
 919 *two species are held at their F_{MSY} when one species' F is varied. White lines are 0.95, 1 and 1.05 yield*
 920 *isoclines (for example, the 1 isocline shows F and T -values where yield is equal to MSY without any*
 921 *warming). The fact that isoclines ≥ 1 occur at relative temperatures below 1 in eight out of nine panels*
 922 *shows that any warming will reduce the MSY. Grey points show at which F yields are maximized across*
 923 *all temperatures (y-values). In three out of nine panels, F_{MSY} declines with warming (for herring when*
 924 *only resource are temperature dependent, and for sprat whenever resources are temperature*
 925 *dependent). Only mean activation energies are used (Table S3, Supporting Information).*