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River dam impacts on biogeochemical cycling

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Abstract

The increased use of hydropower is currently driving the greatest surge in global dam construction since the mid-20th century, meaning most major rivers on Earth are now dammed. Dams impede the flow of essential nutrients, including carbon (C), phosphorus (P), nitrogen (N) and silicon (Si), along river networks, leading to enhanced nutrient transformation and elimination. Increased nutrient retention via sedimentation or gaseous elimination in dammed reservoirs influences downstream terrestrial and coastal environments. Reservoirs can also become hotspots for greenhouse gas emission, potentially impacting how 'green' hydropower is compared to fossil fuel burning. In this Review, we discuss how damming changes nutrient biogeochemistry along river networks, as well as their broader environmental consequences. The influences of construction and management practices on nutrient elimination, the emission of greenhouse gases and potential remobilization of legacy nutrients are also examined. We further consider how regulating hydraulic residence time and environmental flows (e-flows) can be used in planning and operation from dam conception to deconstruction.

[H1] Introduction

River damming has been practiced for millennia, with the first dams built before 2000 BCE in the Egyptian empire[1]. The number of dams increased steadily prior to the Second World War, but expanded rapidly thereafter, peaking in the 1960s and 1970s, with most construction in North America and Western Europe[2]. A second surge in dam construction began in the early 2000s, with over 3,700 hydroelectric dams either planned or under construction worldwide during this construction boom[3], each with a generating capacity of >1 megawatt (MW). Many of the new dams are being constructed in South America, Asia, and the Balkans, largely driven by the need to expand energy production in growing economies[3,4]. Indeed, by 2015, dammed reservoirs supplied around 30–40% of irrigation water globally[5,6], and 16.6% of the world's electricity was generated by hydropower[7]. Almost two thirds of the world's long rivers (that is, those >1000 km) are no longer free-flowing[8], and the current surge in dam construction – motivated by the 2016 Paris Agreement and the need for greater renewable energy generation – is expected to double river fragmentation by 2030 (REF[9]). Accordingly, freshwater ecosystems have been referred to as the 'biggest losers' of the Paris Agreement[10].

Nutrients, such as carbon (C), nitrogen (N), phosphorus (P) and silicon (Si), are transported and transformed along the land to ocean aquatic continuum (LOAC), forming the basis for freshwater and ultimately marine food webs. Dam reservoirs act as 'in-stream' reactors, impeding nutrient flow and thereby increasing residence time along the LOAC. These increases in nutrient residence time enhance: nutrient transformations from dissolved to particulate forms through primary productivity or adsorption; sedimentation and retention; and gaseous elimination **[G]** and/or atmospheric fixation of nutrients in reservoirs. Depending on local or regional goals for nutrient management, enhanced biogeochemical cycling and elimination in reservoirs can be viewed as either an advantage (for example, the reservoir reduces the downstream nutrient flux to eutrophic water bodies) or a problem (if the reservoir itself suffers from eutrophication **[G]** or if it alters nutrient stoichiometry such that it promotes downstream eutrophication).

Dams are often constructed following insufficient environmental impact assessments[11]. Environmental assessments before dam construction typically include an evaluation of water quality, but the impacts on nutrient cycling are rarely included[12,13]. In addition, assessments rarely extend beyond the ecosystems immediately surrounding dam construction[14], and often focus on hydrological connectivity[15-17] or consequences to fish populations[18-20],–and sometimes on greenhouse gas (GHG) emissions from reservoirs[21-25]. For example, the environmental consequences of river damming were markedly misunderstood with regard to the Balbina Dam in Amazonas, Brazil, the construction of which led to the degradation of the flooded forest and the equivalent of ~114 years of hypothetical greenhouse gas emissions from coal or natural gas power generation[26,27]. Meanwhile, in many developing countries, hydroelectric construction projects with generating capacities <10 MW are exempt from any environmental assessment[10].

In this Review, we discuss the impacts of river damming on nutrients, specifically C, N, P and Si, with an emphasis on the impacts of nutrient elimination on biogeochemical cycling along the LOAC. We examine dam-related nutrient management strategies, including dam removal, with a focus on managing tradeoffs at the watershed-scale[28,29]. Our evaluations are based on the hydraulic residence time (HRT, defined as the volume of water divided by the flow through the water body), as it is typically considered the "master variable" governing the relative rates of transport versus biogeochemical reactions[30-34]. The sizes of nutrient loads delivered from upstream are also considered, as they strongly influence nutrient elimination fluxes[31,35]. Finally, we discuss the use of these parameters as simple approaches to enable improved management of biogeochemical processes in dammed river systems.

[H1] Dam nutrient dynamics

Damming impacts both the absolute and relative nutrient loads (often benchmarked against the Redfield ratio[36] stating C:N:P = 106:16:1) and can influence the composition and productivity of an aquatic ecosystem[37,38]. Dammed reservoirs influence nutrient ratios through nutrient elimination from the water column via burial in sediments or gaseous release to the atmosphere (**Fig. 1**)[39,40]. Nutrient elimination is calculated using the equation:

$$E = \frac{F_{in} - F_{out}}{F_{in}} \quad (1)$$

where E is the fraction of eliminated nutrient (unitless), F_{in} is the riverine nutrient influx to the reservoir (M T^{-1}), and F_{out} is the efflux (M T^{-1}) out of the reservoir through the dam(s). Based on this equation, of the total estimated nutrient loads carried by rivers worldwide[41,42], 7.4% of total N (TN; **Fig. 1a**), 12% of total P (TP; **Fig. 1b**), and 5.3% of reactive Si (RSi = dissolved Si (DSi) + biogenic Si (BSi); **Fig. 1c**) were eliminated in reservoirs in year 2000. The increased nutrient elimination compared to undammed states is partially due to dammed watersheds having longer HRTs, fostering biogeochemical and physical transformations that lead to elimination[26,43-46]. In 1997, for example, it was estimated that HRT was an average of 58 days longer than undammed reservoirs[68], though this is now likely to be much higher giventhe recent boom in dam construction.

Compared to N and Si, P is generally eliminated most efficiently in reservoirs at most HRTs, with some reservoirs eliminating nearly all of the P from the water column (**Fig. 2**). For instance, the 400 km^2 Lake Diefenbaker reservoir in central Canada has a relatively long mean HRT of 1.1 years, and 91-94% of the TP[47,48], 64% of the TN[48], and 28% of the DSi[49] are eliminated annually from the water column. Furthermore, in a series of US-based reservoirs, the median N:P ratio is 38:1, and as HRT increases, N:P ratios tended to increase along the freshwater continuum[50]. In this study, at lower HRT they hypothesize that the N:P ratio is altered primarily due to N loss via denitrification **[G]**, while at longer HRT, the loss of P via burial becomes increasingly dominant. The mechanisms driving preferential P elimination in reservoirs are unclear, but could be due to the predominance of P-limitation in freshwater bodies or to the ready sorption of dissolved P species to mineral surfaces[50]. Additionally, the atmospheric fixation source can decrease net N elimination compared to P elimination[40].

Though P is typically the most efficiently eliminated nutrient in reservoirs, a comparison of global elimination relationships with HRT (**Fig. 2**) indicates that at HRTs below ~50 days, Si can be eliminated more efficiently than P and N (as defined by the Redfield-Brezinski ratio[194] **[G]** as C:N:P:Si = 106:16:1:15–20). In the Three Gorges Dam reservoir where the HRT is 27 days, for example, there is preferential elimination of Si (72% of DSi and 16% of BSi) over P (50%) in the Three Gorges Dam reservoir[51,52,53]. Although mechanisms governing preferential Si elimination, including the formation, sedimentation, and eventual preservation of diatoms, in standing freshwater environments are still poorly understood, experimental results show that diatoms dominate over other algal species in these systems as long as Si concentrations exceed 2 µM (global freshwater average ≈ 160 µM; REF[54,55,56]). Therefore, it has been hypothesized that preferential Si elimination at low HRTs is due to the ability of diatoms to establish communities more rapidly than other phytoplankton communities[57,58], conferring the diatoms an advantage in the turbulent, light-limited environments that are characteristic of high-discharge (thus low HRT) hydroelectricity reservoirs[59].

[H2] Dam impacts to downstream ecosystems

In river networks worldwide, rising N and P loads have driven increased eutrophication and harmful algal blooms (HABs) in freshwater and coastal zones[58,60-63]. Often this happens through changes to nutrient ratios that shift the limiting nutrient **[G]**, as seen after the construction of dams. As a consequence of damming altering the limiting nutrients, the phytoplankton species that dominates can also change, often to toxic algae or cyanobacterial species. However, reducing the load of this nutrient through dammed reservoir nutrient retention can help mitigate the extent of eutrophication or HABs[64,65]. Historically, freshwaters have generally been considered P-limited[64,65] and coastal and marine environments have predominantly been considered N-limited[63,66]. Despite P-limitation, reducing both N and P levels in freshwater systems is needed to limit the development of HAB due to seasonal changes to the limiting nutrient[67,68], N and P co-limitation[69,70], and the remobilization of legacy P from sediment to the water column or groundwater[71-74]. Furthermore, reducing P loads alone can force downstream coastal environments to deal with higher N:P ratios, leading to eutrophication and HABs. However, as with freshwater systems, there is a growing understanding that managing only N in coastal zones is not sufficient to mitigate eutrophication[66]. For example, the role of Si-limitation is crucial in the development of coastal HABs.

Dam-driven changes to nutrient stoichiometry operate in conjunction with other anthropogenic influences to modify ecosystem structure and function along the LOAC. A classic example of the interplay between the effects of river damming, changes to nutrient loading, and human activities followed the construction of the Aswan High Dam on the Nile River in 1965. Damming caused a 90% decrease in flow of the Nile to the Mediterranean, dramatically reducing the flux of N, P and Si to coastal waters[75]. This reduction in nutrients led to a decrease in the local diatom communities, followed by subsidence of coastal prawn and sardine populations that fed on the diatoms[75]. Simultaneous dam-driven limitation of the annual flooding (and thus fertilizing) of the Nile's floodplain drove increased agricultural fertilizer application, resulting in a resurgence in N and P delivery to the Nile Delta that ultimately exceeded pre-dam loads and increased fishery catches beyond pre-dam conditions[76].

Concurrent with changing nutrient loading driven by global damming, N and P have been enriched globally due to the use of agricultural fertilizer and wastewater discharge, which have likely doubled or tripled since pre-industrial times[77-79]. Furthermore, global Si loads to the LOAC have decreased two- to threefold due to the removal of Si-rich plant material during deforestation and agriculture (**Fig. 1**)[80,81]. These changes, combined with the impacts of damming, have likely driven the N:Si and P:Si ratios transported down the major world rivers to coastal zones to be notably higher than in pre-human conditions[82-84], thus promoting Si limitation in downstream environments. As a result, natural diatom communities in Si-limited coastal zones are outcompeted by HAB-forming species that do not need large amounts of Si to survive[85-88]. In addition to the human and ecosystem health concerns associated with the shift away from diatom communities towards HABs, this shift has the potential to alter carbon cycling and coastal food chains as diatoms account for up to 40% of oceanic and 25% of global primary productivity[89,90,91].

In a well-known example of the role that dam construction plays in the development of coastal HABs, the damming of the Danube River led to a >60% decrease in Si at the mouth of the river. This decrease was connected to a six-fold increase in the instance of toxic coastal blooms in the Black Sea, compared with only a two-fold increase in diatom populations[92]. Though the HABs were initially attributed to Si elimination in only the Iron Gates I Reservoir (HRT = 7–11 days)[92,93], it was later evident that the decrease in Si was a result of multiple dams constructed along the entire Danube. This phenomenon was subsequently observed in the Baltic Sea[94,95], supporting that idea that multiple dams along one LOAC can have cascading impacts.

The management of both absolute and relative nutrient loads in dammed rivers is an exercise in balancing trade-offs in complicated systems with many interacting, often contradictory, drivers. Watershed management authorities can attempt to manage the dams to: manipulate HRT to select desired downstream nutrient loads and ratios; respond to dam-driven changes in nutrient loads and ratios by altering upstream or downstream nutrient loading management plans; remove existing dams; or (in rare cases) build new dams specifically for nutrient management. In addition to HRT, managers also need to consider other mechanisms that can govern the extent of nutrient elimination such as light availability, inflowing nutrient loads and ratios, reservoir mixing, temperature, micronutrient limitation, the presence of metal oxide minerals, and other locally specific drivers. Finally, as downstream nutrient loads are impacted by upstream changes, management strategies focused on, for example, reducing N- or P-limitation in freshwater systems may inadvertently harm coastal zones. Furthermore, coastal-centric nutrient management that focuses on solely reducing N loads[66,96,97] may prove ineffective in heavily dammed rivers, due to the preferential elimination of P over N in reservoirs. With about 40% of the global population reliant on marine fisheries for at least 15% of their protein[98], the consideration of dam-driven reorganization of nutrient cycling in watershed management plans should be an obvious priority.

[H1] Damming impacts on greenhouse gases

Hydropower has been promoted as a sustainable or "green" energy source for decades, providing an alternative to fossil fuels[99-101]. However, GHGs are often emitted from reservoirs during nutrient elimination through metabolism driving diffusive fluxes from the reservoir surface and ebullition or bubbling from reservoir sediments[23]. Additionally, fluxes are driven by degassing of supersaturated hypolimnion water as it passes through the dam's turbines or spillway[27,102]; and downstream riverine fluxes to the atmosphere[103,104] (**Fig. 3**). Nevertheless, the importance of dam reservoirs as a GHG source has been heavily debated[24,105-107], primarily due to uncertainties in: the mechanisms responsible for GHG production and emission; baseline GHG fluxes of undammed LOACs[108]; the magnitude of both global and local GHG fluxes to the atmosphere[23,109] (**Table 1**); the variability in reservoir GHG emissions through time[26,110]; the potential offset of emissions through burial of C or N in reservoirs[111-113]; and the warming potential of reservoir GHG emissions relative to that of fossil fuel energy sources, per equivalent unit of energy generated[101,114]. We focus this section on processes that lead to GHG emissions from reservoirs in the context of evaluating trade-offs associated with the relationships (or lack thereof) between elimination, reservoir HRT, and inflowing nutrient loads.

[H2] Carbon based emissions.

Global estimates of CO_2 and CH_4 emissions from reservoirs surfaces vary widely (**Table 1**), influenced by emission rates and the reservoir surface area used in global databases. Based on a global reservoir surface area of 1.5 x 10^6 km^2, an estimated 273 Tg C CO_2 yr^{-1} and 52 Tg C CH_4 yr^{-1} are emitted from reservoirs each year[115]. Using a global reservoir area of 3.05 x 10^5 km^2, emissions were estimated to be 36.8 Tg C CO_2 yr^{-1} and CH_4 of 13.3 Tg C CH_4 yr^{-1} (REF[23]). For global hydropower reservoirs (area = 3.4 x 10^5 km^2), annual emissions are estimated to be 48 Tg C as CO_2 and 3 Tg C as CH_4 (REF[26]). However, not all the carbon eliminated in reservoirs is converted to GHG, as organic carbon (OC) burial in global reservoirs has been estimated as 26 Tg C yr^{-1} (area = 3.05 x 10^5 km^2, REF[112]), 60 Tg C yr^{-1} (area = 3.5 x 10^5 km^2, REF[116]), 160–200 Tg C yr^{-1} (area = 4.0 x 10^5 km^2, REFS[117,118,119]), and 290 Tg C yr^{-1} (area = 6.6 x

10^5 km^2, REF[120]). Per unit area, these global emissions fluxes fall within a smaller margin, with global emissions ranging from 120 - 181 g C CO_2 m^{-2} yr^{-1} and emissions ranging from 35 – 44 g C CH_4 m^{-2} yr^{-1}. Conversely, areal burial fluxes range substantially, from 85 – 500 g C m^{-2} yr^{-1}.

Within the global estimates, notable differences in GHG emissions from reservoirs are seen regionally. Gaseous carbon emissions from reservoirs in tropical regions are generally higher than emissions in boreal and temperate reservoirs, partially due to their large surface areas, high volumes of flooded biomass and soil OC, and warmer water temperatures [23,25,110] (**Table 1**). Tropical Chinese reservoirs tend to be the exception due to national policy requiring pre-flooding clearing of vegetation and biomass[121-124]. For example, emission rates of CO_2 (5.81–40.8×10^4 µg C m^{-2} day^{-1}) and CH_4 (0.10–0.30×10^4 µg C m^{-2} day^{-1}) from the cascade of reservoirs in the Upper Mekong River are much lower than the global mean emission rates from reservoirs (106×10^4 and 1.29×10^4 µg C m^{-2} day^{-1} as CO_2 and CH_4, respectively), and decrease linearly with the reservoir's age[125]. Similarly, the Three Gorges Reservoir has a lower CH_4 emission rate (0.38 ×10^4 µg C m^{-2} day^{-}1) than observed in most new tropical (16.0 × 10^4 µg C m^{-2} day^{-1}) or temperate (1.38 ×10^4 µg C m^{-2} day^{-1}) reservoirs[126] (**Table 1**). Unlike these Chinese reservoirs, four of the most heavily studied Amazonian reservoirs (Balbina, Tucuruí and Samuel in Brazil and Petit Saut in French Guiana) were not cleared prior to impoundment and consequently have CO_2 emissions measured as 91.3, 285, 1172 and 123×10^4 µg C m^{-2} day^{-1}, respectively[102,127], all substantially in excess of the worldwide average for reservoir CO_2 emissions (**Table 1**). While the Brazilian government requires biomass clearing before flooding, incomplete clearing can still drive substantial emissions from biomass-rich Amazonian reservoirs[128].

For many dammed river systems, ongoing eutrophication is driving reservoirs towards increased autotrophy **[G]**, as increased nutrient concentrations enable planktonic communities to increase photosynthesis relative to respiration[129-131]. The consequence of this productivity shift is increased carbon sequestration via burial in reservoir sediments[112] (**Fig. 3**), but methanogenesis **[G],** and thus CH_4 emissions, are often increased. The concurrent increase in CH_4 emissions alongside rising autotrophy was seen in a summary of CH_4 emissions measurements from reservoirs worldwide, in which eutrophic reservoirs typically have CH_4 emissions an order of magnitude larger than oligotrophic **[G]** reservoirs[21].

[H2] N_2O emissions.

Globally, reservoirs emit 3.7 Tg N yr^{-1} as N_2 via denitrification[27], bury 1.54 Tg N yr^{-1} in sediments[40], and fix 0.98 Tg N yr^{-1}. Enhanced river network denitrification is beneficial for nutrient-rich river systems when it eliminates excess nitrate from the water column but, along with nitrification **[G],** it can produce N_2O (REF[132]), which has 298 times the global warming potential of CO_2. Global reservoir N_2O emissions are between 20–71.5 Gg N yr^{-1} (REF[23,27]), with higher areal N_2O emissions rates (0.94-1.6 g N m^{-2} yr^{-1}) than lakes[35], rivers, and estuaries (a combined 0.01 – 0.15 g N m^{-2} yr^{-1}), by more than an order of magnitude[27]. Indeed, N_2O emissions from reservoirs account for more than half of the emissions from lentic (freshwater) water bodies (assuming N_2O emissions of 34±21 Gg N yr^{-1} out of 63±41 Gg N yr^{-1}), despite only accounting for 9% of the global lake plus reservoir surface area[35]. These high emission are due in part to the disproportionately high TN load that flows along dammed rivers relative to the load delivered to natural lakes, many of which are located above 50° latitude bands (44%) and tend to be nutrient poor[35]. Furthermore, reservoirs have an average upstream watershed area of > 12,000 km^2 compared to an average of only 617 km^2 for lakes[133], enabling the accumulation of larger nutrient loads in the rivers that feed into reservoirs[35].

Relating HRT to denitrification, nitrification and N_2O emissions is not always straightforward. At long enough HRTs, N_2O produced via denitrification is eventually reduced to N_2 (and not emitted as N_2O), and in reservoirs with HRTs above 6–7 months, more reservoir N_2O emissions are produced via nitrification than by denitrification[23]. Furthermore, there is a strong inverse relationship between the area-normalized N_2O emissions rate and the HRT[35], suggesting that reservoirs with short residence times emit more N_2O per unit area than reservoirs with long residence times. Thus, while many of the ecological impacts related to nutrient elimination could be minimized in small reservoirs with low HRTs, N_2O emissions can be higher than in large reservoirs, which are often conventionally considered environmentally problematic.

[H2] Dam management and GHG.

Reservoirs can be notable sources of GHGs in the years immediately following dam construction[25,125,134] (**Fig. 3**). The decomposition of flooded terrestrial soil and biomass organic matter drive CO_2 and CH_4 emissions for more than a decade after impoundment, and is influenced by the reservoir age, surface area, mass of OC flooded, and temperature[26,135]. Similarly, oscillations in seasonal water levels can contribute to enhanced emissions through repeated wetting and drying cycles. For instance, marshes in the drawdown zone of the Three Gorges Reservoir account for ~19% of total reservoir emissions[136], and the water column acts as an N_2O source for the first 1.5 days of rewetting before switching to a sink for the remainder of wet–dry cycles. These results suggest that newly created (or recreated) flood zones, with organic-rich sediments and frequent variations in water levels, could also become hotspots for GHG emissions after dam removal[105]. This idea is evidenced by the magnitude of hypothetical CO_2-equivalent emissions from the largest 10 reservoirs in the United States once they are decommissioned[137]: after 100 years of damming, post-deconstruction emissions would exceed those of the reservoir's lifetime emissions by 9 times. At present, strategies to avoid this consequence of dam removal have not been developed.

Individual reservoir and watershed-scale assessments can be successfully developed to optimize the local tradeoffs associated with gaseous biogeochemical cycles and reservoir services. For example, Brazil's primarily lowland topography plays a major role in the large magnitude of emissions from its reservoirs[138]; as a result a basin-scale multi-criteria optimization framework, which strategizes dam locations to maximize hydroelectricity generation while minimizing GHG emissions, was proposed for the Amazon River basin[138]. Ultimately, the net worldwide impact of dam construction on GHG emissions is uncertain, and so this approach of focusing on maximizing efficiency for individual basins represents the most feasible course of action.

[H1] Impact of reservoir size

Although there is generally a positive relationship between the magnitude of nutrient elimination and reservoir HRT, small reservoirs may have disproportionately high biogeochemical reactivity **[G]** per unit area or time. For example, first order OC decomposition rate constants (k_{OC}), which describe the reactivity per unit time, increase as HRT decreases[139] (**Fig. 4**). When scaled, this relationship results in decreasing OC mineralization rate constants with distance down the LOAC; this decrease is due to the breakdown of highly reactive material in headwater streams with low HRTs, and the subsequent downstream transport of the less labile **[G]** material to larger water bodies with higher HRTs. For instance, in an analysis of over 200 lakes and reservoirs, inverse relationships between HRT and elimination rate constants for TP, TN, nitrate, and phosphate were identified[46] (**Fig. 4**). Because small water bodies have very low discharges, absolute nutrient fluxes still tend to be small, but when many small reservoirs are linked along the LOAC, their nutrient elimination capacity can be high[140]. The mechanism responsible for greater nutrient reactivity in small water bodies has been attributed to the increasing sediment–water interface contact area to volume ratio as the size of the water body decreases [140,141].

Despite their importance, a spatially explicit estimate of reservoir nutrient and carbon transformation in small reservoirs is virtually impossible to conduct within acceptable uncertainty bounds, largely because there is no complete database of the estimated ~16.7 million reservoirs worldwide[142]. Currently the most complete and spatially explicit, georeferenced dam database is the Global Georeferenced Database of Dams (GOOD[2]), composed of 38,660 manually digitized dams that are visible in Google Earth[143]. However, GOOD[2] is not aligned to an existing river network digitization (such as HydroSHEDS[144]) and that it lacks reservoir physical parameters needed to make biogeochemical predictions (including HRT), making large scale estimate difficult. Other estimates of nutrient retention or elimination in small reservoirs have relied on size distribution functions, typically Pareto, applied randomly to river systems or lumped into watersheds worldwide[145-148]. These estimates provide a foundation for future research investigating the relative importance of small reservoirs in global nutrient cycling. However, due to the lack of reservoir integration within watershed routing networks, predicting nutrient loads to these reservoirs is difficult.

A key outstanding question is whether building a series of cascading small dams in lieu of a single large dam is environmentally preferable. Evidence suggests that multiple small reservoirs with HRTs that sum to the same HRT as a single large reservoir will eliminate nutrients and reduce downstream nutrient loads more efficiently than a single large reservoir[140]. 'Pre-dams' (small upstream dams) that reduce nutrient loads to downstream reservoirs have occasionally been constructed to alleviate downstream eutrophication problems[149,150]. Along these lines, it may be possible to further use dams or pre-dams to mitigate coastal eutrophication problems, particularly if there is a strong need to reduce P loads. The trade-off with this approach is that pre-dams may merely serve to drive eutrophication problems further upstream, whilst further amplifying other ecosystem changes associated with river regulation. Evidence for pre-dam effectiveness is also mixed—even with careful design focused on maximizing P and N retention in pre-dams upstream of German drinking water reservoirs, it was recommended that the pre-dams be emptied and dredged every 5–10 days in order to remain effective[150]. Finally, there is little information available on the elimination of each nutrient element relative to each other in small systems.

[H1] Nutrient management with dams

As reservoirs can eliminate nutrients, there is growing interest in manipulating dam operations to regulate reservoir and riverine trophic conditions, as evidenced by major legislative efforts encouraging the development of new approaches for river flow regulation. The conceptual basis of the environmental-flow (e-flow) approach is to optimise the river flow management to provide services to humans (such as water supply and hydropower) whilst protecting the aquatic environment. In already impacted systems with heavily regulated flows and associated ecosystem effects, such as decreased fish populations or enhanced downstream streambed sediment scouring (**Fig. 5a-c**), e-flow approaches can be applied to restore these systems[151-153]. Generally this approach involves a substantial modification of the flow regime[154] through the maintenance or (re-)introduction of river flow dynamics, based on the objectives for the particular river system[155,156].

One e-flow approach, hydro-peaking **[G]** , has been studied in many parts of the world[157], but the focus of these e-flow studies has typically been ecological, for instance, examining the relationship between flow dynamics and changing temperature[158] on fish or invertebrate populations. Periodic high-flow events (**Fig. 5d-f**), such as annual flooding, have now been incorporated into operational reservoir outflows in many areas, such as the dammed Spöl River in Switzerland[159]. In an 18-year study, most physicochemical variables in the Spöl River followed strong seasonal cycles unrelated to flow regime change[159]. N and P concentrations in outflow waters did increase over the study duration, but the role of the annual floods was negligible in this increase, as nearby unregulated rivers showed similar long-term trends that are likely linked to catchment-scale processes or climate change[160].

Seasonal compensation flow adjustments are a common e-flow regulation method. In these adjustments, reservoir outflow (which is based on the percentage relative to the unmodified flow)[155, 161, 162] provides low flows during dry seasons, with stepped flow increases in wet seasons (**Fig. 5d-f**). Amongst these applications, e-flows designed specifically for downstream water quality management are still rare, but have been examined. For example, in Korean rivers, TP and TN concentrations have been related to storage–release periods of irrigation reservoirs, with downstream TN concentrations elevated during non-irrigation periods when outflows were reduced[163]. Similarly, along the Euphrates River in Iraq, irrigation, subsequent return flows, and reduced flows from upstream reservoirs have been linked with increasing dissolved solid loads over >30 years[164]. In response, maintaining minimum flows into the Euphrates via water diversion has been proposed to mitigate excess dissolved load[164]. Finally, in the Klamath River, USA, flow alterations can be used to modify nutrients, water temperatures and water quantity in order to improve conditions downstream from cyanobacteria bloom-impacted reservoirs, where cyanotoxins and anaerobic conditions can pollute drinking water sources, and harm fisheries and aquatic life[165].

Although these studies suggest that reservoir management for e-flows could ameliorate some downstream water quality issues, there are likely to be local constraints. For example, regulators must consider the seasonality of water quality problems versus water availability for environmental flow allocation, as well as reservoir operational constraints that could limit the volume of water release or the location of water release in the reservoir water column[166,167]. Reintroducing large flow variations might also inundate floodplains and riparian soils, which may lead to the transfer of nutrients and organic matter into rivers or enhance GHG emissions[168]. The limited evidence in this area highlights the need for more studies to systematically examine the use of e-flows in mitigating the effects of dams on river nutrient cycling and downstream fluxes. For instance, high temporal resolution watershed-scale models that represent nutrient flux dynamics along the LOAC could be used to test single and cascading dam operation scenarios with e-flow regimes. Modeling efforts could also be used to select for desirable nutrient elimination by manipulating existing dams to maximize or minimize HRTs (**Fig. 5g-i**) to coincide with high or low nutrient loads.

[H1] Dam removal

In recent years, dam removal in Europe and North America has become commonplace, driven by ageing infrastructure and growing interest in river restoration and environmental concerns[169,170]. For example, in the U.S. alone, more than 1,200 dams have been removed since the year 2000 (REF[171]). Most dam-removal studies have focused on the physical effects of the removal, such as metrics associated with hydraulics, channel morphology, and sediment dynamics, or effects on fish communities. However, despite notable downstream effects associated with nutrient and contaminant release, there is insufficient understanding of dam removal impacts across the LOAC[172], particularly with regard to downstream nutrient dynamics and water quality.

Legacy nutrients and contaminants, typically defined as elements or compounds that remain in the landscape or system beyond a year after their application[173], accumulate in reservoir sediments over the course of a dam's lifespan, and are eroded downstream due to increased flows when dams are removed. The remobilization and downstream impacts of legacy nutrient and contaminant remobilization are increasingly being recognized and discussed in the context of dam construction and removal. For instance, the effects of legacy contaminants have been seen in New York, USA, where industrial use of polychlorinated biphenyls (PCBs) at Ft. Edward and Hudson Falls led to an accumulation of PCBs in reservoir sediments above the Ft. Edward hydroelectric dam. These legacy contaminants were mobilized and released downstream after the dam was removed in 1973 (REF[174]), and PCB transport continues to be documented today[175], despite massive remediation efforts[176]. Legacy nutrients can behave similarly, with multifold increases in downstream N and P concentrations being documented after the release of reservoir sediments due to breaches or changes in management[172]. As an example, flushing of sediments from the Guernsey Reservoir in the western US led to a six-fold increase in downstream P concentrations[177]. In British Columbia, drawdown of water levels of the Capilano Reservoir caused enhanced erosion of reservoir sediments, driving downstream ammonium concentrations to increase by two orders of magnitude[178], and after removal of a low-head dam on the Olentangy River (Ohio, USA), downstream nitrate concentrations were increased three-fold[179].

In addition to mobilizing legacy nutrients or pollutants in reservoirs, dam removal and reservoir drainage cause water tables above the removal site to drop[180]. This drop increases both the downstream river channel depth and cross-sectional area, leading to bed degradation, a lowering of the stream water surface, incision of the stream bed, and erosion of nutrient-rich sediments[172]. As observed in the U.S. mid-Atlantic region, for example, the removal or breaching of thousands of small mill dams resulted in the erosion of stream banks at rates ranging from 0.05 to over 0.2 m yr^{-1} (REF[181]). Furthermore, some of the nutrient-rich sediments released there may account for a substantial portion of current stream nutrient loads in the region[181]. Therefore, dam removal may be at odds with policy goals to reduce watershed nutrient loading[172,182], highlighting the need to consider how and on what timescales that dam removal impacts legacy nutrient remobilization.

Leaving aging dams in place, however, does not ensure that legacy nutrients will remain trapped in upstream reservoirs. When an aging dam is left in place, sediment and nutrient elimination efficiencies can decrease over time due to reservoir infilling[183] (thus decreasing reservoir volume and therefore HRT), so a reservoir that retains 70-80% of incoming nutrient loads early in its lifespan may actually serve as a nutrient source after many years of operation. For example, above the Conowingo dam, constructed in 1928 at the mouth of the Susquehanna River (Maryland, USA)[184], TP concentrations have decreased in the last 10-15 years, likely due to nutrient management strategies implemented to lower nutrient loading to the Chesapeake Bay. Below the dam, however, no such reductions have been observed. Indeed, reservoir output versus input ratios for TP have increased since 2000, with net deposition rates of sediments and TP decreasing across a range of different flows. These findings suggest that the Conowingo reservoir, approximately 90 years after its initial construction, is reaching the end of its "effective life" for sediment removal[184]. In Europe and North America especially, many aging dams and reservoirs are reaching—or have already reached—their sediment-holding capacities. Thus, perhaps the primary concern should not only be whether legacy nutrients will be released as a result of dam removals, but also to what extent existing reservoirs are already beginning to act as nutrient sources (**Fig. 3**), particularly at low flows.

[H1] Future perspectives

Conversations that pitch all dams as problematic are not productive, just as conversations that laud dams as the most viable sustainable energy source in the era of climate change are misleading. Damming rivers to produce energy, control floods, and balance the unequal distribution of water over time is unlikely to stop. If dams are constructed without considering their impacts on nutrient cycling, then changes to coastal nutrient ratios, increased prevalence of HABs, unnecessarily large GHG emissions, and reservoir in-filling and eutrophication will likely continue. However responsible dam construction and management — from conception to deconstruction and in the context of the entire watershed — may be achievable by balancing the environmental impacts of damming with the services provided by it. Based on the biogeochemical impacts of damming discussed in this Review, we posit that LOAC biogeochemistry should be considered at each stage of a dam's life cycle, and ideally during dam conception and planning (**Box 1**).

The inclusion of nutrient elimination and GHG emissions in multi-criteria optimization regimes and quantitative trade-off analyses would be a major step towards achieving sustainable dam construction across entire river basins. These methods to manage trade-offs have successfully have been applied to enable water availability or hydroelectricity generation as well as to maintain flows for river ecosystems[185,186]. Such optimization regimes have also been applied to dam removal scenarios in the Willamette River basin (Oregon, USA), where it was shown that removing 12 dams would hydrologically reconnect 52% of the basin while only eliminating 1.6% of the water storage capacity and hydroelectricity production[200]. Using HRT and nutrient loads to predict the magnitudes of nutrient elimination can be used as a simple starting point to incorporate biogeochemistry into these management methods, and e-flow approaches or dam removal plans can subsequently be considered as implementation strategies within or in addition to these optimization regimes. However, these approaches must be applied across the whole watershed approach in order to avoid transferring nutrient-related challenges to another part of the LOAC.

The relationships between the HRT and nutrient elimination and loading provide a starting point to develop management plans that account for the evolving roles of reservoirs as biogeochemical hot spots on the LOAC. However, the damming-related changes to nutrient cycles represent only one essential priority in responsible dam and watershed management. It is crucial to consider both societal and environmental needs, including maintaining the dam's services, while subsequently ensuring the local and downstream environments and communities are not negatively impacted. Social impacts such as transboundary water quantity and quality disputes, fishery health and drinking water quality, recreation and ancestral or spiritual significance of river systems necessitate the involvement of social scientists working alongside biogeochemists, engineers, biologists, and economists. Interdisciplinary collaboration is necessary to move towards a more complete inclusion of source-to-sea changes to biogeochemical cycles and their consequences in optimizing dam management.

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The authors declare no competing interests.

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Related links

http://globaldamwatch.org/: Public access to GOOD^2, GRanD and FHReD databases of existing and future dams and reservoirs worldwide, as well as links to external global and regional databases.

Key points

- **Nutrient elimination in dam reservoirs modifies global biogeochemical cycles, with consequences to ecosystem structure and function along river networks.**
- **The global importance of reservoirs as greenhouse gas sources and/or sinks remains heavily debated.**
- **The reservoir hydraulic residence time can be used to develop simple relationships to predict nutrient eliminations, though small reservoirs can have large elimination efficiencies.**
- **Dam management strategies impact nutrient cycling at all phases of a dam's life cycle, including removal.**

Table 1: Areal CO_2 and CH_4 emissions from reservoirs*.

Dam region	**CO_2 emissions** ($\times 10^4$ μg C m^{-2} day^{-1})	**CH_4 emissions** ($\times 10^4$ μg C m^{-2} day^{-1})	**References**
		Any purpose	
Global	33.0	4.71 (1.20 – 8.22)	21, 187
Temperate	34.8 (31.3 – 38.2)	1.38 (1.17 – 1.50	115, 104, 187
Tropical	92.6 (89.0 – 95.5)	16.0 (9.44 – 22.5)	115, 104
Boreal	72.4	8.20	24, 104

China	53.2	1.02	188
Hydroelectric			
Global	38.7	2.41	24
Amazonian	110	13.7	24
Non-Amazonian tropical	68.5	4.11	24
Temperate	10.6	0.22	24
Boreal	20.5	0.69	24

*If multiple estimates are available, the mean value across studies is given, with the range of estimates recorded in the literature given in brackets.

Figure 1: Changes to nitrogen, phosphorus, and reactive silicon fluxes along the LOAC. Qualitative river network nutrient fluxes along a simplified dammed land-ocean aquatic system (LOAC) for total nitrogen (TN) (**part a**), total phosphorus (TP) (**part b**), and reactive silicon (RSi) (**part c**), which includes dissolved (DSi) and biogenic (BSi) silica, are shown. The globally averaged reservoir elimination of TN, TP and RSi are shown in the context of major nutrient sources and sinks along the LOAC. Despite preferential elimination of TP in reservoirs, enhanced anthropogenic agricultural and wastewater nutrient loading has resulted in overall net increases in TN and TP in coastal zones. Conversely, reservoir RSi elimination is compounded by RSi loss along the LOAC due to deforestation and cultivation, driving a net decrease in RSi loads to coastal zones compared with pre-human fluxes. Note that the shown river network processes can happen downstream of a reservoir and are shown as upstream here for simplicity, and addition of nutrients via weathering is represented by the gradual widening of the arrows along the entire LOAC. In-reservoir percent changes are relative to the influx and are calculated as arithmetic averages for all reservoirs considered in REFS[55,39,40] for year 2000. Subscript “nat” represents the natural or pre-human

fluxes delivered to coastal zones, and subscript "anthro" represents the anthropogenic or modern-day fluxes delivered to coastal zones.

Figure 2: Elimination of nitrogen, phosphorus and silicon from reservoirs. Elimination measurements and modeled HRT–elimination relationships are shown for ammonium (NH_4^+), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), nitrate (NO_3^-), and total dissolved N (TDN) in reservoirs[40] (**part a**), total phosphorous (TP), total dissolved phosphorus (TDP) and soluble reactive phosphorus (SRP) [39,46] (**part b**), and dissolved silicon[55] (DSi) (**part c**). For all nutrients, published modeled relationships between HRT and elimination are also shown[39,55,40]. On average, TP is the most efficiently eliminated nutrient at most HRTs, with the exception of reservoirs with HRTs below 50 days, where DSi can be more efficiently removed. Elimination measurements show considerably more scatter than modeled relationships, indicating that while HRT is a useful first order predictor, elimination is dependent other mechanisms, including light availability, inflowing nutrient loads and ratios, reservoir mixing, temperature, micronutrient limitation, or the presence of metal oxide minerals. Additional factors that can skew the calculation of worldwide trends from published measurements include inconsistencies in the nutrient species measured, the methods through which reservoir nutrient budgets are calculated, and the seasonality of the reservoir measured. Negative elimination values indicate a net export, such as remobilization or a nutrient source other than the water column, as occurs in N fixation.

Figure 3: Key nutrient processes during a reservoir life cycle. Simplified C (blue, with methane in dark blue arrows), N (green), P (purple), and Si (yellow) dynamics are shown for young (**part a**), middle aged (**part b**), and old reservoirs (**part c**). Young reservoirs are typically characterized by large greenhouse gas (GHG) emissions due to the breakdown of flooded soil and biomass, and tend be dominated by respiration rather than photosynthesis. Nutrients accumulate as the reservoir ages, driving increased photosynthesis

and rising autotrophy, which can develop into algal blooms in middle-aged reservoirs. GHG emissions decrease as flooded biomass is eliminated. Sediment accumulates in the reservoir over time, which can promote downstream streambed scouring due to the under-saturation of suspended sediment in river water. In old reservoirs, sediment accumulation can become severe, serving as a point source for nutrient remobilization to downstream, and nutrient saturation can drive large, potentially harmful algal blooms, causing fish mortality and anoxia.

Figure 4. Relationships between hydraulic residence time, nutrient reactivity and elimination. On the left axis, the first order reactivity rate constants (yr^{-1}) for total nitrogen (TN) removal (k_{TN}), total phosphorus (TP) removal (k_{TP}) and organic carbon (OC) degradation (k_{OC}), are plotted as a function of the hydraulic residence time (HRT) in years[140,139]. On the right axis, the globally modeled average fraction of nutrient elimination (unitless) of the inflowing nutrient load as a function of HRT for denitrification (denit) and TN burial[40], TP burial[39], and allochthonous (allo) or autochthonous (auto) dissolved OC (DOC), particulate OC (POC) or total OC (TOC) mineralization (min)[112]. Reactivity describes the system's ability to remove or transform nutrients per unit time, whereas the elimination is a function of the reactivity and the HRT. Small reservoirs tend to have higher reactivity, while large reservoirs have higher overall elimination due to their long HRTs.

Figure 5. Environmental flow dynamics in different flow regimes and damming scenarios. Natural and dam-altered river flow regimes by month for a hypothetical alpine hydropower dam (**part a**), a temperature zone reservoir used for drinking water (**part b**), and a Mediterranean reservoir used for irrigation[189] (**part c**). Flood-only and seasonal compensation environmental flow (e-flow) scenarios are shown for the same reservoirs (**parts d-f**). The catchment-scale hydraulic residence time (HRT) corresponding to the natural, altered, and e-flow scenarios shown in the left and middle columns are also presented (**parts g-i**). The e-flow scenarios illustrate some reservoir management alternatives to simple

year-round constant flows. The e-flows continue to regulate flows in predictable ways while also allowing for spring flooding or seasonal high flows to better replicate natural flow variations[190,191]. Basin-wide HRT responses to these e-flows scenarios can be used as a starting point to predict how and when nutrient elimination will be maximized or minimized.

[b1] **Dam management considerations**

[H1] Conception and planning

If managed and planned appropriately, from conception to deconstruction and in the context of the entire watershed, dams can come closer to delivering the services for which they are intended with minimized environmental and social consequences. The most responsible dam management plan would address all of the following questions in the before building a dam. Given the current boom in dam construction worldwide, proper planning and management is crucial.

[H2] Size and types of dam(s). Should one large dam be built (one long hydraulic residence time, or HRT), or multiple small dams (many small HRTs)?

[H2] Location(s). Should all dams be built on a single tributary or spread throughout the watershed?[192] Will headwater dams eliminate fewer nutrients and produce fewer greenhouse gases (GHG) than lowland or downstream dams due to lower riverine nutrient and carbon loads?

[H2] Lifespan. How long can we expect the dam in question to maintain the services it provides without increases in its environmental, social, and economic costs? Will the nutrient loads and HRT promote high nutrient elimination in the form of sedimentation in the reservoir?

[H2] GHG emissions. Should biomass be cleared prior to flooding? How do reservoir GHG emissions compare to those from other energy sources with respect to the life cycle analyses? Where can a dam be built within a basin to minimize GHG e missions while maximizing hydroelectricity production?

[H2] Eutrophication. How will reservoir, downstream and coastal nutrient ratios be impacted? Do the predicted reservoir HRT and nutrient loads indicate that there will be substantial nutrient elimination?

[H2] Management. How will existing watershed nutrient management strategies need to change in the context of the new dam? How will the basin-wide HRT change? Will nutrient elimination in the reservoir change nutrient stoichiometry downstream? How will these changes interact with existing nutrient loading management strategies?

[H1] Existing dams

[H2] ***Nutrient load management***. Can we modify existing dam operation to generate desirable basin-wide HRTs using environmental-flows (e-flows), and if so how will different e-flow scenarios influence downstream water quality?

[H2] Is it more feasible to manage the upstream nutrient loads than to attempt to use dam operation for nutrient management?

[H1] Deconstruction

[H2] ***Remobilization:*** How can the remobilization and mineralization and/or emissions of deposited sediment, nutrients, and organic carbon be managed?

Glossary terms

- Elimination: For nutrients, the net removal of nutrients or nutrient species from the water column in reservoirs via sedimentation and burial or gaseous evasion to the atmosphere.

- Eutrophication: The over-enrichment of a water body with nutrients, driving high primary production (photosynthesis) and excessive growth of algae, often resulting in harmful algal blooms or toxic cyanobacterial blooms and the development of anaerobic or anoxic conditions.

- Denitrification: Biological reduction of nitrate (NO_3^-) to N_2 gas through a series of intermediate reaction steps that can produce nitrite (NO_2^-), nitric oxide (NO) and nitrous oxide (N_2O).

- Redfield-Brzezinski ratio: An extension of the Redfield ratio (C:N:P = 106:16:1), the Redfield-Brzezinski ratio describes the average elemental molar composition of diatoms, defined as C:N:P:Si = 106:16:1:15-20.

- Limiting nutrient: The nutrient that is stoichiometrically in short-supply in a system, typically benchmarked in aqueous biogeochemistry using the Redfield or Redfield-Brzezinski ratios.

- Autotrophy: Primary production that derives carbon from carbon dioxide and energy from sunlight (photosynthesis) or an inorganic chemical.

- Methanogenesis: The formation of methane by methanogenic microbes; a form of anaerobic respiration.

- Oligotrophic: A water body characterized by low nutrient concentrations and thus low primary productivity.

- Nitrification: The biological oxidation of ammonium (NH_4^+) to nitrate (NO_3^-). Produces nitrous oxide (N_2O) as a by-product.

- Biogeochemical reactivity: In first order reaction kinetics, biogeochemical reactivity is represented by a rate constant (k) in units of inverse time [T^{-1}] that is multiplied by the nutrient mass or concentration to calculate the rate or flux of a process.

- Labile: Reactive, easily degradable, highly bioavailable chemicals.

- Hydro-peaking: A type of flow regulation that produces short-term, high flow events in river discharge.

ToC blurb

River damming can harness hydropower, control flooding, and store water, but also can alter biogeochemistry in reservoirs and downstream environments. In this Review, the impacts of dams on nutrient cycling and greenhouse production are discussed, emphasising the need to consider biogeochemical cycling at all stages of dam lifespan.