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Contributors: **Erik Jeppesen, Martin Søndergaard, Dennis Trolle, Meryem Beklioglu, Peeter Noges and Rita Adrian**

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PU	Public	X
PP	Restricted to other programme participants (including the Commission Services)	
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CO	Confidential, only for members of the consortium (including the Commission Services)	

Abstract

This deliverable consists of 13 papers, including five comprehensive reviews and a number of original papers on both contemporary limnology and paleoecology. Taken together they allow us to conclude that temperature increases related to global climate change have already had substantial effects on trophic structure and dynamics as well as lake metabolism. In a future, warmer world, these will continue and are likely to increase in magnitude. The current and expected impacts may, to a large extent, negate the effects of nutrient loading reduction measures currently implemented to restore degraded lakes. As a consequence, a considerably greater effort, in terms of management measures, will be required to fulfill the objectives of the Water Framework Directive (WFD) than currently employed. It is therefore of key importance that the next revision of the River Basin Management Plans related to the WFD seriously and practically considers the effects of climate change.

Deliverable 3.2: Manuscript on the temperature effects on trophic structure and dynamics (including metabolism) in lakes.

(AU, METU, EMU, IGB) (month 36).

Erik Jeppesen, Martin Søndergaard, Dennis Trolle, Meryem Beklioglu, Peeter Noges and Rita Adrian

This deliverable include the following 13 research papers presented in order of appearance

1. DeSenerpont Domis L.N., Elser J, Gsell A., Huszar V.L.M, Ibelings B.W., Jeppesen E., Kosten S., Mooij W.M.. Roland F., Sommer U., van Donk E.ʼ Winder M. & M. Lürling, 2013. Plankton dynamics under different climate conditions – Freshwat. Biol., 58: 463-482.

2. Özen A., Michal Šorf, C. Trochine, L. Liboriussen, M. Beklioglu, M. Søndergaard, T.L. Lauridsen, L. S. Johansson & E. Jeppesen, 2013. Long term effect of warming and nutrients on microbial and classical planktonic communities in mesocosms. – Freshwat. Biol, 58:483-492.

3. Bjerring R., J. Olsen, B.V.Odgaard, B. Buchardt, J. Heinemeier, S. McGowan, P.R. Leavitt & E. Jeppesen, 2013. Climate-driven changes in water level: a decadal scale multiproxy recording of the 8.2 kyr cooling event in Lake Sarup (Denmark). – J. Paleolimnology 49:267-285.

4. Adrian R.,D. Gerten, V. Huber, C. Wagner & S.R. Schmidt (2012). Windows of change: Temporal scale of analysis is decisive to detect ecosystem responses to climate change. Marine Biology: 159:2533–2542.

5. González-Bergonzoni I., M. Meerhoff, F. Teixeira-de Mello, A. Baattrup-Pedersen & E. Jeppesen, 2012. Meta-analysis shows a consistent and strong latitudinal pattern in fish herbivory across ecosystems. – Ecosystems 15: 492-503.

6. Laas, A., P. Nõges, T. Kõiv & T. Nõges 2012. High frequency metabolism study in a large and shallow temperate lake revealed seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694:57–74

7. Meerhoff M., F. Teixeira-de Mello, C. Kruk, C.Alonso, I. González-Bergonzoni, J. Pablo Pacheco , M. Arim , M. Beklioğlu, S. Brucet, G. Goyenola, C.Iglesias, G. Lacerot, N. Mazzeo, S. Kosten and E. 10. Jeppesen, 2012. Environmental warming in shallow lakes: a review of effects on community structure as evidenced from space-for-time substitution approaches – Adv. in Ecol. Res. 46:259-350.

8. Iglesias, C. , Mazzeo, N. , Meerhoff, M., Lacerot, G. , Clemente, J. , Scasso, F., Kruk, C., Goyenola, G., Garcia, J., Amsinck S.L., Paggi, J.C., José de Paggi, S. & E. Jeppesen. 2011. High predation is the key factor for dominance of small-bodied zooplankton in warm lakes - evidence from lakes, fish exclosures and surface sediment – Hydrobiologia 667:133-147.

9. Jeppesen E., P. Nõges, T. A. Davidson, J. Haberman, T.Nõges, K. Blank, T.L. Lauridsen, M. Søndergaard, C. Sayer , R. Laugaste, L.S. Johansson ,R. Bjerring & S.L. Amsinck, 2011. Zooplankton as indicators in lakes - a plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). – Hydrobiologia 676:270-297.

10. Nõges P., Nõges T., Ghiani M., Sena, F., Fresner R., Friedl M., Mildner J. 2011. Increased nutrient loading and rapid changes in phytoplankton expected with climate change in stratified South European lakes: sensitivity of lakes with different trophic state and catchment properties. Hydrobiologia. 667:255-270.

11. Trochine C., M. Guerrieri, L. Liboriussen, M. Meerhoff,ʼ T.L. Lauridsen, M. Søndergaard & E. Jeppesen, 2011. Filamentous green algae inhibit phytoplankton and create clear water conditions – particularly when enriched shallow lakes get warmer. – Freshwat. Biol. 56:541-553.

12. Trolle D., D. P. Hamilton, C. Pilditch, I. C. Duggan & E. Jeppesen, 2011. Predicting the effects of climate change on trophic status of three New Zealand lakes – implications for lake restoration. – Environmental Modelling & Software 26:354-370.

13. Wagner C. & R. Adrian 2011. Consequences of changes in thermal regime for plankton diversity and trait composition in a polymictic lake: a matter of temporal scale. Freshwater Biology 56 (10): 1949-1961.

Synthesis

This deliverable consists of 13 papers, including both contemporary limnology and paleoecology – fully or partly covered by REFRESH funding. Taken together they allow the conclusion that temperature increase related to warming already have - and will more so - in a future warmer world have substantial effect on trophic structure and dynamics and likely also on lake metabolism. The changes expected may to a large extent violate the effect of nutrient loading reduction currently implemented to restore degraded lakes. This calls for much stronger measures to fulfil the objectives of the Water Framework Directive (WFD) than needed in the present-day situation. It is therefore of key importance that the planned revision of the Water Plans related to the WFD seriously accounts for the effect of climate change. Some highlights from the papers are given below:

- The consequences of climate change for plankton dynamics are, to a large extent, system specific, depending on characteristics such as food-web structure and nutrient loading. Indirect effects through nutrient loading may be more important than direct effects of temperature increase, especially for phytoplankton. However, with warming a general picture emerges of increases in bacterivory, greater cyanobacterial dominance and smaller-bodied zooplankton that are more heavily impacted by fish predation. (paper 1 and supported by several of the other papers).

- A meta-analysis of published data focusing on change in the relative richness of omnivorous fishes in native fish communities along a broad global latitudinal gradient in streams, rivers, lakes, reservoirs, estuaries, and open marine waters showed a consistent increasing trend in the relative richness of omnivores with decreasing latitude. Furthermore, omnivore richness was higher in freshwaters than in marine ecosystems. Our results suggest that the observed latitudinal gradient in fish omnivory is a global ecological pattern occurring in both freshwater and marine ecosystems. It was hypothesize that this macroecological pattern in fish trophic structure is, in part, explained by the higher total fish diversity at lower latitudes and by the effect of temperature on individual food intake rates; both factors ultimately increasing animal food limitation as the systems get warmer (5,7).

- The mean body size of limnetic cladocerans decreases from cold temperate to tropical regions, in both the northern and the southern hemisphere. This size shift has been attributed to both direct (e.g. physiological) or indirect (especially increased predation) impacts. To provide further information on the role of predation, results from several studies of subtropical Uruguayan lakes using three different approaches were conducted: (i) field observations from two lakes with contrasting fish abundance, Lakes Rivera and Rodo´, (ii) fish exclusion experiments conducted in in-lake mesocosms in three lakes, and (iii) analyses of the *Daphnia* egg bank in the surface sediment of eighteen lakes. The results show that medium and large-sized zooplankton can occur in subtropical lakes when fish predation is removed. The evidence provided here collectively confirms the hypothesis that predation, rather than high-temperature induced physiological constraints, is the key factor determining the dominance of small-sized zooplankton in warm lakes (8,7).

- Using examples from particularly Danish, Estonian, and the UK lakes, it was shown that zooplankton (sampled from the water and the sediment) have a strong indicator value - including the effect of climate change -, which cannot be covered by sampling fish and phytoplankton without a very comprehensive and costly effort. When selecting the right metrics, zooplankton are cost-efficient indicators of the trophic state and ecological quality of lakes. Moreover, they are important indicators of the success/failure of measures taken to bring the lakes to at least good ecological status. Therefore, it is strongly recommend the EU to include zooplankton as a central BQE in the WFD assessments, and undertake similar regional calibration exercises to obtain relevant and robust metrics also for zooplankton as is being done at present in the cases of fish, phytoplankton, macrophytes and benthic invertebrates (9,8,13).

- Changes in plankton species diversity and community structure as a result of globalwarming are of growing concern in ecological studies, as these properties contributesubstantially to key ecosystem processes. The effect of short-term temperature rise and changes in the thermal regime during summer on plankton diversity of the eutrophic and polymictic Muggelsee in Germany showed 1) overall number of stratification events increased significantly across the study period. When the lake was stratified, consistently higher surface water temperatures and lower epilimnetic nutrient concentrations were found. As the length of thermal stratification increased, the phytoplankton shifted towards a higher proportion of buoyant cyanobacteria capable of N-fixation (*Aphanizomenon, Anabaena*), while diatoms declined. Zooplankton species with high thermal tolerances (i.e. *Thermocyclops oithonoides, Thermocyclops crassus*) and /or those that grow quickly at high temperatures (i.e. rotifers) became more common, 2) Minimal changes in diversity, except for an increase in cyclopoid copepods and a decrease in diatom diversity (13,4).

- Filamentous green algae (FGA) may represent an alternative state in high-nutrient shallow temperate lakes. Furthermore, a clear water state is sometimes associated with the dominance of FGA; however, the mechanisms involved remain uncertain. Experimental studies revealed that mesocosms with FGA had lower phytoplanktonic chlorophyll *a* concentrations than those without. Mm experiments demonstrated that FGA strongly suppressed the growth of natural phytoplankton at non-limiting nutrient conditions and regardless of phytoplankton initial concentrations or micronutrients addition. Furthermore, we found that the negative effect of FGA on phytoplankton growth increased up to 49% under high incubation temperatures. The results suggest that FGA control of phytoplankton growth may be an important mechanism for stabilising clear water in shallow temperate lakes dominated by FGA and that FGA may play a larger role when lakes get warmer (11).

- To quantify the effects of a future climate on three morphologically the one dimensional lake ecosystem model DYRESM-CAEDYM was applied and calibrated on three lakes with contrasting nutrient level and scenario run using downscaled regional climate data in the IPCC A2 scenario at the end of this century. The predicted effects on annual mean surface water concentrations of total phosphorus, total nitrogen and Chl *a* is equivalent to the effects of increasing external TN and TP loading by 25 – 50%. Simulations for the polymictic, eutrophic lake further indicate that cyanophytes will be more abundant in the future climate, increasing by >15% in their contribution to annual mean Chl *a*. Therefore, future climate effects should be taken into account in the long-term planning and implementation of lake management as strategies may need to be refined and adapted to preserve or improve the present-day lake water quality (12, 10).

- High-frequency metabolism measurements in the large and shallow polymictic eutrophic Lake Võrtsjärv revealed strong effect of temperature. In the warmer year 2010, the seasonal peaks of GPP, R and NEP were synchronously shifted nearly 1 month earlier compared with 2009. The strong stimulating effect of temperature on both GPP and R and its negative effect on NEP revealed by the multiple regression analysis suggests increasing metabolic rates and increasing heterotrophy in this lake type in a warmer climate (6).

The 13 papers are summarised by their abstracts as follows:

DeSenerpont Domis L.N., Elser J, Gsell A., Huszar V.L.M, Ibelings B.W., Jeppesen E. ,Kosten S., Mooij W.M.. Roland F., Sommer U., van Donk E.' Winder M. & M. Lürling, 2013. Plankton dynamics under different climate conditions – Freshwat. Biol. 58: 463-482

1. Different components of the climate system have been shown to affect temporal dynamics in natural plankton communities on scales varying from days to years. The seasonal dynamics in temperate lake plankton communities, with emphasis on both physical and biological forcing factors, were captured in the 1980s in a conceptual framework, the Plankton Ecology Group (PEG) model.
2. Taking the PEG model as our starting point, we discuss anticipated changes in seasonal and long-term plankton dynamics and extend this model to other climate regions, particularly polar and tropical latitudes. Based on our improved post-PEG understanding of plankton dynamics, we also evaluate the role of microbial plankton, parasites and fish in governing plankton dynamics and distribution.
3. In polar lakes, there is usually just a single peak in plankton biomass in summer. Lengthening of the growing season under warmer conditions may lead to higher and more prolonged phytoplankton productivity. Climate-induced increases in nutrient loading in these oligotrophic waters may contribute to higher phytoplankton biomass and subsequent higher zooplankton and fish productivity.
4. In temperate lakes, a seasonal pattern with two plankton biomass peaks – in spring and summer – can shift to one with a single but longer and larger biomass peak as nutrient loading increases, with associated higher populations of zooplanktivorous fish. Climate change will exacerbate these trends by increasing nutrient loading through increased internal nutrient inputs (due to warming) and increased catchment inputs (in the case of more precipitation).
5. In tropical systems, temporal variability in precipitation can be an important driver of the seasonal development of plankton. Increases in precipitation intensity may reset the seasonal dynamics of plankton communities and favour species adapted to highly variable environments. The existing intense predation by fish on larger zooplankters may increase further, resulting in a perennially low zooplankton biomass.
6. Bacteria were not included in the original PEG model. Seasonally, bacteria vary less than the phytoplankton but often follow its patterns, particularly in colder lakes. In warmer lakes, and with future warming, a greater influx of allochthonous carbon may obscure this pattern.
7. Our analyses indicate that the consequences of climate change for plankton dynamics are, to a large extent, system specific, depending on characteristics such as food-web structure and nutrient loading. Indirect effects through nutrient loading may be more important than direct effects of temperature increase, especially for phytoplankton. However, with warming a general picture emerges of increases in bacterivory, greater cyanobacterial dominance and smaller-bodied zooplankton that are more heavily impacted by fish predation.

Özen A., Michal Šorf, C. Trochine, L. Liboriussen, M. Beklioglu, M. Søndergaard, T.L. Lauridsen, L. S. Johansson & E. Jeppesen, 2013. Long term effect of warming and nutrients on microbes and other plankton in mesocosms.- Freshwat. Biol. 58: 483-492

1. We followed microbial and other planktonic communities during a 4-month period (February–May) in 12 outdoor flow-through mesocosms designed to elucidate the effect of global warming and nutrient enrichment. The mesocosms were established in 2003.
2. Warming had a smaller effect than nutrients on the biomass of the microbial and planktonic communities, and warming and nutrients together exhibited complex interactions.
3. We did not find direct effects of warming on the biomass of bacterioplankton or ciliates; however, warming significantly added to the positive effect of nutrients on these organisms and on heterotrophic nanoflagellates (HNF). No warming effects on any of the other planktonic groups analysed were detected.
4. The zooplankton: phytoplankton biomass ratio was lowest, and the HNF: bacteria and rotifer: bacteria biomass ratios highest in the heated, nutrient-rich mesocosms. We attribute this to higher fish predation on large-bodied zooplankton, releasing the predation on HNF and competition for rotifers.
5. The proportion of phytoplankton to the total plankton biomass increased with nutrients, but decreased with warming. The opposite pattern was observed for the proportion of phytoplankton to the total microbial biomass.
6. As climate warming may lead to eutrophication, major changes may occur in the pelagic food web and the microbial community due to changes in trophic state and in combination with warming.

Bjerring R., J. Olsen, B.V.Odgaard, B. Buchardt, J. Heinemeier, S. McGowan, P.R. Leavitt & E. Jeppesen, 2013. Climate-driven changes in water level: a decadal scale multiproxy recording of the 8.2 kyr cooling event in Lake Sarup (Denmark). – J. paleolimnology 49:267-285.

A two-stage change in lake level during the 8.2-ka event was identified in Lake Sarup, Denmark (55_N), using a multiproxy approach on precise radiocarbon wiggle-matched annually laminated sediments deposited 8740–8060 cal. yr BP. Changes in $d_{13}C$ and $d_{18}O$ indicated closed lake hydrology driven by precipitation. The isotopic, sedimentary and plant macrofossil records suggested that the lake level started to decrease around 8400 cal. yr BP, the decrease accelerating during 8350–8260 before an abrupt increase during 8260–8210. This pattern shows that the climate anomaly started *150 years before the onset of the 8.2-ka cooling event registered in Greenland ice cores, but was synchronous with hydrologic change in the North American Lake Agassiz drainage. The lake level decrease was accompanied by a higher accumulation rate of inorganic matter and lower accumulation rates of cladoceran subfossils and algal pigments, possibly due to increased turbidity and reduced nutrient input during this drier period. Pigment analysis also showed added importance of diatoms and cryptophytes during this climate anomaly, while cyanobacteria became more important when the water level rose. Moreover, Nymphaeaceae trichosclereids were abundant during the period of algal enrichment. Cladoceran taxa associated with floating leaved plants or benthic habitats responded in a complex way to changes in water level, but the cladoceran assemblages generally reflected deep lake conditions throughout the period. The lake did not return to its pre-8.2-ka event status during the period of analysis, but remained more productive for centuries after the climatic anomaly as judged from the pigment accumulation and assemblage composition. The change to more eutrophic conditions may have been triggered by erosion of marginal deposits. Together, these data confirm the chronology of hydrologic changes and suggest, for the first time, that lake levels exhibited both a decline and an increase in rapid succession in response to the 8.2-ka event in southern Scandinavia.

González-Bergonzoni I., M. Meerhoff, F. Teixeira-de Mello, A. Baattrup-Pedersen & E. Jeppesen, 2012. Meta-analysis shows a consistent and strong latitudinal pattern in fish herbivory across ecosystems- Ecosystems 15: 492-503.

Several studies have demonstrated a latitudinal gradient in the proportion of omnivorous fish species (that is, consumers of both vegetal and animal material) in marine ecosystems. To establish if this global macroecological pattern also exists in fresh and brackish waters, we compared the relative richness of omnivorous fish in freshwater, estuarine, and marine ecosystems at contrasting latitudes. Furthermore, we sought to determine the main environmental correlates of change in fish omnivory. We conducted a meta-analysis of published data focusing on change in the relative richness of omnivorous fishes in native fish communities along a broad global latitudinal gradient, ranging from 41_S to 81.5 N_ including all continents except for Antarctica. Data from streams, rivers, lakes, reservoirs, estuaries, and open marine waters (ca. 90 papers covering 269 systems) were analyzed.

Additionally, the relationship between the observed richness in omnivory and key factors influencing trophic structure were explored. For all ecosystems, we found a consistent increasing trend in the relative richness of omnivores with decreasing latitude. Furthermore, omnivore richness was higher in freshwaters than in marine ecosystems. Our results suggest that the observed latitudinal gradient in fish omnivory is a global ecological pattern occurring in both freshwater and marine ecosystems. We hypothesize that this macroecological pattern in fish trophic structure is, in part, explained by the higher total fish diversity at lower latitudes and by the effect of temperature on individual food intake rates; both factors ultimately increasing animal food limitation as the systems get warmer.

Laas, A., P. Nõges, T. Kõiv & T. Nõges 2012. High frequency metabolism study in a large and shallow temperate lake revealed seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694:57–74

Respiratory CO_2 release from inland waters is a major process in the global carbon cycle, retaining more than half of the carbon flux from terrestrial sources that otherwise would reach the sea. The strongly lake type-specific balance between primary production and respiration determines whether a lake acts regionally as a net sink or source of CO_2. This study presents two-year (2009, 2010) results of high-frequency metabolism measurements in the large and shallow polymictic eutrophic Lake Võrtsjärv (area 270 km^2; mean depth 2.8 m). We estimated the net ecosystem production (NEP), community respiration (R) and gross primary production (GPP) from continuous measurements of oxygen, irradiance, wind and water temperature. A sinusoidal model fitted to the calculated metabolic rates showed the prevalence of net autotrophy (mean GPP:R[1) from early spring until August/September, whereas during the rest of the year heterotrophy (mean GPP:R\1) prevailed, characterizing the lake as CO_2 neutral on an annual basis. Community respiration lagged behind GPP by approximately 2 weeks, which could be explained by the bulk of the phytoplankton biomass accounted for by filamentous cyanobacteria that are considered mostly inedible to zooplankton, and the seasonally increasing role of sediment resuspension. In the warmer year 2010, the seasonal peaks of GPP, R and NEP were synchronously shifted nearly 1 month earlier compared with 2009. The strong stimulating effect of temperature on both GPP and R and its negative effect on NEP revealed by the multiple regression analysis suggests increasing metabolic rates and increasing heterotrophy in this lake type in a warmer climate.

Meerhoff M., F. Teixeira-de Mello, C. Kruk, C.Alonso, I. González-Bergonzoni, J. Pablo Pacheco , M. Arim , M. Beklioğlu, S. Brucet, G. Goyenola, C.Iglesias, G. Lacerot, N. Mazzeo, S. Kosten and E. Jeppesen, 2012. Environmental warming in shallow lakes: a review of effects on community structure as evidenced from space-for-time substitution approaches – Adv. in Ecol. Res. 46:259-350.

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.

Iglesias, C. , Mazzeo, N. , Meerhoff, M., Lacerot, G. , Clemente, J. , Scasso, F., Kruk, C., Goyenola, G., Garcia, J., Amsinck S.L., Paggi, J.C., José de Paggi, S. & E. Jeppesen. 2011. High predation is the key factor for dominance of small-bodied zooplankton in warm lakes - evidence from lakes, fish exclosures and surface sediment – Hydrobiologia 667:133-147.

The mean body size of limnetic cladocerans decreases from cold temperate to tropical regions, in both the northern and the southern hemisphere. This size shift has been attributed to both direct (e.g. physiological) or indirect (especially increased predation) impacts. To provide further information on the role of predation, we compiled results from several studies of subtropical Uruguayan lakes using three different approaches: (i) field observations from two lakes with contrasting fish abundance, Lakes Rivera and Rodo´, (ii) fish exclusion experiments conducted in in-lake mesocosms in three lakes, and (iii) analyses of the *Daphnia* egg bank in the surface sediment of eighteen lakes. When fish predation pressure was low due to fish kills in Lake Rivera, large-bodied *Daphnia* appeared. In contrast, small-sized cladocerans were abundant in Lake Rodo´, which exhibited a typical high abundance of fish. Likewise, relatively large cladocerans (e.g. *Daphnia* and *Simocephalus*) appeared in fishless mesocosms after only 2 weeks, most likely hatched from resting egg banks stored in the surface sediment, but their abundance declined again after fish stocking. Moreover, field studies showed that 9 out of 18 Uruguayan shallow lakes had resting eggs of *Daphnia* in their surface sediment despite that this genus was only recorded in three of the lakes in summer water samples, indicating that *Daphnia* might be able to build up populations at low risk of predation. Our results show that medium and large-sized zooplankton can occur in subtropical lakes when fish predation is removed. The evidence provided here collectively confirms the hypothesis that predation, rather than high-temperature induced physiological constraints, is the key factor determining the dominance of small-sized zooplankton in warm lakes.

Jeppesen E., P. Nõges, T. A. Davidson, J. Haberman, T.Nõges, K. Blank, T.L. Lauridsen, M. Søndergaard, C. Sayer , R. Laugaste, L.S. Johansson ,R. Bjerring & S.L. Amsinck, 2011. Zooplankton as indicators in lakes - a plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD)- Hydrobiologia 676:270-297.

With the implementation of the EU Water Framework Directive (WFD), the member states have to classify the ecological status of surface waters following standardised procedures. It was a matter of some surprise to lake ecologists that zooplankton were not included as a biological quality element (BQE) despite their being considered to be an important and integrated component of the pelagic food web. To the best of our knowledge, the decision of omitting zooplankton is not wise, and it has resulted in the withdrawal of zooplankton from many so-far-solid monitoring programmes. Using examples from particularly Danish, Estonian, and the UK lakes, we show that zooplankton (sampled from the water and the sediment) have a strong indicator value, which cannot be covered by sampling fish and phytoplankton without a very comprehensive and costly effort. When selecting the right metrics, zooplankton are cost-efficient indicators of the trophic state and ecological quality of lakes. Moreover, they are important indicators of the success/failure of measures taken to bring the lakes to at least good ecological status. Therefore, we strongly recommend the EU to include zooplankton as a central BQE in the WFD assessments, and undertake similar regional calibration exercises to obtain relevant and robust metrics also for zooplankton as is being done at present in the cases of fish, phytoplankton, macrophytes and benthic invertebrates.

Nõges P., Nõges T., Ghiani M., Sena, F., Fresner R., Friedl M., Mildner J. 2011. Increased nutrient loading and rapid changes in phytoplankton expected with climate change in stratified South European lakes: sensitivity of lakes with different trophic state and catchment properties. Hydrobiologia. 667:255-270.

We hypothesised that increasing winter affluence and summer temperatures, anticipated in southern Europe with climate change, will deteriorate the ecological status of lakes, especially in those with shorter retention time. We tested these hypotheses analysing weekly phytoplankton and chemistry data collected over 2 years of contrasting weather from two adjacent stratified lakes in North Italy, differing from each other by trophic state and water retention time. Dissolved oxygen concentrations were higher in colder hypolimnia of both lakes in the second year following the cold winter, despite the second summer was warmer and the lakes more strongly stratified. Higher loading during the rainy winter and spring increased nutrient (N, P, Si) concentrations, and a phytoplankton based trophic state index, whilst the N/P ratio decreased in both lakes. The weakened Si limitation in the second year enabled an increase of diatom biovolumes in spring in both lakes. Chlorophyll a concentration increased in the oligo-mesotrophic lake, but dropped markedly in the eutrophic lake where the series of commonly occurring cyanobacteria blooms was interrupted. The projected increase of winter precipitation in southern Europe is likely to increase the nutrient loadings to lakes and contribute to their eutrophication. The impact is proportional to the runoff/in-lake concentration ratio of nutrients rather than to the retention time, and is more pronounced in lakes with lower trophy. The hypolimnetic temperature had a strong effect on the anaerobic phosphorus release in both lakes characterised by a Q_{10} value of 2.4. The projected extension of hypolimnetic anoxia and higher bottom water temperatures are likely to enhance internal nutrient loading that may strongly counteract to lake restoration efforts.

Trochine C., M. Guerrieri, L. Liboriussen, M. Meerhoff,' T.L. Lauridsen, M. Søndergaard & E. Jeppesen, 2011. Filamentous green algae inhibit phytoplankton and create clear water conditions – particularly when enriched shallow lakes get warmer.- Freshwat. Biol. 56:541-553.

1. Filamentous green algae (FGA) may represent an alternative state in high-nutrient shallow temperate lakes. Furthermore, a clear water state is sometimes associated with the dominance of FGA; however, the mechanisms involved remain uncertain.
2. We hypothesised that FGA may promote a clear water state by directly suppressing phytoplankton growth, mostly via the release of allelochemicals, and that this interaction may be affected by temperature.
3. We examined the relationships between FGA, phytoplanktonic chlorophyll *a* concentrations and zooplankton in a series of mesocosms (2.8 m_3) mimicking enriched shallow ponds now and in a future warmer climate (0 and c. 5 _C above ambient temperatures). We then tested the potential allelopathic effects of FGA (*Cladophora* sp. and *Spirogyra* sp.) on phytoplankton using several short-term microcosms and laboratory experiments.
4. Mesocosms with FGA evidenced lower phytoplanktonic chlorophyll *a* concentrations than those without. Zooplankton and zooplankton : phytoplankton biomass ratios did not differ between mesocosms with and without FGA, suggesting that grazing was not responsible for the negative effects on phytoplanktonic biomass (chlorophyll *a*).
5. Our field microcosm experiments demonstrated that FGA strongly suppressed the growth of natural phytoplankton at non-limiting nutrient conditions and regardless of phytoplankton initial concentrations or micronutrients addition. Furthermore, we found that the negative effect of FGA on phytoplankton growth increased up to 49% under high incubation temperatures. The experiment performed using FGA filtrates confirmed that the inhibitory effect of FGA on phytoplankton may be attributed to allelochemicals.
6. Our results suggest that FGA control of phytoplankton growth may be an important mechanism for stabilising clear water in shallow temperate lakes dominated by FGA and that FGA may play a larger role when lakes get warmer.

Trolle D., D. P. Hamilton, C. Pilditch, I. C. Duggan & E. Jeppesen, 2011. Predicting the effects of climate change on trophic status of three New Zealand lakes – implications for lake restoration. -Environmental Modelling & Software 26:354-370.

To quantify the effects of a future climate on three morphologically different lakes that varied in trophic status from oligo-mesotrophic to highly eutrophic, we applied the one-dimensional lake ecosystem model DYRESM-CAEDYM to oligo-mesotrophic Lake Okareka, eutrophic Lake Rotoehu, both in the temperate Bay of Plenty region, and highly eutrophic Lake Ellesmere, in the temperate Canterbury region, New Zealand. All three models were calibrated for a three-year period and validated for a separate two-year period. The model simulations generally showed good agreement with observed data for water column temperature, dissolved oxygen (DO), total phosphorus (TP), total nitrogen (TN) and chlorophyll *a* (Chl *a*) concentrations. To represent a possible future climate at the end of this century, mean annual changes in air temperature by 2100, derived from the IPCC A2 scenario downscaled for these lake regions, were added to the daily baseline temperatures for years 2002–2007. Lake model simulations using this future climate scenario indicate differential increases in eutrophication in all three lakes, especially during summer months. The predicted effects on annual mean surface water concentrations of TP, TN and Chl *a* will be equivalent to the effects of increasing external TN and TP loading by 25–50%. Simulations for the polymictic, eutrophic Lake Rotoehu further indicate that cyanophytes will be more abundant in the future climate, increasing by >15% in their contribution to annual mean Chl *a*. Therefore, future climate effects should be taken into account in the long-term planning and implementation of lake management as strategies may need to be refined and adapted to preserve or improve the present-day lake water quality.

Adrian R., D. Gerten, V. Huber, C. Wagner, S.R. Schmidt (2012). Windows of change: Temporal scale of analysis is decisive to detect ecosystem responses to climate change. Marine Biology: 159:2533–2542.

Long-term ecological research has become a cornerstone of the scientific endeavour to better understand ecosystem responses to environmental change. This paper provides a perspective on how such research could be advanced. It emphasizes that a profound understanding of the mechanisms underlying these responses requires that records of ecologic processes be not only sufficiently long, but also collected at an appropriate temporal resolution. We base our argument on an overview of studies of climate impacts in limnic and marine ecosystems, suggesting that lakes and oceans respond to (short-term) weather conditions during critical time windows in the year. The observed response patterns are often time-lagged or driven by the crossing of thresholds in weather-related variables (such as water temperature and thermal stratification intensity). It becomes clear from the previous studies that average annual, seasonal or monthly climate data often fall short of characterizing the thermal dynamics that most organisms respond to. To illustrate such literature-based evidence using a concrete example, we compare 2 years of water temperature data from Muggelsee (Berlin, Germany) at multiple temporal scales (from hours to years). This comparison underlines the pitfalls of analysing data at resolutions not high enough to detect critical differences in environmental forcing. Current science initiatives that aim at improving the temporal resolution of long-term observatory data in aquatic systems will help to identify adequate timescales of analysis necessary for the understanding of ecosystem responses to climate change.

Wagner C. & R. Adrian 2011. Consequences of changes in thermal regime for plankton diversity and trait composition in a polymictic lake: a matter of temporal scale. Freshwater Biology 56 (10): 1949-1961.

1. Changes in plankton species diversity and community structure as a result of global warming are of growing concern in ecological studies, as these properties contribute substantially to key ecosystem processes.
2. We analysed the effect of short-term temperature rise and changes in the thermal regime during summer on plankton diversity of the eutrophic and polymictic Mu¨ ggelsee in Germany, from 26 years of summer records (1982–2007). We tested for changes in community properties, such as species richness, evenness and population size of phytoand zooplankton, during alternating periods of thermal stratification and mixing, which were between 2 and 8 weeks long. Moreover, we tested for overall long-term temporal trends in annual averages of the community properties during stratified and mixed events.
3. We found that the overall number of stratification events increased significantly across the study period. When the lake was stratified, consistently higher surface water temperatures and lower epilimnetic nutrient concentrations were found. As the length of thermal stratification increased, the phytoplankton shifted towards a higher proportion of buoyant cyanobacteria capable of N-fixation (Aphanizomenon, Anabaena). Diatoms were at a disadvantage because of high temperature, exceeding their upper lethal limit and sedimentation losses. Zooplankton species with high thermal tolerances (i.e. Thermocyclops oithonoides, Thermocyclops crassus) and ⁄or those that grow quickly at high temperatures (i.e. rotifers) became more common.
4. During periods of continuous mixing, the community remained largely unchanged, except for some minor increase in the biomass of diatoms.

5. While a noticeable shift towards N-fixing cyanobacteria was observed with increasing length of stratified events, and rotifers and copepods became the main predators, there were minimal changes in diversity, except for an increase in cyclopoid copepods and a decrease in diatom diversity. As for cyanobacteria, the net short-term effect on their diversity was neutral as a result of species replacements. In the long term, however, the diversity of cyanobacteria and cladocerans declined while that of rotifers increased.
6. Overall, our study presents a cautionary example of how we might fail to foresee the impact of climate-induced changes on ecosystem processes if we restrict our studies to seasonal or yearly temporal scales, thus neglecting the impact of substantial changes operating at smaller temporal scales.