



UNIVERSITY OF LEEDS

This is a repository copy of *River dam impacts on biogeochemical cycling*.

White Rose Research Online URL for this paper:

<http://eprints.whiterose.ac.uk/156411/>

Version: Accepted Version

Article:

Maavara, T, Chen, Q, Van Meter, K et al. (4 more authors) (2020) River dam impacts on biogeochemical cycling. *Nature Reviews Earth and Environment*, 1 (2). pp. 103-116. ISSN 2662-138X

<https://doi.org/10.1038/s43017-019-0019-0>

© Springer Nature Limited 2020. This is an author produced version of an article published in *Nature*. Uploaded in accordance with the publisher's self-archiving policy.

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk
<https://eprints.whiterose.ac.uk/>

1 Earth and environmental sciences/Biogeochemistry/Carbon cycle / [URI /704/47/4113]
2 Earth and environmental sciences/Biogeochemistry/Element cycles / [URI /704/47/4112]
3 Earth and environmental sciences/Environmental sciences/Environmental chemistry/Geochemistry [URI
4 /704/172/169/209]
5 Earth and environmental sciences/Environmental sciences/Environmental impact / [URI /704/172/4081]
6

7

8 **River dam impacts on biogeochemical cycling**

9

10 Taylor Maavara^{1,8}, Qiuwen Chen^{2,8}, Kimberley Van Meter³, Lee Brown^{4,5}, Jianyun Zhang², Jinren Ni⁶,
11 Christiane Zarfl⁷

12

13 ¹ School of Forestry and Environmental Studies, Yale University, New Haven, CT, USA

14 ² State Key Laboratory of Hydrology-Water Resources and Hydraulic Engineering, Nanjing Hydraulic
15 Research Institute, Nanjing, China

16 ³ Department of Earth and Environmental Sciences, University of Illinois at Chicago, Chicago, IL, USA

17 ⁴ School of Geography, University of Leeds, Leeds, UK

18 ⁵ water@leeds, University of Leeds, Leeds, UK

19 ⁶The Key Laboratory of Water and Sediment Sciences, Ministry of Education, Peking University, Beijing,
20 China

21 ⁷ Center for Applied Geoscience, Eberhard Karls University of Tübingen, Tübingen, Germany

22 ⁸ These authors contributed equally.

23

24 *e-mail: taylor.maavara@yale.edu; qwchen@nhri.cn

25

26

27 **Abstract**

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

40 **[H1] Introduction**

41 River damming has been practiced for millennia, with the first dams built before 2000 BCE in the Egyptian
42 empire¹. The number of dams increased steadily prior to the Second World War, but expanded rapidly
43 thereafter, peaking in the 1960s and 1970s, with most construction in North America and Western Europe².
44 A second surge in dam construction began in the early 2000s, with over 3,700 hydroelectric dams either
45 planned or under construction worldwide during this construction boom³, each with a generating capacity
46 of >1 megawatt (MW). Many of the new dams are being constructed in South America, Asia, and the
47 Balkans, largely driven by the need to expand energy production in growing economies^{3,4}. Indeed, by 2015,
48 dammed reservoirs supplied around 30–40% of irrigation water globally^{5,6}, and 16.6% of the world’s
49 electricity was generated by hydropower⁷. Almost two thirds of the world’s long rivers (that is, those >1000
50 km) are no longer free-flowing⁸, and the current surge in dam construction – motivated by the 2016 Paris
51 Agreement and the need for greater renewable energy generation – is expected to double river fragmentation

52 by 2030 (REF⁹). Accordingly, freshwater ecosystems have been referred to as the ‘biggest losers’ of the
53 Paris Agreement¹⁰.

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

65 Dams are often constructed following insufficient environmental impact assessments¹¹.
66 Environmental assessments before dam construction typically include an evaluation of water quality, but
67 the impacts on nutrient cycling are rarely included^{12,13}. In addition, assessments rarely extend beyond the
68 ecosystems immediately surrounding dam construction¹⁴, and often focus on hydrological connectivity¹⁵⁻¹⁷
69 or consequences to fish populations¹⁸⁻²⁰,—and sometimes on greenhouse gas (GHG) emissions from
70 reservoirs²¹⁻²⁵. For example, the environmental consequences of river damming were markedly
71 misunderstood with regard to the Balbina Dam in Amazonas, Brazil, the construction of which led to the
72 degradation of the flooded forest and the equivalent of ~114 years of hypothetical greenhouse gas emissions
73 from coal or natural gas power generation^{26,27}. Meanwhile, in many developing countries, hydroelectric
74 construction projects with generating capacities <10 MW are exempt from any environmental assessment¹⁰.

75 In this Review, we discuss the impacts of river damming on nutrients, specifically C, N, P and Si,
76 with an emphasis on the impacts of nutrient elimination on biogeochemical cycling along the LOAC. We

77 examine dam-related nutrient management strategies, including dam removal, with a focus on managing
78 tradeoffs at the watershed-scale^{28,29}. Our evaluations are based on the hydraulic residence time (HRT,
79 defined as the volume of water divided by the flow through the water body), as it is typically considered
80 the “master variable” governing the relative rates of transport versus biogeochemical reactions³⁰⁻³⁴. The
81 sizes of nutrient loads delivered from upstream are also considered, as they strongly influence nutrient
82 elimination fluxes^{31,35}. Finally, we discuss the use of these parameters as simple approaches to enable
83 improved management of biogeochemical processes in dammed river systems.

84

85 [H1] Dam nutrient dynamics

86 Damming impacts both the absolute and relative nutrient loads (often benchmarked against the Redfield
87 ratio³⁶ stating C:N:P = 106:16:1) and can influence the composition and productivity of an aquatic
88 ecosystem^{37,38}. Dammed reservoirs influence nutrient ratios through nutrient elimination from the water
89 column via burial in sediments or gaseous release to the atmosphere (**Fig. 1**)^{39,40}. Nutrient elimination is
90 calculated using the equation:

$$91 \quad E = \frac{F_{in} - F_{out}}{F_{in}} \quad (1)$$

92 where E is the fraction of eliminated nutrient (unitless), F_{in} is the riverine nutrient influx to the reservoir
93 ($M T^{-1}$), and F_{out} is the efflux ($M T^{-1}$) out of the reservoir through the dam(s). Based on this equation, of
94 the total estimated nutrient loads carried by rivers worldwide^{41,42}, 7.4% of total N (TN; **Fig. 1a**), 12% of
95 total P (TP; **Fig. 1b**), and 5.3% of reactive Si (RSi = dissolved Si (DSi) + biogenic Si (BSi); **Fig. 1c**) were
96 eliminated in reservoirs in year 2000. The increased nutrient elimination compared to undammed states is
97 partially due to dammed watersheds having longer HRTs, fostering biogeochemical and physical
98 transformations that lead to elimination^{26,43-46}. In 1997, for example, it was estimated that HRT was an
99 average of 58 days longer than undammed reservoirs⁶⁸, though this is now likely to be much higher given the
100 recent boom in dam construction.

101 Compared to N and Si, P is generally eliminated most efficiently in reservoirs at most HRTs, with
102 some reservoirs eliminating nearly all of the P from the water column (Fig. 2). For instance, the 400 km²
103 Lake Diefenbaker reservoir in central Canada has a relatively long mean HRT of 1.1 years, and 91-94% of
104 the TP^{47,48}, 64% of the TN⁴⁸, and 28% of the DSi⁴⁹ are eliminated annually from the water column.
105 Furthermore, in a series of US-based reservoirs, the median N:P ratio is 38:1, and as HRT increases, N:P
106 ratios tended to increase along the freshwater continuum⁵⁰. In this study, at lower HRT they hypothesize
107 that the N:P ratio is altered primarily due to N loss via denitrification [G], while at longer HRT, the loss of
108 P via burial becomes increasingly dominant. The mechanisms driving preferential P elimination in
109 reservoirs are unclear, but could be due to the predominance of P-limitation in freshwater bodies or to the
110 ready sorption of dissolved P species to mineral surfaces⁵⁰. Additionally, the atmospheric fixation source
111 can decrease net N elimination compared to P elimination⁴⁰.

112 Though P is typically the most efficiently eliminated nutrient in reservoirs, a comparison of global
113 elimination relationships with HRT (Fig. 2) indicates that at HRTs below ~50 days, Si can be eliminated
114 more efficiently than P and N (as defined by the Redfield-Brezinski ratio¹⁹⁴ [G] as C:N:P:Si = 106:16:1:15–
115 20). In the Three Gorges Dam reservoir where the HRT is 27 days, for example, there is preferential
116 elimination of Si (72% of DSi and 16% of BSi) over P (50%) in the Three Gorges Dam reservoir^{51,52,53}.
117 Although mechanisms governing preferential Si elimination, including the formation, sedimentation, and
118 eventual preservation of diatoms, in standing freshwater environments are still poorly understood,
119 experimental results show that diatoms dominate over other algal species in these systems as long as Si
120 concentrations exceed 2 μM (global freshwater average ≈ 160 μM; REF^{54,55,56}). Therefore, it has been
121 hypothesized that preferential Si elimination at low HRTs is due to the ability of diatoms to establish
122 communities more rapidly than other phytoplankton communities^{57,58}, conferring the diatoms an advantage
123 in the turbulent, light-limited environments that are characteristic of high-discharge (thus low HRT)
124 hydroelectricity reservoirs⁵⁹.

125 *[H2] Dam impacts to downstream ecosystems*

126 In river networks worldwide, rising N and P loads have driven increased eutrophication and harmful
127 algal blooms (HABs) in freshwater and coastal zones^{58,60-63}. Often this happens through changes to nutrient
128 ratios that shift the **limiting nutrient [G]**, as seen after the construction of dams. As a consequence of
129 damming altering the limiting nutrients, the phytoplankton species that dominates can also change, often to
130 toxic algae or cyanobacterial species. However, reducing the load of this nutrient through dammed reservoir
131 nutrient retention can help mitigate the extent of eutrophication or HABs^{64,65}. Historically, freshwaters have
132 generally been considered P-limited^{64,65} and coastal and marine environments have predominantly been
133 considered N-limited^{63,66}. Despite P-limitation, reducing both N and P levels in freshwater systems is
134 needed to limit the development of HAB due to seasonal changes to the limiting nutrient^{67,68}, N and P co-
135 limitation^{69,70}, and the remobilization of legacy P from sediment to the water column or groundwater⁷¹⁻⁷⁴.
136 Furthermore, reducing P loads alone can force downstream coastal environments to deal with higher N:P
137 ratios, leading to eutrophication and HABs. However, as with freshwater systems, there is a growing
138 understanding that managing only N in coastal zones is not sufficient to mitigate eutrophication⁶⁶. For
139 example, the role of Si-limitation is crucial in the development of coastal HABs.

140 Dam-driven changes to nutrient stoichiometry operate in conjunction with other anthropogenic
141 influences to modify ecosystem structure and function along the LOAC. A classic example of the interplay
142 between the effects of river damming, changes to nutrient loading, and human activities followed the
143 construction of the Aswan High Dam on the Nile River in 1965. Damming caused a 90% decrease in flow
144 of the Nile to the Mediterranean, dramatically reducing the flux of N, P and Si to coastal waters⁷⁵. This
145 reduction in nutrients led to a decrease in the local diatom communities, followed by subsidence of coastal
146 prawn and sardine populations that fed on the diatoms⁷⁵. Simultaneous dam-driven limitation of the annual
147 flooding (and thus fertilizing) of the Nile's floodplain drove increased agricultural fertilizer application,
148 resulting in a resurgence in N and P delivery to the Nile Delta that ultimately exceeded pre-dam loads and
149 increased fishery catches beyond pre-dam conditions⁷⁶.

150 Concurrent with changing nutrient loading driven by global damming, N and P have been enriched
151 globally due to the use of agricultural fertilizer and wastewater discharge, which have likely doubled or
152 tripled since pre-industrial times⁷⁷⁻⁷⁹. Furthermore, global Si loads to the LOAC have decreased two- to
153 threefold due to the removal of Si-rich plant material during deforestation and agriculture (**Fig. 1**)^{80,81}. These
154 changes, combined with the impacts of damming, have likely driven the N:Si and P:Si ratios transported
155 down the major world rivers to coastal zones to be notably higher than in pre-human conditions⁸²⁻⁸⁴, thus
156 promoting Si limitation in downstream environments. As a result, natural diatom communities in Si-limited
157 coastal zones are outcompeted by HAB-forming species that do not need large amounts of Si to survive⁸⁵⁻
158 ⁸⁸. In addition to the human and ecosystem health concerns associated with the shift away from diatom
159 communities towards HABs, this shift has the potential to alter carbon cycling and coastal food chains as
160 diatoms account for up to 40% of oceanic and 25% of global primary productivity^{89,90,91}.

161 In a well-known example of the role that dam construction plays in the development of coastal
162 HABs, the damming of the Danube River led to a >60% decrease in Si at the mouth of the river. This
163 decrease was connected to a six-fold increase in the instance of toxic coastal blooms in the Black Sea,
164 compared with only a two-fold increase in diatom populations⁹². Though the HABs were initially attributed
165 to Si elimination in only the Iron Gates I Reservoir (HRT = 7–11 days)^{92,93}, it was later evident that the
166 decrease in Si was a result of multiple dams constructed along the entire Danube. This phenomenon was
167 subsequently observed in the Baltic Sea^{94,95}, supporting that idea that multiple dams along one LOAC can
168 have cascading impacts.

169 The management of both absolute and relative nutrient loads in dammed rivers is an exercise in
170 balancing trade-offs in complicated systems with many interacting, often contradictory, drivers. Watershed
171 management authorities can attempt to manage the dams to: manipulate HRT to select desired downstream
172 nutrient loads and ratios; respond to dam-driven changes in nutrient loads and ratios by altering upstream
173 or downstream nutrient loading management plans; remove existing dams; or (in rare cases) build new
174 dams specifically for nutrient management. In addition to HRT, managers also need to consider other

175 mechanisms that can govern the extent of nutrient elimination such as light availability, inflowing nutrient
176 loads and ratios, reservoir mixing, temperature, micronutrient limitation, the presence of metal oxide
177 minerals, and other locally specific drivers. Finally, as downstream nutrient loads are impacted by upstream
178 changes, management strategies focused on, for example, reducing N- or P-limitation in freshwater systems
179 may inadvertently harm coastal zones. Furthermore, coastal-centric nutrient management that focuses on
180 solely reducing N loads^{66,96,97} may prove ineffective in heavily dammed rivers, due to the preferential
181 elimination of P over N in reservoirs. With about 40% of the global population reliant on marine fisheries
182 for at least 15% of their protein⁹⁸, the consideration of dam-driven reorganization of nutrient cycling in
183 watershed management plans should be an obvious priority.

184 [H1] Damming impacts on greenhouse gases

185 Hydropower has been promoted as a sustainable or “green” energy source for decades, providing an
186 alternative to fossil fuels⁹⁹⁻¹⁰¹. However, GHGs are often emitted from reservoirs during nutrient elimination
187 through metabolism driving diffusive fluxes from the reservoir surface and ebullition or bubbling from
188 reservoir sediments²³. Additionally, fluxes are driven by degassing of supersaturated hypolimnion water as
189 it passes through the dam’s turbines or spillway^{27,102}; and downstream riverine fluxes to the atmosphere^{103,104}
190 (Fig. 3). Nevertheless, the importance of dam reservoirs as a GHG source has been heavily debated^{24,105-107},
191 primarily due to uncertainties in: the mechanisms responsible for GHG production and emission; baseline
192 GHG fluxes of undammed LOACs¹⁰⁸; the magnitude of both global and local GHG fluxes to the
193 atmosphere^{23,109} (Table 1); the variability in reservoir GHG emissions through time^{26,110}; the potential offset
194 of emissions through burial of C or N in reservoirs¹¹¹⁻¹¹³; and the warming potential of reservoir GHG
195 emissions relative to that of fossil fuel energy sources, per equivalent unit of energy generated^{101,114}. We
196 focus this section on processes that lead to GHG emissions from reservoirs in the context of evaluating
197 trade-offs associated with the relationships (or lack thereof) between elimination, reservoir HRT, and
198 inflowing nutrient loads.

199 [H2] Carbon based emissions.

200 Global estimates of CO₂ and CH₄ emissions from reservoirs surfaces vary widely (Table 1),
201 influenced by emission rates and the reservoir surface area used in global databases. Based on a global
202 reservoir surface area of 1.5 x 10⁶ km², an estimated 273 Tg C CO₂ yr⁻¹ and 52 Tg C CH₄ yr⁻¹ are emitted
203 from reservoirs each year¹¹⁵. Using a global reservoir area of 3.05 x 10⁵ km², emissions were estimated to
204 be 36.8 Tg C CO₂ yr⁻¹ and CH₄ of 13.3 Tg C CH₄ yr⁻¹ (REF²³). For global hydropower reservoirs (area =
205 3.4 x 10⁵ km²), annual emissions are estimated to be 48 Tg C as CO₂ and 3 Tg C as CH₄ (REF²⁶). However,
206 not all the carbon eliminated in reservoirs is converted to GHG, as organic carbon (OC) burial in global
207 reservoirs has been estimated as 26 Tg C yr⁻¹ (area = 3.05 x 10⁵ km², REF¹¹²), 60 Tg C yr⁻¹ (area = 3.5 x
208 10⁵ km², REF¹¹⁶), 160–200 Tg C yr⁻¹ (area = 4.0 x 10⁵ km², REFS^{117,118,119}), and 290 Tg C yr⁻¹ (area = 6.6 x

209 10^5 km^2 , REF¹²⁰). Per unit area, these global emissions fluxes fall within a smaller margin, with global
210 emissions ranging from 120 - 181 g C CO₂ m⁻² yr⁻¹ and emissions ranging from 35 – 44 g C CH₄ m⁻² yr⁻¹.
211 Conversely, areal burial fluxes range substantially, from 85 – 500 g C m⁻² yr⁻¹.

212 Within the global estimates, notable differences in GHG emissions from reservoirs are seen
213 regionally. Gaseous carbon emissions from reservoirs in tropical regions are generally higher than
214 emissions in boreal and temperate reservoirs, partially due to their large surface areas, high volumes of
215 flooded biomass and soil OC, and warmer water temperatures^{23,25,110} (**Table 1**). Tropical Chinese reservoirs
216 tend to be the exception due to national policy requiring pre-flooding clearing of vegetation and biomass¹²¹⁻
217 ¹²⁴. For example, emission rates of CO₂ ($5.81\text{--}40.8 \times 10^4 \mu\text{g C m}^{-2} \text{ day}^{-1}$) and CH₄ ($0.10\text{--}0.30 \times 10^4 \mu\text{g C m}^{-2}$
218 day^{-1}) from the cascade of reservoirs in the Upper Mekong River are much lower than the global mean
219 emission rates from reservoirs (106×10^4 and $1.29 \times 10^4 \mu\text{g C m}^{-2} \text{ day}^{-1}$ as CO₂ and CH₄, respectively), and
220 decrease linearly with the reservoir's age¹²⁵. Similarly, the Three Gorges Reservoir has a lower CH₄
221 emission rate ($0.38 \times 10^4 \mu\text{g C m}^{-2} \text{ day}^{-1}$) than observed in most new tropical ($16.0 \times 10^4 \mu\text{g C m}^{-2} \text{ day}^{-1}$) or
222 temperate ($1.38 \times 10^4 \mu\text{g C m}^{-2} \text{ day}^{-1}$) reservoirs¹²⁶ (**Table 1**). Unlike these Chinese reservoirs, four of the
223 most heavily studied Amazonian reservoirs (Balbina, Tucuruí and Samuel in Brazil and Petit Saut in French
224 Guiana) were not cleared prior to impoundment and consequently have CO₂ emissions measured as 91.3,
225 285, 1172 and $123 \times 10^4 \mu\text{g C m}^{-2} \text{ day}^{-1}$, respectively^{102,127}, all substantially in excess of the worldwide
226 average for reservoir CO₂ emissions (**Table 1**). While the Brazilian government requires biomass clearing
227 before flooding, incomplete clearing can still drive substantial emissions from biomass-rich Amazonian
228 reservoirs¹²⁸.

229 For many dammed river systems, ongoing eutrophication is driving reservoirs towards increased
230 **autotrophy [G]**, as increased nutrient concentrations enable planktonic communities to increase
231 photosynthesis relative to respiration¹²⁹⁻¹³¹. The consequence of this productivity shift is increased carbon
232 sequestration via burial in reservoir sediments¹¹² (**Fig. 3**), but **methanogenesis [G]**, and thus CH₄ emissions,
233 are often increased. The concurrent increase in CH₄ emissions alongside rising autotrophy was seen in a

234 summary of CH₄ emissions measurements from reservoirs worldwide, in which eutrophic reservoirs
235 typically have CH₄ emissions an order of magnitude larger than oligotrophic [G] reservoirs²¹.

236

237 *[H2] N₂O emissions.*

238 Globally, reservoirs emit 3.7 Tg N yr⁻¹ as N₂ via denitrification²⁷, bury 1.54 Tg N yr⁻¹ in sediments⁴⁰, and
239 fix 0.98 Tg N yr⁻¹. Enhanced river network denitrification is beneficial for nutrient-rich river systems when
240 it eliminates excess nitrate from the water column but, along with nitrification [G], it can produce N₂O
241 (REF¹³²), which has 298 times the global warming potential of CO₂. Global reservoir N₂O emissions are
242 between 20–71.5 Gg N yr⁻¹ (REF^{23,27}), with higher areal N₂O emissions rates (0.94–1.6 g N m⁻² yr⁻¹) than
243 lakes³⁵, rivers, and estuaries (a combined 0.01 – 0.15 g N m⁻² yr⁻¹), by more than an order of magnitude²⁷.
244 Indeed, N₂O emissions from reservoirs account for more than half of the emissions from lentic (freshwater)
245 water bodies (assuming N₂O emissions of 34±21 Gg N yr⁻¹ out of 63±41 Gg N yr⁻¹), despite only accounting
246 for 9% of the global lake plus reservoir surface area³⁵. These high emission are due in part to the
247 disproportionately high TN load that flows along dammed rivers relative to the load delivered to natural
248 lakes, many of which are located above 50° latitude bands (44%) and tend to be nutrient poor³⁵.
249 Furthermore, reservoirs have an average upstream watershed area of > 12,000 km² compared to an average
250 of only 617 km² for lakes¹³³, enabling the accumulation of larger nutrient loads in the rivers that feed into
251 reservoirs³⁵.

252 Relating HRT to denitrification, nitrification and N₂O emissions is not always straightforward. At
253 long enough HRTs, N₂O produced via denitrification is eventually reduced to N₂ (and not emitted as N₂O),
254 and in reservoirs with HRTs above 6–7 months, more reservoir N₂O emissions are produced via nitrification
255 than by denitrification²³. Furthermore, there is a strong inverse relationship between the area-normalized
256 N₂O emissions rate and the HRT³⁵, suggesting that reservoirs with short residence times emit more N₂O per
257 unit area than reservoirs with long residence times. Thus, while many of the ecological impacts related to

258 nutrient elimination could be minimized in small reservoirs with low HRTs, N₂O emissions can be higher
259 than in large reservoirs, which are often conventionally considered environmentally problematic.

260

261 *[H2] Dam management and GHG.*

262 Reservoirs can be notable sources of GHGs in the years immediately following dam
263 construction^{25,125,134} (**Fig. 3**). The decomposition of flooded terrestrial soil and biomass organic matter drive
264 CO₂ and CH₄ emissions for more than a decade after impoundment, and is influenced by the reservoir age,
265 surface area, mass of OC flooded, and temperature^{26,135}. Similarly, oscillations in seasonal water levels can
266 contribute to enhanced emissions through repeated wetting and drying cycles. For instance, marshes in the
267 drawdown zone of the Three Gorges Reservoir account for ~19% of total reservoir emissions¹³⁶, and the
268 water column acts as an N₂O source for the first 1.5 days of rewetting before switching to a sink for the
269 remainder of wet–dry cycles. These results suggest that newly created (or recreated) flood zones, with
270 organic-rich sediments and frequent variations in water levels, could also become hotspots for GHG
271 emissions after dam removal¹⁰⁵. This idea is evidenced by the magnitude of hypothetical CO₂-equivalent
272 emissions from the largest 10 reservoirs in the United States once they are decommissioned¹³⁷: after 100
273 years of damming, post-deconstruction emissions would exceed those of the reservoir’s lifetime emissions
274 by 9 times. At present, strategies to avoid this consequence of dam removal have not been developed.

275 Individual reservoir and watershed-scale assessments can be successfully developed to optimize
276 the local tradeoffs associated with gaseous biogeochemical cycles and reservoir services. For example,
277 Brazil’s primarily lowland topography plays a major role in the large magnitude of emissions from its
278 reservoirs¹³⁸; as a result a basin-scale multi-criteria optimization framework, which strategizes dam
279 locations to maximize hydroelectricity generation while minimizing GHG emissions, was proposed for the
280 Amazon River basin¹³⁸. Ultimately, the net worldwide impact of dam construction on GHG emissions is
281 uncertain, and so this approach of focusing on maximizing efficiency for individual basins represents the
282 most feasible course of action.

283

284 [H1] Impact of reservoir size

285 Although there is generally a positive relationship between the magnitude of nutrient elimination and
286 reservoir HRT, small reservoirs may have disproportionately high **biogeochemical reactivity [G]** per unit
287 area or time. For example, first order OC decomposition rate constants (k_{OC}), which describe the reactivity
288 per unit time, increase as HRT decreases¹³⁹ (**Fig. 4**). When scaled, this relationship results in decreasing
289 OC mineralization rate constants with distance down the LOAC; this decrease is due to the breakdown of
290 highly reactive material in headwater streams with low HRTs, and the subsequent downstream transport of
291 the less **labile [G]** material to larger water bodies with higher HRTs. For instance, in an analysis of over
292 200 lakes and reservoirs, inverse relationships between HRT and elimination rate constants for TP, TN,
293 nitrate, and phosphate were identified⁴⁶ (**Fig. 4**). Because small water bodies have very low discharges,
294 absolute nutrient fluxes still tend to be small, but when many small reservoirs are linked along the LOAC,
295 their nutrient elimination capacity can be high¹⁴⁰. The mechanism responsible for greater nutrient reactivity
296 in small water bodies has been attributed to the increasing sediment–water interface contact area to volume
297 ratio as the size of the water body decreases^{140,141}.

298 Despite their importance, a spatially explicit estimate of reservoir nutrient and carbon
299 transformation in small reservoirs is virtually impossible to conduct within acceptable uncertainty bounds,
300 largely because there is no complete database of the estimated ~16.7 million reservoirs worldwide¹⁴².
301 Currently the most complete and spatially explicit, georeferenced dam database is the [Global Georeferenced](#)
302 [Database of Dams](#) (GOOD²), composed of 38,660 manually digitized dams that are visible in Google
303 Earth¹⁴³. However, GOOD² is not aligned to an existing river network digitization (such as
304 HydroSHEDS¹⁴⁴) and that it lacks reservoir physical parameters needed to make biogeochemical
305 predictions (including HRT), making large scale estimate difficult. Other estimates of nutrient retention or
306 elimination in small reservoirs have relied on size distribution functions, typically Pareto, applied randomly
307 to river systems or lumped into watersheds worldwide¹⁴⁵⁻¹⁴⁸. These estimates provide a foundation for future

308 research investigating the relative importance of small reservoirs in global nutrient cycling. However, due
309 to the lack of reservoir integration within watershed routing networks, predicting nutrient loads to these
310 reservoirs is difficult.

311 A key outstanding question is whether building a series of cascading small dams in lieu of a single
312 large dam is environmentally preferable. Evidence suggests that multiple small reservoirs with HRTs that
313 sum to the same HRT as a single large reservoir will eliminate nutrients and reduce downstream nutrient
314 loads more efficiently than a single large reservoir¹⁴⁰. ‘Pre-dams’ (small upstream dams) that reduce nutrient
315 loads to downstream reservoirs have occasionally been constructed to alleviate downstream eutrophication
316 problems^{149,150}. Along these lines, it may be possible to further use dams or pre-dams to mitigate coastal
317 eutrophication problems, particularly if there is a strong need to reduce P loads. The trade-off with this
318 approach is that pre-dams may merely serve to drive eutrophication problems further upstream, whilst
319 further amplifying other ecosystem changes associated with river regulation. Evidence for pre-dam
320 effectiveness is also mixed—even with careful design focused on maximizing P and N retention in pre-
321 dams upstream of German drinking water reservoirs, it was recommended that the pre-dams be emptied
322 and dredged every 5–10 days in order to remain effective¹⁵⁰. Finally, there is little information available on
323 the elimination of each nutrient element relative to each other in small systems.

324

325 **[H1] Nutrient management with dams**

326 As reservoirs can eliminate nutrients, there is growing interest in manipulating dam operations to regulate
327 reservoir and riverine trophic conditions, as evidenced by major legislative efforts encouraging the
328 development of new approaches for river flow regulation. The conceptual basis of the environmental-flow
329 (e-flow) approach is to optimise the river flow management to provide services to humans (such as water
330 supply and hydropower) whilst protecting the aquatic environment. In already impacted systems with
331 heavily regulated flows and associated ecosystem effects, such as decreased fish populations or enhanced
332 downstream streambed sediment scouring (**Fig. 5a-c**), e-flow approaches can be applied to restore these

333 systems¹⁵¹⁻¹⁵³. Generally this approach involves a substantial modification of the flow regime¹⁵⁴ through the
334 maintenance or (re-)introduction of river flow dynamics, based on the objectives for the particular river
335 system^{155,156}.

336 One e-flow approach, **hydro-peaking [G]**, has been studied in many parts of the world¹⁵⁷, but the
337 focus of these e-flow studies has typically been ecological, for instance, examining the relationship between
338 flow dynamics and changing temperature¹⁵⁸ on fish or invertebrate populations. Periodic high-flow events
339 (**Fig. 5d-f**), such as annual flooding, have now been incorporated into operational reservoir outflows in
340 many areas, such as the dammed Spöl River in Switzerland¹⁵⁹. In an 18-year study, most physicochemical
341 variables in the Spöl River followed strong seasonal cycles unrelated to flow regime change¹⁵⁹. N and P
342 concentrations in outflow waters did increase over the study duration, but the role of the annual floods was
343 negligible in this increase, as nearby unregulated rivers showed similar long-term trends that are likely
344 linked to catchment-scale processes or climate change¹⁶⁰.

345 Seasonal compensation flow adjustments are a common e-flow regulation method. In these
346 adjustments, reservoir outflow (which is based on the percentage relative to the unmodified flow)^{155, 161, 162}
347 provides low flows during dry seasons, with stepped flow increases in wet seasons (**Fig. 5d-f**). Amongst
348 these applications, e-flows designed specifically for downstream water quality management are still rare,
349 but have been examined. For example, in Korean rivers, TP and TN concentrations have been related to
350 storage–release periods of irrigation reservoirs, with downstream TN concentrations elevated during non-
351 irrigation periods when outflows were reduced¹⁶³. Similarly, along the Euphrates River in Iraq, irrigation,
352 subsequent return flows, and reduced flows from upstream reservoirs have been linked with increasing
353 dissolved solid loads over >30 years¹⁶⁴. In response, maintaining minimum flows into the Euphrates via
354 water diversion has been proposed to mitigate excess dissolved load¹⁶⁴. Finally, in the Klamath River, USA,
355 flow alterations can be used to modify nutrients, water temperatures and water quantity in order to improve
356 conditions downstream from cyanobacteria bloom-impacted reservoirs, where cyanotoxins and anaerobic
357 conditions can pollute drinking water sources, and harm fisheries and aquatic life¹⁶⁵.

358 Although these studies suggest that reservoir management for e-flows could ameliorate some
359 downstream water quality issues, there are likely to be local constraints. For example, regulators must
360 consider the seasonality of water quality problems versus water availability for environmental flow
361 allocation, as well as reservoir operational constraints that could limit the volume of water release or the
362 location of water release in the reservoir water column^{166,167}. Reintroducing large flow variations might also
363 inundate floodplains and riparian soils, which may lead to the transfer of nutrients and organic matter into
364 rivers or enhance GHG emissions¹⁶⁸. The limited evidence in this area highlights the need for more studies
365 to systematically examine the use of e-flows in mitigating the effects of dams on river nutrient cycling and
366 downstream fluxes. For instance, high temporal resolution watershed-scale models that represent nutrient
367 flux dynamics along the LOAC could be used to test single and cascading dam operation scenarios with e-
368 flow regimes. Modeling efforts could also be used to select for desirable nutrient elimination by
369 manipulating existing dams to maximize or minimize HRTs (**Fig. 5g-i**) to coincide with high or low nutrient
370 loads.

371

372 **[H1] Dam removal**

373 In recent years, dam removal in Europe and North America has become commonplace, driven by ageing
374 infrastructure and growing interest in river restoration and environmental concerns^{169,170}. For example, in
375 the U.S. alone, more than 1,200 dams have been removed since the year 2000 (REF¹⁷¹). Most dam-removal
376 studies have focused on the physical effects of the removal, such as metrics associated with hydraulics,
377 channel morphology, and sediment dynamics, or effects on fish communities. However, despite notable
378 downstream effects associated with nutrient and contaminant release, there is insufficient understanding of
379 dam removal impacts across the LOAC¹⁷², particularly with regard to downstream nutrient dynamics and
380 water quality.

381 Legacy nutrients and contaminants, typically defined as elements or compounds that remain in the
382 landscape or system beyond a year after their application¹⁷³, accumulate in reservoir sediments over the

383 course of a dam's lifespan, and are eroded downstream due to increased flows when dams are removed.
384 The remobilization and downstream impacts of legacy nutrient and contaminant remobilization are
385 increasingly being recognized and discussed in the context of dam construction and removal. For instance,
386 the effects of legacy contaminants have been seen in New York, USA, where industrial use of
387 polychlorinated biphenyls (PCBs) at Ft. Edward and Hudson Falls led to an accumulation of PCBs in
388 reservoir sediments above the Ft. Edward hydroelectric dam. These legacy contaminants were mobilized
389 and released downstream after the dam was removed in 1973 (REF¹⁷⁴), and PCB transport continues to be
390 documented today¹⁷⁵, despite massive remediation efforts¹⁷⁶. Legacy nutrients can behave similarly, with
391 multifold increases in downstream N and P concentrations being documented after the release of reservoir
392 sediments due to breaches or changes in management¹⁷². As an example, flushing of sediments from the
393 Guernsey Reservoir in the western US led to a six-fold increase in downstream P concentrations¹⁷⁷. In
394 British Columbia, drawdown of water levels of the Capilano Reservoir caused enhanced erosion of reservoir
395 sediments, driving downstream ammonium concentrations to increase by two orders of magnitude¹⁷⁸, and
396 after removal of a low-head dam on the Olentangy River (Ohio, USA), downstream nitrate concentrations
397 were increased three-fold¹⁷⁹.

398 In addition to mobilizing legacy nutrients or pollutants in reservoirs, dam removal and reservoir
399 drainage cause water tables above the removal site to drop¹⁸⁰. This drop increases both the downstream
400 river channel depth and cross-sectional area, leading to bed degradation, a lowering of the stream water
401 surface, incision of the stream bed, and erosion of nutrient-rich sediments¹⁷². As observed in the U.S. mid-
402 Atlantic region, for example, the removal or breaching of thousands of small mill dams resulted in the
403 erosion of stream banks at rates ranging from 0.05 to over 0.2 m yr⁻¹ (REF¹⁸¹). Furthermore, some of the
404 nutrient-rich sediments released there may account for a substantial portion of current stream nutrient loads
405 in the region¹⁸¹. Therefore, dam removal may be at odds with policy goals to reduce watershed nutrient
406 loading^{172,182}, highlighting the need to consider how and on what timescales that dam removal impacts
407 legacy nutrient remobilization.

408 Leaving aging dams in place, however, does not ensure that legacy nutrients will remain trapped in
409 upstream reservoirs. When an aging dam is left in place, sediment and nutrient elimination efficiencies can
410 decrease over time due to reservoir infilling¹⁸³ (thus decreasing reservoir volume and therefore HRT), so a
411 reservoir that retains 70-80% of incoming nutrient loads early in its lifespan may actually serve as a nutrient
412 source after many years of operation. For example, above the Conowingo dam, constructed in 1928 at the
413 mouth of the Susquehanna River (Maryland, USA)¹⁸⁴, TP concentrations have decreased in the last 10-15
414 years, likely due to nutrient management strategies implemented to lower nutrient loading to the
415 Chesapeake Bay. Below the dam, however, no such reductions have been observed. Indeed, reservoir output
416 versus input ratios for TP have increased since 2000, with net deposition rates of sediments and TP
417 decreasing across a range of different flows. These findings suggest that the Conowingo reservoir,
418 approximately 90 years after its initial construction, is reaching the end of its “effective life” for sediment
419 removal¹⁸⁴. In Europe and North America especially, many aging dams and reservoirs are reaching—or
420 have already reached—their sediment-holding capacities. Thus, perhaps the primary concern should not
421 only be whether legacy nutrients will be released as a result of dam removals, but also to what extent
422 existing reservoirs are already beginning to act as nutrient sources (Fig. 3), particularly at low flows.

423

424 **[H1] Future perspectives**

425 Conversations that pitch all dams as problematic are not productive, just as conversations that laud dams as
426 the most viable sustainable energy source in the era of climate change are misleading. Damming rivers to
427 produce energy, control floods, and balance the unequal distribution of water over time is unlikely to stop.
428 If dams are constructed without considering their impacts on nutrient cycling, then changes to coastal
429 nutrient ratios, increased prevalence of HABs, unnecessarily large GHG emissions, and reservoir in-filling
430 and eutrophication will likely continue. However responsible dam construction and management — from
431 conception to deconstruction and in the context of the entire watershed — may be achievable by balancing
432 the environmental impacts of damming with the services provided by it. Based on the biogeochemical

433 impacts of damming discussed in this Review, we posit that LOAC biogeochemistry should be considered
434 at each stage of a dam's life cycle, and ideally during dam conception and planning (**Box 1**).

435 The inclusion of nutrient elimination and GHG emissions in multi-criteria optimization regimes
436 and quantitative trade-off analyses would be a major step towards achieving sustainable dam construction
437 across entire river basins. These methods to manage trade-offs have successfully have been applied to
438 enable water availability or hydroelectricity generation as well as to maintain flows for river
439 ecosystems^{185,186}. Such optimization regimes have also been applied to dam removal scenarios in the
440 Willamette River basin (Oregon, USA), where it was shown that removing 12 dams would hydrologically
441 reconnect 52% of the basin while only eliminating 1.6% of the water storage capacity and hydroelectricity
442 production²⁰⁰. Using HRT and nutrient loads to predict the magnitudes of nutrient elimination can be used
443 as a simple starting point to incorporate biogeochemistry into these management methods, and e-flow
444 approaches or dam removal plans can subsequently be considered as implementation strategies within or in
445 addition to these optimization regimes. However, these approaches must be applied across the whole
446 watershed approach in order to avoid transferring nutrient-related challenges to another part of the LOAC.

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

458

459

460 **References:**

- 461 1 ICOLD. *Dams and the World's Water: An Education Book that Explains how Dams Help to*
 462 *Manage the World's Water.* (International Commission on Large Dams, 2007).
- 463 2 Lehner, B. *et al.* High-resolution mapping of the world's reservoirs and dams for sustainable
 464 river-flow management. *Frontiers in Ecology and the Environment* **9**, 494-502 (2011).
- 465 3 Zarfl, C., Lumsdon, A., Berlekamp, J., Tydecks, L. & Tockner, K. A global boom in hydropower
 466 dam construction. *Aquat. Sci.* **77**, 161-170, doi:10.1007/s00027-014-0377-0 (2015).
- 467 4 Rex, W., Foster, V., Lyon, K., Bucknall, J. & Liden, R. Supporting Hydropower: An Overview of
 468 the World Bank Group's Engagement. (2014).
- 469 5 WCD, W. C. o. D. *Dams and Development: A New Framework for Decision-making: the Report*
 470 *of the World Commission on Dams.* (Earthscan, 2000).
- 471 6 Yoshikawa, S., Cho, J., Yamada, H., Hanasaki, N. & Kanae, S. An assessment of global net
 472 irrigation water requirements from various water supply sources to sustain irrigation: rivers and
 473 reservoirs (1960–2050). *Hydrology and Earth System Sciences* **18**, 4289-4310 (2014).
- 474 7 REN21. Renewables 2016 Global Status Report. (Paris, 2016).
- 475 8 Grill, G. *et al.* Mapping the world's free-flowing rivers. *Nature* **569**, 215-221,
 476 doi:10.1038/s41586-019-1111-9 (2019).
- 477 **Quantified the changes to global river connectivity over time as the global boom in dam**
 478 **construction occurs.**
- 479 9 Grill, G. *et al.* An index-based framework for assessing patterns and trends in river fragmentation
 480 and flow regulation by global dams at multiple scales. *Environmental Research Letters* **10**,
 481 015001 (2015).
- 482 10 Hermoso, V. Freshwater ecosystems could become the biggest losers of the Paris Agreement.
 483 *Global Change Biology* (2017).
- 484 11 Grumbine, R. E. & Pandit, M. K. Threats from India's Himalaya dams. *Science* **339**, 36-37
 485 (2013).
- 486 12 Wang, G. *et al.* Valuing the effects of hydropower development on watershed ecosystem services:
 487 Case studies in the Jiulong River Watershed, Fujian Province, China. *Estuarine, Coastal and*
 488 *Shelf Science* **86**, 363-368 (2010).
- 489 13 Almeida, R. M., Barros, N., Cole, J. J., Tranvik, L. & Roland, F. Emissions from Amazonian
 490 dams. *Nature Climate Change* **3**, 1005 (2013).
- 491 14 Kuemmerlen, M., Reichert, P., Siber, R. & Schuwirth, N. Ecological assessment of river
 492 networks: from reach to catchment scale. *Science of the Total Environment* **650**, 1613-1627
 493 (2019).
- 494 15 Brownell Jr, R. L., Randall, R., Smith, B. D. & Ryan, G. E. Dams threaten rare Mekong dolphins.
 495 *Science* **355**, 805 (2017).
- 496 16 Poff, N. L. & Schmidt, J. C. How dams can go with the flow. *Science* **353**, 1099-1100 (2016).
- 497 17 Poff, N. L., Olden, J. D., Merritt, D. M. & Pepin, D. M. Homogenization of regional river
 498 dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of*
 499 *Sciences* **104**, 5732-5737 (2007).
- 500 18 Stone, R. Dam-building threatens Mekong fisheries. *Science* **354**, 1084-1085 (2016).
- 501 19 Li, J. *et al.* Effects of damming on the biological integrity of fish assemblages in the middle
 502 Lancang-Mekong River basin. *Ecological Indicators* **34**, 94-102 (2013).
- 503 20 Ziv, G., Baran, E., Nam, S., Rodríguez-Iturbe, I. & Levin, S. A. Trading-off fish biodiversity,
 504 food security, and hydropower in the Mekong River Basin. *Proceedings of the National Academy*
 505 *of Sciences* **109**, 5609-5614 (2012).
- 506 21 Deemer, B. R. *et al.* Greenhouse gas emissions from reservoir water surfaces: a new global
 507 synthesis. *BioScience* **66**, 949-964 (2016).
- 508 22 Moran, E. F., Lopez, M. C., Moore, N., Müller, N. & Hyndman, D. W. Sustainable hydropower
 509 in the 21st century. *Proceedings of the National Academy of Sciences* **115**, 11891-11898 (2018).

510 23 Fearnside, P. M. & Pueyo, S. Greenhouse-gas emissions from tropical dams. *Nature Climate*
511 *Change* **2**, 382-384 (2012).

512 24 Barros, N. *et al.* Carbon emission from hydroelectric reservoirs linked to reservoir age and
513 latitude. *Nature Geoscience* **4**, 593 (2011).

514 25 Maavara, T. *et al.* Nitrous oxide emissions from inland waters: Are IPCC estimates too high?
515 *Global change biology* **25**, 473-488 (2019).

516 26 Fearnside, P. M. Hydroelectric dams in the Brazilian Amazon as sources of 'greenhouse' gases.
517 *Environmental Conservation* **22**, 7-19 (1995).

518 27 Kemenes, A., Forsberg, B. R. & Melack, J. M. Methane release below a tropical hydroelectric
519 dam. *Geophysical research letters* **34** (2007).

520 28 Ansar, A., Flyvbjerg, B., Budzier, A. & Lunn, D. Should we build more large dams? The actual
521 costs of hydropower megaproject development. *Energy Policy* **69**, 43-56 (2014).

522 29 Scudder, T. T. *The future of large dams: Dealing with social, environmental, institutional and*
523 *political costs.* (Routledge, 2012).

524 30 Vörösmarty, C., Meybeck, M., Fekete, B. & Sharma, K. The potential impact of neo-
525 Castorization on sediment transport by the global network of rivers. *IAHS Publication* **246**, 261-
526 273 (1997).

527 31 Vollenweider, R. A. Input-output models. *Schweizerische Zeitschrift für Hydrologie* **37**, 53-84
528 (1975).

529 32 Kõiv, T., Nöges, T. & Laas, A. Phosphorus retention as a function of external loading, hydraulic
530 turnover time, area and relative depth in 54 lakes and reservoirs. *Hydrobiologia* **660**, 105-115
531 (2011).

532 33 Finlay, J. C., Small, G. E. & Sterner, R. W. Human influences on nitrogen removal in lakes.
533 *Science* **342**, 247-250 (2013).

534 34 Frings, P. J. *et al.* Lack of steady-state in the global biogeochemical Si cycle: emerging evidence
535 from lake Si sequestration. *Biogeochemistry* **117**, 255-277 (2014).

536 35 Lauerwald, R. *et al.* Natural lakes are a minor global source of N₂O to the atmosphere. *Global*
537 *biogeochemical cycles* **33**, doi:<https://doi.org/10.1029/2019GB006261> (2019).

538 36 Redfield, A. C. On the proportions of organic derivatives in sea water and their relation to the
539 composition of plankton. *James Johnstone memorial volume*, 176-192 (1934).

540 37 Glibert, P. M. Harmful algae at the complex nexus of eutrophication and climate change. *Harmful*
541 *Algae*, 101583 (2019).

542 38 Glibert, P. M. Ecological stoichiometry and its implications for aquatic ecosystem sustainability.
543 *Current Opinion in Environmental Sustainability* **4**, 272-277 (2012).

544 39 Maavara, T. *et al.* Global phosphorus retention by river damming. *Proceedings of the National*
545 *Academy of Sciences* **112**, 15603-15608 (2015).

546 40 Akbarzadeh, Z., Maavara, T., Slowinski, S. & Van Cappellen, P. Effects of Damming on River
547 Nitrogen Fluxes: A Global Analysis. *Global biogeochemical cycles* **33**,
548 doi:<https://doi.org/10.1029/2019GB006222> (2019).

549 41 Mayorga, E. *et al.* Global nutrient export from WaterSheds 2 (NEWS 2): model development and
550 implementation. *Environmental Modelling & Software* **25**, 837-853 (2010).

551 42 Beusen, A., Bouwman, A., Dürr, H., Dekkers, A. & Hartmann, J. Global patterns of dissolved
552 silica export to the coastal zone: Results from a spatially explicit global model. *Global*
553 *Biogeochemical Cycles* **23** (2009).

554 43 Friedl, G. & Wüest, A. Disrupting biogeochemical cycles-Consequences of damming. *Aquatic*
555 *Sciences* **64**, 55-65 (2002).

556 44 Van Cappellen, P. & Maavara, T. Rivers in the Anthropocene: global scale modifications of
557 riverine nutrient fluxes by damming. *Ecohydrology & Hydrobiology* **16**, 106-111 (2016).

558 45 Vörösmarty, C. J. *et al.* Anthropogenic sediment retention: major global impact from registered
559 river impoundments. *Global and planetary change* **39**, 169-190 (2003).

560 46 Hejzlar, J., Šámalová, K., Boers, P. & Kronvang, B. Modelling phosphorus retention in lakes and
561 reservoirs. *Water, Air, & Soil Pollution: Focus* **6**, 487-494 (2006).

562 47 North, R. L. *et al.* Evidence for internal phosphorus loading in a large prairie reservoir (Lake
563 Diefenbaker, Saskatchewan). *Journal of Great Lakes Research* **41**, 91-99 (2015).

564 48 Donald, D. B., Parker, B. R., Davies, J.-M. & Leavitt, P. R. Nutrient sequestration in the Lake
565 Winnipeg watershed. *Journal of Great Lakes Research* **41**, 630-642 (2015).

566 49 Maavara, T. *et al.* Reactive silicon dynamics in a large prairie reservoir (Lake Diefenbaker,
567 Saskatchewan). *Journal of Great Lakes Research* **41**, 100-109 (2015).

568 50 Maranger, R., Jones, S. E. & Cotner, J. B. Stoichiometry of carbon, nitrogen, and phosphorus
569 through the freshwater pipe. *Limnology and Oceanography Letters* **3**, 89-101 (2018).

570 **Quantified changes to nutrient ratios along the land-ocean aquatic continuum, with**
571 **thorough discussion of driving mechanisms.**

572 51 Xu, Y., Zhang, M., Wang, L., Kong, L. & Cai, Q. Changes in water types under the regulated
573 mode of water level in Three Gorges Reservoir, China. *Quaternary international* **244**, 272-279
574 (2011).

575 52 Huang, L., Fang, H. & Reible, D. Mathematical model for interactions and transport of
576 phosphorus and sediment in the Three Gorges Reservoir. *Water research* **85**, 393-403 (2015).

577 53 Ran, X., Yu, Z., Yao, Q., Chen, H. & Guo, H. Silica retention in the Three Gorges reservoir.
578 *Biogeochemistry* **112**, 209-228 (2013).

579 54 Hartmann, J., Lauerwald, R. & Moosdorf, N. A brief overview of the GLObal RIVer CHEmistry
580 Database, GLORICH. *Procedia Earth and Planetary Science* **10**, 23-27 (2014).

581 55 Maavara, T., Dürr, H. H. & Van Cappellen, P. Worldwide retention of nutrient silicon by river
582 damming: From sparse data set to global estimate. *Global Biogeochemical Cycles* **28**, 842-855
583 (2014).

584 56 Egge, J. & Aksnes, D. Silicate as regulating nutrient in phytoplankton competition. *Marine*
585 *ecology progress series. Oldendorf* **83**, 281-289 (1992).

586 57 Hall, R. I., Smol, J. P. & Smol, J. Diatoms as indicators of lake eutrophication. *The diatoms:*
587 *applications for the environmental and earth sciences*, 128-168 (1999).

588 58 Paerl, H. W., Valdes, L. M., Peierls, B. L., Adolf, J. E. & Lawrence Jr, W. H. Anthropogenic and
589 climatic influences on the eutrophication of large estuarine ecosystems. *Limnology and*
590 *Oceanography* **51**, 448-462 (2006).

591 59 Huisman, J. *et al.* Changes in turbulent mixing shift competition for light between phytoplankton
592 species. *Ecology* **85**, 2960-2970 (2004).

593 60 Conley, D. J. *et al.* Controlling eutrophication: Nitrogen and phosphorus. *Science* **323**, 1014-1015
594 (2009).

595 61 Nixon, S. W. Coastal marine eutrophication: a definition, social causes, and future concerns.
596 *Ophelia* **41**, 199-219 (1995).

597 62 Smith, V. H., Tilman, G. D. & Nekola, J. C. Eutrophication: impacts of excess nutrient inputs on
598 freshwater, marine, and terrestrial ecosystems. *Environmental pollution* **100**, 179-196 (1999).

599 63 Justić, D., Rabalais, N. N. & Turner, R. E. Modeling the impacts of decadal changes in riverine
600 nutrient fluxes on coastal eutrophication near the Mississippi River Delta. *Ecological Modelling*
601 **152**, 33-46 (2002).

602 64 Schindler, D. Evolution of phosphorus limitation in lakes. *Science* **195**, 260-262 (1977).

603 65 Schindler, D. W. *et al.* Eutrophication of lakes cannot be controlled by reducing nitrogen input:
604 results of a 37-year whole-ecosystem experiment. *Proceedings of the National Academy of*
605 *Sciences* **105**, 11254-11258 (2008).

606 66 Howarth, R. W. & Marino, R. Nitrogen as the limiting nutrient for eutrophication in coastal
607 marine ecosystems: evolving views over three decades. *Limnology and Oceanography* **51**, 364-
608 376 (2006).

609 67 Chaffin, J. D., Bridgeman, T. B. & Bade, D. L. Nitrogen constrains the growth of late summer
610 cyanobacterial blooms in Lake Erie. *Advances in Microbiology* **3**, 16 (2013).

611 68 Paerl, H. W. *et al.* Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake
612 Taihu, China): the need for a dual nutrient (N & P) management strategy. *Water research* **45**,
613 1973-1983 (2011).

614 69 Paerl, H. W. *et al.* It takes two to tango: When and where dual nutrient (N & P) reductions are
615 needed to protect lakes and downstream ecosystems. *Environmental Science & Technology* **50**,
616 10805-10813 (2016).

617 70 Guildford, S. J. & Hecky, R. E. Total nitrogen, total phosphorus, and nutrient limitation in lakes
618 and oceans: Is there a common relationship? *Limnology and Oceanography* **45**, 1213-1223
619 (2000).

620 71 Nürnberg, G. K. Prediction of phosphorus release rates from total and reductant-soluble
621 phosphorus in anoxic lake sediments. *Canadian Journal of Fisheries and Aquatic Sciences* **45**,
622 453-462 (1988).

623 72 Sharpley, A. *et al.* Phosphorus legacy: overcoming the effects of past management practices to
624 mitigate future water quality impairment. *Journal of environmental quality* **42**, 1308-1326 (2013).

625 73 Maavara, T., Slowinski, S., Rezanezhad, F., Van Meter, K. & Van Cappellen, P. The role of
626 groundwater discharge fluxes on Si: P ratios in a major tributary to Lake Erie. *Science of The*
627 *Total Environment* **622**, 814-824 (2018).

628 74 Orihel, D. M. *et al.* Internal phosphorus loading in Canadian fresh waters: a critical review and
629 data analysis. *Canadian journal of fisheries and aquatic sciences* **74**, 2005-2029 (2017).

630 75 Nixon, S. W. Replacing the Nile: are anthropogenic nutrients providing the fertility once brought
631 to the Mediterranean by a great river? *AMBIO: A journal of the human environment* **32**, 30-40
632 (2003).

633 76 Oczkowski, A. & Nixon, S. Increasing nutrient concentrations and the rise and fall of a coastal
634 fishery; a review of data from the Nile Delta, Egypt. *Estuarine, Coastal and Shelf Science* **77**,
635 309-319 (2008).

636 77 Turner, R. E. & Rabalais, N. N. Linking landscape and water quality in the Mississippi River
637 basin for 200 years. *Bioscience* **53**, 563-572 (2003).

638 78 Compton, J. *et al.* Variations in the global phosphorus cycle. *SEPM Special Publication No. 66*,
639 21-33 (2000).

640 79 Galloway, J. N. *et al.* Nitrogen cycles: past, present, and future. *Biogeochemistry* **70**, 153-226
641 (2004).

642 80 Struyf, E. *et al.* Historical land use change has lowered terrestrial silica mobilization. *Nature*
643 *communications* **1**, 129 (2010).

644 81 Clymans, W., Struyf, E., Govers, G., Vandevenne, F. & Conley, D. Anthropogenic impact on
645 amorphous silica pools in temperate soils. *Biogeosciences* **8**, 2281-2293 (2011).

646 82 Garnier, J., Beusen, A., Thieu, V., Billen, G. & Bouwman, L. N: P: Si nutrient export ratios and
647 ecological consequences in coastal seas evaluated by the ICEP approach. *Global Biogeochemical*
648 *Cycles* **24** (2010).

649 83 Turner, R., Rabalais, N., Justic, D. & Dortch, Q. Global patterns of dissolved N, P and Si in large
650 rivers. *Biogeochemistry* **64**, 297-317 (2003).

651 84 Justić, D., Rabalais, N. N., Turner, R. E. & Dortch, Q. Changes in nutrient structure of river-
652 dominated coastal waters: stoichiometric nutrient balance and its consequences. *Estuarine,*
653 *Coastal and Shelf Science* **40**, 339-356 (1995).

654 85 Billen, G. *et al.* N, P and Si retention along the aquatic continuum from the land to ocean, in
655 *Ocean Margin Processes in Global Change, 1*. 19-44 (John Wiley & Sons) (1991).

656 86 Howarth, R. *et al.* Coupled biogeochemical cycles: eutrophication and hypoxia in temperate
657 estuaries and coastal marine ecosystems. *Frontiers in Ecology and the Environment* **9**, 18-26
658 (2011).

659 87 Conley, D., Schelske, C. & Stoermer, E. Modification of the biogeochemical cycle of silica with
660 eutrophication. *Marine Ecology Progress Series* **101**, 179-192 (1993).

661 88 Billen, G. & Garnier, J. River basin nutrient delivery to the coastal sea: Assessing its potential to
662 sustain new production of non-siliceous algae. *Marine Chemistry* **106**, 148-160,
663 doi:<http://dx.doi.org/10.1016/j.marchem.2006.12.017> (2007).

664 89 Buchan, A., LeClerc, G. R., Gulvik, C. A. & González, J. M. Master recyclers: features and
665 functions of bacteria associated with phytoplankton blooms. *Nature Reviews Microbiology* **12**,
666 686-698 (2014).

667 90 Falkowski, P. G., Barber, R. T. & Smetacek, V. Biogeochemical controls and feedbacks on ocean
668 primary production. *Science* **281**, 200-206 (1998).

669 91 Tréguer, P. & Pondaven, P. Global change: Silica control of carbon dioxide. *Nature* **406**, 358-359
670 (2000).

671 92 Humborg, C., Ittekkot, V., Cociasu, A. & Bodungen, B. v. Effect of Danube River dam on Black
672 Sea biogeochemistry and ecosystem structure. *Nature* **386**, 385 (1997).

673 93 Humborg, C. *et al.* Silicon retention in river basins: far-reaching effects on biogeochemistry and
674 aquatic food webs in coastal marine environments. *AMBIO: A Journal of the Human*
675 *Environment* **29**, 45-50 (2000).

676 94 Humborg, C. *et al.* Decreased silica land–sea fluxes through damming in the Baltic Sea
677 catchment—significance of particle trapping and hydrological alterations. *Biogeochemistry* **77**,
678 265-281 (2006).

679 95 Humborg, C., Smedberg, E., Medina, M. R. & Morth, C. M. Changes in dissolved silicate loads
680 to the Baltic Sea - The effects of lakes and reservoirs. *Journal of Marine Systems* **73**, 223-235,
681 doi:10.1016/j.jmarsys.2007.10.014 (2008).

682 96 Boesch, D. F. Challenges and opportunities for science in reducing nutrient over-enrichment of
683 coastal ecosystems. *Estuaries and Coasts* **25**, 886-900 (2002).

684 97 NRC. *Clean coastal waters: understanding and reducing the effects of nutrient pollution*.
685 (National Academies Press, 2000).

686 98 FAO. *The state of world fisheries and aquaculture, 2002*. (United Nations Food & Agriculture
687 Org, 2002).

688 99 Yüksel, I. Dams and hydropower for sustainable development. *Energy Sources, Part B* **4**, 100-
689 110 (2009).

690 100 Yüksel, I. Hydropower for sustainable water and energy development. *Renewable and*
691 *Sustainable Energy Reviews* **14**, 462-469 (2010).

692 101 Rosa, L. P. & Schaeffer, R. Global warming potentials: the case of emissions from dams. *Energy*
693 *Policy* **23**, 149-158 (1995).

694 102 Guérin, F. *et al.* Methane and carbon dioxide emissions from tropical reservoirs: significance of
695 downstream rivers. *Geophysical Research Letters* **33** (2006).

696 103 Yang, L. *et al.* Progress in the studies on the greenhouse gas emissions from reservoirs. *Acta*
697 *Ecologica Sinica* **34**, 204-212 (2014).

698 104 Hertwich, E. G. Addressing biogenic greenhouse gas emissions from hydropower in LCA.
699 *Environmental science & technology* **47**, 9604-9611 (2013).

700 105 Song, C., Gardner, K. H., Klein, S. J., Souza, S. P. & Mo, W. Cradle-to-grave greenhouse gas
701 emissions from dams in the United States of America. *Renewable and Sustainable Energy*
702 *Reviews* **90**, 945-956 (2018).

703 106 Muller, M. Hydropower dams can help mitigate the global warming impact of wetlands. *Nature*
704 **566**, 315-317 (2019).

705 107 Matthews, J. Dam development: value both wetlands and hydropower. *Nature* **568**, 33 (2019).

706 108 Prairie, Y. T. *et al.* Greenhouse gas emissions from freshwater reservoirs: what does the
707 atmosphere see? *Ecosystems* **21**, 1058-1071 (2018).

708 **A comprehensive discussion of the uncertainties associated with predicting the net impacts**
709 **of dam reservoirs on global greenhouse gas emissions.**

710 109 Hu, Y. & Cheng, H. The urgency of assessing the greenhouse gas budgets of hydroelectric
711 reservoirs in China. *Nature Climate Change* **3**, 708 (2013).

712 110 Galy-Lacaux, C., Delmas, R., Kouadio, G., Richard, S. & Gosse, P. Long-term greenhouse gas
713 emissions from hydroelectric reservoirs in tropical forest regions. *Global Biogeochemical Cycles*
714 **13**, 503-517 (1999).

715 111 Mendonça, R. *et al.* Hydroelectric carbon sequestration. *Nature Geoscience* **5**, 838 (2012).

716 112 Maavara, T., Lauerwald, R., Regnier, P. & Van Cappellen, P. Global perturbation of organic
717 carbon cycling by river damming. *Nature communications* **8** (2017).

718 113 Fearnside, P. M. Do hydroelectric dams mitigate global warming? The case of Brazil's Curuá-
719 Una Dam. *Mitigation and Adaptation Strategies for Global Change* **10**, 675-691 (2005).

720 114 Fearnside, P. M. Greenhouse-gas emissions from Amazonian hydroelectric reservoirs: The
721 example of Brazil's Tucuruí Dam as compared to fossil fuel alternatives. *Environmental*
722 *conservation* **24**, 64-75 (1997).

723 115 St. Louis, V. L., Kelly, C. A., Duchemin, É., Rudd, J. W. & Rosenberg, D. M. Reservoir Surfaces
724 as Sources of Greenhouse Gases to the Atmosphere: A Global Estimate: Reservoirs are sources of
725 greenhouse gases to the atmosphere, and their surface areas have increased to the point where
726 they should be included in global inventories of anthropogenic emissions of greenhouse gases.
727 *BioScience* **50**, 766-775 (2000).

728 116 Mendonça, R. *et al.* Organic carbon burial in global lakes and reservoirs. *Nature communications*
729 **8**, 1694 (2017).

730 117 Cole, J. J. *et al.* Plumbing the global carbon cycle: integrating inland waters into the terrestrial
731 carbon budget. *Ecosystems* **10**, 172-185 (2007).

732 **Landmark paper that develops the framework for including the land-ocean aquatic**
733 **continuum in global carbon budgets.**

734 118 Dean, W. E. & Gorham, E. Magnitude and significance of carbon burial in lakes, reservoirs, and
735 peatlands. *Geology* **26**, 535-538 (1998).

736 119 Mulholland, P. J. & Elwood, J. W. The role of lake and reservoir sediments as sinks in the
737 perturbed global carbon cycle. *Tellus* **34**, 490-499 (1982).

738 120 Stallard, R. F. Terrestrial sedimentation and the carbon cycle: Coupling weathering and erosion to
739 carbon burial. *Global Biogeochemical Cycles* **12**, 231-257 (1998).

740 121 Li, Z. *et al.* Carbon footprints of pre-impoundment clearance on reservoir flooded area in China's
741 large hydro-projects: Implications for GHG emissions reduction in the hydropower industry.
742 *Journal of cleaner production* **168**, 1413-1424 (2017).

743 122 Zheng, H. *et al.* Spatial-temporal variations of methane emissions from the Ertan hydroelectric
744 reservoir in southwest China. *Hydrological Processes* **25**, 1391-1396 (2011).

745 123 Lu, F. *et al.* Preliminary report on methane emissions from the Three Gorges Reservoir in the
746 summer drainage period. *Journal of environmental sciences* **23**, 2029-2033 (2011).

747 124 Rosa, L. P., Dos Santos, M. A., Matvienko, B., dos Santos, E. O. & Sikar, E. Greenhouse gas
748 emissions from hydroelectric reservoirs in tropical regions. *Climatic Change* **66**, 9-21 (2004).

749 125 Shi, W. *et al.* Carbon emission from cascade reservoirs: Spatial heterogeneity and mechanisms.
750 *Environmental science & technology* **51**, 12175-12181 (2017).

751 126 Zhao, Y., Wu, B. & Zeng, Y. Spatial and temporal patterns of greenhouse gas emissions from
752 Three Gorges Reservoir of China. *Biogeosciences* **10**, 1219-1230 (2013).

753 127 Dos Santos, M. A., Rosa, L. P., Sikar, B., Sikar, E. & Dos Santos, E. O. Gross greenhouse gas
754 fluxes from hydro-power reservoir compared to thermo-power plants. *Energy Policy* **34**, 481-488
755 (2006).

756 128 De Faria, F. A., Jaramillo, P., Sawakuchi, H. O., Richey, J. E. & Barros, N. Estimating
757 greenhouse gas emissions from future Amazonian hydroelectric reservoirs. *Environmental*
758 *Research Letters* **10**, 124019 (2015).

759 129 Garnier, J. & Billen, G. Production vs. Respiration in river systems: An indicator of an
760 “ecological status”. *Science of the Total Environment* **375**, 110-124 (2007).

761 130 Wang, F., Wang, Y., Zhang, J., Xu, H. & Wei, X. Human impact on the historical change of CO₂
762 degassing flux in River Changjiang. *Geochemical Transactions* **8**, 7 (2007).

763 131 Jones Jr, J. B., Stanley, E. H. & Mulholland, P. J. Long-term decline in carbon dioxide
764 supersaturation in rivers across the contiguous United States. *Geophysical Research Letters* **30**
765 (2003).

766 132 Beaulieu, J. J. *et al.* Nitrous oxide emission from denitrification in stream and river networks.
767 *Proceedings of the National Academy of Sciences* **108**, 214-219 (2011).

768 133 Messenger, M. L., Lehner, B., Grill, G., Nedeva, I. & Schmitt, O. Estimating the volume and age
769 of water stored in global lakes using a geo-statistical approach. *Nature communications* **7**, 13603
770 (2016).

771 134 Giles, J. Methane quashes green credentials of hydropower. *Nature* **444**, 524 (2006).

772 135 Abril, G. *et al.* Carbon dioxide and methane emissions and the carbon budget of a 10-year old
773 tropical reservoir (Petit Saut, French Guiana). *Global biogeochemical cycles* **19** (2005).

774 136 Chen, H. *et al.* Methane emissions from newly created marshes in the drawdown area of the
775 Three Gorges Reservoir. *Journal of Geophysical Research: Atmospheres* **114** (2009).

776 137 Pacca, S. Impacts from decommissioning of hydroelectric dams: a life cycle perspective. *Climatic*
777 *Change* **84**, 281-294 (2007).

778 138 Almeida, R. M. *et al.* Reducing greenhouse gas emissions of Amazon hydropower with strategic
779 dam planning. *Nature communications* **10**, 1-9 (2019).

780 139 Catalán, N., Marcé, R., Kothawala, D. N. & Tranvik, L. J. Organic carbon decomposition rates
781 controlled by water retention time across inland waters. *Nature Geoscience* **9**, 501 (2016).

782 **Compilation of field and laboratory measurements of organic carbon decomposition shows**
783 **that small water bodies with shorter hydraulic residence times have higher degradation**
784 **than larger water bodies.**

785 140 Cheng, F. Y. & Basu, N. B. Biogeochemical hotspots: Role of small water bodies in landscape
786 nutrient processing. *Water Resources Research* **53**, 5038-5056 (2017).

787 141 Botter, G., Basu, N., Zanardo, S., Rao, P. & Rinaldo, A. Stochastic modeling of nutrient losses in
788 streams: Interactions of climatic, hydrologic, and biogeochemical controls. *Water Resources*
789 *Research* **46** (2010).

790 142 Lehner, B. *et al.* High-resolution mapping of the world's reservoirs and dams for sustainable
791 river-flow management. *Frontiers in Ecology and the Environment* **9**, 494-502,
792 doi:10.1890/100125 (2011).

793 143 Mulligan, M., Saenz-Cruz, L., van Soesbergen, A., Smith, V. & Zurita, L. Global dams database
794 and geowiki. Version 1. <http://geodata.policysupport.org/dams>. (2009).

795 144 Lehner, B., Verdin, K. & Jarvis, A. HydroSHEDS technical documentation, version 1.0. *World*
796 *Wildlife Fund US, Washington, DC*, 1-27 (2006).

797 145 Harrison, J. A., Frings, P. J., Beusen, A. H. W., Conley, D. J. & McCrackin, M. L. Global
798 importance, patterns, and controls of dissolved silica retention in lakes and reservoirs. *Global*
799 *Biogeochemical Cycles* **26**, 12, doi:10.1029/2011gb004228 (2012).

800 146 Harrison, J. A. *et al.* The regional and global significance of nitrogen removal in lakes and
801 reservoirs. *Biogeochemistry* **93**, 143-157 (2009).

802 147 Downing, J. *et al.* The global abundance and size distribution of lakes, ponds, and impoundments.
803 *Limnology and Oceanography* **51**, 2388-2397 (2006).

804 148 Habets, F., Molénat, J., Carluier, N., Douez, O. & Leenhardt, D. The cumulative impacts of small
805 reservoirs on hydrology: A review. *Science of the total environment* **643**, 850-867 (2018).

806 149 Benndorf, J. & Pütz, K. Control of eutrophication of lakes and reservoirs by means of pre-dams—
807 I. Mode of operation and calculation of the nutrient elimination capacity. *Water research* **21**, 829-
808 838 (1987).

809 150 Pütz, K. & Benndorf, J. The importance of pre-reservoirs for the control of eutrophication of
810 reservoirs. *Water Science and Technology* **37**, 317-324 (1998).

811 151 Petts, G. E. Water allocation to protect river ecosystems. *Regulated rivers: research &*
812 *management* **12**, 353-365 (1996).

- 813 152 Arthington, A. H., Bunn, S. E., Poff, N. L. & Naiman, R. J. The challenge of providing
814 environmental flow rules to sustain river ecosystems. *Ecological applications* **16**, 1311-1318
815 (2006).
- 816 153 Chen, W. & Olden, J. D. Evaluating transferability of flow–ecology relationships across space,
817 time and taxonomy. *Freshwater biology* **63**, 817-830 (2018).
- 818 154 Acreman, M. *et al.* Environmental flows for natural, hybrid, and novel riverine ecosystems in a
819 changing world. *Frontiers in Ecology and the Environment* **12**, 466-473 (2014).
- 820 155 Tharme, R. E. A global perspective on environmental flow assessment: emerging trends in the
821 development and application of environmental flow methodologies for rivers. *River research and*
822 *applications* **19**, 397-441 (2003).
- 823 156 Acreman, M. Environmental flows-basics for novices. *WIREs Water* **3**, 622-628 (2016).
- 824 157 Gillespie, B. R., Desmet, S., Kay, P., Tillotson, M. R. & Brown, L. E. A critical analysis of
825 regulated river ecosystem responses to managed environmental flows from reservoirs.
826 *Freshwater Biology* **60**, 410-425 (2015).
- 827 158 Huang, Z. & Wang, L. Yangtze dams increasingly threaten the survival of the Chinese sturgeon.
828 *Current Biology* **28**, 3640-3647. e3618 (2018).
- 829 159 Robinson, C. T., Siebers, A. R. & Ortlepp, J. Long-term ecological responses of the River Spöl to
830 experimental floods. *Freshwater Science* **37**, 433-447 (2018).
- 831 160 Sertić Perić, M., Jolidon, C., Uehlinger, U. & Robinson, C. T. Long-term ecological patterns of
832 alpine streams: An imprint of glacial legacies. *Limnology and Oceanography* **60**, 992-1007
833 (2015).
- 834 161 Tennant, D. L. Instream flow regimens for fish, wildlife, recreation and related environmental
835 resources. *Fisheries* **1**, 6-10 (1976).
- 836 162 Smakhtin, V. U., Shilpakar, R. & Hughes, D. Hydrology-based assessment of environmental
837 flows: an example from Nepal. *Hydrological Sciences Journal* **51**, 207-222 (2006).
- 838 163 Kim, S. M. & Kim, D. H. in *International Conference of Agricultural Engineering* (Zurich,
839 2014).
- 840 164 Rahi, K. A. & Halihan, T. Changes in the salinity of the Euphrates River system in Iraq. *Regional*
841 *Environmental Change* **10**, 27-35 (2010).
- 842 165 Huisman, J. *et al.* Cyanobacterial blooms. *Nature Reviews Microbiology* **16**, 471-483 (2018).
- 843 166 Ashby, S. L., Myers, J. L., Laney, E., Honnell, D. & Owens, C. The effects of hydropower
844 releases from Lake Texoma on downstream water quality. *Journal of Freshwater Ecology* **14**,
845 103-112 (1999).
- 846 167 Nürnberg, G. K. Lake responses to long-term hypolimnetic withdrawal treatments. *Lake and*
847 *Reservoir Management* **23**, 388-409 (2007).
- 848 168 Sabo, J. *et al.* Designing river flows to improve food security futures in the Lower Mekong Basin.
849 *Science* **358**, eaao1053 (2017).
- 850 169 O'Connor, J. E., Duda, J. J. & Grant, G. E. 1000 dams down and counting. *Science* **348**, 496-497
851 (2015).
- 852 170 Pohl, M. M. Bringing down out dams: Trends in American dam removal rationales. *JAWRA*
853 *Journal of the American Water Resources Association* **38**, 1511-1519 (2002).
- 854 171 Bellmore, J. *et al.* Status and trends of dam removal research in the United States. *Wiley*
855 *Interdisciplinary Reviews: Water* **4**, e1164 (2017).
- 856 172 Stanley, E. H. & Doyle, M. W. Trading off: the ecological effects of dam removal. *Frontiers in*
857 *Ecology and the Environment* **1**, 15-22 (2003).
- 858 **Comprehensive review of the broad impacts of dam removal on biogeochemical cycling and**
859 **river ecosystem health.**
- 860 173 Van Meter, K., Van Cappellen, P. & Basu, N. Legacy nitrogen may prevent achievement of water
861 quality goals in the Gulf of Mexico. *Science*, eaar4462 (2018).

862 **Modeled historical and predicted future nitrogen loads for the Mississippi River, indicating**
863 **that legacy nitrogen loading from agriculture may prevent reduction of Gulf of Mexico**
864 **Dead Zone for decades.**

865 174 Shuman, J. R. Environmental considerations for assessing dam removal alternatives for river
866 restoration. *Regulated Rivers: Research & Management* **11**, 249-261 (1995).

867 175 Islam, M. S., Bonner, J. S., Fuller, C. S. & Kirkey, W. Impacts of an extreme weather-related
868 episodic event on the Hudson river and estuary. *Environmental Engineering Science* **33**, 270-282
869 (2016).

870 176 Chateauvert, A., Linnansaari, T., Yamazaki, G. & Curry, R. A. Considerations for Large Dam
871 Removals. (Canadian Rivers Institute, University of New Brunswick, 2015).

872 177 Gray, L. J. & Ward, J. V. Effects of sediment releases from a reservoir on stream
873 macroinvertebrates. *Hydrobiologia* **96**, 177-184 (1982).

874 178 Perrin, C., Ashley, K. & Larkin, G. Effect of drawdown on ammonium and iron concentrations in
875 a coastal mountain reservoir. *Water Quality Research Journal* **35**, 231-244 (2000).

876 179 Bohrerova, Z., Park, E., Halloran, K. & Lee, J. Water Quality Changes Shortly After Low-Head
877 Dam Removal Examined With Cultural and Microbial Source Tracking Methods. *River research*
878 *and applications* **33**, 113-122 (2017).

879 180 Simon, A. & Darby, S. E. Process-form interactions in unstable sand-bed river channels: A
880 numerical modeling approach. *Geomorphology* **21**, 85-106 (1997).

881 181 Walter, R. C. & Merritts, D. J. Natural streams and the legacy of water-powered mills. *Science*
882 **319**, 299-304 (2008).

883 182 Stanley, E. H. & Doyle, M. W. A geomorphic perspective on nutrient retention following dam
884 removal: Geomorphic models provide a means of predicting ecosystem responses to dam
885 removal. *BioScience* **52**, 693-701 (2002).

886 183 Merritts, D., Walter, R. & Rahnis, M. A. Sediment and nutrient loads from stream corridor
887 erosion along breached millponds. *Report to the PA Department of Environmental Protection*
888 (2010).

889 184 Zhang, Q., Hirsch, R. M. & Ball, W. P. Long-term changes in sediment and nutrient delivery
890 from Conowingo dam to Chesapeake Bay: effects of reservoir sedimentation. *Environmental*
891 *science & technology* **50**, 1877-1886 (2016).

892 185 Kiptala, J. K., Mul, M. L., Mohamed, Y. A. & van der Zaag, P. Multiobjective analysis of green-
893 blue water uses in a highly utilized basin: case study of Pangani Basin, Africa. *Journal of Water*
894 *Resources Planning and Management* **144**, 05018010 (2018).

895 186 Mul, M. *et al.* Trade-offs between ecosystem services and hydropower generation, case of the
896 Akosombo and Kpond Dams, Ghana in *International Conference on Water, Energy & Climate*
897 *change* 39 (2016).

898 187 Bastviken, D., Tranvik, L. J., Downing, J. A., Crill, P. M. & Enrich-Prast, A. Freshwater methane
899 emissions offset the continental carbon sink. *Science* **331**, 50-50 (2011).

900 188 Li, S. *et al.* Large greenhouse gases emissions from China's lakes and reservoirs. *Water research*
901 **147**, 13-24 (2018).

902 189 Hayes, D. S. *et al.* Advancing towards functional environmental flows for temperate floodplain
903 rivers. *Science of the Total Environment* **633**, 1089-1104 (2018).

904 190 Yarnell, S. M. *et al.* Functional flows in modified riverscapes: hydrographs, habitats and
905 opportunities. *BioScience* **65**, 963-972 (2015).

906 191 Mannes, S. *et al.* Ecological effects of a long-term flood program in a flow-regulated river.
907 *Journal of Alpine Research| Revue de géographie alpine*, 125-134 (2008).

908

909 192 Jager, H. I., Efroymson, R. A., Opperman, J. J. & Kelly, M. R. Spatial design principles for
910 sustainable hydropower development in river basins. *Renewable and Sustainable Energy Reviews*
911 **45**, 808-816 (2015).

912 194 Brzezinski, M. A. The Si: C: N ratio Of marine diatoms: interspecific variability and the effect of
913 some environmental variables 1. *Journal of Phycology* **21**, 347-357 (1985).
914

915

916

917 **Acknowledgements**

918 T.M. was funded through the Natural Sciences and Engineering Research Council of Canada (NSERC),
919 award number PDF-516575-2018. Q.C. was funded through the National Natural Science Foundation of
920 China (No. 91547206). L.B. was funded from the European Union’s Horizon 2020 research and innovation
921 programme under the Marie Skłodowska-Curie grant agreement No 765553, as part of the Euro-FLOW
922 project.

923 **Author contributions**

924 All authors contributed to the researching data and writing of the manuscript and to the discussion
925 of the content. T.M., Q.C., L.B., K.V.M., and C.Z. reviewed and edited the manuscript before
926 submission.

927 **Competing interests**

928 The authors declare no competing interests.

929 **Peer review information**

930 *Nature Reviews Earth & Environment* thanks Nathan Barros and the other anonymous reviewer(s)
931 for their contribution to the peer review of this work.

932 **Publisher's note**

933 Springer Nature remains neutral with regard to jurisdictional claims in published maps and
934 institutional affiliations.

935

936 **Related links**

937 <http://globaldamwatch.org/>: Public access to GOOD², GRanD and FHReD databases of existing and
 938 future dams and reservoirs worldwide, as well as links to external global and regional databases.

939

940 **Key points**

941

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

951

952

953

954 **Table 1: Areal CO₂ and CH₄ emissions from reservoirs*.**

Dam region	CO₂ emissions (× 10 ⁴ μg C m ⁻² day ⁻¹)	CH₄ emissions (× 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

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

957

958

959

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

973 fluxes delivered to coastal zones, and subscript “anthro” represents the anthropogenic or modern-day fluxes
974 delivered to coastal zones.

975

976

977 **Figure 2: Elimination of nitrogen, phosphorus and silicon from reservoirs.** Elimination measurements
978 and modeled HRT–elimination relationships are shown for ammonium (NH_4^+), dissolved inorganic
979 nitrogen (DIN), dissolved organic nitrogen (DON), nitrate (NO_3^-), and total dissolved N (TDN) in
980 reservoirs⁴⁰ (**part a**), total phosphorous (TP), total dissolved phosphorus (TDP) and soluble reactive
981 phosphorus (SRP)^{39,46} (**part b**), and dissolved silicon⁵⁵ (DSi) (**part c**). For all nutrients, published modeled
982 relationships between HRT and elimination are also shown^{39,55,40}. On average, TP is the most efficiently
983 eliminated nutrient at most HRTs, with the exception of reservoirs with HRTs below 50 days, where DSi
984 can be more efficiently removed. Elimination measurements show considerably more scatter than modeled
985 relationships, indicating that while HRT is a useful first order predictor, elimination is dependent other
986 mechanisms, including light availability, inflowing nutrient loads and ratios, reservoir mixing, temperature,
987 micronutrient limitation, or the presence of metal oxide minerals. Additional factors that can skew the
988 calculation of worldwide trends from published measurements include inconsistencies in the nutrient
989 species measured, the methods through which reservoir nutrient budgets are calculated, and the seasonality
990 of the reservoir measured. Negative elimination values indicate a net export, such as remobilization or a
991 nutrient source other than the water column, as occurs in N fixation.

992

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

998 and rising autotrophy, which can develop into algal blooms in middle-aged reservoirs. GHG emissions
999 decrease as flooded biomass is eliminated. Sediment accumulates in the reservoir over time, which can
1000 promote downstream streambed scouring due to the under-saturation of suspended sediment in river water.
1001 In old reservoirs, sediment accumulation can become severe, serving as a point source for nutrient
1002 remobilization to downstream, and nutrient saturation can drive large, potentially harmful algal blooms,
1003 causing fish mortality and anoxia.

1004

1005 **Figure 4. Relationships between hydraulic residence time, nutrient reactivity and elimination.** On the
1006 left axis, the first order reactivity rate constants (yr^{-1}) for total nitrogen (TN) removal (k_{TN}), total phosphorus
1007 (TP) removal (k_{TP}) and organic carbon (OC) degradation (k_{OC}), are plotted as a function of the hydraulic
1008 residence time (HRT) in years^{140,139}. On the right axis, the globally modeled average fraction of nutrient
1009 elimination (unitless) of the inflowing nutrient load as a function of HRT for denitrification (denit) and TN
1010 burial⁴⁰, TP burial³⁹, and allochthonous (allo) or autochthonous (auto) dissolved OC (DOC), particulate OC
1011 (POC) or total OC (TOC) mineralization (min)¹¹². Reactivity describes the system's ability to remove or
1012 transform nutrients per unit time, whereas the elimination is a function of the reactivity and the HRT. Small
1013 reservoirs tend to have higher reactivity, while large reservoirs have higher overall elimination due to their
1014 long HRTs.

1015

1016 **Figure 5. Environmental flow dynamics in different flow regimes and damming scenarios.** Natural
1017 and dam-altered river flow regimes by month for a hypothetical alpine hydropower dam (**part a**), a
1018 temperature zone reservoir used for drinking water (**part b**), and a Mediterranean reservoir used for
1019 irrigation¹⁸⁹ (**part c**). Flood-only and seasonal compensation environmental flow (e-flow) scenarios are
1020 shown for the same reservoirs (**parts d-f**). The catchment-scale hydraulic residence time (HRT)
1021 corresponding to the natural, altered, and e-flow scenarios shown in the left and middle columns are also
1022 presented (**parts g-i**). The e-flow scenarios illustrate some reservoir management alternatives to simple

1023 year-round constant flows. The e-flows continue to regulate flows in predictable ways while also allowing
1024 for spring flooding or seasonal high flows to better replicate natural flow variations^{190,191}. Basin-wide HRT
1025 responses to these e-flows scenarios can be used as a starting point to predict how and when nutrient
1026 elimination will be maximized or minimized.

1027

1028 [b1] **Dam management considerations**

1029 **[H1] Conception and planning**

1030 If managed and planned appropriately, from conception to deconstruction and in the context of the entire
1031 watershed, dams can come closer to delivering the services for which they are intended with minimized
1032 environmental and social consequences. The most responsible dam management plan would address all of
1033 the following questions in the before building a dam. Given the current boom in dam construction
1034 worldwide, proper planning and management is crucial.

1035 **[H2] Size and types of dam(s).** Should one large dam be built (one long hydraulic residence time, or HRT),
1036 or multiple small dams (many small HRTs)?

1037 **[H2] Location(s).** Should all dams be built on a single tributary or spread throughout the watershed?¹⁹² Will
1038 headwater dams eliminate fewer nutrients and produce fewer greenhouse gases (GHG) than lowland or
1039 downstream dams due to lower riverine nutrient and carbon loads?

1040 **[H2] Lifespan.** How long can we expect the dam in question to maintain the services it provides without
1041 increases in its environmental, social, and economic costs? Will the nutrient loads and HRT promote high
1042 nutrient elimination in the form of sedimentation in the reservoir?

1043 **[H2] GHG emissions.** Should biomass be cleared prior to flooding? How do reservoir GHG emissions
1044 compare to those from other energy sources with respect to the life cycle analyses? Where can a dam be
1045 built within a basin to minimize GHG emissions while maximizing hydroelectricity production?

1046 **[H2] Eutrophication.** How will reservoir, downstream and coastal nutrient ratios be impacted? Do the
1047 predicted reservoir HRT and nutrient loads indicate that there will be substantial nutrient elimination?

1048 **[H2] Management.** How will existing watershed nutrient management strategies need to change in the
1049 context of the new dam? How will the basin-wide HRT change? Will nutrient elimination in the reservoir
1050 change nutrient stoichiometry downstream? How will these changes interact with existing nutrient loading
1051 management strategies?

1052 **[H1] Existing dams**

1053 **[H2] Nutrient load management.** Can we modify existing dam operation to generate desirable basin-wide
1054 HRTs using environmental-flows (e-flows), and if so how will different e-flow scenarios influence
1055 downstream water quality?

1056 **[H2]** Is it more feasible to manage the upstream nutrient loads than to attempt to use dam operation for
1057 nutrient management?

1058 **[H1] Deconstruction**

1059 **[H2] Remobilization:** How can the remobilization and mineralization and/or emissions of deposited
1060 sediment, nutrients, and organic carbon be managed?

1061

1062 **Glossary terms**

1063

1064 • **Elimination:** For nutrients, the net removal of nutrients or nutrient species from the water column
1065 in reservoirs via sedimentation and burial or gaseous evasion to the atmosphere.

1066

1067 • **Eutrophication:** The over-enrichment of a water body with nutrients, driving high primary
1068 production (photosynthesis) and excessive growth of algae, often resulting in harmful algal
1069 blooms or toxic cyanobacterial blooms and the development of anaerobic or anoxic conditions.

1070

1071 • **Denitrification:** Biological reduction of nitrate (NO_3^-) to N_2 gas through a series of intermediate
1072 reaction steps that can produce nitrite (NO_2^-), nitric oxide (NO) and nitrous oxide (N_2O).

1073

1074 • **Redfield-Brzezinski ratio:** An extension of the Redfield ratio (C:N:P = 106:16:1), the Redfield-
1075 Brzezinski ratio describes the average elemental molar composition of diatoms, defined as
1076 C:N:P:Si = 106:16:1:15-20.

1077

1078 • **Limiting nutrient:** The nutrient that is stoichiometrically in short-supply in a system, typically
1079 benchmarked in aqueous biogeochemistry using the Redfield or Redfield-Brzezinski ratios.

1080

- 1081 • Autotrophy: Primary production that derives carbon from carbon dioxide and energy from
1082 sunlight (photosynthesis) or an inorganic chemical.
1083
- 1084 • Methanogenesis: The formation of methane by methanogenic microbes; a form of anaerobic
1085 respiration.
1086
- 1087 • Oligotrophic: A water body characterized by low nutrient concentrations and thus low primary
1088 productivity.
1089
- 1090 • Nitrification: The biological oxidation of ammonium (NH_4^+) to nitrate (NO_3^-). Produces nitrous
1091 oxide (N_2O) as a by-product.
1092
- 1093 • Biogeochemical reactivity: In first order reaction kinetics, biogeochemical reactivity is
1094 represented by a rate constant (k) in units of inverse time [T^{-1}] that is multiplied by the nutrient
1095 mass or concentration to calculate the rate or flux of a process.
1096
- 1097 • Labile: Reactive, easily degradable, highly bioavailable chemicals.
1098
- 1099 • Hydro-peaking: A type of flow regulation that produces short-term, high flow events in river
1100 discharge.
1101

1102

1103

1104 **ToC blurb**

1105 River damming can harness hydropower, control flooding, and store water, but also can alter
1106 biogeochemistry in reservoirs and downstream environments. In this Review, the impacts of dams on
1107 nutrient cycling and greenhouse production are discussed, emphasising the need to consider
1108 biogeochemical cycling at all stages of dam lifespan.