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Global warming: Design of a flow-through shallow lake mesocosm climate experiment

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Abstract

Shallow lakes are likely to be strongly impacted by climate changes and, in particular, by increased temperatures. To enable realistic experimental studies of the effects of higher temperatures on in-lake processes and dynamics, technologically advanced systems are required. This paper presents design details, operating characteristics, and background information on a currently operating experimental flow-through mesocosm system that allows investigation of the interactions between simulated climate warming and eutrophication and their impacts on biological structure and ecosystem processes in shallow lakes. We use 24 mesocosms to combine three temperature scenarios (one unheated and two heated relative to the Intergovernmental Panel on Climate Change climate scenario A2 and A2 + 50%, respectively) and two nutrient levels (enriched and nonenriched). Planktivorous fish (male sticklebacks, *Gasterosteus aculeatus*) are stocked in accordance with the nutrient level. The water residence time is regulated by the semicontinuous addition of water and is approximately 2.5 mo in each mesocosm. For heating, we use electrically powered heating elements. The heating system has performed well over 16 mo of continuous heating, and seasonal and diurnal temperature variations of the unheated reference mesocosms were paralleled well by the heated mesocosms. The performance of the flow-through system and the heating technique are discussed with special emphasis on strengths, limitations, and potential improvements of the system. To illustrate the performance of the system and its potential, we present data for selected periods on total phosphorus retention in the mesocosms and system primary production and respiration.

During the next century, the global climate is expected to undergo significant changes. The forecasts for the Danish region include a temperature increase of 3°C to 5°C, the increase being most pronounced during autumn and winter, with higher precipitation and more extreme climate events (Christensen and Christensen 2001; Jørgensen et al. 2001). Increased temperatures and higher runoff of nutrients predicted on the basis of the expected increase in precipitation are likely to affect lake ecosystems (Straile et al. 2003; Moss et al. 2003). Moreover, the predicted warmer winters will probably substantially reduce the period with ice cover in the coastal situated lakes. This will, especially in shallow lakes, influence the survival of fish and macrophytes, i.e., the key structuring elements in shallow lakes. Such changes may cascade to other trophic levels and, ultimately, affect lake water quality (Moss 1990; Scheffer et al. 1993; Jeppesen et al. 1997). How shallow north temperate coastal lakes will respond to global warming has been debated in recent years. Some argue for increased possibility for a shift occurring in turbid lakes to a clearwater state due to a stimulated plant growth and reduced predation by fish (Scheffer et al. 2001). Others believe that turbid lakes will remain turbid due to enhanced external and internal nutrient loading and higher predation by fish (Jeppesen et al. 2003; McKee et al. 2003; Moss et al. 2003). Yet, the few field experiments conducted so far show that a temperature increase of a few degrees has a modest effect on the

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biological communities, but internal P loading increased (McKee et al. 2003; Moss et al. 2003). Even less is known about the probably different responses of continental situated temperate lakes and subtropical-tropical lakes (Nõges et al. 2002; Jeppesen et al. 2003).

A number of approaches for estimating the effects of climatic changes on lakes exist. These include analyses of interseasonal variations or time series analyses of contemporary data, space-for-time substitution by analyzing data from various climate regions, analyses of paleolimnological records, and controlled experiments in the laboratory and field. All have their potentials and limitations (Schindler 1998; Moss et al. 2003; Battarbee et al. in press).

Several controlled experimental systems have recently been developed to test the effects of global warming on shallow lake ecosystems. Baulch et al. (2003) developed a 700 L lake-based batch enclosure system that is kept open to the sediment. The temperature is controlled by hot water circulated through a network of pipes coiled around the enclosure bottom. The system has run relatively smoothly, although problems in particular in attaining the target temperature difference between the control and the warmed enclosure and controlling the exchange of water between the enclosures and lake have been experienced (Baulch et al. 2003). The latter problem was solved in the land-based batch system described by McKee et al. (2000). That system consists of cylindrical (depth 1 m, diameter 2 m) mesocosms sunk into the ground for insulation, after which sediment was added. Heating was performed by circulating hot water through heating elements placed horizontally on top of the sediment and operating with a sensitivity of ± 0.25°C. Evaporative losses were replaced by deionized water. This system operated smoothly for more than 2 y. However, a drawback of both systems described above is that they are batch systems, whereas natural lakes are typical flow-through systems. Moreover, in both systems, heating elements are fixed in or immediately on top of the sediment to create thermally mixed conditions in the mesocosms without stirring. This construction potentially leads to locally higher temperatures that may influence biogeochemical processes in the sediment (Jensen and Andersen 1992) and, thus, the benthic-pelagic interactions.

Building on the experience of McKee et al. (2000), we have developed a land-based semi-continuous flow-through mesocosm system that takes into account the fact that most shallow lakes are not batch but flow-through systems. Our system allows calculation of mass balances of nutrients and organic matter. Moreover, frequent measurements of oxygen and pH allow estimation of community primary production and respiration, as well as the CO_2 exchange between air and water. Paddles continuously mix the water column in all mesocosms, and the temperature control runs with higher sensitivity than the McKee system. In addition, heating elements are placed above the sediment. The system is equipped with monitoring devices that are supervised by remote control. An alarm system ensures early warning in the case of irregularities in the system functioning. The system allows the simultaneous simulation of warming effects on low nutrient (clear) and enriched (turbid) lakes.

Materials and procedures

General description of the experiment—During spring 2003, we established 24 flow-through outdoor mesocosms in a lowland valley in Central Jutland, Denmark (56°14′N, 9°31′E). The 24 mesocosms allowed a factorial design combining 2 nutrient levels with 3 temperatures in 4 replicates. Aquatic freshwater communities were allowed to establish in the mesocosms before nutrient addition was initiated in early May 2003. By the time heating was initiated (28 August 2003), extensive submerged macrophyte beds had developed in nonenriched mesocosms, while the enriched mesocosms were dominated by phytoplankton or filamentous algae with only sparse macrophyte vegetation. Electrically powered heating is continuously controlled relative to the ambient temperature in the unheated reference mesocosms according to the Intergovernmental Panel on Climate Change (IPCC) climate scenarios A2 (Houghton et al. 2001) and A2 + 50%. Planktivorous fish were stocked in natural densities consistent with the nutrient treatment.

Mesocosm specifications—The mesocosms consist of cylindrical stainless steel tanks 1.9 m in diameter and 1.5 m in total depth (Fig. 1). They are equipped with a flow-through system, where a timer-controlled magnetic valve (Danfoss Group, EV 220B) automatically adds groundwater every sixth hour, while an overflow pipe (diameter = 2.6 cm) drains off excess surface water. A small partly submerged plate (4 × 4 cm) in front of the outflow pipe prevents most snails, floating filamentous algae, and large organic fragments from being washed out of the mesocosm and, also, reduces the risk of clogging the outflow. During winter, the outflow pipe and a small region of water in front of it are kept free of ice by a thermostatically controlled electric warming cable. The flow-through system is thus kept functional throughout the year. Apart from periods of excessive summer evaporation, this flow-system ensures a constant water level of 1.0 m and a total capacity of approximately 2800 L in each mesocosm. The water drained through the overflow pipe is retained in a 500 L covered plastic collection tank placed beside each mesocosm (Fig. 1). Based on the total discharge into these collection tanks, it is possible to calculate the exact water residence time for the individual mesocosms, taking into account water added by the magnetic valve, precipitation, and evaporation. Since the water in the collection tank typically is sampled every 7 to 14 d during the experiment, it can provide integrated information on some of the conservative chemical variables (e.g., iron and total phosphorous) in the water column and permits calculation of highly accurate mass balances.

A 0.1 m layer of washed sand was initially added to each mesocosm and, on top of that, a 0.1 m layer of sediment collected from a nearby nutrient-rich freshwater pond. To remove large fragments of vegetation and avoid uncontrolled

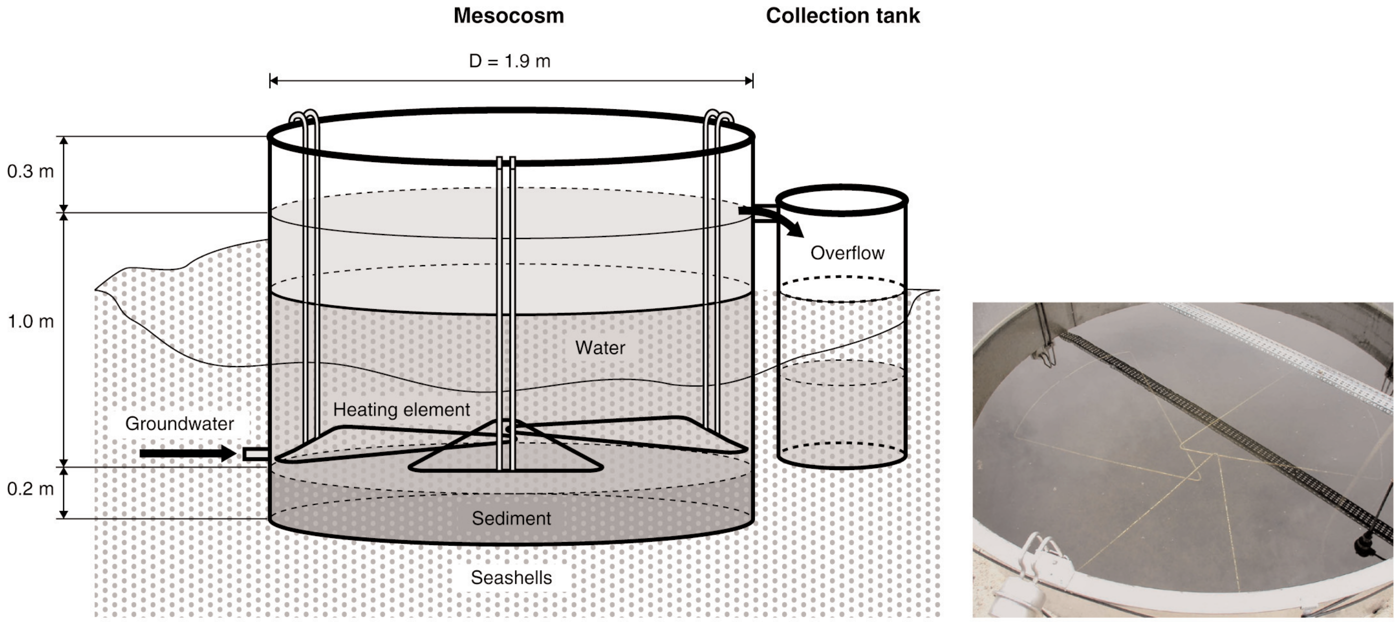

Fig. 1. Illustration and photo of one of the 24 flow-through mesocosms and the collection tank. In the bottom, three heating elements can be seen.

introduction of vertebrates such as fish or amphibians, the sediment was flushed through a net (mesh size: 1 × 2 cm) and drained of excess water before being placed in the mesocosms.

All tanks are located within a 20 × 20 m open area, enclosed at the perimeter by a wire fence and from above by wires strung in rows (distance between wires approximately 0.2 m) over the area (Fig. 2). This prevents the introduction of larger animals and birds to the experimental area. For insulation, the tanks have been embedded into a layer of seashells (*Mytilis edulis*). A major advantage of using seashells as insulation material is that they have a very high drainage capacity. Thus the area between the tanks is dry and accessible even during periods of heavy rain. A fibertex mat covers the shells and on top of that 0.1 m of hard-packed sand provides a stable working area between the tanks and eliminates obnoxious smells from the shells. A metal rim (0.05 m) is fastened around the perimeter of each mesocosm (0.35 m from the ground) to prevent access of smaller animals to the mesocosms. Likewise, a cover on the collection tanks helps prevent them from acting as traps for smaller animals. Inlet and outlet water pipes as well as most electrical wiring have been buried under the shells for insulation.

Heating system—Continuous warming was initiated in late August 2003 and is planned to run until August 2006. Sixteen of the mesocosms are heated under two different warming scenarios: low and high. These are run simultaneously. Three electrically powered (230 V AC) stainless steel heating elements (750 W each) warm the water in each of the heated mesocosms. Unheated mesocosms also contain 'dummy heating elements' that are not connected to the overall heating control system. The heating elements are fixed to the upper rim of the mesocosm and have two bars running parallel to the side before they extend horizontally in an open triangle 0.10 to 0.15 m above the sediment (Fig. 1). This shape was used to distribute the heat evenly near the bottom and to optimize the volume of free water in the middle of the mesocosm and to ensure a minimum of shading on the walls and sediment surface. Placing the heating elements near the bottom of the mesocosms was also predicted to be the optimal setup in terms of its contribution to the vertical mixing of the water within the tank. To supplement this mixing, a paddle-shaped mixer is placed in the upper part of the water column so that there is no visible disturbance of the sediment. The paddles

Fig. 2. Mesocosms to experimentally study how increased temperatures will affect shallow lake systems.

are operated continuously during ice-free periods. However, when the water temperatures approach 0°C, the paddles are stopped so that ice cover and thermal stratification of the water column are allowed to develop.

The mesocosms are grouped in eight blocks of three, including one mesocosm with ambient reference temperature and two mesocosms heated to the low and high warming scenario, respectively. Whether a particular mesocosm is warmed or not was applied in a random design, whereas the blocks were made so that they contain closely sited mesocosms. Within each block, the unheated mesocosm acts as reference for the two heated mesocosms, so that the water temperature in the latter is raised to predescribed target differences over the ambient reference temperature. Temperature control within the distinct blocks, rather than among all mesocosms, is advantageous because a localized failure or breakdown of the temperature recording in one mesocosm can only affect the mesocosms in the same block. It may, however, also potentially induce errors, as a divergence in temperature in only one of the unheated reference mesocosms will, automatically, be transmitted directly to the heated tanks in the block. Natural short-term temperature differences among replicate mesocosms have been observed during the first year of the experiment (August to December: mean 0.0°C to 0.5°C). Nevertheless, as the temperature typically varies with less than 1°C among replicate mesocosms and no systematic differences have been observed to date, it is presumed that these are of minor importance to the overall results.

The heating control system operates through three interlinked components: temperature sensors (PR electronics products: sensor type: Pt 100; maximum error ± 0.15°C at 0°C, temperature transmitter type: TT-5333), a data processor (Siemens S7-ET200 S), and heating elements. Water temperatures are recorded continuously by temperature sensors placed centrally in all mesocosms. Within the data processor, the temperature differences at any given time between warmed and reference mesocosms are compared to the target temperature difference transmitted via a central PC. If the temperature difference is too small, the heating elements in the mesocosm are activated and heating initiated. When the water temperature reaches the target difference to the reference mesocosm, the heating elements are switched off and remain inactive until the temperature difference again drops below the defined target.

In addition to data logging (every 30 min) and temperature control, the computer software has a monitoring function that constantly controls for failures in the information transfer between the computer and the data processor and for temperature deviations from a defined range. Via a local alarm system (FS 944) connected to the computer and the ordinary telephone network, information concerning such errors or notification of power failure is sent to the technician on watch for prompt reaction.

Winter conditions—Controlling the water temperature in the heated mesocosms relative to that of the reference mesocosms presents a problem during winter when the latter become ice-covered. If automatic temperature control continues during periods with severe frost, the heated mesocosms will always remain unfrozen, because the reference water temperature under the ice in the unheated mesocosms will usually remain at 0° to 4°C. Although global warming is anticipated to reduce the frequency and duration of lake ice cover, a scenario where lakes never freeze in Northern Europe is unrealistic according to the predictions of the current climate models (Jørgensen et al. 2001). Therefore, during periods of frost or near-frost, heating is controlled by daily manual adjustments of the target temperature differences according to the prognosis for mean air temperature for the next 24 h. Target temperature differences of 2°C and 3°C at the low and high heating scenario, respectively, are accordingly reduced to only 1°C and 2°C at a mean air temperature of –1°C, while heating is switched off in all mesocosms at mean air temperatures below –3°C. By using the prognosis for mean daily air temperature as reference temperature instead of the actual air temperature, we avoid replication of the considerable temperature fluctuations in air. However, we also eliminate the moderate diurnal variation usually seen for the water temperature. Air temperature is also used as an indicator when stopping the mixing of the water column. At temperatures below zero, the reference mesocosms are no longer mixed and ice cover and thermal stratification are allowed to develop, whereas mixing continues in the heated mesocosms until heating is switched off, according to the criteria described above.

Warming scenarios—IPCC climate scenario A2 (Houghton et al. 2001) and A2 + 50% scaled to local conditions in the region (average over five 25 × 25 km grid cells [pers. comm. O. Bøssing Christensen, Danish Meteorological Institute]) were applied as the low and high warming scenarios, respectively. The climate scenario A2 models actually predict air temperatures. However, because the temperature of surface waters closely follows that of the air in shallow lakes, we chose to use the modeled air temperatures as a surrogate of water temperatures. Warming was calculated as the mean air temperature increases in one particular month with respect to a 30-y reference period (1961 to 1990) and the modeled temperatures in the same month in 2071 to 2100 (Fig. 3). The modeled temperature difference for the A2 scenario is generally higher in August to January (max: 4.4°C in September) than during the rest of the year (min: 2.5°C in June).

Nutrient treatments—Groundwater (total phosphorus: 2 to 20 µg P L^{-1}; total nitrogen: 51 to 70 µg N L^{-1}; total iron: 0.10 to 0.62 mg Fe L^{-1}) collected from a local well is used as inlet water to the flow-through system. To create the two alternative states existing in shallow lake systems, i.e., the plankton dominated (turbid) and the macrophyte dominated (clear) state (Scheffer et al. 1993), half of the mesocosms are enriched with nitrogen and phosphorus while the other half remain unenriched. Throughout the first year, nutrients were added weekly as Na_2HPO_4 and $Ca(NO_3)_2$ solutions with a constant loading of 54 mg P and 538 mg N per mesocosm each week (2.7 mg P m^{-2}

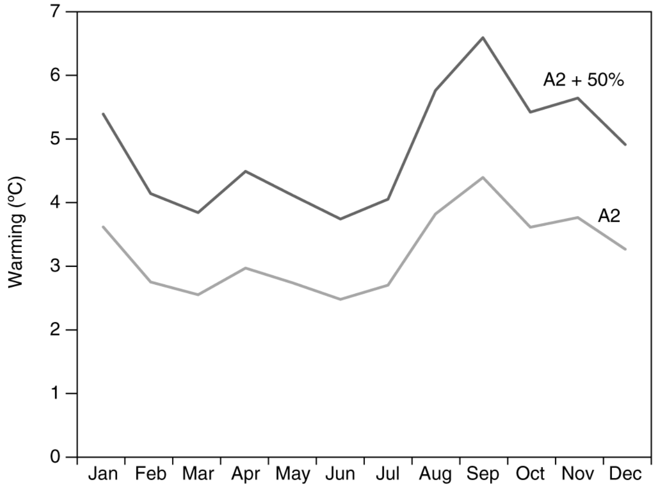

Fig. 3. Modeled monthly temperature increase from the reference period (1961–1990) to 2071–2100 according to the IPCC climate model A2 (gray) and A2 + 50% (dark gray) down-scaled to local conditions around the experimental site. Based on hourly estimates.

d^{-1} and 27.1 mg N m^{-2} d^{-1}). The experiment is still in progress and, depending on the results from the first year, the loading may be changed later in the experiment. The enrichment was initiated in early May 2003 when only sparse submerged vegetation had developed in some of the mesocosms.

Measurements of oxygen and pH—Oxygen and pH probes are rotated among the mesocosms every week and every fourth week, respectively. We use 12 oxygen probes (OxyGuard®, two-wire probe, model 420), and measurements are conducted in all nutrient-enriched mesocosms during 1 week and in all nonenriched mesocosms the following week. At the same time, pH (OxyGuard®, light-duty submersion type connected to a Manta pH measurement system) is measured in six of the mesocosms where oxygen is being measured. A submersible pump (Sicce pumps, model: Micra) connected to the oxygen probe creates continuous horizontal water flow over the membrane and, thus, reduces the risk of instability due to fouling. All probes are calibrated weekly. As for the water temperature, oxygen concentration and pH are measured continuously. However, to reduce the amount of data collected, records are only made every 30 min. The frequent records allow us to describe diurnal variations and to calculate system primary production and respiration using the Odum method (Odum 1956). Re-aeration is a critical factor in these calculations. However, the continuous mixing of the water column allows accurate estimation of the re-aeration coefficient.

Pelagic and benthic communities—Aquatic communities representative of temperate shallow lakes were readily established in the mesocosms before beginning the heating. As inoculum for the benthic populations, sediments from a nutrient-rich plankton-dominated lake (Lake Søbygård) and a less nutrient-rich lake with macrophytes (Lake Stigsholm) were added to the original bulk pool of nutrient-rich pond sediment. In addition to the plankton emerging from resting eggs introduced with the sediment, plankton populations developed from inoculum collected in equal parts from the littoral and pelagic zones of four chemically and biologically different lakes in April 2003. Furthermore, thorough cross-mixing of water among the mesocosms was performed regularly to reduce start community variation among the pelagic communities of the same nutrient treatment. Nevertheless, large snail populations (mainly *Lymnea peregra*) emerged in three mesocosms in the period from May to July, i.e., before initiation of heating. To ensure similar conditions in all mesocosms, we chose to transfer snails to mesocosms with low snail densities.

Macrophytes (mainly *Elodea canadensis* and *Potamogeton crispus*) emerged naturally in most of the nonenriched mesocosms in May to June 2003, whereas sparse shoots of these species appeared in only two of the enriched mesocosms. As the plant populations developed nonuniformly among the nonenriched mesocosms, we manipulated their distribution and coverage before the experiment. In densely vegetated mesocosms, *P. crispus* was thinned out, and intact shoots were transplanted to mesocosms without or with low densities. *E. canadensis* was selectively removed from all mesocosms, but rapid regrowth and colonization prevented complete elimination of this species, and low densities were present in some mesocosms at the start of the experiment. Free-floating and attached filamentous algae developed massively in some of the mesocosms during summer despite our efforts to reduce their abundance during this pre-experimental period. Manipulation of the vegetation was stopped 2 wk before heating was initiated. Yet, 3 to 4 times throughout the experiment sporadically occurring shoots of floating-leaved macrophytes and duckweed were removed from the mesocosms to avoid dominance of floating-leaved plants.

Three-spined sticklebacks (*Gasterosteus aculeatus*) were stocked in the mesocosms in near to natural densities corresponding to the applied nutrient treatment (based on catch per unit effort [CPUE] in gill nets [Jeppesen et al. 2002] in Danish lakes [n = 180]): one individual in nonenriched mesocosms and 12 in enriched mesocosms. The 12 sticklebacks in the enriched mesocosms were added gradually, so that the number increased from mid-May to August (2003) when the heating experiment was initiated. To prevent breeding and, thus, uncontrollable population growth, only sexually mature males with breeding coloration were introduced. This was done because the mesocosms were too small to include piscivorous fish and, in their absence, unnaturally high densities of planktivorous fish were expected to develop if breeding was allowed. Dead or sick fish were replaced when observed. Furthermore, we sought to maintain a constant fish density by additional stocking based on regular visual inspections and the use of minnow traps and catch-recapture estimates. To avoid age-related fish loss, the old fish are replaced by younger males after a year. All sticklebacks came from natural populations and were caught either by traps or drag net.

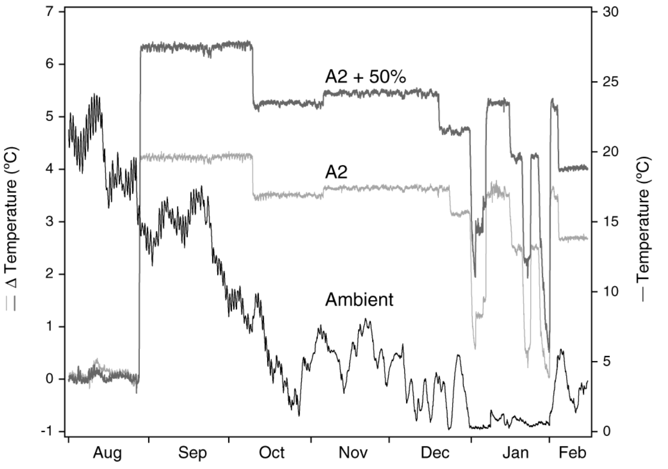

Fig. 4. Temperature difference between the unheated reference mesocosms and those heated according to IPCC climate scenario A2 (gray) and A2 + 50% (dark gray) from August to February. Actual water temperature of the unheated mesocosms is marked in black. Heating was initiated in late August. On frosty winter days (late December to February), the temperature in the heated mesocosms was not raised to a constant difference above the ambient temperature in the reference mesocosm, because the water temperature in the latter would always be ~ 0°C. Alternatively, at mean daily air temperatures, less than 0°C heating was controlled manually by daily adjustments of the temperature difference according to the air temperature. Data logged every 30 min.

Assessment

Both the heating (Fig. 4) and the flow-through system have generally performed well for 16 mo of continuous function. The sensitivity of the heating control system is high, and at the most optimal performance heating cycles run at intervals of 1 to 15 s between on and off, responding to small temperature changes from the target temperature difference. Such frequent cycling allows the heating system to parallel very precisely diurnal and seasonal temperature variation in the control mesocosms. During the first 3 mo with heating, the mean divergence of the measured temperature differences between control and heated mesocosms from the target temperature differences ranged between 0.11°C and 0.26°C (Table 1). In general, the deviation was slightly higher in the high heating scenario. The heating systems previously described by Baulch et al. (2003) and McKee et al. (2000) both controlled temperature by adding hot water through electromagnetic control valves. As pointed out by Baulch et al. (2003), such valves are not suited for continuous cycling between open and closed positions since they will eventually fail due to wear. This limitation, which reduces the sensitivity and accuracy of their systems (deviation from target temperature difference, McKee et al. (2000): margins 0.97°C to –0.63°C, mean = 0.04°C, SD = 0.14; Baulch et al. (2003): mean = –0.5°C), has been overcome in our heating system by using electrical power directly as the heating source.

So far, other freshwater mesocosm experiments on global warming have heated to either a constant temperature (e.g., Beisner et al. 1997), heated to a constant temperature above ambient (McKee et al. 2000; Baulch et al. 2003), or heated only in periods (McKee et al. 2000). By adjusting the temperature difference between the heated and the unheated reference mesocosms every month according to the forecasts of the climate model, seasonal climate warming variation is integrated in our experiment. Heating by on average 1°C to 1.5°C more in August through January than in February through July at the two climate scenarios may be particularly important for the chemical and biological dynamics, because higher temperatures in autumn and winter may extend the growing season of macrophytes, reduce ice covers and the probability of winter anoxia, and increase the survival of various species susceptible to oxygen depletion.

Another strength of our experimental setup compared to most previous mesocosm studies is that the water columns are mixed. Due to weaker surface wave energy mesocosms often tend to have less physical water mixing and, consequently, lower air-water gas exchange than shallow lakes. By constant mixing and semi-continuous inflow of oxygen-rich groundwater to our mesocosms, we attempt to avoid some of the problems frequently seen in unmixed batch system experiments, such as thermal gradients (discussed by Baulch et al. 2003) or total dominance of duckweed (Liboriussen et al. in press)

The flow-through system where each mesocosm has an inlet, an outlet, and a relatively short water residence time was established to mimic the natural passage of water that most lakes

Table 1. Mean temperature difference between unheated reference mesocosms and those warmed to IPCC climate scenario A2 and A2 + 50%, respectively, in August (no heating) to November*

	Scenario A2		Scenario A2 + 50%		
	Target	**Measured ± SD**	**Target**	**Measured ± SD**	***n***
Aug (no heating)	0	0.10 ± 0.10	0	0.04 ± 0.07	1262
Sep	4.39	4.23 ± 0.04	6.59	6.33 ± 0.09	2041
Oct	3.61	3.50 ± 0.03	5.42	5.26 ± 0.04	1253
Nov	3.76	3.64 ± 0.02	5.64	5.45 ± 0.03	2083

*The target temperature difference is calculated as mean temperature increase from 1 month in a 30-y reference period (1961–1990) to the modeled temperatures in the same month in 2071–2100. Measured temperature difference is the actual warming obtained by our heating system. Mean ± SD.

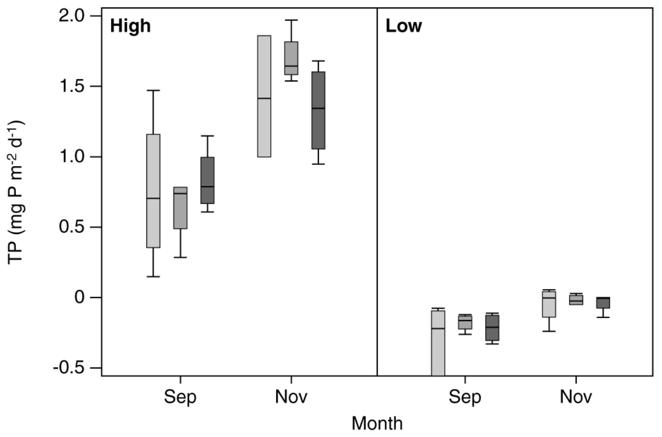

Fig. 5. Box-plot showing examples of mass balances on phosphorus retention in nutrient enriched (high) and nonenriched (low) mesocosms in September and November for unheated reference mesocosms (pale gray) and mesocosms warmed to scenario A2 (gray) and warmed to scenario A2 + 50% (dark gray). Each box shows 10%, 25%, median, 75%, and 90% fractiles.

experience. However, constructing a flow-through system that supplies the same volume of water to all 24 mesocosms was not unproblematic and a continuous flow could not be established due to water pressure differences in connected pipes. Supplying water in pulses, as done in this experiment, allows individual adjustments to be made, not only in the duration of the pulses to each mesocosm but also in the frequency and timing of the pulses. Control of the pulse timing assures that water is only supplied to one mesocosm at the time, thus eliminating variation due to reduced water pressure at simultaneous water supply to several mesocosms. Based on measurements of the total discharge to the collection tanks (September 2003 to March 2004), the average water residence time is estimated to be 74 d (ranging from 68 to 85 d among mesocosms). In addition to the impact of small differences in precipitation into and evaporation from the mesocosms, this variation is probably mainly caused by diurnal variations in water pressure and inaccuracy of the adjustments of the water pulses. The accuracy of the water supply could probably be improved by placing a cistern at each mesocosm to be filled with an exact water volume before emptying at defined intervals. However, due to our relatively frequent measurements (7 to 14 d) of the total water output into the collection tank, we may be able to adjust for the differences in our mass balance calculations.

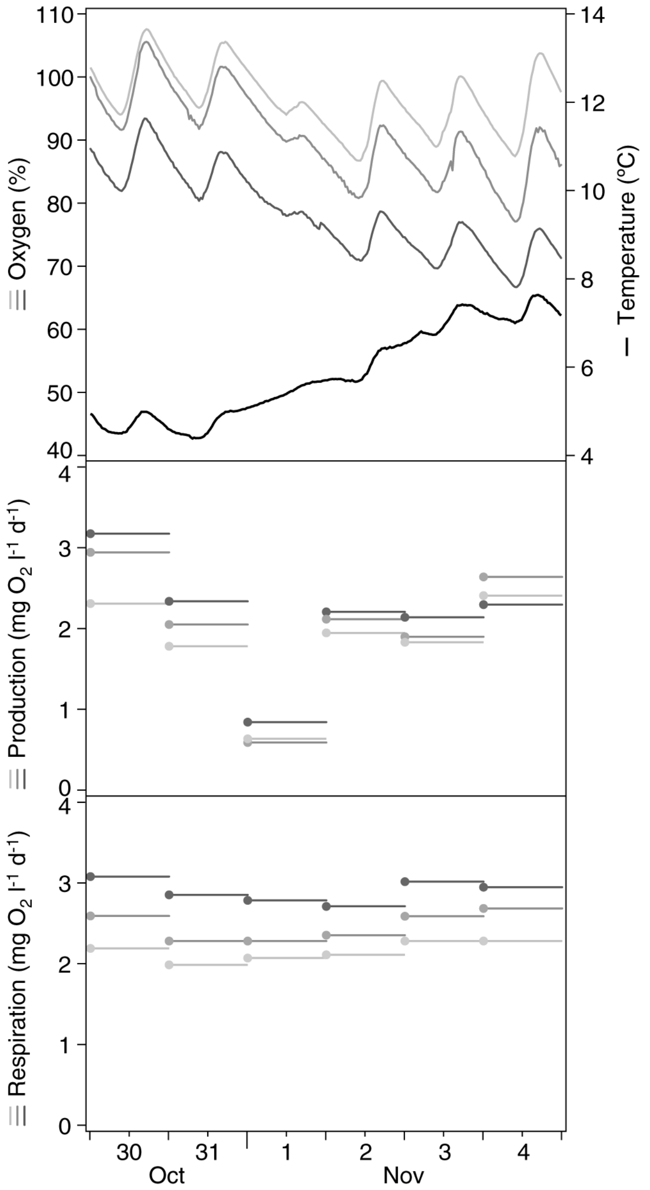

Fig. 6. Example of mean diurnal variation in oxygen saturation and estimated system primary production and respiration in mesocosms being unheated reference (pale gray), warmed to scenario A2 (gray), and warmed to scenario A2 + 50% (dark gray) (*n* = 4). Mean water temperature of the unheated mesocosms is shown in black. All mesocosms are nutrient enriched.

As previously stated, the flow-through system allows us to establish mass balances for some of the conservative chemical variables based on inlet-outlet measurements for the individual mesocosms. An example showing the phosphorus mass balance is given in Fig. 5 for the mesocosms with and without nutrient enrichment, respectively. Nutrient-enriched mesocosms showed positive phosphorus retention, irrespective of temperature, with an increasing trend from September to November. This probably reflects the increased capacity of the sediment to retain phosphorus with decreasing oxygen consumption in the sediment surface due to reduced temperatures. In the mesocosms without nutrient enrichment, phosphorus retention was slightly negative in September at all three temperatures and close to zero in November. This reflects the low inlet concentrations of phosphorus (approximately 12 μg TP L^{-1}) and release from the sediment during summer. Similarly, community primary production and respiration may be calculated from the frequent oxygen monitoring in the mesocosms. As shown in Fig. 6, substantial diurnal variation of the oxygen saturation is evident in all three temperature scenarios. This, along with well-estimated re-aeration caused by constant mixing of the mesocosms, provides us with good opportunities to get year-round information on the metabolic dynamics of the systems and, thus, to describe how heating and nutrients affect systems primary production and respiration. In the period shown, both systems primary production and respiration increased with temperature (Fig. 6).

The use of groundwater as inlet water rather than water from a natural lake may be seen as a weakness of our experiment because groundwater does not carry propagules from upstream waters. However, the main natural water input to many Danish lakes derives either from groundwater or small streams poor in propagules from lentic species. Furthermore, an analysis of metacommunity structure indicates that even in highly interconnected ponds the local communities are often mainly structured by local environmental constraints rather than regional interactions (Cottenie et al. 2003). Lentic propagules in natural lake-inlet waters are thus not only few in numbers, but they can also be expected to have minor effects on the community structure if introduced in natural densities.

The cost of setting up the complete experimental setup including tanks, probes, and the computer-controlled heating and surveillance system has been approximately 140,000 Euro. However, total establishment costs should also include the numerous hours of manpower. Remote access to the computer at the experimental site and, thus, to both past and current data plus several of the vital control functions facilitates easy electronic supervision and allows small adjustments to the software to be made while running the experiment. Despite this advanced technical system, running the experiment is demanding with respect to manpower and requires regular supervision and maintenance of the equipment. Heating expenses are another costly component of the project. On an annual basis, the total electricity consumption of the experiment is approximately 60,000 kWh. This includes electricity supply for heating, mixing, water supply, computer, and control facilities, etc.

Comments and recommendations

We find the system very suitable for describing how changes in temperature and nutrients affect dynamics, storage, and loss of nutrients and carbon in simulated shallow lake system over prolonged time periods and with contrasting trophic structure. Moreover, the design and functional capacity of the flow-through system allow conduction of a range of additional studies not feasible in batch systems, for instance, on how extreme hydrological events or systematic seasonal changes in inflow will affect shallow ecosystems and on the recovery of the ecosystems after such events. The system can also provide both fixed and differential temperature control, just as mixing rate and mixing timing may be minutely controlled. The major drawback of the system is a relatively large variability among mesocosms, particularly at high nutrient loading. Increased replication, albeit costly, would help solve this problem. Another weakness is the relatively small size of the mesocosms. Scale matters (Schindler 1998) and our mesocosms are no exception as we found a tendency for pond forms of, for example, zooplankton to dominate the plankton. Furthermore, relatively high proportions of filamentous algae, more typical for small ponds than for lakes, were observed in the nutrient-enriched mesocosms. In larger systems, such problems could be minimized, and they would also allow stocking of piscivorous fish and, thus, natural development of planktivorous fish. The present system requires restriction of the fish community to single sex small-sized fish to avoid development of unnaturally high fish densities in the absence of piscivores. If the size of the mesocosms were to be increased and the replication strength maintained, alternative heating systems based on wind or sun energy offer an attractive solution. Despite the above-discussed problems and limitations of our technical equipment and of the experiment in general, we believe that the system has a great potential for realistic studies of the effects of global warming and eutrophication on in-lake processes and dynamics in shallow lakes.

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