

Article

Climate Change Will Make Recovery from Eutrophication More Difficult in Shallow Danish Lake Søbygaard

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Abstract: Complex lake ecosystem models can assist lake managers in developing management plans counteracting the eutrophication symptoms that are expected to be a result of climate change. We applied the ecological model PCLake based on 22 years of data from shallow, eutrophic Lake Søbygaard, Denmark and simulated multiple combinations of increasing temperatures (0–6 °C), reduced external nutrient loads (0%–98%) with and without internal phosphorus loading. Simulations suggest nitrogen to be the main limiting nutrient for primary production, reflecting ample phosphorus release from the sediment. The nutrient loading reduction scenarios predicted increased diatom dominance, accompanied by an increase in the zooplankton:phytoplankton biomass ratio. Simulations generally showed phytoplankton to benefit from a warmer climate and the fraction of cyanobacteria to increase. In the 6 °C warming scenario, a nutrient load reduction of as much as 60% would be required to achieve summer chlorophyll-*a* levels similar to those of the baseline scenario with present-day temperatures.

Keywords: climate change; shallow lakes; ecosystem model; PCLake; water quality

1. Introduction

As global surface temperatures are projected to rise by up to 6.1 °C in the worst case scenario by 2100 compared to pre-industrial levels [1], managers of freshwater lakes are faced with challenges to meet the water quality requirements of the EU Water Framework Directive (WFD) [2] and other standards worldwide. Lakes, in most parts of the world already suffering from eutrophication, are expected to experience further water quality deterioration as a result of a warmer climate and altered precipitation patterns enhancing the effects of eutrophication [3–5]. Cross-latitude studies have shown fish to play an essential structuring role, in particular in shallow lakes. In a warmer climate, small

individuals tend to dominate the fish community and predation pressure on zooplankton increases [6,7]. This results in a lower zooplankton biomass and an increasing proportion of benthic-omnivorous fish and consequently greater resuspension of the sediment [8]. Changed fish foraging at increasing temperatures in conjunction with the expectation of increased loadings of nitrogen (N) and phosphorus (P) to the lakes [6,9] may augment trophic cascading effects [10]. As a consequence of higher internal loading and also reduced grazing by zooplankton, higher abundance of phytoplankton and increasing dominance of cyanobacteria are expected, which counteract in part the effort used to restore lakes by nutrient loading reduction [5,6]. Lake mesocosm experiments have given more ambiguous results but often indicate eutrophication symptoms with increasing temperatures, and they emphasize the importance of increased P release from sediments and higher frequency of oxygen depletion events [4,11,12].

In addition to using the knowledge obtained from long-term empirical and experimental research, the application of complex ecological models can be used to project the effects of a future warmer climate on water quality and thus help shape future management plans. The ability to dynamically account for complex responses towards changed climate conditions also makes models a valuable tool in the evaluation of potential mitigation measures. Furthermore, model analysis may help with identifying underlying mechanisms and processes essential for determining the ecological state of lakes. This applies equally well to unique case studies and model studies of different lake types in general, jointly creating a basis for new empirical work and progress in model development [13–19].

Models have previously been applied to quantify the potential effects of temperature and nutrient loads on water quality attributes in lakes [15,16,20,21]. However, these studies have included only a few combinations of temperature increase and nutrient load scenarios. In this study, we focus on the synergetic effects of the fundamental driving variables, temperature and nutrient loading, both external and internal, on a lake ecosystem. Previous modelling studies found interactions between effects of temperature and nutrients in eutrophic and hyper-eutrophic lakes affecting cyanobacterial biovolume [22]. We applied the widely used model PCLake [23] to shallow, eutrophic Lake Søbygaard, Denmark, and calibrated against a comprehensive dataset covering 22 years. During this period the lake was facing recovery from high nutrient loadings of the past. The calibrated model was run with a matrix of temperature increase and nutrient load reduction scenarios in order to (1) assess the effects of increasing temperatures on water quality attributes during summer (May–September) and (2) to estimate the nutrient load reduction needed to mitigate potential negative effects of climate change on the ecological state.

2. Methods

2.1. Study Site

Located in the central part of Jutland, Denmark, ($9^{\circ}48'36''$ E, $56^{\circ}15'20''$ N), Lake Søbygaard is a small (0.38 km^2) shallow lake with a mean depth of 1.1 m and a maximum depth of 1.9 m (Figure 1). The lake receives about 90% of its water from a single inlet, while the remaining 10% derives from groundwater-fed, iron-rich springs. Mean hydraulic retention time is short (summer: 27 days, winter: 22 days). The near-shore surroundings consist of deciduous and coniferous forest, except to the west, allowing for wind exposure. The catchment area (11.6 km^2) comprises mainly agriculture (44%), urban areas (28%), and forest (17%).

During the 1960s and early 1970s, Lake Søbygaard experienced severe eutrophication, receiving mechanically treated sewage from the nearby town of Hammel. Thus, major P deposits accumulated in the sediment [24–26]. In 1976, a biological sewage treatment plant was built, which in 1982 was extended with chemical removal of P. In 1987, the external nutrient load was further reduced following the closing of a local slaughterhouse. In 1996, N removal was implemented at the plant, and in 2006 its outlet was redirected to circumvent the lake completely; yet, the lake is still recipient of storm water. Although the nutrient load has been markedly reduced (from $28\text{--}33 \text{ g P}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$

in 1978–1982 [26] to $2.7\text{--}3.8\text{ g P}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ in 2007–2010 and from $131\text{--}191\text{ g N}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ in 1978–1984 [27] to $35\text{--}45\text{ g N}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ in 2007–2010), submerged macrophytes are still absent, and the lake is characterized by high chlorophyll *a* (chl.-*a*) concentrations ($70\text{--}180\text{ }\mu\text{g/L}$, summer 2010), equivalent to “bad ecological status” according to the WFD.

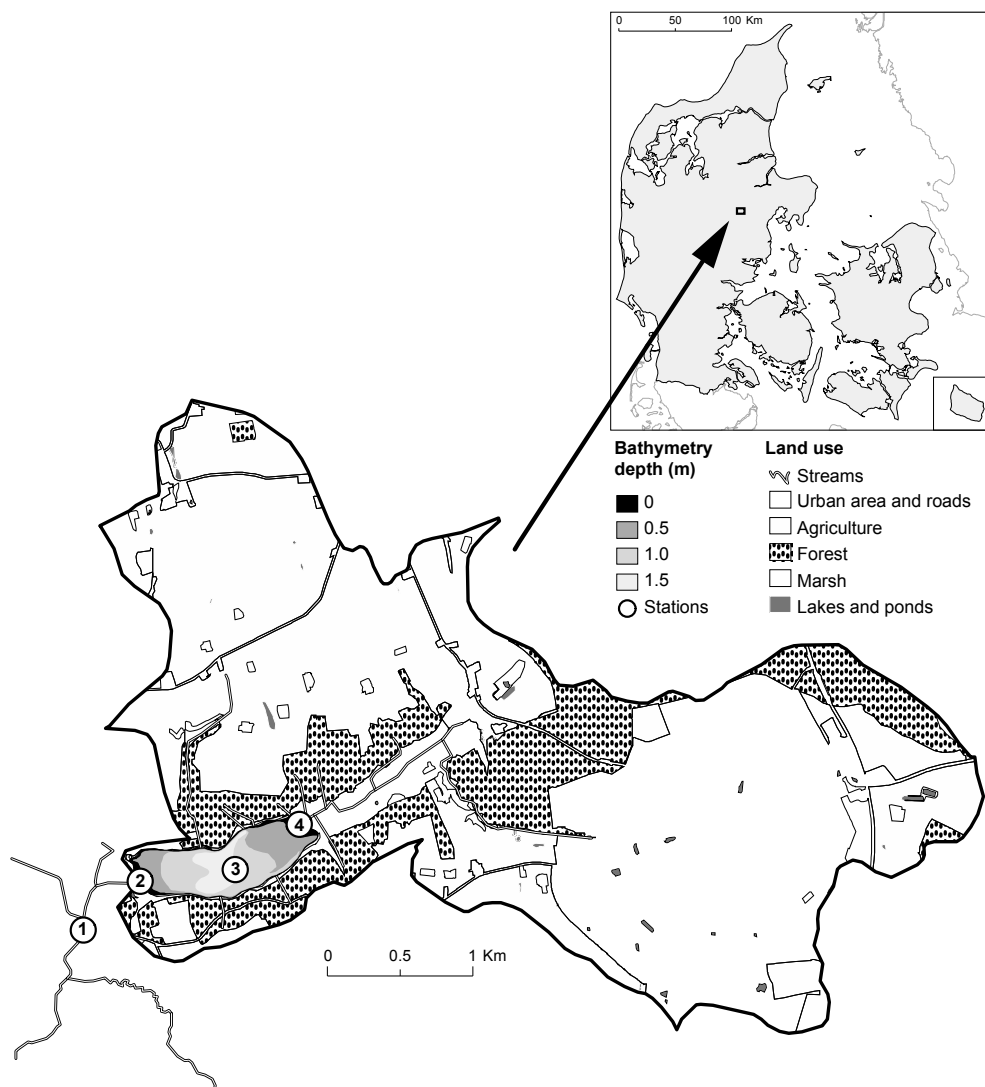


Figure 1. Study area covering the watershed of Lake Søbygaard. Monitoring stations 1, 2 (Outlet) and 4 (Inlet) are hydrometric monitoring stations, station 3 represents an in-lake observation location.

2.2. Model Description

PCLake

PCLake is a dynamic ecological model describing nutrient and simplified food web dynamics in a fully mixed lake. The model was developed for studying eutrophication in shallow lakes with main focus on the phosphorus cycling [28]. It was later extended and now comprises distribution and (external and internal) fluxes of N, P, organic matter and silica in the water column and the upper sediment layer. Dry weight (DW) to nutrient ratios are modeled dynamically and each state variable is expressed mathematically by a differential equation [29]. It has proven capable of predicting lake nutrient concentrations, chl.-*a* content and the quantity of macrophyte vegetation [23,30]. The model was chosen particularly since it explicitly accounts for higher trophic levels, and is able to simulate the

transitions between turbid and clear water states in shallow lakes. The model has previously been calibrated against data from >40 mainly Dutch lakes and also undergone sensitivity and uncertainty analyses [23,31,32]. Essential physico-chemical processes include sedimentation, resuspension, diffusion, adsorption, mineralization, and burial. Collectively, they describe the exchange of detritus, inorganic matter, and nutrients between sediment and water. Resuspension is further affected by the presence of benthivorous fish and submerged macrophytes.

Primary production is described separately for submerged macrophytes and phytoplankton. Macrophytes consist of a root and a shoot fraction, while phytoplankton are split in three functional groups (cyanobacteria, diatoms, and green algae (other edible algae)), differing in their respective traits, for instance growth rate, edibility, physiological composition, nutrient uptake rates and settling rates. Grazing preference of zooplankton on phytoplankton is assumed to differ between phytoplankton groups; cyanobacteria being the least favored. Zooplankton, represented by a single group, is fed upon by juvenile plankti-benthivorous fish, while adult plankti-benthivorous fish feed on macrozoobenthos. Predatory fish feed on both groups of plankti-benthivorous fish and are highly dependent on the presence of macrophytes.

Phytoplankton nutrient limitation is modelled by the Droop equation, which describes the dependence of growth rate on the nutrient content of the phytoplankton group. The growth rate will increase quickly once internal nutrient content of phytoplankton increases above the minimum content [23]:

$$f(P) = aPLimSpec = \left(1.0 - \frac{cPDSpecMin}{rPDSpec}\right) \cdot \frac{cPDSpecMax}{cPDSpecMax - cPDSpecMin} \quad (1)$$

where $f(P)$ represents the fractional growth rate limitation of P , $rPDSpec$ the actual nutrient-to-dry-weight ratio of the phytoplankton group (spec) ($\text{g P} \cdot \text{g}^{-1}\text{DW}$), $cPDSpecMin$ ($\text{g P} \cdot \text{g}^{-1}\text{DW}$) and $cPDSpecMax$ ($\text{g P} \cdot \text{g}^{-1}\text{DW}$) the minimum and maximum phosphorus content of the cells, respectively. The equation for nitrogen limitation is analogous.

The effect of temperature on the various model components is entered through a set of fourteen temperature dependent multipliers. Six of these modify abiotic processes: diffusion, sedimentation of particulate matter (only slightly affected), nitrification, denitrification, and mineralization in the water phase and the sediment. These dependencies are modelled with exponential curves. The eight modifiers that amend the growth rates of biotic components of the model are implemented as Gaussian curves around an optimum temperature. The approach is implemented for the three phytoplankton groups (diatoms, green algae, and cyanobacteria), zooplankton, zoobenthos, plankti-benthivorous fish and piscivorous fish. For macrophytes, an optimum function was implemented by two exponential functions with a higher Q_{10} for respiration than for production. For more details see [16,23].

2.3. General Lake Model

As PCLake cannot calculate water temperature and evaporation from meteorological data, the hydrodynamic 1D model General Lake Model (GLM) was used to provide these data.

GLM [33] employs a Lagrangian layer approach to simulate the vertical structure of temperature, salinity and density of a lake or reservoir. Layers contract, expand and merge freely in response to effects of inflow/outflow, mixing, surface heating and cooling as well as effects caused by the formation of ice. GLM is a reimplement of [34]; however, this version includes various customizations and a modernized code structure [33]. Owing to its one-dimensional design, it is especially suited for lakes with a simple morphology. The average water column temperature predicted by GLM was used as input to PCLake.

2.4. Model Input

2.4.1. Meteorological Data

Daily observations of meteorological variables required for calibration of the two models were obtained from the Danish Meteorological Institute (DMI). Data originated from either a $10\text{ km} \times 10\text{ km}$ (precipitation ($\text{mm} \cdot \text{d}^{-1}$)) or a $20\text{ km} \times 20\text{ km}$ (air temperature ($^{\circ}\text{C}$), wind speed ($\text{m} \cdot \text{s}^{-1}$), shortwave radiation ($\text{W} \cdot \text{m}^{-2}$)) grid, while relative humidity (%) and cloud cover (%) were obtained from a DMI station located within a distance of 50 km from the lake.

2.4.2. Water Flow and Biochemical Properties

As the inlet and outlet stations were not monitored on a daily basis, daily values of in- and outflow volumes were based on linear correlations with a continuous gauge station located immediately downstream of Lake Søbygaard (Figure 1). Daily concentrations of total and inorganic N and P were computed by interpolating concentrations from samples taken with intervals ranging from monthly to weekly, while the organic fraction was estimated as the difference between total and inorganic nutrient concentrations. Silica was assigned a constant concentration (9.2 mg Si/L) representing the mean concentration covering the entire period with data from the inlet (monthly to bimonthly samples except for 1995). Daily inflow temperatures were based on a linear correlation with air temperature.

The water balance residual (15% of the total input) was included as an additional input (assumed to be predominantly a groundwater contribution). Groundwater input was assigned biochemical values equal those of the main inlet.

Model Parameters and Calibration

PCLake was calibrated against observed data covering a 22-year period (1989–2010) for the variables total phosphorus (TP), phosphate (PO_4) represented by soluble reactive phosphorus data, total nitrogen (TN), and chl.-*a*, whereas data for the variables nitrate (NO_3) and ammonia (NH_4) were only available for a 14-year period (1989–2003). Due to the scarcity of phytoplankton biovolume data, these were not used for calibration. The data, although sparse, did however indicate that diatoms and green algae were the dominant taxa in samples collected during summer in the early 1990s, while cyanobacteria appeared to be dominant in samples collected during summer in the early 2000s. Initial test runs were based on parameter values predefined in the PCLake model [23], and initial boundary conditions were derived from field measurements and site-specific literature values. Model performance was evaluated by calculation of the coefficient of determination (R^2) and the relative absolute error in percent (referred to as MARE by [35] and as RE by [36]) for daily output of each of the state variables. As using R^2 for model evaluation suffer potential bias (significant offset errors and differential sensitivity to high values), R^2 is used in combination with RE, providing an indication of the overall model bias [35].

Parameters that were found sensitive (based on test runs and information from the sensitivity analysis by [23,31]) underwent stepwise manual adjustment (i.e., trial-and-error approach) prior to each run (Table 1), until the model error could no longer be appreciably reduced.

Table 1. Parameters adjusted during calibration. Units and descriptions according to [23].

ID	Name	Unit	Parameter Value		Definition	References/Remarks
			Default	Calibrated		
20	cAffNUptDiat	$L \cdot mgDW^{-1} \cdot d^{-1}$	0.2	0.25	Initial N uptake, diatoms	Calibration
21	cAffNUptGren	$L \cdot mgDW^{-1} \cdot d^{-1}$	0.2	0.1	Initial N uptake, greens	Calibration
32	cChDDiatMax	mgChl/mgDW	0.012	0.01	Max chlorophyll/C ratio, diatoms	Calibration
60	cDCarrZoo	mg/L	25	30	Carrying capacity of zooplankton	Calibration
83	cExtSpGren	m^2/gDW	0.25	0.2	Specific extinction greens	Calibration
91	cFiltMax	$L \cdot mgDW^{-1} \cdot d^{-1}$	4.5	4.2	Maximum filtering rate	[37]
104	cMuMaxBlue	d^{-1}	0.6	0.7	Maximum growth rate, bluegreens	[37]
105	cMuMaxDiat	d^{-1}	2	2.6	Maximum growth rate, diatoms	[37]
106	cMuMaxGren	d^{-1}	1.5	3.6	Maximum growth rate, greens	[38]
119	cNDDiatMax	mgN/mgDW	0.05	0.06	Maximum N/day ratio, diatoms	Calibration
124	cNDGrenMax	mgN/mgDW	0.1	0.2	Maximum N/day ratio, greens	Calibration
125	cNDGrenMin	mgN/mgDW	0.02	0.03	Minimum N/day ratio, greens	Calibration
151	coPO ₄ Max	mgP/L	1	6	Maximum SRP concentration in pore water	[39]
191	cPrefGren	-	0.75	0.76	Selection factor for greens	Calibration
234	cThetaDif	-	1.02	1.15	Temperature coefficient for diffusion	Calibration
235	cThetaMinS	-	1.07	1.15	Exponential temperature constant of sediment mineralization	Calibration
236	cThetaMinW	-	1.07	1.15	Exponential temperature constant of mineralization in water	Calibration
237	cThetaNitr	-	1.08	1.103	Temperature coefficient of nitrification	Calibration
253	cTurbDifNut	-	5	5.5	Bioturbation factor for diffusion of nutrients	Calibration
254	cTurbDifO ₂	-	5	7	Bioturbation factor for diffusion of oxygen	Calibration
256	cVNUptMaxDiat	$mgN \cdot mgDW^{-1} \cdot d^{-1}$	0.07	0.1	Maximum N uptake capacity of diatoms	Calibration
257	cVNUptMaxGren	$mgN \cdot mgDW^{-1} \cdot d^{-1}$	0.07	0.11	Maximum N uptake capacity of greens	[40]
266	cVSetDet	m/d	0.25	0.29	Maximum sedimentation velocity of detritus	Calibration
269	cVSetIM	m/d	1	2	Maximum sedimentation velocity of inert organic matter	[38]
281	fDAssZoo	-	0.35	0.33	DW-assimilation efficiency of herbivorous zooplankton	[38]
288	fDepthDifS	-	0.5	0.1	Nutrient diffusion distance as fraction of sediment depth	Calibration
352	hFilt	mgDW/L	1	0.94	Half-saturating food concentration for filtering	[37]
358	hNO ₃ Denit	mgN/L	2	1	Quadratic half-saturating NO ₃ concentration for denitrification	Calibration
360	hO ₂ Nitr	mgO ₂ /L	2	1	Quadratic half-saturating NO ₃ concentration for nitrification	Calibration
367	kDAssFiAd	d^{-1}	0.06	0.04	Maximum assimilation rate of adult fish	Calibration
371	kDMinDetS	d^{-1}	0.002	0.003	Decomposition constant of sediment detritus	Calibration
372	kDMinDetW	d^{-1}	0.01	0.02	Decomposition constant of detritus	[28]
414	kNitrS	-	1	7	Nitrification rate constant in sediment	[37]
415	kNitrW	-	0.1	0.5	Nitrification rate constant in water	[37]

2.4.3. Climate Change and Nutrient Loading Scenarios

A matrix of temperature and (internal and external) nutrient loading scenarios were simulated and compared using the parameter values of the calibrated base scenario. Average daily air temperatures were increased within a range of 0–6 °C in increments of 0.2 °C, applied uniformly throughout seasons. Similarly, the external nutrient load was reduced from the base input within a range of 0%–98% in steps of 2% for either N or P separately (denoted N_{ext} and P_{ext} , respectively) or for both nutrients combined (NP_{ext}). Additionally, the separate external P reduction scenario was combined with elimination of the initial total P pool in the active layer of the lake sediment ($P_{\text{ext+int}}$) yet with all processes of sediment diagenesis still active. This was done as the release from this pool, accumulated during a period with a higher external loading, is of temporary duration and is expected to be eliminated during the coming 1–2 decades [14]. For each combination of temperature increase and nutrient loading reduction, the model was run for the entire simulation period of 22 years.

3. Results

3.1. Base Scenario Calibration

Model output for TP and PO_4 corresponded well with observed values with regard to the timing of seasonal and inter-annual variations (Figure 2A,B), which is also reflected in the R^2 values (Table 2). However, the concentrations of TP and PO_4 were initially (until 1992) overestimated, and the model did not capture the full extent of several peaks during summers.

Table 2. Coefficient of determination (R^2) and mean absolute relative error (RE) between modelled output and observations for daily and monthly time steps based on daily interpolated values from 1989 to 2010. * not significant ($p > 0.05$).

Variable	R^2 Day	R^2 Month	RE Day	RE Month
TP	0.3	0.38	0.55	0.5
PO_4	0.25	0.34	5.24	3.54
TN	0.61	0.72	0.31	0.26
NO_3	0.61	0.7	8.01	10.82
NH_4	0.01	0.0002 *	13.91	26.41
Chl.-a	0.21	0.35	1.9	0.8

As shown by high R^2 values (Table 2), concentrations of TN and NO_3 were captured to a large extent, with the exception of the first year of simulation (Figure 2C,D). However, the model did not succeed in displaying local minima of TN in the beginning of the calibration period until 1996. NH_4 , which as an annual average only constitutes 3% of TN according to observations, was reproduced rather poorly throughout the study period (Figure 2E, Table 2).

RE-values were especially high for variables with very low observation values close to the limits of detection, for instance PO_4 , NO_3 and NH_4 .

Dynamics of total chl.-a concentrations were reproduced reasonably well (Table 2), capturing seasonal and inter-annual variability of observed data. Summer and autumn blooms were occasionally underestimated (Figure 3A). The same applies to spring blooms at the beginning of the calibration period (until 1992).

The simulation suggests that green algae were the dominant phytoplankton group until 1997, after which the proportion of diatoms gradually increased at the expense of green algae (Figure 3B). The sparse data of phytoplankton suggest dominance of diatoms and green algae. (Figure 3C). Thereafter, cyanobacteria appeared in the model output; a tendency also found in observed data, although based on few measurements. The simulation showed diatoms to exhibit both spring and autumn blooms, whereas blooms of cyanobacteria primarily occurred in late summer.

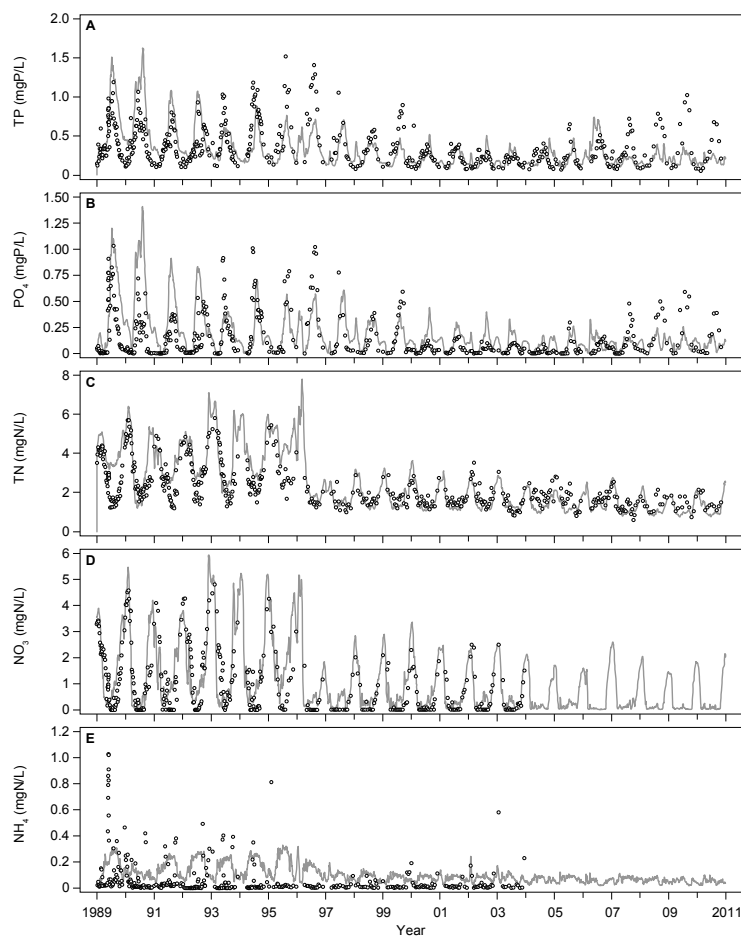


Figure 2. Simulated (lines) and observed (circles) values for calibration. (A) TP; (B) PO_4 ; (C) TN; (D) NO_3 ; (E) NH_4 .

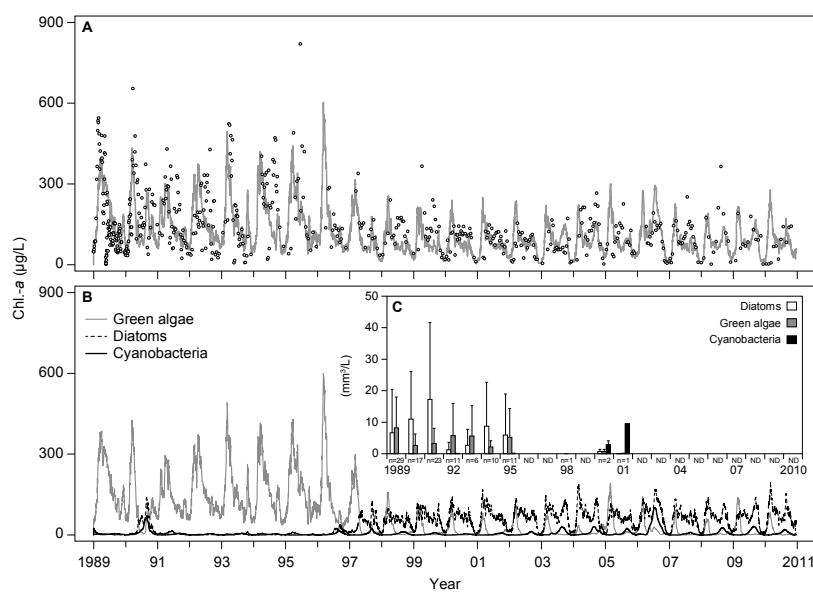


Figure 3. (A) Simulated (line) and observed (circles) values for calibration for chl-*a*; (B) Simulated contribution of green algae, diatoms and cyanobacteria to total chl-*a*; (C) Observed average summer values for phytoplankton biovolume. Values of SE are shown by bars and n indicates sample size. ND = no data.

The simulation indicates that phytoplankton was generally N-limited ($f(N) < f(P)$), except during spring blooms (Figure 4), and green algae appear to be overall more nutrient limited than the other phytoplankton groups.

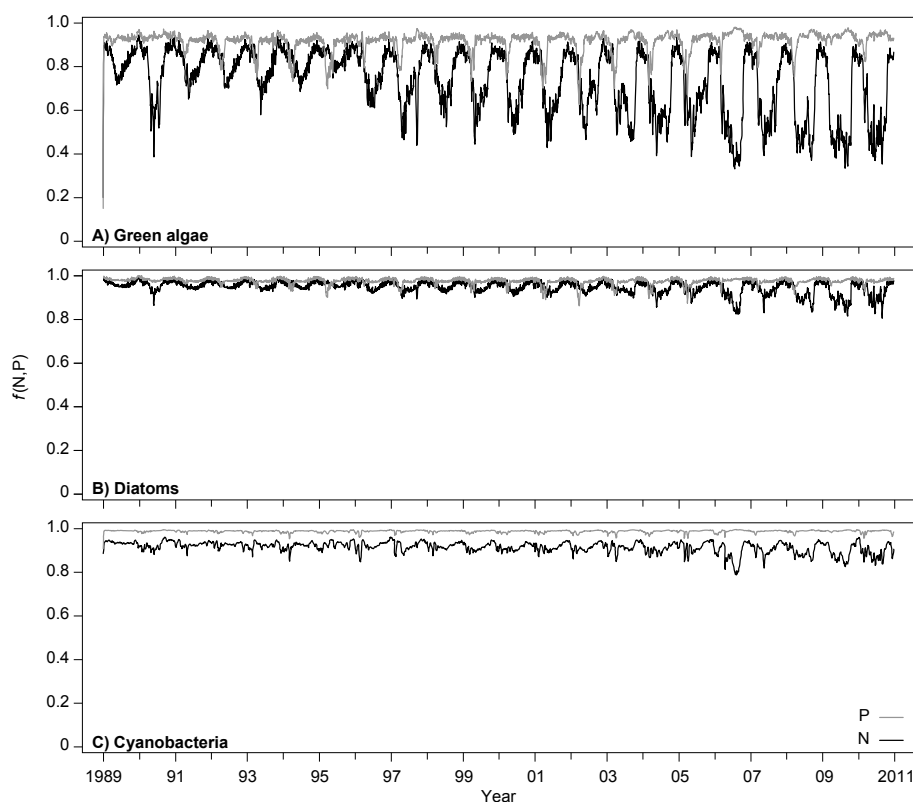


Figure 4. Limitation function (f) of P and N for the base scenario of 1989–2010. (A) Green algae; (B) Diatoms; (C) Cyanobacteria.

3.2. Climate Change and Nutrient Loading Scenarios

Summer mean TP generally increased with rising temperatures and decreased with declining nutrient input (Figure 5A). For PO_4 , however, the pattern was slightly different; the concentration only increased until the temperature increase reached 3 °C with an equivalent decrease from 3 to 6 °C (Figure 5B).

Concentrations of the various N components were predicted to be generally lower during high temperature scenarios, with concentrations of inorganic N fractions declining more steeply than TN (Figure 5C–E). Reductions of nutrient input were followed by a corresponding decrease in all components of N.

Macrophytes were projected to be absent until the nutrient load reduction reached ~70%; mean coverage increased as load reductions reached ~90% after which the coverage decreased again (Figure 5F). The effect of temperature on coverage was negligible according to the model simulations. Mean summer zooplankton:phytoplankton biomass ratio increased with declining nutrient input from low values around 0.3 to substantially higher ratios when macrophyte became abundant, while plankti-benthivorous fish biomass and the proportion of juvenile plankti-benthivorous fish decreased (Figure 6A–C). The enhanced temperatures led to an increase in the proportion of juveniles, whereas the total plankti-benthivorous fish biomass generally decreased. Accordingly the zooplankton:phytoplankton biomass ratio decreased, notably in the high nutrient loading scenarios.

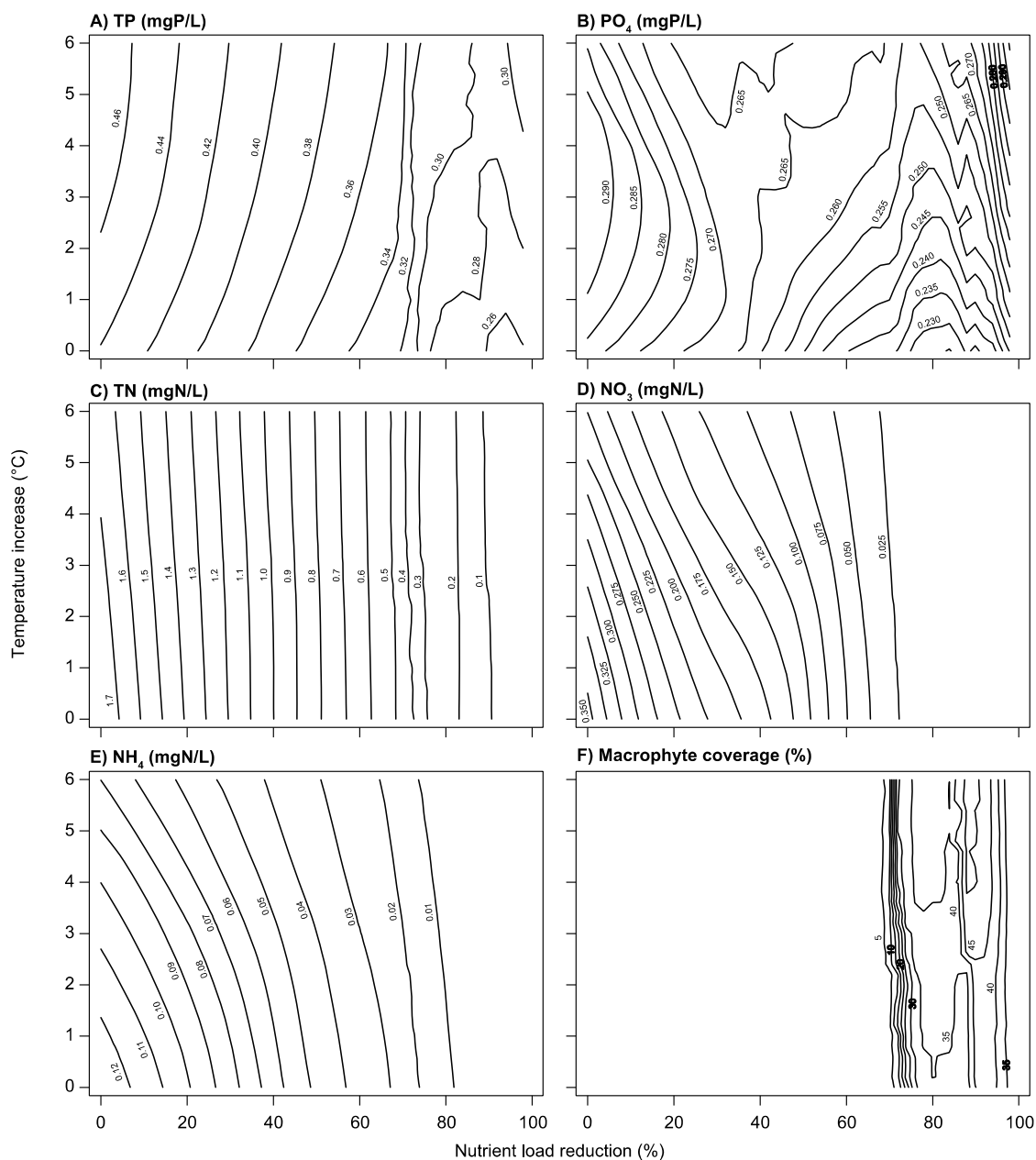


Figure 5. NP_{ext} scenarios. Nutrient load reductions combined with temperature increases. Average summer values for the period 1989–2010. (A) TP; (B) PO₄; (C) TN; (D) NO₃; (E) NH₄; (F) Macrophyte coverage. Value noted by each contour line represents the value of the individual state variable in response to the nutrient load and temperature scenarios.

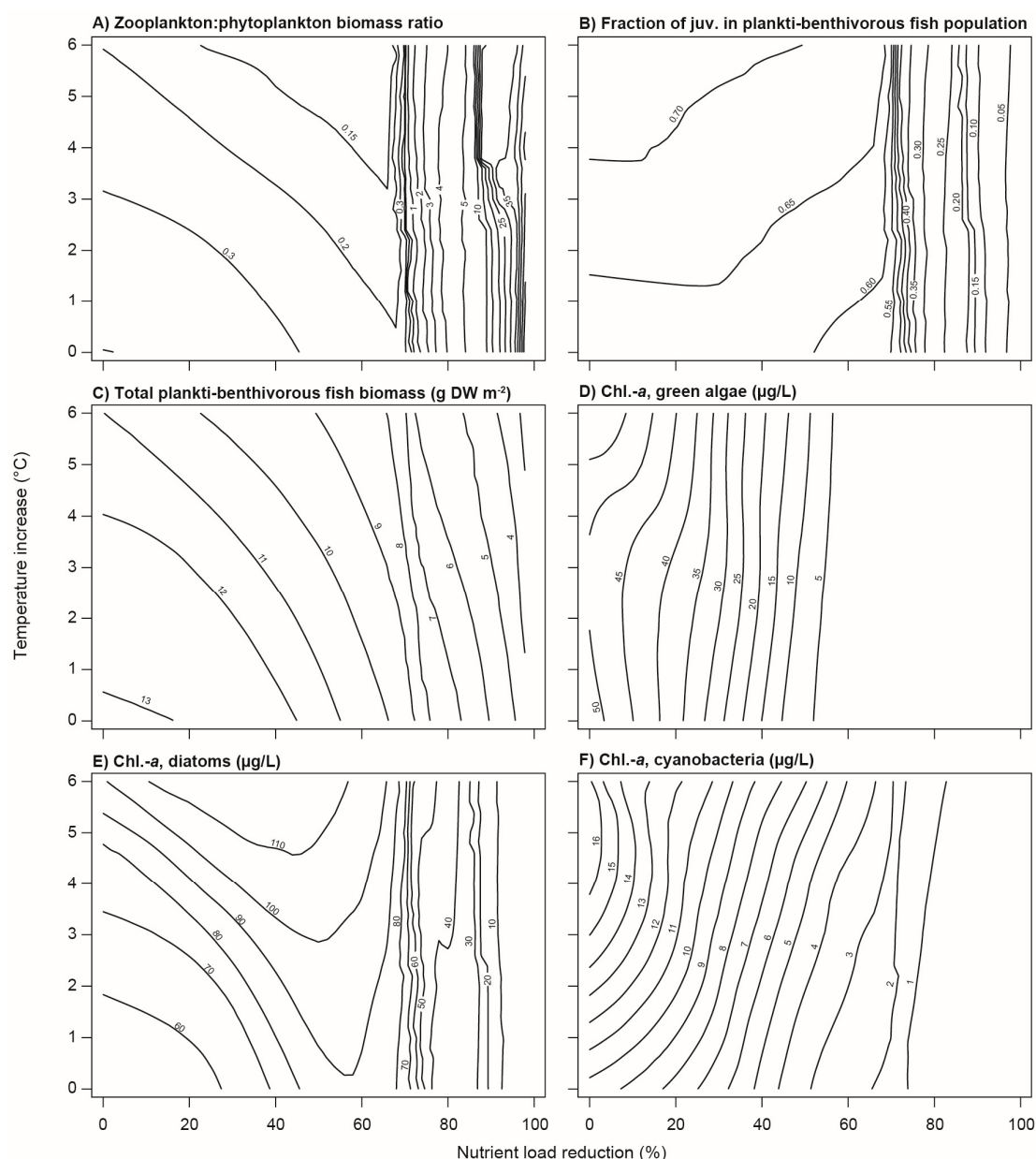


Figure 6. NP_{ext} scenarios. Nutrient load reductions combined with temperature increases. Average summer values for the period 1989–2010. (A) Zooplankton:phytoplankton biomass ratio; (B) Fraction of juveniles in plankti-benthivorous fish population; (C) Total plankti-benthivorous fish biomass; (D) Chl.-a from green algae; (E) Chl.-a from diatoms; (F) Chl.-a from cyanobacteria. Value noted by each contour line represents the value of the individual state variable in response to the nutrient load and temperature scenarios.

Summer mean chl.-a concentration increased with rising temperatures and decreased with declining nutrient input (Figure 7A). Diatoms generally constituted a larger proportion of the entire phytoplankton group with decreasing nutrient input at the expense of both green algae and cyanobacteria (Figure 8). Increasing temperatures generally resulted in higher proportions of both cyanobacteria and diatoms.

The N_{ext} scenario (Figure 7B) appeared to resemble the NP_{ext} (Figure 7A) scenario with regard to chl.-a, while the P_{ext} scenario (Figure 7C) did not produce the same decrease in chl.-a with increasing nutrient load reduction. Only when the lake sediment P pool was eliminated, a decrease in chl.-a occurred when the external P load was sufficiently reduced (P_{ext+int}, Figure 7D).

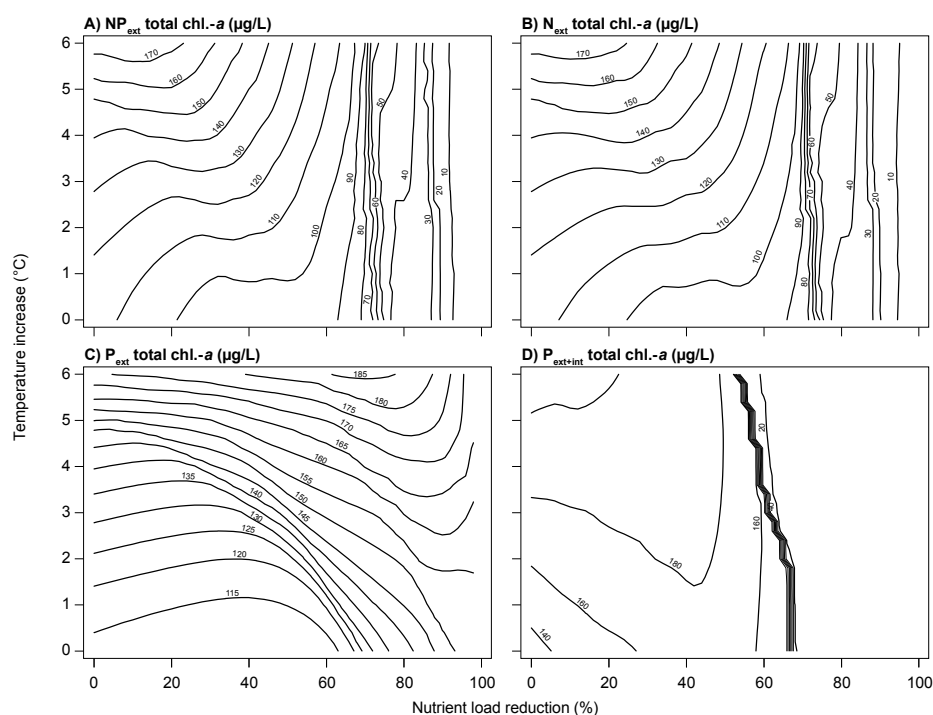


Figure 7. Total chl.-a for NP_{ext} , N_{ext} , P_{ext} and $P_{ext+int}$ scenarios. Nutrient load reductions combined with temperature increases. Average summer values for the period 1989–2010. (A) NP_{ext} ; (B) N_{ext} ; (C) P_{ext} ; (D) $P_{ext+int}$. Value noted by each contour line represents the value of the individual state variable in response to the nutrient load and temperature scenarios.

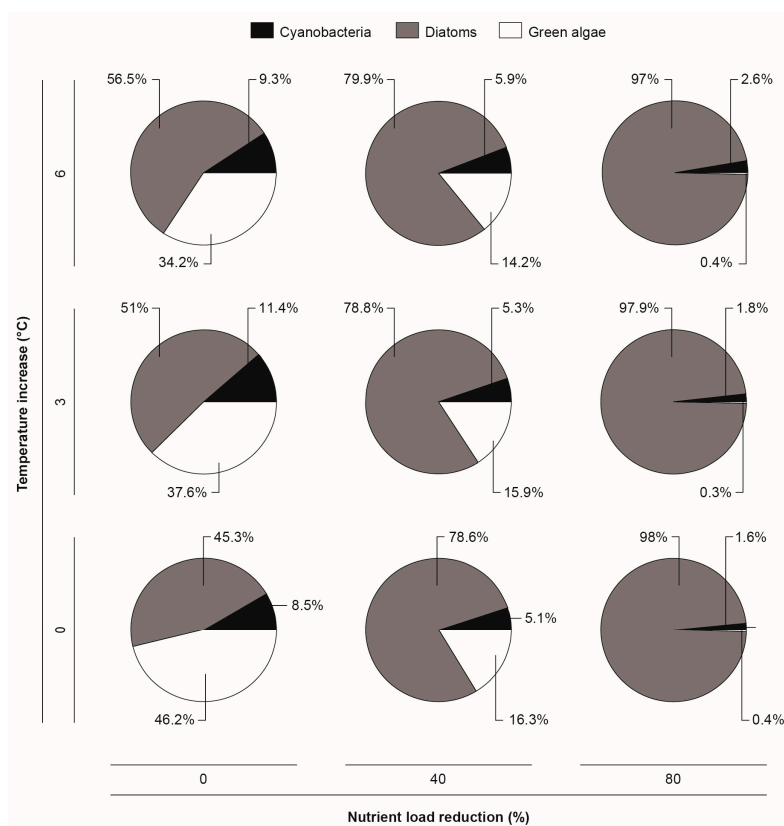


Figure 8. NP_{ext} scenarios. Average summer values for the contribution of chl.-a from different phytoplankton groups.

4. Discussion

4.1. Model Calibration and Performance

The model generally reproduced seasonal and inter-annual variations in nutrient concentrations and chl.-a well albeit some discrepancies between model outputs and observations occurred (Table 2). Arhonditsis et al. [36] conducted a meta-analysis of 153 aquatic modeling studies, summarizing the RE and R^2 values achieved for relevant water quality variables. In comparison, the monthly representation of chl.-a from the present study performs better than 30% of the studies reported in [36] with respect to R^2 values, and $\geq 50\%$ and $\geq 40\%$ for NO_3 and PO_4 , respectively. Statistics on TP and TN were not included in [36]. Compared to a PCLake study published by [30] on shallow Lake Arreskov, Denmark, model performance metrics, and in particular R^2 values, for the Lake Søbygaard model calibration were generally better. It should be noted, however, that a model application should ideally also include a separate validation, where simulated outputs are confronted with observation data collected from a period outside the calibration period. We initially intended to calibrate the model for the period 1989 to 1995, and validate the model for the remaining period, where an abrupt decline in particularly nutrient concentrations were observed as a result of the reduction in external nutrient loads (Figure 2). However, in order to capture the dynamics of this decline acceptably, we had to also compare modelled output and observations for the period 1996-onwards, and adjust model parameters to achieve greater resemblance. Strictly speaking, this means that a separate validation was not performed. Consequently, we also do not report separate model performance statistics for a calibration and a validation period.

Temperature-dependent sediment nutrient release mechanisms were adjusted in accordance with measured high P-release Q_{10} -values from Lake Søbygaard [41], but still the observed P release during summer was not always well captured (Figure 2A,B). This might be attributed to the zero-dimensional design of both the water column and the sediment layer in PCLake and the simplified process of sediment diagenesis as, for example, gradients of dissolved oxygen (apart from an 'aerobic sediment fraction' based on the oxygen concentration in the water and sediment oxygen demand), varying composition of sediment layers, P release induced by high pH, and adsorption of P onto organic material are not incorporated conceptually in the model [23]. These factors have previously been shown to influence P release [42,43], as also demonstrated for Lake Søbygaard [26,44]; particularly high levels of P release can be found in eutrophic lakes during summer [45].

Former studies report substantial N removal due to denitrification in shallow, eutrophic lakes with low hydraulic retention time [46,47]. The extent of annual denitrification previously reported for Lake Søbygaard (35%–47% of total annual N loading [27]) was not fully achieved in this study (only 14%–35% of total annual N loading), which may explain why simulations did not fully reproduce minima of TN and inorganic N fractions during summer (Figure 2C–E). Regular resuspension events caused by wind-induced shear stress and biological disturbances are known to have a major impact on the sediment-water nutrient exchange including nitrogen [48–50], subsequently enhancing denitrification [27,51]. Thus, low denitrification levels might be due to the relatively simple and empirical-based description of resuspension in PCLake [23].

P is often considered to be the limiting nutrient in freshwater lakes [52,53], but phytoplankton in highly eutrophic lakes may also experience stages of N limitation [14,54–56]. According to our simulations (Figure 4), N is a limiting nutrient in Lake Søbygaard. While green algae and diatoms were briefly P limited during spring according to the model results, cyanobacteria showed year-round N limitation. The simulated degree of N limitation of cyanobacteria may be slightly overestimated, though, as N fixation is not considered in PCLake [23,57] summarized data from 17 eutrophic lakes. The average contribution of N (predominantly from autotrophic cyanobacteria) from N fixation in the 17 lakes ($1.73 \pm 2.23 \text{ g N} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) equals up to 5% of the total N budget in Lake Søbygaard, but likely less as cyanobacteria is not always the dominating group of phytoplankton in the lake.

The simulated dominating role of green algae in the beginning of the simulation period is overestimated when compared with measured values. Although not directly comparable, observed

values of phytoplankton biovolume (Figure 3C) indicate a coexistence of green algae and diatoms rather than the modelled dominance of a single algal group until 1996 (Figure 3B). Green algae did, however, dominate the phytoplankton in the lake in the 80's [58].

4.2. Effects of Increasing Temperatures and Reduced Nutrient Loading

Temperature dependence of processes in PCLake allows for studies on effects of climate change [16,59,60]. However, given the large number of adjustable parameters, dynamic models, such as PCLake, may to some extent be subject to non-uniqueness, by which different sets of parameter values yield similar adequate results during calibration, but differing results when applied outside of the domain of calibration [61]. The simulated effects of climate change and reduced nutrient loading should therefore be interpreted with some caution.

A substantial nutrient load reduction of both N and P (~70%) was needed to initiate macrophyte development in Lake Søbygaard in the NP_{ext} scenario (Figure 5F). Although faster recovery might be expected due to greater mobilization of the sediment nutrient pool in a warmer climate, model simulations suggest only negligible importance of temperature on the establishment of macrophyte coverage in this lake. Given the high initial amount of nutrients in the Lake Søbygaard sediment, the sediment will still contain ample amounts of nutrients at the end of the simulation period, even at high temperatures and high nutrient load reductions. Hence, considerable nutrient release will still take place, counteracting the potential effects of a faster depletion of the excess nutrient pool.

The model simulations generally suggest increasing summer concentrations of chl.-a and P in a future warmer climate (Figure 5A,B). Mechanisms responsible for higher P availability include higher mineralization rates and release from bottom sediments triggered by the higher temperatures. Concentrations of N, however, seem to decrease (Figure 5C–E), which may partly be attributed to higher growth rates and thus greater nutrient uptake of phytoplankton, as well as increased bacterial denitrification rates [62]. Diatoms and cyanobacteria generally seem to benefit from higher water temperatures during summer, and diatoms from reduced nutrient conditions, while the effect on green algae is less pronounced (Figure 6D–F). The reduction of chl.-a with declining nutrient load was also accompanied by a shift in the phytoplankton community. This implied increasing dominance of diatoms (Figure 8); a tendency previously reported for lakes undergoing recovery from eutrophication [14]. Steep declines in chl.-a and P occur when macrophytes appear (Figure 5A,F and Figure 7A)—underlining the impairing effect of macrophytes on resuspension, subsequently enhancing sedimentation and reducing sediment nutrient release. Reduction in the predation on zooplankton and thus higher grazing on phytoplankton will have similar effects [6].

N_{ext} and P_{ext} scenarios (Figure 7) predominately suggest N to be the limiting nutrient in Lake Søbygaard during the study period. Reducing the external P load alone did not facilitate a decrease in the amount of chl.-a, as ample release of P from the bottom sediments was able to maintain high concentrations of chl.-a. This effect is also known from numerous recovery studies of freshwater lakes where internal loading delays recovery after a reduction in the external nutrient load [14]. Most lakes reach a new in-lake TP equilibrium after 10–15 years, although heavily impacted lakes may experience significant internal loading for longer periods, even lakes with a relatively short retention time [63]. Simulations with a simple sediment-water P model for Lake Søbygaard [64] has previously indicated that the lake might reach a steady state around 2018, i.e., 36 years after the major P loading reduction. If simulations were run for a much longer time period than in the present study, depletion of the excess P pool would be expected. For Lake Søbygaard, simulations showed that only by eliminating the initial sediment P pool (P_{ext+int}), chl.-a eventually decreased when the external P load was sufficiently reduced. One might expect more drastic effects from eliminating the P pool, even at only moderate external P load reductions. However, due to its high Fe:P ratio [65], the sediment in Lake Søbygaard may be especially prone to retaining phosphorus during oxidized winter conditions and then rapidly releasing it at the onset of biological activity in spring when the oxidized layer decreases [26,66].

Thus, at high external P loadings, the sediment P pool will quickly rebuild to a degree at which it will display negative P retention during summer and help maintain a large phytoplankton population.

In accordance with the empirical studies by [14,67], the model simulations show an increase in the zooplankton:phytoplankton biomass ratio with decreasing nutrient loading, also accompanied by a decrease in the total biomass of plankti-benthivorous fish. With the increasing proportion of juveniles in the plankti-benthivorous fish population with rising temperatures, higher levels of fish zooplanktivory are to be expected, subsequently resulting in lower zooplankton:phytoplankton biomass ratios [10,67,68] as seen at high nutrient loading in the PCLake simulations. The recent data from the lake has shown an increase in the proportion of small fish, attributed to a higher temperature and a reduction in zooplankton size, but no decline in the zooplankton: chl.-*a* ratio [7]. Contradicting cross-latitude studies [69,70], the PCLake simulations show total fish biomass to decline with rising temperatures. PCLake does not incorporate observed changes in phenology, body size and feeding behavior change observed along a temperature gradient [10,71] and therefore likely underestimates the trophic cascade caused by changes in fish community structure.

4.3. Validity of Climate Scenarios

In this study, scenarios of future climate change were represented by a simple increase in air temperature. Undoubtedly, other meteorological variables, seasonality in nutrient loadings and other processes will change as well; some will even show synergistic effects, enhancing symptoms of eutrophication, as e.g., increased precipitation is expected to cause greater nutrient run-off [6]. However, these were not included in order to focus on the relation between temperature and water quality. Moreover, the accuracy of present daily climate projections may not yet be adequate for use in impact studies using simulation models, particularly when a small-scale prediction is needed [72]. With respect to nutrient loading, recent run-off models applied to Danish conditions suggest that a future stronger amplitude and seasonality of run-off events may increase the input of nutrients to streams and lakes; for P this amounts up to 16% increase within a century [6,73], thus further enhancing eutrophication. Less seasonality of P release may be expected, as higher winter temperatures cause less accumulation of P during winter due to a decreased oxidation of the top sediment layer, leaving a smaller P pool to be released during summer [74].

Moreover, the assumption that the temperature increase will have a uniform pattern across seasons may be oversimplified. Danish climate projections are characterized by increasingly warmer weather, with the highest temperature increases projected to occur during winter [75]. Although having received little attention, the consequences of changed winter temperatures may be just as critical as those of their summer equivalents [16]. Since ice cover tends to develop in cold temperate lakes during winter, an increase in temperature will change the timing of ice formation and may reduce the temporal extent of the ice cover [76]. This may enhance fish winter survival and successively reinforce cascading effects on the lower trophic levels of the lake. Thus, reduced population sizes and smaller individuals will come to characterize the zooplankton community structure, leading to a reduced grazing potential. Ultimately, the reduced ice cover duration will increase the occurrence of higher phytoplankton biomass and turbid summer conditions—particularly so in shallow, eutrophic lakes [10,77–79]. It is, therefore, crucial that the fish and zooplankton model representation is adequate and takes into account the changes in community structures—especially as a sensitivity analysis has shown that 25% of the most sensitive model parameters relates to zooplankton dynamics [30].

Due to the aforementioned effects of ice cover and the fact that PCLake does not conceptually incorporate the formation of ice, one might expect larger values of RE in summers immediately following cold winters. This was not the case for the Lake Søbygaard application, though, as no significant linear correlation between mean winter temperature and (chl.-*a*) RE during the following summer was found.

5. Conclusions

We applied the ecological model PCLake based on 22 years of data from shallow, eutrophic Lake Søbygaard, Denmark and simulated multiple combinations of increasing temperatures (0–6 °C), reduced external nutrient loads (0%–98%) with and without internal phosphorus loading. The results of this study were overall consistent with predictions of deteriorating lake water quality by increasing temperatures, as suggested by other studies [10,16,80,81]. An increase of 65% in total chl.-a was projected at a temperature increase of 6 °C. In order to mitigate the effect of such temperature increase, a decrease in nutrient loading of 60% is required to reach chl.-a values similar to those of the baseline scenario with present-day temperatures for Lake Søbygaard. In the 6 °C scenario, the contribution of chl.-a from cyanobacteria increased proportionally to total chl.-a; the cyanobacteria did not, however, demonstrate the same degree of dominance as reported for other climate change studies on lakes [19,82]. These studies have used models that allow a vertical resolution of a water body, meaning that the buoyancy of cyanobacteria can favor these over other phytoplankton under scenarios where water column stability increases, whereas this effect is not accounted for in our study (as PCLake represents a fully mixed water body). Therefore, PCLake may to some extent underestimate the future dominance of cyanobacteria. However, a new development by [83], which can resolve PCLake in a physically explicit structure (e.g., vertically), may allow more realistic predictions by PCLake in future studies. Our results are evidently of a magnitude that indicates strong effects of a future temperature increase and should therefore be considered when planning long-term management of lakes.

Under the prerequisite that PCLake satisfactorily reflects the true behavior of ecological changes during temperature increase and nutrient load reduction, the ecological model proves to be a valuable tool for managers of freshwater lakes. In this study, by relating temperature increase and nutrient load reduction scenarios to summer averages of water quality parameters, a direct link has been established to the ecological classifications of the WFD [84]. Thus, it is possible to estimate the magnitude of nutrient reduction required in a future warmer climate to mitigate eutrophication in order to achieve good ecological status as required by the WFD. However, it is important to continuously improve the conceptual model, and also to take advantage of the diversity of multiple existing models [85], to enhance the reliability of projections, such as, for example, the submodels for fish, fish-zooplankton interactions and sediment nutrient exchange.

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