Earth's Future

Key Points:

- Assumptions regarding how temperature drives biological rates strongly influence food web responses to warming
- Community interactions further modify outcomes to warming which complicate efforts to generalize warming responses across food webs
- Uncertainty in food web temperature dependences should be represented in climate change projections

Temperature-Dependence Assumptions Drive Projected Responses of Diverse Size-Based Food Webs to Warming

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Abstract Food web projections are critical for evaluating potential risks to ecosystems and fisheries under global warming. The temperature dependence of biological processes and regional differences in food web structure are two important sources of uncertainty and variation in climate forced projections of fish communities, but we do not know their magnitude or relative contribution. Here we systematically evaluated a range of different assumptions about temperature-dependence on rates, including size-dependent effects, controlling food intake, metabolism, and non-predation mortality in fishes using species-resolved size spectrum food web models that link individual-level physiological processes to population and community dynamics. We simulated the physiological effect of warming in a range of size-structured food web models calibrated to different marine ecosystems and in simplified trait-based models. Higher food intake in warmed conditions increased total fish biomass, catches, and mean body weight, but these effects were offset by the negative effects of warming on metabolism and mortality, which combined resulted in lower total biomasses and catches for most food webs. These effects were enhanced when warming increased metabolic rates more than food intake, and the outcomes were also sensitive to size dependency of temperature responses. Importantly, these general patterns were not uniform across all food webs—individual functional groups and fish species within food webs responded to warming in different ways depending on their position in the food web and its structure. Hence, caution is warranted when generalizing food web or species outcomes to warming because they are mediated by community interactions. Uncertainty related to temperature dependence and ecological interactions will impact food web projections and should be represented in climate change projections.

Plain Language Summary Multi-species models are often used to predict how climate change will affect marine ecosystems, fisheries yields and conservation. However, temperature can affect species in a variety of ways, making predictions challenging. Moreover, warming driven changes in a fish community will also depend on species interactions, potentially amplifying or dampening warmingdriven effects in individual species. We explored how 2°C of warming may impact fish biomasses, yields and sizes using six models developed for different marine food webs and three theoretical models with different assumptions about species interactions. We found that, overall, warming tended to result in lower biomasses and fisheries yields, but slightly larger average fish sizes. Yet, results differed depending on how we modeled temperature effects on species food intake and energy expenditure. Moreover, even under the same assumptions about temperature impacts, models developed for different ecosystems behaved differently showing that species interactions will modify warming effects, making general predictions difficult. To make better predictions on warming impacts and more informed adaptation strategies we urgently need more work to understand how temperature affects individual species and communities. Meanwhile, models predicting ecosystems responses to warming should more clearly account for the uncertainty in temperature effects on fishes.

1. Introduction

Global mean sea surface temperatures have warmed ~1°C relative to preindustrial levels and an additional warming of ~1.5–3.5°C is possible over the next century depending on future greenhouse gas emission rates (Kwiatkowski et al., 2020). Our ability to project the impacts of future climate change on marine food webs and to make relevant adaptive changes, depends significantly on understanding the effect of temperature on physiological and ecological processes. At the cellular level, temperature drives metabolism and other biochemical

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reaction rates that scale up to influence growth, predation, reproduction, and mortality (Brown et al., 2004; Portner & Peck, 2010). Changes in vital rates, in turn, underpin and depend on community interactions (Gårdmark & Huss, 2020; Ohlberger et al., 2011), and influence population extinction risk and the expansion or contraction of species distributions (Zhang et al., 2017). Warming is projected to increase stratification, leading to a reduced surface nutrient supply and a decrease in primary productivity (Bindoff et al., 2019; Doney et al., 2012). Consequently, models project a decline in global marine biomass (Kwiatkowski et al., 2019; Lotze et al., 2019), but the ultimate outcome of warming on food webs and community structure will also depend in part on the interplay between direct effects of temperature on physiology and indirect effects, transmitted through networks of species interactions (Gilman et al., 2010; Lord et al., 2017).

Given the prevalence of feedbacks and the broad spatial and temporal scales on which food webs operate, models are necessary to project climate impacts on species, evaluate ecosystem-based management under climate change, and assess the potential efficacy of mitigation strategies (Horn et al., 2021). However, food web models vary widely in structure and complexity and emphasize different ecological processes and levels of biological detail depending on the question motivating their development. Consequently, food web projections can range widely among models. In recent global marine food web ensemble studies, end-of-century projections of total animal biomass ranged from no change to a decrease of more than 30% across nine different global models under the high emission scenario (RCP 8.5/SSP5-8.5) (Lotze et al., 2019; Tittensor et al., 2021), and even wider ranges were observed in regional projections (Bryndum-Buchholz et al., 2020). One potential reason for variation in food web projections is the difference in the adopted temperature-dependence assumptions, reflecting uncertainty over the representation of individual-level temperature effects and their scaling to ecosystem-level impacts (Heneghan et al., 2021). Another important source of uncertainty is the effect of interactions among species, as global food web model ensembles typically do not resolve species, but focus on functional or trait groups (e.g., Lotze et al., 2019). To improve projections of global warming impacts on fish communities and ocean food webs we need a better understanding of how different temperature-dependencies alter emergent food web properties and depend on species interactions (Heneghan et al., 2021).

It is typically observed that biological rates in food webs increase exponentially with temperature, following the Van't Hoff-Arrhenius equation (Brown et al., 2004). This assumption is also included in many models. While originally developed to describe temperature effects on chemical reaction rates, the Arrhenius equation is now often applied to many physiological and ecological rates over biologically plausible temperature ranges (Brown et al., 2004; Kooijman, 2000). For example, in physiologically structured food web models, temperature-dependencies have been applied to rates controlling body growth and mortality (Blanchard et al., 2012; Lindmark et al., 2019; Maury, Shin, et al., 2007; Thunell et al., 2021; Zhang et al., 2017). However, biological rates do not all scale with temperature in the same manner. Cross-taxa studies indicate that activation energies associated with parameters controlling animal intake rates (i.e., that control the slope of the relationship between rates and temperature) may be lower than those related to metabolic rates (Englund et al., 2011; Rall et al., 2012; Vucic-Pestic et al., 2011), which suggests that fish feeding rates may increase less strongly with temperature than metabolism. Further, the effects of temperature may also depend on body mass, which means that animals of different weight might have different scaling of intake or metabolic rates (Killen et al., 2010; Lindmark, Ohlberger, & Gårdmark, 2022; Ohlberger et al., 2012). An important consequence is that different life stages may respond differently to warming, which may alter population regulation, stage structure, and species interactions, given that predation in aquatic systems is strongly size-structured (Lindmark et al., 2018, 2019; Thunell et al., 2021). Controlled simulation experiments that systematically test how different individual-level temperature hypotheses propagate through species and food webs have until now only been done in single models (Lindmark, Audzijonyte, et al., 2022; Lindmark et al., 2019; Reum et al., 2020), and we do not know how conclusions from these cases can be generalized across other food web models.

To explore the effect of different size- and temperature-dependence of vital rates on food web responses to warming requires models that account for both intra-specific and population-level processes. This includes the effect of intra-specific variation in body size on individual-level physiological rates and how it propagates to population level rates and species interactions. Size spectra represent the abundance of organisms in a community as a function of individual body size (Sheldon et al., 1972), and dynamic size spectrum models track the flow of biomass up the size spectrum (Andersen, 2019; Blanchard et al., 2017). The models are underpinned by extensive theoretical work and empirical evidence that recognizes body size as the primary trait influencing physiological rates and ecological interactions (Andersen, 2019; Blanchard et al., 2017; Kerr & Dickie, 2001; Peters, 1983;

Sheldon et al., 1972; Trebilco et al., 2013). Importantly, the individual-level processes of size-dependent food consumption, body growth, and mortality are based on bioenergetic principles and are, via intraspecific variation in body size, mechanistically linked to population and community dynamics (Andersen et al., 2016; Blanchard et al., 2017). The framework is therefore well-suited to evaluating individual-level climate stressors on emergent food web properties, such as fish community size structure (Woodworth-Jefcoats et al., 2019) and growth rates (Heneghan et al., 2019), as well as species interactions (Lindmark, Audzijonyte, et al., 2022; Reum et al., 2020). Different versions of size spectrum models have been used to project climate impacts on marine systems and fisheries at both global (e.g., Blanchard et al., 2014; Lefort et al., 2015) and regional scales (e.g., Reum et al., 2020; Woodworth-Jefcoats et al., 2013, 2019). They have also demonstrated that temperature-dependence of rates regulating body growth and mortality increases uncertainty in species long-term biomass projections (Reum et al., 2020), and their effects remain important to resolve as warming outcomes are sensitive to food web structure (Gibert, 2019; Lindmark et al., 2019; Sentis et al., 2014; Thunell et al., 2021).

Here, we systematically evaluated the impact of adopting different individual-level temperature dependence hypotheses for rates controlling fish growth and mortality on emergent food web properties using a diverse set of species-resolved, dynamic size-structured food web models. Specifically, we examined (a) the individual and joint impact of adopting standard exponential temperature dependencies on rates controlling fish body growth and non-predation mortality; (b) the impact of assuming lower activation energies on rates controlling food intake compared to metabolism; (c) the effect of assuming size dependent temperature scaling of food intake and metabolism; and (d) the joint effects of temperature dependences in scenario (b) and (c). These scenarios were also applied to a simplified trait-based size spectrum model (TBM; Andersen et al., 2016) to assess how more realistic resolution of species compares to a generalized TBM community where "species" differ only in their asymptotic size. In TBMs, asymptotic size is considered a master trait that embodies a trade-off between reproductive output and asymptotic size, and theoretical arguments linking the two set predator abundances (Andersen et al., 2016). The multispecies size spectrum models (MSSMs) in contrast were previously developed and calibrated to different regional ecosystems spanning subpolar to tropical latitudes, and included oceanic, continental shelf, and nearshore demersal food webs (Audzijonyte et al., 2023; Blanchard et al., 2014; Lindmark, Audzijonyte, et al., 2022; Novaglio et al., 2022; Reum, Blanchard, et al., 2019; Woodworth-Jefcoats et al., 2019). In MSSMs, species-level detail is richer—parameters controlling growth rates, feeding interactions, and maturation and asymptotic sizes are tuned to improve ecological realism and abundances are adjusted to better match observed levels. Collectively, the MSSMs sample a range of system configurations, but share the same structure regarding the representation of individual energy budgets. Their similarity in modeling framework, yet difference in ecological detail thus provides a robust test of whether the impacts of different assumptions regarding temperature-dependence of biological rates are generalizable across systems.

2. Materials and Methods

We evaluated the implications of adopting different temperature dependence assumptions on rates governing body growth and mortality in three different versions of a general TBM and in six previously developed regional MSSMs (Table 1). The three TBMs differed by just one key parameter—the predator to prey body mass ratio—which strongly influences trophodynamics (Andersen & Pedersen, 2010; Jennings & Blanchard, 2004; Zhang et al., 2017). The MSSMs, while structurally similar to TBMs, represent additional species-specific detail regarding life history traits, energy budget parameters, and prey species and size preferences, which improves their ability to represent differences in community structure between ecosystems (Andersen et al., 2016; Blanchard et al., 2017; Reum, Blanchard, et al., 2019). MSSMs and TBMs were used to evaluate the extent to which the food web structure may alter warming outcomes under the different temperature dependence assumptions. We first outline the temperature dependency assumptions and follow with descriptions of the food web modeling framework and the incorporation of temperature dependence on key rates governing food intake, metabolism, and non-predation mortality. Although biological rates may scale unimodally with warming over large temperature ranges (e.g., Delong et al., 2017), we limited the analysis to exponential scaling relationships which remain relevant when species live at temperatures below their tolerance limits and warming increments are small to moderate (Brown et al., 2004; Kooijman, 2000).

Table 1
Summary of Key Variables in TBMs and MSSMs Included in the Temperature Simulations

Model name	Food web description	Reference	Predators	β	W_{inf}	Links	Connectance
TBM 500	Generic pelagic food web	Scott et al. (2014)	9	500 [500, 500]	1,845 [6, 10,000]	81	1
TBM 2.5K	Generic pelagic food web	Scott et al. (2014)	9	2,500 [2,500, 2,500]	1,845 [6, 10,000]	81	1
TBM 10K	Generic pelagic food web	Scott et al. (2014)	9	10,000 [10,000, 10,000]	1,845 [6, 10,000]	81	1
Coastal Tasmania	Temperate, nearshore rocky reef	Audzijonyte et al. (2023)	17	835 [50, 3,000]	3,855 [39, 16,012]	174	0.6
SE Australia	Temperate, continental shelf	Novaglio et al. (2022)	19	242 [100, 1,000]	8,520 [3, 32,500]	283	0.78
Central North Pacific	Tropical to subtropical, pelagic ocean basin	Woodworth-Jefcoats et al. (2019)	12	125 [100, 400]	108,072 [8,273, 455,400]	142	0.99
Baltic Sea	Subpolar, pelagic inland sea	Lindmark, Audzijonyte, et al. (2022)	3	808 [426, 1,000]	15,016 [21, 44,903]	9	1
North Sea	Temperate, continental shelf	Blanchard et al. (2014)	12	61,011 [22, 398,849]	7,529 [33, 39,851]	144	1
Eastern Bering Sea	Subpolar, continental shelf	Reum et al. (2020)	15	326 [100, 1,000]	7,509 [79, 37,535]	114	0.51

Note. For the predator to prey body mass ratio and maximum body mass (β and W_{inf}, respectively), the mean value of all functional groups or species in the model is given; minimum and maximum values for individual species or functional groups are indicated in brackets. Links correspond to the number of predator-prey pairs within the predator community (excluding predation on resource spectra). Connectance is links/total possible number of linkages (excluding resource spectra linkages). See Table S1 in Supporting Information S1 for details on additional modifications in model structure relative to Scott et al. (2014).
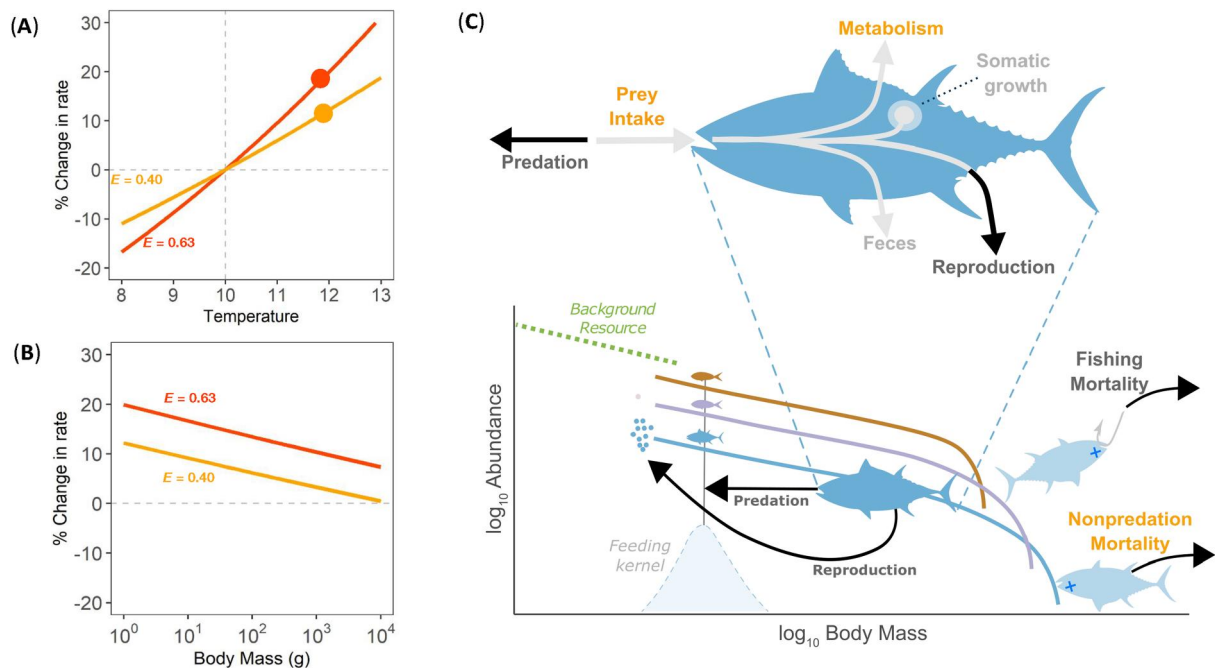
Figure 1. (a) Relative change (%) in temperature-dependent rates predicted by the size-independent exponential (Van't Hoff-Arrhenius) model with activation energy (E) values of 0.40 and 0.63 and a reference temperature (T_{ref}) of 10°C. For reference, the vertical and horizontal lines indicate T_{ref} and no change in rates, respectively; filled points indicate change in rates with 2°C of warming relative to T_{ref}. (b) Relative change (%) in rates under 2°C of warming ($T_{ref} = 10°C$), when temperature scaling is assumed to also depend on body size. The temperature-size interaction parameter c is set to −0.006. (c) Schematic overview of size spectrum food web models. Bioenergetic processes described at the individual-level (gray arrows) are coupled to demographic processes (black arrows) that drive population and community size structure. Temperature-dependencies were incorporated into processes labeled in orange. Predators consume suitably sized prey (selected according to a feeding kernel), and assimilated energy is allocated to metabolism, growth, and reproduction. Intake rates, in turn, set predation mortality rates on prey populations. The smallest individuals feed exclusively on the background resource spectrum. Additional loss of individuals result from fishing and non-predation (e.g., disease, senescence) mortality. Reproduction produces individuals that join the population at the initial weight of a given species or functional group. Full model descriptions are provided in Section 2 and Supporting Information S1.

2.1. Temperature-Dependence

We incorporated temperature dependence using the exponential Van't Hoff-Ahenius equation, which was modified to represent a potential interactive effect of body mass (Brown et al., 2004; Killen et al., 2010; Lindmark et al., 2019). For a given biological rate B, temperature-corrected values for individuals of mass m at temperature T (K) were calculated as:

$$B(m, T) = B(T_{ref}) \cdot A(m, T) \tag{1}$$

where T_{ref} corresponds to the reference temperature at which the correction scalar A is 1. In turn, A is:

$$A(m, T) = m^{c \cdot (T - T_{ref})} \cdot e^{\frac{E_a}{k}\left(\frac{1}{T_{ref}} - \frac{1}{T}\right)} \tag{2}$$

where k is the Boltzmann constant (8.62×10^{-5} eV K^{-1}), E_a is the activation energy (eV), and c is the effect of temperature on the allometric exponent. The exponential term is a modified version of the standard Van't Hoff-Arrhenius temperature correction (Brown et al., 2004) that scales rates relative to the reference temperature (e.g., Maury, Faugeras, et al., 2007). When c is set to 0, the body mass term is unity and the formula reduces to the modified Van't Hoff-Arrhenius correction, with an exponential increase in the rate with temperature that is the same across all body sizes. Different values of c and E_a result in markedly different temperature scalars across body sizes (Figure 1).

2.2. Size Spectrum Models

All models in the comparison were based largely on source code for the R package "mizer" (Scott et al., 2014) which implements TBMs and MSSMs (see https://sizespectrum.org/mizer/ for details). The regional MSSMs included additional modifications from the original source code (Table S1 in Supporting Information S1), but the main equations that compose the models are based on those of Hartvig et al. (2011) as implemented in "R" by Blanchard et al. (2014) and Scott et al. (2014). The models provide predictions of the population dynamics of each ith species (or functional group in the case of TBMs) as described by its size spectrum, denoted $N_i(m)$, where m corresponds to body mass (g). The numerical density of individuals in the body mass range from m_1 to m_2 is calculated from $\int_{m_1}^{m_2} N_i(m)\,dm$ and the total biomass density (g m^{-3}) of individuals is $\int_{m_1}^{m_2} N_i(m)\,m\,dm$. The size spectrum is obtained from a numerical solution of the McKendrick–von Foerster equation (Andersen et al., 2016) in which growth is balanced by mortality:

$$\frac{\partial N_i(m)}{\partial t} + \frac{\partial g_i(m)\,N_i(m)}{\partial m} = -\mu_i(m)\,N_i(m) \tag{3}$$

where $g_i(m)$ is the growth rate (mass per unit time) and $\mu_i(m)$ is the mortality (per unit time). The individual-level processes of growth and mortality are scaled to the population-level size spectrum following Equation 3, thus removing the need for explicit individual-based simulations (Blanchard et al., 2017). The number of individuals recruiting into the population (R_i) is represented as a boundary condition, and individuals enter the population at the smallest population size class, m_0 (here either egg mass, mass at parturition in the case of live-bearing species, or other minimum mass set by the user):

$$g_i(m_0)\,N_i(m_0) = R_i \tag{4}$$

By default, recruitment into the smallest size group is modeled following a Beverton–Holt type stock–recruit relationship (Scott et al., 2014), though constant recruitment or other stock-recruit relationships can be employed (e.g., Jacobsen et al., 2017; Reum et al., 2020). In addition to representing species or functional groups, the model also includes resource spectra to represent other food sources (Andersen et al., 2016; Blanchard et al., 2009). The model allows for species-specific traits that control growth rates, maturation, egg production, recruitment, and maximum size (Scott et al., 2014).

Growth in Equation 3, $g_i(m)$, is calculated from the quantity of ingested prey after accounting for losses owing to assimilation efficiency and metabolism (Hartvig et al., 2011). Metabolism scales with mass allometrically and in most MSSMs it is parameterized to correlate to the maximum food intake rate so that species with higher maximum intake and therefore also potential growth rate also have higher species-specific metabolic rates (Scott et al., 2014). Food intake emerges from the encounter rate of prey and the predator functional response (Scott et al., 2014). Prey encounter rate is the product of the volumetric search rate of predators, prey density, and the predator's prey species and size preferences. The models assume a Holling Type II functional response, and thus capture the effect of predator satiation at high prey encounter rates. Maximum intake rates of the functional response scales with body size allometrically and, where data is available, is derived from species-specific von Bertalanffy growth rate parameters (Scott et al., 2014). In this study we included temperature dependence on metabolic rates and on rates controlling both volumetric search and maximum intake rates, based on earlier studies (Blanchard et al., 2012; Rall et al., 2012), and extensive empirical evidence (Englund et al., 2011; Gillooly et al., 2001; Killen et al., 2010; Rall et al., 2012).

Processes that contribute to mortality in the models include fishing, predation, and non-predation mortality resulting from, for instance, disease or senescence (Andersen et al., 2016; Scott et al., 2014). Non-predation mortality is assumed to depend allometrically on a species maximum body mass, but is constant across body size classes within a species (Scott et al., 2014). The interspecific variation in non-predation mortality reflects expectations from life history theory and empirical findings showing lower mortality rates in larger, longer-lived species compared to small-bodied, short-lived species (Pauly, 1980; Thorson et al., 2017). Imposing constant non-predation mortality across body size classes has the practical benefit of preventing an unrealistic buildup of large-bodied, high trophic level individuals (Andersen et al., 2016), and is perhaps the simplest assumption given the different sources contributing to non-predation mortality and uncertainty with respect to their cumulative

dependency on individual body mass, though other size-dependencies have been explored (e.g., Law et al., 2009). That said, cross-taxa and intra-specific studies show that non-predation mortality and individual lifespans in laboratory and natural populations are temperature-dependent (Keil et al., 2015; Munch & Salinas, 2009). We therefore also incorporated temperature dependence on non-predation mortality rates, assuming higher non-predation mortality at higher temperatures.

2.3. Trait-Based and Regional Multispecies Size Spectrum Models

To explore temperature impacts on marine ecosystems, we used three different versions of trait-based models (TBMs), each with a different value of β, the preferred predator to prey body mass ratio parameter (Table 1). The β parameter is an important determinant of food chain length, size spectrum steepness, and the strength of trophic cascades (Andersen & Pedersen, 2010; Jennings & Blanchard, 2004), and could thus also be important for emergent community responses to warming. When β is low, trophic level increases more rapidly with body mass and the slope of the size spectrum steepens (Jennings & Blanchard, 2004). In low β systems, more trophic levels are present in the size spectrum relative to high β systems (Jennings & Blanchard, 2004), which amplifies the downstream and upstream effects of predator or prey resource perturbations (Andersen & Pedersen, 2010). For TBMs we selected β values of 500, 2,500, and 10,000 which roughly span the magnitude of values of community-wide β inferred from stable isotope and stomach content analyses (Al-Habsi et al., 2008; Coghlan et al., 2022; Reum et al., 2015; Reum, Holsman, et al., 2019; Trebilco et al., 2016) and mean community values from the regional MSSMs (Table 1).

All three TBMs include nine functional groups ranging in maximum size from 6 to 10,000 g, all equally spaced on a logarithmic scale (Table 1). Size at the onset of maturation (in grams) was 25% of their maximum size. We assumed that the community consisted of generalists and that all functional groups were able to feed on each other. Specifically, all species interaction matrix values were set to 1 such that all prey are consumed in proportion to their relative abundances after adjusting for the size selectivity of predators (Hartvig et al., 2011; Reum, Blanchard, et al., 2019). All functional groups were fished assuming a fishing mortality of 0.1 yr^{-1} and a knife-edge selectivity function, where fishing mortality starts at size-at-maturity. Additional details regarding TBM parameterization are provided in Table 1.

Next, we explored temperature effects on community dynamics using six previously developed regional multi-species size spectrum models (MSSMs; Table 1). These models were parameterized to represent ecologically and economically important species composing food webs from the eastern Bering Sea shelf (Reum, Blanchard, et al., 2019), North Sea (Blanchard et al., 2014), Baltic Sea (Lindmark, Audzijonyte, et al., 2022), central North Pacific Ocean (Woodworth-Jefcoats et al., 2019), Southeast Australian shelf and slope (Novaglio et al., 2022), and coastal Tasmania, Australia (Audzijonyte et al., 2023; Table 1). In each MSSM, an effort was made to include species-specific parameters controlling life history, growth rates, fishing mortality, and feeding ecology in terms of the prey and species preference of predators. Overall, the amount of species-specific detail, inclusion of further model refinements, and approach to model calibration and validation (see Table S1 in Supporting Information S1) varied across systems based on data availability and the original ecological or management issue motivating the model. Additional details on distinctions between models and summaries of modifications to model structure relative to Scott et al. (2014) are provided in Table S1 of the Supporting Information S1 and in key references for each system (Table 1). In this study, these regional models were further modified to include the temperature-dependencies described above. No other temperature dependencies or species-specific thermal tolerances were used in the models, and the carrying capacity and growth rate of background resource prey was held fixed to simplify and improve interpretability of the comparisons.

2.4. Temperature Dependence Simulation

We conducted two sets of simulation experiments in which the impacts of temperature dependence assumptions were compared to outcomes under a baseline (non-warming) scenario. Following Equation 2, rates are all scaled relative to the reference temperature for a food web. As the reference temperature increases, the same warming increment results in larger relative correction scalars. However, applying region-specific reference temperatures would weaken our ability to distinguish the effects of food web structure on warming outcomes because model structure would be confounded by reference temperatures. To facilitate comparison between models from different biogeographic regions, we therefore defined a common reference temperature of 10°C and evaluated the

Table 2
Overview of Parameters for Activation Energy E_a and Mass Exponent c (See Equation 2) Parameter Values Applied to Food Intake, Metabolism, and Non-Predation Mortality Rates

		Parameter values				
		c		E_a		
Temperature-dependence	Assumption for rates (code)	Intake	Metabolism	Intake	Metabolism	Mortality
Van't Hoff-Arrhenius	Baseline (Base)	0	0	0	0	0
	Intake (Int)	0	0	0.63	0	0
	Metabolism (Met)	0	0	0	0.63	0
	Mortality (Mort)	0	0	0	0	0.63
	All (All)	0	0	0.63	0.63	0.63
Extensions	Non-uniform scaling (All_E)	0	0	0.4	0.63	0.63
	Allometric scaling (All_c)	−0.006	−0.006	0.63	0.63	0.63
	Combination (All_cE)	−0.006	−0.006	0.4	0.63	0.63

Note. For all temperature-dependence assumptions and models, the reference temperature (T_{ref}) was set to 10°C. The baseline simulations included no warming relative to T_{ref}; the remaining simulations with different temperature-dependence assumptions included 2°C of warming.

effects of 2°C of warming in each of the modeled ecosystems. In doing so, the same relative change in physiological and mortality rates was applied across all systems under a given temperature dependence assumption. The warming increment of 2°C approximates end-of-century global mean sea surface conditions relative to current levels under a future high greenhouse gas emissions scenario (SSP3; Kwiatkowski et al., 2020). For the baseline simulations, the environmental temperature was set equal to the reference temperature, which yields temperature scalars of 1 (see Equation 2).

In the first set of simulation experiments, we applied identical size-independent exponential temperature-dependence to all rates as commonly implemented in food web models (e.g., Blanchard et al., 2012; Maury, Faugeras, et al., 2007; Maury, Shin, et al., 2007; Reum et al., 2020), and evaluated the separate and combined effect of including temperature dependence on food intake, metabolism, and non-predation mortality (Van't Hoff-Arrhenius scenarios in Table 2). This also acted as a sensitivity test to evaluate the effects of turning on and off temperature dependence on one rate at the time. We used an activation energy (E_a) of 0.63 eV for each rate. The value has been adopted previously (e.g., Blanchard et al., 2012; Jennings et al., 2008; Reum et al., 2020) and was obtained from a cross-taxa average of E_a estimates associated with population growth (Savage et al., 2004). For prey intake rates, we assumed temperature-dependencies on volumetric search and maximum intake rates were strongly interlinked and varied with temperature identically (see Section 2.2 for rationale).

The second set of assumptions include temperature-dependencies supported by more recent evidence (Englund et al., 2011; Lindmark, Ohlberger, & Gårdmark, 2022; Rall et al., 2012), but have yet to be widely adopted. Namely, we conducted simulations where E_a varied among rates and where rates scaled interactively with size and temperature for intake and metabolism (Extension scenarios in Table 2). Specifically, values of E_a associated with intake were set to 0.40, reflecting lower activation energies (compared to metabolic temperature sensitivities) reported in experiments (Rall et al., 2012). Values for the temperature-size interaction parameter c were set to −0.006 based on a cross-species average of values for metabolic rates in fishes (Killen et al., 2010). We assumed that, if present, the same temperature-size interaction (c) would apply to both metabolism and feeding rates (search rate and maximum intake rate). This assumption was necessary because experimentally measured values of c are scarce for feeding rates, but deemed reasonable because metabolism drives other biological and ecological rates (Brown et al., 2004) and similar allometric temperature dependence is required for both metabolism and feeding rates to achieve realistic scaling of optimum growth rates with mass (e.g., García et al., 2011).

For each set of temperature assumptions, models were initialized using population size spectra estimated from survey data, stock assessments, or according to analytical solutions for theoretical population size structure at equilibrium (Andersen et al., 2016) and iterated forward for 100 years or until equilibrium or quasi-equilibrium conditions were reached. If present, the effects of oscillatory dynamics were removed by averaging simulation

outputs over 20 years which was sufficient to stabilize mean values and facilitate comparisons between model results.

2.5. Quantifying Food Web Responses and Coherence

For both sets of temperature assumptions, we compared differences in equilibrium total community biomass, spawning stock biomass (SSB), catches, and mean body size between temperature assumption scenarios and baseline outcomes. The same variables (biomasses, mean size, catches) were also evaluated at the species or functional group level to understand their contribution to aggregate community patterns.

To visualize the similarity with which different systems responded to warming across temperature assumptions, we performed ordination on community-level outcomes (total SSB, catches, and mean body mass) using non-metric multidimensional scaling (NMDS; Legendre & Legendre 2012). Outcomes were expressed in terms of percent change relative to the baseline scenario and dissimilarity was calculated as Euclidean distance and submitted to NMDS. Using the same approach, we also visualized similarity of the different temperature assumptions based on outcomes across the different food webs. In the resulting NMDS ordination plots, proximity in ordination space corresponds to similarity in model responses.

To assess the level of qualitative similarity (response direction) in model outputs under the temperature-dependence assumptions, we calculated sign agreement in outcomes for community-level variables (e.g., Lotze et al., 2019; Reum et al., 2020). Outcomes were again expressed in terms of percent change relative to the baseline scenario. Sign agreement for a given variable was calculated following $100 \times |P - N|/(P + N)$, where P and N are the number of models in which the relative change was positive or negative, respectively. If half of the models produce positive outcomes and the other half produce negative outcomes, sign agreement is 0% because every positive outcome is matched by an opposite negative outcome. A value of 100% indicates all outcomes change in the same direction. Within a given model and temperature-dependence assumption, we also evaluated uniformity in the sign responses of individual functional groups or species. This was accomplished by calculating sign agreement across species or functional groups.

3. Results

3.1. Temperature-Dependence Assumptions

The response of total biomass, total SSB, total catches, and mean community body mass to warming was strongly driven by the temperature dependence assumption, with the largest differences across assumptions emerging in the TBMs, and more variable responses in regional MSSMs (Figures 2a and 2b). In all cases, total biomass was closely correlated with SSB; we therefore limit results to SSB to avoid redundancy. Temperature dependence assumptions led to a continuum of responses, depending on how they affected individuals' energy budgets. At one extreme, if warming only led to increased food intake (assumption "Intake"), then biomasses, catches and mean sizes generally increased in most systems (except for catches for the EBS model; Figure 2b; Table 3). The increase in some cases was quite large (>15%), setting the outcomes under this temperature assumption apart from others in ordination space (Figure 2a). Such increases indicate that, at a minimum, abundant species in the systems were not limited by food availability; higher search rates and maximum feeding rates led to higher emergent food intake and therefore body growth on average. At the other extreme, when warming only increased metabolic rates ("Metabolism"), energy available for growth decreased and therefore lowered biomasses, catches and mean sizes in a majority of systems (Figure 2b; Table 3). If temperature only affected non-predation mortality ("Mortality"), responses were also generally negative particularly for biomasses and catches, but not as strong as when only metabolism was affected (Figure 2b; Table 3).

Interestingly, when temperature affected all four rates in the same way ("All"), biomass and catches in TBMs still decreased compared to the baseline simulations, but mean body sizes were relatively unchanged (Figure 2b; Table 3). On average, regional models responded similarly in terms of biomasses and catches (ca. 2%–3% decrease), and mean body mass (ca. 6% increase) but responses were uniform across models only for mean body mass (Figure 2b; Table 3). When temperature affected all rates but metabolic rates increased faster than food intake rates ("All + Ea"), biomasses and catches decreased even further (5%–8% decrease), and the increase in mean body sizes was considerably smaller (0.6% increase). In this case a metabolic mismatch occurred—growth slowed and total SSB and total catches tended to decline with warming relative to the baseline scenario, and all
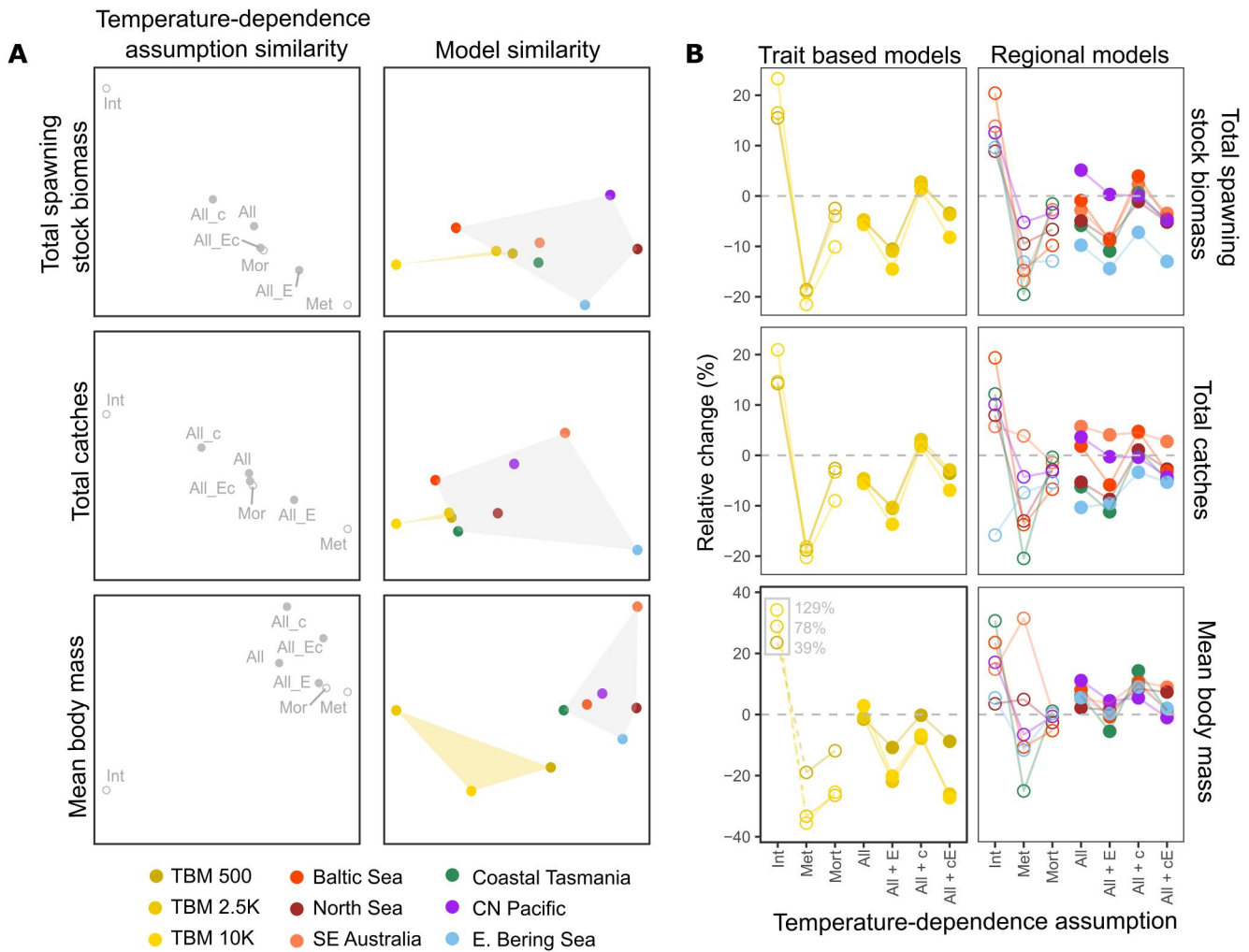
Figure 2. (a) Left column: NMDS ordination plots depicting similarity of temperature dependence assumption (see Table 2 for codes) across systems based on community-wide outcomes for total spawning stock biomass, total catches, and mean body weight; distance between points conveys relative differences in outcomes under the different temperature dependence assumptions averaged across models; open circles: temperature dependence assumption simulations for individual rates; closed circles: simulations with temperature dependence assumptions on all rates. Right column: relative similarity of model outcomes across temperature assumptions. Models that responded more similarly across temperature dependence assumptions are closer in ordinate space. Trait based model and regional MSSMs are demarcated by yellow and gray convex hulls, respectively. (b) Relative change in equilibrium levels of community total spawning stock biomass, catches, and mean body mass with 2°C of warming assuming temperature dependence assumptions on individual rates (open circle) and all rates (open circles; Table 2). Horizontal dashed line corresponds to 0% (no change). Values for mean weight for the trait based models under the Intake scenario are outside the *y*-axis range and are indicated in the figure.

three responses (including mean body size) decreased relative to the case when all rates were affected by temperature in the same way (Figures 2a and 2b; Table 3).

Next, we investigated outcomes of temperature dependence assumptions where activation energies for all physiological rates were the same, but the effect of warming on physiological rates was stronger among small-relative to large-bodied individuals ("All + *c*"). Notably, under this assumption, warming generally led to the smallest changes in total SSB and total catches and a large increase in mean body weight (Figures 2a and 2b; Table 3). These changes tended to be smaller on average compared to when all rates had the same activation energies and no size dependency. Yet, if size dependency was combined with the metabolic mismatch assumption where metabolism increased faster than intake ("All + cEa"), impacts on food webs were more similar to those observed under the "All" assumption (Figures 2a and 2b). This is because the size dependency of the physiological rate increases meant that food intake increased relatively faster in small individuals under warming, but the increase in potential growth was offset by a relatively faster overall increase in metabolic rates (Figures 2a and 2b).

Table 3
Model Averaged Percent Change (and % Sign Agreement Across Models) of Community Total Spawner Stock Biomass (SSB), Catches, and Mean Body Weight

Temperature-dependence assumption	% Change SSB		% Change catches		% Change mean weight	
	TBM	Regional	TBM	Regional	TBM	Regional
Intake	18.4 (100)	13 (100)	16.6 (100)	**6.6 (66.7)**	82.6 (100)	15.9 (100)
Metabolism	−19.7 (100)	−13.2 (100)	−19.1 (100)	**−9.2 (66.7)**	−29.3 (100)	**−2.9 (33.3)**
Mortality	−5.5 (100)	−6.2 (100)	−5 (100)	−3.3 (100)	−21.3 (100)	**−1 (0)**
All	−5.1 (100)	**−3.2 (66.7)**	−5 (100)	**−1.8 (0)**	**0.2 (33.3)**	6.4 (100)
All_*E*	−12 (100)	**−8.5 (66.7)**	−11.5 (100)	**−5.3 (66.7)**	−17.6 (100)	**0.6 (33.3)**
All_*c*	2 (100)	**−0.2 (33.3)**	2.4 (100)	**1.3 (33.3)**	−4.9 (100)	9.7 (100)
All_*Ec*	−5.1 (100)	−6 (100)	−4.5 (100)	**−2.9 (66.7)**	−20.7 (100)	**3.3 (66.7)**

Note. Outcomes for temperature-dependence assumptions with inconsistent directional responses (% sign agreement <100%) are in bold.
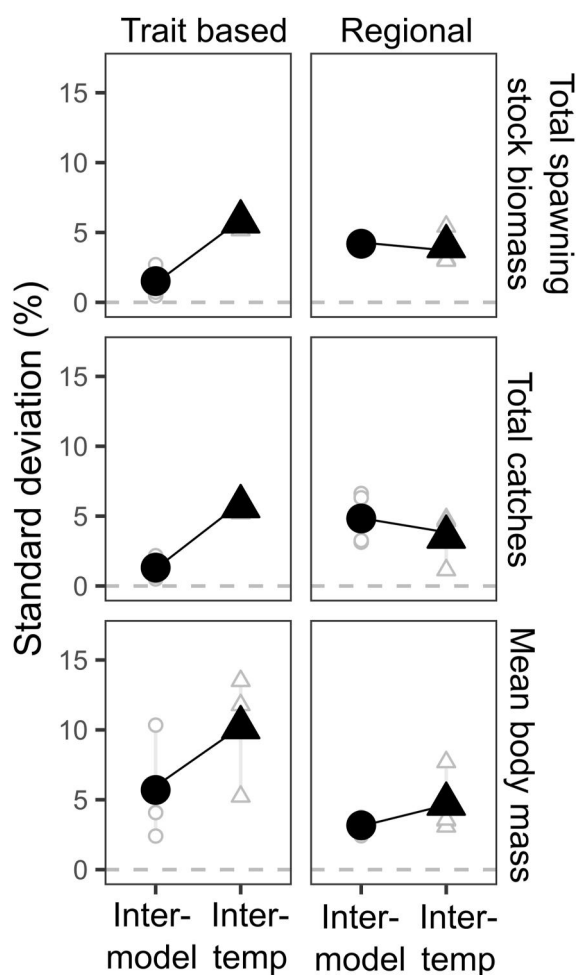

Figure 3. Inter-model variation (expressed as the standard deviation, SD) of relative responses (% change) under warming within individual temperature assumptions (light gray circles) and inter-temperature assumption variation of responses under warming within individual models (gray triangles) for the four simulations where all rates were temperature dependent (All, All + *E*, All + *c*, and All + Ec). Averages of the SDs for inter-model (black circle) and inter-temperature assumptions (black triangle) are provided.

3.2. Variation Across Food Webs

In the three TBMs, the direction of change in total SSB, total catches, and mean body mass were similar under nearly all temperature-dependence assumptions (Table 3), indicating that the large differences in the predator prey mass ratio assumed in these models did not have a major effect on the aggregate food web properties. Averaged across the four main temperature dependence assumptions (All, All + *E*, All + *c*, and All + Ec), inter-model variation for SSB and catches were low (standard deviation: 2.3% and 1.9%, respectively) but somewhat higher for mean body mass (ca. 6.4; Figure 3). In contrast, variation in responses between temperature assumptions, averaged across the three TBMs models, was over twice as high for all response variables (ca. 5.6%, 5.5%, and 12.5%, respectively; Figure 3). This similarity of responses across the TMBs also extended to the biomasses and mean sizes of individual functional groups within the TBMs, which responded to warming in a nonuniform (Table S2 in Supporting Information S1) but highly size-structured manner (Figure 4), reflecting emergence of strong size-based trophic cascades.

In the regional MSSMs, the average direction of change observed for total SSB and catches were largely similar to those for the TBMs under the different temperature dependence assumptions (Figure 2b, Table 3). However, agreement between individual models was lower for most temperature dependence assumptions (Table 3), tempering simple generalizations of the net directional effect of warming on aggregate food web properties in these more ecologically detailed models. Outcomes for mean body mass differed more from those observed for the TBMs: on average, body weight increased when temperature dependence was applied to all four rates, though model agreement was mixed when adopting a lower activation energy value (Table 3). Overall, inter-model variation for SSB and catches within the temperature dependence assumptions was higher than that observed for the TBMs, but not for mean body mass (Figure 3). Further, in MSSMs inter-model variation was more similar in magnitude to the inter-temperature variation, that is, variation in responses across temperature dependence assumptions (Figure 3). Species biomass and body mass responses to warming under the regional models were also not uniform in all cases (Table S1 in Supporting Information S1) but lacked the same degree of size-structuring as in the TBMs (Figure 4), reflecting heterogeneity in both the species and size preference of predators.
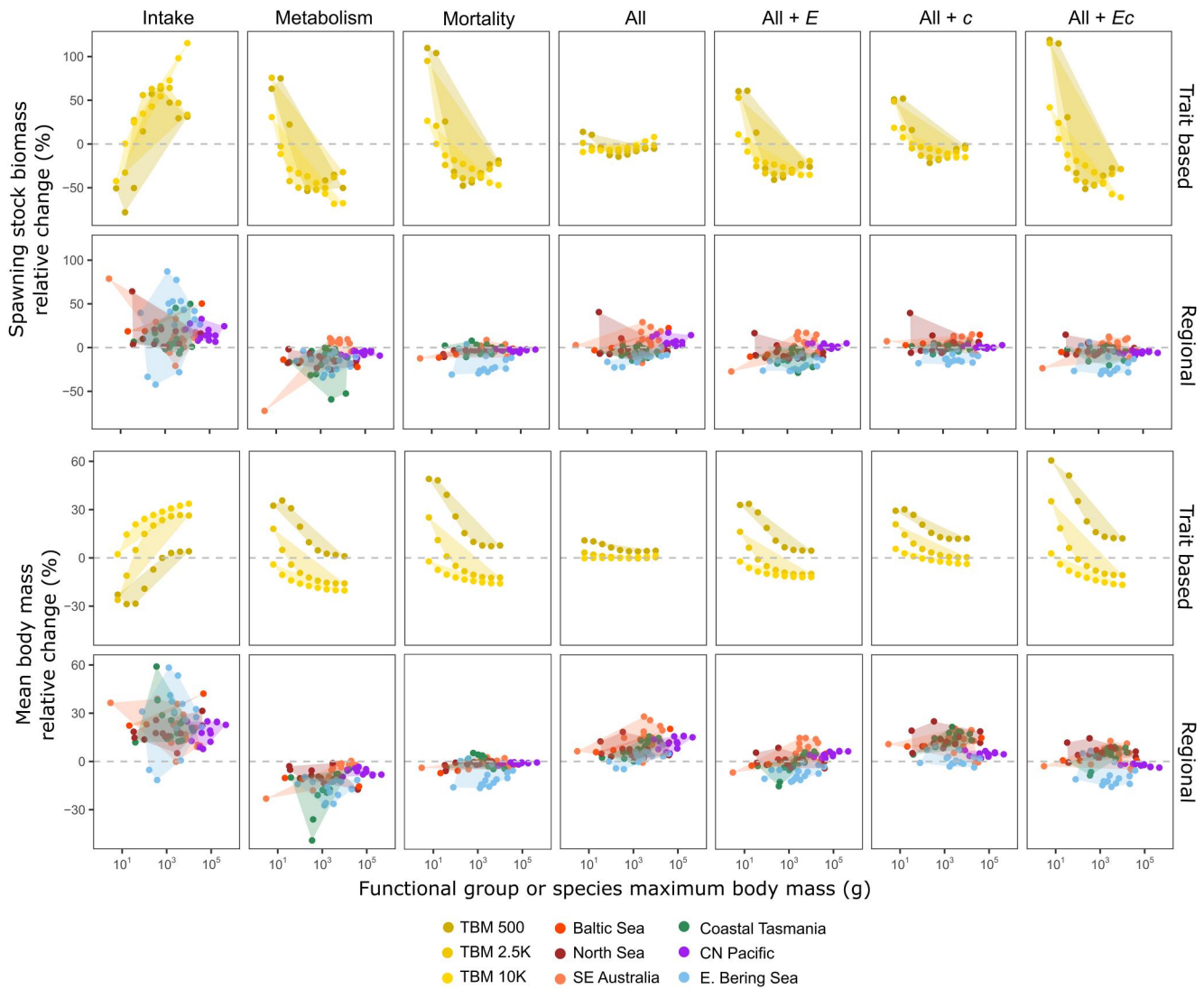
Figure 4. Relative change in functional group or species spawning stock biomass (top panels) and mean body mass (bottom panels) under 2°C of warming and under different temperature-dependence assumptions (columns). Responses are depicted against the maximum body mass of functional groups and species composing the models. Convex hulls demarcate species responses within a food web model. The dashed line corresponds to 0 (no change).

A key distinction between the TBM and regional MSSMs is the intensity of predation pressure (Figure S1 in Supporting Information S1). In TBMs, predation rates are higher than in the regional models across most size classes (Figure S1 in Supporting Information S1), reflecting lower dependence of functional groups on resource spectra for food and stronger trophic interactions between functional groups. Lower predation mortality rates in the regional models is partly explained by the more abundant resources, which also extend into larger size classes in these models. In regional MSSMs, this is often done to account for larger-bodied prey that are not resolved at species- or functional group level. Consequently, warming driven changes in physiological, and especially intake rates in the TBMs are amplified because of stronger feedbacks between the availability of prey and the growth rate of predators; this is clearly seen when only intake is assumed to depend on temperature (Figures 2a and 2b).

4. Discussion

Our comparison of temperature-dependence assumptions across different models yielded at least three important insights. First, we show that the net outcome of warming in food webs is partly dependent on the balance of warming effects on opposing processes that regulate body growth and predation. Ultimately, the direction of the response of aggregate system- and species-level variables will depend on their relative balance under warming.

Second, we show that warming may reduce biomass and catches, but adopting different plausible assumptions regarding activation energy, size-dependent temperature scaling, and their joint occurrence can impact the magnitude and, in some models, the direction of variable responses. Given uncertainty in how the temperature-dependencies should best be captured in ecosystem models, this ambiguity should be acknowledged and incorporated into climate change projections of food webs. Lastly, despite sharing a common size- and physiologically based modeling framework and identical temperature scenarios, we show that the magnitude of variation among temperature assumptions was similar to variation among regional food web models, making simple generalizations on how warming affects fish communities challenging. Rather, our comparisons support the observation that system responses to global warming may require detailed knowledge of species interactions —in particular when considering the differences between the trait-based models and the food web models calibrated to fit a specific system (e.g., Gilman et al., 2010).

Our analysis highlights how adopting temperature dependence assumptions that result in metabolic mismatches or represent size-dependencies in scaling of rates of biological processes are consequential for projecting global warming impacts on food webs. Food web models, including various versions of size spectra models (Blanchard et al., 2012; Jennings et al., 2008; Maury, Faugeras, et al., 2007; Maury, Shin, et al., 2007; Reum et al., 2020), have typically applied the same von Hoff's-Arrhenius temperature corrections to maximum intake, metabolism, and mortality following the metabolic theory of ecology (Brown et al., 2004; Gillooly et al., 2001). However, a metabolic mismatch has been observed in meta-analyses of experimental data (Lemoine & Burkepile, 2012; Rall et al., 2012), and when implemented in size-structured food webs, total SSB, catches, and mean body size generally decreased relative to when uniform activation energies were applied across rates. Moreover, when applying negative body size-dependent scaling, a phenomenon also supported by experimental evidence (Beamish, 1964; García et al., 2011; Messmer et al., 2017; Ohlberger et al., 2012; Strong & Daborn, 1980; Xie & Sun, 1990), the response variables increased slightly. Combined, both measures partially offset each other and system-level variables were more similar to outcomes based on uniform scaling, but importantly, this did not necessarily reflect similarity in outcomes for individual species. Given current uncertainty in how to best represent temperature-dependencies in natural food webs (Lindmark, Audzijonyte, et al., 2022), we suggest analysts acknowledge the uncertainty and carry it through into projections using ensemble modeling frameworks if feasible (Cheung et al., 2016; Gårdmark et al., 2013; Spence et al., 2018). That said, the temperature assumptions we evaluated are not exhaustive and their universality requires further testing. For instance, metabolic mismatch (i.e., faster increase in metabolic rates vs. intake rates) was not supported in an inter-generational experimental study that showed that after three generations baseline metabolic rates of fishes kept at 26 and 30°C remained unchanged, but intake rates were higher at elevated temperatures (Wootton et al., 2022). As empirical evidence accumulates and theory develops, we anticipate that the plausible set of alternative temperature dependence assumptions will also shift.

The use of multiple food web models to evaluate the effects of different temperature dependence assumptions provides a new perspective to previous studies that have explored sensitivities to assumptions using only a single food web (e.g., Lindmark, Audzijonyte, et al., 2022; Reum et al., 2020). Importantly, by using multiple different regional MSSMs but identical temperature dependence assumptions and temperature increase, we show that variability in the magnitude of outcomes of system-level responses across the different assumptions is comparable to variability across food webs. Further, under a subset of assumptions and model combinations, the directional response of system-level variables were inconsistent across food webs; modeled food webs that respond most negatively under warming tended to have higher predation levels and lower reliance on basal resources. Species-level responses, particularly SSB, were also mixed within most food webs and changed across temperature-dependence assumptions. This heterogeneity highlights the importance of species-level interactions in mediating population- and system-level responses to climate change, as also discussed elsewhere (Gårdmark & Huss, 2020; Gilman et al., 2010; Lotze et al., 2019; Tekwa et al., 2022). It also suggests that global food web models that typically consist of simplified, generic functional groups (e.g., Petrik et al., 2019) may have more limited predictive capacity at regional scales than currently assumed. This point can be seen when comparing trait based (TBMs) and multi-species (MSSMs) model outcomes in our study. For biomass and catches the overall direction of responses was often similar across temperature scenarios, but the magnitude differed. In contrast, for mean body sizes TBMs often predicted a decrease with warming (in more complex temperature scenarios), while multi-species regional models overall suggested an increase.

We intentionally limited our temperature-dependency assumption to those associated with individual-level rates impacting body growth and mortality to identify how changing processes at that scale propagate throughout the food web. However, we note that additional processes may exhibit temperature-dependence including maturation (Jonsson et al., 2013), larval survivorship (McLeod et al., 2013), or rates governing dynamics of basal resources (Lindmark, Audzijonyte, et al., 2022). For the latter, in the context of one food web, temperature-dependencies were found to determine whether young age classes responded positively or negatively to warming in terms of size-at-age (Lindmark, Audzijonyte, et al., 2022). Further, an assessment of the total effect of warming on food webs should also address changes in productivity at the base of the food web resulting from, for instance, stronger stratification (Tittensor et al., 2021). Our comparative approach could be adapted to characterize the strength of these and other potential temperature dependence relationships across a variety of food webs. For instance, while we focused our analysis on exponential scalings with temperature, unimodal relationships are also feasible over larger temperature ranges with respect to rates governing feeding (Englund et al., 2011; Portner & Peck, 2010; Rall et al., 2012). Methods for representing and parameterizing unimodal relationships in food webs have been proposed (e.g., Delong et al., 2017; Woodworth-Jefcoats et al., 2019) and could be included in future comparative studies or as part of a model ensemble for a given system (e.g., Reum et al., 2020).

Our findings demonstrate the important role temperature dependence assumptions have on food web responses to warming and indicate the additional uncertainty they may impart into climate-forced projections. Ensemble approaches may help represent this uncertainty (Cheung et al., 2016; Hill et al., 2007) and we encourage continued development of methods to statistically weight ensemble member projections according to skill (e.g., Chandler, 2013; Spence et al., 2018) along with other approaches to better bound and communicate projection uncertainty (Parker, 2013). More generally, our results suggest that past efforts to generate ensemble projections using simplified, generic global food web models (e.g., Bryndum-Buchholz et al., 2020; Lotze et al., 2019; Tittensor et al., 2021) likely underestimate projection uncertainty when alternative temperature-dependence assumptions are not considered in the model set. That said, the models in our study, which explore warming effects on a narrow set of rates, are relatively consistent in projecting reductions in total spawning biomass on average under warming scenarios. This agrees directionally with global ensemble projections consisting of several types of models that differ with respect to structure and forcing variables, and that integrate warming impacts on food availability at the base of the food web (Lotze et al., 2019; Tittensor et al., 2021). While we have focused our analysis on temperature, theoretical frameworks for incorporating oxygen- and CO_2-dependencies on biological rates are also developing (Neubauer & Andersen, 2019; Portner & Knust, 2007; Portner & Peck, 2010), and future studies are needed to evaluate how additional climate-linked changes in marine environments modify food web outcomes under warming.

Data Availability Statement

All simulation outputs analyzed in the present study, along with R code which updates mizer model parameters according to specified temperatures, are available in an online repository [Software] (Reum, 2023, https://figshare.com/s/7ce66c97db8beca8c1c3). Code for the trait-based models and the calibrated North Sea model are available as part of the R package "mizer" (https://cran.r-project.org/web/packages/mizer/). Calibrated regional models are available for: the Eastern Bering Sea [Software] (Reum, 2018); Coastal Tasmania [Software] (Audzijonyte, 2022); SE Australia [Software] (Novaglio, 2021); Central North Pacific [Software] (Woodworth-Jefcoats, 2020); and Baltic Sea [Software] (Delius et a. 2022).

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