Title

Modeling decreased resilience of shallow lake ecosystems towards eutrophication due to microplastic ingestion across the food web

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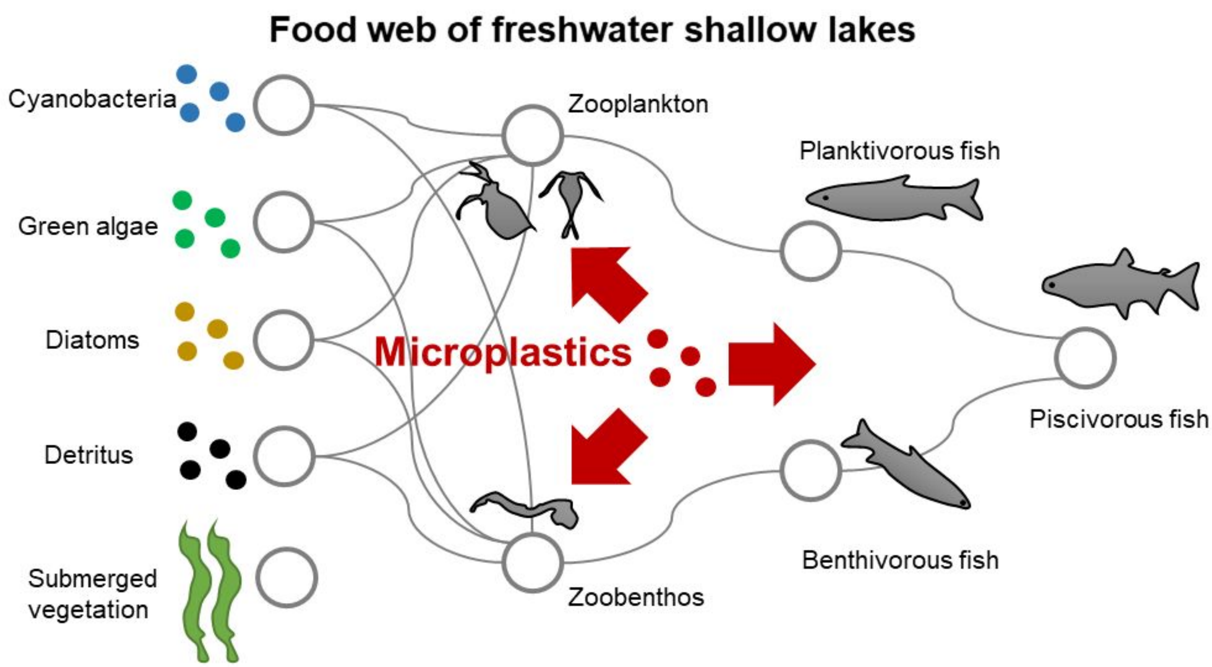

Abstract

The discovery of microplastic (MP) being present in freshwaters has stimulated research on the impacts of MP on freshwater organisms. To date, research has focused on primary effects, leaving questions with respect to secondary effects at the level of freshwater food webs, unanswered. Here, we use a theoretical modeling approach to investigate the hypothesis that MP impose negative impacts on the level of freshwater shallow lake food webs. We find that increasing MP levels have the potential to affect the critical phosphorus loading (CPL), which is defined as the threshold for regime shifts between clear and turbid states of the water column. The possible occurrence of catastrophic cascades due to MP pollution is predominantly driven by the negative effects of MP on zooplankton. We explore the possible states of the food web by scenario analysis and show that the secondary effects of MP at current concentrations are likely to be negligible. However, at the current rate of MP production, a 20 to 40% reduction in CPL would occur by the end of this century, suggesting a loss of resilience in shallow lakes that would be subject to abrupt changes in the food web under lower nutrient loading.

Introduction

Over the last decade, contamination of the aquatic environment with plastic debris has received increasing attention from the public, policymakers and the scientific community.[1] Defined as plastic particles of <5 mm in size,[2, 3] microplastic (MP) is of particular concern since they can be ingested more readily by biota than larger particles.[4] While the implications of MP traditionally have been emphasized for marine systems, the ubiquity of MP in inland freshwater systems such as rivers[5, 6] and lakes[7, 8] has been recognized recently.[9, 10] Studies that evaluate the impact of MP on freshwater organisms are accumulating rapidly,[10] and it has been demonstrated that multiple keystone freshwater organisms can ingest a broad range of sizes and types of MP.[11, 12] Furthermore, ecotoxicological risks of MP to organisms in freshwaters have been suggested,[13] risks that however, remain highly uncertain.[14]

Despite the increasing effort in evaluating biological effects of MP on single species of freshwater organisms, systematic assessments of MP on the level of freshwater ecosystems are scarce. Thus far, ecotoxicological studies of MP for freshwater organisms have been reported for a handful species at higher trophic levels (TL), for invertebrates such as zooplankton (e.g. *Daphnia magna*)[15, 16] and for benthic macroinvertebrates (e.g. *Gammarus pulex* and *Arenicola marina*).[17, 18] As for effects, one major mechanism has been argued to be general and thus crucial across species studied: the dilution of food quality due to the co-ingestion of inert MP together with regular food or prey.[19-22] Based on these limited dose-effect data, preliminary risk assessments for MP have been established using species sensitivity distribution (SSD) models.[13, 23] Nevertheless, increasing levels of MP pollution may not only exert pressure on the level of individuals or populations, but also impose cascading secondary effects on the functioning and services of other communities and ultimately the ecosystem as a whole. After all, ecosystems like those in freshwater shallow lakes are highly interlinked.[24] Hence, systematically assessing impacts of ecological stressors like MP on the ecosystem level is critical to inform risk assessment and management of freshwater ecosystems facing increasing levels of MP pollution.[3]

Shallow lakes are ecosystems that exhibit alternative stable states, i.e. a clear, macrophyte-dominated state, and a turbid, phytoplankton-dominated state.[25, 26] Important implications are that in shallow lakes, responses to eutrophication show nonlinear rather than linear patterns, so that these systems can suddenly shift from one state to another under gradually increasing external pressure.[26, 27] Crossing the threshold of a critical nutrient loading in the water column is generally considered as the dominant mechanism to trigger such abrupt shifts.[24, 28] Other external factors, such as hydrological disturbances[29-31] or climate change[32, 33], can aggravate the negative impact of excess nutrient loading in driving catastrophic shifts. It has also been suggested that toxic chemicals are likely to trigger such regime shifts.[34, 35] Given the potential impact of MP on keystone organisms in shallow lakes, this raises the question whether MP could exert secondary effects on such systems by deteriorating the resilience of shallow lake ecosystems, increasing the probability of abrupt changes, and thereby become another driver of catastrophic shifts in shallow lakes.

Analyzing the effects of MP on food webs comes with several challenges. First, there are no methods available to routinely detect MP concentrations with sufficient reliability in water or biota.[9, 36] Second, environmental MP concentrations are expected to increase, but the actual rate of increase is unclear. Third, experimental approaches are not capable to address regime shifts in lake ecosystems, because the complexity and realisms of such food webs cannot be captured in small-size laboratory or outdoor model ecosystems. Therefore, for the time being, the analysis of secondary MP stressor effects has to rely on prospective modeling. Modeling is the common approach when analyzing food web dynamics and interactions.[37-39]

Here, we provide the first assessment of the impact of MP on freshwater shallow lakes at the ecosystem level. Specific aims are to: 1) evaluate the sensitivity of the critical nutrient loading on the effects of MP, across different species; and 2) quantify the secondary effects of MP on the ecosystems due to food web interaction during pristine, current and business-as-usual future MP pollution scenarios. Given the urgency of the problem of MP and the limited data on effect mechanisms for freshwater organisms, we applied a theoretical mechanistic approach to explore hypotheses on the possible implications of MP on freshwater food webs. We hypothesize that food dilution by MPs alter the energy balance of organisms, decrease resilience towards eutrophication, lead to abrupt change in trophic status of shallow lakes, and overall impose negative impacts on the level of freshwater shallow lake food webs. Model-based scenario analyses were performed to illustrate alternative possibilities that might occur in reality. We used the well-established lake ecosystem model PCLake, which was developed in the context of alternative stable states theory,[24] with the primary goal to estimate critical nutrient loadings for shifts between clear and turbid states in temperate shallow non-stratifying lakes.[40, 41] The model accounts for a fully mixed water column and a sediment surface layer, holds a food web module and the biogeochemical cycles of carbon, nitrogen and phosphorus.[42] MP was implemented in the model as an inert material causing dilution of food, via a new parameter denoting the fraction of MP in food for each biota group in the model in a dose-effect manner. The present study did not address the implications of plastic-associated toxicants in food webs, which however was addressed elsewhere.[43]

Materials and methods

Trophic structure and biogeochemical processes in the PCLake model

The PCLake model[41, 42] comprises of a food web module for both water column and sediment with multiple functional groups (Fig. 1), including three phytoplankton groups (diatoms, greens and blue-green, in both water and sediment), submerged vegetation, zooplankton, zoobenthos, and planktivorous, benthivorous and piscivorous fish. Piscivorous fish predates on the other two fish groups; Benthivorous fish feeds on zoobenthos; Planktivorous fish feeds on zooplankton; Zoobenthos grazes on benthic phytoplankton and detritus without preference; Zooplankton feeds on pelagic phytoplankton and detritus with a preference (green algae>diatom>detritus> cyanobacteria). The food web structure and interactions represent a typical scheme of temperate shallow lakes with four trophic levels.[38] To operate with closed nutrient cycles, each biological component is modeled by three components, namely, dry weight as a surrogate for carbon, nitrogen and phosphorus. Biogeochemical processes, such as conversions of nutrients, detritus and inorganic matter in sediment and water, nutrient recycling from sediment due to diffusion and resuspension caused by processes such as wind shear stress, benthivorous fish disturbance and zoobenthos grazing, are accounted for. We used the original parameter set for PCLake described in literature[40-42] for the present study. The over 400 parameters in the model have been calibrated against field data from over 40 shallow lakes. For a full description of the PCLake model and its parameter set we refer to refs.[38, 41, 42]

Bifurcation analysis with PCLake model

The PCLake model was used to analyze effects of MP on the food web compositions, critical phosphorus loading (CPL) and water quality in shallow lakes via bifurcation analysis.

The model was set up to mimic a realistic default temperate shallow lake,[40, 44] which has a mean depth of 2 m, a hydraulic loading of 20 mm·d^{-1}, a fetch of 1,000 m, barely wetland zone (area fraction = 0.001), and a slightly clayish sediment (30% of dry matter, which contains 10% of organic and 90% of inorganic matter, and 10% of the inorganic matter is clay particles). Following Kuiper et al.[45], nitrogen (N) loading was set at 10 times the phosphorus (P) loading in order to maintain P limitation of primary production. System behavior was simulated for a range of different P loadings (0.1-4.0 mg P·m^{-2}·d^{-1}) with 40 or 400 steps in between, each run for 20 years. The average values during summer time (180 to 270 Julian day) in the final year of simulation were used as the steady state for modeled abundances of biota. An example of bifurcation analysis is provided in the Supporting Information.

Quantifying the effect of microplastic on shallow lake food webs

The effect of MP on the shallow lake food web was assumed to occur via species-specific deterioration of food quality due to dilution of food.[19-22] This dilution was made MP dose dependent via:

$$kDAssGroup = kDAssGroup_{default} \cdot \frac{C_{Food}}{C_{Food} + C_{MP}} \qquad \text{(eq. 1)}$$

where *kDAssGroup* (d^{-1}) is the assimilation rate of the functional group "-*Group*", which is defined as follows: "-*Bent*" for zoobenthos, "-*FiJv*" for planktivorous fish, "-*FiAd*" for benthivorous fish, and "-*Pisc*" for piscivorous fish. $kDAssGroup_{default}$ (d^{-1}) is the default value of the assimilation rate specific for "-*Group*". C_{Food} and C_{MP} (particles·L^{-1}) are the concentrations of the food for the corresponding organism and that of MP in the water column, respectively. Note that for zooplankton, the corresponding parameter in PCLake is *cFiltMax* (d^{-1}):

$$cFiltMax = cFiltMax_{default} \cdot \frac{C_{Food}}{C_{Food} + C_{MP}} \quad \text{(eq. 2)}$$

where $cFiltMax_{default}$ (d^{-1}) is the default value of assimilation rate for zooplankton.

Eq. 1 and 2 quantify how the presence of MP negatively affects the assimilation or the filtration of natural food. They are considered adequate because it is widely accepted in the literature that the mechanism of reduced food quality due to "dilution" of food by low-caloric MP is generic,[46] e.g. for benthic organisms[17, 21, 22] and fish[47, 48]. Suspended and bottom solids themselves (detritus) do not pose food dilution to any modeled group. This is because detritus is modeled as a food resource for zooplankton and zoobenthos, which subsequently has indirect effects on fish groups. The contribution of detritus ingestion for fish groups is assumed minor compared to food consumption in the form of feeding on biota (Fig. 1), which is a valid approach because fish actively search for prey rather than for non-preferred particles as a food source.

The PCLake default values for the parameters are 4.5 for zooplankton ($cFiltMax_{default}$), and 0.1, 0.12, 0.06, 0.025 ($kDAssGroup_{default}$) for zoobenthos, planktivorous fish, benthivorous fish and piscivorous fish, respectively. PCLake thus uses a decreasing assimilation rate of the organisms with increasing trophic level.[42] In the simulations, we modeled the MP dose as a ratio between MP and food abundancy (*rMPF*) as:

$$rMPF = C_{MP}/C_{Food} \quad \text{(eq. 3)}$$

Sensitivity of the effect of microplastic to the critical phosphorous loading across species

We hypothesize that effects of MP on individual species in the food web will affect the CPL, and that this effect will vary across species because: a) species differ in their sensitivity to MP, and b) species occupy a different position in the food web. Therefore, to mimic the potential effects of MP on the CPL of shallow lake ecosystems, first a sensitivity analysis on the mass assimilation rate of species was performed. We designed a range of MP levels in the water column by assigning values of 10^{-3}, 10^{-2}, 10^{-1}, 10^{0}, 10^{1}, 10^{2} and 10^{3} to *rMPF*. For instance, a value for *rMPF* of 10^{-2} means that 1% of the ingested material constitutes MP. By substituting eq. 3 to eq. 1 (or eq. 2), we calculated the corresponding parameter value of *kDAssGroup* (or *cFiltMax* for zooplankton). Subsequently, we performed bifurcation analyses for CPL during eutrophication and oligotrophication for each species (five groups) independently under each value of *rMPF* (seven levels). The sensitivity analysis thus is based on 35 bifurcation analyses.

Relevant scenarios and uncertainty

We further designed three scenarios I (pristine), II (current) and III (business-as-usual) to estimate the potential impact of MP pollution on shallow lake ecosystems (Table 1). We modeled the food dilution by MP as the ingestion of MP by organisms would decrease nutritional value of the food.[15] However, the food dilution effect does not apply to the three algae groups, which after all do not ingest MP.[23] We therefore focused on the food dilution on the other five organism groups.

As for exposure, a case study in the Netherlands showed that MP concentrations (>0.45 μm) in freshwater could range from <5 to 40 particles$\cdot L^{-1}$,[49] while a recent meta-analysis of global data suggested approximately 3 particles$\cdot L^{-1}$ in lakes worldwide on average.[9] Another recent global survey revealed that most measurements on MP in freshwaters were between 10^{-5}-10 particles$\cdot L^{-1}$ excluding several extremes.[13] In the present study, we used the highest reported concentration of 40 particles$\cdot L^{-1}$ as a worst case for MP concentrations in freshwater (current scenario). Furthermore, a recent modeling study suggested that, compared to 2015, MP concentrations in coastal and marine areas would increase by approximately two orders of magnitude by the year 2100, based on the current growth of plastic production (4.5% $year^{-1}$),[50] implying an eventual MP concentration of $4×10^3$ particles·L^{-1} as a worst case under the business-as-usual scenario. For comparison, in typical eutrophic shallow lakes in a turbid state, phytoplankton densities can be up to 10^7 cells·L^{-1}.[51] Successful oligotrophication and restoration of shallow lakes can reduce the density of phytoplankton by approximately three orders of magnitude,[52] which would imply a density of 10^4 cells·L^{-1} in a typical clear shallow lake. Given that the size of algal cells (cyanobacteria: 0.5-60 μm[53]; green algae: highly variable, typical value 4-10 μm for *Chlorella vulgaris* in freshwaters[54]; diatom: 2-200 μm[55]) is similar to that of small-sized MP (>0.45 μm), MP and phytoplankton can be assumed to have the same chance to be ingested by consumers such as zooplankton or zoobenthos, resulting in *rMPF* values of $4×10^{-3}$ and 0.4 for scenario II and III, respectively (Table 1). For other groups, we estimated the *rMPF* between different trophic levels using the parameterization of the MICROWEB model provided by Diepens and Koelmans [43], which is fully parameterized based on empirical data. They estimated that in typical aquatic food webs, if MPs account for 5% of the food (equal to a *rMPF* = 5/(100-5) = 0.053) for organisms at TL=2 (zooplankton and zoobenthos), the fraction of MPs in the total biomass of these organisms would be $3.5×10^{-4}$ (approximately two orders of magnitude lower than 0.053), based on typical values of grazing rate and gut retention time. Because in PCLake, zooplankton and zoobenthos are the only food sources for planktivorous fish and benthivorous fish (TL=3), respectively, we estimated that *rMPF* of planktivorous and benthivorous fish would be two orders of magnitude lower than those of zooplankton and zoobenthos. Likewise, MP fraction in the biomass of planktivorous fish or benthivorous fish is estimated as 0.02, which is approximately 40% of 0.053. As a result, *rMPF* for species at TL=4 (piscivorous fish) predating on planktivorous and benthivorous fish can be determined. These scaling factors across trophic levels allow the design of scenarios described in Table 1. Overall, we assigned *rMPF* values for the five different groups in three scenarios and assumed a normal distribution and a coefficient of variation (CV) of 20% for each *rMPF*. A normal distribution is a typical assumption for composite parameters representing ratios in environmental models,[56] and a CV of 20% is a reasonable estimation on the uncertainty for weakly informative parameters[57] such as *rMPF*. A Monte Carlo simulation was performed with values for *rMPF* randomly sampled for 1,000 times. CPL during eutrophication (CPL_{eu}) and oligotrophication (CPL_{olig}) were assessed as a function of MP pollution for the three scenarios.

All modeling analysis was conducted in Matlab.[58] R program[59] were used for the graphs generation with packages "gplot"[60] and "ggplot2"[61].

Results and discussion

Effects of microplastic on the critical phosphorous loading (CPL) in shallow lakes

We explore the sensitivity of CPL of the lake ecosystem to the impacts of MP ingestion by each of the species, one at a time. Modeling results demonstrate that MP-induced dilution of food can have a profound effect on CPL of shallow lake ecosystems (Fig. 2). For example, for zooplankton, the lower *rMPF* values i.e. up to 10% of MP in food (10^{-3}, 10^{-2} and 10^{-1}) already show a substantial decrease of CPL. Further food dilution by increasing the MP fraction in the food (*rMPF*=10^1,10^2 and 10^3) leads to ultimately four times lower CPL values. Therefore, ecological implications of MP are expected to be triggered especially by the responses of zooplankton, which lead to further interactions in the food web eventually leading to a critical transition. Contrasting results are obtained for benthivorous fish, planktivorous fish and zoobenthos. Food dilution to piscivorous fish by MP ingestion has negligible effects on CPL along the entire gradient of *rMPF*. We explain the patterns for each species in detail below.

We thus find that MP can affect CPL in shallow lakes by restraining the growth of organisms and perturbing the functioning of the whole food web. An example is provided for the effect of food dilution to zooplankton by MP on different groups of organisms (Fig. 3). We show the total abundance of different groups of organisms as a function of P loading and intensity of food dilution to zooplankton by MP (denoted by *rMPF*) at ecological equilibria modeled by PCLake. For instance, the model simulates how zooplankton biomass responds to changing P loading (increasing from 0.1 to 4.0 mg $P \cdot m^{-2} \cdot d^{-1}$ and then returns to 0.1 mg $P \cdot m^{-2} \cdot d^{-1}$) and shifts at the CPL, when zooplankton itself is affected by MP with an *rMPF* value of 10^{-3} (first column of zooplankton panel in Fig. 3). Then, more model simulations can be performed by changing the *rMPF* value of zooplankton across a range of 10^{-3}-10^{3}, which provides the whole subpanel. Likewise, simulation results are depicted for other groups of organisms, which results in eight subpanels. This leads to the outcomes, for instance, that high MP levels cause a decreased abundance of zooplankton, resulting in above average diatom biomass. This explains the yellow panels on the right side of the subpanel for diatom in Fig. 3.

Other results for different target groups of food dilution by MP, including zoobenthos, planktivorous fish, benthivorous fish and piscivorous fish, are provided as Supporting Information (Fig. S2). Reduced assimilation rates due to ingestion of MP result in reduced population density of the corresponding organisms, which are in general more profound when *rMPF* exceeds 1 (10^{0}). The perturbed population of this corresponding organism subsequently affects populations of other organisms via trophic interactions, which are discussed below.

For zooplankton, decreased population density due to increasing MP alleviates the grazing pressure on phytoplankton, particularly on diatoms and green algae, which leads to increased population sizes of both groups (Fig. 3). The absence of zooplankton will in turn reduce the resilience of the shallow lake as indicated by the decreased CPL. In addition, planktivorous fish fed on zooplankton will be largely restrained in response to the loss of zooplankton, which in turn will limit the population of piscivorous fish. Benthivorous fish starts to dominate in the fish community, reducing zoobenthos abundance by predation. This results in stronger perturbation on the sediment and higher water turbidity due to resuspension, which is not favored by macrophytes and not ideal for lake restoration.

We found increasing CPL with increasing *rMPF* values for zoobenthos, which is attributed to their influences on the water quality due to water-sediment interaction. Decreasing zoobenthos biomass due to MP ingestion reduces the population density of their predator (benthivorous fish; Fig. S2), which in turn would largely reduce sediment disturbance. As a result, water turbidity is decreased, which favors the growth of macrophytes. This is the main mechanism for the higher CPL under increasing plastic ingestion by zoobenthos. Similar results are obtained for food dilution of benthivorous fish (except for increased zoobenthos density due to lower predation), for which the same mechanism applies. Furthermore, the loss of zoobenthos causes a higher release of nutrients into the sediment, which are readily available for macrophytes. However, without zoobenthos, cyanobacteria dominate the phytoplankton community with much higher biomass after the lake is tipped into a turbid state. A lower density of benthivorous fish also reduces the density of piscivorous fish, which alleviates predation pressure on planktivorous fish due to apparent competition,[62] but enhances grazing on zooplankton due to trophic cascading.[63] Overall, zoobenthos tends to indirectly influence the water quality in shallow lakes. Note that in the PCLake model, zoobenthos grazes on benthic algae that originate from the sedimentation of pelagic algae, while certain zoobenthos species may directly filter the pelagic water.[64] In this case, loss of zoobenthos may presumably have a higher impact on the CPL and water quality, the outcomes of which remain unclear and need further investigation.

For planktivorous fish, the declined density due to MP ingestion results in an increasing CPL, leaping when *rMPF* equals 10^0, i.e. half of their food is replaced by MP. A low density of planktivorous fish stimulates the growth of zooplankton (Fig. S2), which in turn imposes a high grazing pressure on phytoplankton and increases the CPL for oligotrophication. Note that no critical transition is predicted at a P loading between 0.1 and 4 mg $P \cdot m^{-2} \cdot d^{-1}$ when *rMPF* reaches 10^1,10^2 or 10^3 (Fig. 2). In these cases, high zooplankton densities due to limited predation from planktivorous fish prohibit the growth of phytoplankton. Therefore, the turbid state with phytoplankton dominance does not exist and the lake remains in a clear state irrespective of the P loading. Meanwhile, the clear lake state also facilitates the growth of macrophytes, which in turn enhances the densities of zoobenthos and piscivorous fish by multiple feedback mechanisms.[25]

A lower population size for piscivorous fish due to MP ingestion has little effect on CPL, whereas the density of cyanobacteria increases after the lake shifts to a turbid state (Fig. S2). Less piscivorous fish reduces the predation pressure on the other two fish groups, both of which end up in higher densities. This results in reduced zoobenthos and zooplankton abundance, which in turn leads to an increased cyanobacteria density, demonstrating a typical trophic cascade.[63] Remarkably, trophic cascading does not have an influence on CPL. This finding is in line with an earlier study, in which biomanipulation by fish removal was advocated as a “shock therapy” for shallow lake restoration rather than manipulating the CPL.[25]

Overall, we demonstrate how prospective food web modeling reveals via which mechanisms MP may influence freshwater shallow lake ecosystems. For the first time, we show theoretically to what extent MP induced changes in CPL, which depends on the ecological role of the affected species in the food web. The sensitivity analysis reveals that the loss of resilience due to MP pollution in the shallow lake ecosystem will be caused predominantly by the negative effects of MP on zooplankton. Therefore, priority for ecotoxicological assessment of zooplankton is recommended. In the aforementioned simulations, effects of MP were assessed for species one at a time. However, MP in water dilutes the food for all organisms simultaneously, either directly by ingestion MP or indirectly by consumption of food containing MP. Therefore, below such environmentally realistic scenarios are analyzed.

Scenario studies for current foodwebs with MP levels compared to those for pristine and future MP levels

Scenario analysis suggests that in the condition without MP pollution (pristine scenario), CPL for the default shallow lake would be 2.11 and 1.21 mg $P \cdot m^{-2} \cdot d^{-1}$ for eutrophication (CPL_{eu}) and oligotrophication (CPL_{olig}), respectively (Fig. 4A). Monte Carlo simulations show that lakes with realistic current levels of MPs (current scenario) have CPL_{eu} of 2.08±0.044 mg $P \cdot m^{-2} \cdot d^{-1}$ and CPL_{olig} of 1.20±0.046 mg $P \cdot m^{-2} \cdot d^{-1}$. Although the difference in the value is only marginal, we found that the difference between CPL_{eu} for current and pristine conditions is statistically significant (one-sample t-test, $p<0.05$), and the same applies to CPL_{olig}. In addition, with MP levels that are expected by the end of this century (business-as-usual scenario), both CPL_{eu} (1.62±0.137 mg $P \cdot m^{-2} \cdot d^{-1}$) and CPL_{olig} (0.73±0.155 mg $P \cdot m^{-2} \cdot d^{-1}$) will be substantially lower than those in pristine (one-sample t-test, $p<0.01$) and current conditions (two-sample t-test,

p<0.01) (Fig. 4B). Our results imply that the current levels of MP pollution are not expected to cause an effect on the CPL, whereas, approximately 20-40% reduction in CPL may occur by the end of the century if MP leakage to the environment continues at the current rate.

Our results highlight the potential ecosystem-level effects of MP pollution in shallow lakes due to MP ingestions by organisms and subsequent nutritional dilution. As a result, resilience of the ecosystems is likely to decline, because freshwater lakes would suffer from a critical transition towards an unwanted turbid state already under lower nutrient loading. In addition, restoration of the lake back to its clear state will be more difficult, because the low CPL_{olig} implies more effort of nutrient loading reduction. Furthermore, by modifying CPL, MP pollution may indirectly trigger a regime shift to turbid state in a clear shallow lake (e.g. from S_1 to S_2, Fig. 4C).

The modeling results are subject to several sources of uncertainty in the estimation of *rMPF*. First, uncertainty in the exposure level of MP is large, depending on factors such as location and sampling methods.[13, 23] In the present study, the highest observed concentration was applied representing a "worst case", whereas actual exposure levels will be highly variable. Second, the estimation of 4.5% year^{-1} increase in MP emission[50] and the projection of *rMPF* by the end of this century for the business-as-usual scenario are also uncertain. Nevertheless, it may be plausible that the increasing MP concentration will ultimately reduce the CPL and dampen the resilience of the lake ecosystem, the exact timing of which depends on the rate of increase. Third, discrepancies exist in the biological effects of MP on different organisms. Recent studies report contradicting results on survival and reproduction of zooplankton when they are exposed to MP,[16, 65-68] which may also be linked to other factors such as the MP size and biofouling. In addition, it is also difficult to accurately estimate *rMPF* for all organism groups at certain MP levels. Fourth, our estimation is based on a functional relation between assimilation rate and *rMPF*, which is a fair assumption but still a simplification of reality. More complicated and non-proportional relations may exist. Finally, our uncertainty analysis assumed a normal distribution with a constant CV (20%) for *rMPF* of all organisms. This assumption may be refined when more experimental and field data become available.

Merits and limitations of modeling the effects of microplastic on shallow lake food webs with PCLake

Our modelling results rely on the analysis of a well-evaluated lake ecosystem model (PCLake) and on an additional and validated model component, which quantifies how MP affects assimilation of organisms. The PCLake model is designed for shallow lakes ecosystems. It has been applied to many lakes worldwide and has been validated against field observations in either short- (1-6 years)[69-71] or long-term (20-60 years) time spans.[30, 72, 73] Furthermore, PCLake has been applied to other endpoints, e.g. long-term dynamics of organic contaminants in shallow lakes.[74] The model has shown its ability to provide valid management advices and future prognoses[70, 75], as well as reasonable hypotheses for shallow lakes.[40, 41] This evidence from the literature demonstrates that PCLake in itself is well-evaluated and generally accepted. The equation quantifying how MP affects assimilation of organisms fully complies to the current knowledge about the widely accepted physical effect of MP on the food quality of aquatic organisms, i.e. the “food dilution effect”.[20-22] Consequently, serving as a “virtual mesocosm”, our theoretical modeling approach is powerful in providing and exploring mechanism-based hypotheses regarding the future behavior of natural systems, which is not possible by experimental approaches. Following the view of Epstein[76], the scenarios constitute an example of "good use of modeling" that is consistent with thoughts and philosophies for why we are modeling nature.

Our model simulations for the current scenario can be regarded to be in agreement with field observations, which adds at least some credibility to the "business-as-usual" scenario concerning the future. After all, it has been widely accepted that the present levels of MP in the freshwater environment are too low to cause adverse effects on the population level.[13, 23, 77, 78] Studies show that in the future, MP levels are likely to increase and that critical effect thresholds are likely to be exceeded.[50, 77, 79] However, our model results that relate to this future scenario cannot yet be quantitatively compared with these future observations. Furthermore, field observations addressing how the anticipated increasing MP levels affect ecosystem resilience do not exist. Therefore, for the time being, forecasts of the effects of MP on the level of food webs have to rely on theoretical modeling.

We add some further disclaimers with respect to the modeling results. First, even though PCLake can be "validated" by current observations, the model cannot be "verified", which is in principle not resolvable. Here we follow definitions for "validated" and "verified" models by Oreskes et al. [80] A "validated" model suggests that the model predictions are consistent with observational data, and the model is "internally consistent" but "not necessarily denote an establishment of truth".[80] On the other hand, a "verified" model means that the model can reflect all the truth so that it is reliable for decision-making.[80] This is not possible for an open model system like PCLake because the parameter values are conditional and therefore not fully known. Many parameters in PCLake are obtained from the literature representing an averaged level.[41] Our results reflect the generic effect of MP on a theoretical shallow lake rather than any specific lake. Second, the model scenarios presented in this study are not predictions, but rather illustrations of alternative possibilities that might occur in a real system. We elaborate to explore and generate hypotheses regarding MP effects at the ecosystem level that are open for discussion and criticism. Cautions are needed with respect to decision-making based on the implications suggested by the scenario analyses provided. This, however, is not necessarily a limitation, but rather a feature of such theoretical modeling approaches. Third, there may be mechanisms unaccounted for by the current model. For instance, mechanisms that compensate for MP dilution on food resources for the organisms may exist, such as the adaptive feeding strategy of zooplankton due to MP ingestion. Thus far, we do not know if such speculated selectivity by zooplankton would occur, to what extent it would occur, and how to parameterize it in modeling. In addition, the continuous prevalence of P limitation could indirectly lead to changes in algal assemblages and to an overall food quality improvement for zooplankton. Therefore, the results from the scenario analysis reflect the case when no confounding effects of ecological changes (e.g. animal adaptation) to alleviate the impact are considered. Note that, alternatively, there might be yet unknown processes that could strengthen the effects simulated here. New knowledge on relevant mechanisms needs to be included in the next generation of environmental modeling[81] when new and better information is available. Finally, PCLake assumes that the modeled lake is well mixed horizontally and vertically. Spatial heterogeneity is not accounted for, which however may affect the patterns of CPL, especially in large lakes that are subject to complex hydrological configurations and morphological characteristics.[71] Such limitations in our modeling approach could be resolved by more sophisticated methods such as spatially explicit models[82] and advanced analytic tools,[83] but also may require far more data for model validation.

Implications and perspectives

Our results suggest that, theoretically, MP pollution in shallow lakes can cause effects on the ecosystem level (represented by CPL) beyond impairments on individual species. Present MP concentrations in freshwater shallow lakes do not seem to pose high ecological risks; however, a decrease in resilience of lake food webs upon eutrophication constitutes a plausible hypothesis for the future of shallow lake ecosystems under increasing MP pollution stress. This confers to recently proposed opinions towards MP as an emerging contaminant[9, 14, 23, 77]. Based on model simulations, we hypothesize that by the end of the century, MP concentrations may have reached a level that potentially induce catastrophic shifts in freshwater shallow lakes upon eutrophication.

Our study also has implications for management. It illustrates that we need modeling tools for systems analysis, i.e. supported by models in order to evaluate the risks from MPs and other stressors, because a slow and gradual impairment to individual organisms in shallow lakes due to ingestion of MP may eventually lead to collapse of the whole system. We offer a tool (PCLake parameterized for MP) that is capable of evaluating the effects of MP on shallow lakes, which links the biological effects of MP on freshwater organisms (food dilution) to abiotic environment components including nutrient thresholds that are of high concern for management. Other potential effects of MP, such as physical effects (i.e. shading),[23] have not been evaluated yet but could be relevant and further investigated for the secondary effects of MP on freshwater shallow lakes.

Acknowledgments

We thank Marten Scheffer from Wageningen University for valuable suggestions when the idea of the present study was initially conceived. We thank the editor and three anonymous reviewers who provided constructive comments and suggestions to improve the manuscript. X. Kong is supported by a postdoctoral fellowship from the Alexander von Humboldt Foundation in Germany.

Associated Content

Supporting Information includes: SI Text for an example of bifurcation analysis with PCLake; SI Figures S1-S2.

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Table 1. Scenarios design for PCLake model analysis. The values outside the brackets are assigned for *rMPF* and the values in the brackets correspond to the coefficient of variation (CV).

	Scenario I	**Scenario II**	**Scenario III**
Organism groups	**PRISTINE (No MP)**	**CURRENT**	**Business-as-usual**
zooplankton	0.0 (0%)	4.0×10^{-3} (20%)	4.0×10^{-1} (20%)
zoobenthos	0.0 (0%)	4.0×10^{-3} (20%)	4.0×10^{-1} (20%)
planktivorous fish	0.0 (0%)	4.0×10^{-5} (20%)	4.0×10^{-3} (20%)
benthivorous fish	0.0 (0%)	4.0×10^{-5} (20%)	4.0×10^{-3} (20%)
piscivorous fish	0.0 (0%)	1.6×10^{-3} (20%)	1.6×10^{-1} (20%)

Note: MP concentrations in water (particles$\cdot$$L^{-1}$): 0 (Scenario I), 40 (Scenario II), 4,000 (Scenario III).

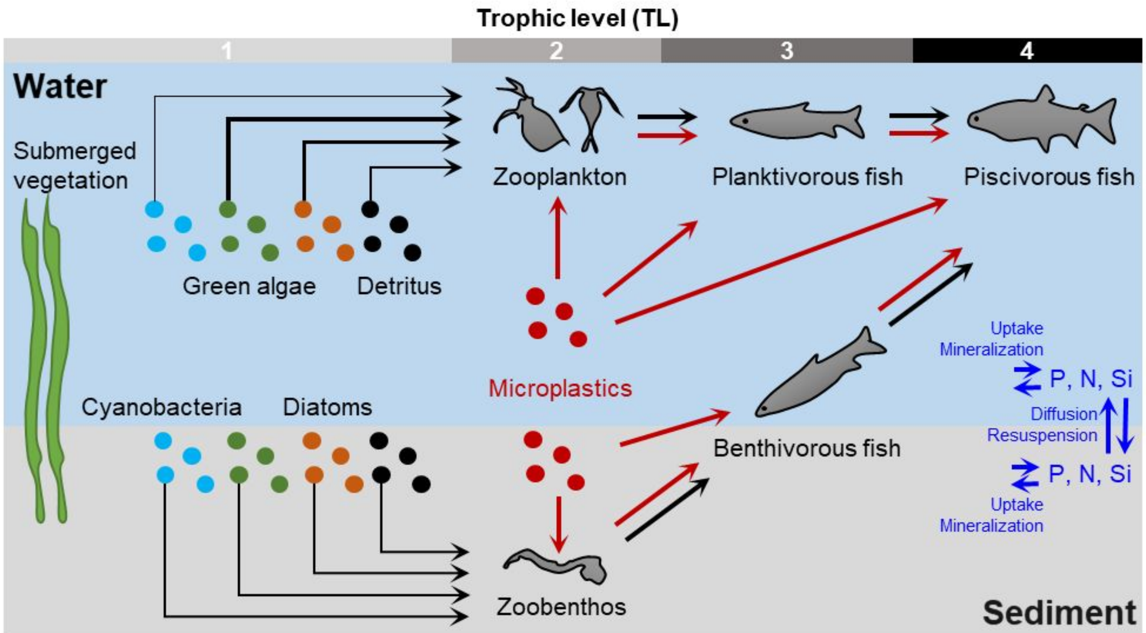

Figure 1. Schematic representation of the nutrient cycling, aquatic food web structure and trophic interactions in the PCLake model modified from Kuiper et al.[38]. The model represents temperate freshwater shallow lake ecosystems comprising a pelagic and benthic food chain linked by a shared top predator. Zooplankton feeds on pelagic phytoplankton and detritus with a preference ranked green algae>diatom>detritus>cyanobacteria, while for zoobenthos no preference is defined. Biogeochemical processes of nutrients (P, N and Si) are explicitly modeled including exchange between water and sediment, affected by e.g. benthic grazing. As a newly added component in the present study, microplastic is ingested by zooplankton, zoobenthos and three fish groups, and transferred between trophic levels by fish predations in the model.

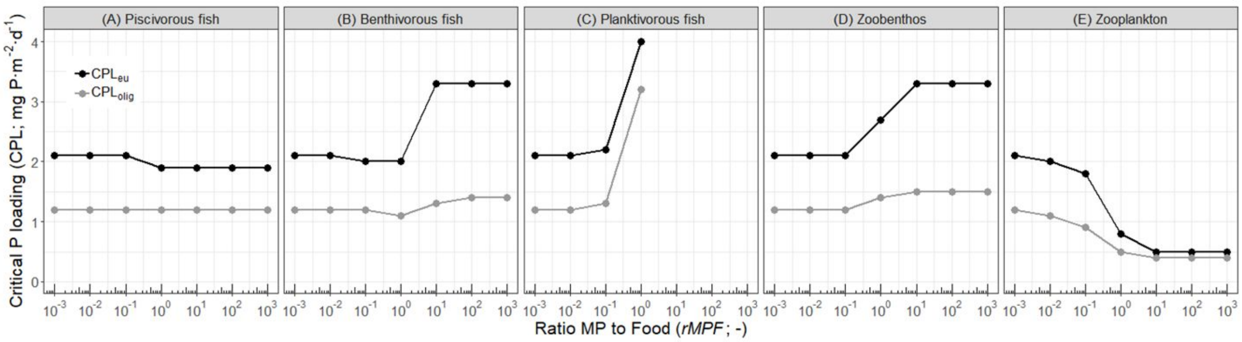

Figure 2. Sensitivity analysis of the critical phosphorous loading (CPL) to MP effects across species. CPL values for a shallow lake between clear and turbid ecological states during eutrophication (CPL_{eu}) and oligotrophication (CPL_{olig}) are given as a function of plastic content of food ingested by (A) piscivorous fish; (B) benthivorous fish; (C) planktivorous fish; (D) zoobenthos; and (E) zooplankton. Note that the same ratio MP to food (*rMPF*) in each group does not indicate the same MP concentration because food density for each group is different.

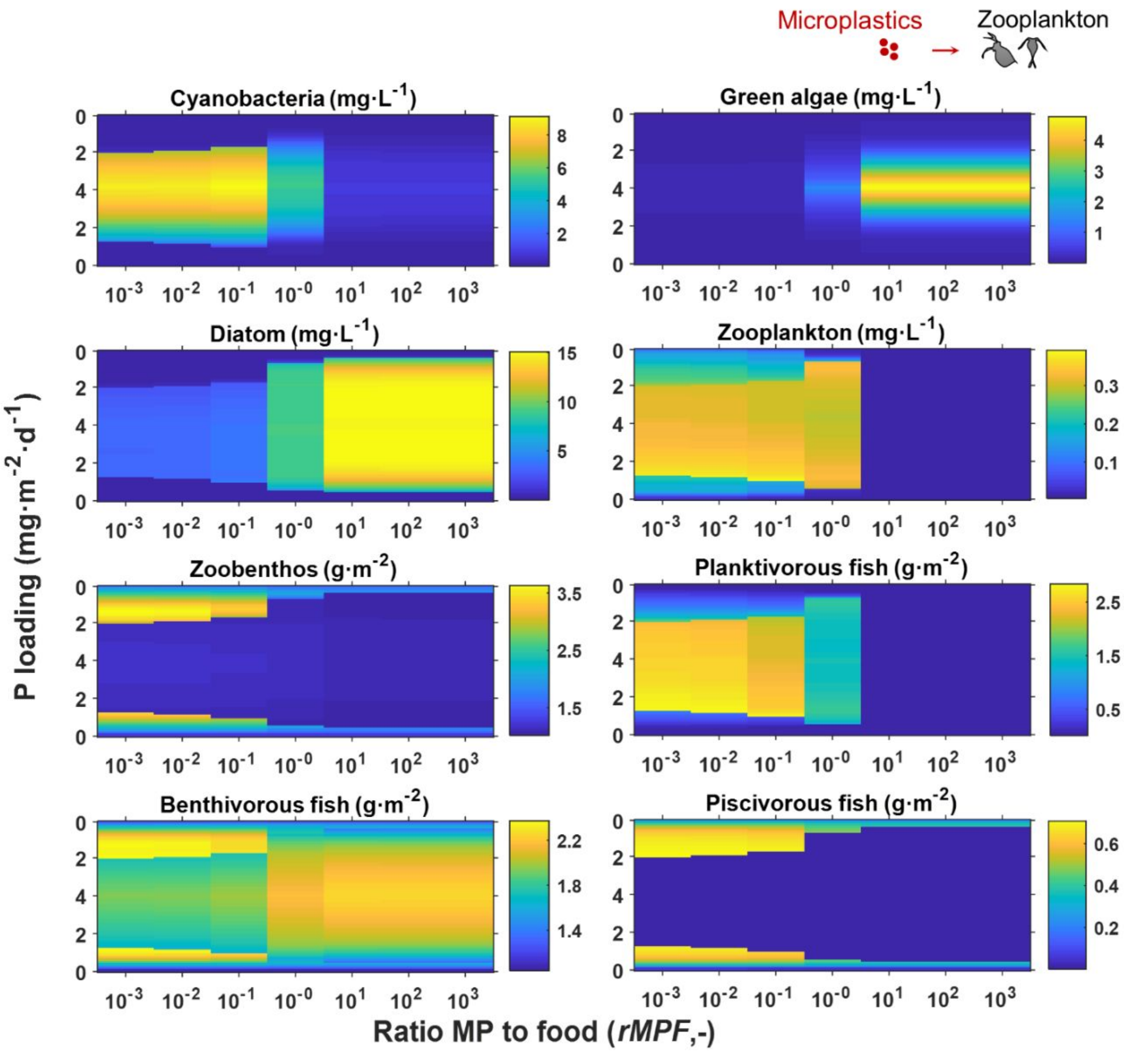

Figure 3. Steady state biomass of eight functional groups as a function of P loading and zooplankton MP-to-food mass ratio (*rMPF*). The panels summarize secondary effects on the biomass of eight different groups of biota, as a result of a primary effect on zooplankton biomass upon MP ingestion. Biomass is indicated by color according to the legend at the right hand side of each panel. P loading (y-axis) follows a sequential eutrophication-oligotrophication scenario from top to bottom, represented by values first increasing from 0.1 to 4.0 and then decreasing again from 4.0 to 0.1 mg P·m^{-2}·d^{-1}. The figure for instance shows that high MP levels cause a decreased abundance of zooplankton, resulting in above average diatom biomass. This is indicated with the yellow color at the right hand side of the diatom subpanel.

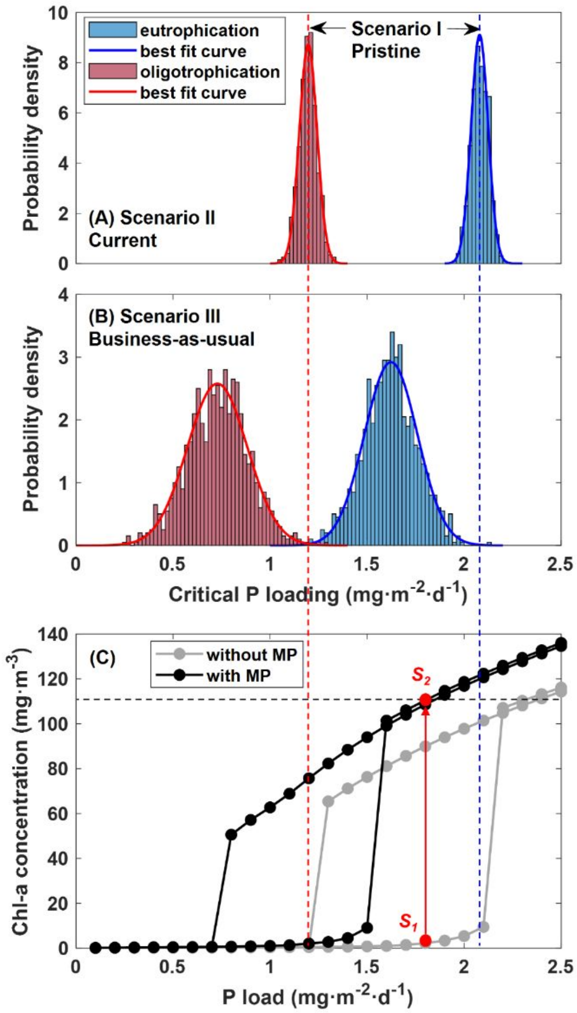

Figure 4. Scenarios analysis for critical phosphorus loading (CPL) with different MP pollution levels and the associated uncertainty. (A) Scenario II (current) with MP pollution at current status as the worst case; (B) Scenario III (business-as-usual) with MP pollution by the end of this century under current production rate; (C) An illustrative example of CPL with and without MP pollution, derived from scenario I and scenario III; Due to MP, a shallow lake in the clear state receiving a P load above ~1.5 mg $P{\cdot}m^{-2}{\cdot}d^{-1}$ (e.g. S_1) could be tipped into the turbid state (S_2) with a summer averaged Chl-a concentration over 100 $mg{\cdot}m^{-3}$. The vertical blue and red dashed lines represent CPL_{eu} and CPL_{olig} in scenario I without MP pollution as the pristine condition, respectively.

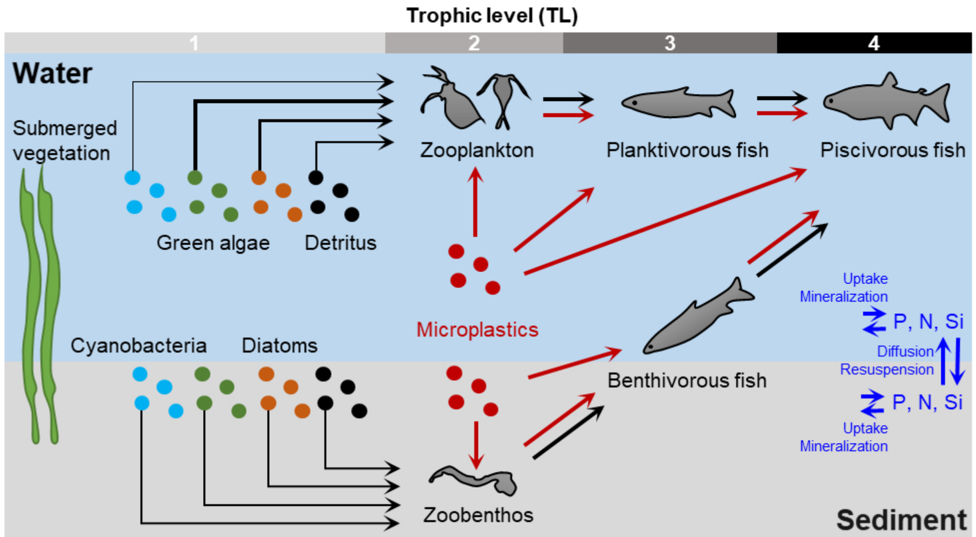

Figure 1. Schematic representation of the nutrient cycling, aquatic food web structure and trophic interactions in the PCLake model modified from Kuiper et al.[38]. The model represents temperate freshwater shallow lake ecosystems comprising a pelagic and benthic food chain linked by a shared top predator. Zooplankton feeds on pelagic phytoplankton and detritus with a preference ranked green algae>diatom>detritus>cyanobacteria, while for zoobenthos no preference is defined. Biogeochemical processes of nutrients (P, N and Si) are explicitly modeled including exchange between water and sediment, affected by e.g. benthic grazing. As a newly added component in the present study, microplastic is ingested by zooplankton, zoobenthos and three fish groups, and transferred between trophic levels by fish predations in the model.

84x47mm (300 x 300 DPI)

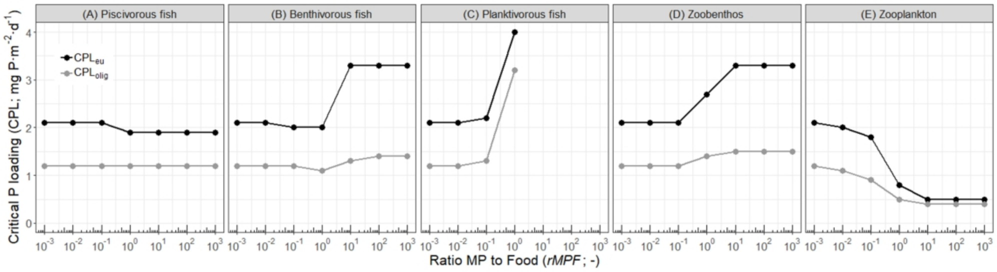

Figure 2. Sensitivity analysis of the critical phosphorous loading (CPL) to MP effects across species. CPL values for a shallow lake between clear and turbid ecological states during eutrophication (CPL_{eu}) and oligotrophication (CPL_{olig}) are given as a function of plastic content of food ingested by (A) piscivorous fish; (B) benthivorous fish; (C) planktivorous fish; (D) zoobenthos; and (E) zooplankton. Note that the same ratio MP to food (*rMPF*) in each group does not indicate the same MP concentration because food density for each group is different.

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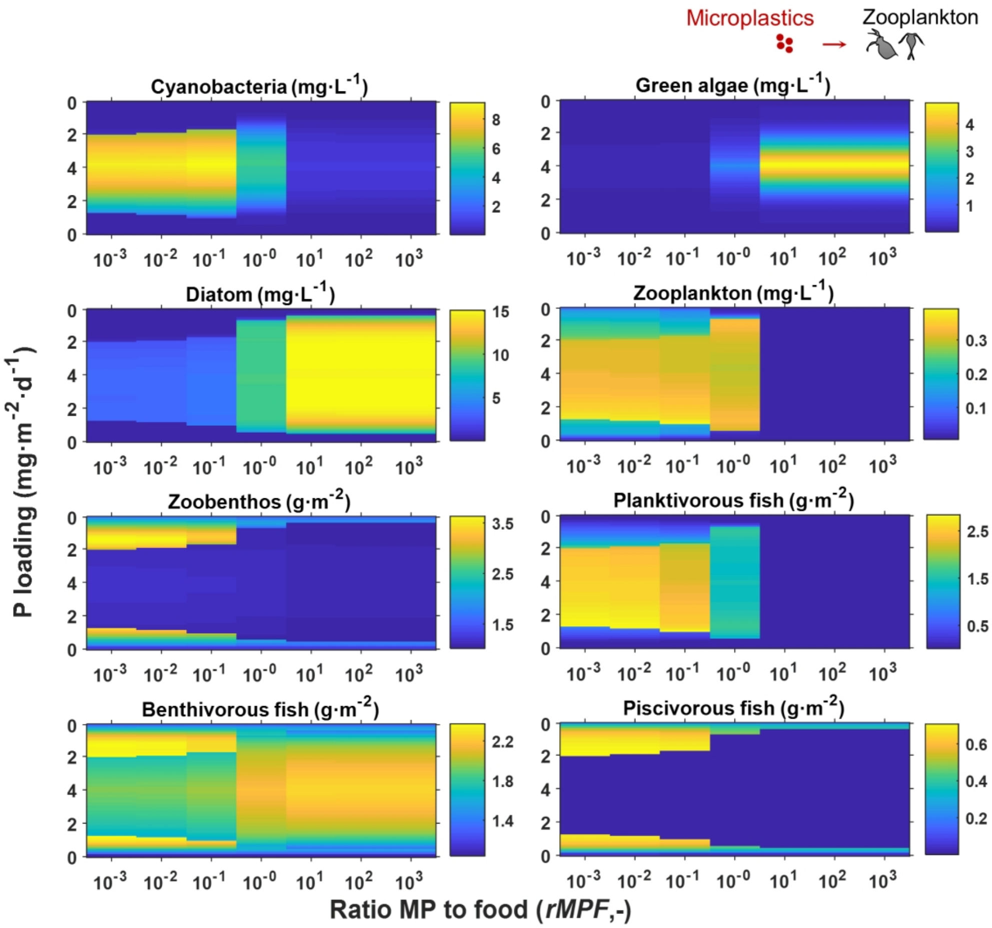

Figure 3. Steady state biomass of eight functional groups as a function of P loading and zooplankton MP-to-food mass ratio (*rMPF*). The panels summarize secondary effects on the biomass of eight different groups of biota, as a result of a primary effect on zooplankton biomass upon MP ingestion. Biomass is indicated by color according to the legend at the right hand side of each panel. P loading (y-axis) follows a sequential eutrophication-oligotrophication scenario from top to bottom, represented by values first increasing from 0.1 to 4.0 and then decreasing again from 4.0 to 0.1 mg P·m^{-2}·d^{-1}. The figure for instance shows that high MP levels cause a decreased abundance of zooplankton, resulting in above average diatom biomass. This is indicated with the yellow color at the right hand side of the diatom subpanel.

175x163mm (300 x 300 DPI)

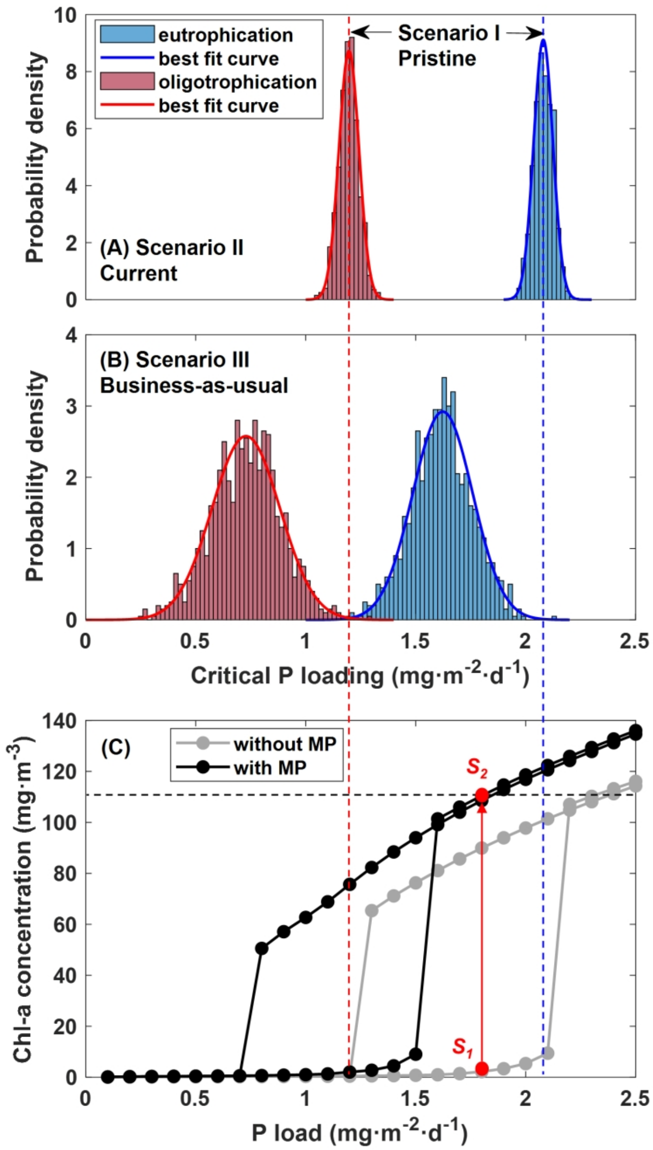

Figure 4. Scenarios analysis for critical phosphorus loading (CPL) with different MP pollution levels and the associated uncertainty. (A) Scenario II (current) with MP pollution at current status as the worst case; (B) Scenario III (business-as-usual) with MP pollution by the end of this century under current production rate; (C) An illustrative example of CPL with and without MP pollution, derived from scenario I and scenario III; Due to MP, a shallow lake in the clear state receiving a P load above ~1.5 mg $P{\cdot}m^{-2}{\cdot}d^{-1}$ (e.g. S_1) could be tipped into the turbid state (S_2) with a summer averaged Chl-a concentration over 100 $mg{\cdot}m^{-3}$. The vertical blue and red dashed lines represent CPL_{eu} and CPL_{olig} in scenario I without MP pollution as the pristine condition, respectively.

141x240mm (300 x 300 DPI)