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Recovery of lakes and coastal marine ecosystems from eutrophication: A global meta-analysis

Michelle L. McCrackin, 1* Holly P. Jones, 2 Peter C. Jones, 3 David Moreno-Mateos 4,5

¹Baltic Sea Centre, Stockholm University, Stockholm, Sweden

²Department of Biological Sciences and Institute for the Study of the Environment, Sustainability, and Energy, Northern Illinois University, DeKalb, Illinois

³Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois

⁴Basque Center for Climate Change, Bilbao, Spain

⁵IKERBASQUE, Basque Foundation for Science, Bilbao, Spain

Abstract

In order to inform policies aimed at reducing nutrient emissions to surface waters, it is essential to understand how aquatic ecosystems respond to eutrophication management. Using data from 89 studies worldwide, we examined responses to the reduction or cessation of anthropogenic nutrient inputs relative to baseline conditions. Baseline conditions were pre-disturbance conditions, undisturbed reference sites, restoration targets, or experimental controls. We estimated recovery completeness (% baseline conditions reached) and recovery rate (annual % change relative to baseline conditions) for plant and animal abundance and diversity and for ecosystem functions. Categories were considered fully recovered if the 95% confidence interval (CI) of recovery completeness overlapped 100% and partially recovered if the CI did not overlap either 100% or zero. Cessation of nutrient inputs did not result in more complete or faster recovery than partial nutrient reductions, due likely to insufficient passage of time, nutrients from other sources, or shifting baselines. Together, lakes and coastal marine areas achieved 34% (±16% CI) and 24% (±15% CI) of baseline conditions decades after the cessation or partial reduction of nutrients, respectively. One third of individual response variables showed no change or worsened conditions, suggesting that achieving baseline conditions may not be possible in all cases. Implied recovery times after cessation of nutrient inputs varied widely, from < 1 yr to nearly a century, depending on response. Our results suggest that long-term monitoring is needed to better understand recovery timescales and trajectories and that policy measures must consider the potential for slow and partial recovery.

Eutrophication is one of the greatest stressors for freshwater and coastal marine ecosystems globally, contributing to increased frequency, duration, and extent of algal blooms and areas with insufficient dissolved oxygen to support life (i.e., dead zones, Smith 2003). The distribution of harmful algal blooms has grown dramatically in the past decades and often tracks the input of nutrients to coastal areas (Anderson et al. 2008; Glibert et al. 2008; Lapointe et al. 2015). Toxins produced by harmful algae can contaminate

drinking water and seafood and kill domestic animals and wildlife (Burkholder 1998; Hoagland et al. 2002; Backer et al. 2015). Dead zones increase invertebrate and fish morbidity and mortality and reduce reproductive success. In the past half-century, dead zones in coastal marine areas have grown dramatically, covering more than 245,000 km² globally (Díaz and Rosenberg 2008).

Eutrophication also has negative economic consequences, such as increased costs for public health, losses in commercially important fisheries, decreases in waterfront property values, and lost tourism revenue. Studies do not always address all impacts of eutrophication, making it difficult to generalize across regions and ecosystems. For example, Dodds et al. (2009) estimated that eutrophication of U.S. freshwaters costs US\$2.2 billion annually, due mostly to decreases in property values and recreational activities, but also resulting from impacts on endangered and threatened species and drinking water. Similar economic damages

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^{*}Correspondence: michelle.mccrackin@su.se

from freshwater eutrophication in England and Wales are estimated to cost US\$105–160 million annually (Pretty et al. 2003). Lastly, hypoxia was responsible for US\$0.25 million in annual welfare losses between 1999 and 2005 in the Neuse River Estuary and Pamlico Sound of North Carolina (Huang et al. 2012).

A number of policies have been implemented to mitigate the ecological and economic effects of eutrophication and restore aquatic ecosystems by reducing anthropogenic nutrient inputs. In the United States (U.S.) and European Union (EU), there has been success in reducing nutrient emissions from agriculture, sewage treatment plants, and fossil fuel combustion. Under the EU Nitrates Directive, for example, average nitrate concentration has decreased in many leaching-vulnerable zones (van Grinsven et al. 2012; European Commission 2013a). Substantial progress has also been made in upgrading sewage treatment facilities to remove nutrients from effluent as a result of the EU Urban Wastewater Treatment Directive and the U.S. Clean Water Act (USEPA 2008; European Commission 2013b). Further, air pollution standards have reduced nitrogen (N) deposition by over 20% in the Eastern U.S. and Europe (USEPA 2013; EMEP 2015) since 1990. Nevertheless, the costs of mitigating eutrophication are significant; in England and Wales, US\$77 million is spent annually to remove nutrients from point sources, adopt new farming practices, and monitor and enforce policy measures (Pretty et al. 2003).

The large body of literature that documents how aquatic ecosystems respond to nutrient management has improved our understanding of recovery from eutrophication for individual study sites or case studies of similar sites (e.g., European lakes, as in Sas 1989 and Bennion et al. 2015 or coastal and estuarine areas, as in Borja et al. 2010). Nutrient management can result in increased water clarity, expanded cover of submerged aquatic vegetation, and reduced plankton biomass and nutrient concentrations (e.g., Bootsma et al. 1999; Søndergaard et al. 2005; Jeppesen et al. 2009). However, many of these previous studies do not track progress against restoration targets (often defined as pre-eutrophic or undisturbed conditions) so the degree and rate of improvement are not known even though this information is critical to assess restoration effectiveness and plan future management actions. Moreover, due to differences in which or how variables are measured and how recovery is defined or assessed, it can be difficult to make generalizations from these studies. Meta-analysis is a powerful tool to summarize results of individual studies (Koricheva et al. 2013) and can, thus, provide useful cross-system information for policy makers and managers aiming to improve eutrophic ecosystems. In this study, we quantitatively assess recovery from eutrophication for both lake and coastal marine ecosystems globally relative to baseline conditions. We estimate recovery completeness, recovery rates, and years to recover for a number of biological and ecosystem function response variables after nutrient management. Our results will be useful to global efforts to mitigate eutrophication and restore aquatic ecosystems.

Methods

Data were obtained by searching the ISI Web of Knowledge database on 01 December 2014 for all years since 1945 using the following search term combinations: ((reduc* OR abate* OR restor*) AND nutrient) OR (eutrophication AND recover*) AND (lake OR coast* OR sea OR marine OR estuary OR bay). The search was refined to the subject "environmental sciences" and returned 8635 references that we assessed for potential inclusion by reviewing the title and abstract. Studies were included in our analysis if data for three conditions were available: (1) baseline conditions, which includes pre-disturbance conditions (prior to the start of nutrient inputs that were ceased or reduced or prior to the appearance of eutrophication symptoms), a nearby undisturbed reference site, a restoration target, or an experimental control; (2) disturbed conditions (those at the nearest time point to nutrient management); and, (3) current conditions (those collected most recently after the cessation or reduction in nutrient inputs). Using these criteria, we identified 562 studies for possible inclusion. We assessed the full manuscript for these studies in detail, finding 89 studies with 1093 response variables (Supporting Information Table S1.1). The scarcity of studies in Asia and the southern hemisphere made it difficult to create a truly global dataset. The most common reason for excluding a study was the lack of baseline data. We extracted graphical data using Data Thief (Tummers 2006) and from tabular data or text within manuscripts. Wetlands, streams, and rivers were excluded from the meta-analysis because preliminary literature searches returned few results and because most restoration activities for these ecosystems focus on hydrological alterations rather than on eutrophication (Moreno-Mateos et al. 2015).

We defined a response variable as any measurement taken by the original authors to document the recovery process. For each study, we recorded the extent of nutrient reduction and the type of nutrient management, nutrient source, metric, life form, ecosystem function, restoration, and ecosystem. We also recorded the latitude of the study site, disturbance duration, and recovery period. Only studies that reported measured data, and not modeled data, were included in our dataset. The extent of nutrient reductions was complete (cessation of aquaculture or agriculture, experimental nutrient additions, and diversion or cessation of sewage effluent) and partial (all else). Nutrient management type was N alone, phosphorus (P) alone, or both N and P. For studies where the original author did not specify which nutrients were managed, we assigned categories based on other information provided in the manuscript. For example, in cases of cessation of sewage, agriculture, and aquaculture we assumed both N and P were affected. Nutrient source types included agriculture, aquaculture, atmospheric deposition, experiments, sewage, and multiple sources. Metric type included abundance, diversity, and ecosystem function. Abundance included biomass and count data and diversity included species richness data (Supporting Information Table S1.2). The life form variable included algae (phytoplankton), submerged aquatic vegetation, invertebrates, and vertebrates. Invertebrates included emergent insects, zooplankton, nematodes, and mollusks, among others (Supporting Information Table S1.3). Vertebrates included only fish and birds. Ecosystem function types included measures of cycling of carbon (C), N, P, and oxygen (O₂) and measures of water clarity. Responses for C, N, and P included fluxes and concentrations in sediments and the water column (Supporting Information Table S1.4). Water clarity included Secchi depth and maximum growing depth of aquatic vegetation. Restoration type included passive restoration (actions taken to reduce nutrient inputs such as improvements in sewage treatment or cessation of aquaculture) and active restoration (additional actions such as replanting vegetation, removal of sediments, or piscivorous fish introductions). Ecosystem type included lakes and coastal marine areas. The latitude of the study site (absolute value of decimal degrees) was used as a proxy for climate. The disturbance duration was the number of years between baseline conditions and when nutrient management occurred. The recovery period was the number of years between nutrient management and when the most recent samples were taken.

We estimated recovery completeness (%) as:

Recovery completeness =
$$(X_c - X_d)/(X_b - X_d) \times 100$$
 (1)

where, $X_{\rm c}$ is current condition, $X_{\rm d}$ is disturbed condition, and $X_{\rm b}$ is baseline condition. Negative values suggest that conditions worsened after anthropogenic nutrients were reduced or ceased. A value greater than 100% suggests that the baseline condition was exceeded (e.g., overshoot).

We estimated the recovery rate (% change yr⁻¹) as the percent change in the mean response variable per year:

Recovery rate =
$$((X_c - X_d)/(X_b - X_d)/t_r) \times 100$$
, (2)

where $t_{\rm r}$ is recovery period, the number of years between the current condition ($X_{\rm c}$) and the disturbed condition ($X_{\rm d}$). A value greater than 100% suggests that recovery occurred in less than 1 yr.

Lastly, we estimated years to recover as:

Years to recover =
$$(X_c - X_b)/((X_c - X_d)/t_r) + t_r$$
, (3)

for response variables with positive recovery rates and for which there were complete nutrient reductions (n=478). We also estimated years to recover for variables that fully recovered, which we defined as having recovery

completeness between 85% and 115% (n=171). This definition is arbitrary, but intended to acknowledge natural variability and measurement error. For fully recovered responses, recovery rates could be under-estimated and years to recover could be over-estimated if the most recent sampling point (X_c) occurred after baseline conditions were achieved and, thus, these values should be interpreted with caution. Recovery from eutrophication is likely not a linear process (e.g., Carstensen et al. 2011; Bennion et al. 2015) and we recognize that our approach to estimating recovery rates and years to recover is a simplification.

Most studies reported multiple response variables for a given category (e.g., abundance data for different species of algae or invertebrates). To account for non-independence, we fit mixed-effect models using maximum likelihood estimation that included each study as a random effect and moderators (sources of heterogeneity) as fixed effects (Nakagawa and Santos 2012). Analyses were conducted in R 3.0.1 (R Core Team 2014) using the nlme package (Pinheiro et al. 2015). Prior to analysis, recovery completeness and recovery rates were inverse hyperbolic sine transformed and years to recover values were log transformed to improve normality, homoscedasticity, and kurtosis. To explore patterns of recovery completeness and recovery rates, we constructed different models with the following moderators: extent of nutrient reductions (complete or partial), nutrient management type (N, P, or both), nutrient source (agriculture, aquaculture, experimental, sewage, or multiple sources), restoration type (active or passive), and ecosystem type (lake or marine). We constructed models for types of life forms and ecosystem functions using subsets of the full dataset. Moderator categories were included if there were more than five response variables from three or more studies. We considered a moderator category to have achieved recovery or not to differ from baseline conditions if the 95% confidence interval (CI) for recovery completeness overlapped 100%. Categories were considered to be partially recovered if the CI did not overlap either 100% or zero and were considered to not to differ from disturbed conditions if the CI overlapped zero. We tested for significant differences among moderator categories with Tukey's test ($\alpha = 0.05$) using the multcomp package (Hothorn et al. 2008).

Note that recovery completeness and recovery rate are either both positive or both negative for each response variable (Eqs. 1 and 2). However, it is possible for the recovery completeness CI for a moderator category to be greater than zero while the corresponding recovery rate CI overlaps zero. In such cases, individual responses with low or negative values for recovery completeness are associated with relatively long periods of time between nutrient management and the most recently collected data (t_r in Eq. 3), which results in low recovery rates for the category as a whole. The reverse true when the CI for recovery completeness overlaps zero and the CI for recovery rate is greater than zero.

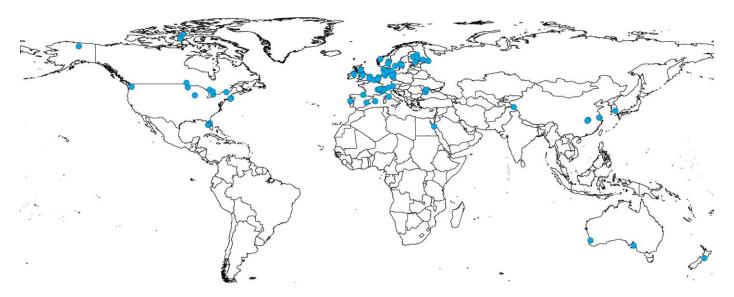


Fig. 1. Map of locations of studies included in the meta-analysis.

Baseline conditions were represented by pre-disturbance conditions for 85% of response variables and by undisturbed reference sites, experimental controls, and restoration targets for 8%, 5%, and 2% of responses, respectively. Combining responses that use different types of baseline conditions could obscure the recovery signal and increase the uncertainty in our results because of inconsistencies in disturbance magnitudes. For example, if the baseline condition was represented as the pre-disturbance condition, then the disturbance magnitude $(X_d - X_b)$ for a given response would be greater than if the baseline condition was represented as a restoration target based on a small improvement over the disturbed condition. We explored this uncertainty in three ways: (1) adding disturbance magnitude as a covariate for recovery completeness and recovery rate; (2) using type of baseline condition as a categorical moderator for disturbance magnitude, recovery completeness, and recovery rate; and, (3) comparing models constructed with the full dataset to those constructed with the subset of data using pre-disturbance conditions. We estimated disturbance magnitude as:

Disturbance magnitude =
$$ln(X_d/X_b)$$
, (4)

for non-zero response variables. First, we found no significant relationship between disturbance magnitude and recovery completeness (p > 0.2) or recovery rate (p > 0.9). Second, there were no significant differences in disturbance magnitude, recovery completeness, or recovery rate among the different types of baseline conditions, although confidence intervals were narrowest for pre-disturbance conditions (Supporting Information Fig. S1.1). Lastly, results were qualitatively the same between models using the full dataset and models using the subset of data associated with

pre-disturbance conditions (Supporting Information Figs. S1.2–S1.5). In the main text, we present the full dataset in order capture a wide variety of study systems and response variables.

Meta-analyses are often weighted by accounting for replication and variance within each study (Gurevitch and Hedges 1999). Weighted analysis requires mean, standard deviation, and sample size information for each response variable. Such data were only available for 98 (9%) individual response variables in our dataset and a weighted analysis would, thus, exclude the majority of our data. We present unweighted models in the main text; however, we explored the effect of unweighted analysis by comparing weighted and unweighted models for recovery completeness using the response variables with variance data. Results were qualitatively similar between the weighted and unweighted models (Supporting Information Figs. S2.1, S2.2). There were wider confidence intervals in weighted models, which is expected given that weighting is intended to account for unequal variances between studies.

Results

The 89 studies were located predominantly in the northern hemisphere (86 studies) and Europe (62 studies, Fig. 1). Studies were concentrated in temperate latitudes except for four sites in arctic regions. Fifty-seven studies were of lakes and 32 were of coastal marine ecosystems. Active restoration occurred in 13 studies. The disturbance period ranged between 0.2 yr for experiments to 220 yr for paleolimnological studies, with a median of 42 yr across the dataset. The periods of time between nutrient management and the final sampling point (t_r) were similarly variable, ranging from 0.1 yr to 380 yr (median = 15 yr).

Fifty-six percent of response variables (n = 615) were measured in response to partial reductions of anthropogenic nutrients and 44% (n = 478) were measured in response to complete nutrient reductions. Inputs of both N and P were managed for nearly two-thirds of response variables (n = 703). Phosphorus alone was reduced or ceased for one-third (n = 359) of variables and N alone was managed for the remaining few (3% of total, n = 31). The majority of response variables (n = 729) were associated with nutrients from sewage and the rest were distributed across multiple sources (n = 149), aquaculture (n = 85), agriculture (n = 68), experiments (n = 60), and atmospheric N deposition (n = 2).

Using extent of nutrient reductions as a moderator, we found the cessation of anthropogenic nutrient inputs did not result in more complete or faster recovery compared to partial nutrient reductions (Fig. 2). Response variables recovered 34% (±16 CI) and 24% (±15 CI) of baseline conditions 13 yr and 16 yr (median) after complete and partial reductions, respectively. Recovery rates were 16% yr⁻¹ (±15 CI) after complete reductions and 4% yr⁻¹ (±9 CI) after partial reductions. We explored the relationship between the extent of nutrient reductions and other moderators for recovery completeness and recovery rates. There was no significant difference between complete and partial nutrient reductions when type of life form or ecosystem function was used as a co-moderator. As a result, we dropped the extent of nutrient reduction as a co-moderator when constructing other models.

Our analysis suggests that biological and chemical components of lake and marine ecosystems can improve toward baseline conditions because the majority of response variables (64%, n = 696) had positive values for recovery completeness and recovery rate. Variables that showed improvement, however, were often masked by those that did not show improvement. As a result, aggregated recovery completeness and recovery rates were statistically indistinguishable from zero across most life form and ecosystem function types (Figs. 3, 4). For example, algae recovered an average of 32% (±15 CI) of baseline conditions, but were not significantly different than submerged aquatic vegetation, invertebrates and vertebrates, none of which differed from zero (Fig. 3). About 40% of individual response variables for algae, invertebrates, and submerged aquatic vegetation and nearly half of those for vertebrates did not improve toward baseline conditions. Compared to life form types a smaller portion of ecosystem function type variables worsened or showed no change after eutrophication management. About 20% of individual response variables for N and P cycling, 30% of responses for water clarity and O₂, and 40% of responses for C did not improve.

Substantial variation in responses to nutrient management can be seen across types of life forms and ecosystem functions. This is not surprising given the heterogeneity associated with the responses we aggregated into these

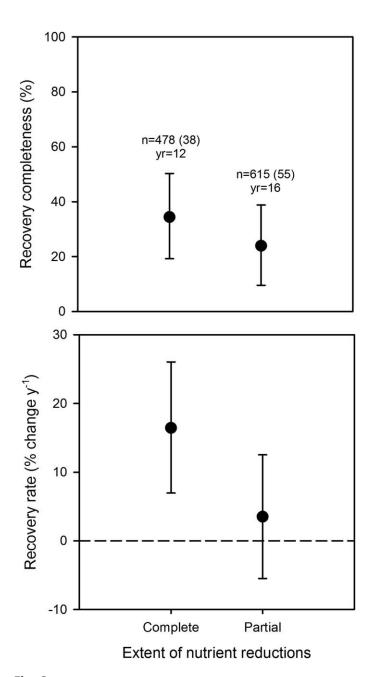


Fig. 2. Recovery completeness (upper panel) and recovery rate (lower panel) by extent of nutrient reduction for the full dataset. Points are mean \pm 95% confidence interval. The number of response variables is indicated by n and the number of studies is in parentheses. Median recovery period (in years) is also noted.

categories. To explain variation in recovery completeness and recovery rates, we explored several other potentially important moderators: latitude of the study site, nutrients sources, and type of nutrient, restoration, and ecosystem. There was a significant (p < 0.05) but small, positive relationship between latitude of the study site for both recovery completeness and recovery rate. For every degree increase in latitude, there was a 0.5% (CI \pm 0.2) and 0.2% yr⁻¹ (CI \pm 0.1)

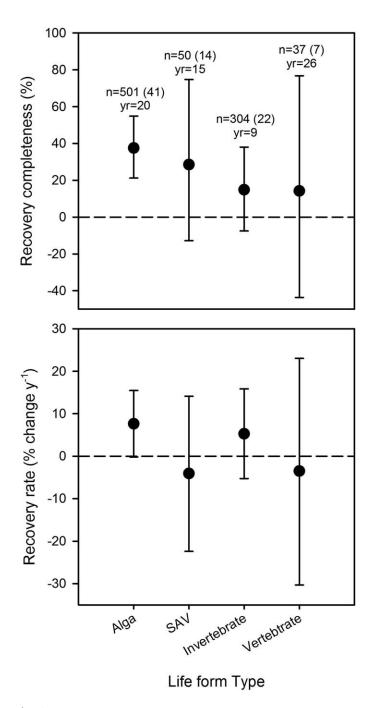


Fig. 3. Recovery completeness (upper panel) and recovery rate (lower panel) by nutrient source for the full dataset. Points are mean \pm 95% confidence interval. The number of response variables is indicated by n and the number of studies is in parentheses. Median recovery period (in years) is also noted.

increase in recovery completeness and recovery rate, respectively. Recovery completeness did not differ across nutrient sources, but recovery rates for aquaculture (45% yr $^{-1} \pm 26$ CI) and experiments (41% yr $^{-1} \pm 23$ CI) were significantly greater than those for sewage (3% yr $^{-1} \pm 8$ CI). Neither single- nor dual-nutrient management was associated with

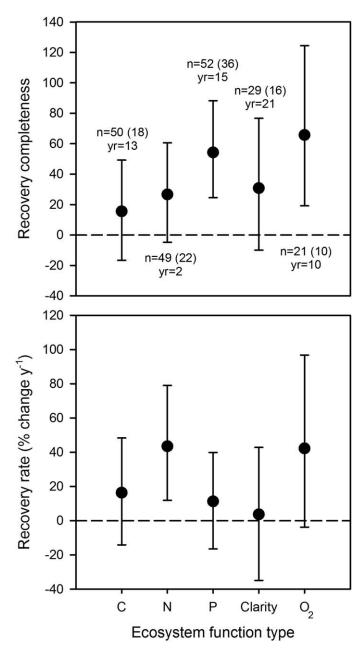


Fig. 4. Recovery completeness (upper panel) and recovery rate (lower panel) by life form type. Points are mean \pm 95% confidence interval. The number of response variables is indicated by n and the number of studies is in parentheses. Median recovery period (in years) is also noted. SAV is submerged aquatic vegetation.

more complete or faster recovery (Supporting Information Fig. S3.1) for lake or coastal marine ecosystems or for the subset of data for autotrophs (algae and submerged aquatic vegetation, data not shown). Recovery completeness ranged between 11% and 56% for management of N plus P and P alone. Results for managing N alone were most variable, 19% (\pm 57 CI) due likely to the small sample size (<3% of response variables). Recovery rates were greater than zero for

dual-nutrient reductions (13% yr $^{-1}\pm9$ CI) but not different from reductions of N or P alone, which overlapped zero. Active restoration was not associated with more complete or faster recovery compared to passive restoration (Supporting Information Fig. S3.2). Responses for both restoration types recovered an average of nearly 30% of baseline conditions, but passive restoration was less variable than active restoration (29% yr $^{-1}\pm12$ CI and 27% yr $^{-1}\pm28$ CI, respectively). Lastly, there were no significant differences in recovery completeness and rates between lake and coastal marine ecosystems and responses were similarly variable (data not shown).

We estimated that baseline conditions could be achieved 15 yr (± 7 CI) after complete nutrient reductions and 31 yr (± 13 CI) after partial nutrient reductions assuming linear recovery trajectories. Years to recover were more variable across life forms, from about 7 yr to 30 yr for algae and invertebrates to 24 yr (± 70 CI) years for submerged aquatic vegetation, compared to those for ecosystem functions, which ranged between 12 yr (± 18 CI) for P cycling to 14 yr (± 37 CI) for water clarity (Fig. 6). Estimated years to recover in response to cessation of nutrients were significantly shorter for aquaculture and experiments (about 2 yr ± 4 CI) than those for sewage (28 yr ± 19 CI).

About 16% (n=171) of individual response variables met conditions of full recovery (recovery completeness between 85% and 115%) but less than half of these variables were associated with complete nutrient reductions. Recovery rates (about 10–38% yr $^{-1}$) and years to recover (about 7–15 yr) did not differ between partial and complete nutrient reductions (Supporting Information Fig. S3.3). There were insufficient data to run mixed-effect models for all moderators and categories within moderators, which limited our analysis. We found no difference in recovery rates and years to recover across types of life forms or ecosystem functions (Supporting Information Figs. S3.4, S3.5).

Discussion

Overall responses

Here we use meta-analysis to explore the responses of lakes and coastal marine ecosystems to reductions in anthropogenic nutrient inputs. Our results are broadly congruent with previous research in finding that recovery is a multidecadal process. Phytoplankton, macroalgae, zooplankton, fish, and water-column nutrient concentrations have shown improvement toward oligotrophic conditions in the years to decades following eutrophication management (Borja et al. 2010; Spears et al. 2011). Past work has also found that biological, chemical, and physical variables can worsen or show no response to reductions in nutrient inputs (Jeppesen et al. 2005; Søndergaard et al. 2007). Indeed, about one-third of the response variables in our dataset made no progress toward baseline conditions, suggesting that improvement may not always be possible.

We make generalizations across 89 studies using a consistent, quantitative approach to estimate recovery completeness, recovery rates, and years to recover relative to baseline conditions. Not surprisingly, our results are less consistent with specific findings of previous work. For example, researchers have reported that phytoplankton and fish respond more quickly to reduced nutrient inputs than submerged aquatic vegetation (Dixit et al. 1992; Jeppesen et al. 2005; Eigemann et al. 2016). Our analysis found no evidence that different types of life forms or ecosystem functions responded more completely or quickly to nutrient management than others (Figs. 3-6). However, confidence intervals for recovery completeness, recovery rates, and years to recover for algae and invertebrates were considerably smaller than those for submerged aquatic vegetation and vertebrates (Figs. 3, 6). This result could be due to differences in sample sizes, but also suggests that algae and invertebrates could respond more consistently to nutrient management than other life forms. Another example is water-column N concentration, which has been found to respond more quickly than P concentration because denitrification can remove N while internal recycling can maintain P concentration despite external nutrient reductions (Søndergaard et al. 2003; Vehtera et al. 2007). We found measures of N and P cycling responded similarly to eutrophication management; P-cycle variables did not recover more completely or quickly than N-cycle variables (Fig. 4) and the number of years to recover were about the same for both (10-34 yr after complete nutrient reductions, Fig. 6).

Factors affecting recovery from eutrophication

The first step in reversing human-caused eutrophication is to reduce or cease anthropogenic nutrient inputs to water bodies. Once nutrient concentrations decrease, algal abundance and growth rates, water clarity, and other components of the ecosystem are expected to progress toward the preeutrophic state. These expectations are based on measured relationships between increasing concentrations of chlorophyll a and nutrients with the assumption that oligotrophication follows the reverse trajectory of eutrophication when nutrients are reduced or ceased (Carstensen et al. 2011). Few of the studies in our dataset reported the magnitude of external nutrient reductions and the lack of such information limited our ability to assess recovery. Complete nutrient reductions were not associated with more complete or faster recovery from eutrophication than partial reductions, possibly because the distinction between these categories was not adequate to detect differences. But this finding could also result from insufficient passage of time, nutrients from alternative or legacy sources in the catchment, and shifting baselines.

After cessation of nutrient inputs, we estimated a recovery period of 25 yr (median; average = 106 yr for n = 277 variables with positive recovery rates) to achieve baseline

conditions, assuming a linear recovery process. However, only 13 yr (median; average = 42 yr) had passed between nutrient management and most recent sampling date (t_r) for these variables. This finding reinforces the need for longterm monitoring to fully understand and document recovery progress. Second, despite cessation of known sources, runoff, groundwater, or atmospheric deposition could have delivered nutrients from other sources. The legacy of past practices also complicates efforts to reduce nutrient inputs to surface waters because the accumulation and subsequent release of nutrients in long-term storage pools, such as agricultural soils, could dampen recovery. Denitrification is thought to remove N from the landscape, so attention has focused on legacy P (Carpenter 2005; Withers et al. 2014). However, there is growing evidence that N can accumulate in soils as well, although the potential for legacy N to leak over long periods is not well understood (Worrall et al. 2015; Van Meter et al. 2016). Lastly, changes in environmental conditions or other pressures, individually or together, could result in shifting baselines that render historical conditions unachievable (Duarte et al. 2008; Bennion et al. 2010; Carstensen et al. 2011). Internal loading of P from sediments is frequently identified as a factor delaying recovery from eutrophication in both lake and marine ecosystems (Jeppesen et al. 2005; Stigebrandt et al. 2014). Climate-driven changes in hydrology, precipitation, and temperature could also alter water residence times, circulation patterns, nutrient concentrations and the distribution and phenology of key species (Scavia et al. 2002). Additionally, non-native species could become established under eutrophic conditions and persist even after nutrient loads are reduced (Higgins and Vander Zanden 2010).

We expected improvement toward baseline conditions after partial nutrient reductions. However, interestingly, about half of the 171 response variables that fully recovered (recovery completeness between 85% and 115%) were associated with partial nutrient reductions. None of the moderators provided insight as to why partial nutrient reductions could lead to full recovery (Supporting Information Figs. S3.4, S3.5). However, these findings are based on a small portion of the dataset and could result from natural variability or our definition of full recovery for individual responses.

Of the moderators we examined, we only found significant differences in recovery rate and years to recover for aquaculture and experiments (Figs. 5, 6). While nutrient inputs from these sources were ceased, it is possible that other factors contributed to the results. For example, the duration of eutrophic conditions could play a role because the disturbance periods for aquaculture and experimental eutrophication were considerably shorter (median = 3 yr and 1 yr, respectively) than those for agriculture and sewage (median = 21 yr and 18 yr, respectively). In the case of aquaculture, it is also possible that areas affected by eutrophication were relatively small (e.g., sediments beneath

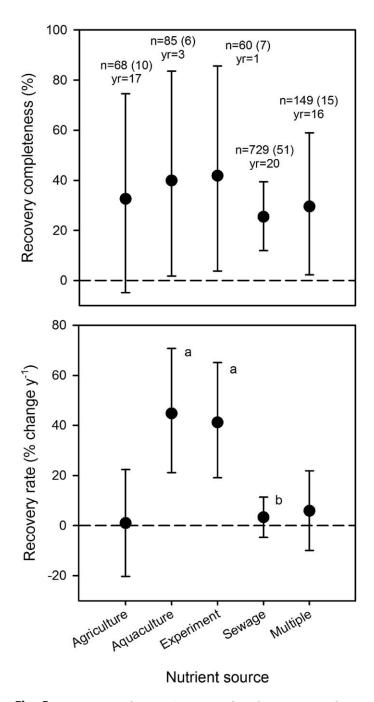


Fig. 5. Recovery completeness (upper panel) and recovery rate (lower panel) by ecosystem function type. Points are mean \pm 95% confidence interval. The number of response variables is indicated by n and the number of studies is in parentheses. Median recovery period (in years) is also noted. Letters denote significant differences (α = 0.05) among categories.

fish pens) and that short water residence times or dilution with surrounding waters sped the recovery process.

Eutrophication management has traditionally focused on controlling P inputs in lakes (Schindler et al. 2008) and N inputs to estuaries and coastal areas (Howarth and Marino

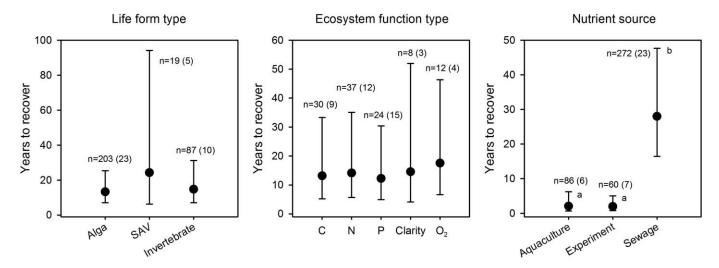


Fig. 6. Years to recover for the subset of individual response variables with complete nutrient reductions. Points are mean \pm 95% confidence interval. The number of response variables is indicated by n and the number of studies is in parentheses. SAV is submerged aquatic vegetation. Letters denote significant differences ($\alpha = 0.05$) among categories.

2006). More recent studies propose dual-nutrient control because of evidence for co-limitation of primary production by both N and P across freshwater and marine ecosystems (Elser et al. 2007; Conley et al. 2009; Smith et al. 2016). Our analysis found no relationship between single- or dualnutrient management and recovery completeness or recovery rates (Supporting Information Fig. S3.1). It is important to note that unlike the meta-analysis by Elser et al. (2007), which examined studies that contained multiple nutrient treatments (e.g., N and P individually and together), the majority of studies in our dataset consisted of environmental sampling in response to one "treatment." The dataset could have been biased if the original authors focused on a particular nutrient thought to be most important for the study system. Overall, our results do not provide insight to discussions on the effectiveness of single- or dual-nutrient reductions.

Over the past several decades, active restoration techniques have been widely used in lakes and to a lesser extent in coastal marine areas. There were insufficient data to evaluate whether certain techniques were more effective than others, but overall we found no evidence that active restoration contributed to more complete or faster recovery from eutrophication than simply managing nutrient inputs alone (Supporting Information Fig. S3.2). Responses to active restoration were more variable than responses to passive restoration, due possibly to differences in sample size between the categories, but could also reflect the mixed results reported in the literature. Studies that examine the effectiveness of active restoration have found that some ecosystems improve, some show initial improvement and then return to eutrophic conditions within 10 yr of restoration, and others show no improvement (Gächter and Wehrli 1998; Gulati and van Donk 2002; Søndergaard et al. 2007; Spears et al. 2015). When active restoration did not achieve the expected results, the original authors hypothesized the likely causes included site-specific factors, internal P loading, or insufficient reduction of cyprinid fish or external nutrient loads (Hansson et al. 1998; Spears et al. 2013; Lüring et al. 2016).

Climate could influence recovery from eutrophication because of temperature effects on the duration of algal blooms and rates of nutrient cycling that sustain eutrophic conditions despite nutrient management. As a result, ecosystems in warm climates could recover more slowly than those in cold areas (Jeppesen et al. 2007). Indeed, we found a small but significant, positive relationship between latitude (as a proxy for climate) and recovery completeness and recovery rates. Similar to previous reviews (e.g., Søndergaard et al. 2005; Borja et al. 2010) the studies in our dataset were concentrated in north temperate regions and the resulting latitudinal gradient was too narrow to fully explore climaterelated patterns. Given the global extent of eutrophication, studies of tropical lakes and coastal ecosystems are needed to improve our understanding of recovery across a broad range of climates.

Conclusion

Reducing anthropogenic nutrient inputs is a necessary first step to address eutrophication. While there has been progress in reducing nutrients from point sources, such as sewage, greater effort is needed to address diffuse sources, especially agriculture. We used meta-analysis to look for patterns across lakes and coastal marine areas and to provide first-order estimates of recovery rates and years to recover for a variety of ecosystem components. Nutrient management

can improve the conditions of eutrophic ecosystems over years to decades, although the large variability in responses we found reflects the complexity of factors affecting recovery. Given the extent to which humans have modified land cover in catchments and continue to use aquatic ecosystems for recreation, transportation, and natural resource extraction, it is critical to establish appropriate restoration goals. The potential for long recovery periods must be considered when eutrophication management actions are planned, implemented, and assessed. Significant opportunity remains to synthesize nutrient-load reconstructions, paleolimnological studies, and long-term datasets to better elucidate load-response relationships and recovery trajectories.

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Conflict of Interest

None declared.

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