



Review

Nitrogen cycling processes and the role of multi-trophic microbiota in dam-induced river-reservoir systems

Nan Yang^a, Chi Zhang^b, Linqiong Wang^c, Yi Li^{a,*}, Wenlong Zhang^a, Lihua Niu^a, Huanjun Zhang^a, Longfei Wang^a

^a Key Laboratory of Integrated Regulation and Resource Development on Shallow Lake of Ministry of Education, College of Environment, Hohai University, Xikang Road #1, Nanjing 210098, P R China

^b College of Mechanics and Materials, Hohai University, Xikang Road #1, Nanjing 210098, P R China

^c College of Oceanography, Hohai University, Xikang Road #1, Nanjing 210098, P R China

ARTICLE INFO

Keywords:

Reservoir impoundment
Stratification
Nutrient cycles
Multiple trophic levels
Microbial food web

ABSTRACT

The nitrogen (N) cycle is one of the most important nutrient cycles in river systems, and it plays an important role in maintaining biogeochemical balance and global climate stability. One of the main ways that humans have altered riverine ecosystems is through the construction of hydropower dams, which have major effects on biogeochemical cycles. Most previous studies examining the effects of damming on N cycling have focused on the whole budget or flux along rivers, and the role of river as N sources or sinks at the global or catchment scale. However, so far there is still lack of comprehensive and systematic summarize on N cycling and the controlling mechanisms in reservoirs affected by dam impoundment. In this review, we firstly summarize N cycling processes along the longitudinal riverine-transition-lacustrine gradient and the vertically stratified epilimnion-thermocline-hypolimnion gradient. Specifically, we highlight the direct and indirect roles of multi-trophic microbiota and their interactions in N cycling and discuss the main factors controlling these biotic processes. In addition, future research directions and challenges in incorporating multi-trophic levels in bioassessment, environmental flow design, as well as reservoir regulation and restoration are summarized. This review will aid future studies of N fluxes along dammed rivers and provide an essential reference for reservoir management to meet ecological needs.

1. Introduction

Rivers are important channels connecting terrestrial and marine ecosystems and serve as transportation systems for large amounts of materials and nutrients. Currently, more than 50% of global rivers are fragmented by dams for hydropower production, water supply, flood control, and navigation (Grill et al., 2019). Dam construction has major effects on hydro-geomorphology, biogeochemical cycles, and the ecological environment. First, dams convert rivers into lentic reservoirs characterized by decreased flow velocity and increased hydraulic residence time (Nilsson et al., 2005). Hydrological variations associated with damming also affect annual runoff, thermal regimes, and sediment loads (Wang et al., 2016; Yigzaw et al., 2019). Second, dams disrupt the river continuum, which increases nutrient loads and induces changes in nutrient stoichiometric ratios along river systems (Wang et al., 2018a). Third, hydrological and biogeochemical variations reshape riparian and

riverine habitats and alter the structure, diversity, and distribution of biological communities (Poff et al., 2007). Ultimately, dams can modify the ecosystem functions (e.g., nutrient cycling and energy flow) and services (e.g., fisheries) of rivers (Turgeon et al., 2019).

Nutrients such as carbon (C), nitrogen (N), phosphorus (P), and silicon (Si) are transported along rivers. Damming can alter riverine nutrient cycles in multiple and complex ways and have positive or negative impacts. For example, reservoirs can eliminate nutrients from the water column via sedimentation or gaseous release, thus alleviating eutrophication pressure on downstream ecosystems (Van Cappellen and Maavara, 2016). However, the longer hydraulic residence time and the higher transparency may promote primary productivity and nutrient transformation within reservoirs, resulting in increased eutrophication downstream (Chen et al., 2018). Reservoirs tend to facilitate the retention of nutrients from rivers in large quantities. Taylor Maavara from the University of Waterloo has quantified the effects of dams on C, P, Si, and

* Corresponding author.

E-mail address: envly@hhu.edu.cn (Y. Li).

<https://doi.org/10.1016/j.watres.2021.117730>

Received 2 August 2021; Received in revised form 25 September 2021; Accepted 27 September 2021

Available online 30 September 2021

0043-1354/© 2021 Elsevier Ltd. All rights reserved.

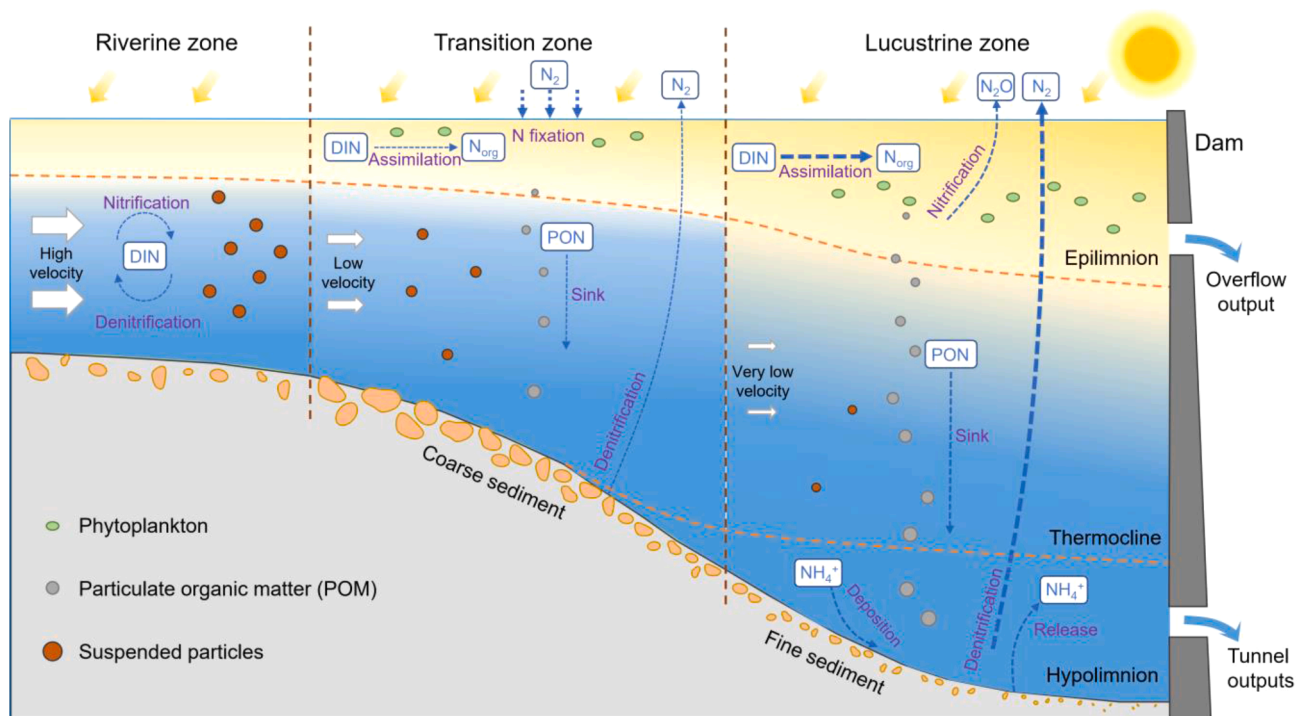


Fig. 1. Conceptual summary of the longitudinal patterns of nitrogen cycling. Variations in environmental factors and major nitrogen cycling processes are shown along the riverine-transition-lacustrine system. The dominant processes in each zone are indicated by bold dashed lines. (DIN, dissolved inorganic nitrogen; PON, particulate organic nitrogen; N_{org} , organismal nitrogen contents).

N fluxes based on global data. They estimated that the global primary productivity and C mineralization ratio (P/R) will double by 2030 because of damming (Maavara et al., 2017). Meanwhile, approximately 17% and 5.3% of the global total P and total reactive Si loading to rivers are expected to be sequestered in reservoirs, respectively (Maavara et al., 2014, 2015). Compared with P and Si, which are eliminated most efficiently in reservoirs through particle sedimentation, N cycling within reservoirs is more complex and is typically dominated by transformation processes. Reservoirs contributed approximately 33% of the total N removed by lentic systems in 2000, and denitrification and burial eliminated 7% of N loading to the global river network; this is predicted to double to 14% by 2030 (Akbarzadeh et al., 2019; Harrison et al., 2009). Recently, a review article by Maavara et al. (2020) discussed the impacts of damming on the biogeochemistry of these nutrients along river networks from a global perspective. The authors emphasized that responsible dam construction and management require consideration of nutrient elimination and loading to achieve a balance between environmental impacts and damming services.

Given the relative complexity of N transformation, a complete knowledge of N cycling processes in reservoirs and dammed river systems is critically important. N inputs to reservoirs are transformed by a series of biotic and abiotic processes, such as nitrification and denitrification, biological assimilatory uptake, sedimentation, and benthic release (Keys et al., 2019; Ran et al., 2017). The cycle of N in river systems was reviewed by Xia et al. (2018), summarizing a series of N transformation pathways active in the water column, suspended particle-water surfaces in overlying water, sediment-water interfaces, and riparian zones. N transformations in rivers and streams are mainly controlled by microbial-mediated oxidation and reduction processes and thus are usually referred to as the microbial N cycle. Several researchers have summarized these biological processes (Kuypers et al., 2018; Zhang et al., 2020b). Briefly, dinitrogen gas (N_2) is first fixed to ammonia N (NH_4^+), which is assimilated into organic N. The degradation of organic N through ammonification can in turn release NH_4^+ , which is subsequently oxidized to nitrite (NO_2^-) and nitrate (NO_3^-) through the

nitrification process and eventually converted back to N_2 via denitrification and anammox processes. The N cycling in river systems is influenced by both natural and man-made disturbances. Rivers are being changed because of human activities, and damming is the most severe anthropogenic disturbance. The widespread construction of dams and reservoirs may impede the hydrologic connectivity of rivers, limit physical exchange, modify the distribution of species, and result in variation in N transformation and flux (Akbarzadeh et al., 2019; Gao et al., 2021b).

The importance of N as a biogenic element and water quality indicator has motivated several studies of N cycling in river systems. As mentioned above, some related review articles have summarized the processes, mechanisms, and drivers of N cycling, as well as the methods for identifying the sources of N or tracing the flux of N (Xia et al., 2018; Zhang et al., 2020b). Dam construction has long been a major focus of research. Published review articles have mainly focused on the entire N budget or flux along rivers and the role of rivers as N sources or sinks affected by damming at the global or catchment scale (Akbarzadeh et al., 2019; Maavara et al., 2020; Van Cappellen and Maavara, 2016; Wang et al., 2018a). However, no studies to date have comprehensively characterized N cycling processes and the controlling factors within a relatively small region, i.e. river-reservoir systems. This review provides a comprehensive overview of N cycling processes along both the longitudinal river flow gradient and the vertical water column gradient for the first time. We summarize the role of multi-trophic microbiota and their biotic and abiotic interactions, which have often been overlooked by previous studies, in controlling N cycling in river-reservoir systems. Learning and mastering these N cycling processes in a single reservoir is key for understanding N patterns along entire rivers. The goal of this review is to promote future research on N cycles along dammed rivers, as well as provide guidance for the restoration of trophic conditions and management of reservoirs from an ecosystem perspective.

2. Nitrogen cycling in longitudinal river-reservoir systems

2.1. Riverine-transition-lacustrine gradient induced by damming

Reservoirs are hybrid systems with pronounced environmental gradients from river inflows to dams and thus are characterized by a mixture of lotic and lentic conditions. Typically, three zones are recognized along the longitudinal axes of reservoirs: riverine (or lotic), transition, and lacustrine (or lentic) (Thornton, 1990). The area of each zone depends on the flow flux, morphology, residence time, season, and geographical location (Soares Guedes et al., 2020).

The upstream riverine zone is a turbulent system characterized by higher flow velocity and shorter hydraulic residence time (Fig. 1). Horizontal flow is dominant in this area and is accompanied by large amounts of suspended particles, resulting in higher turbidity and lower transparency. The transition zone, which has the properties of both natural rivers and large lakes, is characterized by gradually decreasing flow velocity and particulate concentration, as well as increased retention time and light penetration. The lacustrine zone is located close to the dam and remains in an almost stationary state, with longer water residence times, lower turbidity, and a deeper euphotic layer. This region has properties similar to large lakes, and the vertical processes are more pronounced. Vertical stratification may occur because of the weak hydrodynamics and heat transfer in the central reservoir area, which has a high thermal stratification index, especially during the warm seasons (Yu et al., 2010). The lotic to lentic gradient in the reservoir results in shifts in species composition and distribution. Lotic-adapted species prefer upstream riverine and transitional habitats, whereas lentic-adapted species tend to occur in downstream lacustrine habitats (Moitra and Leff, 2015; Pennock et al., 2021; Poznanska et al., 2010; Rychtecky and Znachor, 2011). Overall, physicochemical variations coupled with biotic properties can alter ecosystem functions, such as nutrient cycling, along the riverine-transition-lacustrine system.

2.2. Longitudinal nitrogen cycling processes

The special hydrological and biological properties of reservoirs alter various biogeochemical processes compared with natural rivers. N retention and transformation are closely associated with flow patterns, trophic status, and sedimentation conditions (Xia et al., 2018). Consequently, a series of N cycling processes, such as N fixation, N redox reactions, and N removal, are affected by heterogeneity along the riverine-transition-lacustrine gradient.

2.2.1. Nitrogen fixation

N fixation, in which dinitrogen gas (N_2) is converted to ammonium (NH_4^+), is the only biological route for fixed N creation. In aquatic systems, N fixation is mainly controlled by a subset of taxonomically and metabolically diverse prokaryotes called diazotrophs, which exclusively rely on nitrogenase along with significant amounts of ATP and reductant (Hoffman et al., 2014). Reservoirs are considered hot spots of N fixation, especially in the transition zone. Researchers have found that N fixation is consistently low in riverine and lacustrine zones of reservoirs and peaks in the transition zone; thus, the risk of water quality degradation is probably higher in the transition zone (Doyle et al., 2010; Scott et al., 2009).

Possible reasons for longitudinal variations in N fixation along the riverine-transition-lacustrine system were outlined by Scott et al. (2009). N fixation is closely related to phytoplankton production, which depends on light and nutrient availability. Phytoplankton production is relatively low in the riverine zone and gradually increases in the transition zone because of higher light and nutrient availability but decreases in the lacustrine zone owing to nutrient limitation. These observations may explain the spatial discrepancies in N fixation (Scott et al., 2009). Furthermore, the amount of N fixation is known to be related to the N:P balance in lakes and reservoirs (de Tezanos Pinto and

Litchman, 2010; Vrede et al., 2009). A low external input of N relative to P could stimulate cyanobacteria production and N fixation (Ruan et al., 2014). In the reservoir system, variation in transformation and sedimentation may alter the N:P ratio along the longitudinal gradient. P has generally been considered a limiting nutrient in freshwater (Schindler et al., 2008). Because of the exogenous N inputs from inflow rivers, the riverine zone typically has a high N:P ratio (Cubas et al., 2019). Most N is removed via denitrification or biotic assimilation in the transition zone, which causes the limiting nutrient to shift from P to N (Saunders and Kalff, 2001). However, in the lacustrine zone, N is abundant and active in the overlying water and might be released endogenously from sediments under anaerobic conditions, and P is largely removed from the surface water because of particle sedimentation, thus increasing the N:P ratio in the water column (Maavara et al., 2015; Nowlin et al., 2005). This may also explain the gradual increase and then decrease in N fixation along the riverine-transition-lacustrine system.

2.2.2. Nitrogen transformation

A series of complex and interactive N transformations could occur synchronously in freshwater ecosystems. NO_3^- is the main form of N entering reservoirs. Together with NH_4^+ , these dissolved forms of inorganic N are usually assimilated and transformed into organic N by plants, phytoplankton, and microbes (Glibert et al., 2016; Kreiling et al., 2011; Maia and Moura, 2014). NH_4^+ is more easily assimilated into biomass than NO_3^- , and its accumulation is rarely observed, especially under light and aerobic conditions within central reservoirs (i.e., the static lacustrine zone). The increased production of phytoplankton in central reservoirs can enhance NO_3^- assimilation, thus promoting the formation of particulate organic nitrogen (PON). After organisms die, organic N in residues or detritus is decomposed to NH_4^+ through mineralization, which is mainly carried out by heterotrophic microbes (Zhang et al., 2020b). In the lacustrine zone, high NH_4^+ availability and low flow conditions can promote the nitrification process, which is typically carried out by nitrifying microbes that use NH_4^+ as an energy source (Zhang et al., 2020b). During this process, N_2O is produced and released from the water column, and its concentration significantly varies among the riverine, transition, and lacustrine zones (Chen et al., 2014). Given that N_2O is a highly potent greenhouse gas, some researchers have proposed that reservoirs may exacerbate its greenhouse effects, and this has received increased research attention (dos Santos et al., 2017; Kumar et al., 2019).

In lakes or reservoirs, the surface sediment-water interface is considered a hotspot of N removal, including denitrification and anaerobic NH_4^+ oxidation (Lansdown et al., 2016; Marzadri et al., 2017). Denitrification is the primary route by which fixed N is lost from aquatic systems, and it is controlled by a series of denitrification enzymes and organisms (Zhang et al., 2020b). In reservoirs, the coarse particles tend to settle in the upper riverine zone, and fine sediment is usually carried to the lacustrine zone and settles in the stagnant reservoir. Favorable conditions for denitrification usually exist in the fine sediment close to the dam (Chen et al., 2014; Wallace et al., 2020). In the deep bottom water of the lacustrine zone, hypoxia limits aerobic nitrification and leads to the accumulation of NH_4^+ (Roberts et al., 2012). Overall, the increased hydraulic residence time stemming from dam impoundments alters N transformations in reservoirs and induces a shift in the inorganic N composition from NO_3^- to NH_4^+ .

2.2.3. Nitrogen sedimentation and release

Once the reservoir is formed, the decreased flow velocity and mixing and greater depth lead to the retention or settlement of suspended particles, including particulate organic N and inorganic suspended N (Wang, 2020). The longitudinal heterogeneity of the particulate settlement property causes the sediment size to gradually decrease downstream (Mor et al., 2018). The increased residence time also promotes the growth and assimilation efficiency of pelagic organisms, resulting in the accumulation of endogenous N. These processes, coupled with the

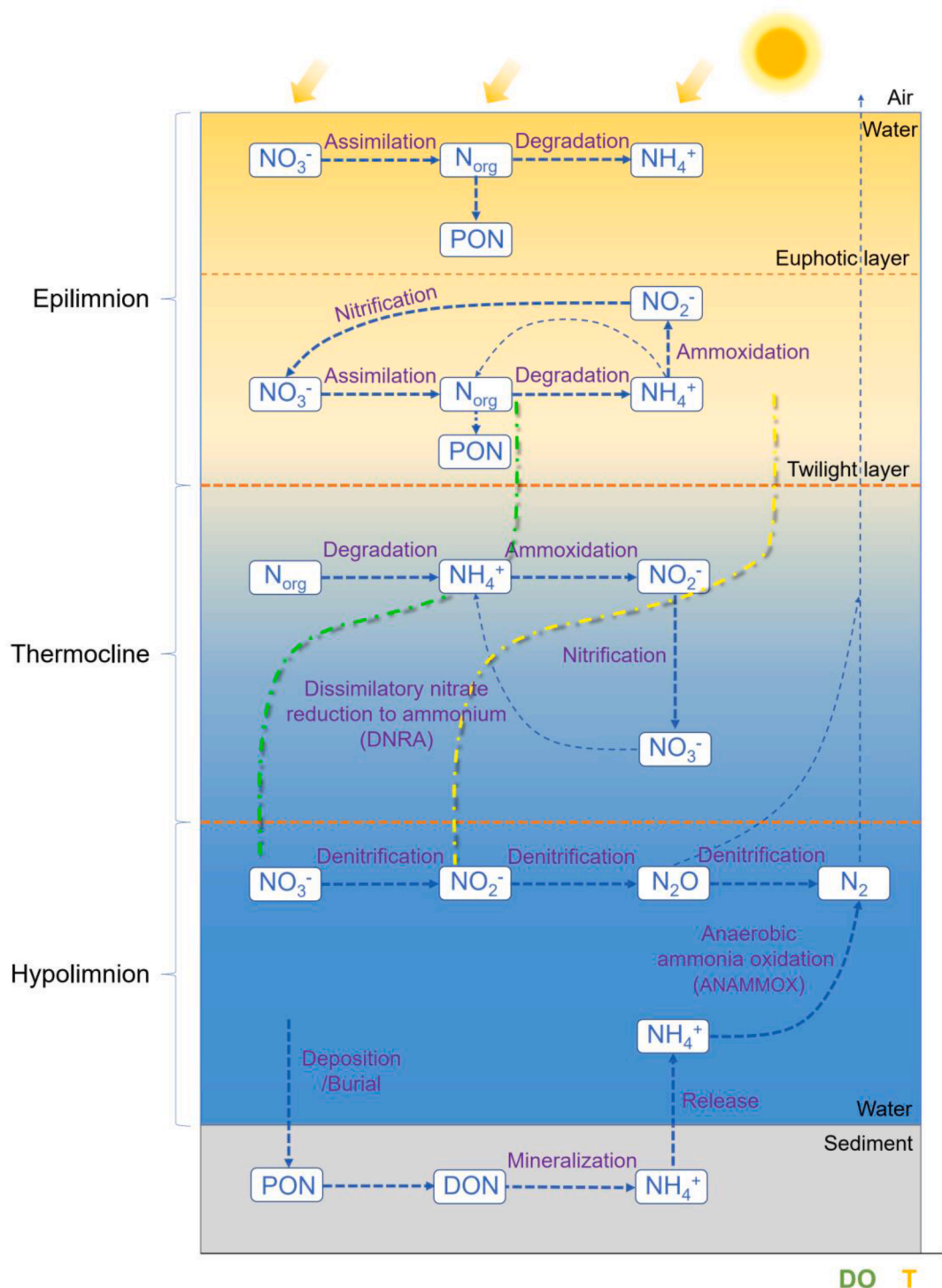


Fig. 2. Conceptual summary of the vertical patterns of nitrogen cycling. The main processes in the epilimnion (including the euphotic and twilight layers), thermocline, and hypolimnion are illustrated, and the dominant processes are indicated in bold dashed lines. Vertical shifts of dissolved oxygen (DO) and water temperature (T) are visualized in green and yellow dot-dash lines, respectively. (DON, dissolved organic nitrogen; PON, particulate organic nitrogen; N_{org} , organismal nitrogen contents).

low degradation rate under hypoxic conditions in the sediment-water interface, are conducive to the accumulation of N in sediment (Chen et al., 2018). Reservoir sediment acts as an important sink of exogenous and autogenous organic matter. The temporary or permanent burial of nutrients along with particulate matter may alleviate N enrichment in the water column. Meanwhile, the anaerobic degradation of organic matter and nutrient mineralization often occur in the water column,

leading to the release of nutrients to the overlying water (Wang, 2020). N is mainly released back into the water as NH_4^+ via sediment resuspension, which is affected by many factors such as bioturbation and the oxygen content. Thus, the balance between deposition and release determines the N load in sediments in the continuum from the upstream riverine system to the downstream lacustrine system.

3. Nitrogen cycling in vertically stratified reservoirs

3.1. Epilimnion-thermocline-hypolimnion gradient induced by stratification

In the lacustrine zone, the classic pattern of lake stratification is typically observed, especially in the deep hydroelectric reservoirs (Wang et al., 2018a). As the water level and ambient temperature increase, seasonal thermal stratification often develops along the water column, creating a well-mixed epilimnion, a thermocline where temperature and density decrease sharply from top to bottom, and a homogeneous hypolimnion (Jin et al., 2019; Xing et al., 2014). Multiple interfaces are observed in the stratified reservoir, including the water-air interface, the photic-aphotic interface based on the light availability, the temperature-transition interface (i.e., thermocline), the oxidation-reduction interface depending on the hydrochemical properties, and the sediment-water interface (Chen et al., 2018). The frequent exchange of material and energy at or near the interfaces has a major effect on the evolution of the eco-environment.

This phenomenon has also led to the development of chemical stratification (dissolved oxygen and nutrient content) and biological stratification (composition and distribution) (Chen et al., 2018). In the stratified reservoir, photosynthesis occurs in the epilimnion, which increases the dissolved oxygen (DO) concentration and pH. In contrast, the thermocline limits the convection exchange between the top and bottom water bodies, thus leading to hypoxia and low pH in deep water (Wang et al., 2015; Zhang et al., 2015b). The temporary stratification can inhibit mass transfer between the upper and lower layers, resulting in different chemical properties, such as the eutrophication status, redox reaction, degradation, and mineralization of organic matter (Chen et al., 2018; Liu et al., 2015; Zhang et al., 2015a). The development of thermal and oxygen stratification also shapes the phylogenetic composition and spatial distribution of microorganism, phytoplankton, zooplankton, and fungi populations (Chen et al., 2014). For example, producers and consumers are usually dominant in the upper layers because of the increased stability and photosynthesis, whereas decomposers are often abundant in the hypolimnion.

3.2. Vertical nitrogen cycling processes

In the vertical profile of the reservoir, the N dynamics are characterized by a series of complex biochemical processes, which are primarily determined by the interaction between N enrichment and removal. The N cycling processes, such as assimilation, benthic release, nitrification, and denitrification, are affected by site-specific environmental conditions in the lentic water. During the period of thermal stratification, the bottom water is usually abundant in reducing substances. These nutrients may react with oxidizing substances in the surface water when seasonal exchange or sudden convective mixing occurs, inducing variation in water quality. Previous studies have confirmed that thermal and oxygen stratification controls the speciation, form, and transformation of N in the water column (Wang, 2020). The shift in the vertical distribution of N cycling processes also depends on the pattern of reservoir operation and is discrepant under high and low flow conditions. The main N cycling processes in different layers during the stratification periods are shown in Fig. 2.

3.2.1. The upper layer

In the upper layer of water bodies, phytoplankton densities often increase because of the longer hydraulic residence time and higher light availability, which provides favorable conditions for aerobic processes (McMillan et al., 2010). Phytoplankton assimilation is a major process controlling the composition of N in the epilimnion. Phytoplankton can utilize dissolved inorganic N, especially NO_3^- and NH_4^+ , for photosynthesis, primary production, and the synthesis of organic compounds (Galloway et al., 2004). Part of the newly formed organic matter is

degraded in this region, and the dissolved N is released back to the water (Wang, 2020). The other part of organic matter is gradually transported to the bottom, which is accelerated under stagnant conditions. The assimilation rate is positively related to phytoplankton abundance, which is the dominant factor controlling the degree of N consumption (Wang et al., 2018b). The growth of phytoplankton in the surface water is limited by nutrient concentrations, particularly dissolved inorganic P, likely because of the sedimentation of particulate P in the central reservoir (Wang, 2020). In addition, during the stratification period, the DO concentration in the upper epilimnion is sufficient for creating an environment conducive to nitrification, in which NH_4^+ is oxidized to NO_2^- and NO_3^- (Galloway et al., 2004; Liu et al., 2018).

In the reservoir system, the main source of N input is NO_3^- , which is consumed through assimilation and produced by nitrification (Yool et al., 2007). The rate of NO_3^- assimilation is light-dependent and increases with NH_4^+ concentration and temperature; the rate of nitrification is partly inhibited by light and is positively affected by water temperature (Wang, 2020). The epilimnion usually contains an upper euphotic layer and twilight layer extending well below the euphotic zone. Assimilation and nitrification are spatially separated between these two layers. The N cycling processes in the euphotic layer are much simpler and are dominated by assimilation. The mixed conditions in the twilight layer allow nitrifiers to compete with phytoplankton for the assimilation of NH_4^+ , suggesting that nitrification and NO_3^- assimilation co-occur in this layer (Fawcett et al., 2015; Fripiat et al., 2015).

3.2.2. The middle layer

The thermocline is a low turbulence region that separates the surface nutrient-depleted layer and the nutrient-replete layer below the thermocline (Ross and Sharples, 2007). This zone affects the physicochemical and biological characteristics of the middle layer, as well as the transfer of DO and nutrients. Deep reservoirs restricted by thermal and oxygen stratification often show seasonal DO scarcity. Therefore, the decomposition of the settled organic matter is usually accompanied by the denitrification process. The upward migration of the reduced N component also contributes to the nitrification process. As a result, nitrification and denitrification often occur in adjacent water layers (Wang et al., 2019). The thermocline or oxycline is considered the center for N transformation and acts as an intermediary between the upper and bottom water. The deposited particulate organic nitrogen (PON) from the surface water can be degraded by microorganisms, thus causing hypoxia in the bottom water. This increases the sediment release of N, mainly NH_4^+ . Part of the released NH_4^+ is used for nitrification in the upper oxidized zone. However, a large proportion of NH_4^+ accumulates in the bottom of the thermocline zone and the hypolimnion. This can be attributed to the depletion of oxygen in the deep layers and limitations in nutrient transfer stemming from stratification.

3.2.3. The bottom layer

The N content in the bottom of the reservoir is controlled by denitrification and sediment release under anoxic conditions. The settled organic matter is decomposed by microorganisms, which consume large amounts of oxygen in the bottom water. The stratified reservoirs also restrict the vertical mixing and oxygen transfer from the upper to the lower layer, thus resulting in hypoxia in the hypolimnion (Maeck et al., 2013). The low saturation degree of DO in the bottom water limits aerobic nitrification and is conducive to denitrification processes (Cubas et al., 2019; Fadhillah et al., 2020; Roberts et al., 2012). The exchange of N between sediment and water and downstream transport are also altered. Consequently, NH_4^+ accumulation is often observed in the bottom water, which shifts the dominant form of dissolved inorganic nitrogen from NO_3^- to NH_4^+ in the dammed reservoirs (Chen et al., 2020).

Denitrification is the primary mechanism of N removal from the reservoirs, which typically takes place in the anoxic hypolimnion and is characterized by high NH_4^+ and low NO_3^- concentrations (Liu et al.,

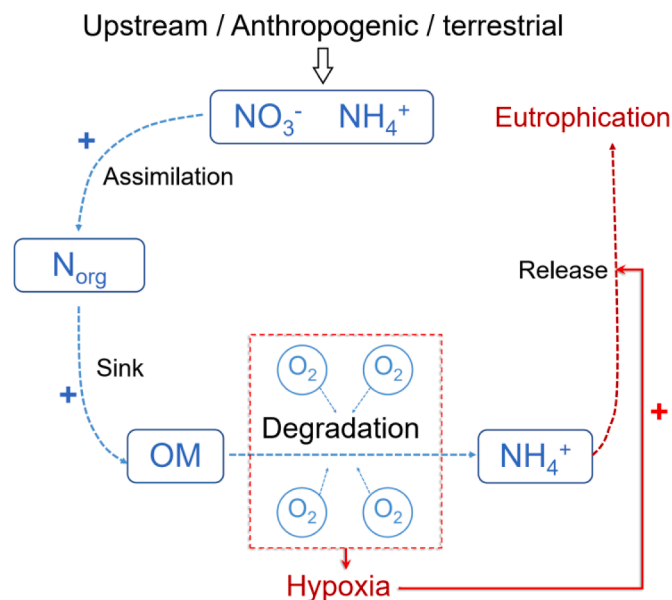


Fig. 3. The positive feedback loop of nitrogen input and release in stratified reservoir. (N_{org} , organismal nitrogen contents; OM, organic matters; +, positive effects).

2018). The first steps of denitrification (nitrate reduction) occur in the suboxic zone and below, where transcripts associated with denitrifiers are usually detected (Suter et al., 2021). Complete denitrification requires the absence of oxygen. Denitrification is positively related to water residence time and N load (Seitzinger et al., 2006). Higher N_2 concentration in bottom water also indicates that N_2 is released in the denitrification process at the sediment-water interface. The vertical

distribution of N_2 is affected not only by the denitrification process but also by the hydrological dynamics controlling fluvial transport through the water mass (Chen et al., 2014). Anammox has been shown to remove N in the reservoirs by oxidizing NH_4^+ with NO_2^- under hypoxic or anoxic conditions, contributing to the production of N_2 (Lin et al., 2020; Xue et al., 2017). The hyporheic zone is another hotspot of N cycling. The increase in the hydraulic residence time and sedimentation of autochthonous organic matter, and the development of hypoxia in the bottom water can jointly affect the N dynamics in the hyporheic zone. Because of the heterogeneity of sediment deposition and riverine-lacustrine transformation, the nutrient supply pattern in the hyporheic zone shifts from horizontal transport to vertical deposition and diffusion (Seitzinger et al., 2006). These processes increase in the anaerobic zone in the sediment, thus enhancing sediment denitrification.

3.3. Nitrogen cycling feedbacks due to stratification

In the stratified reservoir, the thermocline or oxycline inhibits the transfer of DO, resulting in an oxygen deficit in the hypolimnion. N cycling feedbacks may occur in the vertical profile, and this requires more research attention. Zhang et al. (2020b) proposed two types of N cycling feedbacks in marine systems. The first is based on N_2 fixation. In this process, the increase in the newly fixed N increases the N inventory and the N:P ratio, which inhibits N_2 fixation by phytoplankton. The second type of feedback is more likely to occur in the reservoir system given that NO_3^- is the main source of N in the reservoir. In this process (Fig. 3), the high NO_3^- concentration in upstream inputs promotes the assimilation of nutrients by phytoplankton. The increased biological productivity creates an organic matter sink in the bottom water column and the sediments. This organic matter is then degraded to NH_4^+ by decomposers. The degradation processes consume large amounts of oxygen and increase the extent of hypoxia in the hypolimnion. The hypoxic sediment can release more N in the form of NH_4^+ , which further

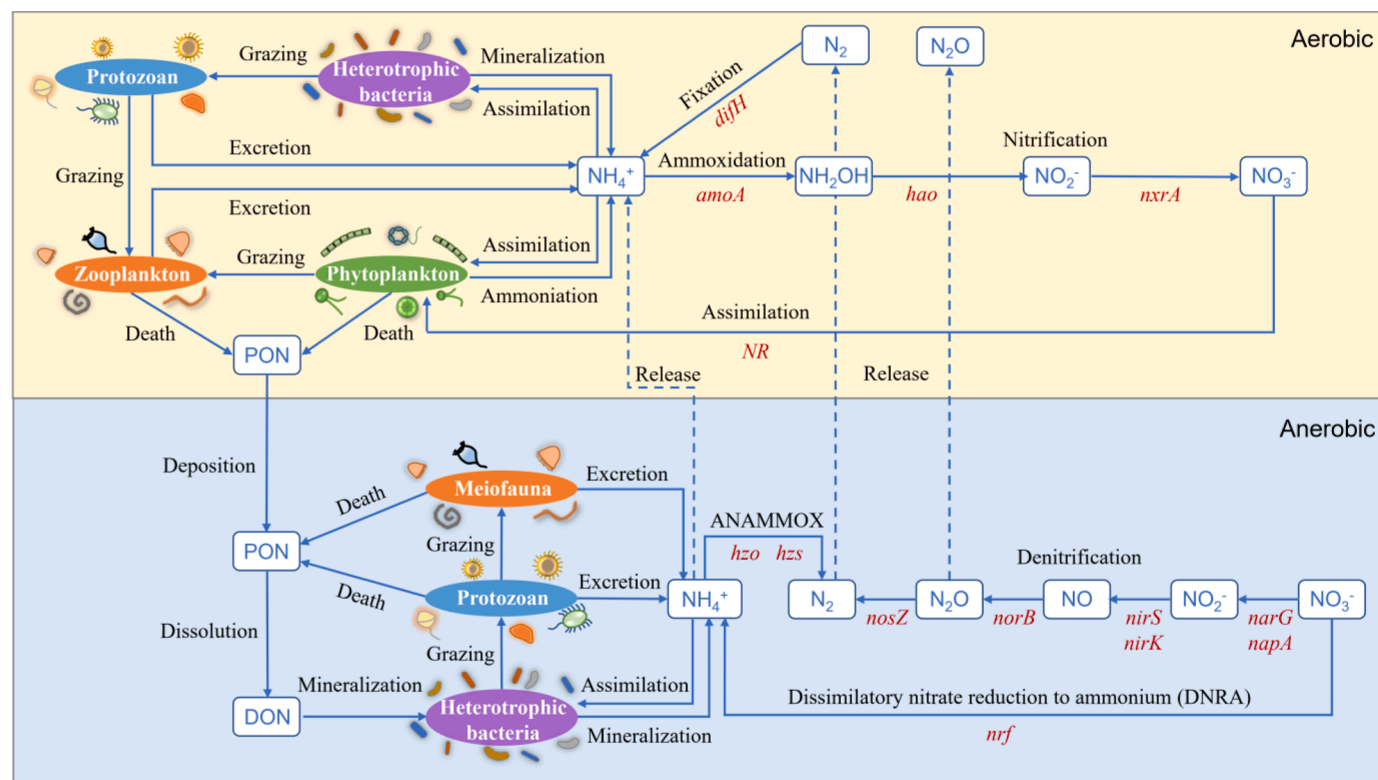


Fig. 4. The role of multi-trophic microbiota in nitrogen cycling. The aerobic and anaerobic nitrogen cycling processes are mediated by multi-trophic microbiota and their interactions. The major genes controlling nitrogen transformation are listed below each process. (DON, dissolved organic nitrogen; PON, particulate organic nitrogen; ANAMMOX, anaerobic ammonium oxidation).

increases N loading in the upper water column. Thus, a positive feedback loop may form among the increased N input, the higher primary productivity, the increased organic matter sedimentation, severe hypoxia in the bottom water, increased N released from sediment, and increased N in the water body (Chen et al., 2018; Rabalais et al., 2010). Given the N cycling feedback loop, ecosystem restoration is difficult if eutrophication occurs in reservoirs. Thus, preventing eutrophication and the formation of a positive feedback loop is critically important, and controlling external inputs and improving the DO level in the bottom water is essential for achieving this. There is also a need to increase the denitrification rate and associated redox processes (e.g., anammox) that remove N from deep reservoirs.

4. Nitrogen cycling processes mediated by multi-trophic microbiota

4.1. Biota-ecosystem interactions from a food web perspective

Ecosystem functions of the riverine system include the processes and properties of a given habitat. These processes are driven by abiotic factors, such as temperature, nutrient concentrations, and hydrological features, but also by biotic factors such as biological composition and diversity (Smeti et al., 2019). Recently, Palmer and Ruhi (2019) summarized the relationships among streamflow, biota, and ecosystem processes and proposed that the three-way “flow-biota-ecosystem processes nexus” interaction should be considered when restoring and protecting river systems. Understanding how biological processes affect and are affected by ecosystem processes under flowing conditions is particularly important, especially in rivers in which the streamflow has been altered by damming.

Nutrient cycling in deep reservoirs is complex, as nutrient concentrations in reservoirs are affected by many factors including nutrient inputs, thermal stratification, primary production, and biological degradation (Wang, 2020). The cycling of C, N, and many other elements is primarily driven by microorganisms, which carry out many important ecosystem functions (Ferrera et al., 2015). The efficiency with which microbes perform these functions is controlled by both bottom-up (physicochemical properties) and top-bottom (higher trophic level species) forces (Kellogg et al., 2019). The microbial food web can regenerate and transfer elements to larger organisms and thus may alter nutrient and energy flows in aquatic ecosystems. Numerous studies and review articles have examined the roles of microbes in nutrient cycling, mostly focusing on bacterial roles in degradation, transformation, and mineralization processes (Arora-Williams et al., 2018; Luo et al., 2017). Other microbes, such as virus (Zimmerman et al., 2020), fungi (Grossart et al., 2019), and other eukaryotic microorganisms (Gadd and Raven, 2010), also participate in nutrient cycling. However, comprehensive reviews on the impacts of multi-trophic microbiota and biotic interactions on nutrient cycles are scarce, especially in river-reservoir systems.

4.2. The role of multi-trophic microbiota in nitrogen cycling

N cycling is a ubiquitous and important element cycle in aquatic ecosystems that has long been thought to be mediated by microorganisms. These microorganisms can convert N compounds spanning redox states from -3 to $+5$ through 14 redox reactions (Kuypers et al., 2018). The growth-limiting nutrients are then transformed to bioavailable N, such as NH_4^+ and NO_3^- , thus facilitating nutrient utilization by other organisms. Previous studies have mainly focused on the prokaryotic contributions to N transformation. However, eukaryotes have also been shown to participate in N cycling in direct (e.g., assimilation and denitrification) and indirect (e.g., predation, excretion, and bioturbation) ways. Here, we focus on multi-trophic eukaryotes and summarize their roles in aquatic N cycling (Fig. 4).

4.2.1. Direct involvement

Eukaryotes are directly involved in the assimilation process of N cycling. Phytoplankton are primary producers in aquatic systems. Bioavailable low-molecular-mass inorganic N, mainly NO_3^- and NH_4^+ , can be assimilated by phytoplankton via photosynthesis. The absorbed N is then transformed through biosynthesis to macromolecules, such as proteins and nucleic acids, which support the growth of phytoplankton (Cai et al., 2019). Phytoplankton assimilation has been shown to contribute to N consumption rates over the entire water column (Molina et al., 2012; Varela et al., 2003).

Eukaryotes are also directly involved in N transformation through reduction reactions. In photosynthetic microbial eukaryotes, the assimilated NO_3^- is transferred to organic N macromolecules. The rate-limiting step of this process is the reduction of NO_3^- to NO_2^- , which is catalyzed by assimilatory nitrate reductase (NR). NR genes are ubiquitous and have been detected in diatoms, dinoflagellates, other flagellates, chlorophytes, and unknown microbial eukaryotes (Comeau et al., 2019). In non-photosynthetic eukaryotic microbes, NO_3^- and NO_2^- can be transferred to N_2 or N_2O through reduction reactions under hypoxic or anoxic conditions. These denitrification processes are carried out via dissimilatory nitrate and/or nitrite reduction. Nitrite reductase gene (*nirK*) has also been shown to catalyze nitrite reduction in several microbial eukaryotes (Gadd and Raven, 2010). New pathways and processes in N cycling mediated by eukaryotic microbes were summarized by Thamdrup (2012) and Kamp et al. (2015). These processes include intracellular nitrate storage, denitrification, anaerobic NH_4^+ oxidation, and anaerobic methane oxidation with NO_2^- , which are carried out by ciliates, fungi, foraminifera, and some algae.

4.2.2. Grazer excretion

The regeneration of nutrients by grazers is important for the growth of both primary producers and other bacteria. The excreted N can release algae from competition with microbes for inorganic N and thus increase primary production (Palmer and Ruhi, 2019). NH_4^+ is the common form of excreted N and is considered recycled N in both pelagic and benthic habitats. Protozoans are small consumers with high turnover and excretion rates and are the main contributors to NH_4^+ excretion (Dolan, 1997). Other grazers, such as metazoans, can also excrete excess nutrients in excess of their growth demands. Eukaryotes can enhance the nitrification potential and proliferation of nitrifying bacteria (Prast et al., 2007; Schratzberger and Ingels, 2018). This can be attributed to the excretion of large quantities of NH_4^+ by grazers, which leads to changes in the C:N ratio and increases in NH_4^+ bioavailability for nitrifying bacteria. The increased availability of NO_3^- and organic compounds can also promote the heterotrophic denitrification process.

4.2.3. Predator-prey interaction

Trophic interactions among microbiota can also affect N cycling processes via top-down forces. Protozoans, which are dominated by heterotrophic flagellates and ciliates, are the direct predators of bacteria in aquatic habitats, and their grazing on bacteria is also an important source of regenerated N (Pernthaler, 2005). They can ingest their body weight in microorganisms per hour. Nitrifying bacteria are more susceptible to predation because of their relatively slow growth rates (Strauss and Dodds, 1997). Therefore, grazing by protozoans can stimulate N cycling by increasing the abundance of recycled limiting nutrients, removing senescent cells, and reducing bacterial competition (Tso and Taghon, 2006). Furthermore, a significant proportion of mineralized N can be passed up to metazoans via the microbial loop. Meiofaunal species are capable of eating their own cell volume of particles per hour daily. They can counteract nitrate reduction associated with grazing microphytobenthos and bacteria; they can also release organic and inorganic N, thus altering the C:N ratio in the water column and the sediment (Stock et al., 2014).

4.2.4. Meiofaunal bioturbation

Macrofaunal species are generally known to enhance the turnover and transport of N via burrowing, ventilation, and bio-irrigation; have a negative effect on denitrification; and have a positive effect on dissimilatory nitrate reduction to ammonium (DNRA) (Stief, 2013). Recent research has examined the effects of meiofaunal bioturbation in superficial sediments on N cycling (Bonaglia et al., 2014). Meiofaunal bioturbation can stimulate the transport of NO_3^- and NH_4^+ in the surface of sediments by a factor of 1.5 to 3.1 compared with molecular diffusion (Schratzberger and Ingels, 2018). The increase in the DO concentration creates an oxic environment that promotes aerobic processes such as nitrification. The denitrification rate is also increased when the abundance and diversity of meiofauna are high. This might be attributed to the increase in bioavailable substrates such as NO_3^- and NH_4^+ , for nitrifying and denitrifying bacteria, which suggests that meiofauna bioturbation promotes benthic N cycling.

4.3. Factors affecting multi-trophic microbiota and their interactions

4.3.1. Hydrological and hydraulic regime

The hydrological regime is a key driver of freshwater ecosystems that structures geomorphological features, riverine connectivity, biological diversity, and stability, thereby altering ecosystem functions. Theoretical research on food-web structure has highlighted the importance of linking flow, biota, and ecosystem processes (Palmer and Ruhi, 2019). Flow-induced variations in dominant resource types, biomass, and the content of nutrients can propagate to higher trophic levels via bottom-up forces and affect biological functions and ecological services.

In reservoir systems, the hydraulic retention time is a key variable structuring planktonic communities, including phytoplankton, heterotrophic bacteria, and zooplankton, that induces the longitudinal succession of these communities along the riverine-transition-lacustrine system. After the building of dams, the increased transparency, water temperature, and nutrient bioavailability, coupled with reduced turbulent mixing, facilitate the development of phytoplankton. The abundance of phytoplankton is usually positively correlated to water retention time (Chen et al., 2020). The composition and succession of phytoplankton are also affected by the periodic operation of reservoirs, which results in shifts from river-dominated species to lake-dominated species (Xu et al., 2020). High hydraulic retention time typically accelerates the deposition of P and organic matter, which inhibits the utilization of biogenic elements by bacteria and alters the availability of food resources to zooplankton (Domingues et al., 2017). Therefore, water retention time may have negative effects on the biomass of heterotrophic bacteria, and the dominant zooplankton may shift from bacterivores to herbivores. In addition, the occurrence, abundance, and composition of zooplankton are all associated with the quality of their environment, including hydrological connectivity and lentic or lotic conditions (Napiórkowski et al., 2019; Wan Maznah et al., 2018).

Reservoir impoundments can also affect the flow regime in benthic habitats. The altered benthic boundary-layer flow may significantly affect sedimentary biogeochemistry and benthos ecology. The abundance, population growth, community structure, and dispersal ability of benthic bacteria, flagellates, ciliates, and meiofauna are closely associated with processes such as sediment resuspension and hydrodynamic disturbance (Shimeta et al., 2001). Because various flow regimes occur along the river-reservoir system, coarse sediments preferentially deposit on the upper reaches of reservoirs, whereas fine particles tend to be transported downward and become deposited in the lacustrine zone (Sang et al., 2019). The particle size distribution can alter the abundance, structure, and spatial distribution of surface-oriented and sediment-inhabiting organisms and has a significant effect on N cycling, especially the denitrification process (Zhang et al., 2020a).

4.3.2. Nutrient conditions

In addition to hydrology, nutrients are a key factor limiting the

metabolic processes of plankton. Given that most nitrifying and denitrifying bacteria are heterotrophs, their N cycling rates are largely dependent on the C:N ratio. The concentration of dissolved organic C in reservoir systems is affected by external inputs upstream or terrestrial sources and internal disturbances induced by the flow regime or natural variations, which lead to variation in primary productivity and zooplankton production (Gao et al., 2021a; Palmer and Ruhi, 2019). Dissolved inorganic N is the fundamental substance of multiple N cycling processes mediated by bacteria and phytoplankton. Thus, the concentration of dissolved inorganic N is closely associated with N transformation efficiency (Domingues et al., 2017).

Nutrient conditions can also alter the interactions of multiple trophic levels. For example, in highly oligotrophic systems, the growth of protistan predators is bottom-up controlled by the low availability of bacteria. By contrast, eutrophic waters can release bacterial communities from predation control, and their growth is largely limited by competition for nutrients (Pernthaler, 2005). In benthic habitats, the altered biological interactions may further affect nutrient and energy transfer through different trophic levels (Yang et al., 2019). Nutrient enrichment is thought to increase bacterial and algal biomass, which in turn enhances the growth of meiofauna and microfauna at higher trophic levels. The shifts in microbial food web components and interactions are also associated with the availability of other essential nutrient elements, such as Si and P, which have received extensive attention in river-reservoir systems (Chen et al., 2020; Van Cappellen and Maavara, 2016).

4.3.3. Thermal stratification

Thermal stratification is an important factor controlling material transformation in dam-induced deep reservoirs. Several studies have shown that seasonal stratification significantly affects the composition and diversity of bacteria, fungi, phytoplankton, and zooplankton (Williams et al., 2014; Zhou et al., 2020). Many factors regulate the vertical distribution of biological communities in stratified reservoirs, such as water column stability, DO, and water temperature (Zhou et al., 2020). Water column stability within reservoirs plays an important role in determining the succession of plankton food web types, which leads to variation between algae-based green food webs and detritus-based brown food webs. The mechanism of bacterial control might be altered from bottom-up control during the water mixing period to top-down control following stratification (Solić et al., 2020). DO and water temperature are the most important factors, as they have been observed to shape the composition of bacterial communities and plankton metabolic processes (Domingues et al., 2017). All these factors can lead to variation in nutrient concentrations, thereby affecting biological community structure and ecological functions.

The N cycles in central reservoirs are mediated by organisms at several trophic levels under stratification. The distinct environmental conditions and biological mechanisms in different layers affect the major factors determining N cycling. For example, phytoplankton assimilation is the major process controlling N composition in the epilimnion, and DO concentration and temperature are the main factors affecting the composition of N in the oxyline and the hypolimnion (Su et al., 2019). Tran et al. (2021) observed sharp contrasts in community composition and metabolic potential between the oxygenated mixed upper layer and deep anoxic water. These differences shape microbial N cycling processes by removing fixed N from water, fixing the upwelled N, and replenishing bioavailable N in the surface water. The abundances of ammonia oxidizers and denitrifying bacteria also show significant variation depending on the content of nutrients, which generates vertical variation in nitrification and denitrification processes (Yue et al., 2021).

Conclusions and future perspectives

N cycling in the dam-induced river-reservoir system involves several complex processes that are affected by longitudinal variation in

Table 1
Applications of DNA metabarcoding in food web analysis.

Methods	Sample types	Target organism	Key points	Advantages	Challenges	References
Correlation network	Environmental samples (water, sediment, soil)	Micro- or Macro-organisms	Identify the nodes (species) and links (correlations) in the networks.	Improve taxonomic resolution; No need to collect single individuals.	Hard to identify biotic interactions, which are usually estimated by correlations.	Steele et al. (2011); Qu et al. (2021)
Diet analysis	Biotic samples (feces, saliva, intestine, stomach)	Macro-organisms (e. g. invertebrate, mammals, fish)	Determine actual predator-prey interactions (i.e. who eats who).	Identify species-level interactions accurately using non-invasive methods.	Rare taxa may be missed because of an incomplete taxonomy database.	Clare (2014); Sheppard and Harwood (2005)
DNA stable-isotope probing (DNA-SIP)	Laboratorial samples (water, sediment, soil)	Micro-organisms (e. g. bacteria, micro-eukaryote)	Trace isotope-labeled DNA across multi-trophic levels.	Track nutrient flows and organic matter decomposition in microbial food webs.	Only small organisms based on specific substrates can be measured.	Kramer et al. (2016); Feng et al. (2011)
Machine learning	Environmental samples (water, sediment, soil)	Micro- or Macro-organisms	Predict biotic interactions and build ecological networks from large sets of data.	Improve the speed of network reconstruction and the precision of measuring interactions.	Require large amounts of background information to code trophic interactions.	Derocles et al. (2018); Bohan et al. (2017)
Biological omics	Environmental samples (water, sediment, soil)	All genetic or metabolic products transcending kingdom barriers	Metagenomics (diversities and metabolic potentials); Metatranscriptomics (gene expression); Metaproteomics (metabolic activity and interactions)	Clarify the compositions, potential and practical functions, and trophic interactions.	Sequencing costs and challenges associated with detection and analysis.	Carradec et al. (2018); Williams and Cavicchioli (2014)

hydrological, nutritional, and particulate conditions, as well as vertical temperature and oxygen gradients. These N cycling processes are mediated by multi-trophic microbiota and their interactions in direct (e. g., assimilation and denitrification) or indirect (e.g., predation, excretion, and bioturbation) ways, which also depend on the unique environmental conditions in river-reservoir systems. Based on the above reviews, the following scientific and technological improvements may benefit the ecological conservation of reservoirs affected by damming.

The collection of long-term observational biological data in river-reservoir systems is essential for protecting the sustainability of ecosystems. The composition and structure of multi-trophic communities (from bacteria to marine mammals) and the complex relationship among species (food web) have already been integrated into bio-assessments and are considered essential for making ecosystem-based ecological protection and restoration decisions (Zhang et al., 2020c; Zhao et al., 2019). However, more work on multi-trophic microbiota and microbial food webs is needed, and qualitative and quantitative methods to detect these organisms require improvement. With advances in molecular methodologies coupled with taxonomically broad sequence repositories, DNA metabarcoding can be used to increase the range of taxa sampled, which would increase the sampling resolution, aid bio-assessments, and provide new insights into functional ecology (Hering et al., 2018). Although this technique has been used to monitor biodiversity, detect rare endangered species, and characterize biotic relationships, this method still needs to be improved for it to be used to describe food web properties. The current applications of DNA metabarcoding in food web analysis are listed in Table 1. The combination of molecular, omics, and machine learning approaches could help unravel hidden patterns in the structure-function-interaction relationships of multi-trophic levels; this approach could also be used to rapidly construct food webs with unprecedented precision and accuracy. Generally, these methods can provide a clear picture of biological patterns in the upstream, downstream, riverine, and lacustrine zones, as well as in front of and behind dams. Subsequently, ecological models that incorporate environmental parameters (e.g., DO concentration, temperature, and flow velocity), biological processes (e.g., composition, diversity, and interaction), and ecosystem functions (e.g., energy flux and nutrient cycles) can be constructed.

The design of river flow (i.e., environmental flow) and the management of dam operations require consideration of various factors, including hydrological properties, morphological features, and biological community structure and functions. Interdisciplinary collaboration

is necessary for enhancing our understanding of damming-related changes to nutrient dynamics and determining how dam operations can be manipulated to regulate trophic conditions (Anderson et al., 2019). The design of environmental flows in impoundment rivers has generally been based on particular organisms, such as fish, vegetation, and invertebrates, rather than through consideration of entire food webs or ecosystems. Although environmental flows in the context of food webs have been studied (Robson et al., 2017), the roles of multi-trophic microbiota have received little attention. Therefore, the direct and indirect biogeochemical impacts of damming discussed in this review underscore the need to consider multi-trophic microbiota when designing environmental flows. In addition, a series of reservoir regulation and restoration approaches have been used to aid the protection of dammed rivers, including temperature control devices, hypolimnic aeration, critical habitats reconnection, and ecological engineering for improving water quality and trophic conditions (Hu et al., 2016; Miles and West, 2011; Naiman et al., 2012; Saito et al., 2001). We suggest that multi-trophic microbiota and food web models be integrated into these interdisciplinary engineering and ecological methods to clarify the impacts of damming on riverine food webs and biogeochemical cycling. Additional studies focused on employing modeling approaches and developing strategies to restore riverine ecosystems in the future are especially needed.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (Grant No. 51779076), the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD), and the Six Talent Peaks Project in Jiangsu Province (2016-JNHB-007).

References

- Akbarzadeh, Z., Maavara, T., Slowinski, S., Van Cappellen, P., 2019. Effects of damming on river nitrogen fluxes: a global analysis. *Glob. Biogeochem. Cycles* 33 (11), 1339–1357.
- Anderson, E.P., Jackson, S., Tharme, R.E., Douglas, M., Flotemersch, J.E., Zwarteveen, M., Lokgariwar, C., Montoya, M., Wali, A., Tipa, G.T., Jardine, T.D.,

- Olden, J.D., Cheng, L., Conallin, J., Cosens, B., Dickens, C., Garrick, D., Groenfeldt, D., Kabogo, J., Roux, D.J., Ruhi, A., Arthington, A.H., 2019. Understanding rivers and their social relations: a critical step to advance environmental water management. *WIREs Water* 6 (6), e1381.
- Arora-Williams, K., Olesen, S.W., Scandella, B.P., Delwiche, K., Spencer, S.J., Myers, E. M., Abraham, S., Sooklal, A., Preheim, S.P., 2018. Dynamics of microbial populations mediating biogeochemical cycling in a freshwater lake. *Microbiome* 6 (1), 165.
- Bohan, D.A., Vacher, C., Tamaddon-Nezhad, A., Raybould, A., Dumbrell, A.J., Woodward, G., 2017. Next-generation global biomonitoring: large-scale, automated reconstruction of ecological networks. *Trends Ecol. Evol.* 32 (7), 477–487.
- Bonaglia, S., Nascimento, F.J.A., Bartoli, M., Klawonn, I., Brüchert, V., 2014. Meiofauna increases bacterial denitrification in marine sediments. *Nat. Commun.* 5 (1), 5133.
- Cai, Y., Cao, Y., Tang, C., 2019. Evidence for the primary role of phytoplankton on nitrogen cycle in a subtropical reservoir: reflected by the stable isotope ratios of particulate nitrogen and total dissolved nitrogen. *Front. Microbiol.* 10, 2022.
- Carradec, Q., Pelletier, E., Da Silva, C., Alberti, A., Seeleuthner, Y., Blanc-Mathieu, R., Lima-Mendez, G., Rocha, F., Tirichine, L., Labadie, K., Kirilovsky, A., Bertrand, A., Engelen, S., Madoui, M.-A., Meheust, R., Poulain, J., Romic, S., Richter, D.J., Yoshikawa, G., Dimier, C., Kandels-Lewis, S., Picheral, M., Searson, S., Jaillon, O., Aury, J.-M., Karsenti, E., Sullivan, M.B., Sunagawa, S., Bork, P., Not, F., Hingamp, P., Raes, J., Guidi, L., Ogata, H., de Vargas, C., Iudicone, D., Bowler, C., Wincker, P., 2018. A global ocean atlas of eukaryotic genes. *Nat. Commun.* 9, 373.
- Chen, J., Wang, J., Guo, J., Yu, J., Zeng, Y., Yang, H., Zhang, R., 2018. Eco-environment of reservoirs in China: characteristics and research prospects. *Prog. Phys. Geogr. - Earth Environ.* 42 (2), 185–201.
- Chen, N., Chen, Z., Wu, Y., Hu, A., 2014. Understanding gaseous nitrogen removal through direct measurement of dissolved N₂ and N₂O in a subtropical river-reservoir system. *Ecol. Eng.* 70, 56–67.
- Chen, Q., Shi, W., Huisman, J., Maberly, S.C., Zhang, J., Yu, J., Chen, Y., Tonina, D., Yi, Q., 2020. Hydropower reservoirs on the upper Mekong River modify nutrient bioavailability downstream. *Natl. Sci. Rev.* 7 (9), 1449–1457.
- Clare, E.L., 2014. Molecular detection of trophic interactions: emerging trends, distinct advantages, significant considerations and conservation applications. *Evol. Appl.* 7 (9), 1144–1157.
- Comeau, A.M., Lagunas, M.G., Scarcella, K., Varela, D.E., Lovejoy, C., Stams, A.J.M., 2019. Nitrate consumers in arctic marine eukaryotic communities: comparative diversities of 18S rRNA, 18S rDNA genes, and nitrate reductase genes. *Appl. Environ. Microbiol.* 85 (14) e00247–00219.
- Cubas, F.J., Holbrook, R.D., Novak, J.T., Godrej, A.N., Grizzard, T.J., 2019. Effective depth controls the nitrate removal rates in a water supply reservoir with a high nitrate load. *Sci. Total Environ.* 673, 44–53.
- de Tezanos Pinto, P., Litchman, E., 2010. Interactive effects of N:P ratios and light on nitrogen-fixer abundance. *Oikos* 119 (3), 567–575.
- Derocles, S.A.P., Bohan, D.A., Dumbrell, A.J., Kitson, J.J.N., Evans, D.M., 2018. Biomonitoring for the 21st century: integrating next-generation sequencing into ecological network analysis. *Adv. Ecol. Res.* 58, 1–62.
- Dolan, J.R., 1997. Phosphorus and ammonia excretion by planktonic protists. *Mar. Geol.* 139 (1–4), 109–122.
- Domingues, C.D., Sampaio da Silva, L.H., Rangel, L.M., de Magalhães, L., Rocha, A.d.M., Lobao, L.M., Paiva, R., Roland, F., Sarmiento, H., 2017. Microbial food-web drivers in tropical reservoirs. *Microb. Ecol.* 73 (3), 505–520.
- dos Santos, M.A., Damazio, J.M., Rogerio, J.P., Amorim, M.A., Medeiros, A.M., Abreu, J. L.S., Maceira, M.E.P., Melo, A.C., Rosa, L.P., 2017. Estimates of GHG emissions by hydroelectric reservoirs: the Brazilian case. *Energy* 133, 99–107.
- Doyle, R.D., Scott, J.T., Forbes, M.G., 2010. Hot spots and hot moments of planktonic nitrogen fixation in a eutrophic southern reservoir. *Lake Reserv. Manage.* 26 (2), 95–103.
- Fadhullah, W., Yacob, N.S., Syakir, M.I., Muhammad, S.A., Yue, F.-J., Li, S.-L., 2020. Nitrate sources and processes in the surface water of a tropical reservoir by stable isotopes and mixing model. *Sci. Total Environ.* 700, 134517.
- Fawcett, S.E., Ward, B.B., Lomas, M.W., Sigman, D.M., 2015. Vertical decoupling of nitrate assimilation and nitrification in the Sargasso Sea. *Deep Sea Res. Part I* 103, 64–72.
- Feng, Y., Lin, X., Zhu, J., Jia, Z., 2011. A phototrophy-driven microbial food web in a rice soil. *J. Soils Sed.* 11 (2), 301–311.
- Ferrera, I., Sebastian, M., Acinas, S.G., Gasol, J.M., 2015. Prokaryotic functional gene diversity in the sunlit ocean: stumbling in the dark. *Curr. Opin. Microbiol.* 25, 33–39.
- Fripiat, F., Elskens, M., Trull, T.W., Blain, S., Cavagna, A.J., Fernandez, C., Fonseca-Batista, D., Planchon, F., Raimbault, P., Roukaerts, A., Dehairs, F., 2015. Significant mixed layer nitrification in a natural iron-fertilized bloom of the Southern Ocean. *Global Biogeochem. Cycles* 29 (11), 1929–1943.
- Gadd, G.M., Raven, J.A., 2010. Geomicrobiology of Eukaryotic Microorganisms. *Geomicrobiol. J.* 27 (6–7), 491–519.
- Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S. P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A. F., Porter, J.H., Townsend, A.R., Vorosmarty, C.J., 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70 (2), 153–226.
- Gao, X., Chen, H., Gu, B., Jeppesen, E., Xue, Y., Yang, J., 2021a. Particulate organic matter as causative factor to eutrophication of subtropical deep freshwater: role of typhoon (tropical cyclone) in the nutrient cycling. *Water Res.* 188, 116470.
- Gao, Y., Zhang, W., Li, Y., Wu, H., Yang, N., Hui, C., 2021b. Dams shift microbial community assembly and imprint nitrogen transformation along the Yangtze River. *Water Res.* 189, 116579.
- Glibert, P.M., Wilkerson, F.P., Dugdale, R.C., Raven, J.A., Dupont, C.L., Leavitt, P.R., Parker, A.E., Burkholder, J.M., Kana, T.M., 2016. Pluses and minuses of ammonium and nitrate uptake and assimilation by phytoplankton and implications for productivity and community composition, with emphasis on nitrogen-enriched conditions. *Limnol. Oceanogr.* 61 (1), 165–197.
- Grill, G., Lehner, B., Thieme, G., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P. H., van Soesbergen, A., Zarfl, C., 2019. Mapping the world's free-flowing rivers. *Nature* 569 (7755), 215–221.
- Grossart, H.-P., Van den Wyngaert, S., Kagami, M., Wurzbacher, C., Cunliffe, M., Rojas-Jimenez, K., 2019. Fungi in aquatic ecosystems. *Nat. Rev. Microbiol.* 17 (6), 339–354.
- Harrison, J.A., Maranger, R.J., Alexander, R.B., Giblin, A.E., Jacinthe, P.-A., Mayorga, E., Seitzinger, S.P., Sobota, D.J., Wollheim, W.M., 2009. The regional and global significance of nitrogen removal in lakes and reservoirs. *Biogeochemistry* 93 (1–2), 143–157.
- Hering, D., Borja, A., Jones, J.I., Pont, D., Boets, P., Bouchez, A., Bruce, K., Drakare, S., Hanfling, B., Kahlert, M., Leese, F., Meissner, K., Mergen, P., Reyjol, Y., Segurado, P., Vogler, A., Kelly, M., 2018. Implementation options for DNA-based identification into ecological status assessment under the European Water Framework Directive. *Water Res.* 138, 192–205.
- Hoffman, B.M., Lukoyanov, D., Yang, Z.-Y., Dean, D.R., Seefeldt, L.C., 2014. Mechanism of nitrogen fixation by nitrogenase: the next stage. *Chem. Rev.* 114 (8), 4041–4062.
- Hu, R., Li, Q., Han, B.-P., Naselli-Flores, L., Padisak, J., Salmazo, N., 2016. Tracking management-related water quality alterations by phytoplankton assemblages in a tropical reservoir. *Hydrobiologia* 763 (1), 109–124.
- Jin, J.X., Wells, S.A., Liu, D.F., Yang, G.L., Zhu, S.L., Ma, J., Yang, Z.J., 2019. Effects of water level fluctuation on thermal stratification in a typical tributary bay of Three Gorges Reservoir. *China. PeerJ* 7, e6925.
- Kamp, A., Hogslund, S., Risgaard-Petersen, N., Stief, P., 2015. Nitrate storage and dissimilatory nitrate reduction by eukaryotic microbes. *Front. Microbiol.* 6, 1492.
- Kellogg, C.T.E., McClelland, J.W., Dunton, K.H., Crump, B.C., 2019. Strong seasonality in arctic estuarine microbial food webs. *Front. Microbiol.* 10, 2628.
- Keys, T.A., Caudill, M.F., Scott, D.T., 2019. Storm effects on nitrogen flux and longitudinal variability in a river-reservoir system. *River Res. Appl.* 35 (6), 577–586.
- Kramer, S., Dibbern, D., Moll, J., Huenninghaus, M., Koller, R., Krueger, D., Marhan, S., Ulrich, T., Wubet, T., Bonkowski, M., Buscot, F., Lueders, T., Kandeler, E., 2016. Resource partitioning between bacteria, fungi, and protists in the detritusphere of an agricultural soil. *Front. Microbiol.* 7.
- Kreiling, R.M., Richardson, W.B., Cavanaugh, J.C., Bartsch, L.A., 2011. Summer nitrate uptake and denitrification in an upper Mississippi River backwater lake: the role of rooted aquatic vegetation. *Biogeochemistry* 104 (1–3), 309–324.
- Kumar, A., Yang, T., Sharma, M.P., 2019. Greenhouse gas measurement from Chinese freshwater bodies: a review. *J. Clean. Prod.* 233, 368–378.
- Kuypers, M.M.M., Marchant, H.K., Kartal, B., 2018. The microbial nitrogen-cycling network. *Nat. Rev. Microbiol.* 16 (5), 263–276.
- Lansdown, K., McKew, B.A., Whitby, C., Heppell, C.M., Dumbrell, A.J., Binley, A., Olde, L., Trimmer, M., 2016. Importance and controls of anaerobic ammonium oxidation influenced by riverbed geology. *Nat. Geosci.* 9 (5), 357–360.
- Lin, J., Chen, N., Yuan, X., Tian, Q., Hu, A., Zheng, Y., 2020. Impacts of human disturbance on the biogeochemical nitrogen cycle in a subtropical river system revealed by nitrifier and denitrifier genes. *Sci. Total Environ.* 746, 141139.
- Liu, H.B., Pan, D., Chen, P., 2015. Spatio-temporal variation of chlorophyll-a in a drinking water reservoir: role of hydraulic conditions and inflow. *Clean-Soil Air Water* 43 (11), 1481–1487.
- Liu, X.-L., Li, S.-L., Wang, Z.-L., Wang, B.-L., Han, G.-L., Wang, F.-S., Bai, L., Xiao, M., Yue, F.-J., Liu, C.-Q., 2018. Sources and key processes controlling particulate organic nitrogen in impounded river-reservoir systems on the Maotiao River, southwest China. *Inland Waters* 8 (2), 167–175.
- Luo, L., Meng, H., Gu, J.-D., 2017. Microbial extracellular enzymes in biogeochemical cycling of ecosystems. *J. Environ. Manage.* 197, 539–549.
- Maavara, T., Chen, Q., Van Meter, K., Brown, L.E., Zhang, J., Ni, J., Zarfl, C., 2020. River dam impacts on biogeochemical cycling. *Nat. Rev. Earth Environ.* 1 (2), 103–116.
- Maavara, T., Duerr, H.H., Van Cappellen, P., 2014. Worldwide retention of nutrient silicon by river damming: from sparse data set to global estimate. *Global Biogeochem. Cycles* 28 (8), 842–855.
- Maavara, T., Lauerwald, R., Regnier, P., Van Cappellen, P., 2017. Global perturbation of organic carbon cycling by river damming. *Nat. Commun.* 8, 15347.
- Maavara, T., Parsons, C.T., Ridenour, C., Stojanovic, S., Duerr, H.H., Powley, H.R., Van Cappellen, P., 2015. Global phosphorus retention by river damming. *Proc. Natl. Acad. Sci. U. S. A.* 112 (51), 15603–15608.
- Maeck, A., DelSontro, T., McGinnis, D.F., Fischer, H., Flury, S., Schmidt, M., Fietzek, P., Lorke, A., 2013. Sediment trapping by dams creates methane emission hot spots. *Environ. Sci. Technol.* 47 (15), 8130–8137.
- Maia, L.B., Moura, J.J.G., 2014. How biology handles nitrite. *Chem. Rev.* 114 (10), 5273–5357.
- Marzadri, A., Dee, M.M., Tonina, D., Bellin, A., Tank, J.L., 2017. Role of surface and subsurface processes in scaling N₂O emissions along riverine networks. *Proc. Natl. Acad. Sci. U. S. A.* 114 (17), 4330–4335.
- McMillan, S.K., Piehler, M.F., Thompson, S.P., Paeerl, H.W., 2010. Denitrification of nitrogen released from senescing algal biomass in coastal agricultural headwater streams. *J. Environ. Qual.* 39 (1), 274–281.
- Miles, N.G., West, R.J., 2011. The use of an aeration system to prevent thermal stratification of a freshwater impoundment and its effect on downstream fish assemblages. *J. Fish Biol.* 78 (3), 945–952.

- Moitra, M., Leff, L.G., 2015. Bacterial community composition and function along a river to reservoir transition. *Hydrobiologia* 747 (1), 201–215.
- Molina, V., Morales, C.E., Farías, L., Cornejo, M., Graco, M., Eissler, Y., Cuevas, L.A., 2012. Potential contribution of planktonic components to ammonium cycling in the coastal area off central-southern Chile during non-upwelling conditions. *Prog. Oceanogr.* 92–95, 43–49.
- Mor, J.R., Ruhi, A., Tornes, E., Valcarcel, H., Munoz, I., Sabater, S., 2018. Dam regulation and riverine food-web structure in a Mediterranean river. *Sci. Total Environ.* 625, 301–310.
- Naiman, R.J., Alldredge, J.R., Beauchamp, D.A., Bisson, P.A., Congleton, J., Henny, C.J., Huntly, N., Lamberson, R., Levings, C., Merrill, E.N., Percy, W.G., Rieman, B.E., Ruggerone, G.T., Scarnecchia, D., Smouse, P.E., Wood, C.C., 2012. Developing a broader scientific foundation for river restoration: columbia River food webs. *Proc. Natl. Acad. Sci.* 109 (52), 21201–21207.
- Napiórkowski, P., Bąkowska, M., Mrozińska, N., Szymańska, M., Kolarova, N., Obolowski, K., 2019. The effect of hydrological connectivity on the zooplankton structure in floodplain lakes of a regulated large river (the Lower Vistula, Poland). *Water* 11 (9), 1924.
- Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. *Science* 308 (5720), 405–408.
- Nowlin, W.H., Evarts, J.L., Vanni, M.J., 2005. Release rates and potential fates of nitrogen and phosphorus from sediments in a eutrophic reservoir. *Freshwat. Biol.* 50 (2), 301–322.
- Palmer, M., Ruhi, A., 2019. Linkages between flow regime, biota, and ecosystem processes: implications for river restoration. *Science* 365 (6459), eaaw2087.
- Pennock, C.A., Hines, B.A., Elverud, D.S., Francis, T.A., McKinstry, M.C., Schleicher, B.J., Gido, K.B., 2021. Reservoir fish assemblage structure across an aquatic ecotone: can river-reservoir interfaces provide conservation and management opportunities? *Fish. Manage. Ecol.* 28 (1), 1–13.
- Pernthaler, J., 2005. Predation on prokaryotes in the water column and its ecological implications. *Nat. Rev. Microbiol.* 3 (7), 537–546.
- Poff, N.L., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proc. Natl. Acad. Sci. U. S. A.* 104 (14), 5732–5737.
- Poznańska, M., Kobak, J., Wolniewicz, N., Kakareko, T., 2010. Macrozoobenthos communities from two types of land-water transition zones in a European lowland dam reservoir. *Fundam. Appl. Limnol.* 176 (2), 115–126.
- Prast, M., Bischoff, A.A., Waller, U., Amann, R., Berninger, U.-G., 2007. Effect of ciliates on nitrification and nitrifying bacteria in Baltic Sea sediments. *Mar. Ecol. Prog. Ser.* 350, 55–61.
- Qu, Z., Forster, D., Bruni, E.P., Frantal, D., Kammerlander, B., Nachbaur, L., Pitsch, G., Posch, T., Proeschold, T., Teubner, K., Sonntag, B., Stoek, T., 2021. Aquatic food webs in deep temperate lakes: key species establish through their autecological versatility. *Mol. Ecol.* 30 (4), 1053–1071.
- Rabalais, N.N., Díaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D., Zhang, J., 2010. Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7 (2), 585–619.
- Ran, X., Bouwman, L., Yu, Z., Beusen, A., Chen, H., Yao, Q., 2017. Nitrogen transport, transformation, and retention in the Three Gorges Reservoir: a mass balance approach. *Limnol. Oceanogr.* 62 (5), 2323–2337.
- Roberts, K.L., Eate, V.M., Eyre, B.D., Holland, D.P., Cook, P.L.M., 2012. Hypoxic events stimulate nitrogen recycling in a shallow salt-wedge estuary: the Yarra River estuary. *Australia. Limnol. Oceanogr.* 57 (5), 1427–1442.
- Robson, B.J., Lester, R.E., Baldwin, D.S., Bond, N.R., Drouart, R., Rolls, R.J., Ryder, D.S., Thompson, R.M., 2017. Modelling food-web mediated effects of hydrological variability and environmental flows. *Water Res.* 124, 108–128.
- Ross, O.N., Sharples, J., 2007. Phytoplankton motility and the competition for nutrients in the thermocline. *Mar. Ecol. Prog. Ser.* 347, 21–38.
- Ruan, X., Schellenger, F., Hellweger, F.L., 2014. Accounting for nitrogen fixation in simple models of lake nitrogen loading/export. *Environ. Sci. Technol.* 48 (10), 5667–5673.
- Rychtecky, P., Znachor, P., 2011. Spatial heterogeneity and seasonal succession of phytoplankton along the longitudinal gradient in a eutrophic reservoir. *Hydrobiologia* 663 (1), 175–186.
- Saito, L., Johnson, B.M., Bartholow, J., Hanna, R.B., 2001. Assessing ecosystem effects of reservoir operations using food web–energy transfer and water quality models. *Ecosystems* 4 (2), 105–125.
- Sang, C., Zheng, Y., Zhou, Q., Li, D., Liang, G., Gao, Y., 2019. Effects of water impoundment and water-level manipulation on the bioaccumulation pattern, trophic transfer and health risk of heavy metals in the food web of Three Gorges Reservoir (China). *Chemosphere* 232, 403–414.
- Saunders, D.L., Kalff, J., 2001. Nitrogen retention in wetlands, lakes and rivers. *Hydrobiologia* 443 (1–3), 205–212.
- Schindler, D.W., Hecky, R.E., Findlay, D.L., Stainton, M.P., Parker, B.R., Paterson, M.J., Beaty, K.G., Lyng, M., Kasian, S.E.M., 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: results of a 37-year whole-ecosystem experiment. *Proc. Natl. Acad. Sci. U. S. A.* 105 (32), 11254–11258.
- Schratzberger, M., Ingels, J., 2018. Meiofauna matters: the roles of meiofauna in benthic ecosystems. *J. Exp. Mar. Biol. Ecol.* 502, 12–25.
- Scott, J.T., Stanley, J.K., Doyle, R.D., Forbes, M.G., Brooks, B.W., 2009. River-reservoir transition zones are nitrogen fixation hot spots regardless of ecosystem trophic state. *Hydrobiologia* 625, 61–68.
- Seitzinger, S., Harrison, J.A., Bohlke, J.K., Bouwman, A.F., Lowrance, R., Peterson, B., Tobias, C., Van Drecht, G., 2006. Denitrification across landscapes and waterscapes: a synthesis. *Ecol. Appl.* 16 (6), 2064–2090.
- Sheppard, S.K., Harwood, J.D., 2005. Advances in molecular ecology: tracking trophic links through predator-prey food-webs. *Funct. Ecol.* 19 (5), 751–762.
- Shimeta, J., Starczak, V.R., Ashiru, O.M., Zimmer, C.A., 2001. Influences of benthic boundary-layer flow on feeding rates of ciliates and flagellates at the sediment-water interface. *Limnol. Oceanogr.* 46 (7), 1709–1719.
- Smeti, E., von Schiller, D., Karaouzas, I., Laschou, S., Vardakas, L., Sabater, S., Tornés, E., Monllor-Alcaraz, L.S., Guillem-Argiles, N., Martínez, E., Barceló, D., López de Alda, M., Kalogianni, E., Elosegi, A., Skoulidakis, N., 2019. Multiple stressor effects on biodiversity and ecosystem functioning in a Mediterranean temporary river. *Sci. Total Environ.* 647, 1179–1187.
- Soares Guedes, G.H., Mattos, T.M., Camilo, G.d.S., Uehara, W., de Paiva Ferreira, D.L., Araujo, F.G., 2020. Artificial flow regime promotes abiotic and biotic gradients: testing the concept of longitudinal zonation in an off-river reservoir. *Ecohydrol. Hydrobiol.* 20 (2), 256–264.
- Šolić, M., Šantić, D., Šestanović, S., Bojanić, N., Grbec, B., Jozić, S., Vrdoljak, A., Orduj, M., Matić, F., Kušpilić, G., Gladan, Z.N., 2020. Impact of water column stability dynamics on the succession of plankton food web types in the offshore area of the Adriatic Sea. *J. Sea Res.* 158, 101860.
- Steele, J.A., Countway, P.D., Xia, L., Vigil, P.D., Beman, J.M., Kim, D.Y., Chow, C.-E.T., Sachdeva, R., Jones, A.C., Schwalbach, M.S., Rose, J.M., Hewson, I., Patel, A., Sun, F., Caron, D.A., Fuhrman, J.A., 2011. Marine bacterial, archaeal and protistan association networks reveal ecological linkages. *ISME J.* 5 (9), 1414–1425.
- Stief, P., 2013. Stimulation of microbial nitrogen cycling in aquatic ecosystems by benthic macrofauna: mechanisms and environmental implications. *Biogeosciences* 10 (12), 7829–7846.
- Stock, W., Heylen, K., Sabbe, K., Willems, A., De Troch, M., 2014. Interactions between benthic copepods, bacteria and diatoms promote nitrogen retention in intertidal marine sediments. *PLoS ONE* 9 (10), e111001.
- Strauss, E.A., Dodds, W.K., 1997. Influence of protozoa and nutrient availability on nitrification rates in subsurface sediments. *Microb. Ecol.* 34 (2), 155–165.
- Su, X., He, Q., Mao, Y., Chen, Y., Hu, Z., 2019. Dissolved oxygen stratification changes nitrogen speciation and transformation in a stratified lake. *Environ. Sci. Pollut. Res.* 26 (3), 2898–2907.
- Suter, E.A., Pachiadaki, M.G., Montes, E., Edgcomb, V.P., Scranton, M.I., Taylor, C.D., Taylor, G.T., 2021. Diverse nitrogen cycling pathways across a marine oxygen gradient indicate nitrogen loss coupled to chemoautotrophic activity. *Environ. Microbiol.* 23 (6), 2747–2764.
- Thamdrup, B. (2012) Annual review of ecology, evolution, and systematics, Vol 43. Futuyma, D.J. (ed), pp. 407–428.
- Thornton, K.W. 1990. Reservoir limnology: ecological perspectives /edited by Kent W. Thornton, Bruce L. Kimmel, Forrest E. Payne.
- Tran, P.Q., Bachand, S.C., McIntyre, P.B., Kraemer, B.M., Vadeboncoeur, Y., Kimirei, I.A., Tamatamah, R., McMahon, K.D., Anantharaman, K., 2021. Depth-discrete metagenomics reveals the roles of microbes in biogeochemical cycling in the tropical freshwater Lake Tanganyika. *ISME J.* 15 (7), 1971–1986.
- Tso, S.-F., Taghon, G.L., 2006. Protozoan grazing increases mineralization of naphthalene in marine sediment. *Microb. Ecol.* 51 (4), 460–469.
- Turgeon, K., Turpin, C., Gregory-Eaves, I., 2019. Dams have varying impacts on fish communities across latitudes: a quantitative synthesis. *Ecol. Lett.* 22 (9), 1501–1516.
- Van Cappellen, P., Maavara, T., 2016. Rivers in the anthropocene: global scale modifications of riverine nutrient fluxes by damming. *Ecohydrol. Hydrobiol.* 16 (2), 106–111.
- Varela, M.M., Barquero, S., Bode, A., Fernandez, E., Gonzalez, N., Teira, E., Varela, M., 2003. Microplanktonic regeneration of ammonium and dissolved organic nitrogen in the upwelling area of the NW of Spain: relationships with dissolved organic carbon production and phytoplankton size-structure. *J. Plankton Res.* 25 (7), 719–736.
- Vrede, T., Ballantyne, A., Mille-Lindblom, C., Algesten, G., Gudas, C., Lindahl, S., Brunberg, A.K., 2009. Effects of N:P loading ratios on phytoplankton community composition, primary production and N fixation in a eutrophic lake. *Freshwat. Biol.* 54 (2), 331–344.
- Wallace, C.D., Sawyer, A.H., Soltanian, M.R., Barnes, R.T., 2020. Nitrate removal within heterogeneous riparian aquifers under tidal influence. *Geophys. Res. Lett.* 47 (10), e2019GL085699.
- Wan Maznah, W.O., Intan, S., Sharifah, R., Lim, C.C., 2018. Lentic and lotic assemblages of zooplankton in a tropical reservoir, and their association with water quality conditions. *Int. J. Environ. Sci. Technol.* 15 (3), 533–542.
- Wang, B., Liu, C.-Q., Wang, F., Liu, X.-L., Wang, Z.-L., 2015. A decrease in pH downstream from the hydroelectric dam in relation to the carbon biogeochemical cycle. *Environ. Earth Sci.* 73 (9), 5299–5306.
- Wang, F., 2020. Impact of a large sub-tropical reservoir on the cycling of nutrients in a river. *Water Res.* 186, 116363.
- Wang, F., Maberly, S.C., Wang, B., Liang, X., 2018a. Effects of dams on riverine biogeochemical cycling and ecology. *Inland Waters* 8 (2), 130–140.
- Wang, H., Wang, T., Yang, S., Liu, X., Kou, L., Huang, T., Wen, G., 2019. Nitrogen removal in oligotrophic reservoir water by a mixed aerobic denitrifying consortium: influencing factors and immobilization effects. *Int. J. Env. Res. Public Health* 16 (4), 583.
- Wang, S., Fu, B., Piao, S., Lü, Y., Ciais, P., Feng, X., Wang, Y., 2016. Reduced sediment transport in the Yellow River due to anthropogenic changes. *Nat. Geosci.* 9 (1), 38–41.
- Wang, W.T., Yu, Z.M., Wu, Z.X., Song, S.Q., Song, X.X., Yuan, Y.Q., Cao, X.H., 2018b. Rates of nitrification and nitrate assimilation in the Changjiang River estuary and adjacent waters based on the nitrogen isotope dilution method. *Cont. Shelf Res.* 163, 35–43.

- Williams, R.L., Wakeham, S., McKinney, R., Wishner, K.F., 2014. Trophic ecology and vertical patterns of carbon and nitrogen stable isotopes in zooplankton from oxygen minimum zone regions. *Deep-Sea Res. Part I-Oceanogr. Res. Pap.* 90, 36–47.
- Williams, T.J., Cavicchioli, R., 2014. Marine metaproteomics: deciphering the microbial metabolic food web. *Trends Microbiol.* 22 (5), 248–260.
- Xia, X., Zhang, S., Li, S., Zhang, L., Wang, G., Zhang, L., Wang, J., Li, Z., 2018. The cycle of nitrogen in river systems: sources, transformation, and flux. *Environ. Sci. -Process. Impacts* 20 (6), 863–891.
- Xing, Z.K., Fong, D.A., Lo, E.Y.M., Monismith, S.G., 2014. Thermal structure and variability of a shallow tropical reservoir. *Limnol. Oceanogr.* 59 (1), 115–128.
- Xu, H., Li, H., Tang, Z., Liu, Y., Li, G., He, Q., 2020. Underestimated methane production triggered by phytoplankton succession in river-reservoir systems: evidence from a microcosm study. *Water Res.* 185, 116233.
- Xue, Y., Yu, Z., Chen, H., Yang, J.R., Liu, M., Liu, L., Huang, B., Yang, J., 2017. Cyanobacterial bloom significantly boosts hypolimnetic anammox bacterial abundance in a subtropical stratified reservoir. *FEMS Microbiol. Ecol.* 93 (10).
- Yang, N., Li, Y., Zhang, W., Lin, L., Qian, B., Wang, L., Niu, L., Zhang, H., 2019. Cascade dam impoundments restrain the trophic transfer efficiencies in benthic microbial food web. *Water Res.* 170, 115351.
- Yigzaw, W., Li, H.-Y., Fang, X., Leung, L.R., Voisin, N., Hejazi, M.I., Demissie, Y., 2019. A multilayer reservoir thermal stratification module for earth system models. *J. Adv. Model. Earth Syst.* 11 (10), 3265–3283.
- Yool, A., Martin, A.P., Fernandez, C., Clark, D.R., 2007. The significance of nitrification for oceanic new production. *Nature* 447 (7147), 999–1002.
- Yu, H., Tsuno, H., Hidaka, T., Jiao, C., 2010. Chemical and thermal stratification in lakes. *Limnology* 11 (3), 251–257.
- Yue, Y., Cai, L., Tang, Y., Zhang, Y., Yang, M., Wang, F., 2021. Vertical distribution of bacterial community in water columns of reservoirs with different trophic conditions during thermal stratification. *Front. Environ. Sci.* 9 (103), 632089.
- Zhang, H.B., Richardson, P.A., Belayneh, B.E., Ristvey, A., Lea-Cox, J., Copes, W.E., Moorman, G.W., Hong, C.X., 2015a. Characterization of water quality in stratified nursery recycling irrigation reservoirs. *Agric. Water Manage.* 160, 76–83.
- Zhang, W., Wang, H., Li, Y., Lin, L., Hui, C., Gao, Y., Niu, L., Zhang, H., Wang, L., Wang, P., Wang, C., 2020a. Bend-induced sediment redistribution regulates deterministic processes and stimulates microbial nitrogen removal in coarse sediment regions of river. *Water Res.* 170, 115315.
- Zhang, X., Ward, B.B., Sigman, D.M., 2020b. Global nitrogen cycle: critical enzymes, organisms, and processes for nitrogen budgets and dynamics. *Chem. Rev.* 120 (12), 5308–5351.
- Zhang, Y., Pavlovskaya, M., Stoica, E., Prekrasna, I., Yang, J., Slobodnik, J., Zhang, X., Dykyl, E., 2020c. Holistic pelagic biodiversity monitoring of the Black Sea via eDNA metabarcoding approach: from bacteria to marine mammals. *Environ. Int.* 135, 105307.
- Zhang, Y.L., Wu, Z.X., Liu, M.L., He, J.B., Shi, K., Zhou, Y.Q., Wang, M.Z., Liu, X.H., 2015b. Dissolved oxygen stratification and response to thermal structure and long-term climate change in a large and deep subtropical reservoir (Lake Qiandaohu, China). *Water Res.* 75, 249–258.
- Zhao, C.S., Yang, Y., Yang, S.T., Xiang, H., Wang, F., Chen, X., Zhang, H.M., Yu, Q., 2019. Impact of spatial variations in water quality and hydrological factors on the food-web structure in urban aquatic environments. *Water Res.* 153, 121–133.
- Zhou, S., Sun, Y., Huang, T., Cheng, Y., Yang, X., Zhou, Z., Li, Y., Li, Z., Cui, J., Xiao, L., 2020. Reservoir water stratification and mixing affects microbial community structure and functional community composition in a stratified drinking reservoir. *J. Environ. Manage.* 267, 110456.
- Zimmerman, A.E., Howard-Varona, C., Needham, D.M., John, S.G., Worden, A.Z., Sullivan, M.B., Waldbauer, J.R., Coleman, M.L., 2020. Metabolic and biogeochemical consequences of viral infection in aquatic ecosystems. *Nat. Rev. Microbiol.* 18 (1), 21–34.