Toward predicting climate change effects on lakes: a comparison of 1656 shallow lakes from Florida and Denmark reveals substantial differences in nutrient dynamics, metabolism, trophic structure, and top-down control


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Toward predicting climate change effects on lakes: a comparison of 1656 shallow lakes from Florida and Denmark reveals substantial differences in nutrient dynamics, metabolism, trophic structure, and top-down control

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Abstract

Rapid climate changes may potentially have strong impacts on the ecosystem structure and nutrient dynamics of lakes as well as implications for water quality. We used a space-for-time approach to elucidate such possible effects by comparing data from 1656 shallow lakes (mean depth <3 m) in north temperate Denmark (DK) and subtropical Florida (FL). The lakes were categorized into 7 total phosphorus (TP) classes within the range of 2 to 300 µg L−1. Physicochemical variables showed significant seasonal differences, which can be attributed to different sunlight regimes and temperatures. The FL lakes had overall higher fish biomasses (notably in the littoral zone) but a substantially lower zooplankton biomass and body mass of microcrustaceans, a much lower zooplankton:phytoplankton biomass ratio (lower grazing on phytoplankton), and a markedly lower biomass of benthic invertebrates, indicating much greater control of consumers by fish in the FL lakes. Accordingly, the summer phytoplankton biomass was higher in the FL lakes. Cyanobacteria in summer were proportionally more important in the FL lakes at all TP levels, whereas the proportion of dinoflagellates, chrysophytes, and cryptophytes was higher in the DK lakes at low TP. Submerged macrophytes occurred at higher TP (>100 µg L−1) in the FL lakes, but coverage was higher in the DK lakes at low TP. We also found lower oxygen saturation in the nutrient-rich FL lakes than in the DK lakes, suggesting lower net ecosystem production in the FL lakes. We discuss our results within the framework of climate warming.

Introduction

Climate change is a reality (IPCC 2007, 2013) and may have strong impacts on the ecosystem structure and nutrient dynamics of shallow lakes, with implications also for the water quality. One of the multiple reasons for these impacts is a higher internal loading of phosphorus (P) in response to the higher temperatures (Søndergaard et al. 2003). Some shallow lakes may also become temporarily stratified due to the rising temperature, which exacerbates the release of P from the sediment. A warmer climate may also lead to a change in wind speed (IPCC 2013), which affects stratification and eutrophication, as seen in Lake Taihu, China (Deng et al. 2018). An increase in the proportion of potentially toxic cyanobacteria among the phytoplankton assemblage is also expected (Huisman et al. 2005, Jöhnk et al. 2008, Jeppesen et al. 2009, Kosten et al. 2012). Moreover, several studies suggest that the biomass of phytoplankton or the concentration of chlorophyll a (Chl-a) per unit of total phosphorus (TP) will increase, which may in part reflect changes in the food web structure (Jeppesen et al. 2009). For example, recent studies indicate that the community assemblage, size structure, and dynamics of fish will change markedly with global warming (Jeppesen et al. 2012). Cross-comparisons of fish populations in similar shallow lakes in subtropical South America and temperate Europe (Teixeira-de Mello et al. 2009), as well as in lakes sampled along a latitudinal gradient within Europe, have collectively shown a higher number of fish at a given TP concentration in warm than in cold lakes (Brucet et al. 2013),
a higher percentage of omnivorous fish (Moss 2010, Gonzalez-Bergonzoni et al. 2012), and more truncated food webs (Iglesias et al. 2011). Such changes in fish assemblages are expected to result in a higher predation pressure on zooplankton and consequently a lower grazing pressure on phytoplankton, producing a higher algal biomass (e.g., Chl-a) per unit of TP (Jeppesen et al. 2009). This trophic structure is further substantiated by an often lower biomass of zooplankton in warm lakes than would be expected from the food resources available (i.e., a low zooplankton:phytoplankton biomass ratio; Gyllström et al. 2005, Havens and Beaver 2011, Meerhoff et al. 2012), although a low food quality (high proportion of cyanobacteria) also may contribute (Ger et al. 2016). Additionally, the abundance of benthic invertebrates is expected to be lower in the warm lakes because of higher fish predation (Meerhoff et al. 2007, 2012), but currently data to justify this assumption are scarce.

Greater abundances of submerged macrophytes often associated with greater water clarity in northern temperate non-humic lakes are also evident. The effect is much weaker in warm temperate (Romo et al. 2004) and subtropical lakes (Bachmann et al. 2002). Bachmann et al. (2002) found no clear differences in Chl-a:TP or Secchi depth:TP relationships in shallow lakes in Florida with low, medium, or high area covered by aquatic macrophytes (COV) or volume infested with aquatic macrophytes (PVI). Jeppesen et al. (2007) found Chl-a at a given nutrient concentration to be overall higher in Florida lakes than in Danish lakes when macrophytes were abundant. In contrast to the northern temperate lakes (Timms and Moss 1984, Burks et al. 2002), macrophytes do not act as a proper refuge for zooplankton in warm lakes because of the higher risk of fish predation and because fish, particularly the smallest species and individuals, aggregate in greater numbers in the vegetation in subtropical and tropical lakes (Meerhoff et al. 2007).

Not only ecosystem structure but also ecosystem metabolism is expected to change with warming because respiration is proportionally more affected by increasing temperature than primary production (Brown et al. 2004). Supporting the view of lower net production in warm lakes, Kosten et al. (2010) found that the partial pressure of carbon dioxide in 83 shallow lakes sampled along a 6000 km climatic gradient in South America was strongly and positively correlated with temperature, indicating a proportionally higher mineralization in warm lakes (or catchments). Moreover, in a cross-European (from Sweden to Turkey) comparative study conducted in shallow lake mesocosms run at 2 contrasting nutrient concentrations representing turbid and clear lakes, Scharfenberger et al. (2019) found a decline in net system production from positive in the colder lakes (mostly northern) to negative in the warmer southern lakes at both low and high nutrient levels.

Most of these studies were based on a modest amount of data and typically did not cover a large nutrient gradient. To elucidate further the robustness of the identified differences between climate zones, we compared a unique set of monitoring data from 1600 shallow lakes in temperate Denmark (DK) and subtropical Florida (FL) with similar depths and surface areas but covering a wide nutrient gradient in both regions. Based on the previous studies, we hypothesized that in warm lakes: (1) top-down control by fish would be greater irrespective of the nutrient level, leading to overall lower zooplankton biomass, lower zooplankton:phytoplankton ratio, higher Chl-a:TP and Chl-a:total nitrogen (TN) levels, and lower zoobenthic biomass; (2) dominance of cyanobacteria would be greater with mass dominance at lower TP; (3) coverage of submerged plants would be higher at high turbidity because of the longer growing season and higher winter survival; and (4) oxygen (O2) concentrations would be lower because the temperature is higher, and O2 saturation would be lower because of the lower net ecosystem production.

Methods

Florida lakes

The 1025 investigated lakes are distributed throughout the state of Florida (Canfield and Hoyer 1988, Canfield and Hoyer 1992). With the exception of a few lakes, water samples for chemical analysis were collected from the surface (0.5 m) at 1–4 open-water sites within each lake and analyzed by Florida LAKEWATCH using standard methods (Canfield et al. 2002). Chl-a concentrations were determined by first filtering water through glass fiber filters. Prior to 1994, extraction was conducted with aqueous acetone, which was replaced by ethanol (Sartory and Grobbelaar 1984). The value of the volunteer program data is often an issue of concern. To elucidate the validity of this concern, professional biologists from the Florida Department of Environmental Protection (FDEP) and Florida LAKEWATCH volunteers sampled 27 FL lakes simultaneously to measure the concentrations of TP, TN, and Chl-a. Each program followed their standard operating procedures for both field and laboratory activities to determine data comparability. The results showed that the LAKEWATCH data were overall similar to those of FDEP collected using stringent quality assurance protocols and analyzed in a National Environmental Laboratory Accreditation Conference (NELAC)-certified laboratory, in compliance with Florida's quality assurance rule (Hoyer et al. 2012).
Secchi depth data were from 2 sources, with one set consisting of samples gathered during a 1979/1980 statewide survey of 165 of the FL lakes (Canfield et al. 1985). Secchi depth at each site was measured with a 20 cm black-and-white Secchi disk, and depth was measured to the nearest centimeter. The other set was LAKEWATCH water clarity data based on samples collected using a 20 cm white Secchi disk. Data on O₂ concentrations were from 2 sources, with one set again consisting of samples gathered during the 1979/1980 statewide survey (Canfield et al. 1985). O₂ concentrations were measured at the deepest point of the lake at 1 m intervals from the surface to the bottom using a YSI Model 51A oxygen–temperature meter (YSI, Inc., Yellow Springs, OH, USA). The other set was from 60 lake surveys (Canfield and Hoyer 1992) in which O₂ concentration was again measured at a deep-water station from the surface to the bottom using the same meter. In our study, only data from the upper 1 m were used.

The phytoplankton data were from 2 sources, with one set consisting of samples gathered during the 1979/1980 statewide survey (Canfield et al. 1985). Water was sampled at 0.5 m depth and fixed in Lugol’s solution. The second dataset was from the Ocklawaha and Kissimmee Chain-of-Lakes (Havens et al. 2019). Phytoplankton was collected with a 2 L Van Dorn bottle from the middle of the water column or with a 2 cm inner diameter PVC tube, enclosing the entire water column to a depth 0.5 m above the bottom. In each case, an aliquot of the water was placed into an amber plastic bottle and preserved with Lugol’s solution. In each dataset, the abundance of common taxa was estimated by random field counts. At least 100 (400 in the second set) units (colonies, filaments, unicells) were enumerated to the lowest possible taxonomic level. Biovolumes were estimated using formulae for solid geometric shapes that most closely matched the cell shape (Hillebrand et al. 1999; for further details see Canfield et al. 1985, Havens and Beaver 2011).

The zooplankton data were also derived from 2 sources, with one set gathered during the same statewide survey of 165 lakes (Canfield and Watkins 1984) using a Wisconsin net (opening diameter 1 cm and 80 µm mesh size). The net was towed vertically through the water column from 0.5 m above the bottom to the surface, and samples were preserved in 80% alcohol. The second set was derived from sampling of Lake Okeechobee and 14 lakes in the Ocklawaha (9 lakes) and Kissimmee (5 lakes) Chain-of-Lakes. Depth-integrated samples were taken with a Van Dorn bottle from a mid-depth station and filtered through a 41 or 75 µm (depending on year) plankton net, and the material retained was preserved with Lugol’s solution or formalin. Zooplankton were counted at 50–100× magnification. Population densities were estimated from the counts as numbers per liter. We assumed 100% sampling efficiency of the hauling. Dry weights were determined from measurements of dimensions and the conversion factors in McCauley (1984; for further details see Havens and Beaver 2011, 2013). Because different mesh-sized nets were used in the different samplings, we only included large-bodied zooplankton (all cladocerans and advanced stages of copepods [adults and copepodites]) to ensure the samples were fully comparable.

Benthic invertebrate datasets were derived from 2 different sources, with one set from surveys of shallow lakes conducted by FDEP (Rutter 1995, 1996, 2005 and references in the latter). Samples were taken in the sublittoral at 12 stations with a Petite Ponar grab (sample area 232 cm²) and pooled. In some lakes, 3 stations were sampled, of which 2 were located in the sublittoral zone and 1 in the middle of the lake. Usually 6 grabs were taken at each station and composited to a single sample (3 grabs to 1 sample when density was high). Each sample was sieved in a box with a No. 30 brass screen (600 µm pore size) bottom and stored in formalin before dividing into subsamples (shallow bottom-gridded pan). Randomly selected fields were counted at 7× magnification. The other dataset was derived from a survey in which samples were taken from 3 littoral and 3 offshore stations in 65 lakes with a Petite Ponar grab (Canfield and Hoyer 1992). The samples were collected between June and October. Each sample was sieved on site with a 500 µm screen, preserved with alcohol, and transported to the laboratory, where they were enumerated under a 10× binocular microscope.

The fish sampling is described in Bachmann et al. (1996). Briefly, rotenone sampling for fish was conducted once during the warm season (May–Nov) in each lake to determine the standing crop and community structure. Two to 6 block nets, each with an area of 0.08 ha, were set in each lake depending on lake size. Most of the lakes were sampled with 6 nets, but one small lake (surface area 2 ha) was sampled with only 2 nets. Equal numbers of block nets were set in the littoral (one side being the shore) and limnetic habitats. Block net sampling followed the procedures outlined by Shireman et al. (1983). Biomass (kg ha⁻¹) estimates were calculated for each fish species in each net and weighted by habitat (littoral and open-water area) to obtain whole-lake estimates.

The percent PVI and percent COV were determined according to modified methods of Maceina and Shireman (1980). LAKEWATCH modified the methods because of advancing technologies. The percentage PVI and COV in deeper, open-water portions of the lakes were measured using sonar bottom transect images recorded with a
Lowrance LCX – 28c HD sonar and GPS system (Tulsa, OK, USA). Random samples from all data points were taken in each waterbody and measured for lake depth and plant height, if plants were present.

Meteorological data were obtained from the National Solar Radiation Database (https://rrdec.nrel.gov/solar/old_data/nsrdb/1991-2010/hourly/list_by_state.html; daily values of sunlight) and from the Florida Climate Center (https://climatecenter.fsu.edu/products-services/data; daily values of precipitation and air temperature), respectively.

Danish lakes

The 631 investigated lakes are included in the National Monitoring and Assessment Programme for the Aquatic and Terrestrial Environments (NOVANA), which has been running since 1989 and includes data on key physical, chemical, and biological variables collected from 1989 to 2010 using well-defined and comparable sampling techniques and analytical procedures (Svendsen et al. 2005). Monitoring and samplings have been conducted by regional or national environmental authorities and intercalibrations, undertaken concurrently.

A depth-integrated epilimnetic sample (covering the entire depth in polymeric lakes) was taken at a mid-lake station and divided into a 1 L or 2 L subsample for water chemistry analyses, and a 100 mL subsample was taken for phytoplankton determination and stored in a dark bottle with added Lugol’s solution. For zooplankton determination, samples were taken at 1–3 mid-lake stations integrating the entire water column, and a subsample from each station was subsequently pooled, after which 4.5–9 L, depending on nutrient level, were filtered through a 90 µm net and stored in Lugol’s solution. A 0.9–1.8 L sample was also taken for determination of small zooplankton. Standard methods were used for chemical variables (Søndergaard et al. 2005a). Phytoplankton was counted on settled (24 h) material using an inverted microscope, and specific algal volumes were then calculated by fitting the different species and genera to geometric forms. Zooplankton were counted in a stereo microscope at 40–100× magnification, and biomass was calculated from length–weight relationships. As with the FL lakes, we only included large-bodied zooplankton (all cladocerans and advanced stages of copepods [adults and copepodites]) in the present analysis.

Benthic invertebrates were sampled in September–October from 2004 to 2006 in the offshore zones of the lakes, restricted to an area between 70% and 90% of the offshore zone, and the depth interval on the hypsography was calculated from the shore to the center, thus avoiding the deepest part of the lake and the littoral zone. Between 8 and 12 samples per lake, depending on program type, were taken randomly with a Kajak sampler (5.9–5.2 cm in width). Each sample was sieved through a 212 µm mesh and stored in alcohol before handling and enumeration in the laboratory.

Fish stock composition was monitored using multiple-sized gill nets with 14 different mesh sizes ranging from 5 to 85 mm. In the most intensive program, the number of nets ranged from 12 to 40, depending on lake size and depth, and in less intense sampling programs from 6 to 22. Nets were set randomly in a lake during late afternoon and retrieved the next morning (Lauridsen et al. 2008). More details about biological sampling methods in DK lakes can be found in Søndergaard et al. (2005b). Catch per net per night was converted roughly to biomass per lake area using conversion factors established for 5 DK lakes in which the mark-recapture method was used simultaneously with the fish survey with gill nets (Fiskeøkologisk Laboratorium 1991).

Macrophytes included floating-leaved and submerged species as well as other species with submerged forms. Macrophytes were recorded along a number of transects and included 150–375 locations in each lake, depending on lake size (for details see Søndergaard et al. 2010).

Meteorological data (daily values of precipitation, air temperature, and sunlight) were provided by the Danish Meteorological Institute, Copenhagen.

Data and statistical analyses

To obtain similar morphometric conditions, we restricted the analysis to shallow lakes with mean depth <3 m, area 10–1800 ha, and average TP <300 µg L⁻¹. We also excluded saline lakes (average >0.5 PSU) and lakes with an average color >40 NTU. The number of lakes and lake-years included varied with the variable considered, ranging from 1597 lakes (1017 from FL) and 7893 lake-years for chemical variables (including Chl-a) to 387 lakes (165 from FL) and 947 lake-years for phytoplankton; 98 lakes (73 from FL) and 492 lake-years for zooplankton; 620 lakes (159 from FL) and 1523 lake-years for macrophytes; 208 lakes (95 from FL) for zoobenthos; and 180 (60 from FL) for fish. Like Carlson (1977) and Canfield et al. (2019), we divided the lakes into TP classes (<15, 15–25, 25–50, 50–100, 100–150, 150–200, 200–300 µg L⁻¹), but for a few variables some classes were merged to obtain sufficient data to test for differences. We used a Wilcoxon 2-variable nonparametric test (NPAR1WAY; SAS) to test for differences among lakes in FL and DK for each TP class (p < 0.05). As an indicator of grazing pressure on phytoplankton, we used the zooplankton:phytoplankton biomass ratio. Because only a few of the
lakes had phytoplankton biomass data, we calculated this ratio of phytoplankton biomass using Chl-a concentrations multiplied by 66 (Jeppesen et al. 2003).

**Results**

**Air temperature, precipitation, sunlight, and lake characteristics**

Air temperature varied along the latitudinal gradient in FL (Table 1) from an average of 13.4 °C in Jacksonville to 21.3 °C in Miami during winter (Dec–Feb) and from 27.8 °C to 28.9 °C, respectively, during summer (Jul–Aug). By contrast, the average temperatures for the latitudinal gradient of DK lakes were 2.0 °C during winter and 16.9 °C during summer. Sunlight hours varied from an average of 171 kWh per month in Miami to 181 kWh per month Jacksonville in summer (Jul–Aug) and from 154 to 158 kWh per month in winter (Dec–Feb). For DK, the sunlight hours were 146 kWh per month in summer and as low as 19 kWh per month in winter (Table 1).

**TP and TN**

In summer, TP was significantly higher in the DK lakes when annual mean TP (aTP) exceeded 25 µg L⁻¹ and, vice versa, higher in FL lakes in winter when aTP exceeded 100 µg L⁻¹ (Fig. 1). TN in summer was significantly lower in the DK lakes when aTP was between 15 and 50 µg L⁻¹ and higher between 100 and 200 µg L⁻¹ aTP. In winter, TN was significantly lower in the DK lakes when aTP was <25 µg L⁻¹ and higher when aTP was >50 µg L⁻¹, and the difference increased markedly with aTP to a 2.6-fold higher TN value in the highest aTP class. TN and TP were similar in the FL lakes in summer (S) and winter (W) in a given aTP class (W:S = 0.90–1.02 for TN and 0.95–1.01 for TP). Accordingly, TN:TP (based on mass) was overall significantly higher in the FL lakes than in the DK lakes in summer and showed a decreasing trend with increasing TP, approaching 10:1 when aTP exceeded 150 µg L⁻¹. In winter, TN:TP was fairly high and constant along the aTP gradient in the DK lakes but showed a declining trend with increasing aTP in the FL lakes, reaching 10:1 at the same aTP level as in summer.

In winter, TN:TP was significantly lower in the DK lakes than in the FL lakes only in the lower aTP classes. TN:TP in a given aTP class was similar in the FL lakes in summer and winter (W:S mean ratio = 0.85–1.02) as a consequence of the TN and TP pattern described earlier.

**Chl-a**

Chl-a concentration during summer was significantly lower in the DK lakes when aTP was <50 µg L⁻¹ and significantly higher when >100 µg L⁻¹, whereas Chl-a in winter was higher in FL lakes with aTP >50 µg L⁻¹ (Fig. 1). However, Chl-a:TP was significantly higher in the FL lakes during summer when aTP was <100 µg L⁻¹ and higher in winter in the FL lakes when aTP was >25 µg L⁻¹. The Chl-a:TN ratio in summer in the FL lakes was significantly higher than the DK lakes for aTP between 25 and 100 µg L⁻¹, but lower for aTP between 100 and 200 µg L⁻¹. In winter the ratio was significantly higher in the FL lakes when aTP was >25 µg L⁻¹. In the FL lakes, the Chl-a:TP and Chl-a:TN ratios did not vary much between summer and winter (W:S = 0.64–0.81 for Chl-a:TP and 0.71–0.89 for Chl-a:TN; Fig. 1).

**Phytoplankton biovolume and proportion of classes**

Generally, the phytoplankton biovolume in summer was significantly higher in the FL lakes than in the DK lakes except when TP >150 µg L⁻¹ (Fig. 2). The variability was particularly high in the FL lakes, possibly attributed to effects of surface water sampling in the majority of the FL lakes, which may have been affected by presence/absence of cyanobacteria blooms. Average Chl-a per unit volume was significantly higher in the DK lakes than in the FL lakes for all TP classes, and the difference was relatively independent of TP.

The proportion of the different classes of phytoplankton showed major differences. Particularly, the proportions of cyanophytes were greater in the FL lakes (average: 25–64%) while those of dinophytes, cryptophytes, and chrysophytes were greater in the DK lakes (Fig. 3). The proportion of cyanophytes was comparatively high in the FL lakes,

<table>
<thead>
<tr>
<th>Period</th>
<th>Jacksonville</th>
<th>Orlando</th>
<th>Miami</th>
<th>Denmark</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp (°C) Dec, Jan, Feb</td>
<td>13.4 (8.8–19.2)</td>
<td>17.1 (12–19.5)</td>
<td>21.3 (17.4–25.0)</td>
<td>2.0 (–2.8–4.0)</td>
</tr>
<tr>
<td>Jul, Aug</td>
<td>27.8 (26.9–28.9)</td>
<td>28.2 (27.4–29.4)</td>
<td>28.9 (28.4–29.5)</td>
<td>16.9 (14.1–18.9)</td>
</tr>
<tr>
<td>Prec (mm) Dec, Jan, Feb</td>
<td>72 (0–128)</td>
<td>56 (0–137)</td>
<td>46 (0–120)</td>
<td>85 (25–127)</td>
</tr>
<tr>
<td>Jul, Aug</td>
<td>178 (73–329)</td>
<td>185 (109–269)</td>
<td>207 (137–315)</td>
<td>79 (27–126)</td>
</tr>
<tr>
<td>Sunlight (kWh per month) Dec, Jan, Feb</td>
<td>155</td>
<td>158</td>
<td>154</td>
<td>19</td>
</tr>
<tr>
<td>Jul, Aug</td>
<td>181</td>
<td>175</td>
<td>171</td>
<td>146</td>
</tr>
</tbody>
</table>

Temp = air temperature; Prec = precipitation.
even in many of the lakes in the low TP class (<15 µg L\(^{-1}\)), and significantly higher in the DK lakes from 15 to 100 µg L\(^{-1}\). The proportion of chlorophytes and diatoms was also greater in the FL lakes than in the DK lakes for TP <15 µg L\(^{-1}\) lakes, and, by contrast, dinophytes, cryptophytes, and chrysophytes constituted greater proportions

**Figure 1.** Selected chemical variables for 2 seasons along an annual mean TP gradient divided into 7 classes, showing 10%, 25%, 75%, and 90% percentiles and a line through the median. Stars indicate significant differences (\(p < 0.05\) to \(p < 0.0001\), not divided further to enhance visibility) among the 2 sets of lakes within the TP class considered.
in the DK lakes than in the FL lakes for TP between 15 and 50 µg L\(^{-1}\) (Fig. 3).

**Secchi depth**

Secchi depth (Fig. 1) was overall greater in the DK lakes than in the FL lakes in summer for aTP <100 µg L\(^{-1}\) (2.1–2.4 times greater, between 15 and 50 µg L\(^{-1}\)) and in winter for all aTP classes (1.5–2.1 times greater).

**Zooplankton biomass, proportion of taxa, and zooplankton:phytoplankton ratio**

Total zooplankton (cladocerans + copepods) biomass increased with aTP in the DK lakes but showed no clear pattern along the aTP gradient in the FL lakes, where it was substantially lower in all aTP classes than in the DK lakes (Fig. 4). This result implies that the difference between the DK and FL lakes increased with increasing aTP. The biomass was 1.5–10-fold higher in the DK lakes. A similar pattern was found when dividing the zooplankton into cladoceran and copepod groupings, with the difference between the DK and FL lakes most pronounced for cladocerans (Fig. 4).

The zooplankton:Chl-\(a\) ratio decreased with increasing aTP in the DK lakes. The ratio was substantially lower in the FL than in the DK lakes when aTP exceeded 15 µg L\(^{-1}\), an extremely low value that did not vary significantly with aTP. Thus, the difference in zooplankton:Chl-\(a\) was greatest at the lowest aTP.
Benthic macroinvertebrate biomass

In the FL lakes, benthic macroinvertebrate density (measured as individuals m$^{-2}$) for samples taken in the sublittoral or littoral zone ranged between 0 and 8588 m$^{-2}$ and for offshore samples in the DK lakes between 357 and 54 341 m$^{-2}$, with no clear changes along the TP gradient in either of the regions. Abundance averaged 1475 [SD 1778] m$^{-2}$ ($n = 95$) in the FL lakes and 10 609 [10 012] m$^{-2}$ ($n = 113$) in the DK lakes and thus was ~7.2-fold greater in DK (Fig. 5), ranging between 4.1- and 7.7-fold in the different TP classes. The difference was significant for TP <100 µg L$^{-1}$ but for higher TP only if assuming a one-sided test (expecting higher values in the DK lakes). For 60 FL lakes, data were also available for the offshore zone (where samples were taken in the DK lakes), where an average density of individuals only reached 50% of those in the littoral zone (394 [473] m$^{-2}$ vs. 781 [1100] m$^{-2}$).

Fish biomass

Compared with the lake averages for the DK lakes, biomass was significantly higher in the pelagic in FL lakes when TP exceeded 50 µg L$^{-1}$ (Fig. 6, right). Fish biomass in the littoral was, however, significantly higher in FL lakes at all TP levels, and the difference increased with TP (Fig. 6, left). In most DK lakes, roach (Rutilus rutilus) and perch (Perca fluviatilis) were the most abundant species, while bluegill (Lepomis macrochirus), largemouth bass (Micropterus salmoides), and warmouth (Lepomis gulosus) were most abundant in the FL lakes.

Macrophyte coverage and plant volume inhabited

For submerged macrophytes, the average coverage percentage (COV%) was relatively constant (19–28%) in the FL lakes along the TP gradient while a shift from 34–38% occurred in the DK lakes between 15 and 50 µg L$^{-1}$ TP to well below 10% at TP between 150 and 300 µg L$^{-1}$ (Fig. 7). A significantly higher COV%...
was found in the FL lakes at TP between 15 and 25 µg L\(^{-1}\) and, vice versa, lower COV% at 100–150 µg L\(^{-1}\). The PVI percentage showed the same trend as COV%, but no statistical differences at \(p < 0.05\) occurred between the 2 regions in any of the TP classes considered (Fig. 7).

**Discussion**

We found TP in summer to be higher at a given aTP in the DK than in the FL lakes and vice versa in winter, and thus likely also the external P loading, despite precipitation being highest in summer in the FL lakes and highest in the winter season in the DK lakes. This seasonal pattern in TP certainly reflects a difference in the seasonal variation of the internal loading due to the much higher winter temperatures in the FL lakes, implying less or no winter retention of P. Mass balance studies of eutrophic DK lakes have shown P retention in winter and a net release in summer, and the difference between summer and winter increased with increasing aTP (Søndergaard et al. 2003). A different picture was found for nitrogen. TN increased with aTP but was similar at a given aTP in summer for the 2 regions and overall was higher in the DK lakes in winter. The elevated TN in the DK lakes can be attributed to higher winter input and lower loss by denitrification due to both a lower temperature and a shorter lake retention time (higher precipitation in winter, Table 1; Søndergaard et al. 2017). Note that the TN and TP level and changes in the FL lakes (and thus TN: TP) along the aTP gradient were relatively similar in

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**Oxygen (metabolism)**

As expected from the difference in temperature, the O\(_2\) concentration in the surface water (upper 1 m) was significantly higher in the DK lakes during both summer and winter in all TP classes (Fig. 8). In summer, O\(_2\) was 29–80% higher in the DK lakes, with the largest percentage difference appearing in the highest TP class (the average O\(_2\) concentration as low as 5.3 mg L\(^{-1}\) in the highest TP class in the FL lakes). In winter, the difference was relatively constant among the TP classes (37–47% higher in the DK lakes), and the minimum O\(_2\) was 8.5 mg L\(^{-1}\) in the FL lakes (Fig. 8). The O\(_2\) percentage differed less. While no significant differences were found in winter, the percentage was significantly higher in the DK lakes in summer when TP exceeded 25 µg L\(^{-1}\), and the difference increased gradually from low to high aTP, from 2% to 7% between 15 and 50 µg L\(^{-1}\) to 15–32% in the 3 TP classes of higher concentration. In the DK lakes, a progressive increase was found in the average O\(_2\) percentage from 93.6% to 102.8% from TP class 2–7.

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**Figure 6.** Measured (Florida) and calculated (Denmark) fish biomass along a TP gradient divided into 4 classes. Stars indicate significant differences (\(p < 0.05\) to \(p < 0.0001\)) among the 2 sets of lakes within the TP class considered.

**Figure 7.** Percent coverage of submerged macrophytes (Coverage) and the percent of water inhabited by plants (PVI) along an annual mean TP gradient divided into 7 classes. Stars indicate significant differences (\(p < 0.05\) to \(p < 0.0001\)) among the 2 sets of lakes within the TP class considered.
summer and winter despite variation in rainfall (Table 1), likely reflecting the overall higher temperature and also a year-round growing season (phytoplankton and macrophytes) modulating seasonality. TN:TP was lower than 10:1 in both seasons in the FL lakes when aTP exceeded 150 µg L\(^{-1}\) but only in summer in the DK lakes, indicating a greater degree of N limitation in the warmer FL lakes (Table 2).

We found the phytoplankton biovolume in summer to be generally higher in the FL lakes for all TP classes, apart from the highest. Moreover, the proportion of cyanophytes was greater in the FL lakes while those of dinoflagellates, cryptophytes, and chrysophytes were greater in the DK lakes. Greater dominance of cyanobacteria in warm lakes is a common pattern observed worldwide (Huisman et al. 2005, Jöhnk et al. 2008, Jeppesen et al. 2009, Canfield et al. 2019), but the higher proportion in FL lakes, even at low TP, is noteworthy (Fig. 3; Canfield et al. 2019). Moreover, average Chl-a per unit of volume was substantially higher in summer in the DK lakes for all TP classes, which may in part reflect the differences in phytoplankton dominance (Kasprzak et al. 2008, Canfield et al. 2019).

We found a major difference in the response of submerged macrophytes to changes in aTP. While the coverage was reduced with increasing aTP in the DK lakes, it was largely independent of aTP in the FL lakes. Moreover, the DK lakes had an overall higher coverage at low aTP and vice versa at high aTP in the FL lakes. In a comparative study of lakes from different climate zones, Kosten et al. (2009) also found that the macrophyte coverage percentage at low TP was overall lower in warm lakes (Brazil, Uruguay, and Florida) than in colder lakes (Argentina, Minnesota, and Denmark), but they did not find coverage to be high at the higher nutrient concentrations as in our FL lakes. Using logistic regressions, they recorded loss of plants at a lower TP concentration in the warmer lakes. Kosten et al. (2009) also found that macrophytes seemed to tolerate lower light conditions in warm lakes, as we found in the FL lakes that we studied. This difference likely reflects a combination of factors, including the fact that submerged macrophytes typically overwinter in warm lakes (high temperatures and more winter light) but often disappear in north temperate lakes in winter. Consequently, the plants are more likely to lose the competition with phytoplankton for light during spring in north temperate lakes because they have to grow from the lake bottom.

The higher macrophyte coverage in summer in the low aTP classes (<50–100 µg L\(^{-1}\)) in the DK lakes coincided with lower Chl-a, Chl-a:TP, and Chl-a:TN values. This finding may partly reflect that grazing on phytoplankton by zooplankton was overall higher in the DK

Table 2. Morphometric data for the included lakes in Florida and Denmark.

<table>
<thead>
<tr>
<th></th>
<th>Florida (n = 1025)</th>
<th>Denmark (n = 631)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Mean depth (m)</td>
<td>2.2</td>
<td>0.6</td>
</tr>
<tr>
<td>Lake area (ha)</td>
<td>204</td>
<td>367</td>
</tr>
</tbody>
</table>

SD = standard deviation.
lakes (higher zooplankton:phytoplankton ratio) and partly that plants in DK lakes act as a daytime refuge for large-bodied zooplankton (Burks et al. 2002). In warm lakes, plants are a poor refuge because fish density among the plants is high (Meerhoff et al. 2007). Consequently, greater water clarity may, in turn, lead to greater macrophyte growth with self-amplifying cascading effects on ratios and clarity. The overall greater coverage at high TP in the FL lakes likely reflects that submerged macrophytes grow year-round and therefore are less sensitive to high turbidity in spring and summer. The finding that submerged macrophyte coverage was greater in more turbid water in the warm than in the cold lakes in our study concurs with a cross-latitude study by Kosten et al. (2009).

We found 1.5–10-fold higher biomasses of total zooplankton (cladocerans and copepods) only in the DK lakes, also when grouping biomasses into cladocerans and copepods, most notably for cladocerans. Accordingly, the zooplankton:phytoplankton biomass ratio was much higher in the DK than in the FL lakes. In these calculations, phytoplankton biomass was calculated from Chl-a using the same conversion factor for the 2 regions; the actual differences are, in fact, even greater given that we found a lower Chl-a:biovolume ratio in the FL lakes. Our results concur with those of Havens and Beaver (2013) in a study of long time series of zooplankton and phytoplankton in 4 large FL lakes. They found that the zooplankton:phytoplankton biomass ratio was overall low compared with those recorded for north temperate lakes, and the ratio was driven largely by variations in zooplankton biomass and only insignificantly affected by variations in phytoplankton biomass. Meerhoff et al. (2012) compiled data from a series of studies in Europe and South America and concluded that the zooplankton:phytoplankton ratio generally decreases from high to low latitudes and that the fish:zooplankton ratio increases. These results are all consistent with the hypothesis of Jeppesen et al. (2003) that in shallow subtropical lakes, fish predation is the major factor controlling the biomass of zooplankton and the zooplankton:phytoplankton biomass ratio. Accordingly, our fish analyses indicated that the total fish biomass was overall higher in the FL lakes, but we emphasize that for the DK lakes the biomass was calculated from catch per unit effort (CPUE), and the estimates are therefore somewhat uncertain. Lower zooplankton biomass may also have contributed to the much higher phytoplankton yield recorded in summer (higher phytoplankton volume per unit TP). Further indications of high fish predation in FL lakes are the substantially lower body mass of planktonic microcrustaceans (cladocerans + copepods), as also evidenced by other cross-system studies (Meerhoff et al. 2012, Jeppesen et al. 2014, Havens et al. 2015).

We found an overall 7.2-fold higher abundance of benthic invertebrates in the DK lakes than in the FL lakes. The few other existing comparative latitudinal gradient studies conducted also suggest lower densities in warm lakes. In a comparative study of invertebrates on artificial plants in a series of lakes in temperate DK and subtropical Uruguayan lakes, Meerhoff et al. (2007) found an 8-fold (on average) higher density of plant-associated macroinvertebrates in the temperate lakes per unit of plant weight. A similar comparative study conducted in brackish DK lakes and south-temperate Spanish brackish lakes also revealed a substantial difference in plant-associated macroinvertebrate density (Bruget et al. 2012). In both cases, the differences were attributed to a much higher fish density in the warmer lakes. In addition, a lower macroinvertebrate density on reeds was recorded in lakes in southern Europe than on similar substrate types in northern Europe (R. Kornijow, unpubl. data). These results collectively show a lower macroinvertebrate density in warm lakes than in north temperate lakes, most likely a result of higher fish predation on macroinvertebrates than on zooplankton. However, sieve mesh sizes differed considerably in our comparative study, 0.5 and 0.6 mm, respectively, in the 2 datasets from the FL lakes and 0.212 mm for the DK lakes. Earlier studies by Jonasson (1955) showed a 2.5-fold higher density using 0.2 mm compared with 0.5 mm sieves, and for chironomids the density was as much as 4 times higher. Therefore, the differences we found are obviously overestimated. The sieve size difference cannot explain the 7.2-fold higher density in the DK lakes. A study of 68 lakes in the Yangtze River catchment (subtropical climate) by Pan et al. (2015) also revealed densities (measured as individuals m$^{-2}$) well below those in most DK lakes, ranging from 1881 m$^{-2}$ (on average) in macrophyte-dominated low TP lakes to 2563 m$^{-2}$ in turbid high TP lakes (average 2222 m$^{-2}$). In their study, a 420 μm sieve net was used, and, even if corrected for sieve size, the densities are much lower in the Chinese than in the DK lakes, with a mean of 10 609 m$^{-2}$.

Our results thus collectively provide strong evidence that differences in fish predation can explain much of the substantial variation found in the zooplankton biomass, the body mass of microcrustacean plankton, the zooplankton:phytoplankton ratio, and the abundance of benthic invertebrates. Stronger predation by fish is also evident by the overall higher biomass of fish in the FL lakes, not least in the littoral zone. However, fish predation risk depends of type of dominant fish, not total biomass. Because of the different fish survey methods
used in the 2 regions, we cannot safely compare the abundance of different fish feeding groups. However, other studies have clearly indicated a shift toward dominance of omnivorous fish and a lower degree of piscivory from cold to warm lakes (Moss 2010, Gonzalez-Bergonzoni et al. 2012), leading to higher predation risk for large-bodied zooplankton and most macroinvertebrates in warm lakes (Meerhoff et al. 2012), as our results also suggest.

As expected, because of the higher temperature, the O2 concentration in surface water was overall much higher in the DK than in the FL lakes, both during winter and summer, reaching low values in the highest TP class (on average 5.3 mg L−1). The difference would have been even larger had we included the entire water column because of a temporal stratification in several of the FL lakes induced by the higher temperature, reaching critically low levels in the bottom water in some of the lakes (authors’ unpubl. data). Also, O2 saturation differed between the DK and the FL lakes in the surface water in summer, especially in the lakes with elevated TP. Although based on only one daytime sampling, the lower O2 saturation in the FL lakes indicates an overall lower net ecosystem production than in the DK lakes, likely reflecting that respiration is a more temperature-dependent process than production (Scharfenberger et al. 2019). The use of O2 saturation as an indicator of net production is supported by a mesocosm study conducted in DK at contrasting temperatures, showing a close relationship (Nielsen et al. 2013) between daytime O2 saturation and the net ecosystem production (calculated from sampling every 30 min for 24 h). Nielsen et al. (2013) further showed that the relationship was independent of nutrient status, macrophyte abundance, or temperature, and field data from shallow lakes exhibit similar relationships. Furthermore, indications of a lower net production in warm lakes are derived from a Pan-European mesocosm study demonstrating a shift from positive net system production in the colder northern lakes to negative net system production in the warm lakes in the south (Scharfenberger et al. 2019). The temperature threshold for a shift to net production depended on the nutrient level and was higher at high nutrient levels (Scharfenberger et al. 2019). Further support for the occurrence of a lower net system production in warm lakes comes from a study of 83 shallow lakes sampled along a 6000 km climatic gradient in South America (Kosten et al. 2010). In that study, the carbon dioxide (CO2) partial pressure was strongly and positively correlated with temperature, indicating a proportionally higher mineralization in warm lakes (and/or in the catchment). Moreover, Lazzarino et al. (2009) found strong CO2 super-saturation in a set of 948 lakes in Florida, and an oxygen mass balance on Lake Apopka, Florida, showed net heterotrophic conditions on an annual scale (Bachmann et al. 2000). In the DK lakes, we found a 9% increase in O2 saturation in summer from 94% to 103% from the lowest to the highest TP class, indicating higher net production in the high TP lakes. By contrast, we found a strong decline in saturation in summer from low to high TP (from 91% to 70% saturation) in the FL lakes, indicating a lower net ecosystem production in the more eutrophic systems. The difference in net production between lakes in the 2 regions would have been even larger if the entire water column had been sampled.

Conclusions, limitations, and perspectives

Our comparative study provides further evidence for the existence of clear contrasts in the structure and functioning of shallow subtropical and temperate lakes as well as major differences in seasonality. A higher fish biomass, a substantially lower zooplankton biomass and zooplankton:phytoplankton ratio (and thus lower grazing on phytoplankton), and a notably lower biomass of benthic invertebrates are all indicative of strong predation in subtropical lakes. Accordingly, the phytoplankton biomass per unit of TP was much higher in the FL lakes. We also found oxygen saturation to be overall lower in the nutrient-rich FL lakes than in the DK lakes in summer and marginally so in winter, suggesting a lower net ecosystem production in the FL lakes.

A potential caveat in our analysis is that the data from the 2 regions derive from various sources and different years (1989–2010) using different methodologies, which we, for valid reasons, have not been able to intercalibrate. However, the results track with the more scattered data from climate effect studies on lakes elsewhere. We are, therefore, confident that the conclusions drawn in this comparative study are robust, taking into account also the comparatively large number of lakes included.

While many of the differences between the FL and DK lakes mimic the expectations of how climate warming may affect shallow lakes (Jeppesen et al. 2009, 2014, Moss et al. 2011, Meerhoff et al. 2012), we acknowledge that the latitudinal difference in light availability (also affecting temperature) plays a role (Lewis 2011). Winter irradiation in the FL lakes allows submerged macrophytes to overwinter and maintain great biomasses while only few lakes in DK have overwintering macrophytes and, in those that do, the plants have poor growth conditions. Thus, in the FL lakes macrophytes will have better growth conditions in spring at a given water clarity because they can grow from higher levels in the water column while macrophytes in the DK lakes must grow
from the lake bottom, where light is lower. In the DK lakes, macrophytes will therefore be more easily outcompeted by phytoplankton in spring than the plants in the FL lakes. Another important effect is a potentially greater winter survival of fish in the FL lakes because of the warmer winter climate than that in the northern climate zone with lower winter solar irradiation. Several studies have shown that a winter fish kill may lead to higher densities of *Daphnia* and stronger grazing on phytoplankton the following summer (Balayla et al. 2010, Ruuhijarvi et al. 2010). Comparative studies of lakes with shorter and longer ice coverage provide similar evidence (Jackson et al. 2007). Winter darkness may also affect trophic interactions and top-down control (Sørensen et al. 2011). More experimental studies of the effects of light on lake ecosystem functioning are needed before we can take full advantage of the space-for-time studies to elucidate the effect of climate change on lakes.

**Acknowledgements**

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**Disclosure statement**

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**References**

Gonzalez-Bergonzoni I, Meehoff M, Davidson TA, Teixeira-de Mello F, Baatrup-Pedersen A, Jeppesen E. 2012. Meta-
analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. Ecosystems. 15:492–503.


[IPCC] Intergovernmental Panel on Climate Change. 2007. Climate change: the physical science basis, summary for policymakers. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. http://www.ipcc.ch


Rutter RP. 1996. A bioassessment of five lakes in Highlands County and one lake in Collier County, Florida, with emphasis on the macroinvertebrate fauna. Punta Gorda (FL): Florida Department of Environmental Protection.


