

Temperature- and body size scaling: effects on individuals, populations and food webs

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Cover: Colourful and surreal illustrations of fishes found in Moluccas (Indonesia) and the East Indies by Louis Renard (1678 -1746) from Histoire naturelle des plus rares curiositez de la mer des Indes (1754)

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Abstract

Climate warming impacts organisms directly through changes in their physiology. Empirical evidence suggest warming has already led to changes in growth, body size, population and community size-structure of natural populations. However, it is difficult to understand the underlying mechanisms from observational data alone. Therefore, it is important to develop mechanistic population- and food web models grounded in a physiological description of individual life history. This requires knowledge on how physiological processes scale with body size and temperature within species and how those are mediated by ecological interactions, which hitherto is largely unexplored.

In this thesis, I collated data sets through standardized literature searches to understand how body growth, metabolism and consumption rate scale with body mass within species of fish using hierarchical modelling approaches. I also expanded population and food web models to include temperature dependence of physiological rates.

I characterize the intraspecific scaling of abovementioned rates and find that the optimum growth temperature of an individual fish declines as it grows in body mass. Using dynamical models, I show that even simple stage-structure within species together with food dependent ontogenetic development can lead to very different responses to warming compared to similar, but unstructured, population and community models. These include sudden shifts in stage-structure, collapses of top predators and bistability. Analysis of a size-structured model reveals that initial warming can lead to faster growth rates, but this does not lead to larger-sized populations if also basal resources decline with warming.

These findings contribute to a broader understanding of the role of intraspecific size-variation for understanding how climate change impacts population and community structure and dynamics. They also highlight the importance of evaluating physiological responses to warming in an ecological context, as optimum temperatures for growth decline with both body size and reduced food availability.

Keywords: Climate change, community dynamics, size-structure, temperature, metabolic scaling, intraspecific interactions, allometry, consumer-resource dynamics, food webs, temperature-size rule

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Temperatur- och storleksberoende biologiska processer: effekter på individer, population och födovävar

Sammanfattning

Klimatuppvärmning påverkar organismer direkt genom deras fysiologi. Empiriska studier har visat att uppvärmning redan har ledd till förändringar i kroppsstorlek, tillväxtmönster, population och samhällsstruktur, men det är svårt att härleda orsak och verkan endast från empiriska studier. Därför är det viktigt att utveckla matematiska populations- och födovävsmodeller som baseras på fysiologiska processer, såsom födo- och temperaturberoende tillväxt i kroppsstorlek och ontogenetisk utveckling. Detta kräver kunskap om hur fysiologiska processer beror på storlek och temperatur inom arter, och hur detta påverkas av ekologiska födovävsinteraktioner, vilket hittills är relativt outforskat.

I den här avhandlingen genomförde jag en standardiserad litteratursökning för att sammanställa experimentella data på metabolism, födointag och tillväxt hos fiskar. Med hierarkiska statistiska modeller beskrev jag generella mönster av temperatur- och storleksberoende allometri. Jag utökade även strukturerade populations- och födovävsmodeller till att inkludera temperaturberoende fysiologiska processer.

Utöver att karaktärisera generella mönster av temperatur-beroende inomarts-allometri hos fiskar visar jag även att den optimala temperaturen för tillväxt minskar med kroppsstorlek. Med dynamiska modeller visar jag att även enkel stadiestruktur och födoberoende tillväxt inom populationer kan leda till drastiskt skilda svar på uppvärmning i jämförelse med liknande, ostrukturerade modeller. Dessa inkluderar drastiska skiften in stadiestruktur, kollapsar av predatorpopulationer och bistabilitet. Analys av en fullt storleksstrukturerad modell visar att uppvärmning kan leda till ökad kroppstillväxt, men trots det en krympande storleksstruktur om födotillgång minskar med uppvärmning.

Dessa resultat bidrar till en utökad kunskap om betydelsen av variation i kroppsstorlek inom arter för att förstå hur uppvärmning påverkar struktur och dynamik av födovävar. De belyser också vikten av att ta hänsyn av fysiologiska processer på individnivå i en ekologisk kontext för att förstå effekten av klimatförändringar, då optimala tillväxttemperaturer minskar med storlek och minskad födotillgång.

Nyckelord: Klimatförändringar, samhällsdynamik, storleksstruktur, temperatur, metabolisk skalering, inomartsinteraktioner, allometri, konsument-resursdynamik, födovävar, temperatur-storleksregeln

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Dedication

To my dad

When we try to pick out anything by itself, we find it hitched to everything else in the Universe.

John Muir

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List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Lindmark*, M., Ohlberger, J., Gårdmark, A. Intraspecific scaling of growth, consumption and metabolism with temperature and body mass across fishes (manuscript)
- II Lindmark*, M., Huss, M., Ohlberger, J., Gårdmark, A. (2018). Temperature-dependent body size effects determine population responses to warming. *Ecology Letters*, 21 (2), pp. 181-189.
- III Lindmark*, M., Ohlberger, J., Huss, M., Gårdmark, A. (2019). Size-based ecological interactions drive food web responses to climate warming. *Ecology Letters*, 22 (5), pp. 778-786.
- IV Lindmark*, M., Audzijonyte, A., Blanchard, J. L., Gårdmark, A. Bottom up and top down effects of temperature on body growth, population size-spectra and yield – an application of a multispecies size-spectrum model (manuscript)

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The contribution of Max Lindmark to the papers included in this thesis was as follows:

- I Conceived the idea, participated in planning and designing the study, collated and analysed data, wrote the first draft.
- II Participated in planning and designing the study, parameterised the model, performed modelling and empirical analysis, wrote the first draft, led the revision of the manuscript.
- III Participated in planning and designing the study, parameterised the model, performed modelling and empirical analysis, wrote the first draft, led the revision of the manuscript.
- IV Conceived the idea, contributed to adapting model code, parameterized and analysed the model, wrote the first draft.

1 Introduction

The unprecedented rate of warming of our planet constitutes major scientific challenges. In order to understand and predict the ecological consequences and societal impacts of climate change, we need to adopt integrated approaches in research. These should link physiology to ecological processes across scales, from individuals to food webs.

1.1 Metabolic ecology

It has long been known that temperature affects the velocity of chemical reactions, and biological processes are no exception. One classical example of this is the observation by astronomer Harold Shapley that the pace at which ants ran at near the Mount Wilson Observatory in California was so linked to the ambient temperature it could be used as a thermometer (Shapley, 1924). The mechanism here is of course that the metabolic rate of individual ants is directly affected by the ambient temperatures. As the ectotherms they are, they do not internally regulate their body temperatures. More formally, the temperature dependence of individual metabolism is often described by $\propto e^{-E/kT}$, where E is the activation energy [eV], k is Boltzmann's constant (8.62×10^{-5} eV K⁻¹) and T is absolute temperature [K] (Gillooly *et al.*, 2001). Biological rates, such as metabolism, therefore increase exponentially with temperature – at least within so called “biologically relevant” temperature ranges (Gillooly *et al.*, 2001).

In addition to temperature, the variation in body mass in the animal kingdom is immense, and an old-established observation is that most characteristics of animals can be described as functions of body mass (Huxley, 1932; Kleiber, 1932; Peters, 1983; Brown *et al.*, 2004). These characteristics can be described by power functions – so called allometric functions – of the form $Y = Y_0 M^b$,

where Y is a response variable, Y_0 is a normalization constant, M is body mass and b is a mass-scaling exponent. This includes also metabolic rate. On a log-log scale, this relationship becomes $\ln(Y) = \ln(Y_0) + b \times \ln(M)$, where $\ln(Y_0)$ now represents the intercept and b the slope in a linear regression. The exact value of b for metabolic rate has for long been subject to much debate, and several hypotheses have been put forward to explain values between $2/3$ and 1 . The surface rule predicts $b=2/3$ based on the assumption that surfaces scale with volumes with a power of $2/3$ and that heat loss is proportional to surfaces (note this hypothesis applies only to endotherms) (Rubner, 1902). By contrast, the metabolic-level boundary hypothesis predicts that the exponent co-varies with the activity level (intercept) so that the actual exponent will vary depending on what constraints metabolism. If metabolism is primarily limited by resource fluxes (e.g. at resting), metabolism scales as surfaces with an exponent of $2/3$, whereas if energy demand limits metabolism (e.g. at peak activity) it scales with mass with an exponent of 1 , i.e. in proportion to mass (Glazier, 2005). A more widely adopted scaling model is the WBE model (West, Brown and Enquist, 1997, 1999), which states that metabolic rate is ultimately constrained by nutrient uptake and transport in fractal-like networks, which causes metabolism to scale with body mass with an exponent of $3/4$. This prediction is in line with the between-species empirical observation that metabolism is proportional to mass with an exponent of $3/4$, known as Kleiber's law (Kleiber, 1932).

The metabolic theory of ecology (MTE) links the fractal scaling model by West et al. (West, Brown and Enquist, 1997) (WBE) with a an exponential temperature scaling factor to correct for the biochemical kinetics of metabolism (Gillooly *et al.*, 2001). Thus, the whole-organism metabolism, B , of any organism, can approximated only from mass and temperature: $B \sim M^{3/4} e^{-E/kT}$. However, while MTE is argued to be derived from first principles, the model has been questioned, both for invoking universal mass-scaling exponents (Bokma, 2004; Glazier, 2005; Downs, Hayes and Tracy, 2008; Isaac and Carbone, 2010; Englund *et al.*, 2011) but also for not being mechanistic (Kozłowski, Czarnołćeski and Dańko, 2004). Despite this, the MTE is undoubtedly the most applied and discussed framework for the emergence and maintenance of allometric scaling laws as well as their implications for biological and ecological processes across scales (Brown *et al.*, 2004). Based on two central ideas, (1) the predictability of individual metabolism from body mass and temperature, and (2) that metabolism represents the uptake, transformation and excretion of energy and materials and thus links individuals to each other and to the environment, it is possible to derive predictions for processes and patterns at higher levels of biological organization. Early applications of the metabolic framework showed it was successful in explaining variation in many macro-

ecological patterns, including the global pattern of declining biodiversity with distance from the equator (Allen, Brown and Gillooly, 2002).

In summary, allometric scaling laws result in non-proportional scaling of individual-level biological rates with body mass. This can be used to predict emergent phenomena, such as population growth rates and population densities (Savage *et al.*, 2004). The consistency with which body size affects biological rates across taxa has for long inspired research aimed to reduce the complexity of natural living systems through generalization based on body mass (Sheldon, Sutcliffe and Prakash, 1973; Peters, 1983; Schmidt-Nielsen, 1984).

1.2 Allometry in population and community ecology

“In the context of science, the well-known adage ‘a picture is worth a thousand words’ might well be ‘a model is worth a thousand datasets’”

- Rackauckas *et al.* (2020)

The main goal of any mathematical model (to which the quote refers), is to allow ecologists to understand why and how patterns inferred from statistical models emerge and are maintained (Rossberg *et al.*, 2019). Models therefore vary immensely on a spectrum ranging from simple abstractions with minimal sets of functions and parameters to complex descriptions of multiple pathways, depending on which processes they are aimed to capture and which patterns to recreate (Yodzis and Innes, 1992). When modelling population and community dynamics, it is for instance important to describe the dynamics of interacting species, traditionally using differential equations (Lotka, 1920; Volterra, 1926). Such consumer-resource interactions constitute the backbone of food webs (De Roos, 2018). Modelling them is however not an easy task, and one might add “good” before “model” in the opening quote. The challenge is that (1) the complexity of a model increases rapidly with the number of interacting species (2) representing species requires many parameters (3) these models are often subject to high parameter- and structural sensitivity. A trade-off emerges here between model tractability and generality (simple) and comprehensiveness and accuracy (complex) (Yodzis and Innes, 1992).

As body size is a key trait of species, parameter complexity can largely be reduced through the use of body mass and allometric scaling relationships. This reduction of complexity is a necessity for deriving general theories of community ecology. As an example of an “intermediate” approach to these trade-offs, Yodzis and Innes (1992) recast the consumer-resource model by Rosenzweig-Arthur model (Rosenzweig, 1971) in terms of biomass. Model parameters were based on allometric $3/4$ power-law scaling of physiological and

ecological rates, such as metabolism and foraging, based on interspecific scaling informed from meta-analyses. Such body-size based approaches to population and food web modelling have resulted in generic models that overcome the issues with species-specific parameters. The body-mass approach has also been expanded to allometric-trophic network models, i.e. by invoking constraints also on the body mass structure of food web networks and “who eats whom” (Brose, 2010; Brose *et al.*, 2016), which has led to new insights into the dynamics of more complex and species rich food webs (Brose, Williams and Martinez, 2006; Brose, 2010)

1.3 Warming and consumer-resource dynamics

In a seminal study, Vasseur and McCann (2005) further developed the bioenergetic framework of Yodzis and Innes for consumer-resource dynamics to account for the effect of temperature on allometric biological and ecological rates. By conforming to the MTE, the model by Vasseur and McCann represents an important step in deriving general understanding on the temperature dependence of consumer resource dynamics. Their modelling framework resulted in three general conclusions on the effects of warming on consumer-resource dynamics: stable systems may turn unstable (cyclic), resource densities always decline, and mathematical extinctions do not occur (although species may be more vulnerable to extinctions when cycling). However, subsequent modelling- and experimental studies within similar bioenergetic frameworks have produced highly diverse predictions. These often contrast the original predictions, e.g. by showing how warming can have *destabilizing* effects and cause consumer extinction (Rall *et al.*, 2010; O’Connor, Gilbert and Brown, 2011; Binzer *et al.*, 2012).

These newer findings can largely be explained by *negative* temperature effects on resource carrying capacity, K (Binzer *et al.*, 2012; Uszko *et al.*, 2017), as well as *reduced* rather than *increased* energetic efficiency of consumers (metabolic costs increasing faster with temperature than energetic gains). These two features were not considered in the model by Vasseur and McCann and will be discussed briefly below.

First, the carrying capacity in these models is a phenomenological parameter, and the temperature-dependence of it is (surprisingly) poorly understood given its importance for ecological dynamics and extinction risks. Metabolic theory does, however, suggest that carrying capacity should decline in proportion to the increase in metabolic rate. This stems from the argument that if metabolic rates increase and all else is constant (mainly the size-structure and nutrient levels), the abundance or biomass at equilibrium must decline (Savage *et al.*, 2004;

Bernhardt, Sunday and O'Connor, 2018). Experimental evidence support this prediction (Bernhardt, Sunday and O'Connor, 2018). However, it should also be noted that more mechanistic resource based approaches reveal that an exponential relationship between K and temperature is a special case of a much more complex set of relationships (Uszko *et al.*, 2017; Lemoine, 2019).

Secondly, in terms of the effects of warming on the energetic efficiency of consumers, the general predictions are very diverse. However, a dominant view seems to be that warming leads to reduced energetic efficiency (Rall *et al.*, 2010; Lemoine and Burkepile, 2012), but see (Angilletta and Dunham, 2003; Englund *et al.*, 2011). In a modelling and microbial experimental study, Fussmann *et al.* (2014) approached this parameter uncertainty by drawing activation energies from a global database. This allowed them to evaluate the probability of obtaining a combination of parameters that lead to energetic efficiency decreasing or increasing, and thus also a prediction on persistence and stability. They found that if warming decreases energy transferred to consumers relative to their losses (e.g. through metabolism or mortality), population dynamics stabilized – at the cost of increased extinction risk. However, it remains uncertain if the global data base used for estimating activation energies represents general scaling across taxa, both within and between species. Another approach to reconciling these diverse predictions was presented in Uszko *et al.* (2017), in which by relaxing the assumption of exponential temperature dependence, the authors were able to map essentially all previous predictions as special cases into a single map of enrichment and temperature.

Despite the challenges of mechanistically describing the implications of warming on the dynamics of the simplest communities, progress has been made to generalize findings through a reduced set of important parameter combinations (Fussmann *et al.*, 2014; Gilbert *et al.*, 2014; Uszko *et al.*, 2017). However, while incorporation of body size and temperature in bioenergetic models allows generalising predictions, climate warming effects are more intricate than that even in simple models, due to the direct, plastic effects of warming on body size itself.

1.4 Climate warming, body size and community dynamics

Declines in body size of organisms with warming is suggested to constitute one of three universal responses to warming, the other being changes in phenology and poleward migration (Daufresne, Lengfellner and Sommer, 2009; Gardner *et al.*, 2011; Sheridan and Bickford, 2011). These predictions on body size stem largely from empirical analysis of climate signals in time series and effects of

warming in experiments. Although, it seems likely that the generality of this prediction has been reinforced by its accordance with other more or less closely related observations and ecological rules. These include (1) the higher efficiency of smaller species at exploiting limiting resources due to the higher surface-to-volume ratio, which could lead to competitive exclusion of larger species of e.g. phytoplankton (Litchman, Klausmeier and Yoshiyama, 2009; Yvon-Durocher *et al.*, 2011), (2) the macro-ecological rules that explain temperature-body size relationships, such as Bergmann's rule (Bergmann, 1847) describing the positive relationship between endotherm body size and latitude (but see (Riemer, Guralnick and White, 2018)) and James' rule, which is the intraspecific equivalent (Blackburn and Gaston, 1996; Saunders and Tarling, 2018), and lastly, (3) the temperature size-rule (TSR), stating that individuals reared at colder temperatures grow to larger body sizes.

What are the implications of climate driven changes on body size in mechanistic population and community models using body size as a generalizing trait? This is a much more recent question, but two studies have investigated this by phenomenologically implementing body size reductions with temperature in line with average effects from the literature, within the bioenergetic framework of Gilbert (Gilbert *et al.*, 2014; Osmond *et al.*, 2017) and Yodzis-Innes (Yodzis and Innes, 1992; Sentis, Binzer and Boukal, 2017). Taken together, these studies indicate body size reductions may buffer from extinctions. Specifically, in a food-chain model, community persistence, measured as number of surviving species (food chain length) generally increases if body sizes decrease in warmer environments, due to weakened interaction strengths between species (Sentis, Binzer and Boukal, 2017). In a consumer-resource model, it was in addition found that smaller mean body sizes can increase community stability (defined as return times from perturbations). This could mean increased resilience of consumer-resource systems, which by extension could buffer against extinctions (Osmond *et al.*, 2017).

Thus, the bioenergetics framework is a promising framework for understanding the implications of body mass reductions at the *interspecific* level, i.e. reductions in the average body size. However, it is at this point extremely relevant to ask how much we can generalize with the interspecific approach to body size-variation, where body size is a trait of a species rather than of an individual. This does not account for intraspecific size-variation nor effects of temperature that vary over ontogeny. These classic assumptions in community ecology may be especially limiting in the light of climate change, because temperature affects individual physiology, and the consequences may vary over ontogeny.

1.5 Body size variation: at which level of biological organization?

1.5.1 Intraspecific temperature responses

The intraspecific and individual-level responses to warming are complex, and the only more or less consistent observation is that responses tend to vary over ontogeny (Ohlberger, 2013; Huss *et al.*, 2019; van Dorst *et al.*, 2019). Responses to warming may therefore turn from positive to negative within a life span (Ohlberger, 2013).

As previously mentioned, the temperature-size-rule (TSR) is the adaptive plastic response of adults reaching smaller body sizes when reared in higher temperatures. It describes a response rather than a macro-ecological pattern, and it has been observed in numerous experimental studies (Atkinson, 1994; Forster, Hirst and Atkinson, 2012), as well as latitudinal gradient studies of insects (Horne, Hirst and Atkinson, 2015). For fishes, however, the empirical findings are somewhat more diverse. If looking at asymptotic body size of fishes rather than average adult body mass, there are some recent examples that can be contrasted. For instance, an experimental study on ontogenetic growth found no clear effect of warming on the asymptotic body size of fish (Barneche, Jahn and Seebacher, 2019). Moreover, Huss *et al.* (2019) did not find any effects on the growth of older and fish (only positive effects on smaller and younger fish), and there does not seem to exist a latitudinal gradient in growth nor asymptotic mass (van Denderen, Gislason and Andersen, 2019), suggesting other factors shape asymptotic size, e.g. temperature selecting for different life histories. However, analyses of times series of asymptotic mass among fishes revealed negative correlations with warming in the North Sea (Baudron *et al.*, 2014), and maximum mass was also found to be negatively related to water temperature in study on Mediterranean fish communities (van Rijn *et al.*, 2017). Moreover, experimental studies of fish have revealed declines in the optimum temperature for both growth and maximum consumption rates with body size (Steinarsson and Imsland, 2003; Björnsson, Steinarsson and Árnason, 2007; García García *et al.*, 2011), which indicates that physiological constraints for individuals at least contribute to species not being able to grow to large sizes in warmer waters.

However, more common than temperature-driven declines in the body size of large or old fish is the positive relationship between temperature and body growth, especially of young individuals. Reconstructed growth histories of individual fish through ageing based on bony structures (otoliths) often show positive correlations between growth rates and warming (Thresher *et al.*, 2007; Neuheimer *et al.*, 2011; Baudron *et al.*, 2014; Huss *et al.*, 2019; van Dorst *et al.*,

2019). This increased growth can also be predicted from the numerous experimental studies showing that growth increases with temperature until a peak is reached, after which additional warming is deleterious (Brett, Shelbourn and Shoop, 1969; Elliott and Hurley, 1995; Jobling, 1997; Morita *et al.*, 2010; García García *et al.*, 2011; Ohlberger, 2013; Barneche, Jahn and Seebacher, 2019).

Can a closer look at the proposed mechanisms reconcile these diverse patterns of the TSR in fishes? The observation of stronger TSR-effects in aquatic compared terrestrial environments led to debate about whether or not physiological constraints (rather than adaptation) played a role in this, specifically oxygen-related constraints, which are more pronounced in aquatic environments (Verberk and Atkinson, 2013; Ern *et al.*, 2015; Hoefnagel and Verberk, 2015; Horne, Hirst and Atkinson, 2015; Audzijonyte *et al.*, 2018). Oxygen limitation has also been suggested as a driver of reduced asymptotic size of fishes, based on the assumption that the limiting resource for body maintenance is oxygen, and large fish are more oxygen limited compared to small due to the allometric scaling of gill surface area and isometric scaling of maintenance costs (Pauly and Cheung, 2018). While the view of asymptotic body growth being the result of resource limitation (be it oxygen or other resources) is fundamental in most mechanistic growth models (Pütter, 1920; von Bertalanffy, 1938; West, Brown and Enquist, 2001; Pauly and Cheung, 2018), it has recently been questioned on physiological grounds for being too simplistic for predictions about growth and size-relationships (Lefevre, McKenzie and Nilsson, 2017, 2018; Marshall and White, 2019a, 2019b). Specifically, scaling relationships do not match empirical data, and if they would, predictions about the effects of warming become very large (Lefevre, McKenzie and Nilsson, 2017).

To increase our understanding about the size-dependent growth responses to temperature, it is important to reconcile mechanistic growth models with intraspecific data. However, our understanding of general or average intraspecific mass- and temperature scaling is limited, in particular for consumption rates. One factor contributing to this is the lack of comprehensive data sets (Dell, Pawar and Savage, 2011). The distinction between intra- and interspecific scaling is important not mainly for conceptual reasons (i.e. because metabolism occurs within the individual), but because scaling relationships may differ within and between species (Glazier, 2005; Jerde *et al.*, 2019) (Figure 1). The consequence of this data limitation is that intraspecific processes are being inferred from interspecific data (Brown *et al.*, 2004) or from single studies or meta-analyses of a subset of experiments (Jerde *et al.*, 2019). The former is potentially misleading as rates can scale differently with body mass and

temperature within and between species (Glazier, 2005; Englund *et al.*, 2011; Rall *et al.*, 2012; Jerde *et al.*, 2019). Moreover, metabolic scaling theories such as the MTE assume fixed scaling relationships rather than fitting multiple regression models when confronting theory to data. This can lead to erroneous estimates when actual scaling parameters deviate from predictions or assumptions (e.g. the mass-scaling exponent is commonly found not to be $3/4$ within species). Lastly, the average metabolic rate of a small species may not be the same as a young individual of a large bodied species. The latter, i.e. using single studies, can lead to inflated variation in general scaling relationships as they do not typically account for taxonomic structure or extreme observations.

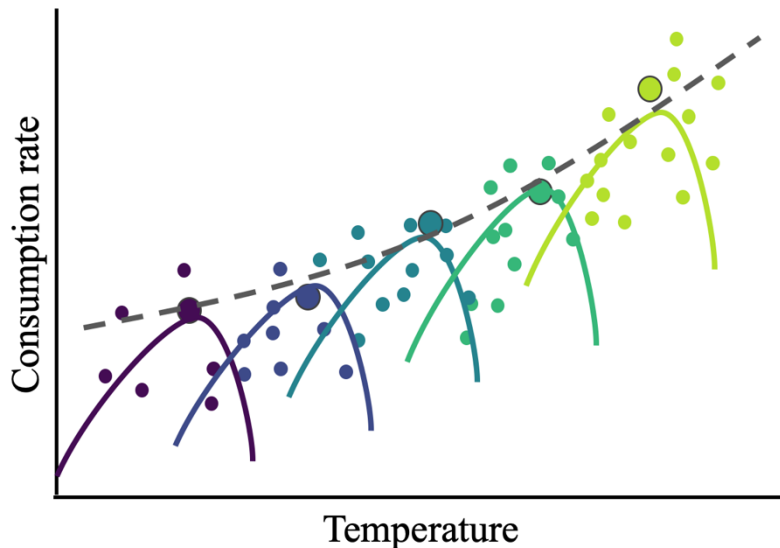


Figure 1. Example illustration of the differences between inter- and intraspecific temperature dependence. Points represent data and colours indicate species. In interspecific approaches, usually one representative observation is taken from each species (indicated with enlarged points), often measured in an adult at a suitable reference temperature for that species. Across all species, exponential curves may be fitted. However, in order to characterize a *response to* rather than a *pattern with* temperature, it is important to evaluate average intraspecific responses across species. In the case of a rate that is unimodal at the intraspecific level, such as consumption, this is especially clear because the thermal responses differ also in form. However, it also applies to other rates, even if they are of the same form within and between species. For instance, metabolism is exponentially increasing with temperature also within species, but the thermal sensitivity (activation energy) may differ within and between species. *Conceptual figure inspired by Rall et al. 2012.*

In summary, while a broader focus on intraspecific processes is important for understanding the size- and temperature dependence of individual-level performance, it is as important to consider the food web aspect of it (Neubauer and Andersen, 2019). The inability of a single physiological framework to

describe *all* aspects of the TSR highlights the importance of the ecological context (Ohlberger, 2013; Neubauer and Andersen, 2019). For instance, it is well known that optimum growth temperatures decline with reduced food availability and experimental studies suggest it also does so with body mass (Brett and Shelbourn, 1975; Björnsson, Steinarsson and Árnason, 2007; García García *et al.*, 2011; Betini *et al.*, 2019; Huey and Kingsolver, 2019).

1.5.2 Population size-structure

The size-based approaches to ecology described so far – the allometric scaling laws and population and community models – typically rely on the large variation in body mass across species. However, body size is not only a trait of a species, but also an individual (Brose *et al.*, 2017). The implications of intraspecific scaling and size-variation on population and community dynamics and structure are perhaps most clear when contrasting size-based allometric models (unstructured at the intraspecific level) to similar models with simple within-species size- or stage structure.

One of the more striking simplifications of unstructured models is the lack of representation of individual life history and ontogenetic development (Hartvig, Andersen and Beyer, 2011; Persson and De Roos, 2013; Brose *et al.*, 2016). In aquatic ecosystems and fish in particular, characterizing a species with a single body mass is seldom warranted. Not only do they grow several orders of magnitude in body size over ontogeny, they also typically undergo several ontogenetic niche shifts and thus also have different ecological functions and interactions depending on their body size (Werner and Gilliam, 1984; Persson and De Roos, 2013). In fact, the range through which a fish increases in body size through its life can be larger than the difference across species with which they interact. This, together with the fact that fish encompass the highest species richness among vertebrates and occupy essentially all aquatic habitats (Froese and Pauly, 2016), makes them great model organisms for size-based ecology. Given the ubiquity of body size variation within species, the follow up question then becomes, when is body size variation important within species for understanding ecological dynamics?

By contrast, structured models (i.e. here referred to as models with structure also within species), take into account variation between individuals within a population with respect to another state, e.g. age, life stage or body mass. Alongside the development of allometric community models (e.g. Yodzis and Innes (1992) and (Brose, Williams and Martinez (2006))), physiologically structured population models, PSPMs, were developed (Metz and Diekmann, 1986; De Roos and Persson, 2001). Founded in dynamic energy budget theory,

these models mechanistically resolve the ontogenetic processes of food-dependent body growth, ontogenetic diet shifts and ontogenetic development into maturing individuals, usually of a single population due to the model complexity (Persson *et al.*, 1998).

Despite the complexity of these models, the work on size-based population and community ecology within the PSPM framework has revealed three main implications of structure (size- or life stage) and ontogenetic development within species. These are population- or stage specific increases in biomass with mortality (De Roos *et al.*, 2007), generation or cohort cycles (Persson *et al.*, 1998) and alternative stable states (De Roos and Persson, 2002). These phenomena are not only predicted from theory but also found in experimental and observational data (Murdoch *et al.*, 2002; Schröder, Persson and De Roos, 2005; Persson *et al.*, 2007; Huss and Nilsson, 2011; Ohlberger *et al.*, 2011; Schröder, van Leeuwen and Cameron, 2014; Reichstein, Persson and De Roos, 2015). In species-poor lake ecosystems in particular, these mechanisms on food-dependent development have been identified as major drivers of the size structure and dynamics. This includes the change in (and maintenance of) population and food web size-structure, and lack of recovery from overexploitation (Persson *et al.*, 2007; Ohlberger *et al.*, 2011). The underlying mechanisms have been made clear through model-simplification, specifically by discretizing the continuous size-structure into discrete stages (size-classes) (De Roos *et al.*, 2008; De Roos and Persson, 2013; De Roos, 2018). This has successfully revealed the minimal necessary conditions behind the observed dynamics and behaviour of complex stage- or size-structured PSPMs, which are juvenile-adult structure and food-dependent development (De Roos, 2018). In the case that individuals in different life stages differ in their efficiency to exploit a shared resource, due to e.g. differences in energetic efficiency, the growth or biomass production of juveniles and adults become unequally limited by food availability (Figure 2). This is referred to as ontogenetic asymmetry in energetics (Persson & De Roos, 2013). The main implication of ontogenetic asymmetry is that it can explain how life stages can increase in equilibrium biomass with increased mortality, due to relaxation of density dependence. It is this mechanism that leads to biomass overcompensation, and it can lead to predictions about alternative stable states in a community.

However, while providing general insights, discretization may also come with a cost, as many processes and features of populations and communities are size rather than stage-based (Hartvig, Andersen and Beyer, 2011). In parallel, other approaches that do not involve discretization has been developed.

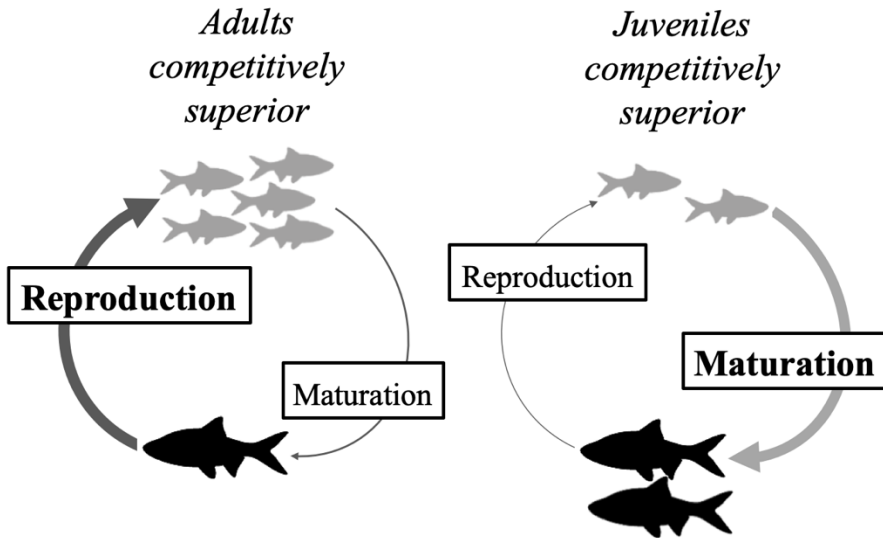


Figure 2. Food- and size dependence of the life history processes reproduction and maturation leads to different resource requirements for development (maturation) and producing offspring. In these figures, density dependence varies over ontogeny, such that energetic bottlenecks emerge in the population. If adults are competitively superior, strong density dependence occurs in the numerous juvenile life stage, which reinforces the low competition in the adult life stage through a slow maturation process. A large recruitment can then be maintained through these feedbacks between population structure and individual-level performance. The opposite phenomenon emerges when juveniles are competitively superior.

As a means of overcoming the issue of species-specific and parameter-rich PSPMs while still maintaining a physiological description of individual life history, Hartvig, Andersen and Beyer (2011) combined the trait-based approach for parameterization (mainly using size at maturity and asymptotic size as traits) with the size-spectrum modelling framework, based on size-spectrum theory (Andersen and Beyer, 2006). This modelling framework constitutes a promising tool for simplifying modelling of species-rich and size-structured food webs (Hartvig, Andersen and Beyer, 2011; Scott, Blanchard and Andersen, 2014; Blanchard *et al.*, 2017; Andersen, 2019) to address the effects of e.g. fishing (Andersen and Pedersen, 2009; Blanchard *et al.*, 2012, 2017; Jacobsen, Burgess and Andersen, 2017). In addition, trait-based size-spectrum models provide great flexibility for implementing more species traits and characteristics, if the aim is to represent a specific food web (Scott, Blanchard and Andersen, 2014; Reum *et al.*, 2019). Such species-based size-spectrum models have been used to evaluate fisheries management scenarios (Blanchard *et al.*, 2014), and for confronting emergent phenomena in models such as realized feeding interactions to empirical diet data (Reum *et al.*, 2019).

The combined effects of multiple stressors, such as fishing and climate change is only recently being researched within this framework (Blanchard *et al.*, 2017; Woodworth-Jefcoats, Blanchard and Drazen, 2019). This is especially true for species-resolved size-spectrum models (in contrast to community-size spectrum models, e.g. Blanchard *et al.*, (2012)). Predictions from size-based food web models on the effects of climate warming are usually tightly linked to changes in productivity, abundance and size-structure of phyto- or zooplankton, which are resources for higher trophic levels (Blanchard *et al.*, 2012; Barange *et al.*, 2014; Canales, Law and Blanchard, 2016; Woodworth-Jefcoats, Blanchard and Drazen, 2019). Results from such models tend to show that declines in resource abundance leads to less energy being transferred to the top of the population or food web. This then results in changes in relative abundance of large individuals (and/or species) and declines in average population and/or community body size (see Figure 3). However, as discussed previously, it is often observed that initial warming leads to faster growth rates, especially for small individuals. Since this is at least partly driven by faster metabolism and food intake rates, it is important to develop models that allow also physiological rates to scale with temperature. These can ideally disentangle these different mechanisms by which population and community size-structure can change with warming.

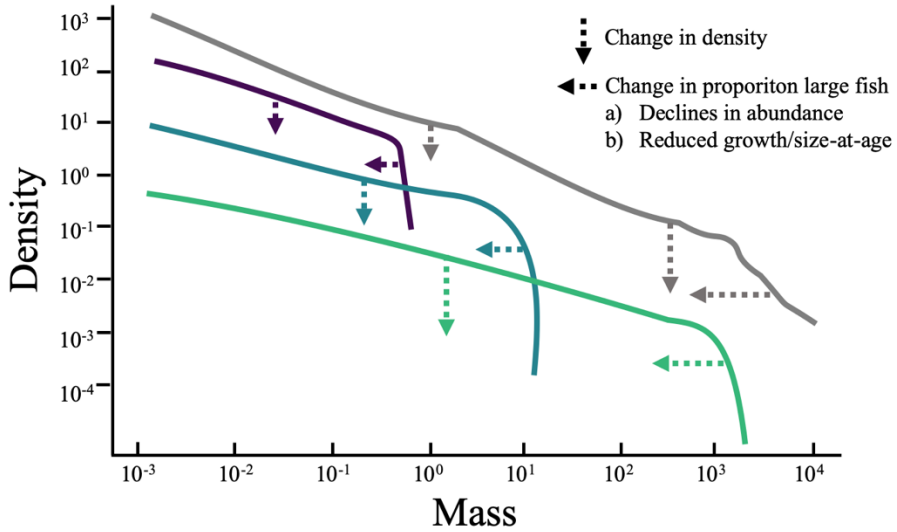


Figure 3. Example illustration of emergent numerical size spectra in a three species food web model (species of different asymptotic mass indicated by colours), and the overall community spectra (grey). The community size structure can change through different mechanisms in a species-resolved food web. Warming can reduce the overall density, if less energy is transferred to the species. This might affect the density of large fish relatively stronger (indicated by longer vertical arrows), which leads to decreases in average community body sizes, and a steeper community size spectrum. This is an interspecific change in relative size-composition. The relative change in size-composition can also occur within species (indicated by horizontal arrows). The horizontal change can emerge from two processes: declines in the relative abundance of large fish, or through changes in growth or size-at-age of the largest fish (individual-level response). How these different processes act in combination is largely unexplored.

2 Goal of the thesis

To summarize this far, intraspecific size variation has the potential to largely drive ecological dynamics, and the importance of intraspecific trait-variation is increasingly acknowledged (Bolnick *et al.*, 2011; Miller and Rudolf, 2011; Persson and De Roos, 2013; Des Roches *et al.*, 2018). Understanding climate impacts on food webs requires mechanistic size-based approaches, as thermal responses vary over ontogeny, body size and food-levels (Pörtner and Knust, 2007; Ohlberger, 2013; Huey and Kingsolver, 2019). However, how intraspecific stage- or size-structure modulate responses to climate change is essentially unexplored.

In this thesis, the overall aim is to (1) increasing the understanding of how key biological rates scale with temperature and body size within species and (2) how intraspecific stage- or size-structure affects the response of populations and food webs to warming, with respect to dynamics and structure. These questions are addressed using both statistical and mathematical modelling approaches to solve more specific research questions, which are described in more detail below.

In **Paper I** I address the knowledge gap of how growth, metabolism and consumption scale with body mass and temperature within species. This is done by first collating data sets from experimental studies using standardized literature searchers. To these data I fit flexible Bayesian hierarchical models to estimate the joint effects of temperature and body mass on these rates with shrinkage, while accounting for variation across and between species. I investigate the following questions: how does intraspecific scaling differ from interspecific scaling (on which most metabolic scaling theory rest)? Do metabolism, consumption and growth scale in similar ways with body mass and temperature? What are the implications of the intraspecific scaling relationships for growth-dynamics?

In **Paper II**, I ask the question: what is the effect of intraspecific stage structure for how a consumer-population responds to warming? How do responses change when life-stages are differently affected by temperature? To answer this, I incorporate temperature-dependence into a bioenergetic stage-structured biomass model. This modelling framework can under special cases resemble unstructured population and community models, but in addition accounts for food dependent ontogenetic development and stage-structure within species. This makes it a good model for contrasting the effects of stage-structure to unstructured models. I analyze how equilibrium population biomass and stage-composition is affected by physiological temperature dependence that is modified through intraspecific competitive interactions.

In **Paper III**, I expand the model in Paper II to a three-species food chain to investigate how stage-structure modifies the effects of warming on community stability and predator persistence. Using a simplified model version, I identify the mechanisms that cause the structured food chain to exhibit different dynamical responses to warming compared to unstructured models. Here I ask: how does stage-structure in the consumer population shape the dynamical responses to warming? Under what circumstances can the dynamical responses to warming of the stage-structured food chain be predicted from theory on unstructured food chains?

In **Paper IV** I expand a size-spectrum food web model (parameterized and calibrated to represent a simplified Baltic Sea food web) to evaluate the combined effect of temperature dependence of physiology and resource dynamics using a set of scenarios representing different assumptions about temperature effects. I investigate the emergent effects of warming on individual-body growth, population size-structure and fisheries yield. With this approach, I am able to address the following research questions: how are individual growth rates affected by warming in the different scenarios? What is the relative effect of changes in size-at-age compared to changes in abundance-at-size for population-level size-structure? How are fisheries reference points and targets affected by emergent changes in growth versus population size-structure? In addition, I also address parameter uncertainty in otherwise deterministic models by performing simulations with random parameterization of temperature-scalars, inferred from Paper I. The findings are discussed with respect to other modelling frameworks and observations of changes in growth trajectories in marine fish.

3 Materials and Methods

3.1 Data analysis

To overcome the knowledge gap about intraspecific scaling of metabolism, consumption and growth, I performed standardized literature searches with the aim to collate experimental data that included both mass and temperature replicates of fishes. This requirement of factorial experimental designs means that only a fraction of all experimental studies could be used in this study. However, it also means that the data I acquired allowed for estimation of the joint effects of temperature and body mass within species. I searched the Web of Science Core Collection for data on individual growth rate, maximum consumption rate (feeding rate at unlimited food supply, ad libitum) and resting, routine and standard oxygen consumption rate as a proxy for metabolic rate (Nelson 2016). The searches are described below.

For growth rate, I used the following topic terms: (growth) AND (mass OR weight OR size) AND (temperature*) AND (optimum), as well as: (growth) AND (mass OR weight OR size) AND (temperature*) AND (optim*). For metabolic rate I used: (metabolism OR "oxygen-consumption" OR "oxygen consumption") AND (mass OR weight OR size) AND (temperature*). For maximum consumption I used: (consumption or feeding\$rate or food\$intake or bio\$energ* or ingestion or food-intake) AND (mass or weight or size) AND (temperature*), as well as: (feeding-rate or bio-energ*) AND (mass or weight or size) AND (temperature*). I also applied additional filters on subject: 'marine freshwater biology', 'fisheries', 'ecology', 'zoology', 'biology', 'physiology'. For growth rates, I in addition included 'limnology' and for maximum consumption I included 'limnology' and 'evolutionary biology'.

Data from these searches were compiled to four datasets: growth-, metabolic- and maximum consumption rate, and the optimum growth rate temperature for each combination of body mass group and species. I acquired in total 154, 2790

and 626 data points from published articles for each rate, from 13, 35 and 18 species, respectively, representing a diverse range of taxonomic groups, habitats and lifestyles (Appendix S1). Data were extracted from published tables or figures using Web Plot Digitizer v. 4.1 (Rohatgi, 2012). A more detailed description of the data collection, criteria and standardization can be found in Paper I of this thesis.

To a subset of these data that included only temperatures below optimum, I fitted hierarchical log-linear models in a Bayesian framework. Biological data often contain some kind of hierarchical clustering or nesting (by individual, taxonomic structure, space, time etc.), and this can be accounted for in a hierarchical model by specifying models both at the global level and per cluster. Some notable features of hierarchical models make them very useful in this context, where the research aim is to identify general intraspecific scaling relationships. First, it means I can define a sub-model on the species-level which avoids pseudo-replication due to observations being clustered by species. Second, parameters are estimated on data from all groups by assuming they come from a common distribution. This has the effect that group-level parameters are driven towards the mean, a phenomenon called “shrinkage” (Gelman and Hill, 2007). Shrinkage is strongest for groups with few data points as information from data-rich groups also inform the global distribution (“partial pooling”). This means that the group-level estimates are not as extreme as they would be with purely single species models where no pooling occurs. Models with no pooling (e.g. species as a fixed effect) introduce a lot more parameters (one per species and parameter), which is not an efficient use of data compared to estimating a distribution, as in the hierarchical model. Given the relatively few data points per species in these data (due to the factorial body mass and temperature criterion), I can still estimate species-level parameters accurately by borrowing information across fishes (Gelman and Hill, 2007). The Bayesian approach also contributes to this, as I specify semi-informative prior distributions to aid model convergence. Third, in contrast to fixed effects models (only one level of variation), hierarchical models allow prediction for a new group – i.e. an unmeasured species, by using the mean of the global distribution for prediction (Harrison *et al.*, 2018). I.e. one can assume that a new fish would be drawn from the same global distribution that we assume the current fishes belong to. Thus, the combination of mass and temperature-treatments within species and the modelling framework allows me to estimate average intraspecific mass and temperature-scaling parameters for fishes in general.

I also fit quadratic models to single species for maximum consumption data, as the thermal response is unimodal over the full temperature range. These models were not hierarchical, due to difficulties in standardizing data across

species with respect to width of thermal response, optimum temperature and distance between habitat and optimum growth temperatures. Thus, models were fitted by species.

All data and R code (data manipulation, analyses and figures) can be downloaded from a GitHub repository (<https://github.com/maxlindmark/scaling>) and will be archived on Zenodo upon publication.

3.2 Mechanistic population and food web models

To investigate the effects of warming on individuals as well as the structure and dynamics of populations and food webs, I expanded two similar models of varying complexity: a stage-structured biomass model (De Roos *et al.*, 2008) and a species-resolved size-spectrum model (Scott, Blanchard and Andersen, 2014). Both modelling frameworks have important features in common: a bioenergetic description of energy flow, food-dependent growth and development and a type II Holling functional response (Holling, 1959). In both cases, the models are focused on higher trophic levels (i.e. fishes in this case) and represent basal resources through a semi-chemostat growth equation described by a turnover rate and a carrying capacity.

I have modified these models to include simple temperature-dependence of key individual-level processes, such as metabolism, background mortality, search rate or attack rate and maximum consumption or handling time (where the latter two are parameters of the functional response), and population-level parameters for the resource dynamics. The mass- and temperature dependence of biological and ecological rates follow a generalized version of the core equation in the MTE: $B = b_0 M^{b+c(T-T_0)} e^{E(T-T_0)/kTT_0}$ (Ohlberger *et al.*, 2012) (but note exceptions occur depending on rate). The second term, $e^{E(T-T_0)/kTT_0}$ becomes 1 when $T = T_0$, meaning I can scale, or “correct” allometric functions measured at T_0 as the modelled temperature deviates from T_0 . The parameter c describes the size-correction of the temperature dependence, which can lead to size-dependent effects of warming on the bioenergetic performance. Below follows a more detailed description of the two modelling frameworks, and how each model was parameterized with respect to allometric functions and temperature scaling.

The stage-structured biomass model used in Paper II-III describes biomass dynamics of species and life stages in terms of ordinary differential equations, and is derived from a fully size-structured population model with a continuous size distribution (Metz and Diekmann, 1986). Under equilibrium conditions, it exactly represents this size-structured model (De Roos *et al.*, 2008). In addition,

the stage-structured biomass model can also represent the dynamics of the unstructured (i.e. with respect to intraspecific structure) Yodzis and Innes model (Yodzis and Innes, 1992; Persson and De Roos, 2013). These two features make it a well-suited model for evaluating the effects of warming on consumer-resource or simple food chain dynamics with intraspecific structure and ontogenetic development. I use this model to describe simple consumer-resource dynamics (Paper II), where the consumer consists of two life stages (juveniles and adults). In Paper III, I extend this model to include an unstructured top-predator, making it a food chain model. The model parameters for the species in the stage-structured biomass models are based on published experimental data on the freshwater fish species common roach (*Rutilus rutilus*) (consumer) and pike (*Esox lucius*) (top predator). When this was not possible, I resorted to using general and/or interspecific parameters (e.g. food conversion efficiency and background mortality). In Paper III, I in addition compared the results from the species-specific model to a more generic parameterization, to more clearly illustrate the mechanisms driving changes in the food chain. With respect to temperature, in Paper II, the focus was on the interaction parameter, c , which determines the difference in the thermal response of life stages. In Paper III, I focused on evaluating the parameter sensitivity of energetic efficiency (activation energies of functional response parameters relative to metabolism and mortality), and the resource dynamics. The models were in both papers analysed using continuation analyses in the MATLAB (MATLAB, 2014) package MATCONT (GUI) (Dhooge *et al.*, 2008). Continuation analysis allows computation of equilibria as a function of a bifurcation parameter and determination of its dynamical stability. It can also be used to compute boundaries between regions of different dynamics, by mapping how bifurcations (such as Hopf bifurcations, branch points and limit points) vary in 2-parameter space (De Roos and Persson, 2013). In most analyses, I evaluated equilibrium biomasses as a function of temperature, or evaluated regions of dynamical stability as a function of temperature and other parameters of interest, e.g. resource carrying capacity. Model files, instructions for viewing and implementing the model in MATCONT, and R-scripts to reproduce the main figures with simulated data have been deposited on https://github.com/maxlindmark/Temperature_Allee.

In Paper IV I investigate the effects of warming on individual growth rates, size-at-age and population size-structure. To do this, I expanded a multi-species size-spectrum model (MSSM) to include similar temperature dependence as described above. MSSMs are similar to trait-based size-spectrum models (Hartvig, Andersen and Beyer, 2011), in that they use the trait-based approach to parameterization but include additional species-specific parameters

(Blanchard *et al.*, 2014; Scott, Blanchard and Andersen, 2014). These include parameters shaping feeding interactions and reproductive potential. As a case study, the model in Paper IV was parameterized and calibrated to the Baltic Sea, where the dominant species (commercially and in terms of biomass) cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) were explicitly modelled. This was done by treating each species maximum recruitment (R_{\max}) as a free parameter. R_{\max} was estimated by an optimization processes that finds the vector of R_{\max} -values that minimizes the residual sum of squares between observed spawning stock biomass (in the calibration time frame, 1992-2002) and the model output at steady state. After calibration and validation (mainly through comparison of predicted versus observed growth, emerging diets and relative biomass), the model was evaluated by projecting it forward to 2050 with annually varying temperatures and long term warming as predicted by the regional coupled model system RCA4-NEMO and the RCP 8.5 emission (Dieterich *et al.*, 2019; Gröger *et al.*, 2019). Note that this means projections are coupled with time-varying temperatures, and the populations are not in exact steady state for most analyses in this study. To contrast direct effects of temperature acting on individual physiology with effects on resource dynamics, I defined five different scenarios that differed in how temperature dependence was modelled. I addressed the uncertainty around temperature sensitivity by simulating each model scenario 200 times, each time with a random set of temperature dependence parameters. These random values were drawn from the posterior distributions estimated in Paper I. This approach allows me to explore emerging results from a probabilistic perspective. The model was built and analysed in R (R Core Team, 2018), using a forked version of the R-package ‘mizer’ (Scott, Blanchard and Andersen, 2014, 2019). All model code (parameterization, calibration and analysis) and data are available on GitHub (<https://github.com/maxlindmark/mizer-rewiring/tree/rewire-temp/baltic>), and will be deposited on Zenodo upon publication.

4 Results and discussion

4.1 Intraspecific size- and temperature scaling of individual processes (Paper I)

When considering temperatures below “optimum” (or more correctly below temperatures where the rate is maximized), I found differences in the mass-dependence (mass-scaling exponent) between metabolism and consumption. Specifically, metabolism scales with an exponent of 0.77 [0.7, 0.83], whereas the mass-exponent for maximum consumption is estimated to be 0.64 [0.56, 0.73], where square brackets indicate Bayesian 95% credible intervals. In addition, I find that the mass-scaling exponent of consumption differs from the “universal” mass exponent of $3/4$, as predicted by the metabolic theory of ecology (MTE). I estimate that there is a 99.5% probability that the mass-exponent of maximum consumption rate is smaller than $3/4$, given the data, model and prior. By contrast, the estimated mass-exponent for metabolism is closer to $3/4$, and I estimate a 70% probability that it is larger than $3/4$. My estimate of 0.77 is slightly lower than what was found in a recent analysis on the intraspecific mass-scaling of metabolism (Jerde *et al.*, 2019), in which it was estimated to be 0.89. A potential reason for this disparity is the different data sets, where they included only recent studies. By contrast, I wanted to evaluate the support for a mass- and temperature interaction within species, and therefore did not differentiate between years to ensure getting a large enough data set. It could also be due to using different model structures, where I used a generalized version of the MTE equation.

One implication of metabolic costs increasing faster with body mass than consumption rate is that as individuals grow in size during ontogeny, their net energy gain declines (all else equal). This is under the assumption that maintenance costs are proportional to standard metabolic rate and energy intake

is proportional to maximum consumption rate (Ursin, 1967; Essington, Kitchell and Walters, 2001; Lefevre, McKenzie and Nilsson, 2018). This finding is important to consider, as it has been questioned recently whether or not this is the case, and instead suggested that hyper-allometric energy investment to reproduction could be the main reason for declines in growth rate with increases in mass (Marshall and White, 2019b). My results indicate that growth efficiency declines with body mass not only due to increased energy allocation to reproduction, but also because gains cannot keep up with costs. This is further supported by observation that individuals in the data sets compiled in this study are in general small, and therefore investment into gonads can be assumed to be minimal. However, to what *extent* declines in net energetic efficiency over ontogeny drives declines in specific growth rate over ontogeny remains uncertain still.

In contrast to the mass-scaling exponents, I find that the temperature sensitivity (activation energy) of growth, metabolism and consumption both overlap and overall conform well to the prediction by the MTE (0.6-0.7 eV), despite the MTE being based on mainly mass-corrected interspecific data. These conclusions are based on the overlapping 95% credible intervals, which correspond to 95% probability that the true parameter value lies within that range, given the likelihood, prior and the data. Specifically, the activation energies of growth rate, maximum consumption and metabolic rate are estimated to be 0.61 [0.56, 0.67], 0.66 [0.49, 0.83], and 0.76 [0.54, 0.99], respectively, where the brackets indicate 95% credible intervals.

While interspecific data may fit an exponential model across species, within each species the thermal response curve is unimodal (Rall *et al.*, 2012) (Figure 1). When considering the full temperature range for maximum-consumption rate, the difference between consumption and metabolism becomes unimodal, and so does growth rate. This effect is well known in the fish biology literature (Jobling, 1997). However, I in addition illustrate this with two different body masses using the empirically estimated body mass and temperature coefficients, where the metabolic costs increase faster with mass than gains. This clearly illustrates that the temperature where growth is maximized declines with body mass. This is also a feature of the widely used von Bertalanffy growth model (von Bertalanffy, 1938), and in fact all Pütter-type growth models, as shown by Morita *et al.* (2010). However, in Morita *et al.* (2010) the unimodal growth curve was assumed to originate from a linear increase in energy assimilation and an exponential increase in maintenance costs (given data provided in Atkinson (1994)), whereas I use unimodal vs exponential curves, as in Jobling (1997). To ensure that declines in optimum growth temperature with mass is not just an artefact from an overly simplistic growth model, it is important to evaluate this

empirically. My results on the analysis of growth rates clearly shown that the optimum temperature for growth within species declines across species as fish grow in size. How much this drives the temperature size-rule or the negative association between asymptotic size or maximum size and temperature depends on the proximity of the environmental temperature and optimum growth temperatures. However, given the lower optimum for large fish, it could be hypothesized that large fish experience negative effects of warming first.

I present results suggesting that unimodal thermal performance curves are indeed close to or even within “biologically relevant” temperature ranges (Savage *et al.*, 2004; Englund *et al.*, 2011). For instance, at the species level, the difference between the predicted average optimum temperature for maximum consumption and the mid-point of their habitat-temperatures is approximately +6°C, which is similar to the corresponding value for growth. This means that the optimum growth and feeding temperatures often are similar to the maximum habitat temperature. It must also be noted that these estimates are based on experiments with optimal conditions, mainly unlimited food supply. Hence, in natural environments the proximity to optimum growth temperatures should be closer, as the optimum declines with reduced food availability (Brett, Shelbourn and Shoop, 1969; Huey and Kingsolver, 2019).

4.2 Effects of warming on stage-structured population and food chains (Paper II and III)

The main finding in Paper II is that in a consumer-resource model with intraspecific juvenile-adult stage-structure in the consumer population, the overall response of a population to warming depends on (1) the competitive dominance between life stages and (2) which life stage is benefitted from warming. Specifically, the population can be dominated by juveniles or adults, depending on if adults or juveniles (respectively), constitute an energetic bottleneck due to competitive inferiority for a shared resource (Figure 2). In turn, warming can affect life stages differently. This can modulate the competitive dominance within the population, with consequences for the density dependence and key life history processes such as maturation and reproduction, and ultimately the relative biomasses of life stages. Another clear qualitative result is that temperature-driven transitions between adult or juvenile dominated consumer populations can be abrupt. This may have implications for the dynamical stability if populations exhibit cohort-driven cycles due intraspecific interactions (Persson *et al.*, 1998; Sanderson *et al.*, 1999; Murdoch *et al.*, 2002; De Roos and Persson, 2013). Moreover, it also means that it is difficult to predict the effect of temperature on population biomass and consumer persistence from

the effect of temperature on energetic efficiency (gains vs losses) alone, without accounting for how density dependence operates in the system.

Thus, it is important to evaluate 1) where density dependence is strongest in a population and 2) how warming affects this density dependence. First, it appears more common in experimental and lake systems that population growth is limited by high density dependence in adult life stages, i.e. limited by reproductive output (Byström, Persson and Wahlström, 1998; Ohlberger *et al.*, 2011; Persson and De Roos, 2013; Schröder, van Leeuwen and Cameron, 2014). This is inferred both from the observation that energetic efficiency declines with body size due to differences in allometric scaling of energy gains and costs (Basset, Cozzoli and Paparella, 2012; Persson and De Roos, 2013; Jerde *et al.*, 2019), and from observations of the stage-specific responses to mortality in lakes that are in line with adult bottlenecks (Ohlberger *et al.*, 2011). Second, several lines of evidence suggest that larger individuals or adults do not benefit from warming in terms of their net energy gain to the same degree as small individuals or juveniles. For instance, temperature effects vary over ontogeny according to the temperature size rule (Atkinson, 1994; Angilletta and Dunham, 2003; Baudron *et al.*, 2014; Tseng *et al.*, 2018), optimum temperatures decline with body size (Panov and McQueen, 1998; Steinarsson and Imsland, 2003; Björnsson, Steinarsson and Árnason, 2007; Handeland, Imsland and Stefansson, 2008; García García *et al.*, 2011) and some evidence exist for changes in the allometric scaling of energy intake and costs that lead to relatively stronger negative effects of body size on net energy gain with warming (Strong and Daborn, 1980; Angilletta and Dunham, 2003). With these two aspects in mind, it could be hypothesised that warming would strengthen the juvenile dominance and the emerging adult bottlenecks.

In Paper II I focus on the physiological aspect of warming by exploring how different levels of size-dependent temperature scaling affect the potential net energy gains for fishes of different body sizes. However, it is worth mentioning that many factors can contribute to life stages responding differently to warming. For simplicity, I implemented different physiological responses by applying a generalized metabolic theory of ecology equation for metabolic rate, with a single parameter added that modifies the size-dependence of a temperature dependent rates (parameter c , see ‘*Materials and Methods*’) (Ohlberger *et al.*, 2012). Although such scaling relationships was found in the study species used here (common roach, *Rutilus rutilus*) (Hölker, 2000; Hölker and Haertel, 2004), the effect size of such size-temperature interactions were found to be smaller in general within species (Paper I). While it leads to the predicted effect of reduced performance of large fish, it is unclear to what degree this mechanism drives temperature-size patterns in general (Audzijonyte *et al.*, 2018). This is because

it does not allow the allometry of net energy gain to *switch* over ontogeny, e.g. going from positive effects of warming to negative as fish grow. To achieve that, the thermal responses should be modelled with unimodal curves with declining optima for net energy gain with body mass (Paper 1). The importance of accounting for such scaling is perhaps stronger in size-structured rather than stage-structured models, as in the temperature-functions are stage-structured models anyway collapsed into discrete scalars.

Combining ontogenetic asymmetry and life-stage specific responses to warming can thus lead to not only drastic changes in population stage-structure, but also somewhat contradicting results, including increasing biomass dominance of the life stage that is experiencing decreased performance with warming. While the effects of stage structure and ontogenetic asymmetry are large for a consumer population, the effects are perhaps even stronger on the community level. In Paper III, I expanded the stage-structured and temperature dependent model to include an unstructured predator. This predator can in turn feed on both life stages (it encounters juveniles with proportion p and adults by proportion $1 - p$). This model is also presented in a more general form that more closely resembles the original stage-structured biomass model (De Roos *et al.*, 2008). The general formulation is simpler, and the ontogenetic asymmetry that determines the population stage-structure is determined by a single phenomenological parameter (q). This generalization makes it easier to illustrate some interesting comparisons to unstructured food chain models.

In the basic case, where the predator feeds on both life stages with equal intensity and temperature has a negative effect on the resource carrying capacity, warming first stabilizes the food chain as limit cycles turn into fixed point dynamics. This phenomenon can be described as an “inverse paradox of enrichment” (Rosenzweig, 1971; Binzer *et al.*, 2012). Here, the temperature response is a mirror of the response to declines in resource carrying capacity. With further warming, the predator population goes extinct. Note also that this scenario is exemplified with a juvenile-adult structure consumer population, but the same qualitative response would have been achieved even if the consumer population had been unstructured, or the qualitatively equivalent of a “symmetrical” consumer population, where there is no difference in the net energy gain of adults and juveniles (De Roos and Persson, 2013). By contrast, when the predator feeds on juveniles, the limit cycles at cold temperatures or high resource carrying capacities disappear. Instead, warming leads first to bistability, where alternative stable states exist and the predator can persist, but not invade, a consumer-resource system. If predators are present in this state, their extinction with further warming is characterized by a sudden collapse rather than a gradual decline. Lastly, if the predator feeds on adults, all else equal, their

persistence is generally favoured compared to feeding on juveniles or equally on both life stages.

The mechanism behind the collapse and the addition of bistability as a response to warming is that the mortality from the predator's feeding induces biomass increases in the juvenile stage, due to relaxations in the density dependence of adults (De Roos *et al.*, 2007). It can therefore be predicted that the opposite pattern should be observed if the consumer population is instead characterized by competitive superiority of adults, which I also show using the general model formulation. Thus, a stage-structured food chain that can qualitatively resemble an unstructured food chain under special-case scenarios (De Roos and Persson, 2013; Persson and De Roos, 2013) can exhibit three different dynamical trajectories along a warming axis. The only ingredients for this to occur is that predators do not feed with equal intensity on both life stages and that the consumer population is at least stage-structured (juvenile-adult). As such, the change in community dynamics with warming is largely driven by intraspecific competition in the consumer and the interplay between predation and stage-structure in this model. These effects can counteract the role of temperature-dependent net energy gain, which recent studies have found to be main predictors of the persistence and stability of similar bioenergetic consumer-resource models (Fussmann *et al.*, 2014; Gilbert *et al.*, 2014; Uszko *et al.*, 2017).

Although all populations exhibit some kind of stage structure as individuals develop before reaching maturity, that does not mean it is a main driver of the ecological dynamics, compared to e.g. environmental drivers and interspecific interactions. However, in many lake ecosystems this has been shown to be important (Byström, Persson and Wahlström, 1998; Sanderson *et al.*, 1999). For example, the mechanisms by which predators promote their own food source through their predation in the model presented here has been shown to drive whole-lake fish size-structure and predator dynamics (Persson *et al.*, 2007). Thus, accounting for intraspecific interactions and life history processes is likely important for understanding population and community dynamics in future climates.

4.3 Impacts of warming on a size-structured food web (Paper IV)

I find that including temperature effects on fish physiological processes has a strong influence on the projected size-at-age in 2050 under the RCP 8.5 emission scenario, relative to the baseline projection (no warming). When only resource dynamics are affected, size-at-age declines for all sizes, and the relative change

is largest for small individuals. The average body size in the populations declines, and this is also driven by declines in abundance-at-size (which in addition are strongest for largest fish). These results are in line with predictions about the consequences for population size-structure when less energy is transferred up in the food web (Lefort *et al.*, 2015; Woodworth-Jefcoats, Blanchard and Drazen, 2019), and also in line with broad-scale predictions about warming-induced “shrinking” (Daufresne, Lengfellner and Sommer, 2009; Sheridan and Bickford, 2011; van Dorst *et al.*, 2019).

However, the declines in size-at-age with warming and stronger negative effects on small or young individuals predicted from this specific scenario are typically not observed in field or experimental data with initial warming, but rather the opposite (Thresher *et al.*, 2007; Baudron *et al.*, 2014; Barneche, Jahn and Seebacher, 2019; Huss *et al.*, 2019). This suggests other important mechanisms are unaccounted for. In scenarios where also physiological rates are temperature dependent (metabolism, background mortality, search rate and maximum consumption rate), I find the opposite result on size-at-age, namely that warming increases size-at-age, and the relative increase is strongest for small individuals. This is a robust result, although the variation due to uncertainty in activation energies is substantial. Typically, the difference relative to a non-warming scenario varies between a factor of approximately 1-1.5 times larger size-at-age for a 1-year old fish.

To what extent can this intraspecific response of faster growth rates (indicated by larger size-at-age) counteract the negative effects of declining resource productivity and carrying capacity on mean population body size? In general, it does not. The only scenario that conclusively leads to larger mean body size within populations is when physiological rates scale with temperature and resource dynamics are independent of temperature. However, for cod, the median body mass in the population in scenarios with both temperature dependence of resources and physiological rates is close to that of the baseline scenario (approximately half of the random simulations lead to larger and half to smaller body sizes with empirical warming), but this is likely due to lower fishing mortalities in projections compared to the calibration time period. This result shows that in general, larger initial size-at-age does not counteract the negative impacts of warming on population size-structure and mean size. However, environmentally driven changes in growth trajectories are not only important to account for projecting individual-level impacts of warming, but also in the context of exploitation.

In fisheries management, growth plasticity is not typically seen as an important factor compared to environmentally driven recruitment variation, density dependence at early life stages and mortality from fisheries for stock

dynamics (Hilborn and Walters, 1992; Lorenzen, 2016). However, due to the empirical evidence of climate-driven changes in vital rates (survival, growth and reproduction), their relative importance for fisheries management reference points and targets has received attention recently (Thorson, Monnahan and Cope, 2015; Lorenzen, 2016). I find that changes in growth affect the management reference points and targets maximum sustainable yield (MSY), fishing mortality leading to MSY (F_{MSY}) and the spawning stock biomass when fished a F_{MSY} (B_{MSY}). Specifically, when temperature affects resources only (i.e. when size-at-age declines), MSY, F_{MSY} and B_{MSY} all decline with warming ($+2^{\circ}\text{C}$ relative to T_{ref}) for sprat and herring. By contrast, when temperature affects physiology and resources, F_{MSY} is higher with warming but B_{MSY} is lower for all species. This is likely due to due faster growth sustaining higher exploitation but leading to a lower yield because of declines in abundance-at-size. When resources do not decline with temperature and only physiology is temperature dependent, all these reference points are higher when temperature is increased by $+2^{\circ}\text{C}$ (reflecting larger size-at-age and larger sized populations). While these results are only qualitative assessments that do not consider other important factors that determine reference points that also might change with warming, they do suggest that it is important to understand climate-driven changes in vital rates. This could be explicitly incorporated in predictions of climate effects on fisheries productivity.

5 Concluding remarks and outlook

In this thesis, I have addressed the importance of intraspecific body size variation when evaluating the impacts of climate change on individuals, populations and food webs. The aim has been to examine how direct effects of warming on individual-level physiology are mediated by size-based interactions within and between species. To achieve that, I have applied statistical models to describe the scaling of biological and ecological rates with body mass and temperature within species, to develop a better understanding of the physiological impacts of warming. I have also analysed the effects of temperature on populations and food webs using stage- and size-structured mathematical models based on a physiological representation of individual life history. These studies have led to novel insights and predictions, which have potential to both reconcile growth theory and observations, as well as point to unexplored dynamical consequences of warming that require more research.

I have demonstrated that the scaling of key biological rates, such as growth, metabolism and consumption with body mass and temperature within species in many key aspects differ both in relation to each other and to what is commonly predicted from metabolic scaling theory. I find that the mass-scaling exponent of maximum consumption rate is smaller than that of metabolic rate, which implies that the net energetic efficiency – all else equal – is a declining function of body size. This can aid in improving mechanistic growth models, as scaling exponents are often discussed or disagreed upon among physiologists and theoretical ecologists. Comparison of the optimum growth temperature with each species' reference temperatures also reveals that optimum temperatures are typically found at the edges of the environmental temperatures experience by species. This suggests two things: first, unimodal thermal responses do occur within biologically relevant temperatures, and second, given that optimum temperatures for growth are lower for large fish within a species, large fish may be the first to experience negative effects of warming, which could have implications for population structure and dynamics. These findings highlight

that size-resolved analyses coupled with spatial structure of sub-populations (e.g. populations living in their thermal ranges and climate-driven range-shifts) is important for predicting effects of warming in natural systems.

Analyses of stage-structured biomass models show that in order to make predictions about the effects of warming consumer-resource systems and food chains, it is important to understand how intraspecific interactions affect the density dependence in the population, and how feedbacks between predation and predator persistence shape the food chain. In other words, population biomass, community stability and predator persistence can in the presence of stage-structure not be predicted from the effect of temperature on the net energy gain relative to resource carrying capacity alone, as can largely be done from models with no stage-structure and food-dependent development. In addition, inclusion of stage-structure also leads to novel dynamical responses to warming, such as bistability and predator collapses. Because of these large effects of stage-structure on community dynamics, it is important to continue the empirical research on the prevalence of these mechanisms and feedbacks between stage-structure and individual performance in real systems, and under what conditions they are the main drivers of the dynamics. As of yet, most empirical support for these drivers and mechanisms stem from fish communities in lakes or experimental studies. It remains unexplored how these feedbacks might change with climate warming in empirical systems.

Moreover, trait or species-based size-structured models constitute a promising framework for linking changes in body growth to population size- and community structure, because of the mechanistic description of food-dependent individual growth. I have shown that simple temperature scaling of physiological rates in combination with declines in resource carrying can explain faster growth rates of young fish but declines in the relative abundance of large fish, causing “shrinking” populations as a whole. These findings are in line with observational studies, and highlight the importance of being explicit about the mechanisms: is the shrinking an inter- or intraspecific response? Is it driven by changes in size-at-age versus abundance-at-size? Imposed physiological constraints or declines in food availability? I here present results regarding the relative contribution of these factors. However, more research needs to be conducted on the generality of these results, for instance by exploring different food web configurations and assumptions about temperature dependence.

Taken together, the size-based and physiological approach to food web dynamics under climate change constitutes a powerful toolbox for explaining observations and for making predictions based on bioenergetic principles. This thesis provides insight into the role of individual size-variation for how populations and food webs respond to warming.

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Popular science summary

Increasing temperatures affects organisms that do not regulate their own body temperatures (“ectotherms”, such as fish) directly by increasing their metabolic rates and thus resource demands. Many studies based on experiments or data from wild fish populations and other ectotherms show that when it gets warmer, the body size of adults and sometimes the average body size of the population declines. Body size is a highly important trait for individuals and species that affects many aspects of individuals populations; how abundant they are, how fast populations grow and who they eat. Therefore, it is important to understand both how body size changes through direct (physiology) and indirect (food availability) effects, and what role body size-variation has for the response of a population to climate warming. Mathematical models are great tools for simplifying complicated processes to their main characteristics, which helps identify the main drivers of a pattern. Experimental studies are similar in that respect, as they can eliminate factors that otherwise could influence an outcome.

In this thesis, I have compiled experimental data sets and analysed them statistically to assess how warming affects individual’s growth, metabolism and feeding rates in fishes. I find that the optimal temperature for body growth declines as individuals grow in size. Thus, while initial warming may lead to faster growth rates, further warming is detrimental for growth, and the large individuals within a population will be the first to experience these negative effects.

By expanding and analysing mathematical models of populations and food webs based on individual-level processes, I find that body size has an important role for mediating the overall response to temperature with respect to stage-structure or dynamics. Specifically, the effect of warming on the size-structure of a population depends on how the population is structured with respect to life stages (e.g. immature juveniles and mature adults) and the competition that occurs between them. If warming benefits the life stage that is most limited by competition, it can lead to the population not declining in total. If warming benefits the competitively dominant life stage, population biomass can decline rapidly. The stage-structure of populations also shapes how food chains respond to warming. It can for instance mitigate the negative effects of warming on the ability of predators to stay alive when conditions are poor, it can stabilize communities and it can explain and lead to predator collapses – all dependent on how the population is structured and on which life stage the predator feeds on.

Results from a size-structured model (not stage structured) show that it is important to consider the combined effect of warming of basal food sources (e.g. phyto- and zooplankton) as well as physiology (e.g. metabolism) for understanding structural changes in food webs to warming. These models also show that warming can lead to initially faster growth rates. However, that does not always lead to larger populations (larger e.g. mean body sizes), because if basal food resources decline, the large fish in the populations become scarcer. Because individual body growth and population size-structure are important factors for how a population responds to exploitation (fishing), these results are important for understanding how climate change might affect the conditions for sustainable fishing.

In summary, these results contribute to an increased knowledge about the importance of body size for understanding how individuals, populations and food webs are affected by warming. It also sheds light on the need to consider temperature effects in an ecological context (accounting for both environmental effects as well as interactions between species), as optimum temperatures for growth decline with body size and food levels.

Populärvetenskaplig sammanfattning

Klimatuppvärmning påverkar växelvarma organismer (såsom fiskar) genom att öka deras ämnesomsättning och därmed också deras krav på miljö i form av resurser. Flera studier på vilda populationer av växelvarma djur har visat att när det blir varmare, så ökar kroppstillväxten hos små eller unga individer, men kroppsstorleken hos äldre eller större individer minskar. Ibland minskar även hela populationens medelstorlek. Kroppsstorlek är ett viktigt karaktärsdrag både för en individ och en art, då det styr hur fort en population växer i antal, vilka arter som äter vilka och hur talrika de är. Därför är det viktigt att förstå både hur storlek förändras genom direkta fysiologiska effekter och indirekta effekter (t.ex. genom födotillgång), samt vilken roll variation i kroppsstorlek har för hur populationer svarar på klimatförändringar. Med hjälp av matematiska modeller är det möjligt att kondensera komplicerade processer till dess beståndsdelar, vilket underlättar förståelsen av orsak och verkan i annars komplexa ekologiska system. Experiment har liknande egenskaper, då det är möjligt att kontrollera för faktorer som annars kan påverka en respons.

I den här avhandlingen genomförde jag en standardiserad litteratursökning för att sammanställa experimentella data på ämnesomsättning (metabolism), födointag och tillväxt hos fiskar. Med statistiska modeller beskrev jag generella mönster för hur både temperatur och kroppsstorlek påverkar fiskars ämnesomsättning, födointag och kroppstillväxt. Resultat från den här studien visar att den optimala temperaturen för kroppstillväxt avtar med kroppsstorlek. Detta innebär att uppvärmning kan leda till ökad kroppstillväxt initialt, men att fortsatt uppvärmning kan leda till minskad tillväxt, och att detta i så fall kommer att märkas först på stora individer inom en art.

Genom att utöka och analysera matematiska populations- och födovävsmodeller baserade på fysiologiska processer på individnivå till att inkludera effekter av temperatur fann jag att kroppsstorlek har en viktig reglerande roll på effekten av uppvärmning. Mer specifikt visar jag att effekten av uppvärmning beror på hur storleksstrukturen (vilka livsstadier, t.ex. omogna och könsmogna individer) och konkurrenssituationen ser ut inom populationen. Om uppvärmning gynnar det livsstadiet som är mest begränsat i konkurrensen om föda kan det leda till att populationen totalt inte minskar, och om uppvärmning gynnar det effektivare livsstadiet kan populationen minska kraftigt i biomassa. Storleksstrukturen har även stora effekter på hur födokedjor svarar på uppvärmning. Den kan till exempel motverka den negativa effekten av uppvärmning på

en toppredators möjlighet att överleva, förklara hur fisksamhällen stabiliseras eller hur predatorpopulationer kollapsar – allt beroende hur variationen i storlek inom en art ser ut och vilket livsstadie predatorm äter av.

Resultat från en storleksbaserad (inte stadiobaserad) modell visar att kombinationen av klimateffekter på födotillgång (till exempel växt- eller djurplankton) och fysiologi (metabolism) är viktig för att förstå effekter av klimatuppvärmning på födovävar. Även här visar resultaten att kroppstillväxt initialt kan öka med uppvärmning. Detta leder dock inte alltid till att populationen i genomsnitt blir större, då stora individer minskar i antal relativt sett. Då individtillväxt och storleksstruktur är viktiga faktorer för hur en population svarar på exploatering (fiske), är dessa resultat viktiga för att förstå hur klimatförändringar kan komma att ändra förutsättningarna för ett hållbart fiske.

Sammanställt så bidrar dessa resultat till en utökad kunskap om betydelsen av variation i kroppsstorlek inom arter för att förstå hur individer, populationer och födovävar påverkas av klimatuppvärmning. De belyser också vikten av att ta hänsyn till den ekologiska kontexten (hur miljöeffekter regleras av interaktioner mellan arter) för att förstå effekten av klimatförändringar, då optimala tillväxttemperaturer minskar med storlek och minskad födotillgång.

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