



Environmental Warming in Shallow Lakes: A Review of Potential Changes in Community Structure as Evidenced from Space-for-Time Substitution Approaches

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Abstract

Shallow lakes, one of the most widespread water bodies in the world landscape, are very sensitive to climate change. Several theories predict changes in community traits, relevant for ecosystem functioning, with higher temperature. The space-for-time substitution approach (SFTS) provides one of the most plausible empirical evaluations for these theories, helping to elucidate the long-term consequences of changes in climate.

Here, we reviewed the changes at the community level for the main freshwater taxa and assemblages (i.e. fishes, macroinvertebrates, zooplankton, macrophytes, phytoplankton, periphyton and bacterioplankton), under different climates. We analyzed data obtained from latitudinal and altitudinal gradients and cross-comparison (i.e. SFTS) studies, supplemented by an analysis of published geographically dispersed data for those communities or traits not covered in the SFTS literature.

We found only partial empirical evidence supporting the theoretical predictions. The prediction of higher richness at warmer locations was supported for fishes, phytoplankton and periphyton, while the opposite was true for macroinvertebrates and zooplankton. With decreasing latitude, the biomass of cladoceran zooplankton and periphyton and the density of zooplankton and macroinvertebrates declined (opposite for fishes for both biomass and density variables). Fishes and cladoceran zooplankton

showed the expected reduction in body size with higher temperature. Life history changes in fish and zooplankton and stronger trophic interactions at intermediate positions in the food web (fish predation on zooplankton and macroinvertebrates) were evident, but also a weaker grazing pressure of zooplankton on phytoplankton occurred with increasing temperatures. The potential impacts of lake productivity, fish predation and other factors, such as salinity, were often stronger than those of temperature itself. Additionally, shallow lakes may shift between alternative states, complicating theoretical predictions of warming effects. SFTS and meta-analyses approaches have their shortcomings, but in combination with experimental and model studies that help reveal mechanisms, the "field situation" is indispensable to understand the potential effects of warming.



1. INTRODUCTION

1.1. Global change and freshwater communities

Anthropogenic impacts on natural ecosystems are increasing apace in both the terrestrial and aquatic (both freshwater and marine) realms, and environmental stressors, such as climate change, threaten to alter community structure and ecosystem functioning from local to global scales (Hagen et al., 2012; Ledger et al., 2012; Mintenbeck et al., 2012; Mulder et al., 2012). The Millennium Ecosystem Assessment (2005) has quantified existing and projected deterioration or loss of natural ecosystems through the intensification of agriculture, urbanization and other anthropogenic impacts that are likely to have significant impacts on most of the terrestrial ecosystems on Earth by the year 2070. The key global drivers include climate warming, changes in precipitation patterns, land use changes (Vitousek, 1994), increasing atmospheric CO₂ concentrations (Rockström et al., 2009), and alterations in the global nitrogen cycle and global fertilization of ecosystems (Galloway et al., 2008; Gruber and Galloway, 2008). Invasive species (Walther et al., 2009) and decreasing biodiversity due to habitat loss and rising water demands (Vörösmarty et al., 2000) are among the most widely reported biological responses to these changes (Parmesan and Yohe, 2003).

The impacts of environmental warming, although increasingly recognized as a key component of climate change following the recent reports from the Intergovernmental Panel on Climate Change (IPCC, 2007), and a growing number of ecological studies, are still poorly understood at the higher (multispecies) levels of biological organization. It is recognized, however, that its impacts are expected to be strongest at high altitude and high latitudes (Phoenix and Lee, 2004; Rouse et al., 1997; Smol et al., 2005; Woodward et al., 2010a,b). Large parts of the polar regions, particularly the Arctic, are expected to show a much faster increase in the mean annual temperature than lower latitudes (Howard-Williams et al., 2006).

Temperature affects a myriad of biological processes, including individual growth and respiration rates (potentially affecting primary production and community respiration, e.g. [Yvon-Durocher et al., 2010](#)), changes in life history traits, changes in phenology and trophic dynamics, with potential temporal or spatial mismatches arising between prey availability and consumer demands (e.g. [Winder and Schindler, 2004](#)). Species may not respond with the same strength or synchronously in time, since they are affected not only by changes in temperature but also by other environmental factors, such as changes in photoperiod ([Winder and Schindler, 2004](#)). However, after accounting for size dependence, temperature explains the largest amount of variation in almost all biological rates ([Brown et al., 2004](#); [Peters, 1983](#)). Given sufficient resource availability, increasing temperatures generally accelerate growth and development rates of individual organisms ([Forster et al., 2011b](#)), although changes in absolute abundances may be species specific or ecosystem specific ([Adrian et al., 2006](#); [Blenckner et al., 2007](#); [Reist et al., 2006](#)).

Warming may also contribute to changes in the latitudinal or altitudinal distributional range of some species, thus likely affecting diversity and community structure. Stenothermal species (narrow thermal range) will most probably shift range or become locally extinct, whereas eurythermal species (wide thermal range) will likely be able to adapt to new thermal regimes ([Lappalainen and Lehtonen, 1997](#); [Woodward et al., 2010a,b](#)). The already observed and the predicted changes in global and regional temperatures make understanding warming effects on ecological communities a priority ([Moss et al., 2009](#); [Petchey et al., 2010](#)). However, the effects of temperature on many aspects of community structure, such as the distribution of diversity and biomass across trophic levels, or the extent and distribution of specialism and generalism across species, are still poorly understood ([Petchey et al., 2010](#); [Woodward et al., 2010b](#)).

1.2. Shallow lakes and ecosystem responses to changes in temperature

Shallow lakes (typically polymictic, maximum depth ca. <5 m) are particularly strongly affected by human activity, as they are key providers of critical ecosystem services that underpin aquaculture, crop irrigation and drinking water supply. Besides being one of the most common and widespread inland water bodies in the world landscape ([Downing et al., 2006](#)), these lakes represent one of the ecosystem types most rapidly affected by external perturbations, including climate change ([Jeppesen et al., 2009](#); [Moss et al., 2009](#)).

Shallow lakes are typically isolated and fragmented in the landscape and are extremely sensitive to climate variability such as evaporation and precipitation balances, since they have a very large surface:volume ratio (Coops et al., 2003), which affects the persistence of climatic signatures. Lake depth and hydrologic residence time, together with stratification and mixing regime, are also physical features that interact to control the duration and strength of climate signals, for instance, in water temperature (Blenckner, 2005). In deep lakes, the winter climate signal (as described, for instance, by the winter North Atlantic Oscillation index, NAO, in the Northern Hemisphere) can persist until late summer, whereas in shallow lakes, the winter temperature signal lasts for much shorter time (Gerten and Adrian, 2001). Identification of climate signals in current measurements may thus be difficult due to time-lags arising from the action of other processes at different scales.

Most lakes are also commonly affected by multiple interacting stressors (Christensen et al., 2006; Yan et al., 2008), potentially confounding the detection of signals due to climate change. Freshwater systems, not least shallow lakes, are subject to increasing deterioration processes in many parts of the world (Feld et al., 2011; Friberg et al., 2011; Hladyz et al., 2011; Moss, 1998; Moss et al., 2011). These include wetland area loss, local extinction of native species and introduction of exotic species, acidification, water level changes due to water extraction or canalization and, especially, eutrophication (nutrient enrichment in the water bodies), among the major drivers of global change that aquatic ecosystems are currently facing (reviewed in, e.g. Carpenter et al., 1998; Dodds, 2007; Friberg et al., 2011; Schindler, 2006; Smith, 2003). While some shallow lakes and ponds might simply dry out (Beklioglu et al., 2007), the lower water level will often concentrate pollutants, enhance resuspension and, together with the higher temperature, amplify the sediment release of nutrients, especially of phosphorus (McKee et al., 2003; Özen et al., 2010). Under increasing precipitation, in contrast, the runoff of nutrients from the catchments may increase (Jeppesen et al., 2009, 2011; Özen et al., 2010). An amplification of eutrophication symptoms by climate warming seems to occur also by changes in trophic dynamics and interactions (Meerhoff et al., 2007a) and shifts in fish community structure (Jeppesen et al., 2010a) and population size structure (Daufresne et al., 2009). As a consequence, the likelihood of dominance of nuisance phytoplankton taxa, such as cyanobacteria and filamentous algae, may rise (Jeppesen et al., 2009; Kosten et al., 2011a; Mooij et al., 2005; Paerl and Huisman, 2009; Trochine et al., 2011).

The interaction of climate signals with nutrient enrichment symptoms has been addressed by several studies based on palaeolimnological records (Bjerring et al., 2009), mesocosm experiments (e.g. Moss et al., 2004 and references herein), latitudinal gradient analysis (Kosten et al., 2009b and references herein) and synthesis papers (Jeppesen et al., 2010a, 2011; Moss, 2010; Moss et al., 2011). However, disentangling the specific effects of environmental warming from nutrient enrichment (as well as from other global changes) is crucial if we are to further our understanding of the responses of freshwater ecosystems to a changing climate and contribute to their conservation with adequate mitigation measures. The interactive effects of warming and other global changes and the indirect impacts on community structure, food web functioning and ecosystem processes are even far less well known (Montoya and Raffaelli, 2010; Woodward et al., 2010b).

The influence of the catchment on within-lake processes can vary depending on land use, the regional climate and geographical location. However, shallow lakes are especially complex due to their numerous internal feedbacks. Shallow lakes may respond differently from other aquatic systems to external perturbations or stressors, given the recognized potential for them to shift between alternative states over an intermediate range of nutrient concentrations, in a typical hysteresis process (Moss et al., 1996; Scheffer et al., 1993, 2001): such extreme regime shifts seem far less prevalent in many running waters, which appear to be far more stable in the face of perturbations or stressors in general (Layer et al., 2010, 2011; Ledger et al., 2012). Biological and physicochemical mechanisms related to the presence or absence of macrophytes and water turbidity maintain either state via a range of positive feedbacks. The stability of such alternative states has been challenged by recent studies conducted in other regions of the globe than the temperate zone (Jeppesen et al., 2007; Kosten et al., 2011a; Meerhoff et al., 2007a), which was the birth place of this theoretical framework, suggesting that they might be modulated by climatic influences. Similar to enhanced nutrient loading, changes in water level, enhanced temperature and longer growing season have been identified as potential weakening factors that may trigger a change from a clear water, macrophyte-dominated state to undesirable states (Beklioglu et al., 2006) involving the dominance by free-floating plants (Scheffer et al., 2003) or filamentous green algae (Trochine et al., 2011). The hysteresis phenomenon complicates our ability to make predictions for the response of a specific community, not least at ecosystem level, to

changing temperatures, as several community and food web configurations may occur under similar environmental conditions.

1.3. Indirect effects of climate on community structure through availability of nutrients

Trends extracted from latitudinal gradient or cross-comparison analyses are based on correlative data. This may render it difficult to disentangle strict climate signals from potential indirect effects of climate and human-related impacts (such as nutrient enrichment and salinization through cultivation, e.g. Bjerring et al., 2009). An increase in nutrient loading may determine a series of important changes in community traits in shallow lake communities. For instance, changes in fish community composition, biomass and body size structure, with non-random loss of predatory species (due to increased turbidity and lower concentrations or larger variations in dissolved oxygen), occur worldwide with eutrophication (Jeppesen et al., 2005). Large increases in nutrient concentrations due to eutrophication thus affect lake trophic webs, from the basal resources to the top predators.

Both the absolute and relative concentrations of nutrients in the water column are essential for the development of phytoplankton communities, as they affect both total biomass and composition. A warmer climate can affect the identity of the limiting nutrient and the availability of nutrients to primary producers: for instance, higher denitrification under warmer conditions could lead to nitrogen limitation (Lewis, 1996, 2000). There are conflicting observations as to which is the main limiting nutrient across different climates. In cross-comparison mesocosm experiments on nutrient and fish addition under different temperatures, the nature of the limiting nutrient varied between temperate and tropical systems (Danger et al., 2009). Addition of phosphorus (P) favoured phytoplankton in temperate lakes, while nitrogen (N) had positive effects in tropical mesocosms, and water N:P ratios tended to be higher in the tropical than in the temperate experiment. However, several latitudinal gradient studies show no clear consistent differences in N or P limitation across large spatial scales in terms of nutrient ratios and chlorophyll-a:nutrient relationships, among other indicators (Huszar et al., 2006; Kosten et al., 2009b; Mazumder and Havens, 1998). Kosten et al. (2011b) showed that while total phosphorus (TP) explained most of the variance in phytoplankton chlorophyll-a (Chl-a) in the cool region of South America, total nitrogen (TN) explained most of the variance in the intermediate and warm regions. A recent work based on an extensive

meta-analysis of various ecosystems has shown equivalence in N and P limitation in freshwater ecosystems and synergistic effects of N and P enrichment (i.e. co-limitation) (Elser et al., 2007). These authors found only a weak negative correlation between latitude and the positive response of primary producers to enrichment in N, but not in P. In summary, our review of nutrient limitation among different climates in the space-for-time substitution (SFTS) approach literature shows no clear or consistent pattern.

1.4. Theoretical predictions

Changes in temperature, due to both anthropogenic activities and natural temperature variations, are a main determinant of community structure and ecosystem processes, via the direct effects on the metabolic demands of individuals and the attendant changes in the distribution of body sizes of organisms (Arim et al., 2007; Charnov and Gillooly, 2004; Forster et al., 2011a,b; Gillooly, 2000; Yvon-Durocher et al., 2011a). The metabolic theory of ecology (hereafter, MTE) considers the effects of both body size and environmental temperature on relevant ecological rates and patterns (Brown et al., 2004). MTE, and other physiologically based theories relating environmental temperature with organisms' performance and community function, provides the basis for predictive analysis of the effect of climate warming on ecosystems (e.g. Angilletta, 2009; Karasov and Martínez del Río, 2007; McNab, 2002; Perkins et al., 2010; Yvon-Durocher et al., 2010). The MTE is based on a set of empirical generalizations about scaling of biological rates with body size (Brown et al., 2004; Peters, 1983), a mechanistic explanation for this scaling (West et al., 1997) and its response to changes in temperature (Dell et al., 2011; Gillooly et al., 2001; Huey and Kingsolver, 2011). This theory remains at the centre of a heated debate (Brown et al., 2005; Etienne et al., 2006; Forster et al., 2011b; Kozłowski and Konarzewski, 2004; Reiss et al., 2010). Nonetheless, despite some deviations from general expectations (e.g. Algar et al., 2007; Caruso et al., 2010), the predictive potential of this ecological theory, which is based on basic principles of biology and kinetics, is notable (e.g. Weber et al., 2011).

MTE quantitatively predicts changes in species (or higher taxa) richness due to changes in environmental temperature and in the mean body size of the individuals composing local communities (Allen et al., 2002; Brown et al., 2004). This theory predicts an increase in richness with temperature

(specifically, a linear relationship between the logarithm of species richness and the inverse of temperature, [Allen et al., 2002](#)) ([Fig. 1, Table 1](#)). The detection of some degree of curvilinear association between these variables in invertebrate and vertebrate ectotherms could be considered as a limitation of the theory or as an area in which further theoretical advances are needed ([Algar et al., 2007](#)). Considering the possible change in species body size and in metabolic rates due to changes in temperature, several predictions can be made.

From a population perspective, the carrying capacity, the growth rates, the incidence among local populations, and the geographic range of species could be potentially affected by temperature. A basic determinant of a population's carrying capacity is the relationship between the demands of individuals and the availability of resources ([Damuth, 1981](#)). The effect of temperature on the demands of an individual predicts a displacement of the density–mass relationship, as well as of the biomass distribution (e.g. [Brown et al., 2004](#)). These displacements take place because the rise in energetic demands with increasing temperature determines that the same amount of resources is divided among individuals that require more from the environment; consequently, fewer individuals can satisfy their demands and a decrease in density and total biomass is expected ([Fig. 1, Table 1](#)). However, if the amounts of available resources and/or predation strength depend on body size and temperature, changes in the slope and modes of the size distribution could also be expected (see [Arim et al., 2011; Brown et al., 2004](#)). In addition to these changes in the carrying capacity of species, population dynamics could also be affected since the maximum growth rate is expected to increase with temperature ([Brown et al., 2004](#)). In this sense, the rise in temperature could lead to less abundant and more variable populations (e.g. [Beisner et al., 1997](#)) with more frequent local extinction, affecting metapopulation dynamics and the fraction of local habitats occupied by the species ([Hanski, 1999](#)).

A causal connection between temperature and body size has long been recognized (reviewed by [Angilletta, 2009; Kingsolver and Huey, 2008](#)), and Bergmann's rule, now more than 160 years old, is one of the first empirical generalizations about ecological patterns ([Gaston and Blackburn, 2000](#)) and still plays a central role in biogeography ([Olalla-Tárraga, 2011](#)). It states that organisms from higher latitudes have large body sizes in comparison with individuals of the same species, related species or assemblages inhabiting lower latitudes ([Olalla-Tárraga et al., 2010](#)) ([Fig. 1, solid line](#)). This trend was conceived for endotherms that obtain a

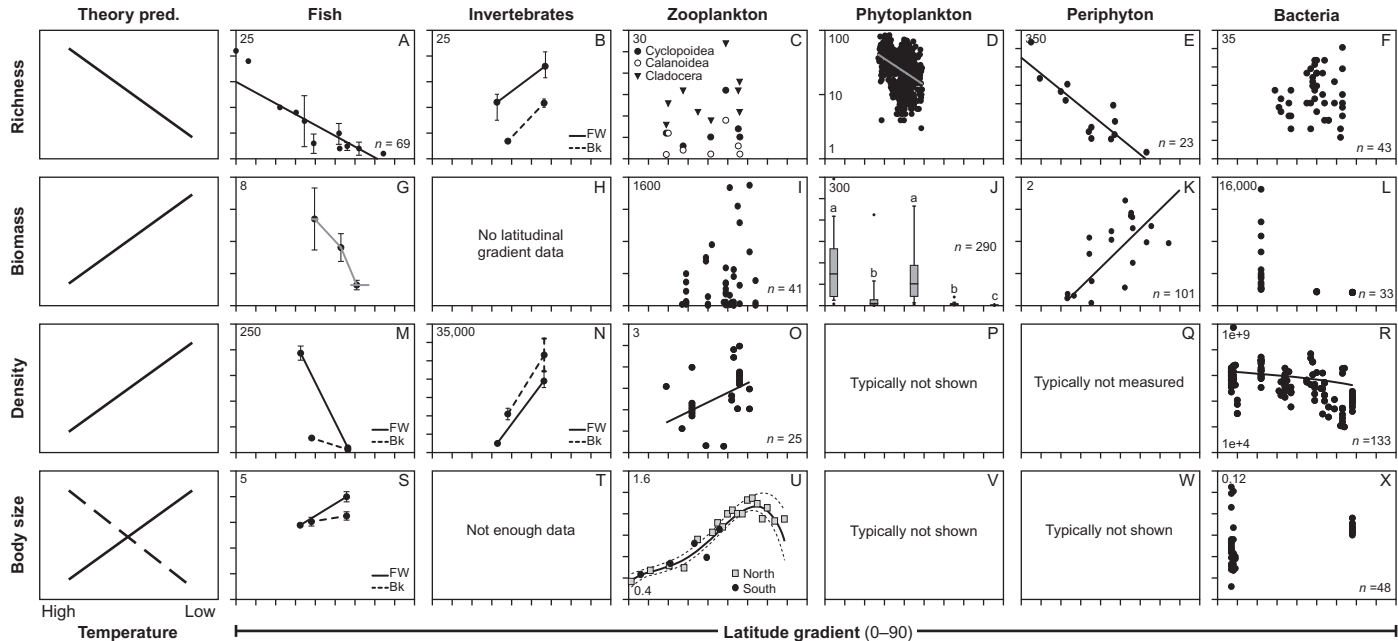


Figure 1 Theoretical expectations and most representative empirical trends in main traits of different communities of shallow lakes along a latitude gradient, as found in space-for-time substitution studies or built on meta-analysis. See [Table 1](#) for a summary of the respective units and references from which data were extracted, and respective Appendixes for the meta-analyses. From right to left: theoretically predicted relationships (solid lines: most supported trend, dashed line: alternative expected trend, see [Section 1](#)), fish, macroinvertebrates, zooplankton, phytoplankton, periphyton and bacterioplankton, and from top to bottom: richness, biomass, density and body size, indicating the maximum scale value on each y-axis, the significant relationships (indicated by a line or an * where appropriate) and the reasons for empty panels. Macrophytes were excluded due to lack of data on all traits. Data on proximate latitudes were averaged and shown as mean value for that latitude range, in the case of fish biomass data (extracted from [Gyllström et al., 2005](#)) after removing the lowest phosphorus values from the analysis in order to have a comparable range among climate zones. To calculate zooplankton dry weight, we used a conversion factor of 48% to transform $\mu\text{g C L}^{-1}$ to $\mu\text{g DW L}^{-1}$ ([Hessen, 1989](#)). Phytoplankton biomass box-plots show mean, mean ± 1 SE, mean ± 1 SD and extreme values. The letters in the right corner of the panels are used for identification in the main text. When shown, error bars correspond to 1 standard error. Codes: Bk=brackish lakes, FW=freshwater lakes.

Table 1 Summary of the data (variables and units) and respective references describing patterns of changes in main community traits along a latitudinal gradient, shown in Fig. 1

	Richness	Biomass	Density	Body size
Theoretical predictions	$\log(s) = (-E/1000k) / (1000/T) + C_1$ C_1 : constant, k : Boltzmann's constant, E : activation energy	$W \sim [R] M^{1/4} e^{E/kT}$ [R]: Supply rate of limiting resource	$K \sim [R] M^{3/4} e^{E/kT}$	See text for explanation
	Allen et al. (2002)	Brown et al. (2004)	Brown et al. (2004)	Gardner et al. (2011), Marquet and Taper (1998), and Olalla-Tárraga and Rodríguez (2007)
Fish	Species number	CPUE (kg net ⁻¹ night ⁻¹)	ind m ⁻²	cm (standard length)
	González-Bergonzoni et al. (2012)	Gyllström et al. (2005)	Brucet et al. (2010) and Teixeira-de Mello et al. (2009)	Brucet et al. (2010) and Teixeira-de Mello et al. (2009)
Macroinvertebrates	Taxa number	No data	ind m ⁻²	No data
	Brucet et al. (2012) and Meerhoff et al. (2007a)		Brucet et al. (2012) and Meerhoff et al. (2007a)	

Continued

Table 1 Summary of the data (variables and units) and respective references describing patterns of changes in main community traits along a latitudinal gradient, shown in [Fig. 1](#)—cont'd

	Richness	Biomass	Density	Body size
Zooplankton	Genera number (cladocerans and copepods)	$\mu\text{g dry weight L}^{-1}$ (total zooplankton)	ind L^{-1} (cladocerans)	mm (cladocerans)
	Brucet et al. (2010) , Meerhoff et al. (2007b) , and Pinto-Coelho et al. (2005)	Gyllström et al. (2005) , Jackson et al. (2007) , and Pinto-Coelho et al. (2005) , and Vakkilainen et al. (2004)	Hansson et al. (2007) , Meerhoff et al. (2007a) , and Meerhoff et al. (2007b) , and Pinto-Coelho et al. (2005)	Gillooly and Dodson (2000)
Phytoplankton	Species number	$\mu\text{g Chl-a L}^{-1}$	No data	No data
	Stomp et al. (2011)	Meta-analysis: Danger et al. (2009) , Ganf (1974) , Kalff and Watson (1986) , Kruk et al. (2011) , and Melack (1976, 1979) plus all references in Table 3		
Periphyton	Species number	$\log \mu\text{g Chl-a cm}^{-2}$	No data	No data
	Analysis of metadata. Appendix A	Analysis of metadata. Appendix A		
Bacterioplankton	DGGE bands	$\mu\text{g C L}^{-1}$	cells ml^{-1}	μm^3
	Analysis of metadata. Appendix B	Analysis of metadata. Appendix B	Analysis of metadata. Appendix B	Analysis of metadata. Appendix B

The equations for the theoretical predictions and their respective references are also shown, while the references used to extract data for meta-analyses are presented in [Appendixes](#). Most data were recalculated or redrawn from the original literature, except the figure from [Gillooly and Dodson \(2000\)](#), republished with kind permission from the Association for the Sciences of Limnology and Oceanography (copyright 2000) and the figure from [Stomp et al. \(2011\)](#), republished with kind permission from the authors (copyright 2011). Abbreviation DGGE, denaturing gradient gel electrophoresis

thermoregulatory benefit by the reduction in the area:volume ratio at larger masses (at high latitudes and thus cold conditions). However, several mechanisms were proposed to account for latitudinal trends in the body size of endo and ectothermic species, focusing on the effects of resource availability and thermoregulation (reviewed by [Watt et al., 2010](#)).

The “heat balance hypothesis” predicts either an increase or a reduction in body size depending on the original size and thermal biology of a given species ([Olalla-Tárraga, 2011](#)). Individuals are typically active at a range of body temperatures that could be achieved by different mechanisms ([McNab, 2002](#)). Thermoconformers, for instance, are those animals that match to their environmental temperature, in contrast to thermoregulators that maintain a nearly constant body temperature via behavioural (ectotherms) or physiological (endotherms) mechanisms (see [Angilletta, 2009; McNab, 2002](#)). Among thermoconformers, a reverse Bergmann’s pattern is expected to reduce heating times in smaller organisms ([Olalla-Tárraga and Rodríguez, 2007](#)). The body temperature of thermoconformers closely fluctuates with ambient temperature with a heating time proportional to body size, being unable to accelerate the heating process. As consequence, large individuals in colder environments have a short activity window (e.g. to forage) while the reduced available energy compromises their viability and, therefore, small individuals might be favoured (see [Olalla-Tárraga and Rodríguez, 2007](#)). Small ectothermic thermoregulators, however, would become larger at lower temperatures to increase heat conservation (from [Olalla-Tárraga, 2011](#)) ([Fig. 1](#), dashed vs. solid lines, respectively). The existence of size thresholds and potential range limits of body size for these processes to occur are not yet defined. While originally focused on amphibians, this hypothesis has the potential to explain observed patterns in fishes ([Belk and Houston, 2002; Blanck and Lamouroux, 2007](#)), invertebrates ([Blanckenhorn and Demont, 2004](#)) and ectotherms in general ([Olalla-Tárraga and Rodríguez, 2007](#)), all of which dominate the fauna of shallow lakes and freshwaters in general.

A common empirical generalization is the “temperature-size rule”, a widely recognized phenomenon, according to which ectothermic individuals growing at lower temperature reach larger body sizes ([Angilletta, 2009; Forster et al., 2011a,b; Kingsolver and Huey, 2008](#)). This process prevails independently of thermoregulatory behaviour and has been reported for unicellular and multicellular organisms, and may arise due to differential thermal responses of development and growth rates, which are not addressed by the MTE ([Forster et al., 2011a,b](#)). From Bergmann’s rule, MTE and the “temperature-size rule”, it is thus expected that for several,

not necessarily exclusive reasons, warming will promote changes in body size (Gardner et al., 2011) although the direction of change will vary depending, among other factors, on the thermal biology of the organisms.

Some macroecological approaches also support a change in body size not only within, but also among, species with global warming. Individual fitness may be summarized, from an energetic perspective, by two processes (Brown et al., 1993), namely, the acquisition of energy from the environment and the transformation of this energy into progeny. While energy acquisition increases with an increase in body size, the individual potential to produce offspring decreases. From the balance between these two processes, an optimum body size requiring less energy to survive in a given environment is expected (Marquet and Taper, 1998; Marquet et al., 2008). In this sense, population viability is determined by the balance between individual energetic demands and the availability of energy in the environment, determining constraints to the maximum and minimum body sizes in local communities (see Marquet and Taper, 1998; Marquet et al., 2008). Based on this energetic context, small species could experience a selection for larger sizes under a relative reduction in the supply–demand balance, whereas the opposite is true for large-bodied species (Marquet and Taper, 1998; Marquet et al., 2008). Specifically, when the resource availability:demands ratio is reduced (e.g. after an increase in temperature), the maximum and minimum size constraints become stronger and the smaller species experience a selection pressure towards larger sizes, while the opposite occurs for larger species (Brown et al., 1993; Marquet and Taper, 1998; Marquet et al., 2008). Within this framework, the optimum body sizes represent a threshold between positive and negative trends in response to changes in environmental conditions (Brown, 1995; Brown et al., 1993; Marquet and Taper, 1998; Marquet et al., 2008). The body size distributions expected from this theory have been evaluated in mammals, birds (e.g. Marquet and Taper, 1998) and fishes (Fu et al., 2004; Knouft, 2004; Knouft and Page, 2003; Rosenfield, 2002).

Trophic interactions may also be affected by temperature in several other ways. The rise in energetic demands with temperature could involve more consumption events (McNab, 2002), an increase in the range of prey consumed and an increase in spatial movements to capture the prey (Petchey et al., 2010; Pike, 1984; Schoener, 1974). In addition, it has been proposed that community food chain length and species trophic position can be negatively associated with environmental temperature (Arim et al., 2007). Temperature might also indirectly affect biotic interactions by

altering the final body size of adults and the time elapsed to achieve this size (Forster et al., 2011a,b). Size refugia from predation is a common phenomenon in aquatic environments (Chase, 1999), where gape-limited predation is prevalent (Gilljam et al., 2011; Woodward et al., 2010c). Smaller prey will likely be more frequently preyed upon at higher temperatures, while smaller predators might face a reduction in the total amount of available resources (Arim et al., 2010, 2011). The relative rate of variation in predator and prey sizes will determine the strength of this effect. These changes in species richness, food chain length, frequency and intensity of trophic interactions, and consequently in connectivity, have a significant potential to alter food webs and create changes in community structure and stability, and ecosystem functioning (Dunne et al., 2002; Fox and McGrady-Steed, 2002; May, 1972; McCann, 2000; Petchey et al., 2010). Contradictory results of models on the responses of community traits and food web metrics to increasing temperatures (such as connectance, Petchey et al., 2010) highlight the need for more and better empirical data to parameterize models, test predictions and produce models of mechanistic effects of temperature change on interspecific interactions, especially in freshwater ecosystems.

1.5. Space-for-time substitution approach

Various methods have been used to investigate the potential effects of global change in natural systems. In particular, a large battery of approaches is used to study the effects of climate warming on shallow lakes, including warming experiments at different scales, from individual-species responses to increased temperature to larger field scale experiments where temperature and associated climate factors are drivers (e.g. Feuchtmayr et al., 2009; Liboriussen et al., 2005; McKee et al., 2002a,b; Netten et al., 2010; Yvon-Durocher et al., 2011a), palaeolimnological surveys (e.g. Smol et al., 2005), long-term contemporary surveys (e.g. Adrian et al., 2006; Winder and Schindler, 2004) and mathematical models (e.g. Mooij et al., 2007; Trolle et al., 2011).

Another research approach to study the potential impacts of climate warming on ecosystems is the so-called SFTS (Pickett, 1989). The origins of this approach, although not meant to analyze biological responses to climate change, can be traced back to the end of the XVIII century with the studies of von Humboldt and Bonpland, who after latitudinal and altitudinal gradient studies in South America suggested that temperature and precipitation played a key role in the spatial distribution of vegetation

(Von Humboldt and Bonpland, 1805, 1807). It has been widely used to gauge community and ecosystem level responses to major environmental gradients in freshwaters, including pH (Layer et al., 2010) and nutrients (Rawcliffe et al., 2010), and many other systems (Olesen et al., 2010).

Within the current context of climate change, this approach is now used to identify key differences between systems located in different climates (slightly warmer or cooler) but otherwise similar (such as in area, trophic state or productivity level, etc.). Comparable ecosystems under different natural climatic conditions showing different ecosystem processes help elucidate the potential long-term consequences of changes in climate, as long-term data are often not available beyond a few years of sampling in most systems (but see Durance and Ormerod, 2007; Jeppesen et al., submitted for publication; Layer et al., 2011). Thus, this approach highlights the structure and interactions of communities arguably at, or close to, equilibrium conditions rather than the responses to short-term perturbations (i.e. experimental increase in temperature) (Woodward et al., 2010a,b). SFTS is a common method used in the attempt to understand change when it is not possible or desirable to wait for years or decades to detect changes (Jackson, 2011). The SFTS approach includes cross-comparison studies, latitudinal gradients (with mean temperature generally increasing towards lower latitudes) and altitudinal (with temperature generally increasing towards lowlands) gradients and has been applied to a series of environments, such as marine and inland ecosystems in Antarctica (e.g. Howard-Williams et al., 2006), Icelandic geothermal streams (Friberg et al., 2009; Woodward et al., 2010a), temperate and subtropical streams (Teixeira-de Mello et al., 2012) and shallow lakes in Europe (Gyllström et al., 2005; Moss et al., 2004; Stephen et al., 2004; and references herein) and South America (Kosten et al., 2009c, 2011a and references herein). SFTS represents one of the most widely used approaches in ecological climate change research, although its potentially weak aspects should be considered before application, including the need for a trait- or size-based approach so as to avoid the potentially confounding effects of geology, biogeography and land use, and the findings should be analyzed carefully since equilibrium or non-equilibrium conditions may be hard to distinguish (Woodward et al., 2010b). We argue that the SFTS approach provides one of the most plausible empirical evaluations for these theories using real-world data and, by the generalization of these theories, provides the potential for inductive advances and the proposition of new mechanisms.

Our aim with this work is primarily to review and summarize the changes in community traits (richness, biomass, density, body size) and in growth, reproduction and strength of trophic interactions in shallow lakes in relation to climate regimes, as shown by studies applying the SFTS approach, either in the form of cross-comparisons studies or investigations along latitudinal and altitudinal gradients and as shown by analyses of published metadata. Extraction of spatial trends that can be associated with climate signals may be done confidently when the sites chosen for comparison are similar as to trophic state, area and other relevant limnological characteristic (e.g. [Brucet et al., 2010, 2012, submitted for publication](#); [Meerhoff et al., 2007a,b](#); [Teixeira-de Mello et al., 2009](#)), or when many sites are sampled with a random distribution of trophic states (e.g. [Kosten et al., 2011b](#) and references herein), so that physicochemical gradients are nested within climate regions (e.g. [Declerck et al., 2005](#)). Thereby, we aimed to detect patterns of change that can be associated with differences in ambient temperature and thus to elucidate changes with warming.

We also analyzed metadata generated in different parts of the world in order to construct gradients for the traits or communities not covered by the current SFTS literature. We searched for shallow lake systems (maximum depth < 5 m, polymictic, or identified by the authors as such) and checked for records on characteristics such as area, trophic state, pH, salinity, turbidity and the presence of exotic species (if identified in the work). The introduction or extraction of species, particularly invertebrates and fish ([Villéger et al., 2011](#)), could blur latitudinal patterns of native fauna and should thus be considered in the analysis. We analyzed trends at different levels of organization, mostly focusing on community structure parameters and compared these findings with theoretical expectations basically from MTE (*sensu* [Brown et al., 2004](#)) and with findings from other research approaches. A significant challenge is to predict the effects of climate warming on lake community structure, since the effects of temperature on a particular community depend on the feedbacks with other communities that are also affected by warming and other aspects of global change ([Moss et al., 2011](#)). It is beyond the scope of this chapter to address all observed or potential climate-driven changes in freshwaters, as many have been reviewed recently for lakes (e.g. [Adrian et al., 2009](#); [Moss, 2010, 2011](#); [Moss et al., 2009](#)) or freshwaters in general ([Perkins et al., 2010](#); [Woodward et al., 2010b](#)). Instead, our target is to highlight the trends in climate-associated changes for community traits that may have profound implications for the functioning of these ecosystems and to identify areas that require further

research and experimental testing of mechanisms, while stressing the limitations and advantages of this research approach.

Being a comprehensive work, this chapter can be read either as a single monograph or in part by considering the self-contained sections, following the axis of community traits (e.g. richness, biomass, density, body size) or the axis of specific shallow lake assemblages (i.e. fishes, macroinvertebrates, zooplankton, macrophytes, phytoplankton, periphyton and bacterioplankton). The articles most frequently cited in the following subsections are briefly described when first mentioned and thereafter referred to for a summary of their main characteristics (Table 2).

Table 2 Summary of the most frequently quoted articles used in the Results section

References	Approach	Type of study	Latitude range	<i>n</i> lakes	Climate
Bécares et al. (2008)	LG	Mesocosm-exp	39–61°N	6	Med–Temp–Cold
Brucet et al. (2010)	CC	Semi exp lit.	38–56°N	8	Med–Temp
Brucet et al. (submitted for publication)	LG	Whole lake	28–69°N	1632	Med–Temp–Cold
Brucet et al. (2012)	CC	Semi exp lit.	38–56°N	8	Med–Temp
Danger et al. (2009)	CC	Mesocosm-exp	14–48°N	2	Trop–Temp
Declerck et al. (2005)	LG	Whole lake	36–56°N	98	Med–Temp–Cold
Griffiths (1997)	LG	Whole lake	29–74°N	474	Subtrop–Cold
Gyllström et al. (2005)	LG	Whole lake	38–68°N	81	Warm–Temp–Cold
Havens et al. (2009)	CC	Whole lake	29–49°N	2	Subtrop–Temp
Heino (2009)	Review		World wide		

Table 2 Summary of the most frequently quoted articles used in the Results section—cont'd

References	Approach	Type of study	Latitude range	<i>n</i> lakes	Climate
Jackson et al. (2007)	CC	Whole lake	51–56°N	252	Temp–Cold
Kosten et al. (2009c)	LG	Whole lake	5–55°S	83	Trop–Subtrop–Cold
Kosten et al. (2011a)	LG	Whole lake	5–55°S, 38–68°N	143	Trop–Cold
Kosten et al. (2011b)	LG	Whole lake	5–55°S	83	Trop–Subtrop–Cold
Lacerot (2010)	LG	Whole lake	5–55°S	83	Trop–Subtrop–Cold
Lewis (1996)	CC	Whole lake	0–70°N	26	Trop–Temp
Meerhoff et al. (2007a)	CC	Semi exp lit.	32.5°S–56°N	10	Subtrop–Temp
Meerhoff et al. (2007b)	CC	Semi exp lit.	32.5°S–56°N	10	Subtrop–Temp
Muylaert et al. (2010)	LG	Whole lake	36–56°N	98	Med–Temp–Cold
Moss et al. (2004)	LG	Mesocosm-exp	36–56°N	6	Med–Temp–Cold
Pinto-Coelho et al. (2005)	LG	Whole lake	19–20°S, 27–55°N	64	Temp–Trop
Schiaffino et al. (2011)	LG	Whole lake	45–63°S	45	Cold–SubPolar
Stephen et al. (2004)	LG	Mesocosm-exp	36–56°N	6	Med–Temp–Cold
Teixeira-de Mello et al. (2009)	CC	Semi exp lit.	32.5°S–56°N	19	Subtrop–Temp

Abbreviations indicate the approach and type of study: LG, latitudinal gradient; CC, cross-comparison; exp, experimental; lit, littoral (i.e. artificial plants were introduced). Broad climate regimes were assigned based on the information given by authors or based on geographic locations, abbreviations: Med, mediterranean; Subtrop, subtropical; Temp, temperate. References are ordered alphabetically.



2. FINDINGS IN SPACE-FOR-TIME STUDIES

2.1. Richness changes with climate

The strong latitudinal relationship of increasing diversity towards low latitudes is one of the most familiar and widespread patterns in ecology and has puzzled many generations of scientists, since Darwin and von Humboldt (e.g. [Allen and Gillooly, 2006](#); [Hillebrand, 2004](#)). Lakes are good model systems for the study of taxon richness in relation to environmental gradients, because they are well-delineated ecological entities in the landscape ([Dodson et al., 2000](#)), yet compared with terrestrial systems studies on diversity patterns in lakes are underrepresented ([Waide et al., 1999](#)), especially in shallow lakes (e.g. [Declerck et al., 2005](#); [Jeppesen et al., 2000](#); [Kruk et al., 2009](#); [Scheffer et al., 2006](#)). In this section, we will briefly cover the findings for shallow lakes, stressing that we do not attempt to explain the patterns in taxonomic richness solely (or mostly) by climate factors, due to the fundamental effects of evolutionary history and biogeography on this particular variable.

2.1.1 Fishes

At a global scale, a meta-analysis detected a decreasing latitudinal pattern in fish assemblage species richness in shallow lakes (linear regression, $n=69$, $r^2=0.88$, $p<0.0001$) (from [González-Bergonzoni et al., 2012](#)) ([Fig. 1A](#)). Greater fish biodiversity in warm climates has also been found in a worldwide latitudinal gradient investigation and in lowland versus high altitude lakes ([Amarasinghe and Welcomme, 2002](#)). This recurrent pattern is also consistent at latitudinal continental scales in Europe ([Brucet et al., submitted for publication](#)) and North America ([Griffiths, 1997](#); [Mandrak, 1995](#)) ([Table 2](#)). Particularly, the broad-scale patterns of fish species richness and diversity in European lakes were mainly explained by environmental temperature together with morphometric variables ([Brucet et al., submitted for publication](#); based on $n=1632$ lakes), while in a wide spatial range of Chinese lakes ($n=109$ lakes, [Zhao et al., 2006](#)), climatic variables (temperature and potential evapotranspiration) were among the most important explanatory variables. Specifically in shallow lakes, cross-comparison studies of littoral communities have found higher fish richness at the warmer locations in a subtropical–temperate investigation ([Meerhoff et al., 2007a](#); [Teixeira-de Mello et al., 2009](#)) and in a temperate versus cold climate comparison ([Jackson et al., 2007](#)).

In brackish lakes, the higher richness of fish at warmer locations seems, however, less pronounced, as found in a similar cross-comparison study of temperate and Mediterranean shallow lakes (Bruçet et al., 2010). Overall, there is an increase in fish richness from cold to warm climates, modulated by hydrology-related factors (such as drought intensity and salinity) that may promote lower relative richness in warm lakes with high hydrological stress (Jeppesen et al., 2010a; M. Beklioğlu et al., unpublished data).

The functional diversity of fish seems also to increase with decreasing latitude, as found in a review of North American freshwaters (Moss, 2010) and in cross-comparison studies (Teixeira-de Mello et al., 2009). In particular, the richness of omnivorous fish species follows a strong and negative worldwide latitudinal gradient in all aquatic ecosystem types, this being associated with the same pattern followed by taxonomic richness (González-Bergonzoni et al., 2012), not least in shallow lakes (Jeppesen et al., 2010a).

2.1.2 Macroinvertebrates

Studies on invertebrate diversity patterns in freshwaters are clearly unbalanced in that they mainly focus on aquatic insects and primarily in running waters. Overall, the few available studies suggest that differences in macroinvertebrate richness between climate regions are ambiguous and depend on taxonomic groups (Heino, 2009). At a global scale, the diversity of some invertebrate groups, such as the orders Ephemeroptera and Trichoptera, seems to show a negative relationship with latitude (Barber-James et al., 2008; de Moor and Ivanov, 2008; data not available for our meta-analysis), while other groups (e.g. Plecoptera, Decapoda, Simuliidae dipterans) do not show any clear trend (e.g. Plecoptera species richness, linear regression $r^2=0.001$, $p>0.05$; with data from Heino, 2009 and Palma and Figueroa, 2008) or seem to increase their diversity towards high latitudes, as in some studies in large biogeographic areas (Crandall and Buhay, 2008; McCreddie et al., 2005). At family level, a latitudinal gradient in assemblage composition of chironomids has revealed the important role of ambient temperature as a key factor for the distribution and relative abundance of different taxa (Larocque et al., 2006). Unfortunately, in most studies, the original data are not shown, the taxonomic resolution achieved differs from paper to paper, or data on lakes and streams are pooled, preventing us from conducting a formal meta-analysis of all published works.

In the few SFTS studies including only shallow lakes, plant-associated macroinvertebrates had much lower richness (at different taxonomic resolution, mostly order level) in the subtropics than in comparable temperate lakes (Meerhoff et al., 2007a), a climate pattern also found in brackish lakes in a similar cross-comparison study between Mediterranean and temperate regions (Brucet et al., 2012) (Fig. 1B, Table 2). Similarly, in a study comparing 16 tropical and 10 temperate lakes, Lewis (1996) found lower diversity and abundance of benthic invertebrates in the tropics, especially among Nematoda and Chironomidae (although data are not available for our meta-analysis). Higher risk of drought and large variations in salinity at the southernmost locations may reduce the species richness in arid or Mediterranean shallow lakes (Boix et al., 2008).

2.1.3 Zooplankton

In contrast to theoretical predictions, the literature shows evidence for a negative or no relationship between mesozooplankton (i.e. cladocerans and copepoda) richness and increasing temperature (in our review, decreasing latitude) (Fig. 1C). Cladoceran species richness exhibited no significant relationship with latitude (from 58.1° to 70.7°N) and altitude (from 0 to 1000 m) over a set of 336 Norwegian lakes, although high latitude and high altitude lakes had relatively low richness (Hessen et al., 2006): these differences were attributed to constraints imposed during colonization and to temperature, although the main explanatory factor was, in fact, productivity. Lewis (1996) reported a similar number of zooplankton species (in total and for cladocerans, copepods and rotifers), with slightly more cladoceran species in temperate than in tropical lakes. A decline in cladoceran and copepod species richness, in this case with increasing surface water temperature, was also observed with a data set of 1042 lake-years collected from 53 lakes in the northern hemisphere (Shurin et al., 2010; showing no latitudinal data and thus unavailable for our meta-analysis). Temperate shallow lakes often host a richer local assemblage of cladocerans (at genus level) than warm shallow lakes (Fig. 1C) as found in different studies (LSmeans $p < 0.001$ in Meerhoff et al., 2007b; no statistics reported in Pinto-Coelho et al., 2005; see details in Table 2). Typically, larger-bodied genera, such as *Daphnia*, *Sida*, *Eurycerus*, *Leptodora* and *Polyphemus*, were missing from both pelagic and littoral habitats in warm shallow lakes (Meerhoff et al., 2007b), which is in accordance with previous studies showing that large zooplankters were rare in tropical lakes (Fernando, 2002; Fernando et al., 1987; Lewis, 1996). In brackish lakes, however, cladoceran species richness was similar

in temperate and Mediterranean regions and salinity emerged as the key controlling factor (Brucet et al., 2009). Overall, local factors such as productivity, salinity and fish predation pressure, despite being factors likely ultimately related to climate often seem better proximate predictors of cladoceran richness than temperature itself.

2.1.4 Macrophytes

The few latitudinal gradient studies on macrophytes diversity are not specific to shallow lakes; they refer to freshwaters in general and often show contrasting results and unclear or no latitudinal pattern. A comparison between temperate and tropical freshwaters revealed higher macrophytes richness in temperate regions, a pattern attributed to the frequent dominance of a particular species within a given water body in the tropics (Crow, 1993). A Finnish study, however, reported a general decline in macrophyte richness in lakes towards the north (Linkola, 1933; reported in Rorslett, 1991), related to the duration of the ice-free period since short growing seasons may not only limit macrophyte growth but their distribution as well (Heino, 2001). Latitudinal changes in macrophyte richness have been recorded in the Great Lakes basin (Canada, USA), largely associated with latitudinal changes in geology and related factors such as sediment composition (Lougheed et al., 2001) rather than climate. Yet another study in North European lakes demonstrated no or only marginal latitudinal changes in macrophyte diversity (Rorslett, 1991), coinciding with the lack of latitudinal pattern in submerged macrophyte species richness in 83 South American shallow lakes (S. Kosten et al., unpublished data). Although regional and continental studies seemed to be inconclusive, a global analysis of the numbers and distribution of vascular macrophytes in freshwaters (not discriminating shallow lakes) showed that their diversity is highest in the tropics (Afrotropics, Neotropics and Orient) and lowest in the Nearctic, Palaeoartic and Australasia (Chambers et al., 2008), suggesting a marked divergence between alpha and gamma diversity.

2.1.5 Phytoplankton

Reports about phytoplankton composition and richness across latitudes, especially those including warm shallow lakes, are very scarce. Altitudinal gradient studies of phytoplankton richness are also limited (but see Wang et al., 2011). However, Stomp et al. (2011) analyzed patterns of species richness of freshwater phytoplankton in 540 lakes and reservoirs across the United States and found strong latitudinal (range: 26–51°N; linear regression: $r^2 = 0.16$,

$p < 0.001$; Fig. 1D), longitudinal and altitudinal gradients, overall showing an increase in richness with rising water temperature. A comparison between temperate and subtropical climates reported a higher richness of species comprising at least 5% of total biovolume in the subtropical lakes (Kruskal–Wallis test $H = 14.31$, $p < 0.002$, see Appendix C).

In terms of composition, warmer phytoplankton communities are often described as overlapping with temperate communities and little endemism (Lewis, 1996). Phytoplankton composition (considering both phylogenetic groups and dominant species) seemed to be affected more by local conditions and nutrient concentrations than by factors associated with latitude *per se*, as found in 27 lakes situated at cold-temperate (56–60°N) and sub-arctic (67–68°N) latitudes (Trifonova, 1998). Local factors such as the presence of submerged vegetation cover may also override latitudinal differences, as described in a European study revealing a negative association between phytoplankton richness and macrophyte cover in 98 shallow lakes (Declerck et al., 2005), although the opposite pattern was traced in subtropical shallow lakes (Kruk et al., 2009).

2.1.6 Periphyton

That periphyton, including all substrata-attached microalgae and associated bacteria and fungi, plays a fundamental role in shallow lake food webs has been demonstrated by several studies during the past decade (Liboriussen and Jeppesen, 2003; Vadeboncoeur et al., 2003, and references herein). However, we did not find any studies on the latitudinal variation on periphytic algae richness. To remedy this, we conducted a meta-analysis of patterns in species richness and biomass (the only community traits measured or shown for this assemblage, as far as we are aware) of periphyton algae over a latitudinal gradient ranging from 68°S to 83°N, including data from a total of 23 publications and 14 countries (see Appendix A for further information). In our meta-analysis, we detected a strong and significant linear decrease in periphyton algae richness with increasing latitude (linear regression: $r^2 = 0.755$, $p < 0.001$, Fig. 1E).

2.1.7 Bacterioplankton

Inclusion of bacteria in the SFTS literature is restricted to a few papers on investigations carried out along gradients in Europe (Declerck et al., 2005; Van der Gucht et al., 2006), Argentina and Antarctica (Schiaffino et al., 2011), and China (Wu et al., 2006). We therefore reviewed the literature and extracted crude data on community traits whenever available

from both gradient and single site studies ($n = 140$ lakes in 17 publications, see [Appendix B](#) for further information). We could not detect significant trends in bacterioplankton richness (usually estimated through molecular fingerprinting methods) along a latitudinal (or temperature) gradient from our dataset (linear regression $n = 43$, $r^2 = 0.008$, $p = 0.58$; [Fig. 1F](#)). Bacterioplankton richness is described in just a few studies, mostly conducted in temperate regions, potentially biasing our results. However, there is increasing evidence for the existence of an inverse relationship of richness with latitude for both continental ([Schiaffino et al., 2011](#)) and marine ([Fuhrman et al., 2008](#); [Pommier et al., 2007](#)) water bodies. Despite the underlying mechanisms still being under debate (e.g. species sorting, history), there are indications that the bacterial community composition in the water column (including shallow systems) changes along latitudinal gradients ([Schiaffino et al., 2011](#); [Sommaruga and Casamayor, 2009](#); [Van der Gucht et al., 2007](#); [Yannarell and Triplett, 2005](#)).

2.2. Climate effects on biomass

2.2.1 Fishes

Fish biomass seems to increase with decreasing latitude, or increasing ambient temperature ([Fig. 1G](#)). Pelagic fishes increased significantly in biomass in warm climates (as CPUE; $\text{g net}^{-1} \text{night}^{-1}$) in a series of shallow lakes of varying nutrient concentrations along a climate gradient in Europe (ANOVA $p < 0.04$, for log-transformed biomass, recalculated from [Gyllström et al., 2005](#)) ([Fig. 1G](#)). Also, cross-comparison studies have found a significantly higher fish biomass (as g m^{-2}) in warmer climates, both in freshwater (ANOVA $F_{1,100} = 40.7$, $p < 0.0001$, [Teixeira-de Mello et al., 2009](#)) and in brackish shallow lakes ([Brucet et al., 2010](#)) at similar TP concentrations in each set under comparison (although brackish lakes seem to have a lower biomass than freshwaters). In a European-scale study ([Brucet et al., submitted for publication](#)), fish biomass was mainly related to lake productivity, but when differences in productivity were taken into account in the analysis, altitude was negatively correlated with biomass.

2.2.2 Macroinvertebrates

Information on changes in the biomass of macroinvertebrates along a climate gradient is extremely scarce in general and almost absent in shallow lake studies: most research records abundance and identity at local scales, rather than biomass. Therefore, we were not able to identify or test a trend of change in macroinvertebrate biomass under different climates or latitudes.

2.2.3 Zooplankton

Although our analysis of published metadata (Table 1) showed no significant relationship, zooplankton biomass exhibits an apparent increase towards colder regions of the globe (Fig. 1I). A latitudinal gradient analysis of 81 lakes in Europe (38–68 °N) documented lower zooplankton biomass levels in the warmer lakes of Mediterranean Spain, with climate being the second most important predictor of zooplankton biomass after TP ($F=19.7$, $r^2=0.49$, $p<0.001$, $n=65$) (Gyllström et al., 2005). Lower zooplankton biomass at lower latitudes was also evident in an outdoor experimental study where nutrient enrichment and fish predation were analyzed in six European lakes (Vakkilainen et al., 2004). A comparison of zooplankton biomass between two eutrophic lakes, one in temperate Italy and the other in subtropical Florida (USA), documented higher biomass in the temperate lake (Havens et al., 2009). The small eutrophic tropical reservoirs in the study by Pinto-Coelho et al. (2005) were the exception to this pattern, with higher zooplankton biomass, particularly of Cladocera, in the warm region. However, the subtropical Florida lakes included in this same study had a lower cladoceran total biomass compared to the colder lakes. Mediterranean brackish lakes also exhibited a remarkably lower biomass of large zooplankton than similar temperate lakes (Brucet et al., 2010). In all cases, colder lakes had a significantly higher proportion of *Daphnia* than similar warmer systems (Brucet et al., 2010; Gyllström et al., 2005; Jackson et al., 2007; Meerhoff et al., 2007b). Trends of change in zooplankton biomass with altitude appear to be less clear than along latitudinal gradients, according to a study of subarctic ponds (Karlsson et al., 2005).

The majority of the articles analyzed address the effect of lake trophic state (i.e. nutrient concentrations) on zooplankton biomass, showing ambiguous relationships between both variables and climate. TP seems the most important predictor of zooplankton biomass and the biomass of large pelagic crustaceans, irrespective of the climatic region considered, as found along a European latitudinal gradient (Gyllström et al., 2005), a latitudinal gradient in Turkey (Beklioglu et al., in prep.) and in cross-comparisons (Jackson et al., 2007): all these studies indicated that increases in TP concentration have a positive effect on zooplankton biomass. However, the response of zooplankton, and particularly that of cladocerans, to increases in TP was more intense in tropical regions (measured as the slope in the regressions) (Pinto-Coelho et al., 2005). Interestingly, intermediate (subtropical) lakes in this study had the flattest slope in the relationship between zooplankton biomass and TP (Pinto-Coelho et al., 2005), as also found in subtropical Lake Apopka (Florida, USA) (Havens et al., 2009).

2.2.4 Macrophytes

Most evidence of effects of warming on macrophyte biomass comes from interannual comparisons rather than from SFTS studies, preventing us from assessing potential latitudinal trends. Early season warm temperatures seem to favour a strong increase in whole-lake submerged macrophyte biomass, as recorded in five lakes in the Eastern Townships of Quebec, Canada, despite increased turbidity in such period (Rooney and Kalf, 2000). However, this temperature effect seems to be overruled by the strong influence of underwater irradiance, which in turn is most often impacted by lake trophic state. In an analysis of data from 139 lakes between latitudes 46° and 69° , underwater irradiance and not latitude explained a large part of the variance in submerged macrophyte biomass (Duarte et al., 1986). For emergent macrophytes, however, lake morphometry is an important factor determining plant biomass; however, no significant positive relationship between the biomass per area colonized and latitude has been found (Duarte et al., 1986).

2.2.5 Phytoplankton

Most studies deal with biomass of phytoplankton in terms of chlorophyll-a (Chl-a) concentrations (indirect estimate of biomass), and, to a lower extent, biovolume (directly related to biomass). We analyzed published data from a large amount of shallow lakes in different climate zones (Tables 1 and 3) and discovered neither linear trends with latitude nor clear differences between climatic regions, except for higher total biomass (as Chl-a) in the tropics and temperate systems, followed by subtropical and subpolar regions (Fig. 1J; $n=90$ lakes, Kruskal–Wallis: $H=205$, $p<0.001$). Larger biomass of phytoplankton in the tropics has been reported before (Danger et al., 2009; Huszar et al., 2006; Lewis, 1996, 2000). Kruk et al. (2010) found that the largest values of Chl-a occurred in subtropical lakes ($n=40$) and the lowest in tropical lakes ($n=42$, over a total of 210 shallow lakes), while Kosten et al. (2011b) recorded a decrease in phytoplankton Chl-a from subpolar regions towards the tropics in South America (83 lakes in total). On the other hand, in a study of 143 shallow lakes along a latitudinal transect ranging from subarctic Europe to southern South America, lakes in warmer climates did not exhibit an overall higher phytoplankton biomass, although cyanobacteria biomass seemed favoured (Kosten et al., 2011a). Along a latitudinal gradient in Europe, both high and low Chl-a concentrations were found in southern and northern lakes (Nøges et al., 2003), while higher Chl-a

Table 3 Relationship between phytoplankton biomass (as chlorophyll-a, Chl-a, $\mu\text{g L}^{-1}$) and total phosphorus (TP, $\mu\text{g L}^{-1}$) in shallow lakes under different climate regimes, as described in published studies

References	Location	Climate	n	Model	R ²	Slope
Antoniades et al. (2003a) *	Canadian Arctic: Ellesmere Island	Polar	31	$\gamma=0.16x-0.22$	0.36	0.16
Antoniades et al. (2003a) *	Canadian Arctic: Prince Patrick Island	Polar	29	$\gamma=0.007x-0.40$	0.00	0.01
Antoniades et al. (2003b) *	Canadian Arctic: Ellef Ringnes Island	Polar	24	$\gamma=0.75x-1.58$	0.36	0.75
Flanagan et al. (2003)	Canada	Cold	113	$\gamma=0.33x-0.42$	0.07	0.33
Kosten et al. (2011b)	Argentina	Cold	11		0.94	
Mazumder and Havens (1998)	North America, Europe	Cold	126	$\gamma=(0.87 \pm 0.05)x + 0.60 \pm 0.07$	0.73	0.87
Ogbebeo et al. (2009) *	Canada	Cold (flooded Arctic-tundra)	10	$\gamma=0.22x+0.25$	0.38	0.22
Ogbebeo et al. (2009) *	Canada	Cold (forest-tundra)	6	$\gamma=0.94x-0.19$	0.84	0.94
Ogbebeo et al. (2009) *	Canada	Cold (non-flooded Arctic tundra)	9	$\gamma=0.50x+0.07$	0.39	0.50
Flanagan et al. (2003)	Canada	Temperate	316	$\gamma=0.92x-0.38$	0.28	0.92
Jackson et al. (2007)	Canadian prairie	Cold	30	$\gamma=0.86x+1.72$		0.86
Jackson et al. (2007)	Denmark	Temperate	222	$\gamma=0.82x+2.35$		0.82
Kruk et al. (2011) **	The Netherlands	Temperate	95	$\gamma=0.91x-0.33$	0.34	0.91
Meerhoff et al. (2007a,b) **	Denmark	Temperate	9	$\gamma=1.64x-1.50$	0.70	1.64

Prairie et al. (1989)	North America, Europe	Temperate	133		0.69 0.87
Mazumder (1994)	North America, Europe	Temperate LH	126	$\gamma = (0.87 \pm 0.05)$ $x + 0.60 \pm 0.07$	0.73 0.87
Mazumder and Havens (1998)	North America, Europe	Temperate SH	235	$\gamma = -(0.97 \pm 0.02)$ $x + 0.21 \pm 0.03$	0.87 0.97
Mazumder and Havens (1998)	Florida, USA	Temperate SH and LH	361	$\gamma = -(0.94 \pm 0.03)$ $x + 0.35 \pm 0.05$	0.71 0.94
Kosten et al. (2011b)	Brazil, Uruguay, Argentina	Temperate–subtropical	34		0.62
Brown et al. (2000)		Subtropical	359		0.67 0.42
Wang et al. (2008)	China	Subtropical	45	$\gamma = 1.04x - 0.97$	0.80 1.04
Kruk et al. (2009)**	Uruguay	Subtropical	18	$\gamma = 0.25x + 0.28$	0.05 0.25
Kruk et al. (2011)**	Uruguay	Subtropical	12	$\gamma = -0.12x + 0.99$	0.00 -0.12
Meerhoff et al. (2007a,b)**	Uruguay	Subtropical	10	$\gamma = 0.71x - 0.59$	0.34 0.71
Mazumder and Havens (1998)	Florida, USA	Subtropical SH	59	$\gamma = -(1.06 \pm 0.07)$ $x + 0.36 \pm 0.09$	0.79 1.06
Huszar et al. (2006)	South America, Africa	Tropical–subtropical	192	$\gamma = 0.70x - 0.15$	0.42 0.70
Kosten et al. (2011b)	Brazil	Tropical	38		0.20
Parinet et al. (2004)	Ivory Coast	Tropical	9	$\gamma = 0.93x + 1.66$	0.32 0.93

The explained variance (R^2), slope and linear models of the relationship between \log_{10} Chl-a (y) and \log_{10} TP (x) in the water column of polar, cold, temperate, subtropical and tropical shallow lakes, indicating the respective references, location, and number of cases (n) are displayed. LH, lakes with large herbivorous zooplankton; SH, lakes with small herbivorous zooplankton, as classified by the authors. * calculated from data available, ** data obtained in the cited references provided by authors. References are ordered by increasing temperature of the region of the data.

concentrations were found in the southern lakes along a latitudinal gradient in Turkey (M. Beklioğlu et al., unpublished data).

Interestingly, the other proxy for total phytoplankton biomass, that is, biovolume, often shows a different pattern to that of Chl-a. In a comparison of a large data set from subtropical and temperate regions, greater total biovolume values appeared in the subtropics than in similar temperate lakes over the same wide gradient in nutrient concentration (Kruskal–Wallis test $H=11.34$, $p < 0.001$, $n = 650$, see [Appendix C](#)). Some works argue the tropics to have a higher frequency of cyanobacteria (Paerl and Huisman, 2009). In the subtropical–temperate lakes comparison (see [Appendix C](#) for analysis information), cyanobacteria and Dinophyceae had a significantly higher relative biovolume in the subtropics, whereas Chlorophyceae, Cryptophyceae, Euglenophyceae, Zygnematophyceae, Chrysophyceae and Xanthophyceae had a higher relative biovolume in the temperate lakes (Kruskal–Wallis tests, [Fig. 2](#)). Mesocosm experiments conducted in different European climate regions have also suggested that warmer climates may increase the relative contribution of cyanobacteria to total phytoplankton biovolume in shallow lakes (Stephen et al., 2004; Van de Bund et al., 2004; [Table 2](#)) as also found in a recent mesocosm warming experiment in southern England (Yvon-Durocher et al., 2011a,b). In contrast, other mesocosm experiments

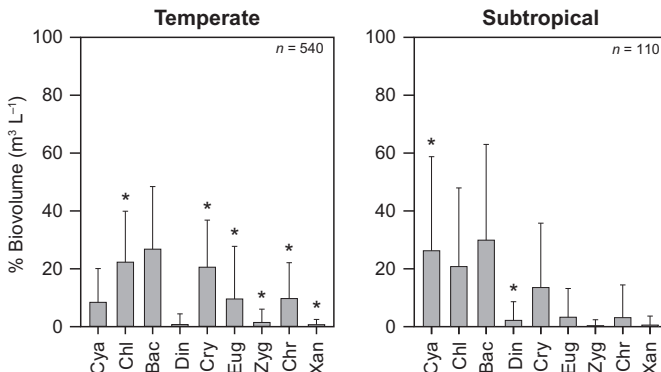


Figure 2 Relative biovolume (%) of phylogenetic classes of phytoplankton in shallow lakes located in temperate ($n = 540$) and subtropical ($n = 110$) climates. Abbreviations: Cyanobacteria (Cya), Chlorophyceae (Chl), Bacillariophyceae (Bac), Dinophyceae (Din), Cryptophyceae (Cry), Euglenophyceae (Eug), Zygnematophyceae (Zyg), Chrysophyceae (Chr) and Xanthophyceae (Xan). Error bars correspond to 1 standard error and * indicates classes with significantly higher biovolume according to the Kruskal–Wallis test ($p < 0.05$). Data were extracted from [Kruk et al. \(2011\)](#), see [Appendix C](#) for a description of methodology.

conducted in tropical and temperate shallow lakes have not revealed any effect on cyanobacteria or any drastic changes in phytoplankton community structure (Danger et al., 2009).

As the relationship between Chl-a and nutrients is directly associated with the predictability of phytoplankton biomass, it is important to analyze its variability and strength under different climatic conditions. The relationship between phytoplankton Chl-a concentrations and nutrients (typically TP) along latitudinal gradients is one of the most commonly reported in the literature of gradients (Table 3). An increase in phytoplankton biomass with increases in TP occurs across climates (positive slope in the regressions) (Fig. 3). However, we found no clear patterns of change in the slope or intercepts across climates (Table 3), even with opposite results being evident in studies at the same latitudinal location (Brown et al., 2000; Gyllström et al., 2005; Huszar et al., 2006; Jeppesen et al., 2007; Muylaert et al., 2010). Although differences were not significant, high variability in the importance of nutrients for phytoplankton biomass (indicated by a wide range of r^2 values in the regressions) emerges in subtropical and also in cold regions (Huszar et al., 2006; Kosten et al., 2009b,c) (Fig. 3), likely suggesting that factors other than TP (or

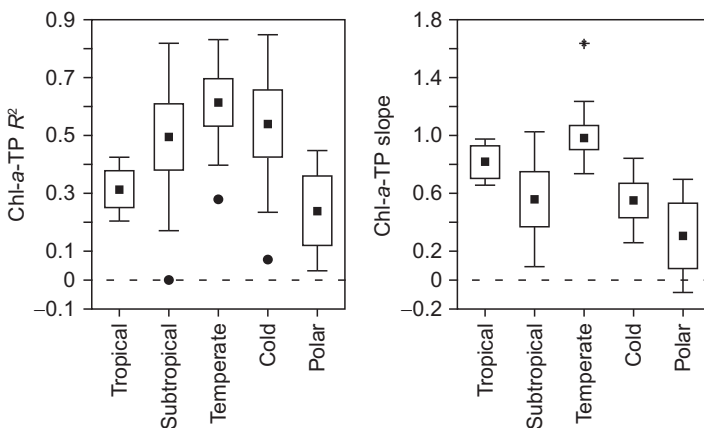


Figure 3 Relationship between phytoplankton biomass and nutrients along a climate gradient, showing the explained variance (R^2) and slope in the linear regressions between total phosphorus (TP) and phytoplankton chlorophyll-a (Chl-a) in shallow lakes from tropical ($n=3$), subtropical ($n=8$), temperate ($n=9$), cold ($n=7$) and polar ($n=3$) regions, according to published works applying the space-for-time approach. Box-plots show mean, mean \pm SE, mean \pm SD and extreme values. Respective references and full regression models are shown in Tables 1 and 3.

nutrients) explain a large proportion of the phytoplankton biomass variation. Besides, the amount of Chl-*a* per unit of TP may be higher in temperate and tropical lakes than in other climatic regions (marginally significant differences, Kruskal–Wallis test, $p=0.07$; Fig. 3).

2.2.6 Periphyton

Only a few published works applying the SFTS approach have included periphyton in their target communities, and those that have, exclusively focus on biomass (Bécares et al., 2008; Brucet et al., 2010, 2012; Meerhoff et al., 2007a). In our meta-analysis, we found a significant and positive linear response of periphyton algae biomass with increasing latitude ($n=16$ publications, $r^2=0.378$, $p<0.01$) (Fig. 1K). This pattern is consistent with findings in other studies based on both field sampling campaigns in temperate, subarctic and Antarctic regions (Hansson, 1992), mesocosm experiments along a latitudinal gradient (Bécares et al., 2008) and cross-comparisons (Brucet et al., 2012; Meerhoff et al., 2007a). Nonetheless, the effects of latitude or temperature might be very complex, because the periphyton response curve to increasing nutrients shows saturation at different points depending on climate regions and is clearly higher in the colder regions of northern Europe than in the Mediterranean zone (Bécares et al., 2008).

2.2.7 Bacterioplankton

In our constructed database, we could not detect any significant relationship between bacterioplankton biomass and latitude, possibly due to the relatively few geographic locations included (despite the fairly high number of systems, $n=33$ lakes, Fig. 1L).

2.3. Climate effects on density

Abundance of individuals is typically measured, but not always reported, for several communities in shallow lakes, particularly animal or single-cell communities. Bacterioplankton represent an exception here, since most works provide numerical counts of abundance rather than estimations of biomass.

2.3.1 Fishes

Published SFTS literature reporting absolute fish density data is rare, and, typically, density and biomass proxies such as CPUE are shown. However, the scarce findings support the trend of higher fish densities towards warmer climates, over a wide range in nutrient concentrations and system area. The

evidence comes from cross-comparison studies in warm and temperate climates, both in freshwater (Teixeira-de Mello et al., 2009) and in brackish (Brucet et al., 2010) shallow lakes (Fig. 1), and from an extensive study including both latitudinal and altitudinal gradients (Brucet et al., submitted for publication). A comparison of fish abundance in cold Canadian lakes to comparatively warmer Danish shallow lakes showed greater abundances in Denmark, as a likely consequence of greater winter mortality in Canada (Jackson et al., 2007). On the other hand, drought-induced fish mortality can also explain the lower fish densities found in southern Mediterranean lakes (M. Beklioglu et al., unpublished data). All these works, despite showing opposite results to general theoretical expectations based primarily on metabolism (Brown et al., 2004; Fig. 1M), discard potential effects of trophic state on the observed patterns, as the cross-comparison studies included lakes paired in terms of nutrient levels and the large spatial gradient study also covered the same gradient in TP for the different locations.

2.3.2 Macroinvertebrates

We found no latitudinal gradient study in shallow lakes including macroinvertebrates, and thus our climate-related data come only from cross-comparison studies. In contrast to fishes, but fitting predictions, the relatively few available data indicate greater densities at colder locations (Fig. 1N). Cross-comparison studies, both in freshwater (Meerhoff et al., 2007a) and in brackish (Brucet et al., 2012) shallow lakes, traced up to eight times lower densities of plant-associated macroinvertebrates in the warmer systems.

2.3.3 Zooplankton

Our meta-analysis of the SFTS studies showed a significant trend of lower microcrustacean abundance towards lower latitudes (linear regression: $r^2=0.16$, $p<0.05$, $n=25$, Fig. 1O), although variability in density patterns was high. The cross-comparison studies detected overall higher cladoceran densities in colder climates, both in freshwater (Meerhoff et al., 2007b) and in brackish shallow lakes (Brucet et al., 2010). However, temperature *per se* did not explain the low abundances of zooplankton in warm lakes in the latter, since low abundances also occurred in cold lakes with high fish densities (Brucet et al., 2010), suggesting a top-down food web effect. In contrast, both cladocerans and copepods were more abundant in the warmer lakes in a comparative study of diel migration patterns of microcrustaceans in similar shallow lakes between latitudes 39° and 61°N in Europe (Hansson

et al., 2007). Both the highest and lowest crustacean densities occurred in the warmer lakes in a study comparing several lakes and reservoirs of different depth in temperate, subtropical and tropical countries (Pinto-Coelho et al., 2005). Reservoirs might exhibit different patterns than true lakes, since deeper sections are common, which might offer a hypolimnion refuge to large zooplankton, thereby masking the otherwise typical patterns in warm shallow lakes. Calanoid copepods, however, were more abundant in the colder lakes (Pinto-Coelho et al., 2005). The patterns followed by other zooplankton groups, such as rotifers, remain unexplained due to the scarce number of works including this fraction. Typically, however, rotifers seem the dominant group in warm lakes (Brucet et al., 2010; Fernando, 2002).

2.3.4 Macrophytes

Different variables that may be used as proxies for density are regularly reported in shallow lakes, such as the percent area covered and the volume of the lake taken up by submerged macrophytes. All these variables are strongly influenced by the underwater light conditions and therefore by lake trophic state but are influenced by temperature as well. High coverage of submerged macrophytes has been related to high spring temperatures in temperate systems (Rooney and Kalf, 2000; Scheffer et al., 1992). In contrast, both space-for-time (Duarte et al., 1986; Kosten et al., 2009a) and inter-annual comparative studies (Hargeby et al., 2004) found that cold winters—typically quantified by the cumulative number of frost—days generally lead to a higher coverage of submerged macrophytes. Even after accounting for the effect of underwater light conditions, however, the variance in coverage among lakes located at similar latitudes remains high (Kosten et al., 2009a), again suggesting action of different processes at a local scale. This likely explains why no latitudinal gradient in submerged macrophyte coverage emerged from the literature, even when variations in lake nutrient status were taken into account, as done for 83 shallow lakes along a latitudinal study in South America (S. Kosten et al., unpublished data) (Fig. 4). The great subjectivity and variety associated with plant cover estimation methods (typically visual, for a brief overview of different methods, see Kosten et al., 2009a) may also prevent the identification of clear patterns.

2.3.5 Phytoplankton

We found only one study reporting microalgal density values in connection to environmental gradients and particularly with latitude (Søballe and Kimmel, 1987). These authors found a negative relationship between algal

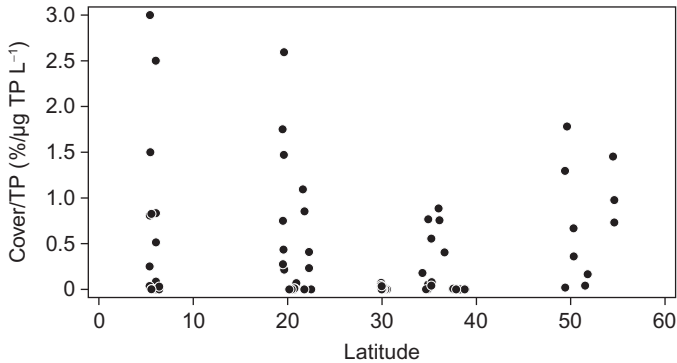


Figure 4 Coverage (%) of submerged macrophytes corrected by the lake total phosphorus concentration in 83 shallow lakes along a latitudinal gradient in South America. S. Kosten et al. (unpublished data), see [Kosten et al. \(2009a\)](#) for details on methodology.

counts (log-transformed) and latitude (correlation $r = -0.45$, $p < 0.01$) for natural lakes all over United States. Due to the lack of raw data and the deeper nature of the lakes including in this study (ca. 8 m *versus* ca. 5 m in our review), we could not include this finding in our analysis ([Fig. 1P](#)).

2.3.6 Bacterioplankton

In our constructed database ([Appendix B](#)), we found a significant increase in bacterial abundance in the water column with decreasing latitude (linear regression: $n = 133$, $r^2 = 0.08$, $p = 0.001$; [Fig. 1R](#)), which is in agreement with a previous latitudinal gradient study specifically including shallow lakes ([Schiaffino et al., 2011](#)). This correlation was also clear when we grouped the lakes according to climatic zones (which do not necessarily overlap with latitude), following the revision by [Leemans and Cramer \(1991\)](#) of the Köppen climate system (1936) ([Fig. 5](#)). We attempted to identify the main factors behind the emerging pattern by applying Spearman's correlations and stepwise multiple regressions with the following parameters: latitude, altitude, lake area, water temperature, conductivity, TP, TN, phytoplankton Chl-a, and dissolved organic carbon (DOC) (see [Appendix B](#) for a summary of results). In particular, the concentration of DOC is a major controlling factor of bacterial production in shallow polar lakes ([Karlsson et al., 2001](#)). Increasing temperatures may stimulate photosynthate extracellular release, thus indirectly contributing to increase DOC concentrations ([Morán et al., 2006](#)). However, in our analysis, temperature and, secondly, Chl-a were the two factors explaining most of the latitudinal variation in

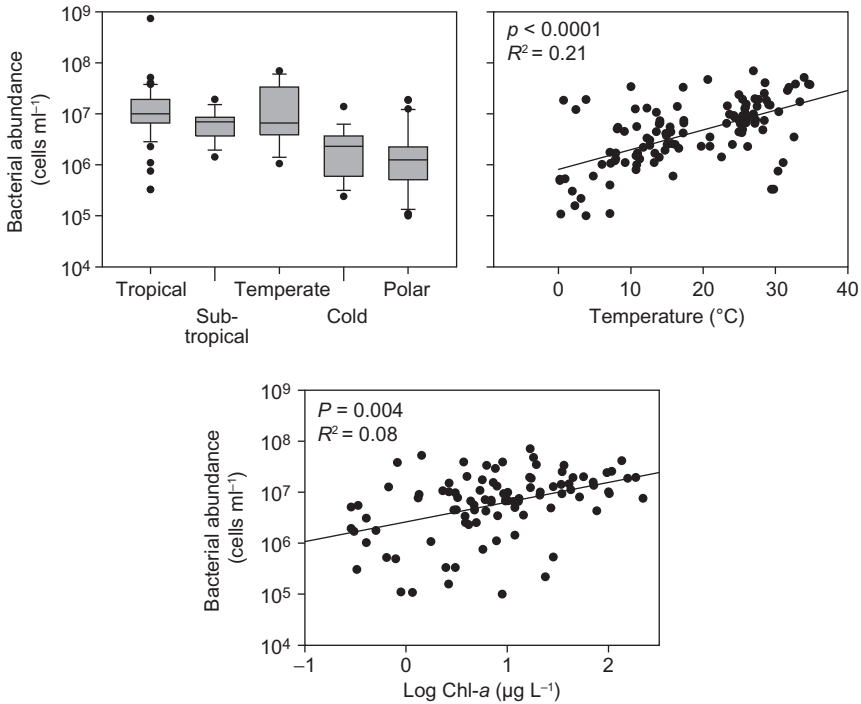


Figure 5 Density of bacterioplankton in lakes along a climate gradient as found in a meta-analysis, showing densities in different climate regions and the relationship between bacterioplankton and temperature and bacterioplankton and phytoplankton biomass (measured as Chl-a). Box-plots show median values (lines), while lower and upper boundaries depict the 25th and 75th percentiles, respectively; whiskers indicate the 10th and 90th percentiles and dots represent outliers. For both regressions, explained variance (R^2) and probability (p) are shown. Respective references are shown in [Appendix B](#).

bacterioplankton abundance (adj. $r^2 = 0.66$, $p = 0.005$) ([Fig. 5](#)). Latitude and DOC, however, co-varied strongly with temperature ($r = -0.83$, $p < 0.0001$, $n = 112$; and $r = -0.94$, $p < 0.0001$, $n = 26$, respectively) and were, therefore, not included in the regression model due to multicollinearity.

Our regression model agrees with results obtained by [White et al. \(1991\)](#), who found strong dependence of bacterial growth rate on temperature and also that a substantial portion of the residual variation was explained by phytoplankton biomass in a broad range of aquatic systems, although no shallow lakes were included in their investigation.

2.4. Climate effects on body size and size structure

The reduction in body size of aquatic organisms seems to be one of the clearest responses to environmental warming, and it has even been described as the third universal response to warming together with changes in phenology and distribution (Daufresne et al., 2009; Gardner et al., 2011). In this review, we sought to test for general trends in body size and community size structure across the different trophic levels that typically constitute shallow lake food webs.

2.4.1 Fishes

Mean body size of fish at the assemblage level tends to decrease with increasing temperature (Fig. 1S), as shown in several latitudinal and cross-comparison studies of lake fish assemblages (e.g. Griffiths, 1997; Meerhoff et al., 2007a; Teixeira-de Mello et al., 2009). Littoral subtropical fishes were significantly smaller than their temperate counterparts in cross-comparison studies (LSmeans $p < 0.0001$ in Meerhoff et al., 2007a; ANOVA $F_{1,94} = 32.5$ $p < 0.0001$ in Teixeira-de Mello et al., 2009). A similar climate pattern occurred in the brackish shallow lakes, although the differences were not statistically significant, most likely due to an overriding effect of salinity over temperature (Brucet et al., 2010). An extensive fish analysis of North American lake fish showed that the proportion of large fish species (> 20 cm TL) within the assemblage increased with latitude and that small fish species (< 20 cm TL) were more common at lower latitudes (Griffiths, 1997). The same trends of an increase in the relative proportion of small fishes (< 10 cm standard length) at lower latitudes occurred along a latitudinal gradient in South America (Lacerot, 2010), and in a review of lake studies from 11 European countries (Brucet et al., submitted for publication). Fish size has been mainly related to altitude, air temperature and amplitude of temperature, whereas trophic state was of little importance in a large study of European lakes (Brucet et al., submitted for publication). Lack of crude data on body sizes (instead of proportions of size classes) prevents us from incorporating several of these studies in our analysis, but the findings support the pattern of a reduction in the mean body size of fish communities with decreasing latitude and increasing temperature.

The body size difference associated with latitude seems clear at the assemblage or community level, whereas the pattern at population level is more ambiguous (Jeppesen et al., 2010a), probably as a result of contingent

effects of species-specific biology and biotic interactions. Typical temperate fish species, such as roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*), show different responses with latitude; perch having the strongest decrease in mean body size with decreasing latitude or increasing temperature, while the mean body size of roach does not exhibit any such changes (Jeppesen et al., 2010a).

2.4.2 Macroinvertebrates

Overall, data on changes in the body size of macroinvertebrates along spatial gradients or changing temperatures are still too scarce and fragmented to permit the drawing of firm conclusions (Fig. 1T), highlighting another important research gap that merits further work.

Using species lists and occurrence data on diving beetles (Coleoptera, Dysticidae) in more than 400 Canadian lakes and ponds, Vamosi et al. (2007) found that the proportion of large species tended to increase at higher latitudes (along a narrow gradient: 49–55°N). Along an elevation gradient, both the proportion of large species and total species richness peaked at mid-altitudes, being exceptionally low at high altitudes (above 2000 m). The authors attributed this to oxygen limitation and low productivity at high altitude locations, overriding the expected temperature effect for body sizes and species richness. In the cross-comparison study of subtropical and temperate shallow lakes, the taxa occurring in the former were characterized by either very small or very large body sizes (such as shrimps, applesnails, crayfish, etc.), whereas the taxa in the set of temperate lakes covered a far wider range in body sizes (Meerhoff et al., 2007a).

2.4.3 Zooplankton

A comprehensive review has shown that cladoceran mean body size decreases towards lower latitudes ($n = 1100$ water bodies, latitudinal gradient between 81°N and 77°S, Gillooly and Dodson, 2000) (Fig. 1U), a pattern mostly driven by differences in body size of individual species of three large and dominant pelagic genera (*Daphnia*, *Ceriodaphnia* and *Diaphanosoma*). In South America, zooplankton mean body size (length), as well as the body size of different taxonomic and functional groups, decreased from temperate to tropical lakes (Lacerot, 2010). This pattern was generated by large differences in the body length of pelagic cladocerans, particularly *Ceriodaphnia*, *Moina*, *Daphnia* and *Diaphanosoma* genera (Lacerot, 2010). Along a latitudinal gradient in Turkey, the mean body size of Cladocera was larger in the

higher latitude lakes (M.Beklioğlu et al., unpublished data). In contrast, despite large differences in biomass, cladoceran zooplankton body size did not vary along climate regions in the European latitudinal gradient analysis by Gyllström et al. (2005), although the large-bodied *Daphnia* spp. were scarce in the warmer lakes. Lack of large pelagic or littoral genera occurred in freshwater subtropical lakes, whereas these taxa were common in similar temperate lakes (Meerhoff et al., 2007b). Similarly, in European brackish shallow lakes, the normalized biomass size spectra of zooplankton exhibited a unimodal pattern with dominance of rotifers in the Mediterranean lakes, whereas cold Danish lakes showed a bimodal distribution, with the second dome corresponding to cladoceran and copepod species (Brucet et al., 2010) (Fig. 6).

2.4.4 Macrophytes

Being a variable most often ignored in the plant community, we found no data reporting changes in plant body size or data allowing us to indirectly estimate body size (e.g. ratio biomass:cover) in the SFTS or in geographically isolated literature.

2.4.5 Phytoplankton

Phytoplankton body size variation with latitude is seldom reported in empirical literature, despite the fact that cells and colonies are routinely measured to estimate biovolume, one of the most typical proxies for phytoplankton biomass (Kruk et al., 2010). Although individual sizes are not available in the literature to construct a latitudinal gradient (Fig. 1V), we compared the biovolume distribution of different size classes of phytoplankton species in shallow lakes in two contrasting climates (subtropical Uruguay and temperate The Netherlands, see Appendix C for a description of the methodology). We found no significant differences in the biovolume of the different size classes, despite a higher total biovolume of phytoplankton in the subtropical lakes (see Biomass). In mesocosm experiments studying the effects of fish addition and nutrient loading on shallow lakes distributed from Finland to southern Spain (Moss et al., 2004), fish shifted the phytoplankton assemblage composition towards smaller phytoplankton, especially chlorophytes and cyanobacteria, presumably by removing large-bodied grazers; however, this effect was not affected by latitude (Moss et al., 2004; Stephen et al., 2004).

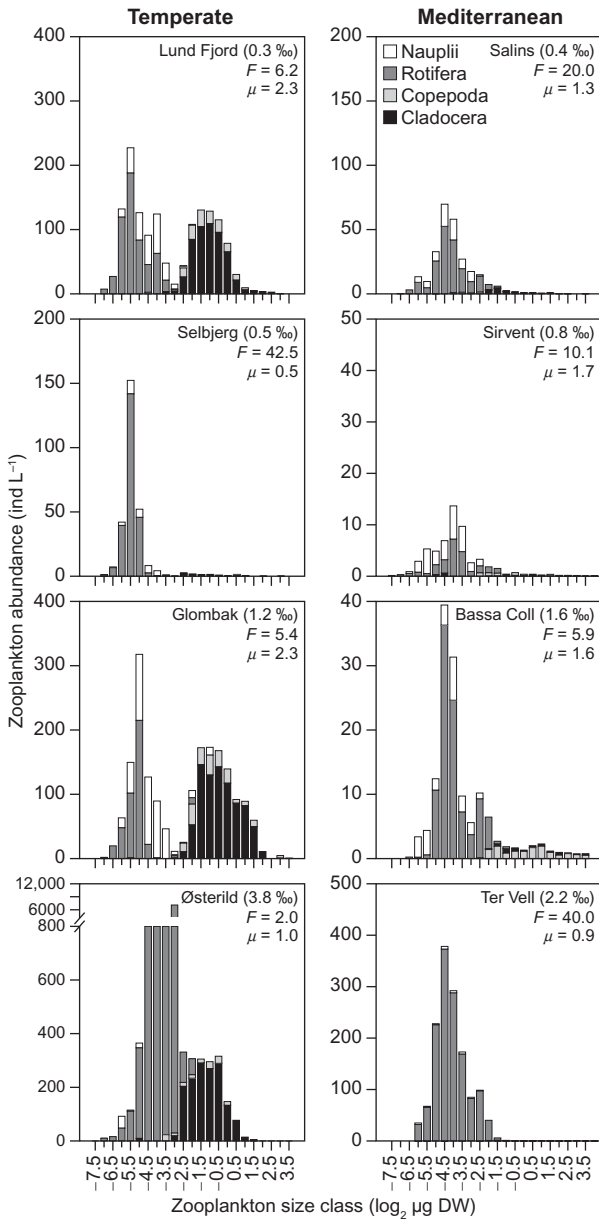


Figure 6 Zooplankton size distribution in temperate (left column) and Mediterranean (right column) brackish shallow lakes, showing the abundance contribution of nauplii, Rotifera, Copepoda and Cladocera (each group shown with a different grey tone). Each panel represents a lake, indicating the respective salinity (‰), mean zooplankton size diversity (μ) and mean fish density (F , ind m⁻²). Modified from [Bruce et al. \(2010\)](#).

2.4.6 *Periphyton*

Neither in the SFTS studies nor in the geographically isolated studies used in our previous meta-analysis have we found published data on periphyton size structure in shallow lakes, preventing us from constructing our own gradient.

2.4.7 *Bacterioplankton*

We found a relatively large number of lakes with data available on body size (cell biovolume) of bacterioplankton ($n = 48$), allowing us to construct a database for the meta-analysis. However, all are derived from two extreme geographic locations and showed strong variability, and no trend in body size could be associated with latitude (Fig. 1X). Nevertheless, a wide range of variation for the tropical locations was observed, indicating either that this trait in bacterioplankton may be more linked to local conditions than to latitude or that variations in this trait are constrained along latitudinal gradients.

2.5. Climate effects on reproduction and growth

2.5.1 *Fishes*

Animals with indeterminate growth experience a life history trade-off in resource allocation between onset and duration of reproduction, fecundity, growth and survival (Gunderson and Dygert, 1988; Heino and Kaitala, 1999). Three primary life history strategies representing essential trade-offs among those demographic parameters, namely, opportunistic, equilibrium and periodic, have been proposed for freshwater fishes (see Winemiller and Rose, 1992) and interpreted as being adaptive to the relative predictability and variability of the environment (Winemiller, 2005).

Most of the large-scale studies of intraspecific variation in the life history traits of fishes focus on single species, grouping populations from lentic and lotic habitats (e.g. Heibo et al., 2005; Lappalainen and Tarkan, 2007; Lappalainen et al., 2003, 2008), with very few studies on life history traits of whole fish assemblages at a continental level (Mims et al., 2010). Different hydrological characteristics of rivers and lakes could potentially influence life history traits in a variety of ways (Lytle and Poff, 2003); however, the work by Blanck and Lamouroux (2007) noted only a slight effect of habitat type on life history traits within European freshwater fishes. In shallow lakes, responses of life history traits of fishes to warming, among other responses, have been reviewed by Jeppesen et al. (2010a). With variations among communities and species-specific responses, empirical evidence indicates that higher-latitude populations grow more slowly, mature later and have longer life and reproductive spans and a greater maximal size than populations at lower

latitudes or higher temperatures (Jeppesen et al., 2010a). Reproductive seasons are limited to periods of the year when limiting physical factors, typically temperature, permit the survival of offspring (Conover, 1992). In temperate systems, most freshwater fish species have seasonal reproduction, with peaks in spring or summer (Wootton, 1984). Breeding and growing seasons, growth rate, number of reproductive events per year and annual reproductive investment are often negatively related to latitude (Fig. 7, Table 4). Smaller, short-lived species with generally opportunistic strategies are more abundant at low latitudes, whereas large, longer-lived species with generally periodic or equilibrium strategies predominate at high latitudes, according to a very comprehensive study of North American fishes (Mims et al., 2010). The general pattern of variation in life history traits with latitude (Fig. 7, Table 4) seems to be common for fishes of inland waters (Conover, 1992; Gotelli and Pyron, 1991; Hubbs, 1985; Morin et al., 1982;

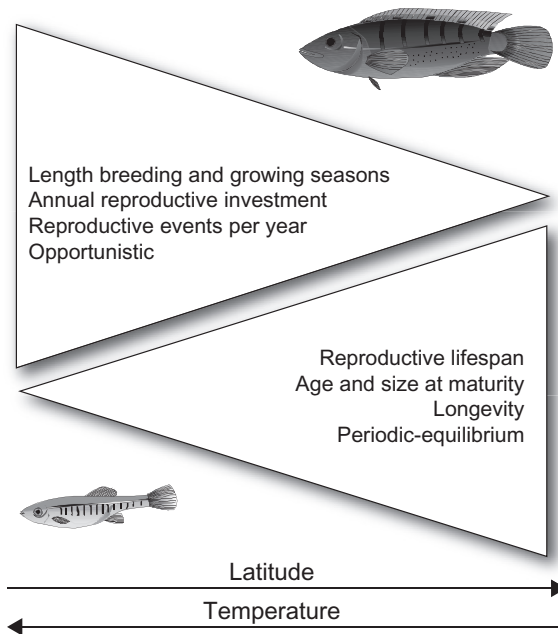


Figure 7 Expected changes in the main life history traits of fish along a temperature and latitudinal gradient based on our review of literature from inland water systems. With increases in temperature, longer breeding and growing seasons, annual reproductive investment and more reproduction events are predicted; a longer reproductive lifespan, greater age and size at maturity and longevity being negatively related with temperature. See text for details and supporting literature.

Table 4 Evidence of variation in reproductive life history traits of fishes with latitude, indicating example species and respective publications

Life history traits	Example species	Respective reference
Length of breeding and growing seasons	<i>Jenynsia multidentata</i> <i>Sander lucioperca</i> <i>Micropterus salmoides</i>	Goyenola et al. (2011), Lappalainen et al. (2003), and Rogers and Allen (2009)
Annual reproductive investment	<i>Jenynsia multidentata</i> <i>Perca fluviatilis</i>	Goyenola et al. (2011) and Heibo et al. (2005)
Reproductive life span	<i>Rutilus rutilus</i>	Lappalainen and Tarkan (2007) and Lappalainen et al. (2008)
Age and size at maturity	<i>Salvelinus alpinus</i>	Malmquist (2004) and Venne and Magnan (1989)
Longevity	<i>Perca fluviatilis</i>	Heibo et al. (2005)

Please see conceptual Fig. 7 for the expected changes.

Paine, 1990; Reznick et al., 2006) as well as marine habitats (Vila-Gispert et al., 2002).

2.5.2 Macroinvertebrates

Patterns on latitudinal changes in reproduction traits of invertebrates in diverse water bodies along a latitudinal gradient (12°N to 30°S) show that life history traits are highly variable and very likely influenced by regional and local factors (Hart, 1985). Despite this, recruitment seems to be more connected with seasonality in temperate climates, as evidenced by the greater timing flexibility in reproduction observed at low latitudes. Most of the evidence for this pattern comes from lotic environments and supports the same general trends as observed for fish, where larger body sizes, later maturity, fewer broods and larger embryos of some macroinvertebrates seem more common towards higher latitudes (reviewed by Sainte-Marie, 1991).

2.5.3 Zooplankton

We found few works on changes in zooplankton reproduction associated with a latitude or altitude gradient. An increase in autumn temperatures, as projected by different climate models, can switch the reproduction of zooplankton from sexual to asexual, resulting in a lower genetic diversity of these organisms (Chen and Folt, 1996). Likewise, studies of sediments

from shallow lakes from Greenland to Spain have shown a 100-times decline in the ratio of resting eggs to carapaces of the pelagic microcrustacean *Bosmina* spp., strongly correlated with changes in summer air temperature, while Chl-a (food resources) and fish density (predation) explained a comparatively minor proportion of the variation (Jeppesen et al., 2003). Studies of chydorids have also shown higher egg:carapace ratios in cold lakes than in warmer waters (Sarmaja-Korjonen, 2003).

2.5.4 Macrophytes

Macrophytes display a range of overwintering strategies (e.g. either in the water column or as seeds, tubers or turions in the sediments), which are differently affected by changes in ambient temperature, particularly in winter. In comparison to other lake communities, there is relatively little information published on phenological changes in macrophytes as a consequence of warming. Both longer (Jeppesen et al., 2010b) and shorter growing seasons (Barko and Smart, 1981) have been reported. At higher temperatures, an enhanced growth rate of submerged macrophytes allows a quick access to the water surface (Barko and Smart, 1981), leading to deeper colonization depths and higher biomass (Rooney and Kalf, 2000). Various studies have indeed found deeper colonization depths towards the equator (Duarte and Kalf, 1987; Kosten et al., 2011b). Duarte and Kalf (1987) attributed the difference in colonization depth to higher irradiance in the tropics. Maximum daily irradiance (which is a combination of light intensity and day length), however, does not vary substantially between lower and higher latitudes (Lewis, 1986). Another factor in favour of the temperature effect is the finding in Canadian lakes where colonization depth increased during a relatively warm year, in spite of increased turbidity (Rooney and Kalf, 2000). Mesocosm investigations have also shown enhanced macrophyte growth as a result of high temperature-mediated reduction in water level (Bucak et al., 2012). Nevertheless, changes in periphyton densities, likely affected by alternate trophic web configurations under different climates (Meerhoff et al., 2007a), may also partially explain changes in colonization depth (Kosten et al., 2011b and references therein).

2.5.5 Phytoplankton, periphyton and bacterioplankton

Life history traits of other assemblages, such as of phytoplankton, periphyton and bacterioplankton, appear less frequently in the SFTS literature. For instance, studies on phytoplankton growth rates along latitudinal transects mainly belong to the marine realm (e.g. Marañón et al.,

2000). One of the reasons lies in the microscopic and unicellular type of life of these organisms, in which sexual reproduction is typically absent or rare. Most of the studies on phytoplankton reproduction deal with particular species (e.g. [Hickel, 1988](#); [Jewson, 1992](#)), without covering many species or their change in different regions, despite the circumstance that this might be important for understanding some community processes ([Eilertsen and Wyatt, 2000](#)). Furthermore, it is relatively easy to develop laboratory experiments to evaluate the effects of temperature on microorganism growth (e.g. [Butterwick et al., 2005](#)), thus making perturbation experiments a more common approach than the SFTS.

2.6. Climate effects on intensity of trophic interactions

Climate warming may affect not only species performances and community traits but also species interactions. Interspecific interactions within food webs or other multi-species networks are highly underrepresented within the context of climate change research ([Woodward et al., 2010b](#)), not least in shallow lakes (but see [Meerhoff et al., 2007a](#)). Indication of changes in the intensity of trophic interactions may be obtained from certain indexes that typically include ratios of biomass or densities between predator–prey pairs relevant to shallow lake functioning (e.g. piscivorous fish:planktivorous fish, zooplankton:phytoplankton biomass ratio) (e.g. [Jeppesen et al., 2000](#)), or between groups of known different sensitivity to predation (such as motile organisms) and the total amount of potential prey (e.g. [Meerhoff et al., 2007a](#)). Also, the changes in size distribution of potential prey are used as indicators of predation pressure (e.g. [Brucet et al., 2010](#)).

Evidence from SFTS studies indicates a clear difference in the strength of trophic interactions with increasing temperature in shallow lakes. A stronger predation pressure by fish under warm conditions was supported by cross-comparison studies where littoral trophic interactions in subtropical and temperate lakes were compared ([Meerhoff et al., 2007a](#)). Several predation indexes constructed based on different sensitivities to predation by several groups, such as the proportion of small fish, the proportion of small snails, the proportion of chironomids, and the proportion of *Daphnia* relative to small cladocerans ([Meerhoff et al., 2007a](#)), suggest stronger effects of fish predation in warm lakes than in similar temperate lakes. The predation pressure exerted by planktivorous fish, particularly on zooplankton (and also on macroinvertebrates), increases with increasing temperature, as also found in European ([Gyllström et al., 2005](#)) and South American ([Lacerot, 2010](#)) latitudinal gradient analyses, and in cross-comparison studies ([Brucet et al.,](#)

2010, 2012; Meerhoff et al., 2007a, b) (Fig. 8). Mesocosm experiments conducted from Finland to southern Spain (Moss et al., 2004) have revealed significant effects of fish on the community structure of zooplankton and phytoplankton (leading towards dominance of smaller algae) along this latitudinal gradient. However, this effect of fish was not influenced by latitude (Moss et al., 2004; Stephen et al., 2004), possibly due to the similar density of fish stocked in all experimental locations.

Cross-comparison studies on *Daphnia ephippia* in sediments of subtropical and temperate shallow lakes indicated that they are also present in warm lakes despite being almost absent from contemporary water samples (Iglesias et al., 2011). These findings support the hypothesis that the typical lack of *Daphnia* in warm climates is more a consequence of high predation rather than of metabolic constraints (Havens and Beaver, 2011; Iglesias et al., 2011; Meerhoff et al., 2007a). Anti-predator behavioural responses by zooplankton also change with climate and the differential associated risk of predation by fish (Brucet et al., 2010; Meerhoff et al., 2007b; Tavsanoğlu et al., 2012).

Most likely as a consequence of increased predation by fish, the size distribution and composition of zooplankton in warm lakes typically change towards dominance of smaller taxa and individuals (Brucet et al., 2010; Gillyooly and Dodson, 2000; Iglesias et al., 2011; Lacerot, 2010; Meerhoff et al., 2007b); consequently, the capacity of zooplankton to control phytoplankton crops (estimated as the zooplankton:phytoplankton biomass ratio) may decrease with increasing temperature or decreasing latitude (Gyllström et al., 2005) (Fig. 8). This last pattern occurred in all freshwater studies we examined, regardless of approach (i.e. latitudinal gradient, cross-comparisons), geographic areas, and use of different biomass estimators (Fig. 8). In brackish lakes, the zooplankton:phytoplankton biomass ratio remained low throughout the year in the temperate regions, whereas the ratio was markedly higher in winter than in summer in the Mediterranean lakes, likely reflecting shifts in zooplankton and fish structure related to a fluctuating hydrology (Brucet et al., 2009). The occurrence of macrophytes in the lakes seems to enhance the grazing pressure of zooplankton in intermediate and cold regions (most likely indirectly via the provision of refugia from fish predation), while no or negligible effect of plants appears at low latitudes (Meerhoff et al., 2006, 2007b; Muylaert et al., 2010; Tavsanoğlu et al., 2012). Similar patterns were found in the gradient analysis in South

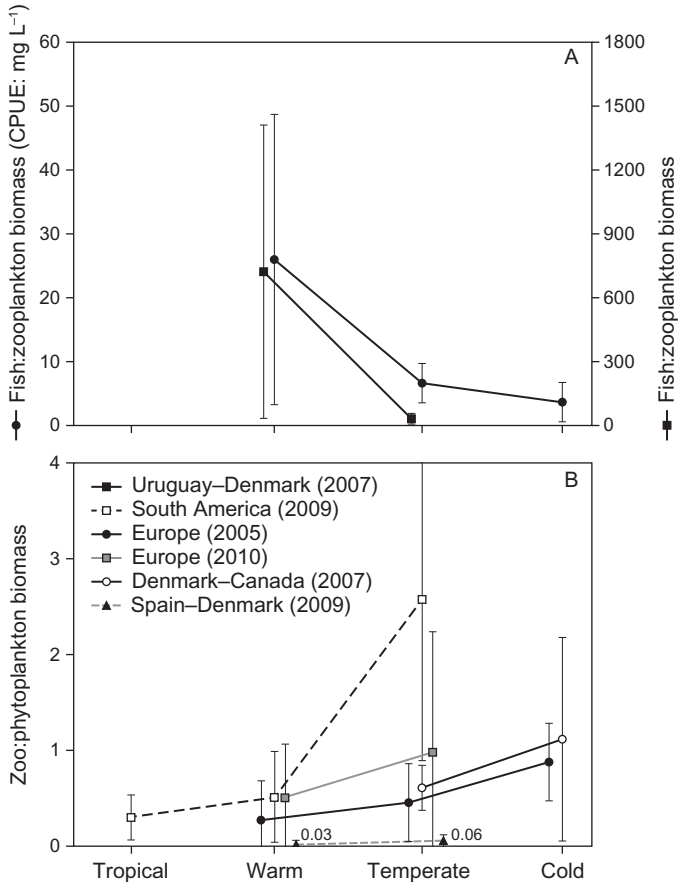


Figure 8 Variation in consumption pressure along a climate gradient, estimated as biomass ratios. (A) predation pressure of planktivorous fish on zooplankton (fish:zooplankton biomass) and (B) grazing pressure of zooplankton on phytoplankton (zoo:phytoplankton biomass). The latitudinal gradient corresponds to ranges from 5° to 55°S and from 38° to 64°N in Europe and America. Data were grouped in wide climate types: Tropical (Brazil), Warm (intermediate Argentina, Uruguay and Spain), Temperate (Denmark, Belgium, The Netherlands, UK and Poland) and Cold (Estonia, Sweden, Finland, Canada and southern Argentina). Zooplankton (either densities or biomass) median values were extracted from the literature and converted into biomass when necessary, according to Jeppesen et al. (1994). Full lines connect the points belonging to the same paper (see symbols). Values were extracted from (A) Fig. 6 in Gyllström et al. (2005) and Table 2 and Fig. 2 in Meerhoff et al. (2007a) and (B) Fig. 6 in Gyllström et al. (2005), Fig. 6 in Brucet et al. (2009), Fig. 2B in Jackson et al. (2007), Fig. 4 in Muylaert et al. (2010) and Fig. 7A in Kosten et al. (2009a). Error bars are 1 SE.

America (Kosten et al., 2009c), where the zooplankton grazing pressure decreased from cold to warm regions; the patterns were, however, influenced by macrophytes and the abundance of fish.

Despite lower total abundances, the relative abundance of herbivorous plant-associated macroinvertebrates was higher in the subtropical climate than in the temperate communities (Meerhoff et al., 2007a). This could imply that a larger proportion of the macroinvertebrates, besides the large numbers of small omnivorous fish, is feeding on periphyton and macrophytes under warmer conditions. On an evolutionary timescale, this could explain the increase in chemical defences of macrophytes at low latitudes, as suggested by Morrison and Hay (2011). On the other hand, grazing can affect periphyton by diminishing its biomass and changing taxonomic or group composition: grazing-mediated changes in composition have been revealed in a study showing a shift to dominance of fast-growing or resistant species (Sumner and McIntire, 1982).

Fully controlled experiments testing fish-mediated trophic cascading effects in shallow lakes under different climates are limited to a few mesocosm investigations. Trophic cascades seem to be weaker in tropical mesocosms, with stronger fish effects on nutrient cycling promoting a more pronounced bottom-up effect than in temperate mesocosms (Danger et al., 2009). Another conclusion of the cross-comparison of littoral food webs was that trophic cascades (concomitant with stronger fish predation pressure) from fish to the bottom of the webs were weaker and with relatively direct effects (perhaps reflecting shorter path lengths through the more reticulate food webs) on most prey communities (Meerhoff et al., 2007a) (Fig. 9).



3. DISCUSSION

3.1. Can we predict changes in community traits with warming?

So far, we have attempted to detect whether common patterns of change in community traits as a response to changes in temperature emerge from the empirical SFTS literature: some traits of a few communities changed in accordance to theoretical predictions, but for most organizational levels, responses were often unclear or non-linear, and only partly supported predictions. Below, we contrast our findings with theoretical expectations and compare them with findings from other research approaches.

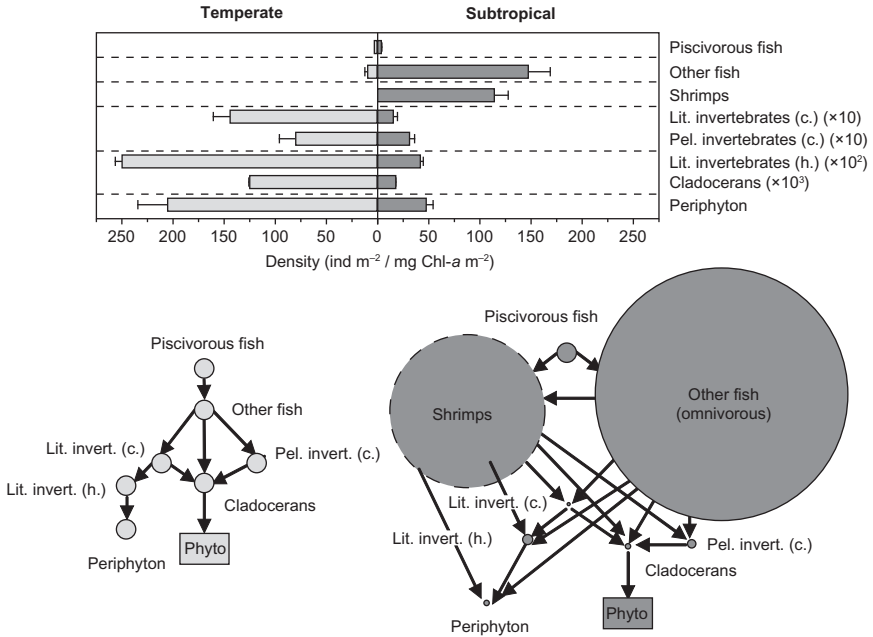


Figure 9 Structure of main communities in temperate (left) and subtropical (right) shallow lakes. (Above) Density of potentially piscivorous fish, all other fish, shrimps, littoral carnivorous invertebrates (Lit. invert. (c)), pelagic carnivorous invertebrates (Pel. Invert (c)), littoral herbivorous macroinvertebrates (Lit. invert. (h)), cladocerans and biomass of periphyton. (Below) Simplified scheme of trophic interactions among the same trophic groups. The densities in the subtropics are expressed relative to those in the temperate lakes (considered as the unit). Except fish, the same taxa share the same trophic classification in both climate zones. Shrimp relative density is dashed due to shrimp absence in the temperate lakes. Phytoplankton (Phyto) box has the same size as it was fixed in the study (surrogate of turbidity) by pairing the lakes in both climates. Data are sample means of five selected lakes and error bars (above) show the standard error. Modified from [Meerhoff et al. \(2007a\)](#).

3.1.1 Congruence of SFTS findings and theoretical expectations

Some of the shallow lake communities surveyed here clearly followed the predictions of an increase in richness with an increase in ambient temperature ([Allen et al., 2002](#)), namely, fish, phytoplankton, and periphyton; whereas macroinvertebrates and cladoceran zooplankton (at genera level) typically showed the opposite trend, and no clear response could be identified for macrophytes and bacterioplankton. Fish taxonomic richness exhibited the clearest pattern (meta-analysis by [González-Bergonzoni et al., 2012](#); [Fig. 1A](#)), with a significant positive relationship with decreasing latitude. Macroinvertebrate richness data are often not available at species

level and latitudinal studies show ambiguous trends, besides being commonly based on pooled data from lakes and streams (e.g. Heino, 2009). In studies including only shallow lakes, however, we found an opposite trend to the expected response (at genus and family levels) (Fig. 1B), with lower local taxon richness in warm lakes (e.g. Brucet et al., 2012; Lewis, 1996; Meerhoff et al., 2007a). Most of the reviewed articles also described a decrease in local cladoceran zooplankton richness (at genus level) at warmer locations (e.g. Brucet et al., 2010; Meerhoff et al., 2007b, Pinto-Coelho et al., 2005) (Fig. 1C). Whether similar or contrasting latitudinal richness patterns occur at species level remains unresolved for these groups. However, richness at different taxonomic resolutions (e.g. species and genera) tends to be highly correlated, as found for, for example, terrestrial vegetation (Enquist et al., 2002), macroinvertebrates (Heino and Soininen, 2007) and phytoplankton (Gallego et al., 2012) and as predicted by theoretical models (Allen et al., 2002).

Microorganisms, ranging from phytoplankton to bacteria, however, are usually considered to either lack or display only weak latitudinal gradients in richness, because of their high abundances and small sizes, enabling them to disperse easily over few geographical barriers and over large distances (Fenchel and Finlay, 2004; Finlay, 2002; Hillebrand and Azovsky, 2001, but see Van der Gucht et al., 2007). The distribution of these groups is suggested to be more strongly driven by local environmental factors (Baas-Becking, 1934; Beisner et al., 2006; Kruk et al., 2009; Ptacnik et al., 2010a,b) than by latitudinal gradients. In our review, however, phytoplankton and periphyton richness increased with decreasing latitude (or rising temperature) (Fig. 1D and E). It has been suggested that most microbial biodiversity is hidden from our observation, because most species will occur at densities below current limits of detection (de Wit and Bouvier, 2006); a limitation increasingly overcome by the application of massive tag-sequencing, which allows for the detection of the microbial components of the so-called rare biosphere (Purdy et al., 2010; Sogin et al., 2006). In our analysis, bacterioplankton richness did not show any clear trend, maybe reflecting the narrow geographic range of the available data (i.e. temperate regions) or, alternatively, the suggested stronger effect of local factors on this diverse group.

MTE predicts a decrease in community biomass and density with an increase in ambient temperature, due to the enhanced metabolic demands and consequent limitation of resources for individuals (Brown et al., 2004; Fig. 1, Table 1). In our review, only periphyton biomass and

macroinvertebrate and zooplankton densities showed a significant decline with decreasing latitudes (Fig. 1K, N and R).

Fish biomass and density showed the opposite pattern (Fig. 1G and M), with a clear increase towards low latitude locations as found in several studies applying different approaches (e.g. Brucet et al., 2010; Gyllström et al., 2005; Meerhoff et al., 2007a; Teixeira-de Mello et al., 2009; see Table 2 for a summary). This is an intriguing phenomenon, since the potential co-variation of lake productivity with latitude was considered in the respective studies (i.e. comparing lakes with similar TP ranges in Brucet et al., 2010; Gyllström et al., 2005, Teixeira-de Mello et al., 2009) and in the data we extracted from the literature. Besides, we found no evidence for limitations of specific nutrients or productivity gradients associated with latitude (reviewed in Section 1.3). Increases in fish biomass and abundance with temperature have also been reported recently from Icelandic geothermal streams, which span a broad thermal gradient within a single catchment (Woodward et al., 2010a).

The meta-analyses of zooplankton (in this case, cladocerans and copepods), however, yielded no significant relationship between biomass and latitude despite that the expected trend of reduction occurred in most reviewed studies (e.g. Gyllström et al., 2005; Havens et al., 2007; Jackson et al., 2007; Meerhoff et al., 2007b; Pinto-Coelho et al., 2005; Vakkilainen et al., 2004).

Contrary to the predictions by MTE, warmer conditions have been argued to lead to higher phytoplankton biomass and yield (Lewis, 1996), not least in shallow lakes. This has been explained by longer growing seasons (Lewis, 1996, 2000), increased availability of phosphorus from internal loading (Jeppesen et al., 2009; Søndergaard et al., 2003) and smaller size of zooplankton grazers (Meerhoff et al., 2007b), resulting in lower grazing pressure as suggested in our review (e.g. Gyllström et al., 2005; Kosten et al., 2009c; Meerhoff et al., 2007a; Fig. 8). In our analysis of large databases from two contrasting climates, we did find higher total phytoplankton biovolume and higher total biovolume of cyanobacteria in subtropical climates than in similar temperate lakes (Fig. 2), as reported in studies following other approaches (Paerl and Huisman, 2009). The general pattern was, however, not maintained for other phytoplankton biomass proxies, such as Chl-a concentration (Fig. 1J), as also reported by Kosten et al. (2012). The typical absence of counts of phytoplankton and periphyton in the shallow lake literature prevented us from testing density predictions on these communities.

The estimation of bacterial biomass relies on the application of conversion factors to translate the volume assessments into carbon values, and these factors are not yet fully established, leading to widely varying estimations when applying the different proposed values to the same dataset (e.g. [Posch et al., 2001](#)). Therefore, bacterioplankton does not seem to be the most appropriate portion of the community with to test predictions of changes in biomass with warming at present, at least not with the information found in this review. Nonetheless, bacterioplankton still showed a significant increase in density with decreasing latitudes (i.e. increasing temperature) ([Fig. 1R](#)). According to our findings, higher temperatures could promote higher bacterioplankton density both through a direct effect (via acceleration of metabolic rates leading to enhanced multiplication) and indirect effects (e.g. via increasing substrate availability, DOC) ([Fig. 5](#)). Higher temperatures could also promote competitive advantages for bacteria over algae ([Carey et al., 2012](#); [Yvon-Durocher et al., 2011a](#)). The fact that temperature and Chl-a appeared in our regression model as separate factors supports the hypothesis that the effects of temperature and resource availability on bacterial biomass production are independent ([Lopez-Urrutia et al., 2006](#)).

Freshwater communities, and particularly shallow lake communities, seem to be strongly size structured ([Hildrew et al., 2007](#)), as recognized in the pioneering works on the effect of fish predation on the size structure of zooplankton in ponds ([Brooks and Dodson, 1965](#); [Hrbacek et al., 1961](#)). Different trends of changes in body size with temperature could be expected according to several theories, which are not necessarily mutually exclusive (see [Section 1](#), [Fig. 1](#), [Table 1](#) and [Daufresne et al., 2009](#)). In our review, fish and zooplankton communities showed a reduction in mean body size with increasing temperatures ([Fig. 1S](#) and [U](#), for fish and zooplankton, respectively), supporting the predictions by MTE ([Brown et al., 2004](#)) and the “temperature-size” rule ([Angilletta, 2009](#)). Bacterioplankton body size, however, revealed no relationship with latitude or temperature, but the data were geographically too restricted and the variability too large to allow detection of latitudinal gradients. The lack of sufficient data for four of our target communities (i.e. macroinvertebrates, macrophytes, phytoplankton and periphyton) prevented us from generalizing a trend for real lake communities. Moreover, at the population level, different mechanisms may occur across latitudinal gradients as predicted by several theories, leading to a decrease in the mean body size of

populations with a concomitant reduction of mean body size across the community as a whole (Daufresne et al., 2009). At the community level, a decrease in average body size with increasing temperature may also reflect competitive exclusion of larger species, size-selective predation (e.g. Brooks and Dodson, 1965) or a reduction of the density of larger species due to inefficient energy transfer along the food web with increasing temperatures (Arim et al., 2007). These mechanisms, however, would not necessarily appear across latitudinal gradients due to local variations in the amount of resources available and the thermal setting in which the communities develop. The trends we found in the SFTS literature mostly refer to changes at assemblage or community level and may thus reflect the effect of temperature through a variety of mechanisms or likely the combined effect of temperature and inter-specific interactions.

3.1.2 Evidence of warming effects obtained by other approaches

Other approaches (e.g. perturbation experiments) to study the potential effects of climate change have shown no effects of increased temperature on richness of some freshwater communities. In outdoor heated mesocosms, cladoceran diversity (McKee et al., 2002a) and phytoplankton richness (Moss et al., 2003) were not significantly affected by experimental warming, although measures of community evenness increased (McKee et al., 2002a). Warming, rather than affecting macrophyte richness, may promote a switch from submerged to free-floating macrophyte dominance in shallow eutrophic lakes, as reported mainly from perturbation experiments (Feuchtmayr et al., 2009; Netten et al., 2010) and previously suggested by models (Scheffer et al., 2003). Warming may thus promote a polewards expansion of the geographical distribution of this type of plants (Scheffer et al., 2003), with potential strong and negative consequences for local biodiversity.

In passively warmed mesocosms in alpine regions, zooplankton biomass was suppressed due to the decline in large cladocerans, even in the absence of fish (Strecker et al., 2004). At the same time, warming did not affect total phytoplankton biomass but significantly altered the assemblage composition by favouring fast-growing phytoflagellates over larger filamentous green algae, supporting the hypothesis that moderate warming can destabilize plankton dynamics in shallow cold-water ecosystems (Strecker et al., 2004). An experimental increase in temperature in mesocosms had also very minor effects on phytoplankton Chl-a and total biovolume, although it significantly decreased the biovolume of Cryptophyceae and Dinophyceae and did not affect the

abundance of cyanobacteria as might be expected (Moss et al., 2003). No obvious effects on the densities of zooplankton (McKee et al., 2002a) and macroinvertebrates (Feuchtmayr et al., 2007; McKee et al., 2003) were observed, suggesting that the overall abundances of most invertebrate taxa will not be severely affected by the predicted temperature rise (Feuchtmayr et al., 2007; but see Dossena et al., 2012). In contrast, in another series of outdoor heating experiments, warming shifted the composition and distribution of phytoplankton size and biomass from assemblages of large individuals with high standing biomass to assemblages with low standing biomass and many smaller-bodied species, including small cyanobacteria (Yvon-Durocher et al., 2011a). In this case, however, such an effect did not occur in the distribution of size and biomass of zooplankton. Warming thus seems to lead to reorganization of the biomass structure in both the benthic and planktonic assemblages (Dossena et al., 2012; Yvon-Durocher et al., 2011a), at least in experimental, relatively simple, food webs with fixed fish densities.

In contrast to our findings (Fig. 1R), in experimental outdoor mesocosms, the abundances of picoalgae, bacteria and heterotrophic nanoflagellates changed in a similar manner over time, with no direct effect of experimental warming (Christoffersen et al., 2006). However, experimental warming modified the effects of nutrient additions (Christoffersen et al., 2006; Özen et al., 2012), indicating that interactive effects may be significant in the future given the current and expected increase in nutrient loading to many shallow lakes worldwide (Jeppesen et al., 2009, 2010b; Moss et al., 2011). The difference between our findings and these experimental studies may reflect the co-variation in nutrient availability (i.e. DOC) and temperature found in our data (Appendix B) rather than different direct effects of temperature on bacterioplankton populations.

A meta-analysis of the effects of warming on body size of ectothermic aquatic organisms, from the individual to the community level, revealed a significant increase in the proportion of small species and organisms at warmer temperatures (Daufresne et al., 2009), as we have found for fish and cladoceran zooplankton (Fig. 1S and U). A study of Cladocera subfossil distribution in 54 European lakes located in different climates showed that small species dominated warm water lakes with high conductivity, macrophyte coverage and fish abundance. In contrast, large pelagic species were more common in low-conductivity high-latitude lakes (Bjerring et al., 2009). Higher summer temperatures have promoted a reduction in the

mean body size of temperate zooplankton (Moore et al., 1996), as also found in heating experiments for phytoplankton communities (e.g. Sommer and Lewandowska, 2011; Yvon-Durocher et al., 2011a). This effect was not found in otherwise similar outdoor experiments, however (Moss et al., 2003). The pieces of evidence showing a reduction in the body size of organisms with increasing temperature suggest that the underlying size structure of aquatic ecosystems might not be robust to global warming (Yvon-Durocher et al., 2011a). The magnitude and sometimes direction of change, however, seem to vary with taxonomic groups and environmental conditions (Gardner et al., 2011). It should be also noted that the spatial scale and range of body sizes under analysis may also affect the generation and testing of congruent predictions (Tilman et al., 2004).

Our review of the SFTS literature revealed trends of a reduction in size at maturity, life-span and the occurrence of more reproductive events in fish towards warmer locations, and although the information on other communities is more scarce, it also suggests comparable changes in the reproduction mode of zooplankton and macroinvertebrates (Section 2.5). In line with these findings, experimental warming can influence the reproduction of fish by affecting embryonic development time and offspring numbers (unimodally linked to temperature) (e.g. García-Ulloa et al., 2011). It can also lead to a reduction in the body size at maturity, as reported for the cladoceran *Simocephalus vetulus* in heated mesocosms (McKee et al., 2002a). Differential effects of temperature on life history traits such as fecundity, development and survivorship will affect the overall fitness of organisms. Mathematical models suggest, for instance, that warming will cause ectothermic species with a high temperature sensitivity of development to reach the age at first reproduction earlier in the year, potentially leading to mismatches between consumers and resources if the latter have a lower temperature sensitivity of development (Amarasekare and Savage, 2012). Studies in other heating experiments (outdoor tanks, Liboriussen et al., 2005) have demonstrated the occurrence of a rapid microevolutionary response of the cladoceran *S. vetulus*, in both survival and subcomponents of individual performance (i.e. age at reproduction and number of offspring), suggesting that populations may persist locally under the predicted scenarios of global warming (Van Doorslaer et al., 2007). According to those results, such microevolutionary responses may buffer changes in community structure under climate warming and help explain the apparent lack of effects in some experiments and field data.

3.1.3 *The importance of local factors and trophic interactions*

Local characteristics have a large potential of blurring latitudinal gradients in traits of, at least, several communities. Some basic relationships, such as the density–mass relationship, might be robust at the level of biomes or at a very large range of body sizes but could exhibit large variations among local communities (e.g. [Arim et al., 2011](#); [Hechinger et al., 2011](#); [White et al., 2007](#); but see, [Brown et al., 2011](#); [Layer et al., 2010](#); [McLaughlin et al., 2010](#); [O’Gorman and Emmerson, 2010](#)).

In particular, the strong imprint of biogeography and local factors may override temperature-related effects on richness and could alter the predicted trends. In many ecosystems, including shallow lakes, explanatory variables that are potentially important as main drivers of local diversity tend to be highly inter-correlated, such as productivity level and the abundance of key structuring organisms, such as aquatic plants ([Declerck et al., 2005](#)) and fish. Besides the potential influence of climatic factors such as the length of the growing season, the annual input of solar radiation and the length of the hydroperiod ([Della Bella et al., 2008](#)), local factors such as lake area (e.g. [Rørslett, 1991](#)), sediment characteristics ([Barko et al., 1991](#)), maximum depth, TP ([Jeppesen et al., 2000](#)) and nitrate concentration ([James et al., 2005](#)) also have strong influences on plant species richness at local scales. Trophic interactions may also indirectly affect submerged macrophytes along latitudinal gradients: the positive effect of long ice cover on macrophyte coverage (e.g. [Kosten et al., 2009a](#)) may thus be due to a cascading effect through anoxia causing fish kills ([Jackson et al., 2007](#)) and subsequent stronger zooplankton and snail control on phytoplankton and periphyton competitors ([Jones and Sayer, 2003](#)). The effect of warming on phytoplankton and periphyton densities, however, also depends on the relative importance of trophic cascading effects, nutrient status and water residence time ([Søballe and Kimmel, 1987](#)).

Our review highlights that several properties of the potential prey communities, from richness to biomass and body size, indicate enhanced predation pressure with increased temperatures. Temperature influences the predator–prey interactions both directly and indirectly, either via the alteration of predator feeding rates and feeding modes ([Beisner et al., 1996](#)) or through changes in both prey and predator body size ([Moore et al., 1996](#); [Woodward et al., 2010b](#)). Experimental warming studies measuring feeding intake rates at different temperatures have demonstrated higher consumption of macroinvertebrates, both on other invertebrates and on periphyton in warmer scenarios ([Kishi et al., 2005](#)).

Warming experiments have also shown that trophic cascade effects may vary with temperature, due to physiological depression of predators (Kishi et al., 2005).

Higher consumption by vertebrate and invertebrate grazers (Lazzaro, 1997; Meerhoff et al., 2007a) could thus also explain our observed local patterns of richness of prey communities in warmer regions, the lower macroinvertebrate densities and lower zooplankton density and mean body size of zooplankton (Meerhoff et al., 2007a) as also suggested by mathematical models (van Leeuwen et al., 2007) and confirmed in our review (Fig. 8). The grazing pressure by zooplankton on phytoplankton showed the opposite trend, being weaker at lower latitudes (Fig. 8). The lack of a relationship or relatively weak latitude effect on phytoplankton biomass could reflect local variations in contrasting mechanisms. The final outcome may be the result at local scales of the balance between temperature effects on metabolism, which should reduce phytoplankton biomass, and the effects of longer growing seasons and lower zooplankton grazing pressure, which would increase it. Ultimately, our results indicate that overall the link between zooplankton and phytoplankton weakens with increasing water temperature. Weak interactions may dampen biomass oscillations between consumers and resources (McCann et al., 1998), implying that not all responses at a specific trophic level are propagated to lower trophic levels or have significant impacts on ecosystem processes (Pace et al., 1999). An increase in the duration of climatic variability effects due to food web interactions seems possible, as the signal of winter climate can be detected in the clear water phase (i.e. a reduction in phytoplankton biomass) in early summer (Straile and Adrian, 2000) or in summer phytoplankton composition and biomass (Blenckner et al., 2002; Weyhenmeyer, 2001) in temperate lakes.

Species higher in the food web are often especially sensitive to changes in ambient temperature (Petchey et al., 1999; Woodward et al., 2010a,b). The decline and maybe the extinction of a top predator, as a potential consequence of warming, may significantly influence the effects of size-structured interactions in food webs and ecosystem functioning. Other temperature-related changes in fish structure and predation pressure might also be expected. After conducting feeding experiments with the omnivore fish species opalaye (*Girella nigricans*) at different ambient temperatures, Behrens and Lafferty (2007) suggested that warming may lead to changes in the diet of fish towards greater consumption and assimilation of plant material. An increase in the relative proportion of

herbivorous and omnivorous species within the fish assemblage with decreasing latitude has been found in meta-analyses of aquatic systems worldwide, not least shallow lakes (González-Bergonzoni et al., 2012; Jeppesen et al., 2010a), giving further support to the previous hypothesis. This change in diet would result in food webs being more truncated, as predicted both theoretically (Arim et al., 2007) and empirically (Meerhoff et al., 2007a). Altogether, the evidence suggests that food webs in temperate or cold shallow lakes will be affected by warming, also due to the current lower number of feeding links (Fig. 9; Meerhoff et al., 2007a) and the lower richness of top species (typically fish) (Fig. 1A). As found in our review, however, the direction of changes seems difficult to predict for the specific communities given the different relative importance of direct or indirect effects of higher temperature under specific local scenarios and the interactions with other environmental stressors.

3.2. Advantages and disadvantages of the SFTS approach

The actual test of theoretical predictions with empirical data from shallow lake literature represents a practical challenge relative to the heterogeneous nature of currently available data. The description of different entities (e.g. populations, communities) and the differences in taxonomic resolution (e.g. species, genera, classes) make comparisons, in our case across studies and different communities, a challenging task (Yvon-Durocher et al., 2011b). Like all other approaches, the SFTS approach has a series of advantages and disadvantages (many already summarized in Woodward et al., 2010b), as it studies communities that have long been exposed to different temperatures, rather than in a transient state in response to warming *per se*. Latitude is probably a better predictor of long-term regimes of climatic variables than current climate values registered by local weather stations (Naya et al., 2008). However, latitude may be correlated with other climatic (e.g. wind speed, seasonality), ecological (e.g. day length and length of growing season), and potentially also historical factors (e.g. biogeographical boundaries) that may affect organisms' physiology (Naya et al., 2008) and, with it, the observed latitudinal patterns. Furthermore, climate is much more than temperature alone, and other potential confounding processes interact with climate to shape communities in lakes. Lake trophic state, as reflected by nutrient levels (more commonly TP), affects community structure by augmenting the fish densities and biomass in increasingly productive systems around the world

(Brucet et al., submitted for publication; Jeppesen et al., 2000, 2005; Mehner et al., 2007; Teixeira-de Mello et al., 2009). Lake productivity thus often overrides the effects of temperature on fish assemblage densities (e.g. Brucet et al., submitted for publication; Mehner et al., 2007). Experimental warming in outdoor mesocosms promoted an increase in TP, total alkalinity, and conductivity, decreased pH and oxygen saturation and increased the frequency of severe deoxygenation (McKee et al., 2003). Several pieces of evidence also support the idea that increasing temperature acts synergistically with eutrophication (e.g. Feuchtmayr et al., 2007; Jeppesen et al., 2010b; McKee et al., 2003; Moss et al., 2011), so these two key drivers could produce outcomes that are not predictable from studying either in isolation.

Climate warming may lead to a higher frequency of dramatic changes in water level, transforming permanent water bodies into temporary systems (Beklioglu et al., 2007) and leading to changes for the whole food web. For example, strong differences in zooplankton assemblage structure appeared between permanent and temporary shallow lakes of the same wetland system, with higher diversity and lower density of large zooplankton in permanent shallow lakes, which was attributed to a higher fish predation pressure compared to temporary lakes (Brucet et al., 2005). Warming may also promote an increase in salinity in shallow lakes due to enhanced evaporation, especially in arid and semi arid climates (Beklioglu et al., 2007), saltwater intrusions into freshwater bodies (Schallenberg et al., 2003) and enhanced use of freshwater for irrigation and industry under a likely increased consumption pressure (Williams, 2001). Trophic structure in shallow lakes typically changes along a salinity gradient (Brucet et al., 2009, 2010; Jeppesen et al., 1994, 2007), as also shown in this review. Indirect effects of climate warming, such as changes in salinity and hydrology, could thus have larger consequences for the diversity, size distribution and abundance of grazers of shallow lake ecosystems than an increase in nutrients or temperature *per se* (Brucet et al., 2009, 2010). Such shifts with increasing salinity and the subsequent decrease in the top-down control on phytoplankton may negatively affect the resilience of brackish lakes to the enhanced nutrient loading (Brucet et al., 2010, 2012).

A further factor that potentially masks natural responses of aquatic communities to temperature variations is the accidental or purposeful introduction of alien species (mostly fishes in freshwaters) by humans. The SFTS approach has clear limitations as to predicting the impact of invasive species

associated with climate warming because a native species may become invasive when expanded beyond its natural distributional range (as expected for large free-floating plants, [Scheffer et al., 2003](#)), and we cannot presume that ecological interactions among species will necessarily be similar in the native and the foreign ecosystem. Climate warming also has the potential to modify the impacts of invasive alien species by affecting the whole process of invasion and further increasing ecosystem vulnerability ([Rahel and Olden, 2008](#)). For instance, climate change may affect aquatic invasive species by altering thermal regimes, reducing ice cover duration, altering stream flow regimes, increasing salinity, and augmenting the demand for water storage and conveyance structures ([Rahel and Olden, 2008](#)). Furthermore, potentially synergistic effects of climate warming and non-native species make forecasting even more difficult ([Woodward et al., 2010b](#)). For example, as pointed out by [Rahel and Olden \(2008\)](#), global climate change will lead to an increase in water temperatures in northern-latitude lakes, which may result in seasonally stressful conditions for coldwater-adapted fish species. On the other hand, however, it may provide suitable thermal conditions for non-native warm water fish species ([Sharma et al., 2007](#)). Such species could prey on or compete with native fishes and this competition may result in a decline or loss of native populations ([Jackson and Mandrak, 2002](#)).

However, potentially confounding factors such as eutrophication, acidification, and the equivalent reverse phenomena generally fluctuate less rapidly than climatic variables. This difference in behaviour and signal-response times can be used to distinguish between climatic forcing and confounding factors, by removing trends and low-frequency fluctuations from relevant time-series by detrending or high-pass filtering, and analyzing only the remaining, higher-frequency fluctuations that are driven mainly by external physical forcing ([Adrian et al., 2009](#)).

Notwithstanding the current shortage of empirical data on all relevant communities or traits in the literature at a truly global scale, a clearer picture of what we should expect with climate warming is starting to emerge, especially when we combine trends from SFTS studies with modelling studies, *in situ* warming experiments and long-term empirical studies (e.g. [Jeppesen et al., 2010a](#); [Jeppesen et al., submitted for publication](#); [Sarmiento et al., 2010](#)). In some cases, however, apparently contradictory patterns emerge, as highlighted here. Experimental warming studies are often of short-term duration, thus showing transient phenomena (i.e. warming as a stressor), whereas SFTS studies in natural systems are more likely to reveal equilibrial

conditions with respect to temperature rather than responses to changing conditions *per se*. Moreover, warming experiments most often simplify food webs and, in particular, the role of predators by using fixed densities of a single predatory fish species (e.g. Liboriussen et al., 2005; McKee et al., 2002a; Yvon-Durocher et al., 2011a), thereby not allowing for the assessment of temperature-driven effects on prey communities through temperature impacts on the assemblage of predators. For instance, the majority of the reviewed SFTS studies suggest that fish predation, rather than temperature alone, is also responsible for the changes in the structure of several communities, mainly as a result of cascading effects of the temperature-driven decrease in fish size (Lacerot, 2010; Meerhoff et al., 2007a) leading to a stronger predation pressure on macroinvertebrates and zooplankton (Gyllström et al., 2005; Meerhoff et al., 2007a,b).

The SFTS approach thus highlights empirical trends that allow researchers to generate hypotheses regarding climate-driven future changes in community and ecosystem processes, thus potentially stimulating further research and the design of appropriate experiments to disentangle effects of potential drivers and to test mechanisms (e.g. Friberg et al., 2009; Liboriussen et al., 2005 and other references mentioned along the text). The combination of empirical data, mechanistic approaches and the framework given by food web and metabolic theories to climate change research in shallow lakes seems also fundamental, as suggested for other ecosystems or in theoretical works (e.g. Montoya and Raffaelli, 2010; Van der Putten et al., 2010; Woodward et al., 2010b).

3.3. Topics for further research

The occurrence of processes acting at different scales renders it difficult to disentangle their specific effects and the relative importance of local and regional characteristics on multispecies richness. In particular, both the experimental evidence and our review of whole lake data might suggest that the effects of nutrient enrichment and predation by fish on zooplankton and macroinvertebrate communities might be stronger than the direct effects of warming. It is thus open for further analysis whether some of our seemingly contradictory findings are a result of temperature-enhanced fish predation in warm locations, and therefore with consequences for a climate warming context, or a result of biogeographic processes or of geographically restricted databases. SFTS studies analyzing changes in community traits in fishless systems could provide some answers to these questions.

Our target community traits (i.e. richness, biomass, density and body size) are very seldom combined in the literature within a given study, and information on the responses of key communities to warming is therefore fragmentary. The common use of proxies for some traits (such CPUE, with different units in different works, as a proxy of fish density and biomass per unit area) also renders it difficult to compare results from different publications and to estimate predation pressure indexes. The lack of reports in the literature of traits typically measured (such as the body size and density of phytoplankton and periphyton) represents information gaps that should be relatively easy to solve. On the other hand, some traits are typically not measured, such as the body size and density of macrophytes or traits of macroinvertebrates at low levels of aggregation (i.e. species and genera), while some assemblages are typically underrepresented in shallow lake research. In particular, and despite the importance of bacteria for geochemical cycles, biomass and nutrient and energy transport within aquatic trophic webs (Azam, 1998), data on microbial communities in shallow lakes are scarce. When present, bacterioplankton community traits are typically not described, reflecting the very different methodological skills and facilities required to evaluate all community traits, which will hopefully become less of a hindrance in the future with the advent of more sophisticated molecular approaches (Purdy et al., 2010). Besides, microbial ecologists have modified their focus, from evaluating bacterioplankton communities in terms of taxaindependent approaches (e.g. measurements of biomass) to elucidating factors controlling the community composition with the aim to understand the role and fate of specific populations (Pernthaler and Amann, 2005), and a move towards more *in situ* characterizations of multispecies systems (Purdy et al., 2010).

Possibly, more serious, though, than the scarcity of data on bacterioplankton is the lack of data on their predators (i.e. heterotrophic nanoflagellates, or HNF). The absence of this link from the literature prevents us from estimating potential changes in energy and nutrient fluxes within the food web of shallow lakes under warming, since these organisms link the microbial loop with the classic food web (i.e. phytoplankton–zooplankton–fish) (Reiss et al., 2010). Changes in lake trophic state could promote a decoupling between bacterioplankton and their potential predators (Gasol, 1994), potentially leading to changes in the efficiency of energy transfer and the occurrence and strength of trophic links (Zingel et al., 2007) in the whole system. The scarcity or lack of data (and large uncertainties associated with laboratory techniques) on the

microscopic components of shallow lakes also renders it very difficult to search for body size thresholds on which to test the predictions of the different theories that relate temperature with body size.

More data on changes in trophic position, diet breadth and feeding rates are needed to test the predicted trends of a reduction in food web length with increasing temperature (Arim et al., 2007) and of changes in key measures of interaction density, such as connectance (Petchey et al., 2010). Climate effects on life history traits other than reproductive characteristics, and seasonal dynamics of lake communities other than plankton (Adrian et al., 2006), are areas that could be usefully investigated applying the space-for-time framework. Another important caveat that deserves further investigation is the effects of climate on host–parasite interactions: several studies suggest that climate strongly influences parasite infection in lake communities (e.g. phytoplankton, Ibelings et al., 2011; fish, Macnab and Barber, 2012), yet this field of trophic ecology is still surprisingly poorly understood (Thompson, Dunne and Woodward, in press). Despite the fact that the overall effects still have yet to be fully elucidated, temperature-mediated changes in parasite infection can potentially alter the expected outcomes of trophic cascades or predator–prey dynamics between the main lake communities. The likely important effects of changes in temperature on the production and action of allelopathic substances represent another research area of great potential.

Arguably, the most familiar characteristic of shallow lake ecosystems is their capacity to shift between alternative, relatively stable, states (Moss, 1990; Scheffer et al., 1993, 2001). This implies path dependency or hysteresis, in which a return to the environmental condition (e.g. a particular nutrient concentration) before the shift is not sufficient to recover the previous ecosystem state. Several pieces of evidence suggest that the differences in the biotic interactions between cold and warmer regions (Meerhoff et al., 2007a) might result in a weaker clearing effect of submerged plants under warmer conditions (Jeppesen et al., 2007), and thus in a weaker stability of the clear water state. Kosten et al. (2009b) assessed whether the effect of submerged plants changes with climate in South America and found that the competitive balance between submerged macrophytes and phytoplankton is not straightforward. However, the effect of submerged macrophytes on water clarity in the lakes (outside the plants beds) was generally lower in South America (Kosten et al., 2009b) than in temperate Northern Hemisphere lakes (e.g. Jeppesen et al., 2007), suggesting that other processes may have been

overlooked. How global changes, including here the changes in C and N cycles and land use, besides climate warming, affect the critical thresholds over which the ecosystems experience such dramatic shifts is thus one of the most relevant questions for ecosystem management in the future, particularly for shallow lakes.

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APPENDIX A. PERIPHYTON LATITUDINAL GRADIENT

We analyzed papers covering a latitudinal gradient range from 68°S to 83°N. All the data come from field sampling campaigns of periphyton on different substrates, either natural or artificial, in freshwater shallow lakes along a nutrient concentration range of 8.0–4050 $\mu\text{g TN L}^{-1}$, 0.4–2750 $\mu\text{g TP L}^{-1}$, and a planktonic chlorophyll-*a* concentration gradient from 0.4 to 400 $\mu\text{g Chl-}a \text{ L}^{-1}$. We performed linear regressions between periphyton data and latitude using the statistical package STATISTICA.

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APPENDIX B. BACTERIOPLANKTON LATITUDINAL GRADIENT

We analyzed 17 publications including information on 140 lakes along a latitudinal gradient from 7° to 64°S and from 29.1° to 68.5°N. The lakes covered a gradient in trophic status from 1.1 to 506 $\mu\text{g TP L}^{-1}$ and 0.29 to 221 $\mu\text{g phytoplankton Chl-a L}^{-1}$. We grouped the lakes according to climatic zones following the revision by Leemans and Cramer (1991) of the Köppen climate system (1936). We performed Spearman's correlations and stepwise multiple linear regressions (after log-transforming relevant data) between bacterioplankton data and relevant environmental variables, latitude, altitude, lake area, water temperature, conductivity, nutrients, such as phytoplankton Chl-a, dissolved organic carbon concentration, etc. We used the statistical packages STATISTICA and SigmaPlot.

The Spearman's correlations indicated that bacterioplankton abundance significantly declined with increasing latitude ($r=0.55$, $p<0.0001$, $n=133$) and increased with DOC ($r=0.90$, $p<0.0001$, $n=34$), temperature ($r=0.67$, $p<0.0001$, $n=112$), conductivity ($r=0.58$, $p<0.0001$, $n=98$) and Chl-a ($r=0.46$, $p<0.0001$, $n=95$). No significant relationships were found for nutrients (TP and TN).

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APPENDIX C. PHYTOPLANKTON UNPUBLISHED DATA AND LATITUDINAL GRADIENT

C.1. Previously unpublished data: The Netherlands–Uruguay comparison

We compiled a database from 650 shallow lakes located within two climate zones in the Netherlands (temperate) and Uruguay (subtropical), covering a wide range of environmental characteristics (Kruk et al., 2011). The sampling and sample analyses protocols were similar in both locations. Lakes were sampled at random points integrating the water column and covering the whole lake area. Water samples for nutrients and plankton were taken integrating the water column with a plastic tube (20-cm diameter) and combining from 3 to 20 random replicates in each lake. Phytoplankton samples were fixed in Lugol’s solution and total phosphorus (TP, mg L^{-1}) was estimated. Details on sample analysis are provided in Kruk et al. (2009).

Phytoplankton populations were counted in random fields from fixed Lugol samples using the settling technique (Utermöhl, 1958). We examined the samples at multiple magnifications and counted until we reached at least 100 individuals of the most frequent species (Lund et al., 1958). Organisms between 5 and 100 μm were counted at 400 \times , larger organisms were counted at 200 \times , and organisms between 5 and 2 μm were counted at 1000 \times . We did not include picoplanktonic species (<2 mm) or species strongly associated

with periphytic communities. For all lakes, we considered the organism as the unit (unicell, colony or filament). Cell numbers per colony as well as organism dimensions, including maximum linear dimension (MLD, μm) were estimated. Individual volume (V , μm^3) and surface (S , μm^2) were calculated according to geometric equations (Hillebrand et al., 1999). For colonial organisms with mucilage, V and S calculations were made for whole colonies including mucilage. Population biovolume was estimated ($\text{mm}^3 \text{L}^{-1}$) and calculated as the individual volume of the species multiplied by the abundance of individuals. Most of the samples were analyzed by the same group of scientists using the same identification keys and a common protocol. However, to diminish the potential taxonomical discrepancies between different data sets, we did not include the organisms that were not identified at least at the class level. Also, organisms from the same genus but not identified to species level were grouped together. We also excluded the species with a contribution of less than 5% to the total community biomass in any individual lake. Richness was estimated as the sum of species per lake.

We classified species into phylogenetic classes following Van Den Hoek et al. (1997), except cyanobacteria (Pérez et al., 1999; Komárek and Anagnostidis, 2005) and Bacillariophyceae (Round, 1992). We also classified the species into size classes, selected to represent the main growing strategies of phytoplankton. Following Reynolds (1988), we plotted the mean values per species of all lakes of $\log S/V$ versus $\log \text{MLD}$ and selected five MLD classes corresponding to < 3 , 3–10, 10–30, 30–100 and $> 100 \mu\text{m}$ that have a more homogeneous distribution of the species. For each class and each size class, the biovolumes were summed per sample. In the case of classes, the biovolume was transformed into percentage to compare the relative contribution in each climatic region.

Total richness of 5% species, total biovolume and the percentage of each phylogenetic group biovolume were tested for differences in their median value between subtropical and temperate regions using Kruskal–Wallis tests.

C.2. Latitudinal gradient meta-analysis

A meta-analysis of data was done searching in published and un-published sources for total chlorophyll-a (Chl-a) and its relationship with total phosphorus (TP), determined using simple linear regression with \log_{10} -transformed data in all studies. The considered studies had comparable sampling procedure and sample analysis. A total of 290 cases were obtained for Chl-a including tropical, subtropical, temperate, cold and polar lakes.

A total of 28 models were calculated from the data available with Statistica software or obtained from the cited references (see Table 3).

Chlorophyll concentration as well as the slope and r^2 of the relation between (\log_{10} -transformed) chl-*a* and TP were tested for differences in their median value among climatic regions (tropical, subtropical, temperate, cold and polar lakes) using Kruskal–Wallis tests and *post hoc* multiple comparisons (*Z* value). We used this type of analysis due to its widespread use in the relevant literature, thus allowing us to increase the power of our comparison. KW test was selected due to the uneven number of cases in each climate region for all categorical variables.

Data on phytoplankton species richness and latitude from Stomp et al. (2011) (Ecological Archives E092-183-S1 in <http://esapubs.org/archive/ecol/E092/183/suppl-1.htm>) were used to estimate the r^2 of the linear relation between richness and latitude.

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