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Climate change impacts on fish communities – how individual responses to climate change are mediated by size-structured interactions

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Front cover: The catch during the fishing after whitefish. Photo: Yvette Heimbrand.

Back cover: Sunset. Photo. Yvette Heimbrand.

Abstract

Global climate change, fueled by human activities, has profound effects on marine ecosystems and food safety, and has already caused large-scale changes in distribution and phenology. Empirical studies suggest that a third universal response of warming is a directional shift towards smaller body sizes of water breathing ectotherms such as fish. This may have implications for fisheries and food security in warming environments, as individual growth and body size are key traits for fisheries yield and management.

However, ectotherm body size is not only governed by temperature, but also biotic factors such as food availability. Experimental and theoretical studies have revealed the importance of differential size-scaling of biological rates for the size-structure and dynamics of animal populations and communities. In turn, these rates are also temperature dependent. Therefore, in addition to direct physiological impacts of warming, warming also induces indirect effects, i.e. feedbacks from altered biotic interactions, as community dynamics and altered population size-structures feed back on individual performance. Thus, climate change impacts on individual performance are mediated by biological interactions which are governed by size- and temperature scaling of vital rates. In addition, it is increasingly acknowledged that the temperature dependence of physiological rates is more multifaceted than what can be inferred from universal temperature- and mass-scaling relationships in terms of shape, size-dependency and effect size.

With a few exceptions, studies on climate change impacts on natural populations ignore ontogenetic- and/or thermal asymmetry between rates. However, these features are both common in natural populations, and important for intraspecific population dynamics and size-structure, which has implications for interspecfic interactions. Thus, current understanding of climate change impacts on community dynamics may be limited to scenarios where the size-structure does not influence intraspecific dynamics, and vital rates show similar temperature dependencies.

Resolving the ecological implications of the asymmetries in thermal responses between and within species, and the feedbacks on food availability emerging from size-dependent interactions and processes, is a key research area for understanding and predicting net effects of climate change. These implications could be explored using individual-based modelling frameworks in a food-web context, such as physiologically structured population models or stage-structured biomass models. Understanding both direct and emerging indirect effects of climate change is a crucial step to advance our ecological knowledge of potential impacts of climate on fish populations and the food webs in which they are embedded.

Keywords: Climate change, food webs, size-structure, inter- and intra-specific interactions, community dynamics, physiology

Table of contents

List of Figures **5**

Abbreviations **6**

1 Introduction **7**

2 Performance of water-breathing ectotherms in warming oceans **10**
2.1 Thermal performance 10
2.1.1 Oxygen- and capacity limited thermal tolerance 11
2.2 The temperature-size rule 13

3 Size-structured population and community ecology **16**
3.1 Growth and ontogenetic scaling of metabolism and food intake 16
3.1.1 Metabolism 16
3.1.2 Energy intake 17
3.1.3 Ontogenetic asymmetry, net energy and growth 18
3.2 Consequences of ontogenetic asymmetry for population dynamics 19
3.2.1 Population bottlenecks and cycles 19
3.2.2 Biomass overcompensation 21
3.2.3 Implications for community structure 22
3.3 Structured or unstructured population models? 23

4 Climate change impacts on ecosystems and the dynamics of size-structured communities **26**
4.1 Temperature effects on the level and size-scaling of biological rates 26
4.1.1 Size- and temperature scaling of functional response parameters 28
4.2 Climate change impacts on ecosystems predicted from metabolic scaling theories 30
4.2.1 Is hotter better? 32
4.3 Implications of intraspecific asymmetries in temperature effects for dynamics and size-structure of communities 32
4.4 Climate change and fisheries yield 35
4.4.1 Effects of warming and size-selective fishing on dynamics and size-structure of fish 37

5 Conclusions **40**

References **42**

List of Figures

Figure 1. Thermal performance plots illustrating A) predicted effects of warming on growth rate depending on the current ambient temperature in relation to predicted increases and optimum temperatures, and B) the effect of food availability for thermal optimum. Redrawn from Ohlberger (2013). 11

Figure 2. Conceptual illustrations of two competing views of the relationship between aerobic scope and optimal temperatures. A) the OCLTT-hypothesis (Pörtner & Farrell, 2008) predicts that maximum aerobic scope coincides with optimal temperature. B) By contrast, Clark et al. (2013) argue that the temperature that maximizes overall performance is lower than that which yields maximum aerobic scope, which in addition continues to increase until critical temperatures are approached. Redrawn from Clark et al., (2013). The pejus (Latin: turning worse) range is the temperature-range of long-term survival of an organism. Denaturation temperature refers to the temperature where the molecular structure is altered. 12

Figure 3. Relationship between the metabolic scaling exponent (b) and metabolic level (L) (proportional to temperature) according to the MLB hypothesis. Over the full range of physiological states, from resting metabolism (white) to active metabolism (gray), the relationship between b and L is U- or V-shaped. Redrawn from Glazier (2010). 28

Figure 4. Conceptual illustration of temperature effects on consumption and metabolism, highlighting the lower temperature at which maximum consumption (Cmax) occurs compared to maximum metabolism (Mmax). 30

Figure 5. Conceptual illustrations of three general types of asymmetry in thermal responses of trait performance or between interacting species. A) Differences in levels (activation energy) between species or rates B) differences in rates of response, such that one species may respond more to warming or differences in temperature effects on the size scaling of rates C) Differences in thermal optimum, either overall fitness for species or for rates. 34

Abbreviations

OCLTT	Oxygen- and capacity- limited thermal tolerance
TSR	Temperature-size rule
MST	Metabolic scaling theory
MTE	Metabolic theory of ecology
UTD	Universal temperature dependence
ONS	Ontogenetic niche shift
IGP	Intra-guild predation
PSPM	Physiologically-structured population model

1 Introduction

As a consequence of the rapid ongoing climate change, sea surface temperatures are predicted to increase by 3° C under the business as usual scenario, RCP8.5 (Riahi *et al.*, 2007; IPCC, 2014). Climate change affects organisms at all levels of biological organization (e.g. cellular, individual, population and community) through individual-level ecophysiology (Pauly, 2010; Pörtner and Peck, 2010; Ohlberger *et al.*, 2011a; O'Gorman *et al.*, 2012). This has caused shifts in distributions (Dulvy *et al.*, 2008; Cheung *et al.*, 2009; Fossheim *et al.*, 2015; Parmesan and Yohe, 2003), phenology (Edwards and Richardson, 2004), body size (Daufresne *et al.*, 2009; Gardner *et al.*, 2011), and productivity (Cheung *et al.*, 2009; Blanchard *et al.*, 2012), as well as disrupted interactions due to species specific responses (Parmesan, 2006; Sheridan and Bickford, 2011). The number of studies on the impacts of climate change are increasing steadily every year, and while the proportion of aquatic studies are increasing, there is still a strong terrestrial bias in the publications (Parmesan, 2006; Hoegh-Guldberg and Bruno, 2010). Furthermore, marine systems are dominated by ectotherms, whose metabolism, and therefore also most other biological rates, is strongly affected by ambient temperatures (Bruno *et al.*, 2015). In addition, warming reduces oxygen availability in aquatic environments which could potentially have a synergetic impact with increasing temperatures and impair individual performance (Pörtner and Knust, 2007). Therefore, the temperature component of climate change is of particular interest for increasing our understanding of how ecosystem dynamics, size-structure and global food safety through fisheries yield are affected by climate change (Cheung *et al.*, 2011; Brander, 2015).

Warming waters are causing directional shifts towards smaller body-sizes of water breathing ectotherms (Baudron *et al.*, 2014; Thresher *et al.*, 2007; Sheridan and Bickford, 2011; Daufresne *et al.*, 2009; Neuheimer *et al.*, 2011). This pattern is often attributed to the temperature-size rule (TSR), which states that warmer temperatures during ontogeny result in smaller individuals at any developmental stage (Atkinson, 1994). As the ability to meet oxygen demand to tissues by oxygen uptake through gill surfaces also is reduced over ontogeny, the TSR is often attributed to gas-exchange limitations (Pörtner and Knust, 2007; Cheung *et al.*, 2013; Baudron *et al.*, 2014; Brander, 2015). Although the underlying mechanisms are still unclear (Atkinson *et al.*, 2006), the physiological basis of the TSR (Pörtner, 2010) and the cross-taxa observations (Gardner *et al.*, 2011), have led to smaller body sizes being proposed as a universal response to warming (Daufresne *et al.*, 2009).

Temperature can induce reductions in mean body size of a population or community from processes other than the TSR. Mean body size of a community can for instance decrease due to altered species compositions (Cheung *et al.*, 2013). Climate change is thought to cause competitively superior smaller species to replace larger

species, and this has been referred to as a *composition shift* (Ohlberger, 2013). Moreover, stage-specific thermal optima can alter the age-structure and hence the mean size of a population, if for instance temperature induces a disproportional increase in mortality on older and larger individuals (Pörtner and Knust, 2007). This is referred to as a *structure shift*, in contrast to the *size-at-age shift* associated with the TSR (Ohlberger *et al.*, 2011a; Ohlberger, 2013). Importantly, somatic growth of individuals is food dependent, and therefore also depends on competition for shared resources within and between species. In turn, the strength of such competitive interactions depends on size- and temperature scaling of vital rates, such as food intake, metabolism and mortality.

Body size largely determines the ecological role of an individual (Peters, 1983; Calder, 1984; Brown *et al.*, 2004), and 75% of vertebrate species grow during their whole life cycle (Werner, 1988: in de Roos and Persson, 2013), a phenomena referred to as indeterminate growth. All ectotherm populations are size-structured (de Roos and Persson, 2013), and often exhibit ontogenetic asymmetry in energetics, i.e. differential size-scaling of foraging rates and metabolism. This leads to size-dependent differences in net energy gain (difference between metabolic costs for maintenance and energy intake) and mass-specific biomass production. Asymmetry in size-scaling of vital rates causes asymmetry in competitive strength among differently sized individuals, as the impacts of food-limitation becomes size-dependent. Ontogenetic asymmetry is a life history feature of paramount importance for the dynamics of size-structured populations and communities, because of the implications for intraspecific interactions. Intraspecific competition coupled with ontogenetic asymmetry has been linked both experimentally and theoretically to population cycles, bottlenecks in life-histories, positive responses of biomass to mortality, and stabilizing feedbacks on community states (Hamrin and Persson, 1986; Persson *et al.*, 1998; Persson *et al.*, 2007; de Roos *et al.*, 2007). Thus, biotic interactions generate feedbacks on individual performance and consequentially population size-structure through density dependent processes.

Current metabolic scaling theories, such as the metabolic theory of ecology (Brown *et al.*, 2004), predict that biological rates related to food intake should be driven by metabolism. Therefore, these rates also show similar, predictable allometric scaling relationships and temperature dependencies as metabolism, according to the theory (Brown *et al.*, 2004; Glazier, 2010, 2005). Such theories are derived from interspecific relationships. However, it is increasingly acknowledged that deviations from these general rules are widespread both between and within-species (Killen *et al.*, 2010; Ohlberger *et al.*, 2012; Englund *et al.*, 2011). Temperature does not only increase the rate of most biological rates at sub-optimum temperatures, but it can also affect the size-scaling of most biological processes (Ohlberger *et al.*, 2012;

Glazier, 2005, 2010). Within species, this interaction between body mass and temperature does not necessarily have to be present in all rates affected by temperature, and the form of the temperature-dependencies of vital rates may also be species-specific.

Our understanding of size-structured population and community ecology through ontogenetic asymmetry has increased substantially in the past 20 years. Only recently has the variability in terms of temperature impacts on vital rates within species been highlighted (e.g. Ohlberger *et al.*, 2012). Given the importance of intraspecific variability in size-dependent physiological rates for community dynamics and structure, increasing temperatures could result in a multitude of possible biotic feedbacks at the community-level. The form of these feedbacks likely depends on the within-species relationships between the mass- and temperature-scaling of the species embedded in the community, as well as the regulation and structure of the populations.

Changes in the size-structure of populations in warming environments depend on both direct physiological impacts of increasing temperatures on individual level rates, and the feedbacks on food-availability that emerge from size-dependent interactions. The interplay between these direct and indirect effects is, however, largely unexplored, in particular in a multi-species context, and this restricts our ability to predict net consequences outside very simplified situations.

In this essay I first review universal scaling theories and the limitations of such approaches for understanding both direct and indirect effects of temperature on population and community dynamics. Secondly, I present size-based community theory to identify the potential to integrate this theory with intraspecific temperature- and mass scaling relationships. This appears a promising venue to gain new ecological understanding about climate change impacts on the dynamics and structure of natural communities.

2 Performance of water-breathing ectotherms in warming oceans

2.1 Thermal performance

Direct, individual-level impacts of increasing temperature can be described with the concept of thermal performance. Thermal performance curves describe how biological rates, such as metabolism, growth rate and reproduction, depend on temperature (Ohlberger, 2013; Dell *et al.*, 2014). Typically these are unimodal over a large temperature range, and an increase in performance occurs until a maximum is reached (referred to as optimum temperature), whereafter it rapidly declines (Fig. 1) (Kingsolver, 2009). Therefore, the effect of warming (i.e. whether it is positive or negative) on a specific trait of an individual depends on the current ambient temperature relative to the optimal temperature for the trait (Fig. 1 A) (Ohlberger, 2013). Moreover, the thermal optima of growth rate often change during ontogeny in such a way that juveniles have higher optimum temperatures compared to adults (Björnsson and Steinarsson, 2002; Pörtner and Peck, 2010; Pörtner *et al.*, 2008). Consequently, warming may increase growth rate for juvenile stages but have a negative impact on growth rate at larger sizes (Baudron *et al.*, 2011). In addition, juveniles generally have wider thermal performance curves than adults, meaning that juveniles are more capable to endure acute heat stress, as for example shown in eelpout (*Zoarces viviparous*) (Pörtner and Knust, 2007). Food supply can also alter the thermal performance curve (Fig. 1 B). For instance, the optimum temperature for growth is lower when food is limiting, and higher when food supply is not limiting growth (Elliott, 1982). Therefore, the net effects of temperature on growth cannot be studied in isolation without considering that growth is food-dependent (Jobling, 1997).

Interestingly, both experimental and tagging studies have revealed that species do not normally occupy temperatures that maximize performance of a specific trait, i.e. the thermal preference is not necessarily close to temperatures that maximize physiological performance (Neat and Righton, 2007; Killen, 2014). This may reflect differences in thermal optima of different physiological processes and that the thermal preference is a trade-off between multiple optima. The resulting thermal preference then depends on species- or developmental stage-specific priorities (Clark *et al.*, 2013; Killen, 2014), as well as size dependent mortality from predation (Ohlberger, 2013). Habitat selection may also be linked to temperature indirectly (i.e. not through thermal physiology), for instance through inter- and intraspecific interactions and food availability.

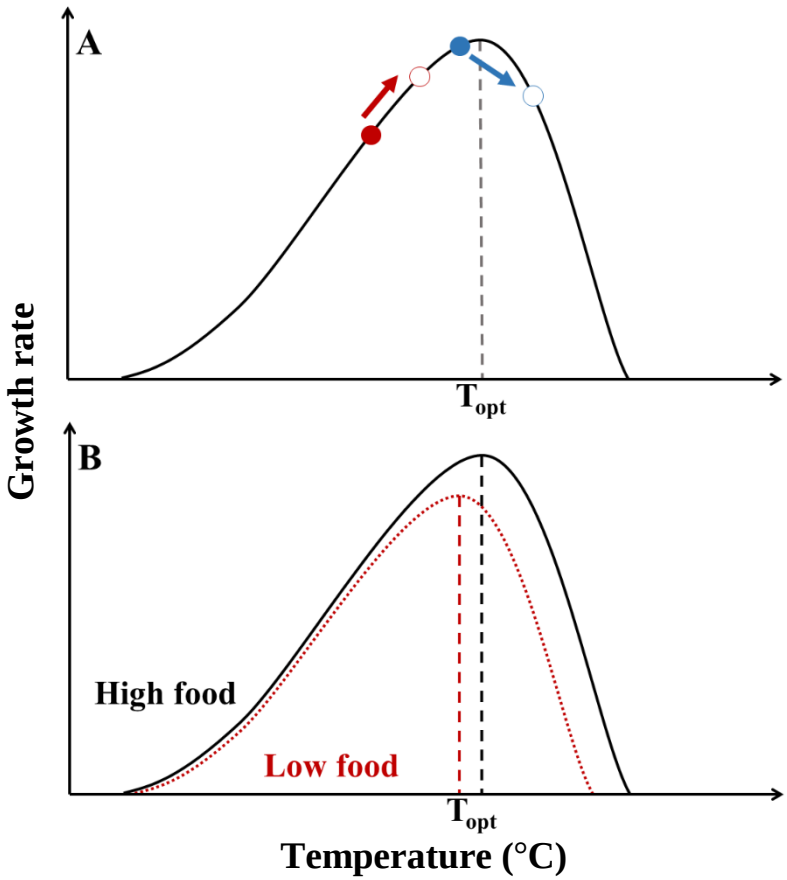

Figure 1. Thermal performance plots illustrating A) predicted effects of warming on growth rate depending on the current ambient temperature in relation to predicted increases and optimum temperatures, and B) the effect of food availability for thermal optimum. Redrawn from Ohlberger (2013).

2.1.1 Oxygen- and capacity limited thermal tolerance

Oxygen shapes the thermal performance, in particular at high temperatures (Pauly, 1979; Hoefnagel and Verberk, 2015; Atkinson *et al.*, 2006; Pörtner and Knust, 2007). The oxygen- and capacity limited thermal tolerance (OCLTT) concept provides a framework in which the impacts of various climate-related stressors are integrated to mechanistically explain how individual-level processes are affected by warming (Pörtner and Knust, 2007; Pörtner, 2010; Deutsch *et al.*, 2015; Verberk *et al.*, 2015). More specifically, the OCLTT hypothesis predicts that warming at sub-optimum temperatures increases metabolic rate and therefore also growth capacity. After an optimum is reached, growth rates then decline due to loss of aerobic scope (difference between standard and maximum metabolic rate) (Clark *et al.*, 2013), as

individuals cannot increase oxygen supply correspondingly (Fig. 2A) (Pörtner and Knust, 2007; Pörtner and Farrell, 2008).

While the OCLTT is generally adopted to explain observed large-scale climate-induced changes in growth trajectories of marine fishes (Cheung *et al.*, 2013; Baudron *et al.*, 2014), it remains a debated topic (c.f. Clark *et al.*, 2013; Farrell, 2013; Pörtner, 2014; Wang *et al.*, 2014). Until recently, relatively little research effort has been invested in trying to disentangle the relative contribution of oxygen and of temperature on the observed directional changes in growth trajectories (Hoefnagel and Verberk, 2015). If a temperature-induced oxygen constraint causes

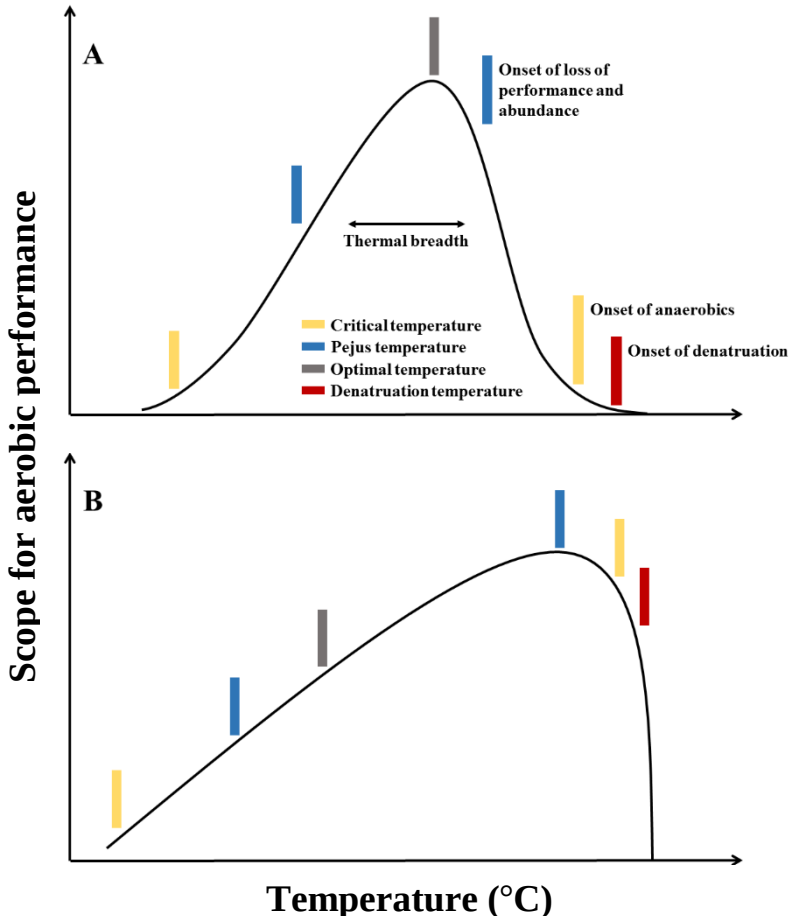

Figure 2. Conceptual illustrations of two competing views of the relationship between aerobic scope and optimal temperatures. A) the OCLTT-hypothesis (Pörtner & Farrell, 2008) predicts that maximum aerobic scope coincides with optimal temperature. B) By contrast, Clark et al. (2013) argue that the temperature that maximizes overall performance is lower than that which yields maximum aerobic scope, which in addition continues to increase until critical temperatures are approached. Redrawn from Clark et al., (2013). The pejus (Latin: turning worse) range is the temperature-range of long-term survival of an organism. Denaturation temperature refers to the temperature where the molecular structure is altered.

the temperature-size rule (i.e. the observation that higher temperatures increase growth rates but decrease asymptotic body size), growth would not cease in a warming environment if ample oxygen is supplied, and vice versa; hypoxia would induce a stronger TSR (Hoefnagel and Verberk, 2015). Some support for these predictions was found in an experimental study, where oxygen limitation caused a stronger TSR. However, the opposite (reduced TSR in hypoxic environments) was not evident. The authors argued this could be due to an adaptation of the study species (the isopod *Asellus aquaticus)* to regulate oxygen uptake in changing oxygen levels, or difficulties in assessing oxygen relative to the species' preferred range (Hoefnagel and Verberk, 2015). Other recent experiments have found results contradictory to the OCLTT-hypothesis. For instance, aerobic scope can be decoupled from ambient temperatures, and can actually increase continuously to near lethal temperatures (Gräns *et al.*, 2014; Norin *et al.*, 2014). A decoupling of aerobic scope and growth has also been reported in experimental studies (Gräns *et al.*, 2014; Wang *et al.*, 2014; Ern *et al.*, 2015) (see Fig. 2B for an alternative view on the role of aerobic scope for thermal performance). Tests of the OCLTT are limited on wild animals in natural environments due to the difficulty of obtaining performance data. Recently, however, Payne *et al.* (2016) showed that performance of wild fish closely matched the laboratory derived thermal sensitivity of aerobic scope. However, to which degree thermal sensitivity of aerobic scope influences overall thermal tolerance could not be estimated in the study.

These studies reveal the complexity and species-specific variability in how oxygen and temperature interact at non-lethal temperatures (i.e. at temperatures where oxygen limitation may not be the most influential variable.). Moreover, knowledge of potential thermal acclimatization is generally lacking (Gräns *et al.*, 2014; Sandblom *et al.*, 2014) despite that it has been proposed to be the prime determinant of winners and losers in future ecosystems (Sandblom *et al.*, 2014; Somero, 2010). It may also be that discrepancies of the OCLTT reflect that ecological impacts often are studied outside the species' food web context, given how biotic and abiotic effects interact.

2.2 The temperature-size rule

The inverse relationship between higher temperatures during ontogeny and reduced body size at any developmental stage (size-at-stage henceforth) has been termed the temperature size-rule (TSR) (Atkinson, 1994). The TSR has been proposed to be a universal response to warming in water breathing ectotherms. This is primarily due to the large cross-taxa support, its accordance with other related empirical temperature-size relationships, such as Bergmann's rule (Bergmann, 1847; Bertalanffy, 1960), paleontological comparisons and experimental evidence (Gardner *et al.*,

2011; Daufresne *et al.*, 2009; Ohlberger, 2013; Hoefnagel and Verberk, 2015). Empirical studies show support of temperature-induced increases in growth rate of species inhabiting below-optimum temperatures, but a decline in asymptotic body size of marine fishes, in line with the TSR (Thresher *et al.*, 2007; Baudron *et al.*, 2014; Neuheimer *et al.*, 2011). As an example, Baudron *et al.* (2014) collated times series on growth trajectories of 8 fish species with different life histories spanning over 40-years in the North Sea, a large marine ecosystem that has experienced a rate of warming among the highest globally (Belkin, 2009). The time series of 6 out of 8 species were positively associated with a common trend of declining asymptotic size, despite variation in species-specific histories of food availability and fishing intensity (which also influences growth potential). This common trend, i.e. the synchronous component of reduced asymptotic body size, in turn coincided with a steep temperature increase in the North Sea.

Despite the long tradition of studying temperature and size relationships in the animal kingdom, and the widespread conformation of the TSR in ectotherms, it remains debated what mechanisms are causing the TSR (Atkinson and Sibly, 1997; Kingsolver and Huey, 2008; Angilletta and Dunham, 2003). Interestingly, if other variables that affect growth are increased, such as food supply, both growth rates and asymptotic body size generally increase. However, the TSR implies that increasing temperatures result in faster growth rates but smaller asymptotic body size (Angilletta and Dunham, 2003). In addition, ectotherms mature later and grow to larger sizes when temperature is limiting growth. However, when growth limitations arise from limited food supply, ectotherms mature later at smaller sizes. This observation has been referred to as the 'life-history puzzle' (Berrigan and Charnov, 1994). In the same paper, Berrigan and Charnov (1994) argued from a life history perspective that the TSR can arise if growth rate and asymptotic body size are negatively correlated – an assumption that is not easily validated empirically as growth rate and asymptotic size are themselves determined by the life history of the species (Angilletta and Dunham, 2003). Perrin (1995) approached this issue by going back to the general form of von Bertalanffy's growth equation (Bertalanffy, 1960) where absolute growth rate is given by the difference between anabolism (increase in body mass) and catabolism (decrease in body mass):

$$dW/dt = aW^{2/3} - bW \quad (1)$$

where W is body mass and a and b are coefficients of anabolism and catabolism respectively. The ability of this equation to explain a TSR is based on two assumptions: anabolism increases with body mass less rapidly than does catabolism (through a lower exponent), and that the temperature coefficient of catabolism is

higher than that of anabolism (i.e. $b > a$). The latter was given a mechanistic explanation in Perrin (1995). This results in reduced growth rates with increasing body size as anabolism can never catch up with catabolism, leading to a negative relationship between growth rate and asymptotic body size (Bertalanffy, 1960; Pauly, 2010; Perrin, 1995; Angilletta and Dunham, 2003).

As the assumption of the 2/3 scaling exponent of anabolism in Eq. 1 is derived from the scaling of a surface with volume (determining oxygen uptake), the TSR has been hypothesized to be caused by growth constraints at high temperatures due to increased difficulties to balance oxygen supply and demand. Therefore, the TSR is sometimes discussed within the concept of OCLTT (Cheung *et al.*, 2013; Baudron *et al.*, 2014; Pauly, 2010). However, oxygen supply becomes so limiting at extreme temperatures that it decreases overall growth and thus body size at all developmental stages, unlike what is predicted by the TSR (Pörtner, 2002; Berrigan and Charnov, 1994; Ohlberger, 2013). The TSR has also been suggested to be caused by variation in cell size and number (Zuo *et al.*, 2012; Atkinson *et al.*, 2006; Hoefnagel and Verberk, 2015).

Due to the many interacting biotic and abiotic variables that determine thermal performance and life histories that are associated with growth rates, such as food availability, oxygen and species-specific adaptations, deviations from the TSR are expected (Berrigan and Charnov, 1994; Angilletta and Dunham, 2003; Atkinson and Sibly, 1997; Kuparinen *et al.*, 2011; Angilletta *et al.*, 2004). Food availability for instance is largely determined by size-dependent intra- and inter-specific interactions. In addition to reduction in size-at-stage, low food availability through competitive interactions can also shift the size-distribution in a population. If increasing temperatures further strengthen the competitive ability of juveniles, or smaller size classes, compared to larger size classes, a consequence may be a higher proportion of young individuals and a reduced maximum and mean body size (Ohlberger *et al.*, 2011a). At temperatures close to a species' thermal tolerance limit, increasing temperatures can cause acute thermal stress and mortality on larger individuals (Pörtner and Knust, 2007), also reducing the mean body size of a population. These processes can generate an apparent 'TSR' at the population level without a reduction in size-at-stage.

3 Size-structured population and community ecology

3.1 Growth and ontogenetic scaling of metabolism and food intake

Growth in size and ontogenetic development after independence from parental energetic investment occurs in most, if not all, fish species (de Roos and Persson, 2013). Analogous to the formulation of von Bertalanffy's equation for growth rate (Eq. 1), the growth potential of an individual is given by the net energy gain. The net energy gain is the difference between energy intake through feeding and energetic costs of routine tasks. If the size-scaling differs between metabolism and food intake, the potential net energy gain is size-dependent.

3.1.1 Metabolism

If size is the master trait, metabolism is the master rate. The metabolic rate is the result of various biochemical processes that transform energy for basic structural needs and functions of an organism. It determines how energy is transformed and allocated within an organism, and it shapes all other biological rates, which is why it sometimes is referred to as "*the pace of life*". It also determines ecological interactions, through energy exchange between organisms in an ecosystem (Brown *et al.*, 2004; Glazier, 2010). Not surprisingly then, the scaling of metabolic rate with body mass has since the classic work by Bergman, Sarrus and Rameaux and others (cited in Bertalanffy (1957)) been an intensively researched and debated topic. Metabolism (or respiration, R) depends on mass, and, as most rates dependent on body size it can be described using the general form: $R = aM^b$, where M is body mass, a is a mass scaling constant and b the mass-scaling exponent. In 1883, Rubner showed that metabolic rate scales with an exponent of 2/3 in dogs, hypothesizing that this could be explained by geometrical features. In order to maintain a constant body temperature, heat-generating metabolism scale as $M^{2/3}$, just as surfaces, which determines how heat loss scales with volume or mass (Rubner, 1883: cited in Glazier (2005)). Subsequent research aimed to explain observed scaling coefficients greater than 2/3, and for poikilotherms (organisms whose internal temperature depend on the ambient temperature). Similar negative allometric metabolic scaling was found for poikilotherms, however for such organisms arguments based on thermoregulation do not apply (Bertalanffy, 1957). Later this exponent was identified as being closer to 3/4 for both mammals (Kleiber, 1932; Brody and Procter, 1932) and unicells (Hemmingsen, 1960: cited in Glazier (2005)), after which it became known as "the 3/4-power law" or "Kleiber's law". After the endorsement of a universal 3/4 scaling relationship in three major reviews in the 1980's (Peters, 1983; Calder, 1984;

Schmidt-Nielsen, 1984), the hypotheses founded in Euclidian geometry of surface-area to volume ratios (scaling as 2/3) fell out of flavour (Glazier, 2005; O'Connor *et al.*, 2007). Since then, much effort has been put to explain the lack of a biological basis of a 3/4 mass scaling exponent, with mixed results (Glazier, 2005). In a series of highly influential papers by West and colleagues, a mechanistic model based on constraints in distribution networks in animals was developed to explain the universality of scaling exponents as multipliers of 1/4 rather than 1/3, including metabolic rate (West *et al.*, 1997, 1999). These models are derived from interspecific comparisons and ignore any within-species variation. Intraspecific data are inherently more difficult to acquire, hence, only recently has the broad within-species variation been acknowledged. However, in terms of community dynamics and size-structure, within-species variation in the size-scaling of biological rate have proven crucially important.

3.1.2 Energy intake

Energy intake depends on the relationship between consumer capture rate and resource density, i.e. the functional response (Solomon, 1949; Holling, 1959). While there are many ways to describe the functional response and its components, it is commonly given by attack rate and handling time, which, in turn, depend on various sub-components (Persson *et al.*, 1998; Brose, 2010; Rall *et al.*, 2012). For an extensive review on functional responses, see Jeschke *et al.* (2002).

Attack rate depends primarily on reaction distance, speed of consumer, food source and capture success (Brose, 2010), and it describes the feeding rates where handling time is negligible (Rall *et al.*, 2012). Empirical evidence suggest that size-structured consumers feed on size-structured resources (Werner and Gilliam, 1984). In these circumstances, the prey sizes that are available to the predator are set by a lower and an upper boundary. For visual gape-limited predators, the lower boundary depends on the predator's detectability of the prey, and ability to perform fine-scale manoeuvers. The upper boundary is set by morphological feeding constraints (Persson *et al.*, 1998; Vucic-Pestic *et al.*, 2011). The attack rate is usually assumed to be a hump-shaped function of predator size for a given prey size (or for the consumer-food source size ratio) (Persson *et al.*, 1998; Brose, 2010). The decreasing section of the function has been assumed to in part be due to an increased difficulty to perform fine-scale manoeuvers (Persson *et al.*, 1998). Persson *et al.* (1998) highlighted the importance of the components of attack rate for determining the competitiveness of an individual, as other rates appears to be less variable in terms of mass scaling.

Handling time is defined as the time it takes to capture, eat and digest the food source (Brose, 2010; Jeschke *et al.*, 2002). Increasing consumer to resource body size ratios reduce handling time, as subduction, ingestion and digestion are faster

compared to small consumer resource ratios (Mittlebach, 1981; Brose, 2010). The exact shape of this decreasing handling time with increased ratios can vary from linear to power-law and exponential relationships (Brose, 2010). Using a general form of a rate-size relationship, the decreasing handling time (H) with mass (Claessen *et al.*, 2000), can be represented by the function: $H = \varepsilon_1 M^{\varepsilon_2}$, where M is body mass and ε_1 and ε_2 are constants. This equation stems from the assumption that maximum intake rate is given by the inverse of the handling time, i.e. that at maximum feeding, the intake rate is limited only by digestion capacity (Claessen *et al.*, 2000). As such, handling time in modelling studies is often defined as the process of digesting prey rather than the time spent on capturing and handling the prey (Persson and de Roos, 2006).

3.1.3 Ontogenetic asymmetry, net energy and growth

Metabolic rates (maintenance costs) generally increase faster with body size than does food intake (Persson and de Roos, 2006). Therefore, the ratio of energy intake to maintenance costs, or net energy gain, decreases with body size. This can result in ontogenetic asymmetry in energetics through intrinsic processes, if differently sized individuals feed on a shared resource (de Roos and Persson, 2013). Ontogenetic asymmetry can also arise from external processes. If the size-dependencies of vital rates are identical, ontogenetic asymmetry can still be present if differently sized individuals utilize different resources with different productivities (Reichstein *et al.*, 2015). An implication of ontogenetic asymmetry is that performance, such as growth, becomes size-dependent, regardless of the underlying mechanism (intrinsic or external, or a combination of both) (Persson and de Roos, 2006).

Growth in size generally induces sequential niche shifts during a lifetime, i.e. ontogenetic niche shifts (ONS). The act of feeding by one species on resources at different trophic levels, but different throughout life, is referred to as life history omnivory (Werner and Gilliam, 1984). Efforts to adapt to size-dependent energetic requirements and physiological limitations to capture and handle prey (Claessen and Dieckmann, 2002), and a trade-off between foraging gains and mortality risks of different habitats (Werner and Gilliam, 1984; Mittlebach, 1981), have been proposed to cause ONS. ONS causes increasing complexity of food webs (vertical heterogeneity) compared to the traditional representation of interactions as a set of static links, with a (+) or (–) sign, between species pairs, as the same species can feed on different trophic levels (de Roos and Persson, 2001; Wilbur, 1988).

Ontogenetic asymmetry also has implications for competitive interactions for a shared resource between differently sized individuals. This can be understood through critical resource densities, the resource density needed to acquire enough energy to sustain routine tasks (Persson *et al.*, 1998). Given that metabolism in-

creases faster with body size than the energy intake does, the critical resource density generally increases with size. This results in smaller individuals being superior competitors for a shared resource as they can reduce the resource densities to levels where larger individuals cannot meet basic metabolic demands.

Therefore, growth and size, governed by size-dependent metabolism and food intake rates, largely determine an individual's ecological role. This generates feedbacks between individual performance, such as growth, and the ecological consequences of growing in size.

3.2 Consequences of ontogenetic asymmetry for population dynamics

3.2.1 Population bottlenecks and cycles

If ontogenetic asymmetry is present, either adults or juveniles form a population-level bottleneck, given low mortality rates and a shared resource pool. Where in the population the bottleneck emerges can be inferred from the size-scaling of biological rates if the two stages are competing for the same resource, such that the biomass will be dominated by the energetically inferior stage. For instance, if juveniles are competitively superior, the maturation rate exceeds the reproduction rate within the population due to the higher net energy gain of juveniles compared to adults (Persson and de Roos, 2013). The high competition in the adult stage when an adult bottleneck is present further reduces the net energy gain of individuals in this stage, resulting in low energetic investments in offspring. This population-regulation mechanism is referred to as *reproduction control*, which implies that reproduction is more limited than maturation. By contrast, when adults are superior competitors, the population is regulated by *development control*, characterized by high juvenile competition, low maturation rates and high energetic investment in reproduction (de Roos *et al.*, 2007).

Empirical observations and modelling studies have revealed that the dynamics of size-structured populations can exhibit stable equilibrium with coexistence of multiple cohorts as well as numerical dominance of strong year classes. Single cohort dominance in populations often follows a cyclic pattern, driven by intrinsic processes such as size-dependent predation, mortality and competitive dominance (Hamrin and Persson, 1986; Sanderson *et al.*, 1999; Persson *et al.*, 1998). Moreover, it has been shown that single cohort cycles can arise from both recruit- and non-recruit driven processes (Persson *et al.*, 1998). In a modelling study, Persson *et al.* (1998) explored the role of ontogenetic asymmetry for these dynamics through intrinsic processes by manipulation of the size-scaling exponents of food intake relative to metabolism. More specifically, they investigated the consequence of varying

the mass-scaling exponent of attack rate, α, while keeping the exponents of metabolic rate and handling time constant, in low mortality scenarios. This allowed them to determine the type and degree of ontogenetic asymmetry in a consumer-resource food-web. At the lower end of the spectrum of α (i.e. at scenarios of juvenile competitive superiority in energetics, as metabolic costs increase faster relative to food intake with body mass) high amplitude, recruit-driven cycles emerge in the population as strong year classes produce large recruitment pulses as they become mature. The numerical dominance, and the high attack rate relative to metabolism compared to for larger specimens, causes a depletion of the resources. Due to their lower critical resource density, the recruits can survive the resource depletion. However, larger individuals cannot and eventually perish, leaving a population largely consisting of a single cohort. At intermediate levels of α, populations with multiple coexisting cohorts emerge due to similar competitive abilities of differently sized individuals. As α is further increased, cyclicity reappear, but now driven by older individuals (but of lower amplitude than recruit-driven cycles), as the relatively lower attack rate of the recruits cannot deplete the resources for the adult cohorts. Juvenile- and adult-driven cycles resemble the equilibrium population states of reproduction- and development control, respectively. Also, these cycles are qualitatively different from cycles emerging from unstructured predator-prey cycles (de Roos and Persson, 2013; Murdoch *et al.*, 2002), in that juveniles and adult cycles are out of phase.

These examples are derived from simple communities exemplified using a size-structured consumer and a single shared unstructured resource. However, in natural systems, life history complexity can alter the types of intra- and interspecific interactions, and competitive ability can be defined by means other than size-scaling exponents, for instance through stage-specific resources with different productivities and/or energetic content (van Leeuwen *et al.*, 2013; Reichstein *et al.*, 2015; Claessen *et al.*, 2000; Persson *et al.*, 2000). This was shown in a multigenerational experimental study by Reichstein *et al.* (2015), in which the competitive superiority shifted from juvenile to adult when a proportion of the shared resource was partitioned to the otherwise competitively inferior adult stage.

In terms of life history omnivory, cannibalism is a common phenomenon of animals, in particular in piscivorous fish populations (Polis, 1981; Fox, 1975; Smith and Reay, 1991). The capacity for a cannibal to prey on a victim depends on cannibal:victim size ratios (Polis, 1981; Claessen *et al.*, 2000). In particular the lower size boundary of cannibalism has been shown to be important for the dynamics of such populations. This boundary is positively correlated with cannibalistic capacity, which in turn is associated with low efficiency feeding on invertebrate prey (Wahlström *et al.*, 2000). Therefore, the lower size boundary could indicate if potential cannibals will be outcompeted by the smaller sized fish on which they would

prey as cannibals. If this is the case, the dynamics will resemble the cohort-driven cycles previously described (Persson and de Roos, 2006). At higher cannibalistic capacities, cannibals can reduce intercohort competition through predation on abundant recruits. This can cancel out the larger biomass reaching maturation compared to reproduction that otherwise would occur given juvenile superior competitiveness, and hence stabilize the dynamics of the population (Persson and de Roos, 2006; Persson *et al.*, 2004). If cannibalistic capacity is further increased, cohort-driven cycles can reappear in the population. This can occur if the cannibals have grown too large to prey down the abundant newborns, which prey on the resource so that it reaches densities close to the critical resource density of the newborns (Claessen *et al.*, 2000)

3.2.2 Biomass overcompensation

The population cycles in the previous section assumed low mortality rates. As mortality rates increase from low levels in size-structured populations with ontogenetic asymmetry, hump-shaped increases in stage-specific biomass, and even total population biomass under certain circumstances, can follow. This phenomenon is termed biomass overcompensation. Stage-specific biomass overcompensation has been shown to occur regardless of whether the mortality is targeted at juveniles, adults or equally distributed over the population. Importantly, the asymmetry in energetics that is crucial for this phenomenon to occur can arise from foraging capacity, inferred from intrinsic size-scaling relationships, through stage-specific resources productivities or a combination of both (Reichstein *et al.*, 2015; de Roos and Persson, 2013).

If *development control* is present, increased mortality will reduce juvenile biomass, either by direct mortality on juveniles or indirectly through reduced recruitment if mortality is targeted at adults. This releases the population bottleneck which in this case occurs at the maturation of juveniles because of high juvenile intra-stage competition. Consequently, a higher proportion of juveniles can mature, and that way the adult biomass (although not the abundance) can increase, even if mortality targets the adults (de Roos *et al.*, 2007). Similarly, if a population is under *reproduction control*, increased mortality results in higher fecundity of surviving adults through released competition, which translates to a higher per capita biomass increase through increased reproductive output. The stage which constitutes the population-level bottleneck is also the stage that will decrease most in biomass as a response to increased mortality, regardless of where it is directed (de Roos and Persson, 2013; de Roos *et al.*, 2007). Moreover, the magnitude of the biomass increase in the stage that generates the overcompensatory response (i.e. the energetically superior stage) depends on where the mortality occurs, and the highest increase occurs when the mortality is targeted at the bottleneck (de Roos *et al.*, 2007). At the

population level, however, overcompensatory biomass responses to mortality appear to be limited to scenarios when mortality is not affecting the energetically superior juvenile stage and when juveniles are resource unlimited. In all other scenarios with a shared resource or adult-specific resources, the total consumer population biomass decreases with mortality (de Roos *et al.*, 2007).

Biomass overcompensation has been identified in both natural systems (Ohlberger *et al.*, 2011b), experimental systems (Schröder *et al.*, 2009) and in various modelling studies (de Roos *et al.*, 2007). Considering the widespread pattern of faster increase in metabolic rate with mass compared to food intake rate (resulting in competitive superiority of juveniles in terms of energetics) (Rall *et al.*, 2012; Persson *et al.*, 1998), it could be hypothesised that reproduction control is more common in natural systems, which seem to be in line with preliminary reviews (Persson and de Roos, 2013; Schröder *et al.*, 2014).

3.2.3 Implications for community structure

Stage-specific biomass overcompensation induced by ontogenetic asymmetry is a fundamental feature for understanding community structure and dynamics. In size-structured prey populations, this can lead to positive feedbacks between a predator and its prey through increased stage-specific mortality, resulting in higher prey biomass when a predator is present compared to a system without a predator (Persson and de Roos, 2013). Thus, predators can through their predation induce higher food densities, which is also known as an *emergent Allé effect*, irrespective of the presence of size-structure in the predator population (de Roos *et al.*, 2003). In addition, this implies that predators can persist at high densities, but not invade from low densities as the impact of feeding at low predator densities is not large enough to induce an overcompensatory response in the prey (de Roos *et al.*, 2003). Given that a predator can induce stage-specific biomass-increases in the prey population, stage-specific overcompensation may facilitate the presence of another predator feeding on the stage that is increasing with mortality. The second predator would not be able to persist had ontogenetic symmetry been present in its prey (and consequently no biomass overcompensation). This phenomena is referred to as emergent facilitation (de Roos *et al.*, 2008a), and has been shown in both theoretical (de Roos *et al.*, 2008a) and experimental studies (Huss and Nilsson, 2011).

Stage-specific overcompensation was demonstrated in the now classic “Lake Takvatn” in northern Norway. As a consequence of overharvesting and stocking, the lake underwent a shift to an alternative stable state, constituted by a stunted consumer, Arctic char (*Salvelinus alpinus*), and its predator, brown trout (*Salmo trutta*). The brown trout fed on juvenile Arctic char, and had been reduced to low biomass levels. By harvesting the Arctic char population, growth capacity and recruitment of Arctic char was increased, and subsequently, juveniles of the size-class

on which trout fed upon also increased. The trout biomass then increased to levels where trout predation maintained the size-structure of the Arctic char population in such way that it facilitated the now larger trout population, and the previous stable state was restored and maintained by the predator (Persson *et al.*, 2007). This is an example of how abundant predators can stabilize one of the alternative stable states through predator-induced biomass overcompensation. The same mechanism has also been suggested and partly indicated to govern the dynamics of Atlantic cod (*Gadus morhua*) (de Roos and Persson, 2002; Gårdmark *et al.*, 2015).

In communities where a predator both competes with and feeds on a prey during ontogeny, i.e. intra-guild predation (IGP) (Polis *et al.*, 1989), a predator can also stabilize a steady state through "cultivation". Cultivation refers to the release of competition for a predator's offspring through predation on the competing prey (Walters and Kitchell, 2001; Gårdmark *et al.*, 2015). At low biomasses, it then follows that predators are unable to "cultivate" a suitable environment with low competition between the juvenile predators and the prey of adult predators (which often are competitively superior). This limits population growth of a predator at low density, and may also constitute a stabilizing feed-back impairing biomass recovery of a depleted predator (van Leeuwen *et al.*, 2013; Walters and Kitchell, 2001).

3.3 Structured or unstructured population models?

Despite the widespread within-species variation in body size, and the (often) associated implications for individual performance through asymmetry in energetics, this feature has long been overlooked in population ecology (de Roos and Persson, 2013). Historically, population models, such as those formulated by Alfred Lotka and Vito Volterra, have not included body growth and intraspecific variability in size. Hence, they have not included the variability in vital rates of the individuals that constitute the population (de Roos and Persson, 2013). The assumptions of such unstructured population models, more specifically that all individuals within a population contribute equally to reproduction and are equally susceptible to mortality, may severely limit the understanding of population-dynamical patterns if juveniles and adults exhibit asymmetry in energetics (de Roos and Persson, 2013; de Roos and Persson, 2001). Structured population models on the other hand take into account not only abundance, but also the size structure, or the distribution of individuals of different sizes or developmental stages.

Yodzis and Innes (1992) developed an individual-based bioenergetic consumer-resource model that can be regarded as a population model structured by a single stage. It can also be shown that the dynamics in this population model are identical to a special case of a structured population model that exhibits ontogenetic symmetry (de Roos and Persson, 2013). In the Yodzis and Innes model, ontogenetic

symmetry arises from the assumption of identical mass scaling exponents of biological rates, more specifically 3/4 (see section 4.1). It then follows that per gram of body weight, rates scale as $M^{-1/4}$. Both inter- and intraspecifically, this assumption appears to constitute a very limiting scenario albeit with large consequences for population regulation and responses to mortality (de Roos and Persson, 2013). While the Yodzis and Innes model is different from earlier unstructured models by Lotka, Volterra and others (in de Roos and Persson, 2013), as it does not represent a population simply by a number, it could be argued whether this model is structured *per se*. An important point here is that without ontogenetic asymmetry, the size-distribution does not influence the dynamics of the population and, hence, the body size is not a structuring factor in terms of population dynamics. For it to be so, ontogenetic asymmetry must be present, as discussed in section 3.2 (de Roos and Persson, 2013).

Physiologically structured population models (PSPMs), developed by de Roos & Persson and colleagues, building on the work by Metz and Diekmann (1986), constitute a framework for individual based population models that are fully size-structured (de Roos and Persson, 2001; de Roos *et al.*, 2008b). Founded in dynamic energy budget theory (Kooijman, 1993; Persson *et al.*, 1998; de Roos and Persson, 2013), PSPMs explicitly and mechanistically link performance to the physiological state of the individual, for instance size, and its environment, generally characterized by food density. This is a desirable feature considering the importance of food-dependent growth and ontogenetic development for population dynamics and how that is regulated by biotic feedbacks.

More recently, the framework of PSPMs was simplified into a stage-structured biomass model. The latter allows for an easier model analysis, in particular in multi-species systems, while maintaining within-species differences in size- and food-dependencies of key life history processes such as growth (de Roos *et al.*, 2008b). As the name indicates, rather than accounting for the complete size-distribution of a population, the population size-distribution is represented by discrete stages. It has been shown to produce identical predictions to the PSPM under equilibrium and even similar dynamics under certain conditions, but not when the PSPM predicts juvenile-driven single generation cycles. These models have, for example, been used to identify mechanisms behind juvenile biomass overcompensation in a natural perch (*Perca fluviatilis*) population following increased mortality due to a pathogen outbreak (Ohlberger *et al.*, 2011b).

The formulation of the size-dependent individual-level processes that govern the population dynamics (e.g. energy acquisition, maintenance costs and energy allocation) often requires complex and parameter-rich equations derived from experimental studies (de Roos *et al.*, 2008b). Although this means that the parameterization then becomes species-specific as such experiments have been conducted for a

limited number of species, it has been shown that the number of significant mechanisms driving the dynamics of size-structured populations are relatively few. In addition, these mechanisms are also generally robust to specific model assumption (de Roos and Persson, 2001) and parameter ranges (Ohlberger *et al.*, 2011a). This implies that these models have the potential to achieve a high degree of generality when representing the dynamics of size-structured communities (de Roos and Persson, 2001). Using the framework of PSPMs and stage-structured biomass models, several empirically observed properties of size-structured populations and communities, of fish in particular, have been explained mechanistically. This has contributed greatly to the understanding of population and community ecology, and the importance of ontogenetic development for the dynamics and size-structure of populations.

4 Climate change impacts on ecosystems and the dynamics of size-structured communities

4.1 Temperature effects on the level and size-scaling of biological rates

Like all chemical reactions, biological rates depend on temperature. While the effect of body size on metabolic rate has a long tradition in ecology and physiology, resulting in many attempts to derive universal laws, research on the temperature component of the scaling of biological rates is more recent (although see Clarke and Johnston (1999) for temperature scaling of metabolism). Perhaps this has been fueled by an increase in research directed towards climate change impacts on natural systems (Englund *et al.*, 2011). Gillooly *et al.* (2001) approached this by expanding the model by (West *et al.*, 1997, 1999) (see section 3.1.1) describing the allometry of metabolism to include a temperature effect using the Arrhenius equation (Arrhenius, 1889). Because this model was able to approximate metabolic rate in organisms ranging from microbes to plants and endothermic vertebrates, the temperature dependence in the equation was termed "the universal temperature dependence of metabolism" (UTD). More specifically, the metabolic rate, R, of any organism can be approximated by:

$$R = b_0 M^b e^{E_i/kT} \tag{2}$$

where b_0 is a scaling constant, b is 3/4, M is body mass, E_i is the activation energy of metabolism, k is Boltzmann's constant (eV) and T is the absolute temperature (K) (Gillooly *et al.*, 2001). The activation energy, averaging around 0.65 eV (Brown *et al.*, 2004), describes the rate of increase with temperature (at temperatures below optimum). The model of a temperature- and size-dependent metabolism developed in the series of papers by West, Brown and colleagues is summed in the metabolic theory of ecology (MTE) (Brown et al, 2004). The MTE can be regarded as an attempt to build a "theory of everything" in ecology based on the fundamental influence of size and temperature on metabolic rate, which in turn drives essentially all other biological rates (Brown *et al.*, 2004; Harte, 2004). Indeed, extensions of the MTE has been used to model phenomena on virtually all scales of life, from DNA-evolution (Gillooly *et al.*, 2005) to macroecology (Allen *et al.*, 2005; Allen *et al.*, 2002; Walters *et al.*, 2012). Thus, the Arrhenius equation is commonly used to add temperature dependence to biological rates that are driven by metabolism, including consumption rates (Englund *et al.*, 2011; Gillooly *et al.*, 2006; Öhlund *et al.*, 2015).

Despite being widely used, the reception of MTE has been mixed and its components has received much criticism on various points (Harte, 2004). These include mathematical (Kozłowski and Konarzewsk, 2004; Agutter and Wheatley, 2004) and logical (Makarieva *et al.*, 2005) inconsistencies; whether it truly is mechanistic (as opposed to phenomenological) (O'Connor *et al.*, 2007); and the invoking of a universal mass scaling exponent of 3/4 for metabolic rate (Glazier, 2005; Killen *et al.*, 2010; Isaac and Carbone, 2010). Moreover, as the MTE has provided a framework for studies on climate change impacts on marine ecosystems (e.g.Vasseur and McCann, 2005; Bruno *et al.*, 2015), it is important to resolve inconsistencies with the theory concerning the UTD. The UTD has been criticized for the use of the Arrhenius equation to explain metabolism mechanistically (Clarke, 2006; Clarke and Fraser, 2004; Clarke, 2004) and its inability to capture temperature effects on functional response parameters (Englund *et al.*, 2011; Rall *et al.*, 2012). Furthermore, the UTD assumes that the mass-scaling exponent (b) is independent of temperature (Gillooly *et al.*, 2001; Eq. 2), despite the numerous studies showing that it indeed can be temperature dependent (Ohlberger *et al.*, 2012; Twomey *et al.*, 2012; Lemoine, 2012; Hölker, 2000).

Alternative scaling-theories, such as the metabolic-level boundary hypothesis (MLB) (Glazier, 2005, 2010), acknowledge that the mass scaling exponent may not be universally centered around 3/4 interspecifically. Instead, it varies systematically between and within species (Glazier, 2005, 2006; Isaac and Carbone, 2010; Twomey *et al.*, 2012), and with ecological factors such as temperature (Killen *et al.*, 2010; Ohlberger *et al.*, 2012; Twomey *et al.*, 2012) and activity level or lifestyle (Glazier, 2009). Thus, the MLB-hypothesis (Glazier, 2010, 2005) takes an entirely different, more flexible approach compared to the MTE, to address the allometry of metabolic rate (and consequently other rates as well), and the temperature-dependence of such rates. Rather than focusing on central tendencies, the variability within- and between species are central to the theory. The broad diversity in scaling exponents is in those not treated as statistical artefacts, but rather systematic features that can be predicted from the ecology of the species. More specifically, the MLB hypothesis suggests that the exponent b depends on the relative influence of two extreme boundary constraints: surface area limits and volume limits on energy use (Fig. 3). The relative influence of the boundary limits is determined by the metabolic activity level of the species, L. L, in turn, is proportional to ambient temperatures, and thus maintenance costs for basal functions and processes. This pattern has previously been overlooked as it has been assumed that the exponent is centered around 3/4 regardless of metabolic level (Glazier, 2010). As L increases in resting organisms, the relative influence of surface-related resources fluxes (scaling allometrically as $M^{2/3}$) increases. In the other extreme, a low L in resting organisms makes

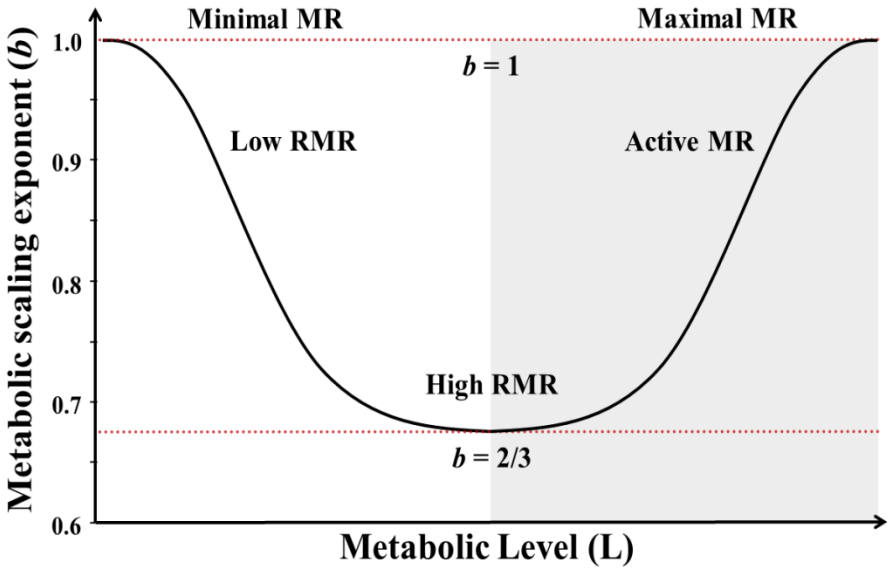

Figure 3. Relationship between the metabolic scaling exponent (b) and metabolic level (L) (proportional to temperature) according to the MLB hypothesis. Over the full range of physiological states, from resting metabolism (white) to active metabolism (gray), the relationship between b and L is U- or V-shaped. Redrawn from Glazier (2010).

such organisms primarily limited by volume-related resource demand (scaling allometrically as M^1). In active organisms the pattern is the opposite, which gives a u-shaped relationship between b and L over different activity levels.

Interspecifically, there is support for a systematic temperature dependent mass scaling exponent of metabolism. Killen *et al.* (2010) collated data on ecological variables and values of b (one per species) for 89 species of teleost fishes and found that for resting metabolism, b was negatively correlated with temperature, and related to the lifestyle of the species. However, if this negative relationship holds at the within-species level is not as clear. For instance, Ohlberger *et al.* (2012) reported independent effects of temperature and mass for two cyprinid species (as predicted by the MTE), while two coregonid species showed linear and negative relationships between b and temperature (in line with what the MLB predicts interspecifically). While the MLB is still being developed and tested, the recognition of within-species variability in the size-scaling of rates is important, given the influence of such variation for population and community dynamics.

4.1.1 Size- and temperature scaling of functional response parameters

Although equally important for understanding competitiveness through differential scaling of biological rates, in contrast to metabolic rate, few unifying explanations exist for linking size and temperature dependencies of feeding rates (Rall et al., 2012). This is partly due to that consumption depends on various other traits, such as visual capacity, locomotor ability, and morphological traits (e.g. such as gape size

and digestive capacity) – all of which can vary greatly in terms of allometry (Persson *et al.*, 1998). In addition, scaling theories such as the MTE generally do not capture the variability in temperature effects on functional response parameters (Englund *et al.*, 2011).

A meta-analysis by Englund *et al.* (2011) of temperature dependencies of functional response parameters identified a steeper scaling with temperature in attack rate compared to maximum intake rate, i.e. digestion capacity or the inverse of handling time. In contrast to the exponential temperature effect on metabolism, functional response parameters were hump-shaped over a larger temperature range (Fig. 4). This is also in line with what Rall *et al.* (2012) found for both attack rate and handling time. Both Rall *et al.* (2012) and Englund *et al.* (2011) found that activation energies of functional response parameters (see Eq. 2) were systematically lower and more variable than that of metabolism. In fact, roughly 90 % of values reported by Englund *et al.* (2011) were outside the range predicted by the UTD of the MTE, which predicts that all biological rates are constrained to values of activation energies between 0.6 and 0.7 (Gillooly *et al.*, 2006; Brown *et al.*, 2004).

The consequence of a lower activation energy is a less steep increase of feeding rates with temperature compared to metabolism, which implies that organisms may not be able to meet the higher metabolic demand caused by increasing temperatures. This pattern, i.e. reduced net energy gain in warmer environments, appears to be a general response for both terrestrial and marine ectotherms at the within-species level (Lemoine, 2012; Rall *et al.*, 2012; Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011; Twomey *et al.*, 2012). Lemoine (2012) found that within species, ingestion efficiency (or net energy gain), can drop significantly after a threshold temperature. In the same study, a meta-analysis was conducted, showing that the ratio of metabolism to consumption decreased with temperature between species. This was also found in experiments with terrestrial ectotherms (spiders and beetles) (Rall *et al.*, 2010). Twomey *et al.* (2012) showed that not only do increasing temperatures increase the proportion of animals that are not able to meet metabolic demands through accelerated consumption rates, but also that the temperature- and mass effects are not necessarily independent for metabolism and consumption. Also, the temperature- and mass effect on metabolic rate differed between the five marine ectotherms of different phyla that were studied.

Thus, a UTD of functional response parameters may not be meaningful in a strict sense. This is because the use of the Arrhenius equation limits the temperature range to below optimum, because in this range the hump-shaped temperature dependence could be approximated with the exponential Arrhenius term. Proponents of the UTD argue that it is aimed to be used within biologically relevant temperature ranges, where near optimum temperature are not included (Savage *et al.*, 2004). However, this temperature range may be important to consider, in particular for species living

close to their thermal optima ("thermal specialists"), such as warm-adapted species with a narrow temperature range (Payne *et al.*, 2016; Walters *et al.*, 2012).

For a narrow temperature range which does not include near T_{max}-temperatures for consumption, this decoupling of metabolism and consumption may not be detected as metabolism increases exponentially with temperature according to the UTD (Gillooly *et al.*, 2001) (Fig. 4). Still, the UTD predicts a much narrower variation in the temperature effect on food intake rates than what is observed, thus constituting a limiting scenario where vital rates increase almost symmetrically. In addition, as a consequence of a hump-shaped temperature dependence, the relationship between temperature and the rate depends on the temperature for the observation relative to the species' optimum temperature for that rate (Englund *et al.*, 2011). Interestingly, this is in turn food dependent, which highlights the need to study impacts of warming in a food-web context.

4.2 Climate change impacts on ecosystems predicted from metabolic scaling theories

Despite the limitations of the MTE concerning temperature-independent size-scaling of rates, and symmetry between rates in terms of temperature dependence, it is often used to address climate change impacts on communities (Bruno *et al.*, 2015). The MTE predicts that temperature increases top-down control through increased metabolism and consequentially feeding rates of consumers, potentially strengthening consumer-resource interactions (Brown *et al.*, 2004). Increased top-down regu-

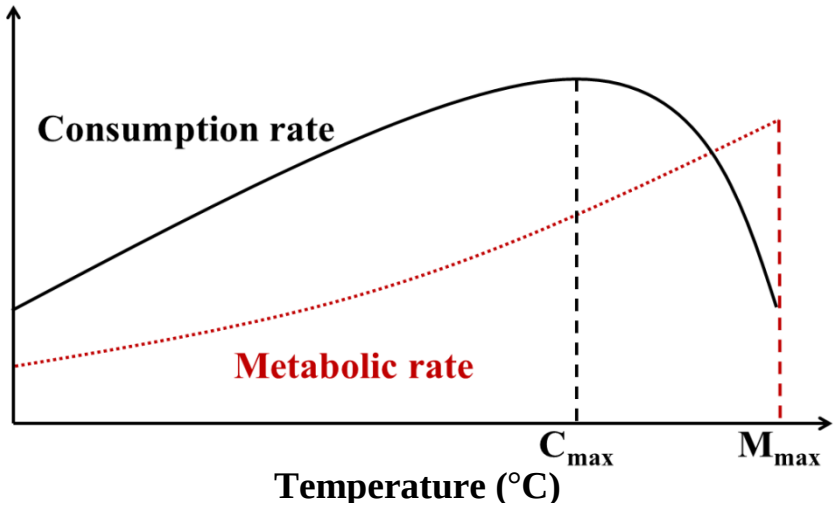

Figure 4. Conceptual illustration of temperature effects on consumption and metabolism, highlighting the lower temperature at which maximum consumption (Cmax) occurs compared to maximum metabolism (Mmax).

lation was partly identified in an experimental study by Shurin *et al.* (2012), investigating the effects of eutrophication and warming on relative bottom-up and top-down control of freshwater ponds. It was also identified in a modelling study using one value for the activation energy for all rates driven by metabolism, including feeding rates (i.e. food intake rates and metabolic rates increased symmetrically with temperature) (O'Connor *et al.*, 2011). There may also be scenarios where maximum food intake rates has a higher activation energy compared to metabolism and thus increases faster with temperature. This setup was used by Vasseur and McCann (2005) in a consumer-resource bioenergetics model coupled with temperature-dependent rates. Naturally, this suggests that top-down control is even stronger in warming environments than what a strictly general interpretation of the MTE predicts. Vasseur and McCann (2005) argue that their configuration is more common (higher activation energies of feeding rates than metabolism), but that contrasts to more recent studies showing the opposite (Lemoine, 2012; Rall *et al.*, 2012; Englund *et al.*, 2011). Vasseur and McCann (2005) also identified that the relationship between the temperature dependence of food intake and metabolism determined whether a grazing-induced biomass reduction was found in the resource density or not. Metabolism and feeding rates often start to decouple as temperatures increase further, due to the lower temperature optima of consumption compared to metabolism (Fig. 4) (Twomey *et al.*, 2012; Lemoine, 2012; Rall *et al.*, 2012; Vucic-Pestic *et al.*, 2011). Therefore, as temperatures approach optimum, relaxation of top-down control could be induced regardless of the initial increase in top-down control (Brose *et al.*, 2012).

The net impacts of a potential temperature-induced increase in consumption on prey populations, i.e. on interaction strength, also depend on the ability of the resource to increase population growth rate in synchrony with increased per capita consumption from predators (O'Connor *et al.*, 2011; Bruno *et al.*, 2015). As photosynthesis has a roughly 50% lower activation energy than that of respiration, the MTE predicts faster increases in primary production with warming (Allen *et al.*, 2005; O'Connor *et al.*, 2011). However, the faster increases in primary production can be masked, or even outweighed (Ohlberger *et al.*, 2011a), by the temperature-induced increased grazing. However, the predictions of faster resource growth rely on the assumption that primary production is not limited by other abiotic factors such as nutrients and light. In addition, a relatively large grazer biomass may still be sustained, as an assemblage shift to smaller species and sizes with higher competitive advantage and faster turnover rate is also predicted and observed in warmer aquatic environments (Reuman *et al.*, 2014; Yvon-Durocher *et al.*, 2011; Shurin *et al.*, 2012). As this is also generally predicted at higher trophic levels as well, consumer population growth rate can be reduced at high temperatures due to the pro-

portionally stronger negative effect on large individuals that contribute more to population growth (Angilletta, 2009; Peck *et al.*, 2009). This could also govern the impact of increased per capita grazing on top-down control. In addition, if size-specific feeding is present, it could be hypothesized that a concurrent shift in size-structure may reduce availability of suitably sized prey for consumers, thus limiting the potential for top-down control. The consequences of such feeding patterns for the dynamics of populations are, however, not possible to estimate without considering within-species variations in size as well as size-dependent processes such as foraging.

4.2.1 Is hotter better?

The *hotter-is-better*-hypothesis states that as reaction rates increase with temperature due to higher kinetic energies of warmer systems, species that are warm-adapted should exhibit a higher absolute fitness. More specifically, the intrinsic rate of increase, r_{max}, is higher in warm-adapted species compared to cold-adapted species when both are measured at their optimal temperature (Savage *et al.*, 2004; Kingsolver and Huey, 2008; Hamilton, 1973). The MTE predicts that r_{max} is ultimately limited by metabolism, and therefore it should scale with the average activation energy of metabolism (Walters *et al.*, 2012; Brown *et al.*, 2004; Savage *et al.*, 2004). Cross-taxa studies of activation energies for r_{max} (the slope of r_{max}~*1/kT*, see Eq. 2) measured at the species thermal optima generally conform to a positive relationship between r_{max} (or fitness) and temperature (Frazier *et al.*, 2006; Angilletta *et al.*, 2010). However, large variations in the strength of the "hotter-is-better" pattern have been reported both intra- and interspecifically (Savage *et al.*, 2004; Frazier *et al.*, 2006). This has been suggested to be due to local adaptations (Walters *et al.*, 2012). Assuming these occur, it is unclear why r_{max}should increase with average body temperature (Walters *et al.*, 2012).

These potential differences between warm- and cold-adapted species may play an important role for future competitive interactions in a climate change context. In particular considering the observed concurrent range shifts in species, with tropical species moving into temperate biomes. This could introduce new species with, at least potentially, higher absolute performance (but a narrower thermal window) to established communities (Kingsolver and Huey, 2008; Kingsolver, 2009; Parmesan, 2006).

4.3 Implications of intraspecific asymmetries in temperature effects for dynamics and size-structure of communities

Asymmetry in thermal responses can be described both within and between species, and empirical evidence (Englund *et al.*, 2011; Lemoine, 2012; Twomey *et al.*, 2012)

point to the conclusion that thermal asymmetry is most likely present in communities one way or another. Asymmetry can exist within species in terms of activation energies of rates, which determines how fast they increase with temperature (Englund *et al.*, 2011). Asymmetry between rates, within species, can also arise from differential temperature-effects on mass scaling exponents (Ohlberger *et al.*, 2012). If these patterns are species-specific, and possibly related to the lifestyle and ecology of the species (Glazier, 2010, 2005), this generates interspecific asymmetry in temperature-effects on rates within multispecies communities (Dell *et al.*, 2014, 2011). Fig. 5 illustrates three general types of asymmetries of thermal responses that can represent asymmetry both between rates (e.g. food intake and metabolism) and between species.

Within the context of size-based community ecology, the ecological consequences of differential temperature effects on mass scaling exponents of vital rates are either relaxations or enhancements of competitive superiority of smaller size-classes in warmer environments (Ohlberger *et al.*, 2011a). These interactions between differently sized individuals, both between and within species, have strong implications for population dynamics and size-structure. For instance, in vendace (*Coregonus albula*) there is a negative relationship between the mass-scaling exponent and temperature for metabolism (Ohlberger *et al.*, 2012). Thus, if assuming temperature-independent scaling of food intake, adult vendace may actually become relatively less inferior in terms of energetics as temperature increases (Ohlberger *et al.*, 2012). In perch on the other hand, the size-scaling exponent of rates appear to be hump-shaped, meaning that at sub-optimum temperatures, juvenile competitiveness is enhanced with warming (Lessmark, 1983; Ohlberger *et al.*, 2011a). By contrast, in roach (*Rutilus rutilus*), the mass scaling exponent of metabolism is temperature independent, but for maximum intake rate the exponent is negatively related to temperature (Ohlberger *et al.*, 2012; Hölker, 2000). If assuming that other functional response parameters follow the same relationship as maximum intake, juvenile competitive superiority may be enhanced also in roach in warmer environments.

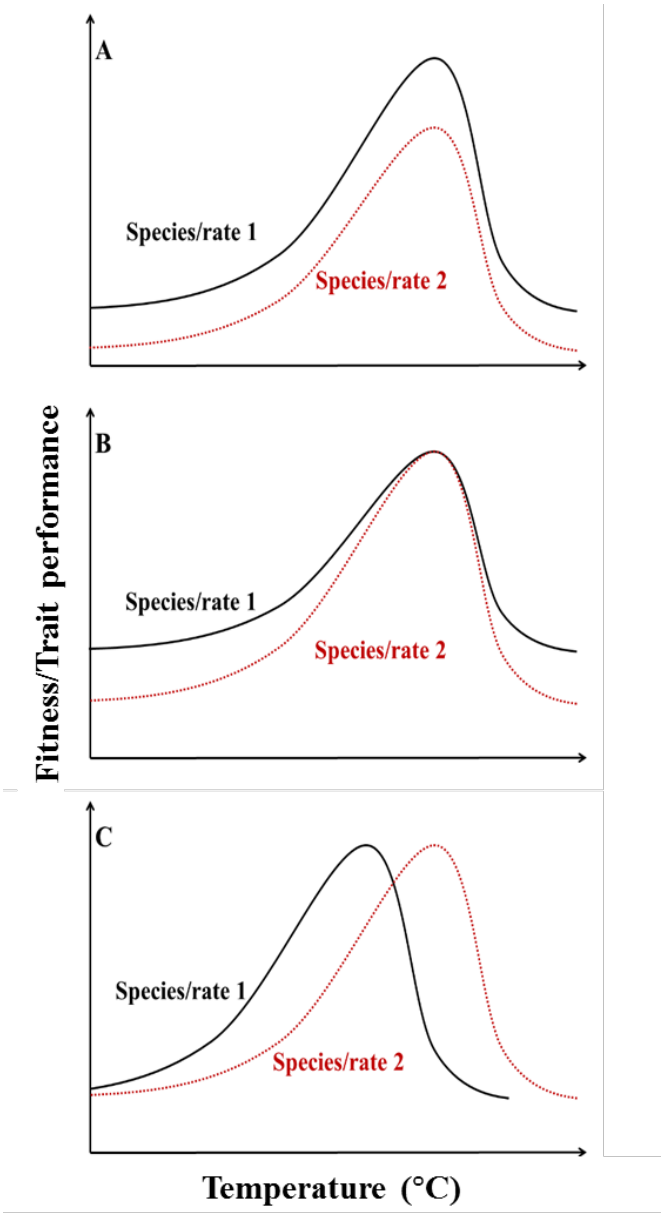

Figure 5. Conceptual illustrations of three general types of asymmetry in thermal responses of trait performance or between interacting species. A) Differences in levels (activation energy) between species or rates B) differences in rates of response, such that one species may respond more to warming or differences in temperature effects on the size scaling of rates C) Differences in thermal optimum, either overall fitness for species or for rates.

Notably it is not the sign of the temperature effect on the mass-scaling exponent *per se* that determines the temperature impacts on the energetic efficiency between differently sized individuals within a population. Rather, it is the effect of temperature

on the ratio of the mass-scaling exponents of metabolism and food intake, which can either decrease or increase with temperature.

Vasseur and McCann (2005) argued on the basis of their temperature-dependent consumer-resource model that warming may drive stable systems to exhibit cyclic dynamics, and decrease both consumer and resource biomass. Since the model was an extension of the Yodzis and Innes population model (see section 3.3) it did not exhibit a size-structure with ontogenetic asymmetry. Hence their approach could not capture dynamics emerging from intraspecific interactions. This may be a strong limitation considering the ubiquity of ontogenetic asymmetry and the fundamental importance of it for driving dynamics of size-structured populations. Ohlberger *et al.* (2011a) coupled a PSPM of a cannibalistic perch population (originally described in (Claessen *et al.*, 2000)) with temperature effects on biological rates and mass-scaling exponents, as well as on the resource population. Their findings were qualitatively similar to Vasseur & MacCann's unstructured model, in that the dynamics went from stable to cyclic as temperature increased. Furthermore, a reduction in average body-size was found after a population-level shift in size structure due to stronger competitive superiority of smaller individuals in warmer environments. The positive relationship between mass-scaling exponents and temperature in Ohlberger's parameterization represents one of many possible temperature effects on the mass-scaling exponents of rates within species. Given the apparent within-species variation in such temperature effects, knowledge about the community-dynamical consequences of differential temperature effects is missing. Furthermore, the addition of multiple species within the framework of physiologically structured population models coupled with temperature dependencies remains unexplored. We do know, however, that it is crucial to consider the food web in which single species are embedded, as the dynamics of communities depend on, and feed back on, individual-level physiological processes and performance. This knowledge gap poses a major limitation to our ability to understand and predict impacts of climate change on natural food webs and the changes we observe in species within them.

4.4 Climate change and fisheries yield

Climate change impacts on global and regional fish production and fisheries yield have primarily been estimated using recently developed end-to-end models that integrate physical-biogeographical models with food-web models (Cheung *et al.*, 2011; Blanchard *et al.*, 2012; Brander, 2015). Such projections of fisheries yield in future climates are uncertain because of large uncertainties in key processes and feedbacks between trophic levels (Brander, 2015). For example, Sarmiento *et al.* (2004) predicted primary production to increase by 2050 by 0.7-8.1% compared to

2005 levels, while Chust *et al.* (2014) predicted a decrease in both primary production and zooplankton by 9% and 11%, respectively, by the end of the century, given an increase in sea surface temperatures by 2.29 °C. These projections of primary production also show large regional differences (Sarmiento *et al.*, 2004; Steinacher *et al.*, 2010; Chust *et al.*, 2014).

A decrease in fishable biomass in tropic regions has been predicted in multiple end-to-end studies due to changes in primary production and distributional shifts. By contrast, increases in potential fisheries yield have been projected in temperate regions, following an increase in primary production (Blanchard *et al.*, 2012; Cheung *et al.*, 2011). In addition, consumer body size at low- and mid-latitude is thought to decrease as larger specimens become unable to meet metabolic demands due to dwindling resource availability, as well as due to changes in species composition in fish communities, favoring smaller species (Cheung *et al.*, 2013; Lefort *et al.*, 2015). Using a dynamic size-based food web model coupled with temperature-dependencies from the MTE, Blanchard *et al.* (2012) were able to estimate the effects of fishing mortality within and between ecosystems experiencing warming. They found that regions characterized by slow individual growth (either due to low primary production or cold waters) were more susceptible to fishing effects in a warmer climate, and also less likely to sustain heavy exploitations. In addition, fishing effects resulted in more variable dynamics due to disrupted ecosystem size-structures, increased individual growth and smaller body sizes. Ultimately, this resulted in reduced resilience to climate change impacts (Blanchard *et al.*, 2012).

The size-structured and physiologically based approach develop by Blanchard *et al.* (2012) is derived from size-spectra models (Blanchard *et al.*, 2011; Blanchard *et al.*, 2009), and is therefore different from the size-structured and physiologically based models described so far (see section 3.3). Both approaches are individual- and size-based dynamic models based on dynamic energy budgets. In size-spectra models the individual is indexed by its size rather than taxa (but see Blanchard *et al.* (2014) for a multispecies example). The size-dependent processes are thus accounted for at the community level. This simplification has its advantages, in particular when analyzing multispecies systems. However, it also eliminates the possibility to capture intraspecific dynamics that are driven by size-dependent processes, which are also important for multispecies community dynamics and size-structure. On the other hand, PSPMs and physiologically structured biomass models have previously been limited to species-poor systems, as model interpretation becomes increasingly challenging as more species are included.

4.4.1 Effects of warming and size-selective fishing on dynamics and size-structure of fish

Many major fish stocks show no or little sign of recovery from severe overharvesting (Myers and Worm, 2003), despite various management approaches to reduce overall fishing mortality. These include, but are not limited to, seasonal closures and overall reductions in fishing mortality, either through effort regulations or quota reductions (Hutchings, 2000). As trawl fisheries generally are restricted by minimum mesh-size regulations only, fishing mortality often increases with size (Huss *et al.*, 2014). This is in contrast to natural predators, which usually predate on a specific "size-window" of the prey. Consequently, for a given fishing mortality, increasing selectivity (i.e. increasing mesh sizes and minimum catch-sizes) will increase fishing mortality in larger size-classes. Depleted fish stocks are often managed with increasing mesh-sizes, with the belief that such actions increase the number of spawners (Svedäng and Hornborg, 2014). Svedäng and Hornborg (2014) showed that increasing selectivity as a management tool for recovering fish stocks may increase the actual fishing mortality on larger size-classes, despite an overall reduction of fishing mortality. They further suggested that this harvesting pattern has induced the reduced growth potential of cod just below the minimum conservation reference size (<37 cm) that is currently evident in Eastern Baltic cod, through density dependent processes. Their study points to an interesting issue with current fisheries management, particularly of recovering fish stocks, i.e. that of size-selective fishing and size-specific mortality versus overall fishing mortality. However, it is impossible to point to density dependence and intraspecific competition without considering stage-specific food availability, and other factors affecting growth potential of cod, which were not accounted for in Svedäng and Hornborg (2014).

Size-structured population- and community theory on the other hand provides important insights in the dynamics of overharvested populations, in particular through biomass overcompensation. For instance, overharvesting of a top predator such as cod could remove any predator-induced biomass overcompensation (emergent Allé effect) in the size-structured prey population upon which they feed (van Leeuwen *et al.*, 2008; Gårdmark *et al.*, 2015; de Roos and Persson, 2002). This will depend on the population regulation of the prey population (where in the population the bottleneck occurs) and the size-classes upon which the predator feed, as that governs the biomass response of mortality (de Roos and Persson, 2005; van Leeuwen *et al.*, 2008; de Roos *et al.*, 2007; de Roos *et al.*, 2003).

The inhibition of a prey-overcompensation could reduce the biomass of suitably sized prey. It could also reduce the energetic content if the condition is reduced as well, due to high intraspecific competition in the prey population, which in turn could reduce fitness of cod and limit its recovery. This has been hypothesized to occur in Eastern Baltic cod and cod in the Northwest Atlantic (Gårdmark *et al.*,

2015; de Roos and Persson, 2002). If also the predator population is size-structured, an additional mechanism can inhibit predator recovery. At low adult predator biomass, prey populations that either compete with, or prey on, juvenile predators may increase. This could reduce fitness or abundance of predators growing into adult stages, and limit predator recovery. At high densities however, the predator "cultivates" the environment by reducing competition for its offspring through its predation (Bundy and Fanning, 2005; Gårdmark *et al.*, 2015; Walters and Kitchell, 2001). This mechanism has been suggested to occur in Northwestern Atlantic cod (Swain and Sinclair, 2000), Baltic cod (Casini *et al.*, 2009), cod from the eastern Scotian Shelf (Bundy and Fanning, 2005) and North Sea cod (Fauchald, 2010).

In addition to understanding factors that stabilize alternative states, these mechanisms can also aid in multispecies fisheries management. In such management strategies, the objective is partly to understand the consequences of size-selective harvesting not only on the target species but also for interacting species. One example where size-based community theory may aid the understanding of feedbacks from harvesting and interspecific predations was given by Huss *et al.* (2014). In a modelling study, they showed that if a predator-induced biomass overcompensation is present in the prey species, the predator that often is seen as a competitor with fishers, may actually facilitate larger biomasses and, hence, fisheries yields of the prey species (Huss *et al.*, 2014).

Recent studies show that the mechanisms behind the lack of recovery of predator fish species may be caused by feedbacks from size-dependent mechanisms, such as emergent Allé effects, which unstructured models cannot capture (van Leeuwen *et al.*, 2008; Gårdmark *et al.*, 2015; Schröder *et al.*, 2009). Understanding the combined effect of (size-selective) fishing and the possible feedbacks through biotic interactions in a warming environment is of top priority for estimating future food security. This will require joint efforts from fisheries ecologists and marine ecologists, as the interplay between temperature and size-structured multi-species communities is largely unexplored. And, in addition, fisheries management relies heavily on unstructured (at least with respect to size) quantitative stock assessment models (Persson *et al.*, 2014). These do not include within-species variation in size, and importantly, variation in size- and food-dependent processes such as reproduction, mortality and growth. This is a major limitation in current fisheries management, as many commercially important fish stocks show limited potential for recovery, despite reduced fishing mortality. In addition, global projections of fisheries yield in future climates often lack key processes and exhibit large uncertainties (Brander, 2015). However, these uncertainties associated with fisheries projections were not acknowledged in the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (Brander, 2015). Thus, providing ecologically-based advice and

projections of management options in climate change scenarios will require development of tools that account for the potentially interactive effects of size- and temperature dependent biotic feedbacks in fish communities.

5 Conclusions

This review points to the link between within-species variation in size- and temperature-dependence of vital rates and size-based community theory. This link is crucial for understanding and predicting climate change impacts on animal communities, as it may increase our understanding of how direct effects of warming on individuals are mediated by biotic interactions.

Ontogenetic asymmetry drives community dynamics and size-structure within species, and the form of the asymmetry can be affected by temperature through either size-scaling of vital rates or through effects on resource productivities. However, most individual-based, bioenergetics models that aim to predict climate change impacts do not account for ontogenetic asymmetry. Therefore they do not consider community feedbacks from size-based competitive interactions on food availability, which affects individual performance.

Universal temperature- and size scaling frameworks derived from interspecific data, such as the MTE, are frequently used to address the effect of warmer temperatures on communities through accelerated individual-level rates. However, more important than universal scaling relationships is the variation in size scaling of rates for population dynamics. Increasing evidence suggest deviations from universal scaling theories are widespread, both intra- and interspecifically. This thermal asymmetry between the rates that, in turn, drive the dynamics of size-structured populations may have large implications for individual performance and the dynamics of communities in warming environments. Thus, universal scaling relationships represent cases of thermal- and ontogenetic symmetry, which may not be common in natural fish populations. It is therefore important to critically consider the community-dynamical consequences of these assumptions in order to understand the limitations of predictions founded in universal scaling theories.

Meeting projected food requirements from fisheries in the next decades introduces large challenges for fisheries management. Size-based approaches are currently lacking in traditional stock assessment methods, despite the importance of accounting for size-dependencies of key processes. This is an important area to develop in fisheries ecology, in particular in a climate change context as the effects of temperature interact with the processes that are fundamental for size-based community dynamics.

To the best of my knowledge, temperature-dependent size-structured population models have never been developed to account for interacting populations, including both intra- and interspecific interactions. PSPMs and stage-structured biomass models in particular constitute a promising framework for combining size-based community theory with universal or species-specific temperature dependencies in multispecies contexts.

Some important aspects of climate change in natural systems have not been covered in this essay. These include evolutionary consequences of warming, thermal acclimatization of physiological processes, spatiotemporal distributions and range shifts, and changes in phenology – all of which influence species interactions. Given the role of biotic interactions for community dynamics, this is important to consider. Neither has the question of temperature-ranges and temporal scales for predictions been thoroughly revised.

In conclusion, the interplay between two widespread features, namely ontogenetic- and thermal asymmetry, may be an important driver of the size-structure and dynamics of animal communities in warming environments.

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