Oecologia Australis
26(2):187–198, 2022
https://doi.org/10.4257/oeco.2022.2602.08

HUMAN IMPACTS ON AQUATIC ECOSYSTEMS FROM THE LENS OF ECOLOGICAL STOICHIOMETRY

Layla Mayer Fonseca[1], *Gabrielle Rabelo Quadra*[1], *José R. Paranaíba*[1], *Otávio Augusto Lacerda Ferreira Pimentel*[2], *James B. Cotner*[3] & *André Megali Amado*[1,4]*

[1] Universidade Federal de Juiz de Fora, Departamento de Biologia, Pós-Graduação em Biodiversidade e Conservação da Natureza, Laboratório de Ecologia Aquática, Rua José Lourenço Kelmer s/n, CEP 36036-900, Juiz de Fora, MG, Brazil.

[2] Universidade Federal do Rio Grande, Instituto de Oceanografia, Pós-Graduação em Aquicultura, Av. Itália, CEP 96203-900, Carreiros, RS, Brazil;

[3] University of Minnesota, Department of Ecology, Evolution and Behavior, Como Avenue, 55455, Twin Cities, United States;

[4] Universidade Federal do Rio Grande do Norte, Departamento de Oceanografia e Limnologia, Avenida Senador Salgado Filho, 3000, CEP 59014-002, Lagoa Nova, RN, Brazil.

E-mails: layla.mayer@ecologia.ufjf.br; gaby_quadra@hotmail.com; jose.paranaiba@ecologia.ufjf.br, otavio.lacerda13@hotmail.com; cotne002@umn.edu; andre.amado@ecologia.ufjf.br (*corresponding author).

Abstract: Aquatic ecosystems are under different anthropogenic pressures, such as climate change, eutrophication, chemical pollution, overfishing, and introducing exotic species. Human activities have accelerated biogeochemical cycles forcing organisms and ecosystems to adapt. Most ecological stoichiometry studies are focused on carbon, nitrogen, phosphorus, and their relative proportions. Still, the possibilities for investigations using other elements to better understand the impacts of human pressures on aquatic ecosystems are vast. Therefore, here we explore how different anthropogenic activities influence ecosystem balance in terms of nutrient composition and stoichiometry. We conclude that human interventions have affected the functioning of aquatic ecosystems in terms of energy flow due to stoichiometric imbalances. We also conclude that the interplay between macro and micronutrient stoichiometry might raise important axioms to predict and understand human impacts on the functioning of aquatic ecosystems.

Keywords: biogeochemical cycles; elements; nutrient stoichiometry; pollution.

INTRODUCTION

Ecological stoichiometry (ES) focuses on ecosystem functioning targeting nutrients ratios and how they mediate the relationships between consumers (biological requirements) and resources (availability) (Sterner & Elser 2002). Alfred Redfield was one of the first researchers to make the connection among organisms, the quality and ratios of resources, and the ecosystem functioning (Redfield 1934, 1958). This was achieved by establishing the classic and conservative "Redfield ratio", which is the relative abundance of carbon (C) to nitrogen (N) and to phosphorus (P) (*i.e.*, C: N: P of 106: 16: 1 in planktonic organisms of the ocean) (Redfield

1934, 1958). One of the key points from Redfield's work was to highlight that planktonic organisms are essentially able to manipulate the marine environment to reflect their biomass composition (Redfield 1934, 1958). The relative uniformity of biomass composition that Redfield highlighted and the long residence time of water in the ocean leads to a feedback mechanism whereby the carbon and nutrient pools reflect the elemental composition of the plankton (Redfield 1934, 1958). However, these feedbacks work much less efficiently in freshwater systems that can have residence times on the order of weeks to decades rather than hundreds of years to millennia (They *et al.* 2017). Consequently, these systems can have greater stoichiometric imbalances, especially when short residence time is coupled with ecological stressors (Welti *et al.* 2017). Imbalances in C: P and N: P ratios can occur among different trophic levels or among organisms and the environment (Sterner *et al.* 1998, Sterner & Elser 2002), which has significant ecological consequences for population dynamics, nutrient cycling and, finally, for ecosystem metabolism (Elser & Urabe 1999, Sterner & Elser 2002).

One of the axioms of the ES is to examine relationships between the chemical composition of organisms and their resources (Sterner & Elser 2002). For instance, homeostatic organisms have the ability to keep their chemical composition relatively uniform, despite changes in the environment or resource, while non-homeostatic organisms have their chemical composition varying with the resource composition (Kooijman 1995). It is also common to observe different degrees of homeostasis among organisms (Godwin & Cotner 2015).

Anthropogenic activities have accelerated biogeochemical cycles and increased aquatic pollution worldwide (Quadra *et al.* 2019). Pollution can be understood as a manifestation of a stoichiometric imbalance. For instance, the nutrient concentrations and ratios of N: P, C: N, and C: P have been changing due to eutrophication, driven primarily by agriculture, untreated sewage, and human population growth, with important implications for aquatic metabolism and biological interactions (Dodds & Cole 2007, Welti *et al.* 2017).

Most ecological stoichiometry studies are currently related to C, N, and P, but organisms typically require more than 20 elements, and much less is known about these other elements such as zinc (Zn), iron (Fe), and copper (Cu) (Jeyasingh *et al.* 2017). Very similar to N and P, a low relative abundance of trace elements may also represent changes in ecosystem function. For example, in the Southern Ocean, where N and P are found in excess in relation to the needs of plankton, Fe limits primary production (Behrenfeld & Kolber 1999). Unlike N and P, trace elements are much less prevalent in biomass, and excess concentrations may be toxic. For instance, several marine cyanobacteria species had reduced reproduction due to high Cu and cadmium (Cd) concentrations (Brand *et al.* 1986; and for a more recent review see Sunda 2012). Thus, trace elements toxicity is a reflection of a stoichiometric imbalance (Bradshaw *et al.* 2012). The excess of N and P in aquatic ecosystems usually boost microbial community growth rate and respiration (Del Giorgio & Cole 1998), while high concentrations of trace elements may result in toxicity (Kolarova & Napiórkowski 2021). Recently, anthropogenic activities have been increasing the concentration of several trace elements in surface waters, bringing up consequences for ecosystem services, such as carbon sequestration, nutrient recycling, self-purification, and supporting biodiversity (Gerbersdorf *et al.* 2011, Chen *et al.* 2015, Schuler & Relyea 2018).

Even though it was recently shown that ES is a powerful tool to look at ecosystem functioning (Welti *et al.* 2017), there are not many studies addressing the effects of human interventions on aquatic ecosystems referring to ES theories. Therefore, our objective is to discuss how human activities may trigger stoichiometric changes in aquatic ecosystems using the following anthropogenic pressures as case studies: climate change, cultural eutrophication, aquaculture, invasive species, and overfishing. Furthermore, considering that anthropogenic interventions potentially affect organism growth rates and nutritional composition, we discussed consequences for energy flow and energy pyramids in aquatic ecosystems and how ES can help predict environmental changes caused by anthropogenic influences.

CLIMATIC EVENTS AND STOICHIOMETRY

In the last century, the intense human fossil fuel burning has been causing the atmospheric accumulation of greenhouse gases, such as carbon dioxide (CO_2) and methane (CH_4), leading to changes in the planetary climatic patterns. Climate models have systematically shown temperature increase as a major climatic response in the Brazilian territory and biomes (Marengo *et al.* 2010, 2020) with great consequences to hydrology (Brito *et al.* 2018) and biogeochemical cycling in inland waters (Roland *et al.* 2012). For instance, temperature increase may change organisms' growth rates and affect their chemical composition (*i.e.*, stoichiometric imbalance) and, consequently, can affect ecosystem functions as primary production or decomposition (Cotner 2019).

Climate change is affecting ecosystem stoichiometry and ecological processes in several ways. Recently, it has been shown that increased N, P, and CO_2 availability may 'dilute' micronutrients in crops with important implications for human health (Medek *et al.* 2017; Myers *et al.* 2014). Increasing CO_2, as well as N and P (from cultural eutrophication, another global environmental issue discussed below) concentrations, may have a similar effect in aquatic ecosystems (Cotner 2019), a phenomenon referred to as 'environmental obesity'; *i.e.*, higher proportions of C fixed by primary producers (*i.e.*, higher C:nutrient ratios) due to the higher atmospheric CO_2 concentrations with consequences to nutrient recycling and energy flow through the aquatic food web (Van Der Walls *et al.* 2010; Cotner 2019). Moreover, increasing temperatures can directly affect aquatic metabolism (Brown *et al.* 2004) by altering growth rates. For instance, increasing temperatures resulted in increased bacterial biomass and higher C: P and N: P ratios (Phillips *et al.* 2017). Therefore, higher temperatures may lead to P deficit in organism biomass resulting in energy flow changes due to stoichiometric imbalance between resources and predators, such as zooplankton grazing high C: P biomass phytoplankton (as in the plankton paradox energy; Sterner *et al.* 1998). Moreover, increasing temperature and N and P availability may affect heterotrophic bacteria respiration (Scofield *et al.* 2015, Berggren *et al.* 2010), increasing CO_2 and nitrous oxide (N_2O) emissions from freshwaters (Marotta *et al.* 2014, Liengaard *et al.* 2013).

As an indirect consequence of climate change, hydrological and rainfall patterns will also be altered, and these changes were predicted to drastically affect ecological processes such as nutrient cycling, energy flow, and spatial ecological gradients in inland waters (Roland *et al.* 2012). The reduction of the annual precipitation in the Brazilian semi-arid, for example, has caused drastic changes in water volume and resuspension of sediments, reducing light availability to primary producers but also increasing P concentrations in the water column during droughts (Costa *et al.* 2019). On the one hand, these frequent and prolonged droughts can shift the phytoplankton community to the dominance of mixotrophic organisms and affect the trophic chain energy flow (Costa *et al.* 2019). On the other hand, it can also affect seston and bacterial stoichiometry by increasing water residence time in aquatic ecosystems (They *et al.* 2017). With prolonged water residence time, bacterial and seston increased their nutritional quality by reducing C: P ratios, affecting nutrient cycling, such as the increase in C mineralization rates (They *et al.* 2017).

CULTURAL EUTROPHICATION

The load of nutrient-rich anthropic effluents, such as those from domestic, agriculture, and aquaculture activities, have resulted in higher concentrations of N and P in freshwater ecosystems (Glibert 2012, Quadra *et al.* 2019). How water resources rich in N and P affect the stoichiometry of organisms is still unknown and deserves more attention in future work (Sardans *et al.* 2012, Sitters *et al.* 2015). When N and P occur in high concentrations and out of stoichiometric balance with other nutrients, they favor the rapid proliferation of fast-growing microorganisms. The Growth Rate Hypothesis connects the nutritional needs of organisms to elementary disproportion represented in nucleic acids, which are central for growth (Elser *et al.* 2000). Fast-growing organisms require large amounts of N and mainly P, resulting in low N: P, C: N and C: P ratios, which supports the high protein synthesis rates necessary for rapid growth (Elser *et al.* 1996, 2000, Sterner & Elser 2002). Fast-growing organisms are usually connected to ecological imbalances such as harmful algae that have the ability to cause severe damage to the ecosystems functioning and biodiversity (Glibert & Burkholder 2011).

Sewage effluents can be a key source of N and P to aquatic ecosystems (Jarvie *et al.* 2006, Xu *et al.* 2008, McCrackin *et al.* 2013), increasing growth rates of both autotrophs and heterotrophs and selecting fast-growing P-rich species (according to the growth rate hypothesis; Smith *et al.* 1999, Sterner & Elser 2002, Smith & Schindler 2009, Welti *et al.* 2017). At the beginning of the eutrophication process, the primary producers grow quickly and facilitate the growth of the higher trophic levels; however, changes in the biological and/or physicochemical conditions, such as higher relative accumulation of P than N, can alter ecosystem behavior (Vinçon-Leite & Casenave 2019). For instance, the dominance of non-edible cyanobacteria, such as *Cylindrospermopsis raciborskii*, could shift zooplankton community composition and, perhaps, drastically affect the energy flow through the aquatic food web in eutrophic ecosystems (Neumann-Leitão *et al.* 2018, Rangel *et al.* 2020). Additionally, increased availability of N and P can stimulate both autotrophic and heterotrophic metabolism affecting CO_2 formation and consumption rates in freshwaters, such as in humic and clearwater coastal tropical lagoons (Peixoto *et al.* 2013), which may represent positive feedback to climate changes in those ecosystems (Scofield *et al.* 2015).

An under-appreciated aspect of eutrophication is the effect of N and P imbalances on other biogeochemical cycles. Noteworthy, relieving N and P limitations could potentially increase recycling rates of all elements, including non-limiting ones. Unlike Redfield's ocean C:N:P rate, where the microbiota regulates elemental cycling due to internal processing and long residence times, externally supplied N and P may disrupt the close coupling between these elements and others, such as C, Fe, and Zn. Presumably, this would lead to increased retention of these elements, but it is likely complicated by temporal and spatial complexities (Yang *et al.* 2020). For example, increased demand for micronutrients with N and P enrichment could potentially be offset by changes in the water column or sediment redox potential (Cotner *et al.*1990, Burgin *et al.* 2011), which may happen due to extreme droughts or precipitation, acidification, quality and quantity of organic matter shifts, effluents inputs to aquatic ecosystems, among others (Riedel *et al.* 2013). Nonetheless, changes in nutrient availability are likely to affect ecosystem processes that become more or less favorable with N and P addition. For example, N and P addition facilitate algal growth (Cotner & Wetzel 1992) but negatively affects nitrification and denitrification depending on Fe and Mn availability (Browning *et al.* 2021). While ecologists examined competition between organisms with similar metabolic strategies such as photo-synthesizers or aerobic heterotrophs, studies addressing how micronutrient limitation affects metabolism and processes with ecosystem-scale implications, such as competition between N-fixers and denitrifies for Fe, are still needed. The implications of these dynamics are important not only for a given freshwater system but also for downstream environments such as the ocean (Maranger *et al.* 2018).

Noteworthy, anthropogenic effluents are a complex mixture that contributes not only to N and P addition but also trace elements to the environment (Quadra *et al.* 2019). Hence, it could be expected that these other elements would interact with high N and P concentrations and could also express other important, but still unrevealed, features in ES. For instance, Karimi & Folt (2006) showed that the variation of C: N: P ratios were lower among benthic macroinvertebrates, while non-essential metals (lead (Pb), mercury (Hg), and cadmium (Cd)) presented a higher variation among the same groups (Karimi & Folt 2006). Furthermore, it was found that the green algae presented similarities in their composition of Fe, Cu, and Zn, while the red algae presented similarities in their composition of Cd, cobalt (Co), and manganese (Mn) (Quigg *et al.* 2003). The authors attributed these differences to environmental pressures on photosynthetic devices once trace elements may substitute each other depending on environmental concentrations. Furthermore, it has been demonstrated that different evolutionary mechanisms may have selected macronutrients and trace elements stoichiometry in marine eucaryotic phytoplankton since the Proterozoic era (Quigg *et al.* 2003).

Thus, including micronutrients stoichiometry, such as trace elements, in the ES approaches may bring new insights into the role of organisms in ecosystem functioning. For example, Fe plays a key role in photosynthesis and phytoplankton growth and has the potential to increase N_2 fixation by phytoplankton (Martin & Fitzwater 1988, Martin *et al.* 1990a, 1990b, 1991, Mills *et al.* 2004, Somes *et al.* 2010). Moreover, Fe availability affects bacterial growth efficiency (Tortell *et al.* 1996). Other trace elements are also crucial for ecosystem functioning; *e.g.*, in the absence of oxygen (O_2), microorganisms tend to use nickel (Ni) in the production of urease to obtain N (Price & Morel 1991). When Cu is limited, N_2O accumulates due to denitrifying microorganisms' growth reduction. Many enzymes that participate in the phytoplankton respiration process (Mechanism of Carbon Concentration) need Zn, and other groups need Co or Cd (Lane & Morel 2000). Therefore, it is possible to observe the fundamental role of trace elements in regulating C and N cycles and in the production of gases in aquatic ecosystems (Granger &Ward 2003). We reinforce that the other elements (other than C, N, and P) may improve ES ability to predict ecosystem functioning (Jeyasingh *et al.* 2017). It could be possible to draw new functional axioms as the growth rate hypothesis and better predict how human activities can affect aquatic ecosystem functioning by combining trace elements with the well-known macronutrient stoichiometry.

STOICHIOMETRY AND AQUACULTURE

Aquaculture is growing worldwide because it enables the production of high-quality animal protein for society (FAO, 2020). However, it usually discharges organic matter and nutrient-rich effluents in aquatic ecosystems without previous treatment, contributing to cultural eutrophication (Páez-Osuna 2001, Gesteira & Paiva 2003, Boyd 2003). The Biofloc technology (BFT) was developed based on stoichiometric manipulations of cultivation water to improve shrimp production and reduce the need for water exchange (Emerenciano *et al.* 2013). Basically, C-rich fertilization strategies (*e.g.*, by addition of molasses, sugar, or vegetable bran), stimulate autotrophic and heterotrophic microbial communities to form biological aggregates (bioflocs) that oxidize (for less toxic compounds for animals, such as nitrate) and assimilate (converting into microbial biomass) the ammonia produced by the feed addition and by the animal's excretion, providing adequate water quality (Avnimelech 2012, Romano *et al.* 2018, Samocha, 2019). High nutrient availability and temperature can affect microbial growth rates in shrimp ponds that use the BFT, increasing P concentration and reducing C: P and N: P ratios (Pimentel *et al.* 2020). Thus, besides BFT has become an important alternative food source to shrimp growth, it has also become an environmentally friendly alternative for reducing nutrient-rich water disposal (Emerenciano *et al.* 2013, Rajkumar *et al.* 2016, Samocha 2019). Therefore, ES knowledge has been opening large avenues to improve the operation of intensive shrimp farming systems and minimize or avoid eutrophication.

INVASIVE SPECIES

Invasive species are considered a huge threat to biodiversity, affecting not only biological communities but also the economy and human health (Gallardo *et al.* 2016, Pimentel *et al.* 2001, Walsh *et al.* 2016). The introduction of new species has the potential to alter biogeochemical cycles and affect stoichiometry (Cucherousset & Olden 2011). For example, Nile tilapia (*e.g.*, *Oreochromis niloticus*) was introduced globally in inland waters for aquaculture purposes (Vicente & Fonseca-Alves 2013), which may significantly affect energy flow through the trophic chain. Although tilapias' role in trophic interactions is not straightforward due to their omnivorous habit, their excretion may have important consequences to N and P stoichiometry (Attayde *et al.* 2007). A study showed that phytoplankton P limitation was reduced in a lake with an invasive omnivorous fish species (*Astyanax bimaculatus*), showing higher chlorophyll-a concentrations than neighboring environments without the invasive fish. The P limitation of the phytoplankton was alleviated due to the high P content present in the fish excretion (Nobre *et al.* 2019). Another study performed in a tropical reservoir also showed that Nile tilapia increased N and P availability via excretion and promoted algae growth (Figueredo & Giani 2005). After a massive fish kill of two invasive tilapia species from a Brazilian reservoir, researchers found an improvement in water quality, with a decreased chlorophyll-a and P concentrations (Starling *et al.* 2002).

OVERFISHING

Whether for consumption or ornamental purposes, overfishing is a big threat to aquatic ecosystems (Arthington *et al.* 2016). Fishing is undoubtedly important at different scales, but the natural stocks are not being able to reestablish, and overfishing together with other stressors threatening freshwater and marine ecosystems (Jackson *et al.* 2001, Möllmann & Diekmann 2012). Overfishing influences the stoichiometry of aquatic ecosystems when it acts synergistically with other stressors such as eutrophication or changes in water temperature (Moy & Christie 2012). Zaneveld *et al.* (2016) showed that overfishing in nutrient-polluted environments might alter the stoichiometry of reef regions in the ocean, increasing coral-algal competition and, consequently, reducing coral recruitment, growth, and survival, through several mechanisms, including coral microbiome disruption. As mentioned in previous sections, the misbalance in N and P may lead to algae growth and dominance of some phytoplankton species. Moreover, removing predatory phytoplankton species can also boost this algal growth. Overfishing oysters to the level of extinction in the ecosystem is an example of how eliminating organisms that exercise top-down control can affect the stoichiometric balance of the environment (Ibrahim *et al.* 2018). Bivalve populations that feed on phytoplankton limit the blooms, preventing eutrophication (Officer *et al.* 1982). A classic example of how overfishing can impact inland waters is the Laurentian Great Lakes (North America), which has experienced nutritional imbalances and invasion of non-native species since the beginning of overfishing records (Smith 1968). It is expected that the biodiversity decreases even more over time, as well as the size of the organisms and chemical composition, in which both can influence the energy flow throughout trophic levels.

CONCEPTUAL MODELS: ENERGY PYRAMIDS IN AQUATIC ECOSYSTEMS

Charles Elton elaborated the trophic pyramid in 1927 to describe the trophic efficiency and energy loss at each trophic interaction, afterward demonstrated in 1942 by Raymond Lindeman in the "Trophic-dynamic aspect of ecology" paper (see Elton 2001, Lindeman 1942). Lindeman has also discussed different trophic efficiencies among different environments. In fact, freshwater ecosystems have higher trophic efficiency than most terrestrial ecosystems, with lower energy loss through trophic levels. This higher efficiency is achieved due to differences in the stoichiometric balance of C to nutrient ratio between primary producers and herbivores, with terrestrial primary producers showing higher C: nutrient ratios in biomass than aquatic primary producers (Del Giorgio *et al.* 1998, Sterner *et al.* 1998, Sterner & Elser 2002). Furthermore, the life cycle of aquatic organisms is generally shorter, making nutrient cycling faster. In this way, the classical theoretical energy pyramid of a given freshwater ecosystem that undergoes different anthropogenic pressures may be altered with consequences to the energy flow, matter cycling, and functioning (see Dudgeon *et al.* 2006). For instance, as mentioned before, at the beginning of the eutrophication process, the primary producers overgrow and, consequently, the following trophic levels also grow since the amount of energy available is larger. The introduction of new species also affects the ecosystem pyramid. For example, introducing a top predator fish in the third trophic level would increase the consumption of the second trophic level and allow the growth of the first trophic level. When overfishing occurs on the third, the second trophic level may gain in biomass, accumulating energy and increasing consumption of the first trophic level.

CONCLUSION

Human interventions may lead to stoichiometric imbalances in aquatic ecosystems with implications for ecosystems functioning. Ecological stoichiometric alterations are also related or reflected in energy flow and trophic alterations. Multielement stoichiometry approach, beyond C, N, and P, is important because while C, N, and P are probably with the most increased availability (Falkowski *et al.* 2000), it is likely to be driving major changes in the cycling of other elements. The intensification of unrestrained human activities such as the increase in land use and occupation in an unsustainable manner and the discharge of not-properly treated effluents (from industrial, agricultural, and urban areas) can lead to environmental imbalances at elementary levels, changing natural biogeochemical processes. This may have consequences not only to global climate but also impacts aquatic ecosystem functioning.

ACKNOWLEDGMENTS

A. Amado gratefully acknowledges continuous funding through Research Productivity Grant provided by CNPq (Process 312772/2020-3). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) Finance Code 001. This paper resulted from a graduate course on Aquatic Ecology in the Biodiversity and Nature Conservancy Graduate Program at UFJF (2018).

REFERENCES

Arthington, A. H., Dulvy, N. K., Gladstone, W., & Winfield, I. J. 2016. Fish conservation in freshwater and marine realms: status, threats and management. Aquatic Conservation: Marine and Freshwater Ecosystems, 26, 838–857. DOI: 10.1002/aqc.2712

Attayde, J. L., Okun, N., Brasil, J., Menezes, R., & Mesquita, P. 2007. Os impactos da introdução da tilápia do nilo, *Oreochromis niloticus*, sobre a estrutura trófica dos ecossistemas aquáticos do bioma caatinga. Oecologia Brasiliensis, 11(03), 450–461. DOI: 10.4257/oeco.2007.1103.13

Avnimelech, Y. 2012. Biofloc Technology – A Practical Guide Book, 2d Edition. The World Aquaculture Society, Baton Rouge, Louisiana, United States. p. 272.

Behrenfeld, M. J., & Kolber, Z. S. 1999. Widespread iron limitation of phytoplankton in the South Pacific Oceanic. Science, 283(5403), 840–843. DOI: 10.1126/science.283.5403.840

Berggren, M., Laudon, H., Jonsson, A., & Jansson, M. 2010. Nutrient constraints on metabolism affect the temperature regulation of aquatic bacterial growth efficiency. Microbial ecology, 60(4), 894–902. DOI: 10.1007/s00248-010-9751-1.

Boyd, C. E. 2003. Guidelines for aquaculture effluent management at the farm-level. Aquaculture, 226, 101–112. Elsevier. DOI: 10.1016/S0044-8486(03)00471-X

Bradshaw, C., Kautsky, U., & Kumblad, L. 2012. Ecological Stoichiometry and Multi-element Transfer in a Coastal Ecosystem. Ecosystems, 15(4), 591–603. DOI: 10.1007/s10021-012-9531-5

Brand, L. E., Sunda, W. G., & Guillard, R. R. 1986. Reduction of marine phytoplankton reproduction rates by copper and cadmium. Journal of Experimental Marine Biology and Ecology, 96(3), 225–250. DOI: 10.1016/0022-0981(86)90205-4.

Brito, S. S. B., Cunha, A. P. M., Cunningham, C. C., Alvalá, R. C., Marengo, J. A., & Carvalho, M. A. 2018. Frequency, duration and severity of drought in the Semiarid Northeast Brazil region. International Journal of Climatology, 38(2), 517–529. DOI: 10.1002/joc.5225

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. 2004. Toward a metabolic theory of ecology. Ecology, 85, 1771–1789. DOI: 10.1890/03-9000

Browning, T. J., Achterberg, E. P., Engel, A., & Mawji, E. 2021. Manganese co-limitation of phytoplankton growth and major nutrient drawdown in the Southern Ocean. Nature communications, 12(1), 1-9. DOI: 10.1038/s41467-021-21122-6

Burgin, A. J., Yang, W. H., Hamilton, S. K., & Silver, W. L. 2011. Beyond carbon and nitrogen: how the microbial energy economy couples elemental cycles in diverse ecosystems. Frontiers in Ecology and the Environment, 9(1), 44–52. DOI: 10.1890/090227

Chen, G., Shi, H., Tao, J., Chen, L., Liu, Y., Lei, G., Liu, X., & Smol, J. P. 2015. Industrial arsenic contamination causes catastrophic changes in freshwater ecosystems. Scientific Reports, 5(1), 1-7. DOI: 10.1038/srep17419.

Costa, M. R., Menezes, R. F., Sarmento, H., Attayde, J. L., Sternberg, L. da S.L., & Becker, V. 2019. Extreme drought favors potential mixotrophic organisms in tropical semi-arid reservoirs. Hydrobiologia, 831(1), 43–54. DOI: 10.1007/s10750-018-3583-2

Cotner Jr, J. B., & Heath, R. T. 1990. Iron redox effects on photosensitive phosphorus release from dissolved humic materials. Limnology and Oceanography, 35(5), 1175–1181. DOI: 10.4319/lo.1990.35.5.1175.

Cotner Jr, J. B., & Wetzel, R. G. 1992. Uptake of dissolved inorganic and organic phosphorus compounds by phytoplankton and bacterioplankton. Limnology and Oceanography, 37(2), 232–243. DOI: 10.4319/lo.1992.37.2.0232

Cotner, J. B. 2019. How increased atmospheric carbon dioxide and 'The Law of the Minimum'are contributing to environmental obesity. Acta Limnologica Brasiliensia, 31. DOI: 10.1590/S2179-975X6519

Cucherousset, J., & Olden, J. D. 2011. Ecological impacts of nonnative freshwater fishes. Fisheries, 36(5), 215–230. DOI: 10.1080/03632415.2011.574578

Del Giorgio, P.A. and Cole, J.J., 1998. Bacterial growth efficiency in natural aquatic systems. Annual Review of Ecology and Systematics, 29(1), 503–541.

Dodds, W. K., & Cole, J. J. 2007. Expanding the concept of trophic state in aquatic ecosystems: It's not just the autotrophs. Aquatic Sciences, 69(4), 427–439 DOI: 10.1007/s00027-007-0922-1

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., Naiman, R. K., Prieur-Richard, A., Soto, D., Stiassny, M. L., J., & Sullivan, C. A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological reviews, 81(2), 163–182. DOI: 10.1017/S1464793105006950

Elser, J. J., Dobberfuhl, D. R., MacKay, N. A., & Schampel, J. H. 1996. Organism size, life history and N:P stoichiometry. BioScience, 46(9), 674–685. DOI: 10.2307/1312897

Elser, J. J., Sterner, R. W., Gorokhova, E., Fagan, W. F., Markow, T. A., Cotner, J. B., Harrison, J. F., Hobbie, S. E., Odell, G. M., & Weider, L. W. 2000. Biological stoichiometry from genes to ecosystems. Ecology Letters, 3(6), 540–550. DOI: 10.1046/j.1461-0248.2000.00185.x

Elser, J.J. & Urabe, J. 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. Ecology, 80, 735–751. DOI: https://doi.org/c76gbg

Elton, C. S. 2001. Animal ecology. University of Chicago Press. p. 296.

Emerenciano, M., Gaxiola, G., & Cuzon, G. 2013. Biofloc Technology (BFT): A Review for Aquaculture Application and Animal Food Industry. In: Matovic, M.D. (Ed.). Biomass Now – Cultivation and Utilization. pp. 301–328. InTechOpen. DOI: 10.5772/53902

FAO. 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in action. Rome. p. 244.

Figueredo, C. C., & Giani, A. 2005. Ecological interactions between Nile tilapia (*Oreochromis niloticus*, L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil). Freshwater Biology, 50(8), 1391–1403. DOI: 10.1111/j.1365-2427.2005.01407.x

Gallardo, B., Clavero, M., Sánchez, M. I., & Vilà, M. 2016. Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology, 22, 151–163. DOI: 10.1111/gcb.13004

Gerbersdorf, S. U., Hollert, H., Brinkmann, M., Wieprecht, S., Schüttrumpf, H., & Manz, W. 2011. Anthropogenic pollutants affect ecosystem services of freshwater sediments: the need for a "triad plus x" approach. Journal of Soils and Sediments, 11(6), 1099–1114. DOI: 10.1007/s11368-011-0373-0

Gesteira, C. T. V., & Paiva, M. P. 2003. Impactos ambientais dos cultivos de camarões marinhos no nordeste do brasil. Arquivos de ciência do mar, 36, 23–28. DOI: 10.32360/acmar.v36i1-2.6487.

Glibert, P. M. 2012. Ecological stoichiometry and its implications for aquatic ecosystem sustainability. Current Opinion in Environmental Sustainability, 4(3), 272–277. DOI: 10.1016/j.cosust.2012.05.009

Glibert, P. M., & Burkholder, J. A. M. 2011. Harmful algal blooms and eutrophication: "strategies" for nutrient uptake and growth outside the Redfield comfort zone. Chinese Journal of Oceanology and Limnology, 29, 724–738. DOI: 10.1007/s00343-011-0502-z

Godwin, C. M., & Cotner, J. B. 2015. Stoichiometric flexibility in diverse aquatic heterotrophic bacteria is coupled to differences in cellular phosphorus quotas. Frontiers in Microbiology, 6(FEB), 159. DOI: 10.3389/fmicb.2015.00159

Ibrahim, A. M., David, S., Bruno, G., Mark, C.,

& Mohammed, A. M. 2018. Decline in oyster populations in traditional fishing grounds; is habitat damage by static fishing gear a contributory factor in ecosystem degradation?. Journal of Sea Research, 140, 40–51. DOI: 10.1016/j.seares.2018.07.006

Granger, J., & Ward, B. B. 2003. Accumulation of nitrogen oxides in copper-limited cultures of denitrifying bacteria. Limnology and Oceanography, 48(1), 313–318. DOI: 10.4319/lo.2003.48.1.0313

Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., & Warner, R. R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. science, 293(5530), 629–637. DOI: 10.1126/science.1059199

Jeyasingh, P. D., Goos, J. M., Thompson, S. K., Godwin, C. M., & Cotner, J. B. 2017. Ecological stoichiometry beyond Redfield: An ionomic perspective on elemental homeostasis. Frontiers in Microbiology, 8. DOI: 10.3389/fmicb.2017.00722

Karimi, R., & Folt, C. L. 2006. Beyond macronutrients: Element variability and multielement stoichiometry in freshwater invertebrates. Ecology Letters, 9(12), 1273–1283. DOI: 10.1111/j.1461-0248.2006. 00979.x

Kooijman, M., Van Amerongen, H., Traub, P., Van Grondelle, R., & Bloemendal, M. 1995. The assembly state of the intermediate filament proteins desmin and glial fibrillary acidic protein at low ionic strength. FEBS Letters, 358(2), 185–188. DOI: 10.1016/0014-5793(94)01419-2

Lane, T. W., & Morel, F. M. M. 2000. A biological function for cadmium in marine diatoms. Proceedings of the National Academy of Sciences of the United States of America, 97(9), 4627–4631. DOI: 10.1073/pnas.090091397

Liengaard, L., Nielsen, L. P., Revsbech, N. P., Priemé, A., Elberling, B., Enrich-Prast, A., & Kühl, M. 2013. Extreme emission of N2O from tropical wetland soil (Pantanal, South America). Frontiers in microbiology, 3, 433. DOI: 10.3389/fmicb.2012.00433

Lindeman, R. L. 1942. The Trophic-Dynamic Aspect of Ecology. Ecology, 23(4), 399–417. DOI: 10.2307/1930126

Maranger, R., Jones, S. E., & Cotner, J. B. 2018. Stoichiometry of carbon, nitrogen, and phosphorus through the freshwater pipe. Limnology and Oceanography Letters, 3(3), 89–101. DOI: 10.1002/lol2.10080

Marengo, J. A. 2010. Vulnerabilidade, impactos e adaptação à mudança do clima no semi-árido do Brasil. Parcerias estratégicas, 13(27), 149–176.

Marengo JA., Espinoza JC., Alves LM., Ronchail J., Lavado-Casimiro W, Ramos AM., Molina-Carpio J., Correa K., Baez J., Salinas R. 2020 Regional Climates - Central South America. In: Blunden, J. & T. Boyer (Eds.). State of the Climate in 2019. Bulletin of the American Meteorological Society, 101(8), S321–S420, DOI: 10.1175/2020BAMSStateoftheClimate_Chapter7.1

Marotta, H., Pinho, L., Gudasz, C., Bastviken, D., Tranvik, L. J., & Enrich-Prast, A. 2014. Greenhouse gas production in low-latitude lake sediments responds strongly to warming. Nature Climate Change, 4(6), 467–470. DOI: 10.1038/NCLIMATE2222

Martin, J. H., & Fitzwater, S. E. 1988. Iron deficiency limits phytoplankton growth in the north-east pacific subarctic. Nature, 331(6154), 341–343. DOI: 10.1038/331341a0

Martin, J. H., Broenkow, W. W., Fitzwater, S. E., & Gordon, R. M. 1990a. Yes, it does: A reply to the comment by Banse. Limnology and Oceanography, 35(3), 775–777. DOI: 10.4319/lo.1990.35.3.0775

Martin, J. H., Fitzwater, S. E., & Gordon, R. M. 1990b. Iron deficiency limits phytoplankton growth in Antarctic waters. Global Biogeochemical Cycles, 4(1), 5–12. DOI: 10.1029/GB004i001p00005

Martin, J. H., Gordon, M., & Fitzwater, S. E. 1991. The case for iron. Limnology and Oceanography, 36(8), 1793–1802. DOI: 10.4319/lo.1991.36.8.1793

McCrackin, M. L., Harrison, J. A., & Compton, J. E. 2013. A comparison of NEWS and SPARROW models to understand sources of nitrogen delivered to US coastal areas. Biogeochemistry, 114(1–3), 281–297

Medek, D. E., Schwartz, J., & Myers, S. S. 2017. Estimated effects of future atmospheric CO 2 concentrations on protein intake and the risk of protein deficiency by country and region.

Environmental Health Perspectives, 125(8), 087002. DOI: 10.1289/EHP41

Mills, M. M., Ridame, C., Davey, M., La Roche, J., & Geider, R. J. 2004. Iron and phosphorus co-limit nitrogen fixation in the eastern tropical North Atlantic. Nature, 429(6989), 292–294. DOI: 10.1038/nature02550

Möllmann, C., & Diekmann, R. 2012. Marine ecosystem regime shifts induced by climate and overfishing: a review for the Northern Hemisphere. Advances in ecological research, 47, 303–347. DOI: 10.1016/B978-0-12-398315-2.00004-1

Moy, F. E., & Christie, H. 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. Marine Biology Research, 8(4), 309–321. DOI:10.1080/17451000.2011.637561

Myers, S. S., Zanobetti, A., Kloog, I., Huybers, P., Leakey, A. D., Bloom, A. J., E. Carlisle, L. H. Dietterich, G. Fitzgerald, T. Hasegawa, N. M. Holbrook, R. L. Nelson, M. J. Ottman, V. Raboy, H. Sakai, K. A. Sartor, J. Schwartz, S. Seneweera, M. Tausz, & Y. Usu. 2014. Increasing CO 2 threatens human nutrition. Nature, 510(7503), 139–142. DOI: 10.1038/nature1317

Neumann-Leitão, S., Melo, P. A., Schwamborn, R., Diaz, X. F., Figueiredo, L. G., Silva, A. P., & Thompson, F. 2018. Zooplankton from a reef system under the influence of the Amazon River plume. Frontiers in microbiology, 9. DOI: 10.3389/fmicb.2018.00355

Nobre, R. L., Caliman, A., Guariento, R. D., Bozelli, R. L., & Carneiro, L. S. 2019. Effects of the introduction of an omnivorous fish on the biodiversity and functioning of an upland Amazonian lake. Acta Amazonica, 49, 221–231. DOI:10.1590/1809-4392201804131

Officer, C. B., Smayda, T. J., & Mann, R. 1982. Benthic filter feeding: a natural eutrophication control. Marine Ecology – Progress Series, 9, 203–210.

Páez-Osuna, F. 2001. The environmental impact of shrimp aquaculture: A global perspective. Environmental Pollution, 112(2), 229–231. DOI: 10.1016/S02697491(00)00111-1

Peixoto, R. B., Marotta, H., & Enrich-Prast, A. 2013. Experimental evidence of nitrogen control on pCO2 in phosphorus-enriched humic and clear coastal lagoon waters. Frontiers in microbiology, 4, 11. DOI: 10.3389/fmicb.2013.00011

Phillips, K. N., Godwin, C. M., & Cotner, J. B. 2017. The Effects of Nutrient Imbalances and Temperature on the Biomass Stoichiometry of Freshwater Bacteria. Frontiers of Microbiology, 8, 1692. DOI: 10.3389/fmicb.2017.01692

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., & Tsomondo T. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agriculture, Ecosystems and Environment, 84, 1–20.

Pimentel, O. A. L. F., Amado, A. M., & They, N. H. 2020. Higher nitrogen and phosphorus immobilization in bioflocs is associated with higher temperature and increased suspended solids in shrimp farming with biofloc technology. Aquaculture Research, 51(9), 3888–3899. DOI: 10.1111/are.14737

Price, N. M., & Morel, F. M. M. 1991. Colimitation of phytoplankton growth by nickel and nitrogen. Limnology and Oceanography, 36(6), 1071–1077. DOI: 10.4319/lo.1991.36.6.1071

Quadra, G. R., Teixeira, J. R. P. V. A., Barros, N., Roland, F., & Amado, A. M. 2019. Water pollution: one of the main Limnology challenges in the Anthropocene. Acta Limnologica Brasiliensia, 31. DOI: 10.1590/S2179-975X5118

Quigg, A., Finkel, Z. V., Irwin, A. J., Rosenthal, Y., Ho, T. Y., Reinfelder, J. R., Schofield, O., Morel, F. M. M., & Falkowski, P. G. 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. Nature, 425(6955), 291–294. DOI: 10.1038/nature01953

Rajkumar, M., Pandey, P. K., Aravind, R., Vennila, A., Bharti, V., & Purushothaman, C. S. 2016. Effect of different biofloc system on water quality, biofloc composition and growth performance in *Litopenaeus vannamei* (Boone, 1931). Aquaculture Research, 47(11), 3432–3444. DOI: 10.1111/are.12792

Rangel, L. M., Silva, L. H. S., Faassen, E. J., Lürling, M., & Ger, K. A. 2020. Copepod prey selection and grazing efficiency mediated by chemical and morphological defensive traits of cyanobacteria. Toxins, 12(7), 465. DOI: 10.3390/toxins12070465

Redfield, A. C. 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. James Johnstone memorial volume, University Press of Liverpool, 176–192.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. American Scientist, 205–221

Riedel, T., Zak, D., Biester, H., & Dittmar, T. 2013. Iron traps terrestrially derived dissolved organic matter at redox interfaces. Proceedings of the National Academy of Sciences, 110(25), 10101–10105. DOI: 10.1073/pnas.1221487110

Roland, F., Huszar, V. L. M., Farjalla, V. F., Enrich-Prast, A., Amado, A. M., & Ometto, J. P. H. B. 2012. Climate change in Brazil: perspective on the biogeochemistry of inland waters. Brazilian Journal of Biology, 72(3), 709–722. DOI: 10.1590/S1519-69842012000400009

Romano, N., Dauda, A. B., Ikhsan, N., Karim, M., & Kamarudin, M. S. 2018. Fermenting rice bran as a carbon source for biofloc technology improved the water quality, growth, feeding efficiencies, and biochemical composition of African catfish *Clarias gariepinus* juveniles. Aquaculture Research, 49(12), 3691–3701. DOI: 10.1111/are.13837

Samocha, T.M. 2019. Sustainable Biofloc Systems for Marine Shrimp. The Texas A&M AgriLife Research Experience. Baton Rouge: The World Aquaculture Society. p. 463.

Sardans, J., Rivas-Ubach, A., & Peñuelas, J. 2012. The C: N: P stoichiometry of organisms and ecosystems in a changing world: A review and perspectives. Perspectives in Plant Ecology, Evolution and Systematics, 14(1), 33–47. DOI: 10.1016/j.ppees.2011.08.002

Schuler, M. S., & Relyea, R. A. 2018. A review of the combined threats of road salts and heavy metals to freshwater systems. BioScience, 68(5), 327–335. DOI: 10.1093/biosci/biy018

Scofield, V., Jacques, S., Guimarães, J. R., & Farjalla, V. F. 2015. Potential changes in bacterial metabolism associated with increased water temperature and nutrient inputs in tropical humic lagoons. Frontiers in Microbiology, 6, 310. DOI: 10.3389/fmicb.2015.003

Sitters, J., Atkinson, C. L., Guelzow, N., Kelly, P., & Sullivan, L. L. 2015. Spatial stoichiometry: Cross-ecosystem material flows and their impact on recipient ecosystems and organisms. Oikos, 124(7), 920–930. DOI: 10.1111/oik.02392

Smith, S. H. 1968. Species Succession and Fishery Exploitation in the Great Lakes. Journal of the Fisheries Research Board of Canada, 25(4), 667–693. DOI: 10.1139/f68-063

Smith, V. H., & Schindler, D. W. 2009. Eutrophication science: where do we go from here?. Trends in ecology & evolution, 24(4), 201–207. DOI: 10.1016/j.tree.2008.11.009

Somes, C. J., Schmittner, A., & Altabet, M. A. 2010. Nitrogen isotope simulations show the importance of atmospheric iron deposition for nitrogen fixation across the Pacific Ocean. Geophysical Research Letters, 37, L23605. DOI: 10.1029/2010GL044537

Starling, F., Lazzaro, X., Cavalcanti, C., & Moreira, R. 2002. Contribution of omnivorous tilapia to eutrophication of a shallow tropical reservoir: evidence from a fish kill. Freshwater Biology, 47(12), 2443–2452. DOI: 10.1046/j.1365-2427.2002.01013.x

Sterner, R. W., Clasen, J., Lampert, W., & Weisse, T. 1998. Carbon: phosphorus stoichiometry and food chain production. Ecology Letters, 1(3), 146–150. DOI: 10.1046/j.1461-0248.1998.00030.x

Sterner, R. W., Elser, J. J. 2002. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. United States of America: Princeton University Press, p. 464.

Sunda, W. 2012. Feedback interactions between trace metal nutrients and phytoplankton in the ocean. Frontiers in microbiology, 3, 204. DOI: 0.3389/fmicb.2012.00204.

They, N. H., Amado, A. M., & Cotner, J. B. 2017. Redfield Ratios in Inland Waters: Higher Biological Control of C:N:P Ratios in Tropical Semi-arid High Water Residence Time Lakes. Frontiers in Microbiology, 8, 1505. DOI: 10.3389/fmicb.2017.01505

Tortell, P. D., Maldonado, M. T. & Price, N. M. 1996. The role of heterotrophic bacteria in iron-limited ocean ecosystems. Nature, 383(6598), 330. DOI: 10.1038/383330a0

Vicente, I. S., & Fonseca-Alves, C. E. 2013. Impact of introduced Nile tilapia (*Oreochromis niloticus*) on non-native aquatic ecosystems. Pakistan Journal of Biological Sciences: PJBS, 16(3), 121–126. DOI: 10.3923/pjbs.2013.121.126

Vinçon-Leite, B. and Casenave, C., 2019. Modelling eutrophication in lake ecosystems: a review. Science of the Total Environment, 651, 2985–3001.

Walsh, J. R., Carpenter, S. R. & Vander Zanden, M. J. 2016. Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences, 113(15), 4081–4085

Welti, N., Striebel, M., Ulseth, A. J., Cross, W. F., Devilbiss, S., Gliber, T. P. M., Guo, L., Hirst, A. G., Hood, J., Kominoski, J. S., MacneilL, K. L., Mehring, A. S., Welter, J. R. and Hillebrand, H. 2017. Bridging Food Webs, Ecosystem Metabolism, and Biogeochemistry Using Ecological Stoichiometry Theory. Frontiers in Microbiology, 8. DOI: 10.3389/fmicb.2017.01298

Xu, J., Ho, A. Y., Yin, K., Yuan, X., Anderson, D. M., Lee, J. H. & Harrison, P. J. 2008. Temporal and spatial variations in nutrient stoichiometry and regulation of phytoplankton biomass in Hong Kong waters: influence of the Pearl River outflow and sewage inputs. Marine pollution bulletin, 57(6-12), 335–348. DOI: 10.1016/j.marpolbul.2008.01.020

Yang, J., Holbach, A., Wilhelms, A., Krieg, J., Qin, Y., Zheng, B., Zou, H., Qin, B., Zhu, G., Wu, T. and Norra, S. 2020. Identifying spatio-temporal dynamics of trace metals in shallow eutrophic lakes on the basis of a case study in Lake Taihu, China. Environmental Pollution, 264, 114802. DOI: 10.1016/j.envpol.2020.114802

Zaneveld, J. R., Burkepile, D. E., Shantz, A. A., Pritchard, C. E., McMinds, R., Payet, J. P., Welsh, R., Correa, A. M. S., Lemoine, N. P., Rosales, S., Fuchs, C., Maynard, J. A., & Thurber, R. V. 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. Nature Communications, 7(1), 1–12. DOI: 10.1038/ncomms11833

Submitted: 20 July 2021
Accepted: 12 March 2022
Invited Associate Editors: Rayanne Setubal, Reinaldo Bozelli and Vinícius Farjalla