

REVIEW

Climate warming and ectotherm body size – from individual physiology to community ecology

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Summary

1. Accumulating evidence suggests that the average body size of many organisms is declining in response to climate warming. This phenomenon has been suggested to represent a universal response to warming that may impose significant adverse effects on ecosystem functioning and services.
2. However, we do not have a thorough understanding of why body sizes are commonly declining, and why some organisms show the opposite response. Because ectotherms constitute the vast majority of organism biomass and about 99% of species worldwide, it is particularly important to understand how ectotherms respond to a warming climate.
3. This review discusses the underlying physiological mechanisms of changes in ectotherm body size and addresses observed responses within a broad ecological context at different levels of organization, from individuals to communities, particularly in aquatic systems.
4. Warming-induced responses in average body size are not only determined by changes in rates of individual growth and development, but also mediated through size-dependent feedbacks at the population level, as well as competitive and predatory interactions within the community. Emergent properties at higher organizational levels have already been observed in both experimental and natural systems.
5. Various approaches will be required for enhancing our knowledge about the importance of such processes in natural systems. These include controlled semi-natural experiments and phylogenetic comparisons as well as statistical models of time-series data and theoretical models linking climate effects at the individual, population and community levels.
6. Understanding causes of observed changes in organism body sizes and how these depend on the ecological context is essential for improving our predictions and the management of ecosystems in the face of a warming climate.

Key-words: climate change, community, ectothermic, growth, size structure, temperature

Introduction

Climate warming affects virtually all ecosystems worldwide. Global mean temperatures and the frequency of extreme temperature events are predicted to increase within the twenty-first century (Meehl & Tebaldi 2004; IPCC 2007). Although climate change occurs naturally over time, contemporary rates of warming are unprecedented and believed to have severe impacts on many biota (Parmesan 2006; IPCC 2007). The best-known and most studied ecological responses to climate warming are shifts

in species' distribution ranges (Parmesan & Yohe 2003; Root *et al.* 2003; Perry *et al.* 2005) and changes in phenology (Stenseth *et al.* 2002; Walther *et al.* 2002; Durant *et al.* 2007). Recently, warming-induced declines in mean body size have been reported in a number of organisms (Gardner *et al.* 2011; Sheridan & Bickford 2011) and have been suggested to represent a third universal response to global warming (Gardner *et al.* 2011). However, we do not have a thorough understanding of why this trend prevails. Thus far, research within the field has remained largely descriptive without considering the interplay between physiological mechanisms and the broader ecological context. A better understanding of the causes of observed changes

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in mean body sizes in response to climate warming is required to enable predictions about the future and improve our management of natural systems in the face of rapid climate change. This review highlights that observed changes in mean body size emerge at different levels of biological organization and that warming may cause such responses through different mechanisms.

Smaller mean body sizes in response to contemporary climate warming have been reported for a number of organisms in both aquatic and terrestrial environments (Gardner *et al.* 2011; Sheridan & Bickford 2011), including crustaceans (Moore & Folt 1993), fishes (Todd *et al.* 2008; Genner *et al.* 2010; Cheung *et al.* 2013), amphibians (Reading 2007), birds and mammals (Yom-Tov & Geffen 2011). These size shifts have been observed at different levels of biological organization, from individuals to communities (Millien *et al.* 2006; Daufresne, Lengfellner & Sommer 2009; O’Gorman *et al.* 2012). Besides studies linking observed declines in body size to current climate trends, circumstantial evidence inferred from paleontological studies, geographic comparisons, or experiments suggests that warmer temperatures are associated with smaller body sizes. For instance, paleontological records and trace fossils of invertebrates indicate reductions in body sizes during past periods of warming (Hunt & Roy 2006) and larger sizes during periods of climate cooling (Smith *et al.* 2009). Second, organisms in colder climates tend to be larger than their counterparts at lower latitudes, both across species and across populations of the same species (Bergmann 1847; James 1970). However, the opposite trend of increasing body size associated with climate warming has also been reported, for instance in marine fishes (Thresher *et al.* 2007), and in lizards (Chamaille-Jammes *et al.* 2006), and even phylogenetically similar species within the same habitat may show opposite trends in response to warming (O’Gorman *et al.* 2012).

Negative effects of increased temperature on organism body size have been observed in ectotherms as well as endotherms, but the mechanisms through which temperature affects individual physiology and body size differ fundamentally between the two groups. The body temperature of ectotherms closely tracks that of their immediate surrounding whereas endotherms maintain a constantly high core temperature. Because ectotherms constitute the vast majority of organism biomass and about 99% of all species worldwide (Wilson 1992; Atkinson & Sibly 1997), it is of particular importance to understand how ectotherms respond to a warming climate. This review discusses temperature effects on individual growth and development of ectothermic metazoans, with a focus on aquatic systems and particularly fish, and it highlights how these effects are modified by population feedbacks, community interactions and the potential for evolutionary change. The goal of the study is to provide a better understanding of the mechanisms underlying observed changes in mean organism body sizes across ecosystems, and to stimulate further research.

From individual physiology to community ecology

INDIVIDUAL GROWTH AND DEVELOPMENT

Climate warming affects an organism’s growth and development, and ultimately body size, through direct effects of temperature on biochemical reactions, which are integral to energetic processes such as metabolism and resource acquisition. Biochemical reaction rates increase steadily with temperature up to an optimum and rapidly decrease thereafter, resulting in an asymmetric thermal sensitivity curve (Hochachka & Somero 2002; Angilletta 2009). The thermal sensitivity of biochemical reaction rates implies that trade-offs exist between performance at high and low temperatures, and that thermal specialization comes at the cost of reduced performance at other temperatures (Angilletta 2009). These thermal constraints lead to similar asymmetric temperature sensitivity curves at higher organizational levels, from cellular functions to whole-organism performances such as growth (Angilletta 2009; Kingsolver 2009).

Thermal performance curves, which describe the variation in fitness-related traits across a range of temperatures, can theoretically be used to assess an organisms’ sensitivity to rising temperatures (Fig. 1). The direction and magnitude of an organisms’ response to climate warming, for instance in growth rate, is determined by the thermal optimum relative to the actually experienced environmental temperature. Currently lower than optimal temperatures thus imply positive effects of warming, while currently optimal or higher than optimal temperatures imply negative effects of increasing temperatures on individual growth performance. Hence, higher temperatures can lead to faster or slower growth, depending on the optimal temperature range relative to current conditions (Fig. 1a), and the magnitude of climate warming (Fig. 1b). Importantly, the thermal sensitivity is further modified by acclimatory processes in response to changing environmental conditions, that is, phenotypic plasticity. Ectotherms acclimate by adjusting their biochemical composition and physiological rates, thereby favouring the maintenance of function and capacity at the acclimation temperature, but not necessarily at other temperatures (Guderley 2004). Short-term exposure to very high or low temperatures (heat or cold shock) usually causes increased tolerance to acute thermal extremes, whereas long-term exposure to moderate temperatures can induce sustained changes in thermal sensitivity (Huey *et al.* 1999; Angilletta 2009). For instance, seasonal changes in environmental temperature may lead to acclimatory responses that enhance performance under seasonal conditions (Packard, Packard & McDaniel 2001; Guderley 2004). The potential for acclimation thus influences an organisms’ response to climate warming.

Within the range of non-extreme temperatures that allow an organism to develop and reach maturity but do not lead to a decline in growth rate, the thermal reaction

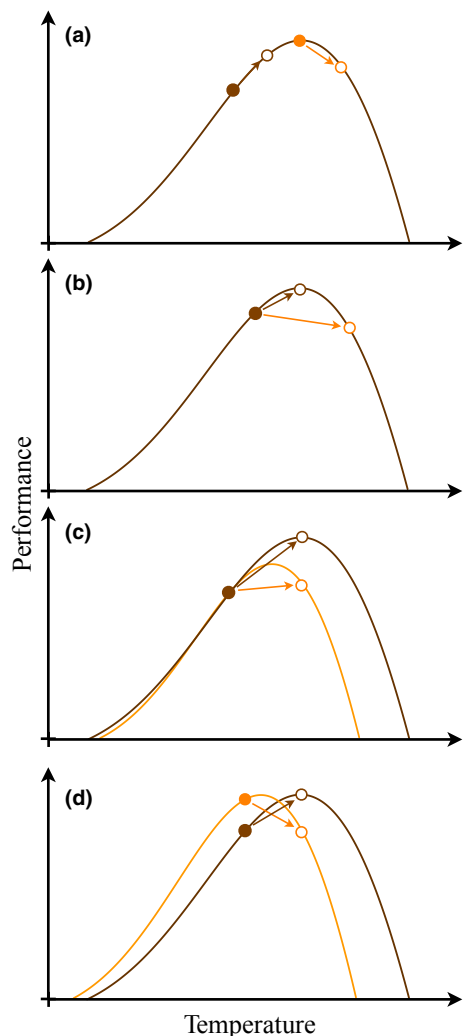


Fig. 1. The concept of thermal performance curves illustrates the impact of climate warming on the growth capacity of ectotherms: (a) climate warming is expected to increase growth capacity for organisms currently experiencing lower than optimal temperatures, but decrease growth capacity for those experiencing close to optimal temperatures; (b) while moderate warming may increase growth performance, severe temperature increases lead to a reduction in growth in the absence of adaptation; (c) because optimal temperatures are lower when food is limiting, positive effects on growth may be compromised by reduced food availability; (d) thermal optima often differ between life stages, resulting in different responses in growth performance to rising temperatures.

norm of most ectotherms is well described by the temperature–size rule (TSR) (Atkinson 1994). The TSR describes an organisms’ phenotypic response to the thermal environment during ontogeny: higher temperatures increase growth rate (increase in somatic mass) and development rate (differentiation from egg to adult), but decrease adult body size. The consequence of temperature change is therefore a shift in size-at-age, not ‘body size’ per se, and the observed response depends on when during ontogeny body size is measured (Berrigan & Charnov 1994) (Fig. 2). Size-at-stage (e.g. size-at-maturity) may thus be the most

useful measure when determining an organisms’ response to changing thermal conditions. Although the opposite trend of larger adult size at higher temperatures seems to be the exception, it has been described for some organisms, particularly species in seasonal environments that experience strong constraints on their life cycles (Chown & Klok 2003). Furthermore, at extreme temperatures, growth is usually impaired by insufficient energy or oxygen supply, which decreases growth and body size at any developmental stage and may thus lead to a reverse temperature–size relationship (Pörtner 2002).

The proximate reason for smaller adult body size at warm temperature is a decrease in cell size, a decrease in cell number, or a combination thereof (Partridge *et al.* 1994; James, Azevedo & Partridge 1995). It has been suggested that the TSR is caused by different temperature sensitivities for cell growth and cell division (van der Have & de Jong 1996). Observed responses to temperature, including both the TSR and the reverse trend, could in fact be mediated by any combination of variation in cell size and/or cell number (Zuo *et al.* 2012). In line with theory, empirical work suggests that ectotherms show different thermal dependences of growth and development [e.g. crustaceans (Forster, Hirst & Woodward 2011), insects (Davidowitz & Nijhout 2004)] and that temperature can affect the age at maturation (development time) independently of growth [e.g. fishes: Kuparinen *et al.* (2011)]. Although the ultimate causation might be an adaptive advantage of smaller body size at higher temperatures (Kozowski, Czarnoleski & Danko 2004), differences in body size are realized through cell growth and division, and these two processes do not necessarily show the same temperature dependence. It is thus crucial to determine how rates of growth and development contribute to changes in size-at-age across thermal gradients (Fig. 2).

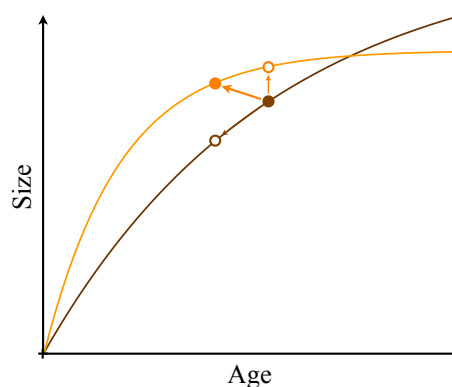


Fig. 2. Conceptual illustration of the impact of climate warming on individual body size via differential effects of temperature on rates of growth and development. Size at a given life-history transition such as maturation, increases due to faster growth (orange/grey open circle), decreases due to faster development (brown/black open circle), and is ultimately determined by the relative importance of the two processes (orange/grey filled circle).

POPULATION FEEDBACKS AND COMMUNITY INTERACTIONS

The impact of climate warming on individual development and growth may translate into changes in mean body size at the population level either as a direct consequence of decreased size-at-age of the individuals ('*size-at-age shift*') or through changes in the relative abundances of different age-classes or life-stages within the population ('*structure shift*'). Such changes also lead to a shift in the mean size of the community if they occur consistently across populations, for instance through indirect effects on interacting species. In addition, climate warming may alter the mean body size within the community through a shift in the relative abundances of differently sized species ('*composition shift*'), including extinction and migration (Fig. 3) (Daufresne, Lengfellner & Sommer 2009). These shifts can be mediated by various mechanisms, including density-dependent growth, size-dependent survival, asymmetric competition between size-classes and size-selective predation (Fig. 4).

Field studies have shown that the interplay between temperature and population density can alter the impact of climate warming on ectotherm growth and body size. The body size response to temperature depends on population density, because higher individual growth capacity only translates into increased growth rate when sufficient resources are available to fuel increasing metabolic demands, which increase roughly exponentially with temperature (Gillooly *et al.* 2001). Accordingly, experimental studies have demonstrated that the optimum temperature for growth is lower when food is scarce compared to unlimited food supply (Fig. 1c) (Elliott & Hurley 2000). Increased temperature may therefore affect individual biomass in opposite ways, resulting in lower body weight in

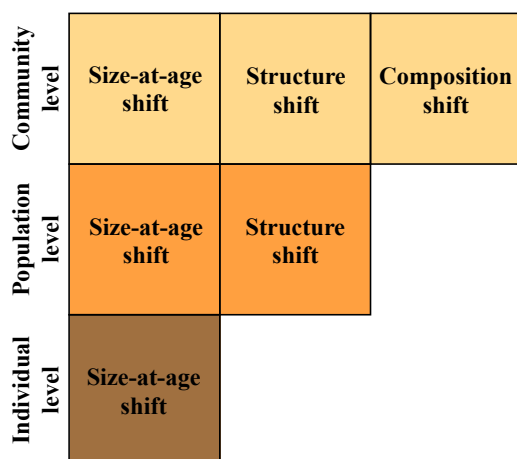


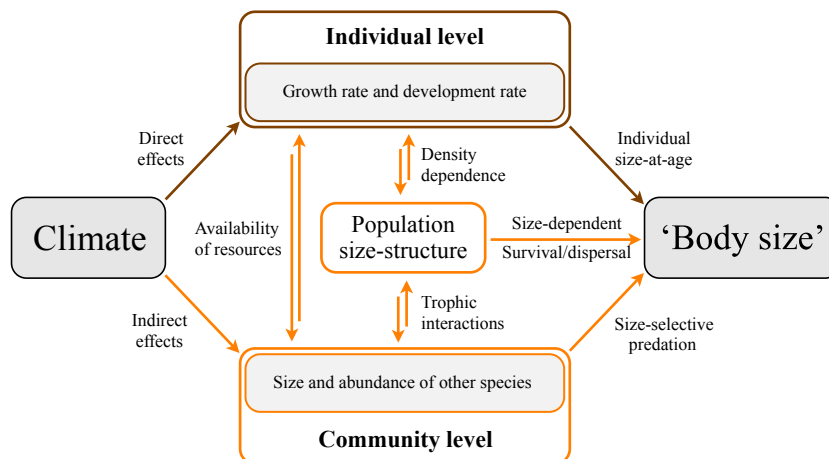
Fig. 3. Changes in average body size occur at different levels of organization (individuals, populations and communities). Declining body sizes may result from a decreased size-at-age of individuals ('*size-at-age shift*'), an increased proportion of smaller/younger individuals ('*structure shift*'), and/or a higher abundance of small-bodied species ('*composition shift*').

the absence and higher body weight in the presence of food (Brodersen *et al.* 2011). In fact, the growth rate of multiple populations of Chinook salmon (*Oncorhynchus tshawytscha*) was found to increase with temperature at low population densities, but decrease at high densities (Crozier *et al.* 2010). Similarly, reductions in body size at high population densities have been reported for Atlantic cod (*Gadus morhua*) (Rogers *et al.* 2011). Climate effects on early life stages, including temperature-induced increases in growth rate, may further be attenuated through density dependence later in life (Stige *et al.* 2010). These 'contemporary' observations are supported by long-term catch records of Atlantic salmon (*Salmo salar*) showing that warm temperature regimes in the past were associated with larger size and low abundance, whereas cold climates were characterized by the opposite pattern (Huusko & Hyvärinen 2012).

Temperature further influences the outcome of intraspecific competition between size-classes that differ in thermal sensitivities. The relative competitive abilities of differently sized individuals largely depend on the size scaling of physiological rates, specifically metabolism and consumption, and size scaling relationships themselves may depend on temperature (Strong & Daborn 1980; Persson *et al.* 1998; Ohlberger *et al.* 2012). Increasing temperatures may therefore shift the population size distribution towards smaller individuals if these have higher thermal optima and are better competitors for shared resources (Fig. 1d) (Ohlberger *et al.* 2011), as suggested by higher optimum temperatures for growth in juveniles compared to adults (Panov & McQueen 1998; Björnsson & Steinarsson 2002).

Climate warming may affect the population size structure through life-stage-specific responses in survival probability, because thermal limits typically differ between life stages of an organism [e.g. insects: (Kingsolver *et al.* 2011); fishes: (Peck *et al.* 2009)]. For instance, thermal tolerance windows of fish tend to be narrow in early life stages due to developmental constraints, widen out for juveniles and young adults as performance capacity increases, and narrow down again in larger and particularly in reproducing individuals due to the rapidly increasing energy demand for reproductive tissue (Pörtner & Farrell 2008; Peck *et al.* 2009; Righton *et al.* 2010). Accordingly, heat stress due to extreme summer temperatures in a population of eelpout (*Zoarces viviparus*) in the southern North Sea caused a selective loss of large individuals and limited the remaining individuals to a location-specific maximum body size (Pörtner & Knust 2007). Similarly, an analysis of 14 marine invertebrate species revealed that smaller individuals survived at higher temperatures than larger conspecifics in acute temperature treatments, suggesting that juveniles cope better with warming than larger, older individuals (Peck *et al.* 2009). Organisms may also experience different degrees of warming if they display ontogenetic shifts in habitat use associated with changes in nutritional and/or thermal conditions (Schreiber & Rudolf 2008; Kingsolver *et al.* 2011). Importantly, the combined effects of

Fig. 4. Mechanisms through which climate warming may affect mean organism body size. Warming directly affects rates of individual growth and development and thus body size (brown/black pathway). Individuals also compete for resources, experience size-dependent survival and dispersal, and interact with other species in the community through competition and predation, all of which may depend on temperature as well (orange/grey pathway).



temperature on rates of growth, fecundity and/or survival may alter population size structure in complex ways. For instance, while higher growth rates may translate into larger body sizes at maturation and thus higher fecundity, negative effects of warming on juvenile survival may outweigh these positive effects on individual growth and reproductive output, as suggested for Atlantic salmon (Friedland & Todd 2012). Furthermore, changes in population age- or size structure can be mediated through shifts in the timing of seasonal events (Sebastian *et al.* 2012). Finally, size-specific dispersal can lead to changes in size structure, because the ability of individuals to disperse often depends on the phenotype, and particularly body size (McCauley & Mabry 2011). The importance of life-stage-specific responses to climate warming is now increasingly recognized (Zeigler 2013). In conclusion, warming may strongly affect certain life stages but not necessarily others, and small changes in life-stage-specific survival (or dispersal) can severely affect population abundance and mean body size.

Changes in the size structure of populations, especially top predators, may lead to cascading effects that drive the response of entire food webs (Estes *et al.* 2011). Population size-structure determines how species are embedded in their food web (Brose *et al.* 2012). Due to species-specific thermal tolerance windows, warming differentially affects the physiology of interacting species and thus their responses at different trophic levels (Voigt *et al.* 2003; Yvon-Durocher *et al.* 2011). Warming therefore changes the strength and dynamics of trophic interactions such as predation and competition (Vasseur & McCann 2005; Finstad *et al.* 2011; Lang, Rall & Brose 2012), as well as trophic cascades (Kratina *et al.* 2012), and the timing of these interactions via phenological shifts (Freitas *et al.* 2007). Rates of foraging, prey ingestion and handling, which depend on environmental temperature, determine the strength of competitive and predatory interactions (Emmerson *et al.* 2005; Englund *et al.* 2011; Rall *et al.* 2012), which are commonly size-based in many food webs (Persson & de Roos 2007; Thierry *et al.* 2011). For example, a warming-induced decline in the mean body size of zooplankton populations reduced vulnerability to visually

feeding fish, but increased vulnerability to invertebrate predators, thereby affecting higher trophic levels in opposite ways (Moore & Folt 1993). In summary, warming affects the type and strength of species interactions in both aquatic and terrestrial ecosystems, and has the potential to modify trophic cascades, which in turn may cause consistent changes in the size structure of communities.

Changes in community size structure due to shifts in relative species composition or species losses have also been reported in a number of experimental studies (Petchev *et al.* 1999; Dossena *et al.* 2012), as well as natural ecosystems (Strecker, Cobb & Vinebrooke 2004; Li *et al.* 2009; Woodward *et al.* 2010a). Especially for plankton communities, warming is associated with increasing abundances of smaller sized species or taxa in both freshwater and marine ecosystems (Li *et al.* 2009; Yvon-Durocher *et al.* 2011; Taylor *et al.* 2012). Climate warming was further shown to alter the community composition in geothermal streams, where brown trout (*Salmo trutta*) replaced invertebrates as the top predators in warmer streams (Woodward *et al.* 2010a). Smaller, faster growing organisms also became dominant in warm compared to cold experimental alpine ponds (Strecker, Cobb & Vinebrooke 2004). Furthermore, invasions of non-native species, migrations of resident populations, and the spread of diseases may change the size composition of communities (Walther *et al.* 2002; Thomas *et al.* 2004; Ellis *et al.* 2011). If community size spectra are largely determined by phylogenetic constraints and colonization history that are linked to the species' life histories, warming may induce regime shifts that result in the reorganization of species assemblages once a thermal threshold is reached. Consequently, size distributions of entire communities may show non-linear responses to climate warming (Allen *et al.* 2006).

EVOLUTIONARY RESPONSES

An important question in the context of changes in mean body size due to warming is whether these changes represent phenotypically plastic or genetic responses. Evolutionary responses could either alleviate or reinforce ecological

changes in body size due to climate warming. It has been suggested that differences in growth and adult size represent adaptive responses to temperature with a fitness advantage of being smaller in warmer environments (Atkinson 1994; Kozowski, Czarnoleski & Danko 2004). One explanation for the adaptiveness of changes in body size with temperature is the optimal allocation of resources to somatic vs. reproductive growth, assuming that organisms are selected for maximum lifetime reproductive success (Kozowski, Czarnoleski & Danko 2004). Optimal rates of individual growth and development in a given environment are determined by energetics in terms of resource acquisition and metabolic demands as well as size-dependent mortality. Thus, evolutionary responses in growth and body size may result from temperature-dependent mortality rates and/or changes in the thermal sensitivities of energy acquisition and metabolism (Kozowski, Czarnoleski & Danko 2004). There is in fact evidence for both mechanisms operating in nature (Strong & Daborn 1980; Belk & Houston 2002; Munch & Salinas 2009; Ohlberger *et al.* 2012).

Evolution in growth and development rates in response to contemporary climate warming is likely considering that (i) thermal adaptation via changes in thermal performance functions has been described for several organisms (Pörtner 2002; Angilletta 2009), (ii) closely related species commonly display variation in temperature-related physiological traits as a result of past adaptation (Davis, Shaw & Etterson 2005; Ohlberger *et al.* 2008), (iii) warming differentially affects the survival of small versus large individuals (Pörtner & Knust 2007; Peck *et al.* 2009), (iv) laboratory experiments have demonstrated the evolution of growth and development in response to selection on body size (Partridge *et al.* 1994; Teuschl, Reim & Blanckenhorn 2007) and (v) evolutionary responses can occur on time-scales over which climate is expected to change (Yoshida *et al.* 2003; Hairston *et al.* 2005). Nevertheless, conclusive evidence of genetic change in response to increasing temperature is still rare for natural populations (Bradshaw & Holzapfel 2006; Gienapp *et al.* 2008), probably due to the limited amount of data suitable for tests of changes in allele frequencies in genes functionally linked to traits under selection (Hoffmann & Sgrò 2011).

GEOGRAPHY, SEASONALITY AND HABITATS

The effects of climate warming on the growth capacity and body size of an organism also critically depend on its geographic location. Within species that are distributed over a wide latitudinal range, individuals at higher latitudes commonly experience lower than optimal temperatures, whereas those at lower latitudes experience average temperatures closer to the upper thermal limit (Pörtner 2002; Righton *et al.* 2010). Accordingly, growth capacity is expected to increase at high but decrease at low latitudes relative to the species distribution range. However, local adaptation of populations of the same species may

alleviate adverse effects on growth. For instance, different stocks of cod are known to exhibit polymorphisms in haemoglobin type (Righton *et al.* 2010) with different thermal optima. Therefore, studies of single populations within a limited geographic area may reflect location-specific responses to climate warming.

Geographic ranges are further important in the context of Bergmann's rule, which originally described a positive relationship between endotherm body size and latitude (Bergmann 1847). The cause of this common relationship was attributed to thermoregulation and optimization of endotherm body size, stating that cold environments favour larger size due to reduced mass-specific heat loss at larger body volume-to-surface ratios. Only later was the concept extended to intraspecific size clines (James 1970) and to ectotherms (Atkinson 1994). The TSR, which describes the phenotypic response of an organism during ontogeny, has been associated with observed patterns of latitudinal clines in ectotherm body sizes (Kingsolver & Huey 2008). However, the mechanisms causing size clines in endotherms cannot apply to ectotherms that are unable to produce considerable metabolic heat. Furthermore, the generality and adaptive significance of Bergmann's rule remain highly debated (Angilletta & Dunham 2003; Kingsolver & Huey 2008; Stillwell 2010), and patterns of latitudinal size clines cannot be used to 'explain' changes in ectotherm body size in response to climate warming.

Across species, body size responses to temperature changes also strongly depend on species-specific thermal requirements (Pörtner 2002). Especially cold-adapted polar stenotherms that are restricted to narrow temperature ranges appear most vulnerable to climate warming and will likely experience reductions in growth performance (Somero 2010). In contrast, eurythermal species, including many temperate ectotherms, are capable of surviving over wide ranges of temperature. Even though temperatures are projected to rise faster in temperate compared to tropical ecosystems (IPCC 2007), warming may have the most severe effects on ectotherms in the tropics. The relative increase in metabolic costs with temperature is greater in warmer climates due to the exponential increase in metabolic rate, and thermal windows tend to be narrower in tropical compared to temperate environments due to lower temperature variability (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008). Tropical species typically have an upper thermal limit for survival closer to the optimum temperature than their temperate counterparts. Temperate species have broader thermal tolerances and generally experience climates with average temperatures below their thermal optima [e.g. insects: Deutsch *et al.* (2008); lizards: Huey *et al.* (2009)]. One possible explanation is that optimal temperatures higher than those actually experienced function as a safety margin in more variable climates (Kingsolver 2009).

Because stronger temperature variation is associated with wider thermal tolerances (Deutsch *et al.* 2008), and because organisms in temperate regions commonly show

seasonal shifts in thermal windows (Pörtner 2002), environmental variability plays an important role in determining the impact of warming on organism body size. Seasonality also implies that the observed effects of climate warming may depend on the season for which the growth response is measured. Accordingly, contrasting effects of seasonal temperatures on ectotherm body size have been reported in a number of studies (Kari & Huey 2000; Rogers *et al.* 2011; Sebastian *et al.* 2012). For instance, warm summer temperatures off the southern coast of Norway during the last century have limited growth of juvenile Atlantic cod while warmer springs have resulted in larger individuals (Rogers *et al.* 2011). Furthermore, organism responses to climate warming may depend on regional patterns in climate warming, and the increasing frequency of extreme events (Helmuth *et al.* 2002; Hoffmann, Sorensen & Loeschcke 2003). Such extreme temperature events can increase mortality rates and reduce growth capacity in specific years (Mallet *et al.* 1999) and may have the strongest impact on terrestrial, coastal and shallow freshwater ecosystems.

In general, the mechanisms through which warming affects ectotherm body size differ between aquatic and terrestrial environments. Oxygen limitation as determinant of thermal tolerances is more important in water breathing animals that experience lower levels of oxygen, slower oxygen diffusion, as well as higher energetic costs of ventilation and circulation. Accordingly, evidence that thermal tolerance limits are set by limited oxygen supply to tissues is strong for aquatic, but less conclusive for terrestrial ectotherms (Pörtner 2002; Stevens *et al.* 2010). The combined effects of oxygen limitation and increasing temperatures may thus lead to reductions in average body size particularly in water-breathing ectotherms (Cheung *et al.* 2013). In fact, a recent meta-analysis found that reductions in body size in response to warming are greater in aquatic (freshwater and marine) than terrestrial species (Forster, Hirst & Atkinson 2012). Because most terrestrial ectotherms experience stronger short-term variability in temperature than aquatic/marine species due to the lower thermal buffering, they use thermoregulation to maintain body temperature within their tolerance range. In contrast, aquatic ectotherms commonly show stronger thermal acclimation (Angilletta 2009), or migrate between shallow and deep waters and thereby choose preferred thermal habitat (Dulvy *et al.* 2008). Consequently, growth rates of aquatic species in deeper habitats may be less affected by warming than those in coastal or littoral habitats (Thresher *et al.* 2007), and changes in body size may depend on local adaptation associated with fine-scale differences in habitat use (Mehner, Emmrich & Kasprzak 2011).

CONSEQUENCES AND FUTURE ROADMAP

Shifts in organism body sizes or population size spectra can have important consequences for ecosystem functioning and thus the services ecosystems provide for humans (Woodward *et al.* 2005; Petchey & Belgrano 2010). Body

size is one of the most important traits determining individual performance and life history and is linked to population stability, extinction risk and distribution patterns (Peters 1983; Calder 1984). Due to species-specific thermal requirements, interacting species respond differently to climate warming, with direct implications for size-based competition and predation, especially between species with different life-histories (Tylianakis *et al.* 2008; Traill *et al.* 2010). Shifts in size structure may further change the type and strength of top-down or bottom-up control of ecosystems (Brose *et al.* 2012; O'Gorman *et al.* 2012). Because food web stability is tightly linked to the strength of species interactions, such warming-induced imbalances may destabilize the dynamics of food webs and affect ecosystem functioning (Strecker, Cobb & Vinebrooke 2004; Emmerson *et al.* 2005; Woodward *et al.* 2010a). Besides more general changes in ecosystem status, declining body sizes may decrease food supply or economic profits. For instance, in fisheries the mean sizes of many fish species seem to be declining in response to climate warming (Todd *et al.* 2008; Daufresne, Lengfellner & Sommer 2009; Genner *et al.* 2010; Cheung *et al.* 2013). However, the impact of a decline in fish body size would depend on the population dynamical consequences of warming, as an increase in abundance could offset adverse effects of smaller sizes. This further emphasizes the need to understand causes of past and contemporary changes in body size in order to assess the consequences of potential future declines. Further, warming will interact with the other ecological and evolutionary impacts imposed on natural populations by humans, for instance through harvesting or habitat alteration.

A better understanding of how evolutionary responses and ecological interactions modify the effects climate warming on individual physiology is required for making useful predictions about expected changes in mean organism body sizes. Predictions of the impact of continuously increasing temperatures on the body size of a single individual under otherwise constant environmental conditions are rather simple given that sufficient experimental data exist. However, as elaborated in this review, predictions about changes in the mean body size of populations and communities are challenging due to the complexity of biological systems, specifically the potential for emergent properties at higher organizational levels (Woodward, Perkins & Brown 2010b; Woodward *et al.* 2010a), relatively rapid evolutionary change (Hairston *et al.* 2005), and non-linear ecological dynamics in response to abiotic changes (Smol *et al.* 2005). Nevertheless, considering such emergent properties may improve predictions of warming-induced changes in body size, as intra- and interspecific interactions are part of the biology of most organisms (Zarnetske, Skelly & Urban 2012).

To improve our understanding of the underlying causes and to facilitate the management of ecosystems in the face of climate change, hypotheses about warming-induced changes in body size need to be developed and tested empirically. Based on the arguments developed in this

study, changes in the average body size of populations and entire communities are likely and may be mediated via different mechanisms. Some expectations emerge based on recent empirical evidence and general considerations as presented in this review. Adult body sizes of the majority of ectotherms are expected to decline as temperature increases due to the underlying thermal reaction norms ('size-at-age shift'). Warming is expected to most severely decrease the survival of adults due to lower stage-specific thermal tolerances, and to strengthen competitive asymmetry in favour of smaller-sized individuals ('structure shift'). Within communities, smaller species are expected to replace larger competitors, which themselves may migrate polewards to avoid above-optimal temperatures ('composition shift'). However, these expectations about organism responses to warming may depend on geographic location, life history and phylogenetic constraints, as outlined above. For instance, climate warming is expected to most severely affect body sizes of cold-adapted stenotherms and tropical species that are specialized on narrow temperature ranges and live close to optimal temperatures, reduce individual growth rates at lower latitudes while promoting growth at higher latitudes within eurythermal species that spread over a range of climatic conditions and have weaker impacts on deep-water species compared to aquatic species inhabiting shallow and surface waters.

Improving our understanding of the causes of observed size shifts will require diverse expertise and targeted research efforts. Theoretical models, although necessarily simplistic, are a basic tool for linking thermal dependence of individual growth and development to population dynamics and ultimately community interactions (Clark *et al.* 2003). Simulation models such as size-structured population models that are based on individual physiology and calibrated to empirical data are a useful tool for studying population-level effects of rising temperatures, but require well-studied model organisms (Ohlberger *et al.* 2011). Integral projection models provide a great opportunity to study the temperature dependence of vital rates, and how these interact to determine population growth and size structure (Rees & Ellner 2009). Although paleoclimate studies can detect effects of long-term climate fluctuations on average population body sizes (Hunt & Roy 2006; Smith *et al.* 2009), their value may be limited if current rates of warming outpace historic climate trends. Experimental studies that control temperature regimes in mesocosms are important for characterizing changes in size structure at the population and community levels under semi-natural conditions (Petchey *et al.* 1999; Dossena *et al.* 2012). Statistical analyses of long-term data series are further needed as they can provide the most direct evidence for changes in size-at-age, size structure or size composition caused by climate warming while accounting for the complexity of natural systems (Daufresne, Lengfellner & Sommer 2009). In this context, hierarchical models that simultaneously test for temperature effects at different levels of organization may be particularly promising.

Conclusions

This review suggests that widely observed declines in the mean body size of organisms result as a direct consequence of changes in physiological rates, from size- and density-dependent population feedbacks, and changes in trophic interactions. While the thermal dependence of growth and development leads to shifts in individual size-at-age, emergent effects through ecological interactions lead to shifts in size distributions of populations and changes in community composition of differently sized species. Consequently, considering the broader ecological context of observed changes in body sizes based on empirical data is critically important when trying to draw conclusions about the underlying causes. Doing so will improve our understanding of the importance of the various processes and our ability to predict responses in body size to future climate warming.

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