Long-term nutrient load reductions and increasing lake TN : TP stoichiometry decrease phytoplankton biomass and diversity in a large shallow lake

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Abstract

Nutrient loading of freshwater and marine habitats has increased during the last century as a result of anthropogenic activities. From the 1980s onwards, following implementation of new policy targeting eutrophication, total phosphorus (TP) and total nitrogen (TN) loads were reduced in many European waters. Often, however, decreases in TP were stronger as compared to TN, leading to increased TN : TP ratios. Our analysis shows that the large and shallow lake IJsselmeer (the Netherlands) experienced a similar trend, whereas TN was reduced by 50%, TP was reduced by 89% between 1975 and 2018. Most of this nutrient load reduction was achieved before the year 2000, changes in nutrient concentrations in the lake became smaller afterwards, especially for TN, leading to a further increase in stoichiometric imbalance up to a yearly averaged TN : TP (molar) of 296 in 2018. The observed changes in nutrients were accompanied by a decline in total phytoplankton biomass, and slight declines in phytoplankton genus evenness and diversity. Although biomass decreases likely resulted from the overall decrease in nutrient availabilities, the reduced diversity may have resulted from the shift toward very high TN : TP ratios that indicate relatively low TP levels and enhanced competition for phosphorus. Overall, our findings demonstrate long-term trends with decreased phytoplankton biomass and diversity following reduced nutrient concentrations and enhanced stoichiometric imbalance. Ultimately, such changes at the food web base may alter the structure and functioning of the entire aquatic food web in lake IJsselmeer.

Anthropogenic activities strongly influence nutrient cycling in ecosystems and have resulted in eutrophication of the European coastal marine and freshwater environments during the last century (Smith 2003; Ferreira et al. 2011). Phosphorus (P) and nitrogen (N) loads generally increased until the end of the 1980s, but were reduced following a ban on household detergents containing phosphates, improved nutrient removal in sewage treatment plants, and implementation of European legislation regulating fertilizer application (Rozemeijer et al. 2021). Reduction of nutrient loading generally improves ecological conditions in lakes (Kronvang et al. 2005). Since the aforementioned measures generally targeted total P (TP) loads more than those of total N (TN), many lakes, rivers and coastal waters experienced a shift in nutrient balance toward higher TN : TP ratios (Jeppesen et al. 2005; Grizzetti et al. 2012; Tong et al. 2020).

Changes in nutrient loads and ratios have consequences for phytoplankton biomass and community composition. Phytoplankton biomass is often high when both N and P loads are high, since these are often (co)limiting factors for growth (Elser et al. 2007; Dolman et al. 2012). Shifts in TN : TP ratios were shown to induce changes in phytoplankton community composition and diversity (Jeppesen et al. 2005; Elser 2009; Ptacnik et al. 2010). Waters that are relatively N limited and have excess P exhibit low TN : TP ratios, which may favor dominance of N2-fixing cyanobacterial taxa (Smith 1983; Levine and...

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Additional Supporting Information may be found in the online version of this article.

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Schindler 1999; Vrede et al. 2009). At the same time, low TP conditions with high TN : TP ratios may also benefit cyanobacterial blooms, for instance if prevailing cyanobacteria populations are physiologically adapted to P limitation (Gilbert et al. 2014; Gobler et al. 2016). Changes in TN : TP ratios are also expected to affect phytoplankton diversity, as shifts toward imbalanced ratios will increase competition for either of the nutrients and may thereby reduce species richness (number of species) and/or evenness (relative abundance of species) (Hillebrand et al. 2014). Indeed, imbalanced resource ratios, including TN and TP, across a range of Norwegian lakes reduced species richness of phytoplankton communities (Cardinale et al. 2009). In a more recent meta-analysis, however, species richness and evenness in natural systems remained largely unaffected by imbalanced (mainly TN : TP) resource ratios (Lewandowska et al. 2016). This may have resulted from limited gradients in TN : TP ratios, as only annual means were incorporated. Including seasonal dynamics in long-term data analyses may possibly reveal larger variability in TN and TP concentrations and thereby allow testing how diversity will change along wider ranges in TN : TP ratios.

Here, we assessed how long-term decreases in TN and TP concentrations, and associated increases in TN : TP ratios, affected phytoplankton biomass, community composition, and phytoplankton genus evenness and diversity. To this end, we used a unique dataset containing > 40 yr of monthly monitoring data on lake IJsselmeer, a shallow ~ 1100 km² freshwater lake in the Netherlands in which toxic cyanobacterial blooms were a common phenomenon until the 2000s (Leeuwhang et al. 1983; Berger and Sweers 1988; Ibelings et al. 2005). Throughout 1970s till the 1990s, new legislation was implemented, among others the Dutch Pollution of Surface Waters Act, the European dairy produce quota (leading to reduced amounts of cattle and manure), and a ban on P detergents in Germany and the Netherlands (Rozenmeijer et al. 2021). As a result of these, P input and concentration in lake IJsselmeer strongly decreased in the 1980s and was reduced down to 50% by the 1990s. N reductions and changes in phytoplankton biomass and community composition were less pronounced during the same period, and, as a result, the lake could still be classified as hypertrophic (Hosper 2001; Lammens et al. 2001) based on chlorophyll a (Chl a).

Our objectives are to (1) determine how the observed long-term (40 yr) reductions in TN and TP concentrations, and accompanied increases in TN : TP molar ratios, affect phytoplankton biomass, and (2) how the prolonged reductions (recent 14 yr) in TN and TP concentrations, and associated increases in TN : TP ratios, affect the phytoplankton community and cyanobacterial dominance therein. More specifically, we evaluate how a set of environmental parameters have changed over the entire monitoring period of 40 yr, including lake temperature, nutrient concentrations, and TN : TP ratios, and test how this influenced phytoplankton biomass over the entire monitoring period and cyanobacterial abundances between 2004 and 2018 using generalized additive models (GAMs). Moreover, changes in phytoplankton species diversity and evenness were also assessed between 2004 and 2018, as data on phytoplankton community composition was only available for this period. Overall, we expect reduced phytoplankton biomass over the course of the monitoring period, associated with long-term decreases in TN and TP. Moreover, with stronger decreases in TP as compared to TN, we anticipate associated increases in TN : TP, resembling a stronger competition for P and thereby a decrease in phytoplankton diversity.

Methods

Study site and sampling

Lake IJsselmeer is a former shallow bay which was closed off from the North Sea in 1932 by the construction of a 32-km-long dam built for flood protection and reclamation of land (Fig. 1, map created using https://maps.co/). The lake is polymictic and shallow, with an average depth of about 4.5 m, and an average water residence time of 0.4 yr (Berger and Sweers 1988; Ibelings et al. 2005). The rate of eutrophication of lake IJsselmeer increased drastically during the 1950s, as it is fed mainly through the river IJssel, a branch of river Rhine (de Kloe 1978; Dijker 1982). The Rhine River drains a 185,000 km² watershed covering eight countries in which the majority of land is used for agriculture (Wessel 1995). Due to high nutrient concentrations in the water, blooms of potentially toxic cyanobacteria have been present since the formation of the lake, which were dominated by genera such as Microcystis, Anabaenopsis, and Planktothrix until the end of the 1990s (Ibelings et al. 2005). Since lake IJsselmeer was formed it hosted a dense population of freshwater mussels; however, from 2006 onwards, the lake was invaded by the quagga mussel, which quickly reached an almost complete dominance within the Dreissend community (bij de Vaate et al. 2013; Matthews et al. 2014). For our analyses, we used publicly available monitoring data collected by the Directorate-General for Public Works and Water Management (Rijkswaterstaat) between 1972 and 2018, via https://waterinfo.rws.nl/. We focused on the central monitoring station of lake IJsselmeer “Vrouwezand” (Fig. 1; 52°48’37.3,N, 5°23’35.3’E), since this is the only station that covers the entire period for both macronutrients (TN, TP), temperature, and Chl a (1975–2018), and for which phytoplankton cell counts and species composition are available for a subset of years (2004–2018). Due to large sets of missing data during late autumn and winter, phytoplankton community composition could only be analyzed for the months April–October.

Because the dataset covers a long sampling period, the specific methods inevitably have changed over the years. Current and historical methods are described in standard protocols by the Royal Netherlands Standardization Institute (NEN), and are available through https://www.nen.nl/en/. In general, water samples were taken monthly by sampling the upper 1 m from the surface using a tube sampler according to NEN 6600. Samples for Chl a were taken by filtering water over glass fiber...
filters, kept in the dark at 4°C, and analyzed within 24 h or otherwise stored at −18°C and analyzed within 14 d. Chl $a$ was determined spectrophotometrically after 80% ethanol extraction and a correction for phaeophytin according to NEN 6520. Phytoplankton community composition was determined in Lugol-preserved samples using inverted light microscopy and sedimentation chambers according to NEN-EN 13395 and NEN 6646. TP was determined according to NEN-EN-ISO 15681. Dissolved inorganic nitrogen and phosphorus were measured with a continuous flow analyzer.

Average yearly N and P input to the lake from river IJssel was estimated by multiplying the average monthly discharge from station “IJsselkop” with nutrient monitoring data from station “Kampen,” which were subsequently summed per year (data also retrieved from https://waterinfo.rws.nl/). Average yearly N-deposition data were downloaded from website of Environmental Data Compendium (https://www.clo.nl).

**Fig. 1.** Map of the Netherlands (A) and lake IJsselmeer (B, in blue). The black circle denotes the central monitoring station.

### Statistical analyses

All statistical analyses were performed in R version 4.0.3 (Team 2010). Two GAMs were established to examine the relationships of Chl $a$ (biomass) between 1975 and 2018 and cyanobacterial abundances (counts) between 2004 and 2018 with variation in the environmental parameters temperature, TN, and TP across years and months (Wood 2017). We note that long-term data on dissolved nutrients and pH were available (Supporting Information Figs. S1–S3) but not included in the model as these parameters respond more strongly to phytoplankton growth and hence are not suitable as predictive variables. Moreover, other parameters, such as time, were excluded from the model as this showed too much curvilinearity (GAM equivalent of collinearity) with temperature and total nutrients. The models have the following structure:

$$g(Y) = f_1(T) + f_2(TN, TP)$$

where $g$ is a link function, $Y$ the response variable, which is either Chl $a$ (mg/L) or phytoplankton abundance (cells L$^{-1}$), and $f_i$ are the smoothing functions for predictor variables, temperature, TN, and TP, respectively. We used a thin plate regression spline for temperature, while the multivariate smooths $f_2$ is based on a tensor product smooth and integrates the respective main effects and interactions between those covariates with a penalized cubic regression spline. This approach was used as it allows to model a series of nonlinear smoothing functions, which is ideal for ecological data (Pedersen et al. 2019). The model was fitted using the R packages “mgcv” and “mgcViz” (Fasiolo and Nedellec 2020; Wood 2023), where we used REML to estimate model coefficients and smoothing parameters and a Tweedie distribution (Supporting Information Figs. S4, S5). GAMs are increasingly used in recent years for analyzing ecological trends, as they have the advantage of being able to deal with complex nonlinear response relationships (Wood 2006; Liu et al. 2019; Zhang et al. 2021).

In addition, we quantified if significant trends were present in the dataset, specifically for temperature, TN, TP, TN : TP, Chl $a$, and cyanobacterial abundances and abundances of other algal groups over the years, and during specific months of the year over the years with a Mann–Kendall test and a seasonally corrected Mann–Kendall test (all months over the years), respectively using the R package “Kendall” (McLeod 2022). A non-parametric Mann–Kendall test is widely used for assessing climatic time series data, as it can cope with outliers (Douglas et al. 2000; Atta-ur-Rahman and Dawood 2017; Nashwan and Shahid 2019). In addition, it is also used for analyzing phytoplankton data over time (Marshall et al. 2009; Lynam et al. 2010; Winter et al. 2011).

Moreover, phytoplankton community composition data over the period 2004–2018 was also used to assess shifts in phytoplankton evenness and diversity. To this end, data were first grouped on a genus level for consistency over time.
and to avoid potential biases due to changes in phytoplankton taxonomist and to account for large variations caused by low species abundances that may appear just below or above detection levels. Subsequently, shifts in evenness and diversity were calculated with the \textit{R} package “\textit{vegan}” (Vinet and Zhedanov 2011), where Pielou’s evenness and the Simpson biodiversity index were used, respectively. Significant changes over time (both across years and over specific months) were again assessed by a seasonal Mann–Kendall and a Mann–Kendall trend test, respectively.

\textbf{Results}

\textbf{Nutrient loading and stoichiometry}

\textit{Long-term annual trend}

Input of N and P by river IJssel into lake IJsselmeer was reduced considerably since the 1970s (Fig. 2). Cumulative yearly N input was reduced by 58% and total P by 88% as compared to their maxima at the end of the 1970s and beginning of 1980s. TN and TP concentrations in water of lake IJsselmeer follow a similar trend (Fig. 2, Table 1), where TN was reduced roughly from > 4 mg L$^{-1}$ to an average 2.5 mg L$^{-1}$ (50% reduction) and TP was reduced from around 0.30 to 0.05 mg L$^{-1}$ (89% reduction). Whereas both TN and TP were reduced significantly over the entire monitored period, TN was not reduced substantially from 2004 to 2018 (Table 1B). Atmospheric N-deposition into lake IJsselmeer decreased by about 43% over the last 40 yr (Supporting Information Fig. S6), but contribution of deposition to TN loads of lake IJsselmeer are negligible, ranging between 0.03% and 0.05% throughout time, as when compared to the amount of TN transported into the lake by the river IJssel. Since TP was reduced comparatively more than TN, TN:TP displays an increasing trend (Fig. 2). Average

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{fig2.png}
\caption{Long-term annual TN (A) and TP (B) loads into lake IJsselmeer via river IJssel, and TN : TP ratio of water in river IJssel (C). Concentrations of TN (D), TP (E), and TN : TP ratio (F) of lake IJsselmeer surface water. Trend lines represent loess-smoothed conditional averages. Note that (C) and (F) are plotted on a logarithmic scale.}
\end{figure}
Phytoplankton biomass dynamics and drivers

**Phytoplankton trends**

Phytoplankton biomass (Chl $a$) shows a very strong decreasing trend over 1975–2018, reducing from an average of close to 100 $\mu$g L$^{-1}$ at the start of the 1980s to 20 $\mu$g L$^{-1}$ in 2018 (Fig. 4). Chl $a$ was reduced significantly for the months January, March, May, June, August, and September, and for the year overall (Table 1). While no significant trend was observed in the phytoplankton group composition of cyanobacteria and diatoms, other groups decreased slightly, and both genus diversity and evenness showed a small reduction during the period 2004–2018 (Fig. 5; Table 1B). A significant decrease in evenness was also specifically apparent in October, while we did not observe significant decreases in diversity over other months (Table 1).

The 15 most dominant taxa (by cell counts) over the period 2004–2018 comprised mostly of cyanobacteria (Supporting Information Table S1), notably including small coccolid, colonial, and nontoxic species, such as those belonging to Chroococcales, with specific genera including *Aphanizomenon*, *Cyanodictyon*, *Aphanocapsa*, and *Cyanocaten* that represented 51–78% (by cell counts) of the 15 most dominant taxa. There were no diazotrophic cyanobacteria dominant during the monitored period, although *Aphanizomenon* and *Pseudanabaena* are observed at times.

### Table 1. Long-term trend for each month of the year (Mann–Kendall test), and the year overall (seasonal Mann–Kendall test), for different variables measured in lake IJsselmeer over the period 1975–2018 (A) and 2004–2018 (B). For the latter, phytoplankton group composition data is available (cyanobacteria, diatoms, other), which were used to calculate genus diversity and evenness. Numbers in the table represent the Kendall rank correlation coefficient, which measures the monotony of the slope. Gray cells: no data or not enough data. White cells: no statistically significant change. Colored cells: statistically significant increase (red) or decrease (blue; $p < 0.05$).

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<table>
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<th>Variable</th>
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</table>

yearly lake water surface temperature showed a slight upwards trend over the 40-yr period, although this was not significant for specific months (Table 1).
Potential drivers of biomass

GAM results showed that temperature, TN, and TP were all significant predictors for estimating Chl a ($R^2$ of 0.36; deviance explained 37%; 43 yr) and cyanobacterial abundances ($R^2$ of 0.44; deviance explained 56%; 14 yr) across years and months. Positive effects of temperature on Chl a concentrations were already apparent from 10°C onwards, while the effect of these temperature gradients on cyanobacterial abundances shows a clear optimum between 13°C and 20°C (Fig. 6a, b). Nutrient responses for overall Chl a and cyanobacteria were quite different, where highest Chl a concentrations are found during high TN and TP, and highest cyanobacterial abundances under low TN and intermediate TP (low TN : TP) conditions (Fig. 6C,D). Both Chl a and cyanobacterial abundances were generally lowest at low TP conditions.

Discussion

Decadal trends

Policy focusing on nutrient load reductions has been shown to be very effective in terms of lowering both TN and TP loads of lake IJsselmeer during the 1980s until the early 2000s (Table 1B), accompanied by further declines in phytoplankton biomass during the last two decades (Fig. 4). Furthermore, the high TN : TP ratios well above 50 most of the year (Fig. 3) suggest that P is likely most limiting and thereby the predominant nutrient controlling phytoplankton biomass in lake IJsselmeer (Guildford and Hecky 2000). This is supported by year-round relatively low concentrations of dissolved inorganic P, while dissolved inorganic N availability remains generally higher (Supporting Information Figs. S1, S2). In addition, although cyanobacteria such as Aphanizomenon and Pseudanabaena are observed at times, the phytoplankton community was never dominated by diazotrophic species (Supporting Information Table S1), furthermore suggesting that N-deficiency in lake IJsselmeer may be rare.

We applied GAMs to estimate the effects of TN and TP, together with temperature, on Chl a and cyanobacterial abundances. As such, the GAM results integrate the effects of seasonality and long-term changes in TN and TP, as well as in temperature, and the observed relationships are therefore linked to both. Based on the GAM output, highest cyanobacterial abundances in lake IJsselmeer were associated to low TN and intermediate TP conditions (Fig. 6). Although other studies often find an association of high cyanobacterial abundance with high TP conditions (Schindler 1975; Schindler et al. 2016; Chorus et al. 2020), this trend may in part be explained by the

![Fig. 3.](https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lno.12428) Seasonal trends of TN : TP ratio and temperature in lake IJsselmeer over the last four decades. Trend lines represent loess-smoothed conditional averages. Dashed reference lines in (A) represent TN : TP thresholds for N deficient (<20) and P deficient growth (>50).
Fig. 4. Long-term (A) and seasonal trend (B) of Chl a in lake IJsselmeer. Trend lines represent loess-smoothed conditional averages.

Fig. 5. Trends of phytoplankton genus evenness (A) and diversity (B) from 2004 until 2018. Trend lines represent loess-smoothed conditional averages.
Fig. 6. GAM smooth response curves of Chl a and cyanobacterial abundances to temperature (A, B) and nutrients (C, D), showing only the effect these specific parameters have on Chl a and cyanobacterial abundances. The dashed 0 line in (A) and (B) indicates no effect on the abundances. The black diagonal line in (C) and (D) represents the Redfield ratio at 16 : 1 (molar).
lack of domination by diazotrophic species discussed above. The highest overall biomass of phytoplankton corresponded to both low and high TN and intermediate TP conditions. The high biomass with high TN is mainly driven by the decadal trend and is in line with overall eutrophication effects with higher nutrient concentrations leading to higher phytoplankton biomass (Vollenweider 1968; Smith 2003; Moss et al. 2011). The high biomass with low TN is driven by seasonal dynamics, where summers correspond to higher phytoplankton biomass but also low TN likely as result of enhanced denitrification (Scott and McCarthy 2010; Shatwell and Köhler 2019).

Seasonal trends

Our results show clear seasonal shifts in TN : TP ratios, which are particularly high during spring (i.e., well above 50 for the period 2008–2018; Guildford and Hecky 2000) and lower in summer and fall. Therefore, phytoplankton was likely P limited during spring, and decreases in TP concentrations may possibly explain the large decrease in phytoplankton spring bloom biomass over the last 43 yr (Fig. 4b). Although phytoplankton biomass also decreased in summer and fall, the relative reduction seems less pronounced, which likely results from other (co-)limiting factors. For example, pH increased up to values of around 9, which may correspond to under-saturating CO2 concentrations and potential CO2 limitation (Verspangen et al. 2014). Similarly, high phytoplankton biomass in summer may cause strong self-shading and result in light limitation (Huisman and Hulot 2005). We note that our analysis involves overall patterns with monthly data, and future data collection and analyses with higher frequency data on a wider range of parameters, including phytoplankton bio-volumes, are required to fully elucidate the role of climatic conditions in explaining year-to-year variation in phytoplankton biomass.

Besides phytoplankton biomass, we also observed a slight decrease in genus diversity over the last two decades. More pronounced shifts may have become apparent if we could compare to data of the 1970s and 1980s. Changes in diversity may possibly result from enhanced imbalances in TN : TP ratios, which reflect relatively low P availabilities and thereby stronger competition for P (Ptacnik et al. 2008; Hillebrand et al. 2014). Consequently, fewer species may reach higher relative abundances, and possibly cause blooms. We do not see such shifts at higher taxonomic levels (i.e., cyanobacteria, diatoms, others), and the phytoplankton community was consistently dominated by small coccoïd cyanobacteria during the period 2004–2018. Rather, observed declines in diversity resulted from changes in species and genera within these larger taxonomic groups.

Implications for the food web

The observed changes in lake TN : TP and associated shifts in phytoplankton biomass may affect higher trophic levels in lake IJsselmeer. For example, enhanced P limitation as well as reduced diversity of phytoplankton in their diet may decrease fitness, growth, and reproduction of zooplankton (Boersma et al. 2008; Striebel et al. 2012). Consecutively, zooplankton feeding on lower food quality items may also be nutritionally less valuable itself to zooplanktivorous fish (Malzahn et al. 2007). For lake IJsselmeer, zooplankton monitoring data is not available, as this is not required for the European Water Framework Directive (Jeppesen et al. 2011), and it thus remains elusive how shifts in the phytoplankton community may have affected higher trophic levels in this lake. Yet, monitoring of fish stocks indicate strong declines in a range of planktivorous fish species, particularly over the last decade (de Leeuw and Van Donk 2020). Additional monitoring of the zooplankton community is required to test whether changing nutrient loads, and associated shifts in phytoplankton biomass and diversity, can cascade through the entire food web. Besides consequences for ecosystem services in lake IJsselmeer itself, changes may also impact downstream systems. Indeed, water from lake IJsselmeer flows into the Wadden Sea National Park, and TN and TP from lake IJsselmeer are responsible for a significant share of the total nutrient loading of the western parts of the Wadden Sea, especially for TN (Philippart and Cadée 2000; Van Raaphorst and De Jonge 2004). Such a relative high load of TN may induce P limitation, as was shown for Dutch coastal waters, which shifted from P limitation nearshore to co-limitation of N and P in a transitional region, to N limitation offshore (Burson et al. 2016). Hence, reductions in TN in lake IJsselmeer may also have consequences for the structure and functioning of the food web of the Wadden Sea and nearshore regions of the North Sea.

Warming of lake IJsselmeer

In agreement with global trends (Schneider and Hook 2010; O’Reilly et al. 2015), lake IJsselmeer yearly average temperature also showed an upwards trend over the last 40 yr (Fig. 3). It is often assumed that increased temperature may be translated into shifting dominance of phytoplankton groups toward cyanobacteria due to their higher optimal growth temperatures, and their ability to exploit their buoyancy in a more stable water column when temperatures are higher (Huisman et al. 2018). No direct response, however, could be observed in cyanobacterial counts in our dataset (Table 1), maybe because cyanobacteria were already dominant throughout the entire tested period, or due to overlapping optimum growth temperatures of cyanobacteria with other phytoplankton present in the lake (Butterwick et al. 2005; Lürling et al. 2013). Moreover, changes in water temperature may also cause shifts in the timing and magnitude of phytoplankton top-down control by herbivores or pathogens, and thus affect phytoplankton biomass and community composition (Adrian et al. 2006; Frenken et al. 2016, 2020). Consequently, any potential increase in phytoplankton biomass and even group composition may have been masked by shifts in top-down control. Although in lake IJsselmeer this did not lead to marked shifts
in phytoplankton groups, such changes in timing may underlie changes in the observed evenness and diversity, and the decreasing trend of phytoplankton other than cyanobacteria and diatoms (Table 1).

Nutrient mitigation strategies

It is still under debate on which nutrient(s) policy makers should focus to have the highest potential to control phytoplankton biomass and cyanobacterial blooms. There are many case studies pointing toward N (Moss et al. 2005; Scott and McCarthy 2010; Newell et al. 2019), P (Schindler 1975; Schindler et al. 2016; Chorus et al. 2020) or both (Shatwell and Köhler 2019; Lewis et al. 2020). By achieving low enough concentrations of N and P in the water, mitigation strategies to limit severe bloom formation may suffice focusing on either N or P (Chorus and Spijkerman 2021). Lake IJsselmeer may be approaching that status now. But, although concentration of nutrients in lake IJsselmeer have been reduced very significantly, the lake still classifies as eutrophic during the last years of the dataset, still reaching Chl a concentrations in the range of 60 μg L⁻¹ during summer. Moreover, the phytoplankton community remains dominated by cyanobacteria. Even though these are not notorious toxic genera, they might impede trophic transfer as they generally represent poor food quality (Lampert 1987; Von Elert et al. 2003). Based on our dataset, we cannot disentangle whether ongoing P reductions alone, or dual N and P reductions, are required to induce a shift toward lower phytoplankton biomass and, importantly, stimulate growth of phytoplankton species of higher food quality. Moreover, the cyanobacterial community is dominated by genera with similar traits as some notorious toxin producers, notably Microcystis, while declines in TN concentrations have largely stopped since the start of this century. Thus, to improve the food web functioning, and reduce the risk of harmful cyanobacterial bloom development, it would be advisable to continue P load reductions and increase efforts for mitigating N.

Conclusion

Our analysis on long-term data from the large and shallow lake IJsselmeer (the Netherlands) describes marked decreases in TN and TP concentrations that are associated to a decline in overall phytoplankton biomass. Nutrient load reductions effectively reduced TN and TP concentrations between 1980 and 2000, and continued to decline for TP but not TN, hence leading to marked increases in TN:TP ratios. These increased TN:TP ratios suggest enhanced P limitation, which may increase competition for P and underlie the observed reduction in phytoplankton evenness and diversity. The phytoplankton community is dominated by small coccoid, colony forming cyanobacteria, that may represent a low-quality food source for higher trophic levels. Future studies combining monitoring data with modeling should reveal whether TP and, particularly, TN load reductions might lead to more balanced nutrient concentrations, increased phytoplankton diversity, and a shift toward more favorable phytoplankton groups, thereby improving the structure and functioning of the lake IJsselmeer food web.

Data availability statement

All the data used in this study are openly available in data repositories of Dutch government agencies, as specified in “Methods” section.

References


Chorus, I., and E. Spijkerman. 2021. What Colin Reynolds could tell us about nutrient limitation, N:P ratios and...


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Conflict of Interest

All authors declare that they have no conflicts of interest.

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