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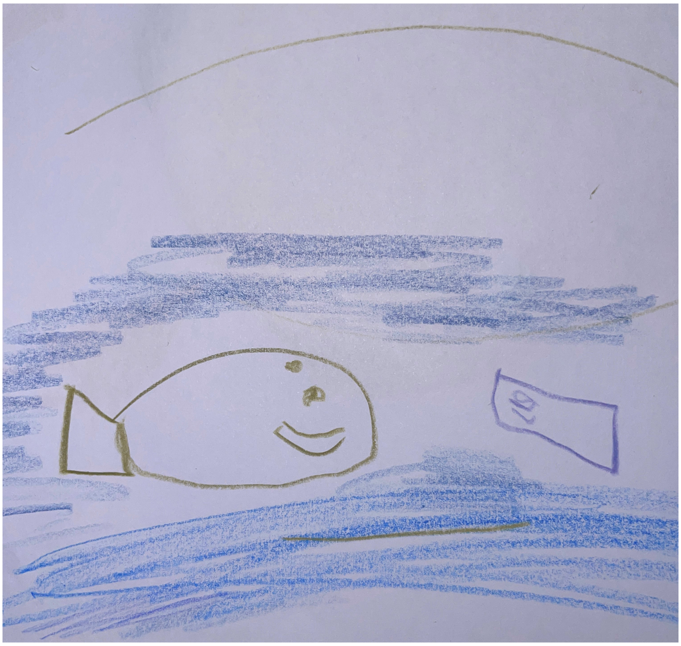
Fish life histories in a warming climate: a mechanistic basis of change and a community context

Viktor Thunell



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Abstract

Body size dependent interactions structure food webs, and these are changing with climate warming. We cannot yet predict how warming affects many aspects of life history evolution and species ecology, despite a longstanding interest in the structuring effects of temperature and body size in food webs. This is in part due to not recognizing the temperature dependence two aspects, namely that 1) within-species differences govern species interactions and 2) processes of adaptation depend on body size. In this thesis, I assess how body size dependent effects of temperature govern such interactions and processes using theoretical models of individual growth and reproduction. First, I study effects of warming on the energy allocation trade-off between somatic growth and energy reserves and find that warming favours allocation to reserves and reproduction through increasing importance of early life history processes. Specifically, failing to adapt to warming winters compromises viability of population through juvenile mortality. Second, I study how effects of warming on consumer-resource systems depend on energy allocation strategies. Here, energy allocation can modulate temperature dependent competition for food between stages, but competition mediated by diet is the main determinant of effects of warming. Last, I show how effects of warming affect the feedback mechanism of stage dependent competition and predation on interacting species and thus prevent adults from cultivating a low competition environment for their young. I conclude that linking underlying individual body size dependent physiological responses to warming to effects in population and communities provides novel mechanistic understanding of adaptation and food web processes. While these mechanistic predictions form a basis for, and require, empirical tests, I propose that diversity and function of aquatic food webs are at stake.

Keywords: climate change, energy allocation, species interactions, food webs, life history, temperature-size-rule, scaling, energy budget, dynamic model, integral projection model

Livshistorier i ett varmare klimat: mekanismer för förändringar hos fisk och deras artsamhällen

Sammanfattning

Näringsvävars struktur beror på storleksberoende interaktioner mellan arter och förändras i ett varmare klimat. Det saknas i nuläget prediktioner om uppvärmningens effekter på livshistorieevolution och ekologi trots ett historiskt vetenskapligt intresse för rollen av temperatur och storlek i näringsvävar. En bidragande orsak är att forskning i många fall inte sett till att de storleksskillnader inom arter som styr interaktioner mellan arter och evolutionära processer är temperaturberoende. I den här avhandlingen beskriver jag individers tillväxt, reproduktion och mortalitet i teoretiska modeller för att utvärdera storleksberoende effekter av temperatur på sådana interaktioner och processer. Först studerar jag effekter av uppvärmning på energiallokering mellan somatisk tillväxt och energireserver. Jag visar att allokering till energireserver gynnas i en varmare miljö på grund av en ökande betydelse av tidig könsmognad och reproduktion. Större energireserver krävs också för att juveniler ska överleva varmare vintrar. Jag studerar även hur temperatureffekter på predator-bytessystem beror på energiallokering. Jag visar här att energiallokering påverkar temperaturberoende konkurrens om föda mellan levnadsstadier men att ontogenetiska dietskiften är mer avgörande för temperatureffekter. Avslutningsvis visar jag att uppvärmning påverkar mekanismer för stadieberoende konkurrens och predation på interagerande arter och därmed hindrar vuxna från att begränsa sin avkommas födokonkurrens. Sammantaget visar resultaten att kopplingen mellan storleksberoende fysiologiska svar på uppvärmning och effekter på artsamhällen ökar den mekanistiska förståelsen av naturlig selektion och näringsvävsprocesser. Dessa mekanistiska prediktioner kräver ytterligare empiriskt stöd men tyder på negativa effekter på biologisk mångfald och näringsvävars.

Nyckelord: klimatförändringar, energiallokering, artinteraktioner, näringsvävar, livshistoria, temperatur-storleks-regeln, skalering, energibudget, dynamisk modell, integralprojektionsmodell

Dedication

To whom it may concern.

Contents

List of publications

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

I. Viktor Thunell, Anna Gårdmark, Magnus Huss, Yngvild Vindenes (Forthcoming). Optimal energy allocation trade-off driven by size-dependent physiological and demographic responses to warming. *Ecology.*

II. Viktor Thunell. Fitness consequences and optimal energy allocation strategies for fish in warming seasonal environments (Manuscript)

III. Viktor Thunell, Magnus Huss & Anna Gårdmark. Energy allocation strategies mediate individual- and population responses to warming via intraspecific competition. (Manuscript)

IV. Viktor Thunell, Max Lindmark, Magnus Huss & Anna Gårdmark (2021). Effects of Warming on Intraguild Predator Communities with Ontogenetic Diet Shifts. *The American Naturalist*, 198(6), 706-718.

Papers I and IV are open access publications (CC-BY 4.0).

1. Introduction

On evolutionary timescales, the rate of current global warming implies an abruptly changing environment for organisms and their ecosystems (Visser 2008). It is a scientific challenge, and a pressing issue, to describe how this change affects organisms within their ecosystems. Historically, an important development of modern ecological science begins with August Pütter constructing an individual growth model based on physical and physiological principles (Pütter 1920; Kearney 2021). His work also included a model of why species grow to larger sizes in the cold. A substantial amount of evolutionary and ecological research has since centred on how body size and temperature shape animal communities and increasingly so in the light of climate change. By defining the physiological constraints and capacities that a warmer environment involves and evaluate associated trade-offs, we can understand how warming shapes animal communities (Jørgensen et al. 2016). This provides theoretical ecological and evolutionary frameworks with direct mechanisms from which we can test predictions (Marquet et al. 2014).

1.1 Temperature, body size and community ecology

Temperature is the kinetic energy of the particles in a physical body. With increasing temperature, the rate of any process within that body increases. For ectotherms, i.e. animals with a body temperature that varies with that of the surrounding environment, the rate of internal biological processes increases with environmental temperature. The core biological processes is metabolism, which includes transformation of ingested food into an energy carrier (ATP), the use of that energy to build (anabolism) and break down (catabolism) material supporting cellular processes (Clarke & Fraser 2004).

The higher the temperature, the higher the metabolic rate with implications for turnover, demand and use of energy.

A larger body has more cells to support, thus demands more oxygen to maintain metabolism, which causes a higher metabolic rate. Metabolic rate scales supralinearly (an exponent less than 1) with body size meaning that per unit body mass, a larger organism has a lower metabolic rate than a small (Brown et al. 2004). Proposed theory as to how and why metabolic rate scales with body size suggest a surface to volume ratio, i.e. $m^{2/3}$ (Rubner 1908), or fractal like supply networks to explain a statistical mean of $m^{3/4}$ (Kleiber 1947; West et al. 2001). Considering the variation of metabolic rate and body size between and within species, it is likely that metabolic rate and body size coevolve making the scaling exponent variable (Kozłowski et al. 2020; White et al. 2022). The latter explanation provides freedom in trying to explain patterns at higher hierarchical levels. Given the complexity of biochemical and cellular processes involved, and the evolution that shaped those, there is substantial evidence that questions the basis of theories based on thermodynamic first principles (Clarke & Fraser 2004; Glazier 2015). From an ecological point of view, statistical estimates of the scaling of metabolic rate with body size (and temperature) rather than proximate mechanisms, are however just as useful in providing a general and delimited expectation of effects.

For the individual, the implications of increasing rates of metabolic processes is increases in the rate of interactions with the external environment. Metabolic rate scales energy use to power activity, somatic maintenance and growth, development and reproduction and the rate of senescence (Brown et al. 2004). In turn, this defines individual body size and energy use and therefore performance in interactions between individual organisms by scaling the rate of resource consumption (Rall et al. 2012; Hein et al. 2014). By basing ecological models (as mathematical representations) of organism communities on the scaling of body size and temperature, realism of how food webs function and are structured greatly increases (Yodzis & Innes 1992; Gillooly et al. 2001; Vasseur & McCann 2005). This improves the applicability of those models. Consequently, acknowledging the effects of body size and temperature on metabolism makes for more accurate theory of community ecology in a changing climate.

A general prediction of food webs under warming is a reduced energetic efficiency. Energetic efficiency, also termed “Ecological scope”, is the ratio between consumption and metabolic rate (Yodzis & Innes 1992; Vucic-Pestic et al. 2011). In a food web, reduced energetic efficiency under warming is the mismatch between respiration and biomass production within and between trophic levels (O'Connor et al. 2009). In other words, while system productivity is increasing, standing stock biomass is constrained (e.g. Blanchard et al. 2012). At different trophic levels however, relative changes in biomass depend on differences in temperature sensitivity of energetic efficiency and on system primary production (O'Connor et al. 2009; Brose et al. 2012; Gilson et al. 2021). As body size determines the energy demand and temperature sensitivity of energetic efficiency, size differences between trophic levels can determine how system carrying capacity (a system's ability to hold standing biomass based on environmental conditions) respond to warming (Arim et al. 2007; Binzer et al. 2012). Because of responses in primary production, carrying capacity should be unimodal over the full biological temperature range, and thus decrease in the higher temperature range (Lemoine 2019; Uszko et al. 2022). Consequently, food web responses to warming are predicted to depend on the temperature range examined, how warming changes energetic efficiency across trophic levels, on effects on primary production but also on biomass loss via mortality affecting competition for resources (Vasseur & McCann 2005; Binzer et al. 2012). Uszko et al. (2017) showed that by considering study-specific assumptions regarding these effects, it is possible to map previous theoretical studies (all using Rosenzweig–MacArthur predator-prey models) onto a space of temperature and prey carrying capacity. Such general predictions provides understanding of large-scale changes of food webs, paving the way for more detailed and system specific predictions in which environmental conditions vary.

Because body size scales metabolism and because of other life stage (i.e. ontogeny) dependent energetic differences, the susceptibility of individuals to changes in environment govern population responses (de Roos & Persson 2013). Importantly, as juveniles and adults, or individuals of different sizes, differ in their competitive ability or may have different diets, it is unlikely that their production rates are equal (Arim & Marquet 2004; Persson & de Roos 2013). This is however the assumption which development of ecological community theory is often based on (Lotka 1925; Volterra 1926; Rosenzweig & MacArthur 1963). By applying the concept of body size dependent energetic efficiencies to individuals within populations, theory can be developed to understand the effects of size dependent species interactions and asymmetric competition on animal communities. The concept of energetic efficiency is often referred to as an energy budget in models that account for such within-species variation (Kooijman & Metz 1983; Kooijman 1993; de Roos et al. 2008). By considering life history variation in body size, the applicability of predictions from models on natural communities can greatly improve (Persson et al. 2007; Ryabov et al. 2017).

An increasing number of studies of dynamic food web models account for within species differences in temperature responses to generate predictions of how a warming climate may reshape animal communities (Ohlberger et al. 2011; Lindmark et al. 2018, 2019; Uszko et al. 2022). This development shows for example that system stability changes in response to temperature can depend on size dependent competition within populations (Ohlberger et al. 2011), that warming induces alternative stable states via size dependent predation (Lindmark et al. 2019), and that body size dependent effects of warming within populations determines population responses to warming and size shifts towards smaller species through competition (Lindmark et al. 2018; Uszko et al. 2022). These advances of exploring the implication of between and within species processes for responses to climate warming calls for further assessment, in particular of food webs that rely strongly on body size for species interactions (Werner & Gilliam 1984; Gårdmark & Huss 2020).

1.2 Warming induced size shifts in aquatic animal communities

Currently, climate change is directly affecting ecosystem diversity through shifts in species ranges, and shifts in phenology (Perry et al. 2005; Parmesan 2006; Asch 2015). While these two categories of change can be inferred directly from the thermal preference of species, their predictive power in terms of the structure and function of communities is limited. A third category of effects is changes in size distributions (Daufresne et al. 2009). These effects largely fall (with modifications) under the term temperature-size-rule (TSR), which states that small individuals grow faster and large individuals may achieve smaller sizes in a warmer compared to a cold environment (Atkinson 1994), or “Larger size in cold is attained by a prolonged growth period overcompensating slow growth.” (Kozlowski et al.

2004). Research on the underlying cause to the TSR has been extensive (reviewed by Audzijonyte et al. 2018; Verberk et al. 2021). TSR effects are more common in aquatic than in terrestrial species suggesting constraints in aerobic capacity linked to body size or feeding ability (Forster et al. 2012; Tirsgaard et al. 2015; Norin & Clark 2017; Christensen et al. 2020). Increasing temperature may thus have varying effects on energetic efficiency dependent on body size (Holt & Jorgensen 2014; Lindmark et al. 2022). Furthermore, as development rate increases with temperature and juveniles thus mature at an earlier age, this can affect the temperature dependence of growth trajectories (Daufresne et al. 2009; Glazier 2015). Despite proximate physiological cause, TSR-type growth trajectories are more pronounced, common and easy to measure in laboratory conditions than in the field (Atkinson 1994). This provides uncertainty in the importance of this phenomenon for predicting climate change effects in food webs. Trophic interactions, their strength and function in food webs are however body size dependent and affected by warming (Shurin et al. 2012; DeLong et al. 2015; Sentis et al. 2017). Consequently, it is relevant to understand the origin and effects of the underlying processes of size-shifts as it should affect food web function and structure. In addition, shifts in species ranges and phenology is contingent on how species ecology change with warming, highlighting the need for knowledge of how size shifts in turn affect their food webs (Lurgi et al. 2012; Hein et al. 2014; Gilson et al. 2021)

Knowing where (spatially, temporally and in what part of a food web) and how size shifts emerge in response to warming is a key to understand their origin (Doak & Morris 2010). Here, long-term time series can predict effects of climate change across body sizes both within and between species. For example, studies from North Atlantic fish communities show that temperature-size-rule type growth trajectories are common and that smaller species are more susceptible to temperature change than large in terms of growth rate (Genner et al. 2010; Baudron et al. 2014; Ikpewe et al. 2020). However, temperature responses may be weaker than predicted from metabolic theory showing the importance of ecological or evolutionary processes (van Denderen et al. 2020). These time series are however rare or may provide little mechanistic understanding. For fish communities, another issue with studies of such temporal patterns of climate change inferred from time series data are that they are heavily biased because of fishing (Pomeranz et al. 2022). The effects of intensive harvest on individual growth trajectories, maturation, reproductive patterns and population structure may obscure potential effects of climate change and thus demands a more diverse methodological approach (Enberg et al. 2012; Audzijonyte et al. 2016). By coupling temporal empirical observations on size shifts in nature to spatial patterns, we may instead gain mechanistic ecological and evolutionary knowledge on the origin of size shifts.

Spatial, e.g. latitudinal differences, used to infer temperature effects on trophic interactions and body size shifts could in part overcome drawbacks of temporal more local analyses but instead reflect evolutionary patterns. Such space-for-time approaches are less consistent in their detection of TSR-type growth trajectories across species in a system (van Rijn et al. 2017; Audzijonyte et al. 2020). Accordingly, effects of climate warming on body size may thus be stronger than spatial gradients (Audzijonyte et al. 2020). However, maximum and mean body size generally decreases with temperature over latitudinal gradients, in communities (Blanck & Lamouroux 2006; Emmrich et al. 2014) and within species (Heibo et al. 2005; van Dorst et al. 2019). Also maturation occurs at a smaller size, growth rate and mortality increases, which in turn skews the population towards smaller individuals (van Dorst et al. 2019; Pomeranz et al. 2022). The possible effects of other environmental factors such as productivity or light conditions may however bias the analysis of effects of temperature on size-at-age. Rare opportunities for natural or semi-natural experiments in which such environmental differences are negligible, in part corroborates adaptive responses in terms of increasing growth rate of small individuals (O'Gorman et al. 2017; Huss et al. 2019). These populations also show metabolic and respiratory adaptation to warming that in turn should interact with other life history components affecting body size (Sandblom et al. 2016; Kozłowski et al. 2020; Kordas et al. 2022). Theory based on body size dependent effects of temperature on metabolic processes and subsequent energy gain can function as drivers of population demographics and species interactions. In turn, this contributes to understanding of how adaptation in life histories is linked to the use of available energy to grow and reproduce.

1.3 Adaptation to a warmer climate

Energy allocation trade-offs, primarily between growth, survival and reproduction, is defining animal life histories (Charnov et al. 2001). Varying with body size, generation time or reproductive mode, allocation strategies between species is a central aspect of their ecology and evolution (Pianka 1970; Stearns 1992; Winemiller & Rose 1992; Healy et al. 2019). Allocation strategy varies also between and within populations of the same species, e.g. with body size or age and in changing environments (Heibo et al. 2005; Barneche et al. 2018). In turn, this variation affects the body size and life stage structure of a population (Kozlowski 1997; Heibo et al. 2005; Finstad et al. 2006). Consequently, temperature dependent energy allocation strategies will have consequences for animal populations and communities in a warmer climate but this has received little scientific attention.

Energy allocation as a part of life history optimization is difficult to assess empirically because of its natural variability (Heino & Kaitala 2001). Available energy reserves, the size of reproductive organs and energy allocation is highly variable throughout the year and varies between years and individually (Lambert 2008). Furthermore, energy reserves are used to cover maintenance metabolic costs in times of starvation prior to reproduction, increasing the uncertainty of energy allocation strategies in nature (Schultz & Conover 1999; Fernandes & McMeans 2019; Corriero et al. 2021). Theoretical models of life histories and adaptation therefore fills an important role in recreating how energy allocation and other life history components may vary dependent on how external conditions affects both metabolic demands, growth rate and demographic processes (Heino & Kaitala 2001; Kozlowski et al. 2004; Holt & Jorgensen 2015).

The optimal energy allocation strategy is the energy allocation scheme that maximizes reproductive output under the constraints of the environment (e.g. resource availability) and by adapting other life history components (Kozłowski 1992). These components include body size dependent metabolic rate, growth, maturation, reproduction and mortality (Kozłowski et al. 2020). By assuming that metabolic rate is non-adaptive, energetic efficiency (the difference between consumption gains and maintenance costs) varies predictably with body size and temperature and the optimal energy allocation strategy should make best use of allocable energy via growth, maturation and reproduction throughout life. Experimentally derived statistical estimates of consumption and maintenance over body size and temperature predicts an energetic efficiency (or energy budget) that produces a temperature-size-rule type growth trajectory (Lindmark et al. 2022). In other words, increasing temperature means increasing costs or energetic constraints for large body sizes and increasing gains or energetic capabilities for a small body size. In addition, mortality is a main driver of adaptive responses in body size (e.g. through predation) and typically increases with temperature (Brown et al. 2004; Thorson et al. 2017; Alfonso et al. 2021). The optimal energy allocation strategy therefore depends on temperature, and the temperature and body size dependence of available energy and mortality are suitable predictors of changes in energy allocation strategies with warming.

It is becoming increasingly evident that higher energy allocation to reproduction at the cost of growth is a likely response to increasing temperature (Loisel et al. 2019; Fryxell et al. 2020; Wootton et al. 2022; Niu et al. 2023). However, we do not know what temperature driven energetic changes, what demographic processes and species-specific ecology drives selection on energy allocation strategies in response to warming. Additionally, we know little of how such life history components in turn affect community responses to warming.

2. Aim of the thesis

Growth throughout life has consequences for the chance of surviving and successfully reproducing and therefore determines the role of an organism in its population, community and ecosystem. Body size and temperature are predictors for the underlying metabolic processes for growth (e.g. feeding rate and maintenance costs). This makes them general factors explaining how species and communities respond to climate warming across ecosystems. By developing mechanistic body size and temperature dependent frameworks of warming effects on short-term ecological and evolutionary processes, we can build general theory useful for predicting effects in the long term.

The overall aim of this thesis is to make predictions of how warming can affect ontogenetic development in terms of species interactions and life history and how those changes at the individual level affect their populations and communities. Specifically, the thesis aims to answer the following questions:

How does warming affect the optimal allocation of energy between growth and reproduction, and what are the underlying fitness trade-offs? (**Paper I**)

How does winter temperature and feeding conditions affect population viability and optimal energy allocation to growth and energy storage and how does this depend on summer temperature? (**Paper II**)

How does the level of energy allocation between reproduction and somatic growth affect responses to temperature in two consumer-resource populations that differ in the timing of ontogenetic changes in diet? (**Paper III**)

What are the consequences, and the underlying mechanisms of warming on predation and competition in an intraguild predator community with ontogenetic diet shift? (**Paper IV**)

3. Methods

To assess how body size and temperature affect ontogenetic development in terms of species interactions and life history, I use two mathematical frameworks: Stage Structured Biomass Models (SSBM, de Roos et al. 2008) and Integral Projection Models (IPM, Ellner et al. 2016). While both frameworks are developed to assess population growth dependent on within species differences in body size in ontogenetic development and life history, they recreate different ecological and evolutionary processes, which I describe below. In this thesis, I make the body size and temperature dependent energy budget the common denominator of the two frameworks. The energy budget represents the internal biological processes responsible for energy available for growth, reserves and reproduction. The energy budget thus sets the conditions for effects of body size and temperature on external ecological processes shaping population responses, species interactions and community composition. In turn, these processes shape natural selection.

3.1 Temperature effects on metabolic processes determine warming effects on the energy budget and on mortality

In the energy budget, temperature affects allometric (body size dependent) metabolism dependent rates (maintenance and consumption), resource productivity and mortality. These effects are key components of the temperature driven changes in the population (**Paper I** and **II**) and community models (**Paper III** and **IV**).

To incorporate temperature effects on the energy budget, on resource productivity and on mortality, I use the Arrhenius equation

($e^{E_A(T-T_{\mathrm{ref}})/kTT_{\mathrm{ref}}}$) formulated using the Boltzmann constant (k) and expressed in relation to a reference temperature (T_{ref}) (Gillooly et al. 2001). Here, activation (set by E_A) through increasing temperature (T) predicts an exponentially increasing rate of change in these three processes. This is a common assumption that makes a general prediction for how temperature affects physiology driven by the temperature activation of enzymatic processes such as maintenance rate and mortality (Brown et al. 2004; Jørgensen et al. 2022). Physiological activity dependent processes however, such as the functional response or maximum consumption rate, are commonly not exponential but unimodal over the full temperature range (Englund et al. 2011; Buba et al. 2022). This distinction is important as the difference between maintenance metabolic rate in relation to consumption rate makes temperature effects on the energy budget size dependent.

In **Paper I**, **II** and **III**, I assume that feeding performance, i.e. maximal consumption rate, is unimodal over temperature (Englund et al. 2011; Lindmark et al. 2022). I model this relationship using the Sharpe-Schoolfield equation as expressed by Padfield et al. (2020) in which exponential temperature activation is counteracted by exponential inactivation at high temperature:$C_{T_{\mathrm{ref}}} e^{E_A(T-T_{\mathrm{ref}})/(kTT_{\mathrm{ref}})} \cdot \left(1 + e^{E_{DC}(T-T_D)/kTT_D}\right)^{-1}$ (Schoolfield et al. 1981). In combination with the assumption that maintenance rate increases faster than consumption rate with increasing body size, the unimodal change of consumption rate over temperature results in a body size dependent effect of temperature on energy gain. This interaction imposes a relative negative effect of warming on larger individuals compared to small. In **Paper IV,** I instead use a phenomenological approach to model this interaction. By adding a linear scalar to the exponential effect (the Arrhenius equation), I decrease the maximum consumption rate of large (adult predators) individuals relative to small with increasing temperature.

In **Paper III** and **IV**, I model temperature dependent food web feedbacks via resources and assume exponential increases in resource productivity but decreases in maximum resource levels. Here I assume that the resource turnover rate has a lower activation energy (E_a) than maintenance metabolic rate, and that the maximum biomass density of resources (sensu carrying capacity) decreases over temperature. This assumption results in that resource density declines over temperature, negatively affecting the energy budget.

Regarding mortality, **In Paper I-II,** I use field based statistical estimates of temperature effects on survival probability in the model species (Windemere Northern Pike, *Esox Lucius*, Vindenes et al. 2014). In **Paper III**, I assume no direct effects of temperature on natural mortality. In **Paper IV** however, I assume that per capita mortality rate scales as maintenance rate with temperature (i.e. the same with the same value of E_A, Savage et al. (2004).

3.2 The size and temperature dependent energy budget

An energy budget is a bioenergetic model of rates of consumption of prey, the conversion or assimilation of the prey into energy and the storage and use of that energy to maintain (somatic maintenance) or build structure (somatic growth), to develop (mature) and to produce offspring (reproductive output). I use two energy budget models in this thesis, differing little in how they generally represent size dependent energy gain and energy allocation (Kooijman 1993; de Roos & Persson 2013)

I deviate in my model in a few assumptions compared to the original formulation of the DEB and the SSBM regarding the energy budget. In Kooijmans (1993) dynamic energy budget model, which I apply in **Paper I** and **II**, the assimilation efficiency is independent of (making it proportional to) consumption rate which scales with body size and temperature (see previous section). Maintenance and somatic growth here competes for energy, which in turn and together compete with the respective demands of development and reproductive reserves. The energy no longer spent on development in adults is spent on reproduction. An important assumption of the DEB- model is the “κ-rule”, stating that a fixed proportion (κ) of energy is spent on maintenance and somatic growth and the rest to storage (e.g. reproduction). The standard DEB-model assumes that no maintenance costs are paid on reserves. This results in that the theoretical individual final size is a result of the competing demand of somatic maintenance and growth (Kooijman 1993). It is however, commonly found in both terrestrial and aquatic species (importantly in fish), that reproductive output strongly increases with size suggesting increasing allocation to reserves with increasing size (Honěk 1993; Kozlowski 1997; Barneche et al. 2018). I therefore assume that kappa decreases with size. In addition, this also allows me to reproduce growth and reproductive patterns in my model species in

Paper I and **II** (Windermere Northern pike, *Esox lucius*). The SSBM as formulated by de Roos et al. (2008) relies on similar energetic principles as DEB-theory but assumes that consumption scales proportional to metabolic rate. I depart from this assumption in **Paper IV** by using the linear scalar of consumption rate and in **Paper III** by using differential body size and temperature scaling of maintenance and maximum consumption rate. This causes growth to slow down with increasing size and temperature - an important assumption considering the aim of my thesis. Furthermore, in the stage-structured model, κ is stage-dependent and is zero for the largest adult stage (i.e. all energy is allocated to reproduction). Consequently, growth mainly ceases due to reproduction being the main component, both in the SSBM and in the DEB-IPM (Kozlowski 1997). The differences in assumptions of the energy budget in the DEB and the SSBM and my departures from these models should be negligible. Importantly, the deviations from the original assumptions that I make allows me to recreate size dependent growth and reproduction over temperature in the DEB.

3.3 The Integral Projection model (IPM)

In **Paper I** and **II**, I used the long-term population growth rate (λ) to assess fitness consequences of different allocation strategies in fish populations in warmer waters. I used the Integral Projection Model framework to build matrices from which λ is calculated as the principal eigenvalue representing mean fitness in the population. To assess what mechanisms contribute to the change in optimal energy allocation, I decompose the sensitivity of λ (assessed through perturbation) to a change in κ $(\frac{d\lambda.}{d\kappa_0^*.})$ between demographic functions across size.

IPMs are structured by a continuous variable, commonly size and/or life stage, that defines demographic rate functions for reproduction, offspring size, growth and survival. Compared to the stage-structured analog (matrix models), IPMs avoid the bias that can be introduced when discretizing size-structured populations with large size ranges into relatively few stages. Like matrix models however, IPMs projects transitions between years of the population structure in discrete time. The demographic rate functions are commonly data-driven, i.e. built on statistical estimates. I instead used the DEB framework to build models for offspring size, growth and reproduction and then a statistically derived survival probability model.

The two DEB-IPMs differ in two important aspects. First, in **Paper I**, I focus on demographic processes taking place between spring and late autumn. In particular, this model does not include winter mortality. This is instead the focus of **Paper II**, where winter survival probability from starvation is multiplied with the summer survival function. In **Paper II**, winter starvation also decreases reproductive output through the use of energy reserves. Furthermore, how energy reserves are allocated temporally differ between **Paper I** and **II**. In **Paper I**, I use the standard DEB-model approach in which energy allocation is constant throughout the season, while in **Paper II**, I instead assume that individuals first grow and then apply a discrete shift to allocation to energy storage. This makes allocation level a fraction (κ) of daily consumed energy in the first case and a fraction of the total seasonal available energy in the second case. The two approaches produce similar and reasonable estimates of growth, fecundity and of κ at mean temperature and of λ over temperature for the model population.

The DEB-IPM in **Paper I** and **II** is inspired by a similar model proposed by Smallegange et al. (2017) but differs in significant aspects. I developed their framework to be able to account for the size dependent temperature effects described above. In principal, the DEB provides a differential equation for the rate of energy available for growth and reproduction. Projecting size dependent growth and reproduction in time is done by integrating this equation. Smallegange et al. (2017) solved the integration of the differential equation for growth rate analytically and quantified parameters for the von Bertalanffy growth equation that they could fit to data. This approach is mathematically convenient but requires that maintenance rate scales proportional to mass and that mass-dependent rate scales proportional to the cube of length (Kooijman & Metz 1983; Essington et al. 2001; Smallegange et al. 2017). However, the fact that maintenance rate scales with both temperature and mass generates such functions without closed form, and consequently without analytical solutions. Furthermore, the von Bertalanffy is unable to incorporate the consequences for reproductive allocations (Czarnoleski & Kozlowski 1998). Consequently, I instead solve the differential equation numerically to incorporate the mass and temperature scaling of maintenance and consumption and size dependent allometric scaling. The DEB-IPM in **Paper I** and **II** therefore provides a novel framework for mechanistic assessments of temperature effects on demographic and evolutionary processes.

The DEB-IPM is based on the life history of the Windermere Northern pike population (*Esox Lucius*), a large growing, spring-spawning capital breeder that breeds annually. I fit the demographic functions for the size of age 1 individuals (offspring), somatic growth, fecundity (reproduction) in the DEB to data on the Windermere pike (Winfield et al. 2013b; a). This requires parameters estimates on the size and temperature dependence of metabolism, consumption and allocation. The temperature effects in the DEB are based on the meta-analysis of Lindmark et al. (2022), the size dependence of metabolic rate are based on parameters from Armstrong et al. (1992). As consumption rate is naturally highly variable and allocation (κ) is unknown, I consider parameters describing the size scaling of these processes in the DEB as free (sensu Essington et al. 2001). To this end, I use numerical optimization of the model to estimate these parameters at mean temperature to fit the data on weight-at-age and fecundity-at-weight observed in the Windermere pike. While the resulting IPM is largely based on a specific population, the overall temperature effects on the physiological rates that in turn predicts responses in demographic rates are more general and should apply to a broader range of similar populations and species.

3.4 Stage structured Biomass models (SSBM)

To assess how temperature effects on the size dependent energy budget affects communities via interactions within and between species (**Paper III** and **IV**), I used stage structured biomass models (SSBM, de Roos et al. 2008).

The SSBM framework is a simpler and more condensed development of the Physiologically Structured Population Models (PSPMs, Persson et al. 1998). PSPMs are based on partial differential equations modelling growth and mortality continuously, but maturation and reproduction in discrete time. This detailed approach requires keeping track of the dynamics of the population based on the state of its individuals. The realistic representations of life histories trades off however for complex analysis and limits possibilities of modelling multispecies systems (de Roos et al. 2008). SSMBs on the other hand are based on ordinary differential equations and are stage-structured versions of the energetic biomass model of Yodzis & Innes (1992). Here, maturation and reproduction is continuous and the state variables (species or stages within species) are based on individual level rates. This makes for less detail in life history but allows for keeping track of how within-species asymmetric biomass production between stages, dependent on body size, shapes the population via environmental conditions. Furthermore, it allows for direct assessment of alternative stable states even in the simplest consumer-resource models over environmental gradients, which is a major enhancement of unstructured models (Miller & Rudolf 2011). I use this approach to understand how changes in temperature via the size dependent energy budget and resource productivity affects interactions both within and between species.

In **Paper III**, I assessed the response to a continuous increase in temperature of a consumer-resource model with a three-stage structured consumer population consisting of juveniles, small and large adults. Here, I vary energy allocation discretely in small adults and also analyze how warming and energy allocation affect two consumer populations that differ regarding at what life stage they change diet, early at maturation or late at transition from small to large adult.

In **Paper IV**, to study how warming affects intraguild predator communities, I assess how temperature affects community composition and biomass structure in a system consisting of a two-stage-structured predator (juveniles and adults), an unstructured intermediate consumer and their shared resource. In the main analysis, the predator undergoes a discrete ontogenetic diet-shift: the juvenile predator feeds on the shared resource and the adult predator feeds on the consumer only. In the extended analysis, I vary the extent of the ontogenetic diet-shift, i.e. the extent to which the adult feeds on both the consumer versus the shared resource.

4. Results and discussion

4.1 Changes in energy allocation with warming

In Paper I and II, I find that optimal energy allocation to reproduction increases with warming at the cost of growth. There is support for this finding, in both controlled and natural experiments (Loisel et al. 2019; Fryxell et al. 2020; Wootton et al. 2022) and in previous theoretical work (Kozlowski et al. 2004; Audzijonyte et al. 2018). My methodological approach however allows an improved understanding of how physiological responses in the energy budget affect demographic processes that in turn shape selection for energy allocation strategies.

I identify four mechanisms by which warming drives increasing allocation to energy reserves (Paper I and II): 1) Warming induced increased growth rate of small individuals, 2) increased winter starvation rate, 3) energetic constraints of larger sizes and 4) increased adult mortality.

The first mechanism, increased growth rate of small individuals, makes juveniles grow and mature faster. Selection for high growth rates is strong early in life, a high growth rate both increases survival probability (as this is size dependent) and juveniles can reach maturity faster (Heino et al. 2002). Consequently, I find that the sensitivity of the long-term population growth rate to change in allocation strategy is strongest among juvenile individuals (Paper I). A positive temperature effect on the energy budget releases selection pressure on high somatic growth rate, making juvenile growth rate correlate with higher energy allocation to reproduction (van Noordwijk & de Jong 1986; Conover & Present 1990). Juveniles that increase their reproductive reserve at the cost of somatic growth before next year's probable maturation and onset of reproduction will contribute more to population growth. I did not assess, but it is possible, that negative effects of warming on reproductive output, e.g. via factors reducing survival of eggs and larvae would lower the slope of change in optimal energy allocation with warming (Bry et al. 1991; Alix et al. 2020).

The importance of juvenile growth and survival for the viability of the population motivates better understanding of the processes that shape increased winter starvation rate which is the second warming driven identified mechanism that affects allocation strategy (Hurst 2007). Winter survival in young-of-the-year or juvenile fish is threshold like over body size, where a larger body size increases survival through larger energy storage and a lower mass-specific maintenance rate (Shuter & Post 1990; Schultz & Conover 1997, 1999). In Paper II, I identify the corresponding threshold of energy allocation to somatic growth that puts a limit on population viability through individual juvenile survival. The allocation parameter in the DEB-model makes the energy allocation trade-off between body growth and winter energy storage explicit as opposed to being a correlate of body size. I find that increasing winter temperature and unfavourable summer temperature lowers the threshold of energy allocation to somatic growth, i.e. requires larger energy reserve. In contrast, increasing food availability in winter favors the energy budget and raises the threshold to higher energy allocation to growth. That increasing summer temperature increases the allocation threshold for population viability means that favorable growth conditions via energy storage, and not necessarily via body size, provides better chances of survival (Post & Parkinson 2001; Huss et al. 2008).

The optimal energy allocation strategy in Paper II can differ from the allocation threshold for population viability. Different optimal energy allocation strategies can thus emerge dependent on food availability (or feeding ability) in winter, and on summer temperature (Post & Parkinson 2001; Byström et al. 2006; Mogensen & Post 2012). This is likely caused by that energy allocation to reserves, which reduces winter temperature dependent survival, trades off against somatic growth, which increases body size dependent survival (e.g. predation) in summer (Persson 1986; Post & Parkinson 2001). When winter survival is high, juveniles can maximize growth to increase the probability of reaching maturity and survive to next year (Heino & Kaitala 2001). Therefore, if food availability in winter is high, the optimal strategy tracks (is very close to) the energy allocation threshold for population viability. When food is scarce however, the optimal energy allocation strategy and threshold for population viability are separated and they become more separated with increasingly warm winters. This means that the selection pressure(s) for minimum energy requirements differ from the energy storage optimum for population growth. The current analysis does not reveal why this is the case. A more detailed analysis could possibly disentangle underlying causes of selection in response to warming, e.g. age of juveniles, or temperature dependent selective pressure (survival, future feeding conditions or reproductive potential).

The third mechanism, energetic constraints of large adults, contributes to the change in optimal energy allocation in Paper I by increasing reproductive effort. I find however that this contribution is smaller than temperature dependent mortality and juvenile growth. As large or old adults are often relatively few, they do not contribute as much as small to population growth (Andersen et al. 2019). The growth rate of large individuals is constrained in my model because warming increases the deviation from their temperature optimum for growth, which declines with increasing size (Morita et al. 2010; Lindmark et al. 2022). This is in turn due to a reduced energetic efficiency at high temperature. In Paper II, where I separate adult and juvenile allocation, the decline in energy allocation to growth among adults appears only at high winter temperatures. I did not asses the contribution of demographic processes to this increase in optimal energy allocation to reserves but a likely cause is reduced reproductive output through starvation effects on reproductive reserve (Farmer et al. 2015; Wright et al. 2017). Unfavourable (cold or hot) summer conditions exacerbate the decline in energy allocation to growth with increasingly warm winters. What demographic processes that balance negative effects of warming at lower winter temperature in my model, resulting in no change in optimal energy allocation, is also unknown.

Increasing adult mortality with increasing temperature is the fourth mechanism that increases the selection pressure for an increased allocation to reproduction (Paper II). Mortality increases with temperature via metabolic processes increasing the rate ecological sources of mortality (e.g. predation and disease) and senescence (Brown et al. 2004; Jørgensen et al. 2022). When mortality rate increases, chances of a long life and a large size decreases. Such effects of adult mortality on change in growth and reproductive strategies (e.g. energy allocation) is well described within life history theory and my prediction regarding this mechanism should be fairly consistent (Stearns 1992; Charnov et al. 2001). However, how temperature driven increases in mortality affects energy allocation strategies can be context dependent, e.g. depend on the effects of temperature on growth (Kozlowski et al. 2004).

As mortality is the strongest selective agent of body size, the warming induced net change in size dependent mortality is the key to understand changes in life histories such as energy allocation (Grainger & Levine 2022). Whether observations of warming induced changes in maximum or mean size depend on allocation strategies can only be fully understood in the context of changes in mortality (direct or indirect via growth) affecting the prospect of future reproductive output (Kozlowski et al. 2004). My results of a change in energy allocation strategy implies changes in body size structure and generation time of a population (c.f. Röpke et al. 2021). This in turn affects its susceptibility to variation in the environmental (including climatic) conditions and to harvesting (Hsieh et al. 2010; Hidalgo et al. 2011).

4.2 Effects of warming dependent on energy allocation strategy

My results address three aspects of how effects of warming on population structure and viability depend on energy allocation strategy: the ontogenetic life stage affected, seasonal differences in temperature change (Paper I and II) and if resource feedbacks are taken in into account (Paper III).

Seasonality affects population growth via possible biomass gains in summer and constraints of winter. When accounting for demographic processes taking place in summer (Paper I), an increase in energy allocation to reproduction reduces somatic growth rate without strongly reducing population viability. In contrast, the analysis of increasing winter temperature in Paper II shows that failure to meet higher energy storage requirements can have drastic negative effects on population viability. This is particularly the case if the energy storage threshold for population viability is close to the juvenile energy storage that results from an allocation strategy favoured by natural selection. Consequently, how a population responds to warmer winters, will depend on the history of adaptation to the local winter environment (e.g. seasonal temperature changes or food availability) that has shaped allocation strategy.

Adapting by increasing energy allocation to reserves at the cost of somatic growth keeps the population viable in Paper II. This suggests however that warming selects for reduced growth rate and smaller sizes (to meet the need of energy storage requirements and increase of reproductive output). Reduced energy allocation to growth can thus trade-off for a reduction in growth rate and body size, negatively affecting survival (e.g. via predation Sewall et al. 2019), probability of maturing in the approaching season (Morita & Fukuwaka 2006) or resource availability (Nunn et al. 2012; Callahan et al. 2021). Intermediate warming directly increases growth rate of small individuals and causes earlier maturation and can therefore compensate for these effects. High summer temperatures however, have negative effects on growth rate independent of size. Consequently, when warmer summers constrain biomass production and winter demands higher energy storage, warming selects for further reduced growth rate and body sizes, in turn forcing higher mortality and reduced population growth.

How temperature affects population growth rate depends on how resource competition shapes ontogenetic growth bottlenecks (Lindmark et al. 2018). I did not assess density dependent processes in Paper I and II (using the temperature dependent DEB-IPM). In Paper III however, using a dynamic model (SSBM), I studied how energy allocation might affect such growth bottlenecks.

I find that by shifting biomass between stages, and thereby modulating intraspecific competition and the strength of ontogenetic growth bottlenecks, energy allocation affects the population response to temperature. If juveniles change diet early in life, warming shifts population regulation, from a juvenile to an adult bottleneck, via negative size dependent effects of warming on adults. This shift occurs independent of energy allocation strategy despite that reduced energy allocation to growth releases competition for food among adults. An important change preceding the shift in population regulation (i.e. the switch from juvenile to adult bottlenecks), is a decrease in total reproductive output, increasing individual juvenile growth rate. Density dependent growth is common in juvenile stages of fish populations and empirical work support that climate change may reduce such density dependence (Bassar et al. 2016; Zimmermann et al. 2018). That the underlying cause however may be size dependent effects of warming on energy budgets of adults in relation to that of juveniles is to my knowledge based on theoretical predictions (Lindmark et al. 2018; Uszko et al. 2022).

Other, more easily measured processes that may affect density dependent competition among juveniles have better support, e.g. that warming reduces reproductive success via increased mortality of eggs and sperm (Alix et al. 2020; Dahlke et al. 2020; Parratt et al. 2021), larval and juvenile survival (Killen et al. 2007) and increased energetic costs of winter (Farmer et al. 2015; Wright et al. 2017; Goodsman et al. 2018). These effects combined warrant a change in competitive bottlenecks in response to warming.

The negative effects of warming on adult growth that drive change in population regulation in Paper III, i.e. that declining energetic efficiency of adults makes biomass starts to accumulate, could in part be reversed. For example, if energy allocation to growth decreases in response to warming, biomass density is reduced, lessening negative effects on adult biomass competition, their biomass production and reproductive output (Sentis et al. 2017). Paper III however shows that this comes at the cost of further loss of larger and adult individuals (i.e. large adults in the model), population biomass and biomass production. The loss of biomass of large individuals through warming induced competition increases with increasing energy allocation to growth predicting species dependent responses in size shifts with warming.

For most combination of species- or population-specific life history traits in Paper III (energy allocation strategy and ontogenetic diet shifts) biomass of large individuals is lost. Furthermore, with high energy allocation to growth and an early diet shift (at maturation), warming results in a shift, from large to small adults. While studies on natural fish populations often (but not always) support this prediction, these cross scale patterns are biased because of fishing on those populations (Baudron et al. 2014; Ikpewe et al. 2020). This obscures detailed analysis of warming driven mechanisms underlying size shifts (Pomeranz et al. 2022). I identify that negative effects of warming on the energy budget of large individuals, amplified by resource competition, increase with allocation to growth. Fishing, which often targets adult and larger individuals may release them from competition (Morrongiello et al. 2021). This would obscure negative effects of warming on their energy budget. In fish populations with low fishing mortality however, the underlying mechanisms to loss of large individuals could depend on natural mortality or reflect adaptation to climate warming to avoid such growth constraints (Heibo et al. 2005; Audzijonyte et al. 2018; Ikpewe et al. 2020). Considering variation in species-specific ecology in terms of the ontogenetic niche apart from their thermal adaptation can be a fruitful way forward to understand how such adaptations evolve.

4.3 Warming induced changes in population and community structure

The upper thermal sensitivity of populations depends on the effect of high temperature on their ontogenetic stages, i.e. on the ability of successful reproduction of adults and on the growth and maturation of the offspring (Dahlke et al. 2020; Parratt et al. 2021). Better knowledge of how community interactions are driven by differences in the underlying metabolic responses between ontogenetic stages therefore help predict population tolerances to increasing warming (Sunday et al. 2022).

In Paper IV, I identify a mechanism that exposes predatory fish species to negative effects of warming: warming induced loss of cultivation. Cultivation is a feedback mechanism where larger individuals of a predator population cultivate a favourable environment for their juveniles by feeding on their competitors (Walters & Kitchell 2001). These favourable conditions enhances predation rate on the competitors via a high growth rate and maturation rate of smaller individuals. When the predation effect on the competitors is lost, e.g. by intense harvesting of predators or as shown in Paper IV, via warming effects on competition and predation, this has “depensatory” (i.e. negative effects) on the population growth rate (Walters & Kitchell 2001; Gårdmark et al. 2015; Thunell et al. 2021). Consequently, this causes alternative stable states in community composition, i.e. with or without predators present (van de Wolfshaar et al. 2006). I show that at intermediate temperatures, the cultivation mechanism enables coexistence of the predator population and its consumer prey but that warming makes the predator go extinct at higher temperature. The warming induced increased competition and reduced predation rate causes a juvenile bottleneck preceding extinction of the predator. Similar shifts in within-species population regulation of prey with warming precedes extinction of predators feeding on smaller prey individuals in tri-trophic food chains (Lindmark et al. 2019). From either shift, whether in the predator or in the prey, follows a collapse of the predator. The collapse (as opposed to a smooth decline in biomass preceding extinction) and coupled alternative stable states are results of taking into account within species differences in species interactions (de Roos & Persson 2002; Binzer et al. 2012; Lindmark et al. 2019). Comparable to size specific predation, IGP resulting from ontogenetic diet-shifts are common, not only in fish but in other aquatic and terrestrial communities (Nakazawa 2014; Sanchez-Hernandez et al. 2019). This warrants collapses of predators following warming. Not considering ontogenetic diets-shifts and its effects on predation and competition in food-webs limits understanding of under what environmental and food-web specific conditions collapses occur (Nakazawa 2014).

Warming leads to a shift in species composition, favouring a lower trophic position in the multispecies IGP community in Paper IV and an accumulation of biomass in the smaller adult stage in the consumer-resource community in Paper III. This supports the prediction of smaller species and larger stages when accounting for size dependent effects of warming (Uszko et al. 2022). Considering theoretical expectations of reduced energetic efficiency from warming in higher trophic levels (Vucic-Pestic et al. 2011; Fussmann et al. 2014), there is an important difference in how temperature shapes the energetic efficiency within species preceding the extinction in the two models. While warming reduced energetic efficiency in larger stages in consumer resource model (Paper III), it increases slightly in the adult intraguild predator (Paper IV). This discrepancy is due to that different ontogenetic stages constitute the ontogenetic bottleneck in response to warming.

Evidence is accumulating for changes in population regulation with climate change. For example, Myrvold and Kennedy (2015) attributed stronger juvenile competition and bottleneck in wild Steelhead (*Oncorhynchus mykiss*) with increasing metabolic rate driven by warming, while Watz et al. (2019) linked a warming driven ontogenetic bottleneck in early life to interspecific competition from White-spotted charr (*Salvelinus leucomaenis*) on Dolly Varden trout (*Salvelinus malma*). On the other hand, Bassar (2016) showed that climate induced reductions in early survival might outpace density dependent early growth regulating populations of Eastern brook trout (*Salvelinus fontinalis*). Consequently, despite similar systems and related species, different climate driven mechanisms govern the ontogenetic bottlenecks highlighting the importance of a mechanistic basis predicting population or species-specific responses to warming.

My analyses in Paper III and IV highlight the importance of inter- and intraspecific competition for how warming shapes populations and food webs. While the underlying metabolic mechanisms are very similar in Paper III and IV, the change in population regulation with warming depends on whether inter- or intraspecific competition is accounted for. In Paper III, a smaller body mass increases mass-specific consumption rate and energetic efficiency with warming, making juveniles superior to adults in resource competition. In Paper IV, the consumer species is superior in foraging on the shared resource compared to the juvenile predator (via a higher mass-specific maximum consumption rate) and favoured when warming increases resource demands in relation to supply. When the adult predator stage can no longer control interspecific competition via predation, a change in population regulation, from an adult to a juvenile bottleneck precedes the extinction of the intraguild predator. In contrast to how interspecific competition shapes the temperature response of the predator population in Paper IV, warming effects on intraspecific competition can precede extinction via an opposite change in regulation in Paper III. Here, adults are productive enough to maintain a juvenile bottleneck (for a diet shift at maturation) at intermediate temperature but adult competition for food compromises productivity at high temperatures. While reflecting opposite mechanisms of change in these two studies, the similarity is the importance of the function of adults in these models: reproductive output and top-down control. Maintaining a juvenile as opposed to an adult bottleneck via reproductive output is common in fish populations and is important for adult growth rate and thus population size structure (van de Wolfshaar et al. 2008; Zimmermann et al. 2018). However, intraguild predation and ontogenetic diet shifts are both common ecological features in fish communities providing stabilizing functions in food webs (Finke & Denno 2005; Nakazawa 2014; Sanchez-Hernandez et al. 2019). My results suggest that warming compromises both reproductive output and top-down control, in turn affecting the functional role of larger individuals and adults in populations and in food webs. The scale of inter- and intraspecific competition in natural communities should thus be a key to understand how size shifts emerge and food webs function in response to climate change.

5. Conclusions and future perspectives

In this thesis, I have inferred changes in species interactions and changes in selection pressure from size and temperature dependent energy budgets, mortality and temperature effects on resource productivity. The energy budget is based on common effects of temperature and body size on maintenance and consumption rates among fish species. Using these approximations of physiological effects on individuals, the body size structure of populations can change towards an increasing amount of juvenile (Paper I, IV) or small, instead of large adult individuals (III). The change in body size structure depends on what warming dependent processes are accounted for. Here, species interactions are a particularly strong force shaping how changes in body size structure occur. In summary, I have identified a set of novel predictions: That changes in energy allocation strategies with warming depend on demographic and environmental processes taking place early in life; that energy allocation strategies sets the conditions for loss of larger individuals due to growth constraints but may, in comparison to competition for food, be a weak predictor of how ontogenetic bottlenecks change with warming; that the cultivation/depensation mechanism common in fish communities should be temperature dependent.

I find that energy allocation to growth should decrease to favour increased reproduction and to serve as energy reserves during winter when feeding conditions are poor and warming increases maintenance demands. This finding is based on well-known predictions from life history theory regarding changes in mortality, growth and reproduction and thus quite intuitive. However, the link to the size and temperature dependent energy budget based on metabolic rates is interesting in the light of recent theoretical advances of metabolic life history theory. While my predictions on energy allocation and warming seem correct, underlying drivers may differ (c.f. Wootton et al. 2022). Kozlowski et al. (2020) suggested that the body size dependence of metabolic rate reflects life history optimization of allocation based on mortality. This was formalized in a model by White et al. (2022) which could predict statistical correlations of metabolic allometry with reproductive output and growth rate. Similar work show the relationship between metabolic rate, temperature and life style of fishes (Killen et al. 2010; Jørgensen et al. 2016). Furthermore, metabolic rate in response to temperature is adaptive and results in population specific adaptation of life histories, and possibly speciation on long evolutionary times (Jutfelt 2020). These collective circumstances render the direction of causality in my models (i.e. changes in metabolism and mortality affects energy allocation) uncertain but spurs questions about short- and long-term implications of adaptation of metabolic rates of life histories following contemporary climate warming. This is a topic for future investigation.

From body size dependent effects of warming on the energy budget in dynamic models, I predict loss of intraguild predator biomass, extinction via a collapse and species shifts that depend on the form of ontogenetic diet-shifts. The more realistic account of community structure in this case enables species-specific accounts of effects of warming resulting from density dependent processes. Extending previous approaches of addressing alternative stable states in natural communities (e.g. Gårdmark et al. 2015) with predictions based on effects of warming could guide empirical assessments of changes occurring in fish communities. Such an approach would be a suitable test of my predictions of warming effects on species interactions in this thesis. In my models however, I did not account for the larger community context where additional species interactions are at play, that may lower extinction risk and stabilize the community (McCann et al. 1998). The stage-structure of species in which a change precedes the collapse of the intraguild predator, is stabilizing in larger species communities (de Roos 2021). And so is ontogenetic diet shifts (Reum et al. 2019). By focusing on more realistic accounts of ontogenetic diet-shifts, their effects on asymmetry in energetics between life stages and associated species interactions could consequently favour understanding of large-scale changes in food webs under warming.

I conclude that by accounting for predictable effects of body size and temperature on individual energetics, we gain mechanistic understanding for change in food webs with climate warming. This approach can be used to infer general or system specific effects of temperature on species interactions and on evolutionary processes. My thesis thus forms a basis for future work consisting of empirical tests. With established links between empirical tests and theory, phenomenological observations in response to warming can become mechanistic knowledge, in turn providing science with predictive power, and management and conservation with sharper tools.

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Popular science summary

How do species and ecosystems evolve under climate change? To explore this question we need take into account how the direct effects of temperature on physiological processes affect individual growth, reproduction and mortality. These effects can predict how species interactions are shaped by temperature. Species interactions affect the composition of animal communities; from predators, their prey and down to the smallest animals or plants that form the energy base of ecosystems. The joint effects of these processes shape natural selection and evolution in response to a warmer climate.

A common observation from climate warming so far, and over natural temperature gradients is changes in body size both within and between species, for example smaller adults or loss of large bodied species. How and why these changes occur, and what consequences it has for ecosystems and the services they provide us with is a challenge for ecological and evolutionary research.

In this thesis, I use mathematical models to represent a few core physiological processes to fill critical knowledge gaps in ecological and evolutionary research related to climate warming. The purpose of theoretical models of ecology and evolution is to generate predictions (or expectations) of complex processes that are difficult to measure in the field and in the laboratory. I use these models to study how the body size compositions of populations affect natural selection and how individuals feed and compete with other individuals, from the same or from other species. The overall aim of the thesis is to predict how warming affects 1) natural selection for division of available energy between growth and reproduction to maximize individual reproductive success and 2) the structure of animal populations and the species composition of their communities.

I find that in a warmer environment, the growing fish will use more available energy to increase the production of eggs and offspring instead of growing large. This is mainly because small and juvenile individuals grow and become mature faster in an increasingly warmer climate and contribute more to the growth of the population at smaller sizes or younger ages. At the same time, large adults die earlier and may become limited in their production of eggs in a warmer environment. Smaller adults that produce many offspring early in life are thus favoured by natural selection. I also find that warmer environments demand more energy reserves for fish to survive starvation in winter and this can further increase the need for energy that could otherwise be used for individuals to grow large. The change in energy allocation and warming affects the size structure of fish populations, and can in turn increase their sensitivity to changes in the environment.

Regarding changes in population and species community composition, I show that changes in diet throughout life is important for how species respond to a warmer environment. Fish and other ectotherm (cold-blooded) animals commonly change diet as they grow in size or become mature, and this is an important ecological aspect of how ecosystems are structured. I show that diet shifts matter for how warming affects the competition for food between different sizes of individuals and for feedbacks mechanisms between predators and prey. These feedbacks maintain growth of large growing predatory fish and if they are disrupted, this leads to collapses of fish populations.

In conclusion, these findings contribute to knowledge on why and how temperature dependent individual growth can affect natural selection and animal communities in a warmer climate. The theoretical predictions of temperature dependent mechanisms identified in this thesis can serve as guidance when designing experiments and assessing field survey data. Overall, I predict that fish communities will continue to change in size structure and species composition with negative effects on ecosystem services and biodiversity at the current rate of climate warming.

Populärvetenskaplig sammanfattning

För att förstå hur arter och ekosystem påverkas av klimatförändringar måste vi ta hänsyn till hur temperatur direkt påverkar fysiologiska processer och hur det i sin tur påverkar individuell tillväxt, reproduktion och livslängd hos fiskar och andra arter. Den kunskapen kan sedan användas för att förstå hur artinteraktioner påverkas av temperatur vilket formar ekosystems sammansättning, från predatorer, deras byten och ner till de minsta organismer som utgör ekosystemens energibas. Den sammanlagda effekten av dessa processer formar sedan det naturliga urvalet och evolution i ett varmare klimat.

Över naturliga temperaturgradienter och i och med ett allt varmare klimat observeras förändringar i kroppsstorlek hos ektoterma (växelvarma) djur. Det syns både som förlust av storväxta djurarter eller individer inom arter. Hur och varför dessa förändringar sker, och vilka konsekvenser det har på ekosystem och på ekosystemtjänster, är en viktig fråga och stor utmaning för ekologisk och evolutionär forskning.

I den här avhandlingen använder jag matematiska modeller vilka återskapar fysiologiska nyckelprocesser för hur djur växer, reproducerar sig och dör för att fylla kunskapsluckor i hur ekologi och evolution påverkas av uppvärmning. Sådana modeller inom ekologisk och evolutionär forskning syftar till att göra teoretiska prediktioner (förväntade effekter) av komplexa processer som är svåra att mäta i fält och i experiment. Jag använder dessa modeller för att studera hur populationernas kroppsstorlekssammansättningar påverkar det naturliga urvalet och hur individer äter och konkurrerar med andra individer från samma population eller från andra arter. Avhandlingens syfte är att göra prediktioner baserade på sådana modeller för hur uppvärmning 1) påverkar det naturliga urvalet för hur tillgänglig energi används till individuell tillväxt och reproduktion och

2) påverkar djurpopulationers struktur och näringsvävars artsammansättning.

Jag visar att det i en varmare miljö är bättre för en växande fisk att använda tillgänglig energi till att producera mer avkomma istället för att växa sig större. Orsaken är framförallt att små och unga individer växer och blir könsmogna snabbare i en varmare miljö vilket gör att de kan bidra till populationstillväxt redan vid mindre storlek eller i yngre åldrar. Samtidigt begränsar en varmare miljö storväxta individers produktion av avkomma och de dör tidigare. Det naturliga urvalet gynnar alltså de vuxna individer som producerar mycket avkomma tidigt i livet. Jag visar också att ett varmare klimat kräver mer energireserver för att fiskar ska kunna överleva svält under vintern vilket ytterligare ökar behovet av energi som annars skulle kunna användas för att individer ska växa sig stora. De här processerna påverkar fiskpopulationernas storleksstruktur vilket i sin tur ökar deras känslighet för förändringar i miljön.

För att förstå hur en varmare miljö påverkar djurpopulationers struktur och artsammansättning visar jag att arters födobyten genom livet är viktiga att ta hänsyn till. Fiskar och andra ektoterma djur byter vanligtvis föda när de växer i storlek eller blir könsmogna vilket är en viktig aspekt av hur ekosystem är uppbyggda. Jag visar att sådana dietskiften påverkar uppvärmningens effekter på födokonkurrens mellan individer beroende på storlek och hur predator-bytes-mekanismer förändras. Dessa mekanismer upprätthåller tillväxt hos storväxta rovfiskar och när de störs leder det till att fiskpopulationer påverkas negativt och drastiskt (kollapsar).

Sammanfattningsvis bidrar avhandlingen till kunskap om hur och varför individuell temperaturberoende tillväxt kan komma att påverka evolution och artsammansättning i ett varmare klimat. De prediktioner jag gör av temperaturberoende mekanismer kan också användas som vägledning vid utformning av experiment och för analyser av fältundersökningsdata. Baserat på dessa prediktioner förutspår jag att fisksamhällen kommer fortsätta att förändras i storleksstruktur och artsammansättning med negativa konsekvenser för ekosystemtjänster och biodiversitet.

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ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

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Body sizes vary within and between species, they structure food webs via feeding interactions and are changing with climate warming. In this thesis, I use theoretical models of individual growth, reproduction and mortality based on temperature and body size dependent metabolic rates, to infer effects of warming on species interactions and natural selection. Subsequently, I identify mechanisms of life history evolution and species ecology by which fish individuals and their food webs are changing with an increasingly warmer environment.

Viktor Thunell received his undergraduate degree at Stockholm University.

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SLU generates knowledge for the sustainable use of biological natural resources. Research, education, extension, as well as environmental monitoring and assessment are used to achieve this goal.

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