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Climate change impacts on lakes: an integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes

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ABSTRACT

Freshwater ecosystems and their biodiversity are presently seriously threatened by global development and population growth, leading to increases in nutrient inputs and intensification of eutrophication-induced problems in receiving fresh waters, particularly in lakes. Climate change constitutes another threat exacerbating the symptoms of eutrophication and species migration and loss. Unequivocal evidence of climate change impacts is still highly fragmented despite the intensive research, in part due to the variety and uncertainty of climate models and underlying emission scenarios but also due to the different approaches applied to study its effects. We first describe the strengths and weaknesses of the multi-faceted approaches that are presently available for elucidating the effects of climate change in lakes, including space-for-time substitution, time series, experiments, palaeoecology and modelling. Reviewing combined results from studies based on the various approaches, we describe the likely effects of climate changes on biological communities, trophic dynamics and the ecological state of lakes. We further discuss potential mitigation and adaptation measures to counteract the effects of climate change on lakes and, finally, we highlight some of the future challenges that we face to improve our capacity for successful prediction.

Key words: eutrophication, water level change, predictions, salinity, modelling, trophic dynamics, space for time substitution, palaeolimnology.

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INTRODUCTION

Freshwater ecosystems and their biodiversity are presently seriously threatened by global changes (Millennium Ecosystem Assessment, 2005; Bellard *et al*., 2012). As the world population grows, pressure to produce more food, whilst simultaneously producing crops for biofuel, will likely lead to further increases in nutrient inputs and intensification of eutrophication problems in receiving fresh waters. Despite large variability and uncertainty in the projections of current climate models (Knutti and Sedláček, 2013), a substantial change in climate is predicted to occur in this century (IPCC, 2007), and effects are already visible in many ecosystems (Parmesan and Yohe, 2003; Thackeray *et al*., 2010). Climate change is expected to alter directly and indirectly the community structure and ecosystem functioning of fresh waters worldwide (Jeppesen *et al*., 2010a, 2010b, 2012b; Woodward *et al*., 2010). Changes are to be expected in species distribution (Parmesan and Yohe, 2003) and food-web dynamics (Perkins *et al*., 2010), phenology (Thackeray *et al*., 2010), life history traits especially in body size (Amarasekare and Savage, 2012; Daufresne *et al*., 2009; Gardner *et al*., 2011), growth and respiration of organisms and ecosystem metabolism (Yvon-Durocher *et al*., 2012). In addition to changes in mean ambient temperature, major changes in precipitation patterns are expected worldwide based on multiple climate models (Knutti and Sedláček, 2013). This will lead to enhanced net precipitation in, for instance, vast areas in the North temperate zone (IPCC, 2007), particularly during winter. In cultivated areas, this will most probably be accompanied by higher nutrient loading from the catchment to the lakes (Jeppesen *et al*., 2009, 2011). Increases in dissolved organic carbon (DOC) can also result from increased precipitation and runoff, depending on the changes in terrestrial vegetation cover, wetlands, ice melting, *etc*. (Tranvik *et al*., 2009). In other parts of the world, in contrast, net precipitation is expected to decrease, not least in the Mediterranean region where as much as a 25-30% decrease in freshwater runoff is expected by 2040-61 (Giorgi, 2006; Giorgi and Lionello, 2008). While such a reduction may decrease the nutrient input to lakes in this region, the concentrations may still remain high, particularly in shallow lakes, due to higher internal loading associated with warmer conditions along with the concentration of nutrients in less water (Özen *et al*., 2010). As there is a strong linkage between climate and the hydrological cycle, warming can also enhance drought (Wrona *et al.*, 2006; Trenberth *et al.*, 2014) with strong implications for water level and salinity in lakes in arid and semi-arid climates (Wantzen *et al*., 2008 and references therein; Beklioğlu *et al*., 2011). During prolonged periods of drought, salt accumulates each year and may ultimately cause a shift to oligosaline or mesosaline conditions (Beklioğlu *et al*., 2011; Beklioğlu and Tan, 2008; Jeppesen *et al*., 2009; Kazancı *et al*., 2008). In the most extreme circumstances, drought will transform permanent water bodies into temporary systems (Beklioğlu *et al*., 2007), with strong consequences for the biota even at complex, multispecies levels (Ledger *et al*., 2013) and the provision of ecosystem services.

Climate warming and other components of global change, such as a growing population demanding a higher food production, will lead to major changes in agricultural land use and management, including changes in the choice of crops, crop rotation and use of cash crops, and in agricultural practices, including tillage and fertilisation as well as the rates and timing of fertilisation (Howden *et al*., 2007; Olesen *et al*., 2007). Autonomous adaptation to climate change in the agricultural sector is likely to lead to intensified production in areas with increased precipitation such as the temperate zone of the northern hemisphere and some areas of the southern hemisphere (*e.g.*, centre and southeast of South America; Marengo *et al.*, 2009) and to less intensive production in warm temperate and Mediterranean regions, largely as a result of reduced availability of water for irrigation (Olesen and Bindi, 2002; Alcamo *et al*., 2007; IPCC, 2007). In the latter areas or at locations with enhanced summer drought and increased winter precipitation mostly in the form of rain instead of snow, especially at high-elevated parts with uncertainties in water availability, the construction of reservoirs for water storage will likely become a common method to secure irrigation for crops, with negative consequences for biodiversity and water quality of previously running fresh waters (Sen *et al*., 2013; Baxter, 1977).

It is evident from recent studies that some climate change impacts on fresh waters are similar to the effects of eutrophication (Chen *et al*., 2003; Meerhoff *et al*., 2007a; Jeppesen *et al*., 2009; 2010a,b; Moss *et al*., 2011), although the influence of the processes in the catchment and the effects of climate change can vary depending on geographical location, regional climate, land use in lake basins and variations in lake characteristics, such as surface area, depth and fetch. Besides the expected effects of changes in temperature and net precipitation, more projected frequent extreme events (heatwaves, storms, extreme rain) may potentially affect also ecosystem stability (Thompson *et al*., 2013) (*e.g*., by enhancing mismatch of species distributions and interactions; Kishi *et al*., 2005; Durant *et al.,* 2007) and lead to greater sensitivity to increasing nutrient loading and fish kills (Moss *et al*., 2011). To further our understanding of the responses of freshwater ecosystems to a changing climate and contribute to their conservation with adequate mitigation measures (Jeppesen *et al*., 2010a, 2010b; Montoya and Rafaelli, 2010), it is therefore of utmost importance to be able to disentangle the specific effects of environmental warming from nutrient enrichment and other global changes, and even from the effects of climate change adaptation measures (Destouni *et al.*, 2013), and to search for coherent signals that may be associated with climate change (Parmesan and Yohe, 2003; Adrian *et al*., 2009). Studies of lakes provided some of the early indications of the effects on ecosystem structure and function (Magnuson *et al*., 2000; Verburg *et al*., 2003) and the consequences for ecosystem services (O'Reilly *et al*., 2003) resulting from the current climate change, adding to the changes by the already substantial human impact. From the studies conducted so far, it is evident that a combination of approaches, overcoming each individual weakness (Tab. 1), is needed to gain deeper insight into climate change effects on lake ecosystems. Lakes are considered particularly appropriate for climate change investigations because: i) lake ecosystems are well defined and are often studied following more or less standard protocols; ii) lakes respond directly to climate change but also to integrated climate-driven changes in the catchment; iii) lakes typically integrate responses over time, thus reducing inter-annual variability; iv) lakes are globally distributed, thus capturing different aspects of climate change (*e.g*., rising temperatures, changing precipitation patterns, glacier retreats, permafrost melting) (Adrian *et al*., 2009); and v) lakes have a sedimentary record which can be used to either infer past changes in climate or to track ecological responses to climate change on decadal to millennial timescales (Schindler, 2009). Consequently, lakes offer a particularly unique opportunity to detect climate-driven changes (Adrian *et al*., 2009).

In this paper, we first describe the strengths and weaknesses of the various approaches that are presently available for elucidating the role of climate change in lakes, including space-for-time substitution, time series, experiments, palaeoecology and modelling. By combining knowledge gained from the different approaches highlighted in Tab. 1, we subsequently discuss the potential effects of climate change on the response of biological communities and trophic dynamics and the consequences for ecological state. We particularly focus on warming since comparatively few studies have addressed other aspects of climate change. These other climate change-related drivers include change in UV radiation (Williamson *et al*., 2010), CO_2 enrichment (Andersen *et al*., 2005), precipitation or water level (Berger *et al*., 2007, 2010; Bucak *et al*., 2012) and acidification (Christensen *et al*., 2006), either in isolation or interacting with some of the more obvious aspects of climate change (Christensen *et al*., 2006; Williamson *et al*., 2010). Such studies are, however, too scarce to extract clear patterns of the likely impacts of such changes.

Strengths and weaknesses of approaches to elucidate climate change effects on lakes

To date, most empirical evidence of climate change effects in lakes is derived from space-for-time substitution (SFTS) studies using cross-comparisons of data sampled along climate (latitude or altitude) gradients (Gyllström *et al*., 2005; Jeppesen *et al*., 2007b, 2010a; Meerhoff *et al*., 2007a, 2007b, 2012; Kosten *et al*., 2009a, 2009b, 2012; Brucet *et al*., 2009, 2010, 2012) or from sites with temperature contrasts due to thermal heating (Hillbricht-Ilkowska and Zdanowski 1988; Protasov *et al*., 1997; Socha and Hutorowicz, 2009). The strength of this approach is that the biological assemblages *per se* have had time to evolve and adapt to the climate in which they live. However, a potential weakness is that they may not yet have reached a mature state. This is especially true for the cold regions where speciation is currently occurring, for instance among the dominant fish species (Hudson *et al*., 2011). Moreover, and probably more significant, a weakness of SFTS is that regional biogeographical constraints are not taken into account (Tab. 1). Current patterns in species richness and assemblage composition are strongly influenced by past glaciations, their present distance from the refuges available during those periods and the dispersal barriers that emerged following deglaciation, such as the mountains of Europe (Griffiths, 2006; Abell *et al*., 2008). Additionally, the occurrence of marine regression and transgression events and geomorphological events (such as mountain formations) plays a key role in the current patterns of species richness even in areas that acted as glacial refugia (Lomolino *et al*., 2006). Moreover, although the differences in life history traits between populations at varying latitudes may reflect long-term evolution, they may not indicate how local populations might respond to accelerated climate warming at decadal to centennial scales. In this sense, rapid microevolution of life history traits, such as survival and other aspects of individual performance (*e.g*., age at first reproduction and number of offspring), has been experimentally tracked for zooplankton (Van Doorslaer *et al*., 2007), suggesting that at least some populations may buffer changes in community structure and persist locally under the conditions of the predicted climate warming, either permanently or until some critical environmental conditions are passed. Finally, the accelerated species invasions due to globalisation and warming have implications for the generalisations that can be drawn from STFS. Invasive species may, for example, alter natural lake assemblages at several scales (Burlakova *et al*., 2000; Witte *et al*., 2000; Gurevitch and Padilla, 2004), and the stability and system maturation state depend on the time since first invasion (Strayer *et al*., 2006). Another weakness of the STFS approach is that the influence of co-variates of temperature and the latitudinal variation in other climate-related variables, such as seasonality and the length of growing seasons, may go undetected. Overall, causal relationships are very difficult to identify with SFTS approaches because of their reliance on inferential data. Nonetheless, the SFTS studies have collectively, and more than any of the other methods discussed,

Tab.1. Strengths and weaknesses of different approaches to elucidate climate change effects on lakes.

Approach	Strengths	Weaknesses
Space-for-time substitution (SFTS)	Long-term response and adaptation of communities to ambient temperatures. High spatial resolution.	Inferential – not mechanistic. Steady state of communities and potential non-mature state. Potential confounding factors (biogeography, latitude, major disturbances, co-variates).
Time series (monitoring)	No biogeography effect. True temporal changes (decadal).	Inferential – not mechanistic. Typically short-term records. Created for other purposes.
Palaeo records	True temporal changes (millennial, centennial, decadal).	Inferential. Potential confounding gradients (*e.g*., eutrophication).
Controlled experiments	Mechanistic test of effects.	Oversimplicity, lack of complex interactions. Short-term biological responses to stressor.
Mathematical models	Prediction ability.	Oversimplicity, often lack of potentially relevant ecological variables.

provided new knowledge on how the structure and function of lake ecosystems might be expected to change with global warming.

Other approaches also have their strengths and weaknesses (Tab. 1). Long-term time series hold some potential with better temporal resolution. On the positive side, they are free of biogeographical problems and provide information on the changes to be expected in the short term for different lake characteristics and biological complexity levels (Wagner and Adrian, 2009). Numerous time series studies have provided insight into the impacts of climate-induced changes (*e.g.,* summarised in George, 2010 and Kernan *et al*., 2010), and they indicate, for instance, that the current warming has already had major implications for stratification (and thus, indirectly, for plankton; Verburg *et al*., 2003), enhanced cyanobacterial dominance (Chen *et al*., 2003) and lengthened the growing season and/or altered the timing of spring peaks of phytoplankton and zooplankton (with potential mismatch) (Winder *et al*., 2009). However, these instrumental records are typically short (<30-40 years at the most) and often established for other reasons (*e.g*., monitoring of eutrophication or acidification trends), rendering it difficult to disentangle a climate change signal from the changes related to the other pressures or to lake-specific characteristics. However, the shift in trophic structure, phenology and life histories of organisms (*e.g*., age and size of first reproduction, longevity, seasonal dynamics) in such time series can be used as biological indicators of warming effects (Thackeray *et al*., 2010) as the changes will typically be more profound than expected from those resulting from, for example, nutrient loading reduction (Kernan *et al*., 2010). A clear weakness of this approach, compared to the SFTS approach, is that the effect of long-term changes in flora and fauna expected with global warming cannot be evaluated.

Palaeolimnological approaches have traditionally focussed more on inferring past environments rather than on tracking within-lake ecological change. More recently, however, the utility of a longer-term perspective of ecological change provided by the sediment records has become more apparent. The strength of this approach is that it is holistic, recording real world change with no space-for-time substitution, which also leads to its main drawback, *i.e.* the question of how to disentangle the multiple drivers behind the observed patterns. In addition, sediment resuspension is often thought to smooth the signal of change contained in the sediment record, in particular in shallow lakes. Separating climate effects from other human-induced pressures can be problematic, which is particularly evident for the past 200 years in the more developed areas of the world (Kernan *et al*., 2010). It is, however, possible to track ecosystem change with negligible anthropogenic impact if the records cover several centuries (Gregory-Eaves and Beisner, 2011) or are obtained from the currently more pristine ecosystems of the globe, such as lakes and ponds in the Arctic (Smol *et al*., 2005). In the sub-tropics (with a short history of anthropogenic impacts), analysis of sediment cores has suggested that climate amelioration (*i.e.,* warmer and more humid conditions) has co-occurred with events of natural eutrophication (García-Rodríguez *et al*., 2004; Inda *et al*., 2006). However, in more populous regions with a long history of catchment activity, it has generally proved very difficult to separate the effects of recent climate change from other anthropogenic pressures, in particular point and diffuse source nutrient addition (Bennion *et al*., 2012), acidification (Simpson and Anderson, 2009) and atmospheric nitrogen deposition (Hobbs *et al*., 2010). A comparison of the nature, magnitude and rate of ecosystem change driven largely by climate in the past, for example around the Little Ice Age, with current warming could potentially help identify the climate signal in contemporary datasets.

Controlled experiments can separate distinct effects in relatively simple, though not necessarily very unrealistic, systems (Moss *et al*., 2003; Liboriussen *et al*., 2005; Yvon-Durocher *et al*., 2010). Despite a potentially high degree of realism, several aspects of true ecosystems are typically not reflected in experiments, such as the coupling with other habitats (terrestrial, littoral, benthic, *etc*.), including several trophic levels and the wide range of species richness and body sizes that occurs naturally in most freshwater systems due to scale limitation. This limitation is clearly demonstrated as most experimental studies have focussed on elucidating the responses to warming of plankton communities. Furthermore, in real ecosystems the many pressures act not only simultaneously but also interactively, rendering it difficult to make firm predictions about climate warming effects from experiments alone. Additionally, observations reflect the short-term responses of an immature system as most experiments run for a season or for a few years. Accordingly, despite a similar level of complexity, current climate-warming mesocosm experiments have shown quite contrasting results (summarised in Stewart *et al*., 2013). In general, climate change experiments in fresh waters have focused on increases in mean temperature as the main external stressor, leaving aside other components of climate change including temperature variability and precipitation changes as well as the occurrence of extreme events (Stewart *et al*., 2013; Thompson *et al.*, 2013). In all cases, researchers need to make decisions about which global circulation models to use and under which emissions scenarios, downscaled to local conditions, to design more realistic experiments (Thompson *et al.*, 2013).

Mathematical modelling includes a wide variety of approaches and complexity that are highly relevant for describing, among other processes, the trophic dynamics and metabolism in lakes (Mooij *et al*., 2005, 2010). A range of modelling approaches have been developed during the past three decades, including, for example, individual-based models, minimal dynamic models and complex dynamic ecosystem models, as reviewed in detail by Mooij *et al*. (2010). As individual-based models and minimal dynamic models typically focus only on a subset of an ecosystem, these models are typically used for simple hypothesis testing, while the more complex dynamic ecosystem models are used in attempts to make projections of future ecosystem states given future changes in external forcing. Today, these mechanistic numerical models, integrating the complex physico-chemical responses to climate change, play an important role for both the testing of hypotheses (system understanding) and for projecting the future state of ecosystems, and the conceptual models and modelling approaches undergo continuous development (Mooij *et al*., 2010, Trolle *et al*., 2012). While the complex dynamic ecosystem models may be useful for making general predictions, these are still simplistic descriptors of reality and therefore also have their limitations (Mooij *et al*., 2010; Trolle *et al*., 2008, 2011). Moreover, lack of good quality data to parameterise the model is one of the main disadvantages currently faced by this approach. Hence, the prediction of climate change effects on lakes by modelling is typically based on a single model set-up and on one set of model parameters (calibrated or with default values) without taking into account uncertainties. This limitation can, however, be at least partly overcome by compiling an ensemble of model runs (*e.g*., with multiple sets of parameter value combinations) (Nielsen, 2013), which enables uncertainty estimations and also helps identify key areas of uncertainty (and sensitivity) that will be critical for further research and model development. This ensemble technique is therefore likely to become a commonplace methodology in the near future and may thus help accelerate model development.

Trophic structure and dynamics in the pelagic zone of lakes

Based on theoretical expectations and empirical evidence, we can expect major changes in pelagic ecosystem structure and dynamics with climate change, having implications for the ecological state of lakes. Although evidence is often lake-specific, several studies using SFTS, time series, snapshot monitoring data and experiments together indicate that the fish community assemblages, size structure and dynamics will change markedly with global warming and that changes have already occurred in the past decades coinciding with elevated temperatures (Tab. 2).

A study of time series data from 24 European deep and shallow lakes indicates major changes in composition, especially a decline in the abundance of several cold-stenothermal species, in particular in shallow lakes, and an increase in the proportion of eurythermal species, even in deep, stratified lakes (Fig. 1; Jeppesen *et al*., 2012a). This change has occurred despite a reduction in nutrient loading in most of the case studies arising from efforts to reduce eutrophication and its symptoms in European lakes, which otherwise favour the fish typically living in cold-water, low-nutrient lakes. The cold-stenothermic Arctic charr (*Salvelinus alpinus*) has been particularly affected, showing a population decline in, for example, Lake Elliðavatn in Iceland, Lake Windermere in the UK (Winfield *et al*., 2010) and Lake Vättern in Sweden (Jeppesen *et al*., 2012a), and also the growth rate of Arctic charr has declined in Scandinavian hydroelectric reservoirs (Milbrink *et al*., 2011). Other cold-water adapted species, such as coregonids and smelt (*Osmerus eperlanus*), have also been affected at the southern edge of their geographical distribution. The harvest of whitefish (*Coregonus* spp.) has declined substantially in Lake Vättern as well as in Lake Peipsi in Estonia (Jeppesen *et al*., 2012a; Kangur *et al*., 2007; Kangur *et al*., 2013). In the UK and Ireland, a decline in the coregonid pollan (*Coregonus autumnalis*) in recent decades has also been attributed to warming (Harrod *et al*., 2002). A drastic reduction in the population of smelt has occurred in shallow Lake Peipsi, as judged from commercial harvests, the decline being particularly remarkable in years with extensive heat waves (Kangur *et al*., 2007; Jeppesen *et al*., 2012a). By contrast, the abundance of eurythermal species, including the thermo-tolerant carp (*Cyprinus carpio*), roach (*Rutilus rutilus*) and pikeperch (*Sander lucioperca*), has increased in several lakes in Europe (Lehtonen, 1996; Jeppesen *et al.*, 2012a). Monitoring data covering three decades in Lake Ontario, Canada, also revealed that climate change might have resulted in a substantial reduction in the recruitment of cold-water and cool-water species and an increase in the recruitment of warm-water species (Casselmann *et al*., 2002). Higher recruitment of warm-water species in warm years has been demonstrated in some lakes in Europe (Lehtonen and Lappalainen, 1995).

Although most aspects of life history are related to climate at an evolutionary scale, several trends are consistent with observed changes at short term, ecological scale. A reduction in body size of fishes with increasing water temperature has been detected with time series in French rivers (Daufresne and Boet, 2007) and for some (but not all) typical species in Danish lakes (Jeppesen *et al*., 2010b). Cross-comparisons of fish populations in similar shallow lakes in subtropical South America and temperate Europe (SFTS) (Teixeira-de Mello *et al*., 2009) and in lakes of varying depth along latitudinal gradients within Europe have shown that lower-latitude fish species are often not only individually smaller (Griffiths, 1997; Jeppesen *et al*., 2010a; Brucet *et al*., 2013) but also grow faster, mature earlier, have shorter life spans and allocate

Tab. 2. Expected trends in buffer mechanisms that help maintain clear water in shallow lakes with climate change, as suggested by different research approaches. Empty cells highlight the absence of data in the climate change literature consulted for this review. See Fig. 5 for a graphical representation of the different mechanisms and their typical effects on the environmental state of lakes in the temperate zone.

	Theoretical expectations	Palaeo	SFTS	Time series	Heating expectations	Models
Sediment resuspension	Increased if more precipitation and changes in fish community					Deeper thermocline and changes in mixing (4,34)
Internal loading	Increased due to higher decomposition rate and sediment release with temp.				Increased phosphorus (25,27)	Increased phosphorus (4,26,36,44)
Competition	Enhanced due to higher metabolism					Faster nutrient limitation for nutrients to phytoplankton (13,34)
Competition for light	Enhanced due to increased turbidity (more runoff, mixing regime, change in trophic structure)	Enhanced (54)		Enhanced (3)		Enhanced (deep lakes, 34)
Submerged plant biomass	Depends on theory and on balance between direct and indirect effects		Reduced biomass in cold lakes and higher sensitivity to nutrients (30)	Reduced in cold lakes (due to lower fish kills with warming) (22)	No effect (15,38)	Decreased due to increasing turbidity (44,50)
Free-floating plant biomass	Increased due to higher air temp.				Increased (15,48)	
Phytoplankton biomass	Depends on theory and outcome of direct and indirect factors	Increased (54,55)	No clear latitudinal effect (42)	Increased (9)	Increased (28); no effect (15,47); decrease (32,60); effect depending on trophic length (21)	Increased (36,44,59); no annual change but increase in spring (13)
Cyanobacteria	Enhanced biomass		Increased (27,31,42)	Increased (9,27)	Increased (11,21); no effects (47); no competitive advantage (35)	Increased (1,11,13,50,59)
Allelopathy	Likely enhanced due to enhanced metabolism				Increased (filamentous algae on phytoplankton) (58)	
Fish assemblage	Smaller fish; enhanced omnivoroy		Smaller size (7,28,40,56); increased omnivory (18,40,46,55)	Reduced size (10,28); changes in community composition (29)	Decreased biomass (45); decreased fitness (24)	Increased predation capacity (23,43); changes in distribution (52)
Grazing macro-invertebrates	Smaller invertebrates, reduced densities		Reduced densities (6,40)	Unclear effects (2); changes in community composition (8)	Unclear effects (2); no effects on densities (14,39); differential seasonal effects on size (12); advanced phenology (19)	
Zooplankton	Smaller size, reduced biomass and lower grazing capacity	Increased pelagic taxa (54); smaller taxa (49)	Reduced size and grazing capacity (5,17,20,33,41)		No clear effect (37,51); enhanced grazing (32,53)	Decreased abundance (44)
Refuge by plants to zooplankton	No prediction		Decreased (5,41)		Changed phenology (16)	
Benthic/pelagic balance	Enhanced pelagic production	Increased pelagic (54,57)			Increased pelagic production (53)	

The numbers in the table correspond to the following references, in alphabetic order: 1. Arheimer et al.*, 2005; 2. Baulch* et al.*, 2005; 3. Beklioğlu* et al.*, 2006; 4. Bleckner* et al.*, 2002; 5. Brucet* et al.*, 2010; 6. Brucet* et al.*, 2012; 7. Brucet* et al.*, 2013; 8. Burgmer* et al.*, 2007; 9. Chen* et al.*, 2003; 10. Daufresne and Boet, 2007; 11. De Senerpont Domis* et al.*, 2007; 12. Dossena* et al.*, 2012; 13. Elliot* et al.*, 2005; 14. Feuchtmayr* et al.*, 2007; 15. Feuchtmayr* et al.*, 2009; 16. Feuchtmayr* et al.*, 2010; 17. Gilloly and Dodson, 2000; 18. González-Bergonzoni* et al.*, 2012; 19. Greig* et al.*, 2011; 20. Gyllström* et al.*, 2005; 21. Hansson* et al.*, 2012; 22. Hargeby* et al.*, 2004; 23. Hill and Magnuson, 1990; 24. Hopkins* et al.*, 2011; 25. Jensen and Andersen 1992; 26. Jensen* et al.*, 2006; 27. Jeppesen* et al.*, 2009; 28. Jeppesen* et al.*, 2010b; 29. Jeppesen* et al.*, 2012a; 30. Kosten* et al.*, 2009a; 31. Kosten* et al.*, 2012; 32. Kratina* et al.*, 2012; 33. Lacerot, 2010; 34. Lehman, 2002; 35. Lürling* et al.*, 2012; 36. Malmaeus* et al.*, 2006; 37. McKee* et al.*, 2002a; 38. McKee* et al.*, 2002b; 39. McKee* et al.*, 2003; 40. Meerhoff* et al.*, 2007a; 41. Meerhoff* et al.*, 2007b; 42. Meerhoff* et al.*, 2012; 43. Mehner, 2000; 44. Mooij* et al.*, 2007; 45. Moran* et al.*, 2010; 46. Moss, 2010; 47. Moss* et al.*, 2003; 48. Netten* et al.*, 2010; 49. Nevalainen* et al.*, 2013; 50. Nielsen, 2013; 51. Özen* et al.*, 2012; 52. Sharma* et al.*, 2007; 53. Shurin* et al.*, 2012; 54. Smol* et al.*, 2005; 55. Sorvari* et al.*, 2002; 56. Teixeira de Mello* et al.*, 2009; 57. Thies* et al.*, 2012; 58. Trochine* et al.*, 2011; 59. Trolle* et al.*, 2011; 60. Yvon Durocher* et al.*, 2011.*

less energy to reproduction than species at higher latitudes (Blanck and Lammouroux, 2007) (Fig. 2, from Meerhoff *et al.*, 2012). Additionally, a greater number of fish for a similar TP concentration was found in warm compared to cold lakes at a European continent scale (Brucet *et al.*, 2013). Moreover, global analyses indicate that the percentage of omnivorous species within the fish assemblage is higher at lower latitudes and in warmer climates [Fig. 3 (modified from González-Bergonzoni *et al*., 2012); Moss, 2010] and that food webs likely are more truncated. Similarly, in an SFTS study covering 30 shallow Turkish lakes, clear evidence has been found of higher fish predation and stronger cascading effects of fish in southern than in colder northern lakes. Such changes along a latitudinal gradient appear also at the species level (Blanck and Lammouroux, 2007; Lappalainen *et al*., 2008; Volta *et al*., 2013) and for assemblages within the same biogeographical area (González-Bergonzoni *et al*., 2012).

When fish have been included in heating experiments [either as a response variable (Moran *et al*., 2010), or as a predation treatment (McKee *et al*., 2002a, 2002b; Liboriussen *et al*., 2005)], a single, small species has been used, thus limiting the comparability of the results with real world data. The scarce evidence coming from experiments has shown changes in the behaviour of the three-spined stickleback (*Gasterosteus aculeatus*), including a reduction in nesting, time spent at nest sites and incubation success with increasing water temperature (Hopkins *et al*., 2011) and a strong reduction in their biomass, leading to massive mortality if warming interacts with nutrient enrichment (Moran *et al*., 2010). Therefore, changes in life history traits and body size of fishes can be expected with warming and may already have occurred at different organisation levels (from individuals to communities), even for quite resilient species such as those typically used in the heating experiments. Changes in fish assemblages and traits typically have major cascading effects in lake ecosystems, increasing the predation pressure on zooplankton and, consequently, reducing the grazing pressure on phytoplankton, consequently resulting in higher algal biomass (and chlorophyll *a*) per unit of phosphorus, as judged from SFTS studies in Europe and elsewhere (Gyllström *et al*., 2005; Jeppesen *et al*., 2010a, 2010b; Meerhoff *et al*., 2012) (Fig. 4). Increased fish predation on zooplankton with warming has also been predicted by models (Mehner, 2000). Similarly, a major decrease in fish size along a temperature gradient associated with a decrease in zooplankton mean size was found in the SFTS study of the 30 shallow Turkish lakes, suggesting future changes in fish size structure as a consequence of climate change that may cascade to the whole aquatic

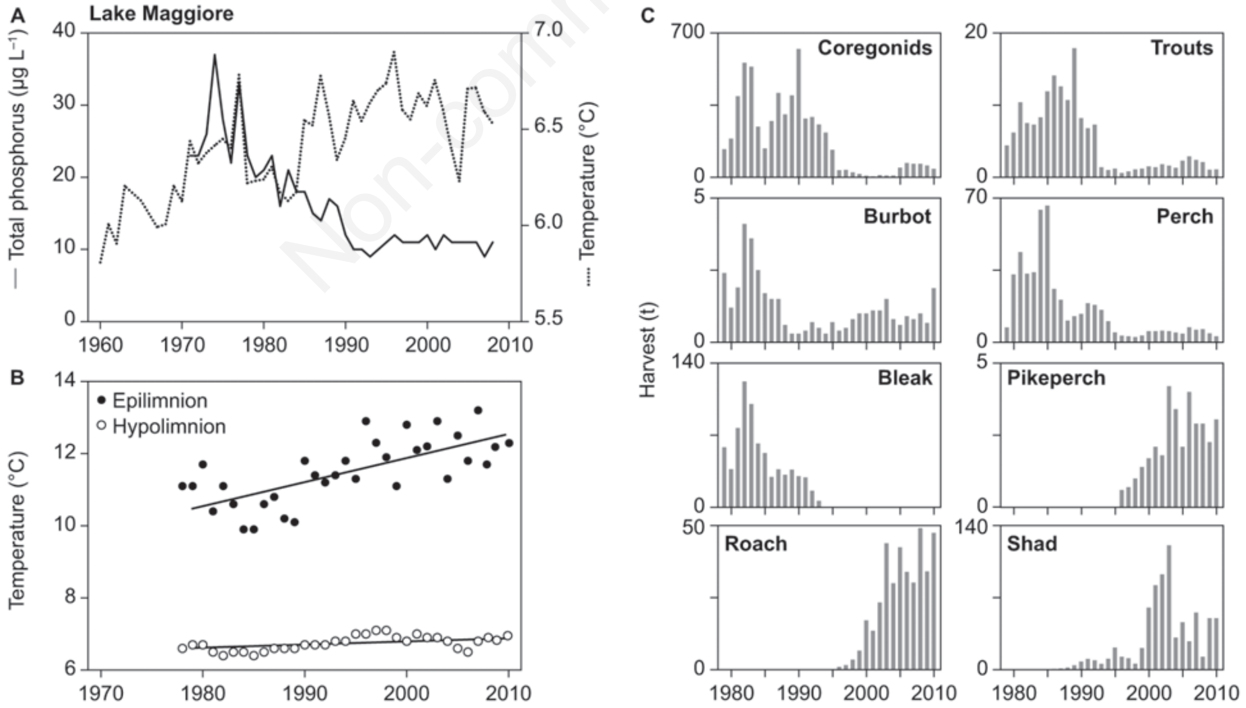

Fig. 1. Lake Maggiore. A) Mean water temperature and total phosphorus at the spring overturn. B) Annual mean water temperature of the epilimnion (0-25 m depth) and hypolimnion (25-360 m depth). C) Annual commercial harvest (in tonnes) of the most important fish species as registered in the fishery statistics by CISPP (Italian Swiss Commission for the Fisheries). From Jeppesen *et al.* (2012a).

food web. Such interactions are particularly relevant for shallow lakes where changes in the fish community can trigger dramatic shifts in the environmental state of the ecosystem (Fig. 5; Scheffer *et al*., 1993; Jeppesen *et al*., 1998).

Latitudinal gradient studies (not necessarily designed to test climate change impacts) (Gillooly and Dodson, 2000) have shown a decrease in the size of cladoceran zooplankton from high to low latitudes, which is supported by findings from time series from cold summers to warm summers (Jeppesen *et al*., 2012b). While dominance of small-bodied forms with higher water temperature is in accordance with the predictions by the metabolic theory of ecology (Brown *et al*., 2004) and several other theories and rules (Daufresne *et al*., 2009), recent studies have shown a more complex pattern involving major changes in zooplankton body size related to differences in trophic dynamics and interactions under different climates (Meerhoff *et al*., 2007a, 2007b; Brucet *et al*., 2010, 2012; Iglesias *et al*., 2011). Supporting the view of enhanced predation-induced changes in cladoceran mean size under warm climates (Meerhoff *et al*., 2007a, 2007b), Iglesias *et al*. (2011) found that large-bodied *Daphnia* became dominant, albeit briefly, after summer fish kills in a subtropical Uruguayan lake and in experiments ran at low fish abundances, despite high water temperatures in both cases. Furthermore, the biomass of zooplankton is often lower in warm lakes than would be expected from the available food resources (*i.e.,* low zooplankton: phytoplankton biomass ratio) (Gyllström *et al*., 2005; Havens and Beaver, 2011; Meerhoff *et al*., 2012), which is considered a clear indication of high fish predation (Jeppesen *et al*., 2004). Lower mean body size of zooplankton may also di-

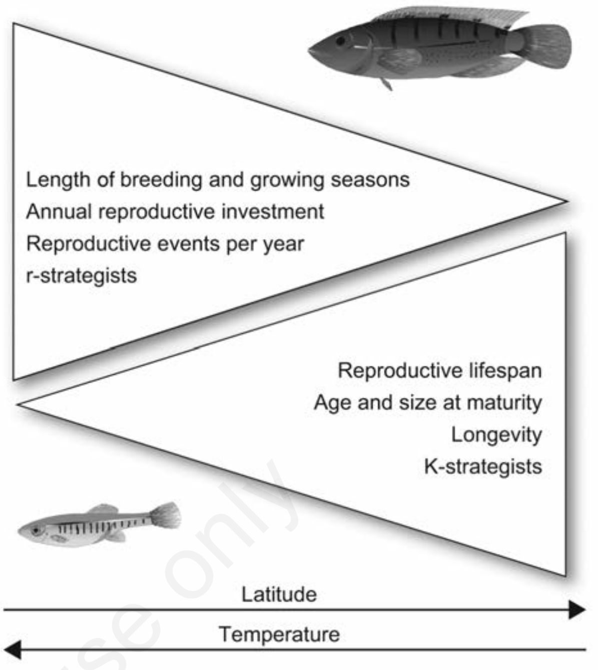

Fig. 2. Expected changes in the main life history traits of fish along a temperature and latitudinal gradient based on our review of literature from inland water systems. With increases in temperature, longer breeding and growing seasons, annual reproductive investment and more reproduction events are 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. From Meerhoff *et al.* (2012).

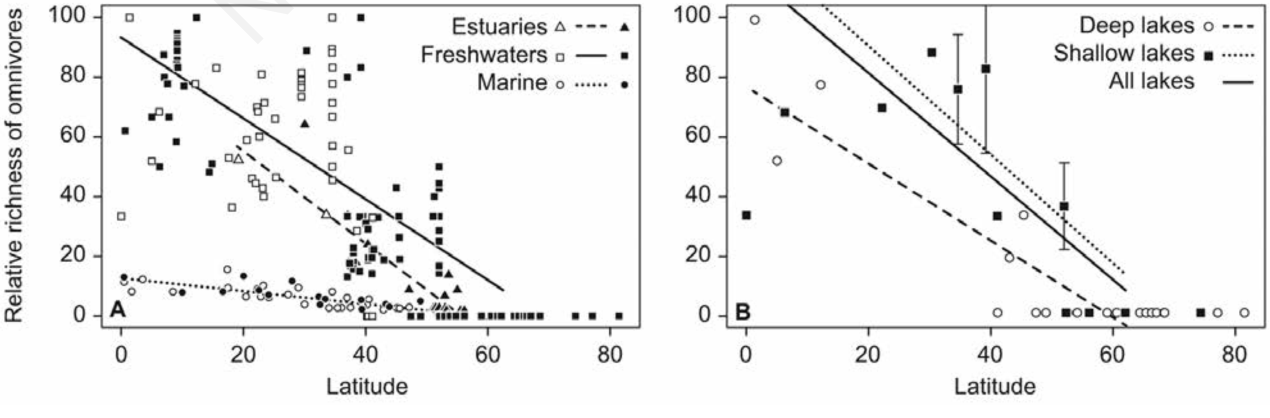

Fig. 3. Relationship between latitude and relative richness of omnivorous fish species. Left panel: for freshwater (n=162, r^2=0.51), estuarine (n=22, r^2=0.80) and marine systems (n=44, r^2=0.67). Right panel: relationship for deep lakes (r^2=0.81 n=26), shallow Lakes (r^2=0.47, n=62) and all lakes grouped (r^2=0.51, n=88). Data from multiple lakes at same latitude are shown as mean and standard deviation. All linear regressions are significant (P<0.001), although the relationship seems to become steeper with decreasing salinity and to be steeper in shallow lakes than in deep lakes. Modified from González-Bergonzoni *et al.* (2012).

minish the grazing pressure on large-sized phytoplankton, for instance some cyanobacteria species, which may themselves affect zooplankton body size due to physical interference with their feeding apparatus, the production of toxins, *etc*. (DeMott *et al*., 2001; Sarnelle *et al.*, 2010).

Fish abundance, and thus predation on zooplankton, may also be influenced by changes in the duration of ice cover in cold lakes. Comparative studies of Danish coastal lakes and continental Canadian lakes with similar summer but lower winter temperatures revealed much higher zooplankton: phytoplankton biomass ratios and much lower yield expressed as chlorophyll a:TP ratios in the Canadian lakes, likely due to lower winter survival of zooplanktivorous fish under ice (Jackson *et al*., 2007). Reduced ice cover in winter, as expected with climate warming, might, therefore, enhance fish survival. This would potentially have strong cascading effects through the food web, reaching phytoplankton and thus altering water clarity (Balayla *et al*., 2010; Ruuhijärvi *et al*., 2010), not only during the summer season but also during winter (Sørensen *et al*., 2011). This cascading effect would reinforce the symptoms of eutrophication in the nutrient-rich systems.

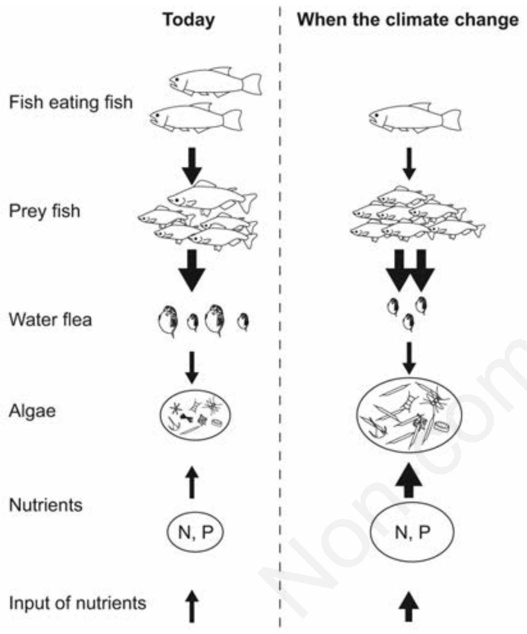

Fig. 4. Conceptual model showing trophic structure in meso-eutrophic temperate lakes and the suggested changes resulting from climate warming. Today, top-down control by piscivorous fish is medium to low depending on nutrient level, and the abundance of cyprinids feeding on large-bodied zooplankton is, conversely, medium to high. Accordingly, *Daphnia* biomass is moderate to low as is the grazing pressure on phytoplankton. Such lakes are sensitive to additional nutrient loading but somewhat buffered by grazing by zooplankton and other stabilising mechanisms (*sensu* Scheffer *et al.*, 1993) at low nutrient levels. As lakes warm, a variety of processes will lead to increasing dominance by small fish, with less abundant and smaller zooplankton. Accordingly, the lakes will be more sensitive to addition of nutrients and other external stressors, such as changes in water level. Moreover, cyanobacteria will likely be stimulated by both higher temperature and higher external and internal nutrient loading (from Jeppesen *et al*., 2012b).

Although no clear current latitudinal pattern of phytoplankton biomass emerged in an SFTS meta-analysis (Meerhoff *et al*., 2012), phytoplankton may be less grazed in a warmer climate, while their growth may furthermore be stimulated markedly by enhanced nutrient loading and higher temperatures. We can expect higher internal loading of phosphorus in response to the higher temperatures in shallow lakes, more prolonged stratification in deep lakes or temporary stratification in more shallow lakes (Jensen and Andersen, 1992; Søndergaard *et al*., 2003). Such processes can boost the decomposition of organic matter and thus oxygen depletion at the water-sediment interface, further exacerbating the release of phosphorus from the sediment (Søndergaard *et al*., 2003). Supporting this view, palaeoecological studies showed an increase in pelagic relative to benthic algal production with warming in a lake in the highlands of Austria (Thies *et al*., 2012) and in Arctic lakes (Smol *et al*., 2005), followed by a shift in community composition to taxa reflecting a more enriched trophic status. Considering most available evidence, we can further expect a higher proportion of potentially toxic cyanobacteria among the phytoplankton assemblage in a warmer climate. Studies during heat waves in the northern hemisphere indicate a positive temperature effect on cyanobacteria biomass (Huisman *et al*., 2005; Reynolds, 2006; Jönk *et al*., 2008; Wagner and Adrian, 2009), while a study of numerous Danish lakes (>800 lake-years sampled in summer) also indicates a higher likelihood of cyanobacterial dominance in warmer years (Jeppesen *et al*., 2009). Further support comes from SFTS studies (Jeppesen *et al*., 2010b; Kosten *et al*., 2012; Meerhoff *et al*., 2012) and long-term data series (Chen *et al*., 2003; Kernan *et al*., 2010).

It is important to note, however, that experimental results have provided more ambiguous results than STFS and palaeoecological studies (Tab. 2), despite being conducted under relatively controlled conditions. In a two-year warming experiment undertaken in the UK (Moss *et al*., 2003, Feuchtmayr *et al*., 2009), warming had only minor effects on phytoplankton chlorophyll-a and on total phytoplankton biovolume with a 3°C temperature rise. Effects were greater at 4^{o}C, although the temperature increase did not affect the abundance of phytoplankton, including cyanobacteria. In another series of outdoor heating experiments in the UK, warming shifted the composition and distribution of phytoplankton size and biomass from assemblages dominated by large species with high standing biomass to assemblages with low standing biomass and many smaller-bodied species, including small cyanobacteria (Yvon-Durocher *et al*., 2011). A weakening of the summer phytoplankton bloom was found in heating experiments by Kratina *et al*. (2012). An experiment conducted in Denmark showed, in contrast, a strong positive effect of warming (IPCC A2 and A2+50% scenarios downscaled to local predictions) on phytoplankton chlorophyll-a after two years of warming under low nutrient concentrations. The same held true at high nutrient concentrations in the A2 scenario, but not in the A2+ 50% scenario where filamentous algae became dominant (Jeppesen *et al*., 2010b). Allelopathic effects of these filamentous algae on phytoplankton would explain the low phytoplankton biomass in these mesocosm experiments (Trochine *et al*., 2011), highlighting other unpredicted responses to warming.

In contrast, no clear effects on the densities of zooplankton were detected in the mesocosms in the UK (McKee *et al*., 2002a, 2002b) or in Denmark (Özen *et al*., 2013). In other cases, experimental warming has enhanced the effects of zooplankton grazing, which may reduce the occurrence of algal blooms under eutrophic conditions (Kratina *et al*., 2012; Shurin *et al*., 2012). The outcome may, however, depend on the trophic structure recreated in the experiments. In short-term outdoor experiments run at different temperatures in Sweden, Hansson *et al*. (2012) found that phytoplankton benefitted from warming in three-trophic-level but not in two-trophic-level systems. However, in their experiment, cyanobacteria, in contrast to other taxa, again benefitted from a higher temperature irrespective of the food chain length. It is striking, though, that cyanobacteria and green algae grow equally well under experimental warming according to laboratory competition experiments, suggesting that competitive advantages are linked to other characteristics besides temperature-mediated growth rates (Lürling *et al.*, 2012). The contradictory findings from these experimental approaches are largely to be expected with differences in underlying experimental conditions (including duration) and fish treatments, and they should not be overemphasised without corresponding *real world* patterns.

Results of modelling studies of the long-term effects of climate change on temperate lakes (Elliott, 2012; Mooij *et al*., 2007; Trolle *et al*., 2011) generally concur with the empirical evidence that phytoplankton biomass will increase and that cyanobacteria will become a more dominant feature of the phytoplankton species composition. Using three different models on shallow lake Engelsholm, Denmark, a yet unpublished study by Trolle *et al*. demon-

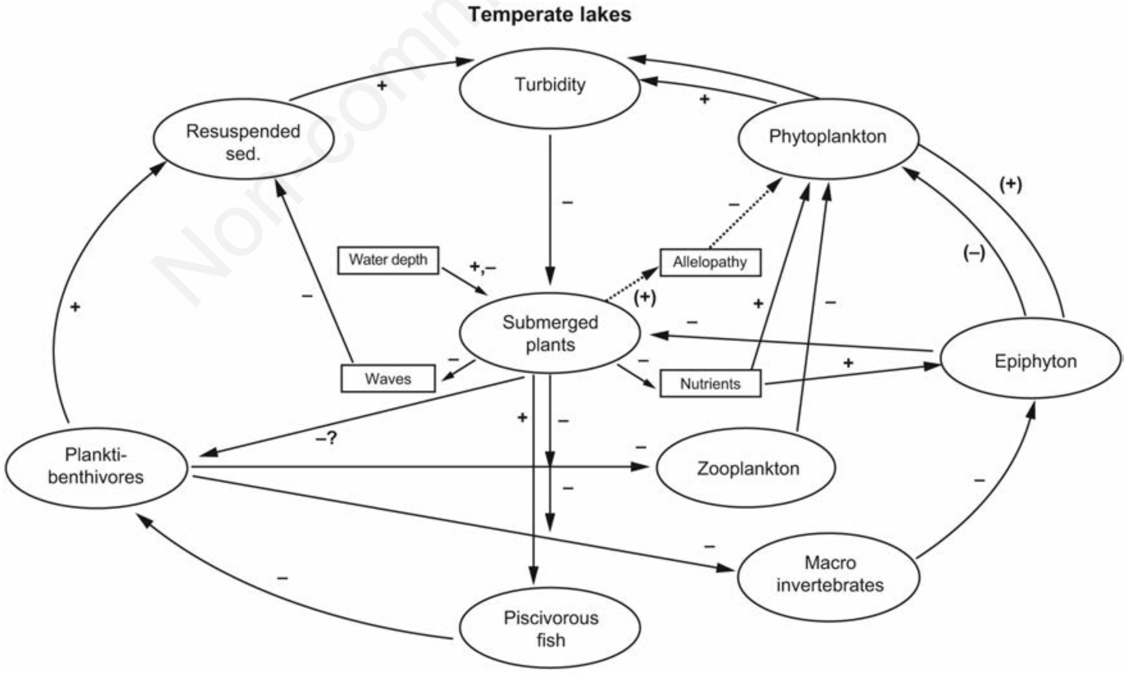

Fig. 5. Role of submerged plants in the functioning of currently temperate shallow lakes and ponds; the effects on different physical, chemical and biological processes that ultimately stabilise a clear water state are shown. Note that the benthic-pelagic coupling is included in the scheme in a partial manner. The qualitative effect of each route can be determined by multiplying the signs along the way. +, positive; –, negative; dotted line, occasionally. Modified from Meerhoff and Jeppesen (2009) (originally based on Scheffer *et al*., 1993). See Tab. 2 for the trends to be expected with climate change and the available evidence as suggested by different research approaches.

strated that a better fit to the seasonal data was obtained when using averages of the output from all the models rather than that obtained from any of the individual models. The ensemble of models predicted that the number of days in which cyanobacteria biomass exceeds the highest World Health Organization (WHO) limit (50 mg chlorophyll a m^{-3}) may increase dramatically from 8 to 23 days per year, given even relatively modest increases in annual mean air temperature of a near-future scenario (*e.g*., 1.5°C increase relative to 1999-2001, representing 2050 under the ICCP A2 scenario down-scaled to Denmark). How the microbial community and processes are affected has so far only been studied in a few large-scale experiments. In a set of experimental ponds in Canada, higher temperatures (ca. 3°C increase) produced top-heavy food webs with a lower biomass of pelagic producers, an equivalent biomass of zooplankton and pelagic bacteria and more pelagic viruses (Shurin *et al*., 2012). In the mesocosms in Denmark, the abundances of picoalgae, bacteria and heterotrophic nanoflagellates showed no direct effect of experimental warming (Christoffersen *et al*., 2006). However, warming modified the effects of nutrient addition (Christoffersen *et al*., 2006; Özen *et al*., 2013), 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, 2010a; Moss *et al*., 2011).

In the Mediterranean and other arid and semi-arid regions, the warmer temperatures may also promote other effects, such as enhanced evaporation and evapotranspiration processes, and lead to increased salinity (Williams, 2001), with negative effects on the diversity of phytoplankton, zooplankton, macroinvertebrates and fishes (Jeppesen *et al*., 1994; 2007a; Brucet *et al*., 2009, 2012). As salinity increases, a shift occurs from dominance of large and more efficient filter-feeding cladoceran species to dominance of copepods and small cladoceran species (Jeppesen *et al*., 2007a; Brucet *et al*., 2009; Jensen *et al*., 2010). The reduction in the size and abundance of zooplankton grazers due to enhanced salinity may further negatively affect the resilience of lakes to enhanced nutrient loading (Brucet *et al*., 2010, 2012; Bezirci *et al*., 2012).

Dynamics in the littoral zone of lakes

Processes in the littoral zone, or more broadly, areas with aquatic plants, are crucial for the overall environmental state and stability of lakes, particularly shallow lakes and ponds (Scheffer *et al*., 1993; Burks *et al*., 2006), but also for the biodiversity of deep lakes. As with the pelagic zone, different components of climate change may directly and indirectly affect the littoral habitat with consequences at different ecological scales. The positive effect of submerged macrophytes on lake clarity typically seen in shallow lakes in temperate to cold climates (Fig. 5; Moss, 1990; Scheffer *et al*., 1993) seems weaker in similar lakes in warm climates (Bachmann *et al*., 2002; Jeppesen *et al*., 2007b; Meerhoff *et al*., 2007a), even though high clarity may occur inside the macrophyte stands in such lakes (Kosten *et al*., 2009b) or in the whole lake when the cover of submerged plants is very extensive and nutrient concentrations are low to moderate (Kruk *et al*., 2009). The diel link between littoral and pelagic zones made by migrating zooplankton in search for refuge from visual predators is considered one of the main mechanisms by which submerged plants may indirectly outcompete phytoplankton and thus help maintain clear water in shallow lakes in cold and temperate climates (Fig. 5; Timms and Moss, 1984; Lauridsen and Lodge, 1996; Burks *et al*., 2002). SFTS studies have shown that such movement is far less common in similar lakes in warm climates (Meerhoff *et al*., 2007b; Brucet *et al*., 2010), as also suggested by laboratory behavioural experiments (Meerhoff *et al*., 2006; Tavsanoglu *et al*., 2012), probably due to key differences in fish assemblage structure and behaviour (Meerhoff *et al*., 2007a; Teixeira de Mello *et al*., 2009). Macrophyte growth and colonisation depth are in general positively affected by temperature (Rooney and Kalff, 2000). In an SFTS study, Kosten *et al*. (2009a) found that submerged vegetation in the warm regions reached relatively deeper zones than in the temperate region, which may indicate a lower light requirement likely due to higher growth at higher temperatures. However, other SFTS (Duarte *et al*., 1986) 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. The apparently conflicting effects of an increase in temperature on submerged macrophytes seem, again, to depend at least partly on the trophic structure in the lakes (Meerhoff *et al*., 2007a; Jeppesen *et al*., 2007a, 2007b). The greater density of omnivorous and herbivorous fishes (Teixeira-de Mello *et al*., 2009; González-Bergonzoni *et al*., 2012), which are typically more abundant among the aquatic plants (Meerhoff *et al*., 2007a; Brucet *et al*., 2010), may lead to higher mechanical disturbance and grazing on competing periphyton (Meerhoff *et al*., 2007a; Brucet *et al*., 2012), thus facilitating submerged plant growth in warm climates. Furthermore, plants growing in warm climates seem to be less palatable to macroinvertebrates both in marine (Bolser and Hay, 1996) and freshwater systems (Morrison and Hay, 2012), most likely due to greater presence of some form of chemical defence (Morrison and Hay, 2012).

However, fish may also promote opposite effects in other climate regions. A study of 782 lake-years in different climate zones in North America, South America and Europe, testing for systematic differences along a latitude gradient in the relationship between the abundance of submerged macrophytes and environmental factors, such as lake depth and nutrient levels, suggested that the effects of nutrient loading are not independent of climate effects (Fig. 6; Kosten *et al*., 2009a). In the pooled dataset, the proportion of lakes with substantial submerged macrophyte coverage (*i.e*., >30% of the lake area) decreased in a sigmoidal way with increasing total phosphorus concentrations, falling most steeply between 0.05 and 0.2 mg L^{-1} TP. However, the maximum TP concentration allowing substantial submerged macrophyte coverage was higher in cold regions with more frost days (Kosten *et al*., 2009a), perhaps due to partial winter fish kills. In cold eutrophic lakes where

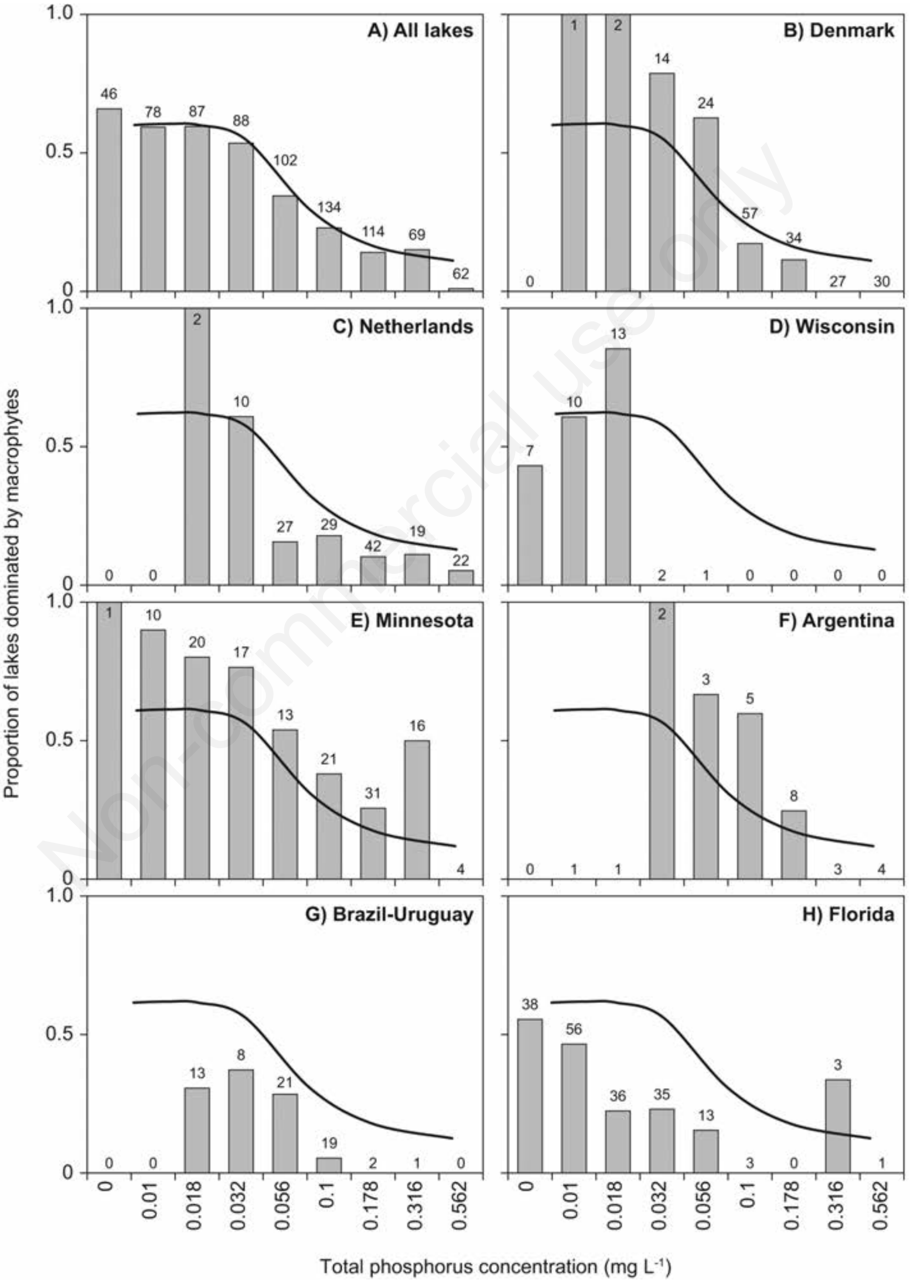

Fig. 6. Proportion of lakes dominated by macrophytes (coverage ca. 30%) at different total phosphorus (TP) concentrations. The curve represents the average proportion of lakes dominated by macrophytes in the different regions (panel A) and is reproduced in the other panels to facilitate comparison only. Class widths are equal on a logarithmic scale. The number of lakes in a certain TP class is represented on top of the bars. From Kosten *et al.* (2009).

fish assemblages are typically dominated by planktivorous species (Persson *et al*., 1991; Jeppesen *et al*., 2000), higher survival of fish would lead to decreased zooplankton biomass and an indirect enhancement of competing phytoplankton, as described in the above section. In cold regions where climatic warming is projected to lead to fewer frost days, macrophyte cover could decrease unless nutrient levels are lowered (Kosten *et al*., 2009a).

A shallow lake model (PClake; Janse, 1997), including macrophytes and their effects on the ecosystem, has also been used to quantify the effects of warming (Mooij *et al*. 2007), the conclusion being that warming may lead to a higher risk of a shift from a clear, macrophyte-dominated state to a turbid, phytoplankton-dominated state. Nielsen, 2013 (submitted) applied a compiled ensemble approach based on the PClake model to Danish, shallow Lake Arreskov and found in future projections that the lake has a lower probability of exhibiting a clear-water, vegetation-rich state and greater likelihood of cyanobacteria dominance at elevated warming and nutrient levels. For instance, in a 6°C warming scenario the nutrient loading of nitrogen and phosphorus would have to be reduced by about 75% to maintain the present ecological state of the lake, but even in a near-future 2°C warming scenario,

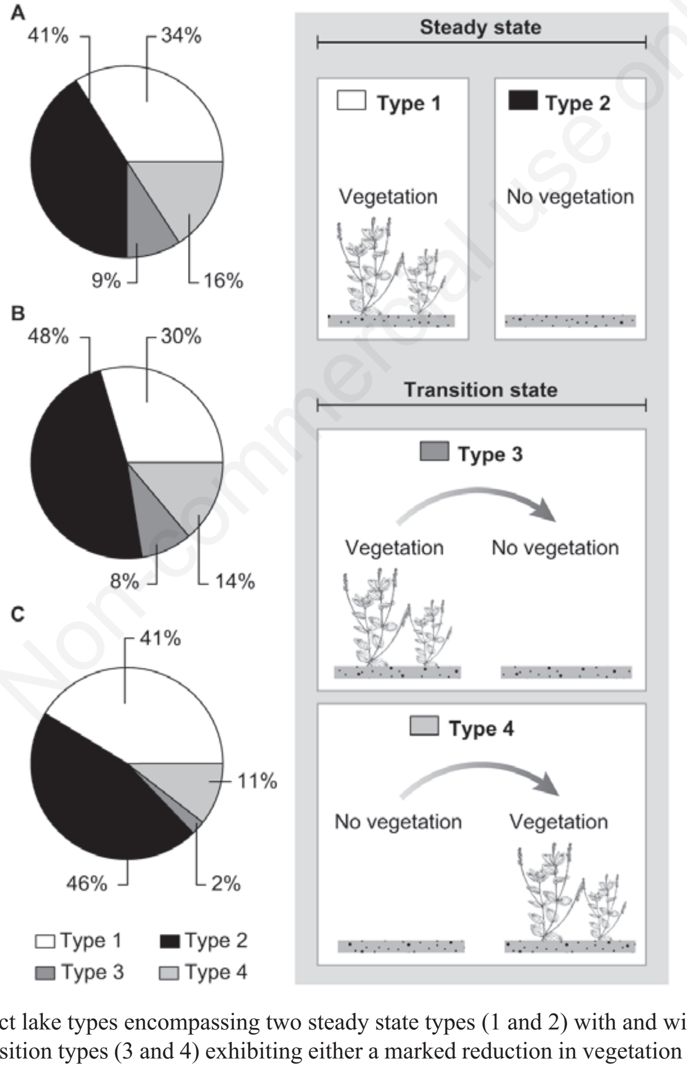

Fig. 7. Proportion of four distinct lake types encompassing two steady state types (1 and 2) with and without submerged vegetation in all simulated years and two transition types (3 and 4) exhibiting either a marked reduction in vegetation coverage or a marked increase in vegetation coverage between two neighbouring years. These lake types have been extracted from the ensemble simulation using PClake in which the model, due to multiple sets of parameter values, produced various plausible simulation representations of the ecosystem in Danish Lake Arreskov (Nielsen, 2013). The multiple sets of parameter values rendering current conditions (A) were retained and utilised in scenarios where (B) represents the current nutrient loading to the lake, with a 2°C temperature increase above present climatic conditions and (C) a 75% reduction of the current nutrient loading with a 6°C increase in temperature above present climatic conditions. Responses to these scenarios are the changes in the proportion of the four distinct lake types. From Nielsen (2013).

there is a higher probability of a turbid, cyanobacteria dominated state (Fig. 7).

While some SFTS and modelling results point to higher risks of losing submerged macrophytes or of weakening their buffering effects in shallow lakes in a warmer climate (Fig. 5), due to both direct and indirect factors, the experimental results are, again, much more ambiguous (Tab. 2). In experiments in the UK, the response of submerged macrophytes (measured as volume inhabited by the plants) to nutrient addition was temperature-independent (McKee *et al*., 2002a, 2002b). Others have found that a warmer spring stimulates macrophyte growth (Scheffer *et al*., 1992) and the development of macrophytes at low nutrient levels (Jeppesen *et al*., 2010b). Conversely, in comparative enclosure experiments, macrophytes in shallow Mediterranean lakes gave way to phytoplankton dominance at lower nutrient concentrations than in similar studies conducted in North European lakes (Romo *et al*., 2004), giving experimental support to the idea of an interaction of nutrient effects with climate regime and, particularly, mean ambient temperature. On the other hand, the role of water level fluctuation and its compensation for eutrophication and strong top-down control have to be taken into account in hydrologically variable lakes (see Beklioğlu *et al*., 2006; Özkan *et al*., 2010; Bucak *et al*., 2012, for details).

The composition of the plant community may also be affected by warming. In one of the UK heating experiments, plant diversity and species richness of macrophytes decreased with warming and the plant community became dominated by warm-water exotics, such as *Lagarosiphon majo*, as well as *Ceratophyllum demersum*, and free-floating plants such as lemnids (Moss, 2010; Feuchtmayr *et al*., 2010). Other experiments also highlight a higher risk of increased importance of free-floating plants (Netten *et al*., 2010) and filamentous algae (Trochine *et al*., 2011) with warming. Fewer experimental studies have focused on other groups relevant to littoral or benthic processes, such as macroinvertebrates (Baulch *et al*., 2005; Feuchtmayr *et al*., 2007; Greig *et al*., 2012; Dossena *et al*., 2012). In the UK mesocosms no clear effects on the densities of macroinvertebrates were detected (Feuchtmayr *et al*., 2007; McKee *et al*., 2003), whereas Greig *et al*. (2012) in a Canadian mesocosm experiment found that experimental warming in ponds advanced the phenology of insect emergence (while treatments with predatory fish delayed it) but had no effect on the biomass of zoobenthos. In the latter experiment, warming also reduced the effects of eutrophication on periphyton, leading to a lower biomass of benthic producers (Shurin *et al*., 2012). In Mediterranean and other hydrologically variable lakes, submerged macrophytes may also be strongly affected by water level fluctuations altering the underwater light climate (Blindow, 1992; Nõges and Nõges, 1999; Coops *et al*., 2003; Beklioğlu *et al*., 2006). Vulnerability of macrophytes to turbidity may increase during high water level periods due to reduced light penetration to the lake bottom, whereas low water levels during summer may enhance macrophyte growth as seen in different geographical locations (Blindow, 1992; Engel and Nichols, 1994; Gafny and Gasith, 1999; Mazzeo *et al*., 2003, Havens *et al*., 2004; Beklioğlu *et al*., 2006; Tan and Beklioğlu, 2006). Two recent mesocosm studies undertaken in Mediterranean shallow lakes with strong water level fluctuations by Özkan *et al*. (2010) and Bucak *et al*. (2012) have shown higher resistance of macrophytes to nutrient loading than expected from studies of northern temperate lakes. Similar evidence comes from long-term studies of lakes Uluabat and Marmara in Turkey (Fig. 8; Beklioglu *et al*., 2006) where an overall high abundance of submerged macrophytes in periods with low water level and low or no plants in high water level periods were recorded (Beklioglu *et al*., 2006). In Mediterranean eutrophic shallow lakes and in other regions with summer declines in water level, it seems likely that a negative effect of climate warming on water clarity due to enhanced eutrophication and augmented top-down control of fish may be, at least partly, counteracted by a reduced water level due to reduced precipitation and enhanced evaporation, provided that the physical disturbance of plants is not severe. Other indirect effects of climate change, such as increased salinity in lakes in arid and semi-arid regions, may also affect macrophyte growth and littoral processes. Salinity appeared to be a critical factor for aquatic plant occurrence in an SFTS study of Mediterranean shallow lakes. In accordance with this, a comprehensive study that included both the contemporary plant community and surface sediment remains of aquatic plants collected from 35 shallow lakes showed that conductivity was the most important environmental factor determining the composition of the macrophyte community (Levi *et al*., 2014). Increased salinity may negatively affect the diversity of submerged plants, for example by reducing germination (Brock *et al.,* 2005), and can even lead to a change in lake status from dominance by aquatic plants to phytoplankton and microbial mat dominance (Davis *et al*., 2003). As described before for pelagic communities, SFTS studies have demonstrated changes also in the littoral trophic structure within increasing salinity, both in temperate and in Mediterranean shallow lakes (Brucet *et al*., 2009, 2010, 2012).

Challenges for the future

A number of challenges exist in the process of improving the predictions of climate change effects on lakes derived from the various existing approaches:

Space-for-time substitution. There is a great need for more cross-system analyses of data from lakes worldwide, which will be facilitated by the increasing computer capacity and the construction of large global databases. A key challenge of SFTS is to separate the climate effects from other anthropogenic effects, natural variability and biogeographical effects. Concerning the latter, studies in species-poor areas such as islands along a climate gradient may be a useful strategy to reveal how the ecosystem function of lakes depends on species assemblages and biodiversity, as long as potential strong (and often disproportionate) variations in, for instance, effects of introduced exotic species can be taken into account and controlled. To be more effective, this approach should be based on a clear theoretical framework and defined expectations.

Time series and monitoring. A serious threat to our understanding of the impacts of climate change is that water authorities around the globe are bringing long-term studies of lakes to a halt exactly at the time when they are most needed, as a consequence of general budget cutting. It is of outmost importance to stop and reverse this practice. Key aspects to consider, however, are the variations in taxonomic resolution and detection limits as well as differences in the experience of the staff in charge of the monitoring, which may produce serious inconsistencies in databases (Straile *et al*., 2013) and thus prevent the extraction of clear climate effects. Nowadays and even more so in the future, high-frequency sampling technology and remote sensing will permit less time-consuming monitoring. Until probes have been developed to cover all necessary key variables (*e.g*., including molecular measurements), such monitoring cannot stand alone but must be supplemented with frequent monitoring of biological variables, such as fish abundance, zooplankton, phytoplankton and macrophytes, to obtain ground-true data for calibration.

Experiments. While most experimental studies on climate change effects on lakes have been conducted at small scale and are of short-term duration, focus in the future should be on long-term and large-scale experiments, potentially including natural gradients in warming (Jeppe-

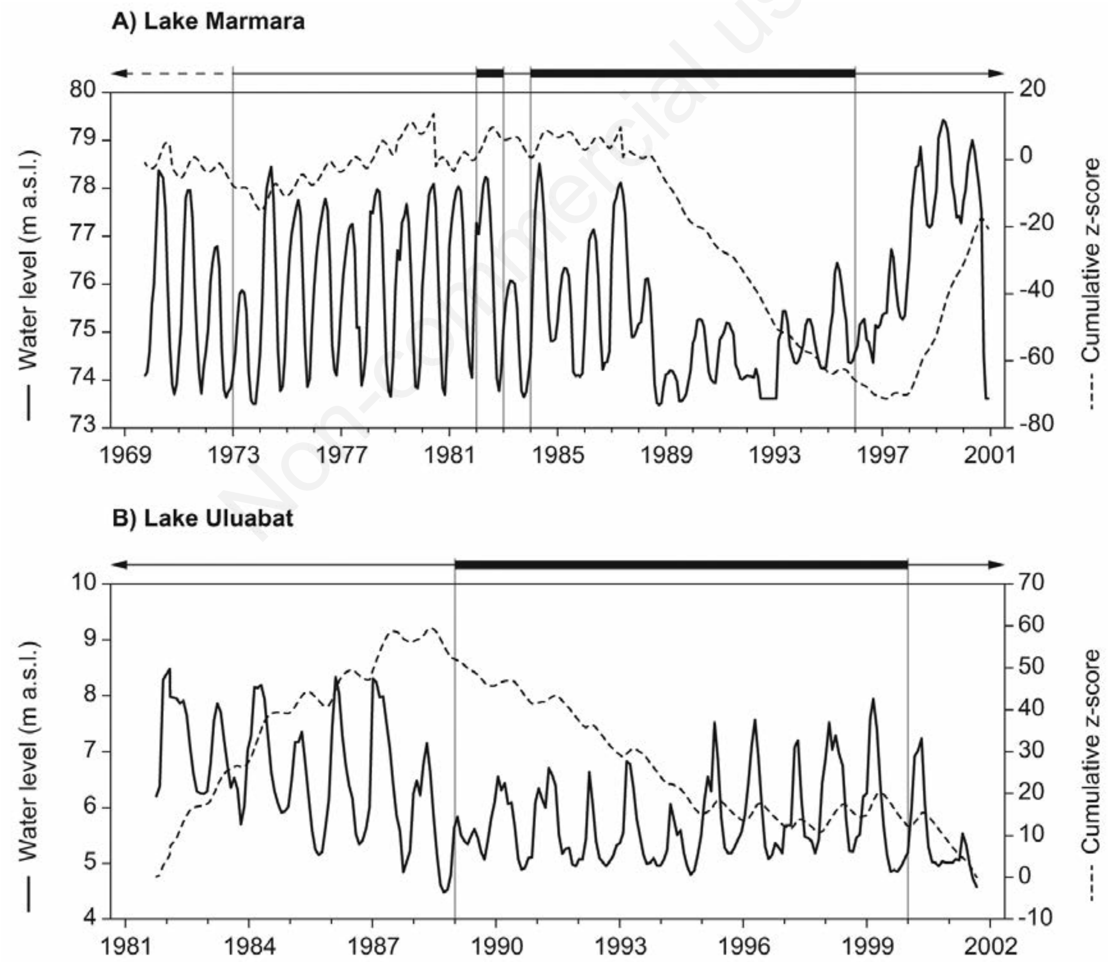

Fig. 8. Changes in water level (m asl) (WL) and the cumulative z-scores of water levels for a) Lake Marmara and b) Lake Uluabat. Lines on the second X-axis indicate the state of submerged plant development (thick dark line, high vegetation cover; thin dark line, low vegetation cover; broken line, lack of data). From Beklioglu *et al.* (2006).

sen *et al*., 2009; Stewart *et al*., 2013) and standardised cross-climate region approaches (Moss *et al*., 2004; Meerhoff *et al*., 2007a, 2007b). Incorporation of other climate-related drivers (*e.g*., precipitation, cloudiness, CO_2 concentrations, frequency and magnitude of extreme events), to supplement the typically studied effects of warming, as well as more natural predator assemblages (*i.e*., more diverse in terms of species and body sizes), is the main challenge for experiments. Choice of appropriate global circulation models and emission scenarios to define the projected values of target climate variables is also a key challenge in order to obtain comparable results.

Palaeoecology. It is a major challenge to disentangle the climate effect signals from eutrophication, not least when studying the past 150 years where major changes have occurred in both the nutrient loadings to lakes and in climate (particularly in Europe). A number of studies have attempted to isolate climate effects from nutrient loading and other anthropogenically induced pressures, such as fish stocking, with mixed success (Simpson and Anderson, 2009; Buchaca *et al*., 2011; Bennion *et al*., 2012; Dong *et al*., 2012; Guilizzoni *et al*., 2012; Thies *et al*., 2012). Palaeo approaches can provide information on the degree, nature and, in some cases, the speed of change in the biological group (or groups) analysed and demonstrate how these changes relate to independently inferred past climatic variation (Anderson *et al*., 2008). Future work will require closer integration of contemporary, in particular the use of independent historical climate data, and palaeo techniques and investigation of change at multiple sites to counter local heterogeneity as a response (Reuss *et al*., 2013) when investigating ecological change at ecosystem level. This can be assessed in numerous ways (such as species turnover, biodiversity, the balance of benthic *vs* pelagic production) along climate and nutrient gradients in both space and time.

Models. The present complex dynamic lake models are too rigid to account for all the structural shifts in ecosystems triggered by climate warming. However, progress is underway *via* the development of a model framework (FABM, Framework for Aquatic Biogeochemical Models, http://sourceforge.net/apps/mediawiki/fabm/), which readily enables development of new ecological modules (open source and freely available) that are easily coupled to a physical model through FABM (Trolle *et al*., 2012), thereby enabling compositional flexibility in both the ecosystem structure and the physical environment. This will also allow rapid implementation of changes in the outline of the models concurrently with new knowledge gained from the other approaches. A set of models on the same lake ecosystem can also be used to improve prediction capacity. As has already been seen for weather forecasts and global circulation models, an ensemble approach using different models (multi-model ensemble) or a range of different parameterisations for an individual model (single-model ensemble) can provide more robust and reliable predictions of the future state of aquatic ecosystems than an individual model (Nielsen, 2013). It is evident that the models being developed, based mainly on experiences from temperate lakes, are currently not able to tackle the major shift in trophic structure and dynamics of the lake ecosystems to be expected when lakes get warmer. Improvements are needed in order to build reliable models and good quality data must be obtained to allow better parameterisation for predicting the effect of climate change on lakes.

The use of bioclimatic models to predict changes in the geographical distribution of species as well as the likelihood of biological invasions under the predicted climate change scenarios (Jeschke and Strayer, 2008) should ideally incorporate biotic interactions (Fernandes *et al*., 2013). However, in many cases, basic niche information on several species is completely lacking, making this task currently impossible. Besides, predicting distribution changes by present niche characteristics might not always result in an effective prediction as the flora and fauna may adapt to the new conditions, in part by microevolution, even in the short term.

Mitigating climate change effects

Our summary in brief in Tab. 1 indicates that different approaches may sometimes yield similar and sometimes different results. This suggests that several approaches should be taken in order to provide strong predictions, *i.e*., if two (or more) approaches clearly point in the same direction, we can be relatively certain that this is a solid base for predictions. With this in mind, there seems to be strong evidence that climate change will enhance eutrophication in mesotrophic and eutrophic lakes as a result of physico-chemically and biologically induced higher internal loading and, in North temperate lakes, enhanced external nutrient loading as well. The effects on phytoplankton of such changes are ambiguous; most approaches indicate an increase in biomass, but the results generally point to a major increase in the risk of dominance and blooming of potentially toxic cyanobacteria species. If the biomass of phytoplankton and/or the amount of suspended matter increases, we can expect a shift in production within the ecosystem, from benthic and littoral processes to pelagic processes, as has also been found as a result of eutrophication (Liboriussen and Jeppesen, 2003; Vadeboncoeur *et al*., 2003). The role of macrophytes for maintaining clear water conditions will likely diminish, although water level reduction as in semi-arid lakes may counteract this effect. Enhanced salinity is to be expected in the Mediterranean lakes, which may reduce species diversity and adversely affect the provision of key ecosystem services (Levi *et al*., 2014).

Changes in species distribution (Parmesan and Yohe, 2003) due to climate warming are difficult to counteract. There may, however, be opportunities to compensate for some of the cascading effects of the changes in lake ecosystems as many of the symptoms of warming are similar to those following from enhanced nutrient loading. Measures should be aimed at increasing the natural resilience of ecosystems against external perturbations (Moss *et al*., 2011). For instance, measures taken to reduce the nutrient input to fresh waters, beyond those already implemented or planned, are straightforward and may include: i) application of fertilisers as determined by soil retention capacity and crop needs, leading to less intensive land use in catchments with sensitive fresh waters (or sites of particular conservation priority, such as drinking water sources or biodiversity hot spots, *etc*.) in order to reduce diffuse nutrient inputs; ii) (re)-establishment of riparian vegetation to buffer nutrient transfers to water bodies, iii) re-meandering of channelised streams to increase retention, decomposition and loss of organic matter and nutrients; iv) improvement of land management and agricultural practices to reduce sediment and particulate and dissolved nutrient export from catchments; v) improvement of the design of sewage works to cope with the consequences of flood events and low flows in receiving waters; vi) more effective reduction of nutrient loading from point sources by proper sewage water treatments and from the atmosphere, the latter by reducing emissions from industry and agriculture; vii) in warmer regions, application of severe restrictions on alterations of natural hydrological cycles and water use, in particular for irrigated crop farming so as to reduce the risk of severe salinisation and eutrophication; viii) increased control of dispersal, arrival and establishment of exotic species. Some of these adaptation measures have been integrated in the River Basin Management Plans required under the European Water Framework Directive, but since they are largely qualitative (Nõges *et al*., 2010a, 2010b) they will certainly stir a heated debate among different stake holders.

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