



The Rings of Power: managing nutrient cycles in aquatic food webs above and beyond primary producers

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Abstract. Global nutrient cycles (biogeochemical flows of nitrogen and phosphorus; N, P) are at a tipping point. In aquatic systems, natural food webs facilitate nutrient digestion and decomposition, but nutrient assimilation is poor. The current approach to understanding and managing nutrient cycles in aquatic systems needs to integrate animal nutritionist thinking. It is not the supply or stoichiometry of elements (carbon (C), N, P) in the food web but the supply and stoichiometry of specific biomolecular packages in which they come (aka Rings of Power) that decides the state of nutrient cycles (slow/fast, low/high) in all trophic levels above primary producers. Animal nutritionists often maximize N and P retention efficiency in animal production systems by expanding the scope of homeostatic control of nutrient deposition in animals. By spiking specific biomolecular packages in the diet (e.g., Rings of Power, such as specific amino acids, lipid classes, carbohydrate subfractions like starch), it is possible to alleviate energy–nutrient transfer barriers from food to biomass. Under the influence of “Rings of Power”, free N and P excretion is minimized and protein (N-bound), phospholipid, and apatite-rich (P-bound) biomass is maximized. Combining such expertise with food web (plankton) ecology, we can develop nature-based, regenerative aquaculture solutions in hypertrophic inland standing waterbodies (which accumulate nutrients) to slow down N and P cycles by curbing the metabolic N and P throughput of consumer communities (omnivorous fish, zooplankton) and suppress eutrophication.

1 Introduction

Global nutrient cycles are at a tipping point. We are already overshooting Earth’s safe operating space (planetary health boundaries) for carbon (C; climate change), nitrogen, and phosphorus flows (N and P; biogeochemical cycling) (Steffen et al., 2015; Richardson et al., 2023). To slow down or restrict nutrient cycles, the current approach to understanding and managing eutrophication processes in diverse ecosystems (Elser et al., 2007) needs an urgent integration of animal nutritionist thinking. Elements and elemental ratios are used across trophic levels to understand and manipulate nutrient cycles in terrestrial and aquatic food webs. Ecologists concern themselves with elements (e.g., C, N, P) and elemental ratios (e.g., the Redfield ratio, ecological stoichiometry theory) across trophic levels and predator–prey/consumer–

producer interactions to understand nutrient cycles in our global food web (Sterner and Elser, 2003).

To some extent, it is valid up to the primary producers’ trophic level, but not beyond. Our biosphere is not composed solely of primary producers; it also includes consumers. To restrain global nutrient cycles (C, N, P) from tipping points, the general focus on and reductionist approach to the elements C, N, and P have limitations. The supply–demand relationships of elemental C, N, and P are straightforward for plants, fungi, and protists that require these elements for biomass accretion. The more fertilization of these elements in free forms, the greater their response to growth. However, animals do not grow on free forms of elemental C, N, and P, and the supply–demand relationships of elemental C, N, and P are not straightforward for animal systems. For example, in fish, the mean effect size of diet elemental propor-

tion (N:P) on excretion N:P was not significantly different from 0 (meaning no effect) in either diet manipulation studies or field surveys (Moody et al., 2015). Seeing this, it was hypothesized that testing stoichiometric theory might require that future work examining dietary effects on excretion rates and ratios considers not only dietary N:P ratios but also the forms in which these nutrients are present (Moody et al., 2015). Therefore, a re-focus is necessary on the various packaging(s) or biomolecular forms of these elements, in which C, N, and P are available to consumers from the resource pool (food web). One can supply the same amount of nitrogen to fish mainly via non-essential amino acids, while the other can supply mainly via essential amino acids, rendering the growth response higher in the latter (Peres and Oliva-Teles, 2006). Similarly, one can supply more carbon to fish through a high-protein diet or through non-protein fractions (lipids, carbohydrates) on an isoenergetic intake basis; the growth response would be higher in the latter (Heinitz et al., 2018). One can supply the same amount of phosphorus to fish, but with low and high background levels of essential-amino-acid-bound N or low and high levels of non-protein-bound C fractions, the phosphorus storage is always low under the “low” supplies of key biomolecular packages (Roy et al., 2024a; Ruohonen et al., 1999). These interactions in animal systems are overlooked, and a generalist focus on elements only (quantity $\times$ stoichiometry) in the “animal-type” food web makes it redundant. Not all C, N, or P is equal in animal systems or their food webs; mathematically, we keep treating those data as if they were equal, but their biomolecular packaging matters a lot. For example, essential-amino-acid-bound N or non-protein-bound C (that is digestible and not a fiber) should have more weightage or be disentangled from the total N or total C measured in the food or body. Such a weighting or disentangling approach is not often seen in food web ecology (C, N, P flow) calculations. It is well realized that it is time to look beyond C:N:P (Van de Waal et al., 2018) and that animal nutritionists are necessary in ecology.

2 Concept

Ecology and nutrition are two discrete fields that rarely interact. So far, ecologists have taken the lead in bridging the nutrition gap. Limited interdisciplinary relationships have resulted in seminal biochemical views of the food web (Müller-Navarra, 2008; Ruess and Müller-Navarra, 2019), bridging nutritional geometry with ecological stoichiometry theory (Sperfeld et al., 2017; Meunier et al., 2017) and contemplating nutrient form/quality over quantity (Danger et al., 2022; Müller-Navarra and Ruess, 2019). So far, while bridging nutrition and ecology (by ecologists), too much emphasis has been on viewing one biomolecule at a time, rather than on their proportions relative to other biomolecules or metabolizable energy. For example, there is an overemphasis on

fatty acids in the aquatic food web, while amino acids are discussed negligibly. Also, biomolecule groups in the food web (e.g., lipids) are often discussed alone, not considering complex bioenergetics principles such as protein- and lipid-sparing effects, protein quality for tissue synthesis, or what mitochondria prefer as easy metabolic fuel (e.g., starch, saturated fatty acids) and what is too complex to burn as metabolic fuel (e.g., long-chain polyunsaturated fatty acids).

Plants, or primary producers, need elements (N, C, and P) (Parent et al., 2013), while animals, or consumers, require biomolecules such as proteins, carbohydrates/lipids, and phospholipids/non-apatite P as sources of those elements, respectively. The trophic levels above primary producers have lost half of their amino acid synthesis or nitrogen re-packing capabilities (e.g., essential amino acids) (Jennings, 1972; Wu, 2017). Unlike primary producers, consumers cannot reflect the elemental composition of their food base in their bodies, due to homeostatic control (Van de Waal and Boersma, 2012). Consumers cannot use photonic energy to synthesize and store matter from absorbed elements (e.g., the photosynthesis principle); instead, they need a combination of metabolic energy and catabolism first to be able to synthesize and store new matter (e.g., the nutritional bioenergetics principle) (Bureau et al., 2003). Also, the fates of C, N, and P in consumers in terrestrial and aquatic food webs, whether released from or retained in the body, are dictated by a handful of key biomolecules containing such elements. The minimum requirement of those key biomolecules (e.g., essential amino acids, long-chain polyunsaturated fatty acids, cholesterol, phospholipids) changes relative to the availability of energy from non-key biomolecules. Surplus energy provided by dietary non-key biomolecules (e.g., non-essential amino acids, starch, glycogen, and saturated or monounsaturated fats) lowers the requirement of dietary key biomolecules, and more of dietary C, N, and P could remain trapped in the body of consumers. While inadequate energy from non-key biomolecules increases the need for and catabolism (destruction) of key biomolecules to supply energy, more C, N, and P could be released from consumers' bodies due to a loss of nutritional bioenergetic efficiency. The fundamentals of nutrient ingestion–excretion cycles in the animal body are better understood by nutritionists, who strive to provide a balanced diet or nutrition optimized for bioenergetics. Aquatic animal nutritionists concern themselves with a wider set of biomolecules (not elements) and biomolecule ratios (e.g., amino acids, fatty acids, starch/glycogen, energy profiles) across digestive and metabolic axes to understand C, N, and P cycles (retention, excretion) (Roy et al., 2022, 2023, 2024a; Kaushik and Seiliez, 2010; Bureau et al., 2003; Kaushik and Schrama, 2022; Heinitz et al., 2018; Ruohonen et al., 1999; Kaushik et al., 1995; Kim and Kaushik, 1992; Watanabe et al., 1987). In nature, we now understand that the natural food web helps digest nutrients (Roy et al., 2024c). However, metabolic assimilation is rather poorly constrained by stoichiometric errors and consumer homeostasis in an im-

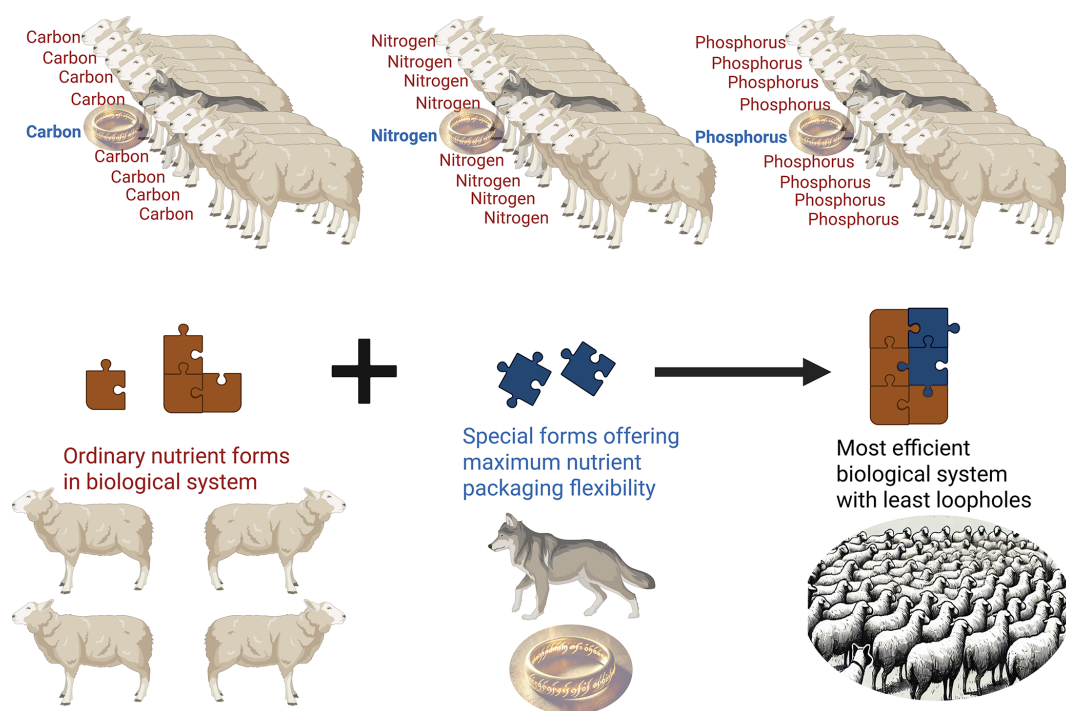


Figure 1. Rings of Power philosophy, metaphorically portrayed as a sheepdog (special biomolecules containing C, N, P) among sheep (average biomolecules containing C, N, P), holding the power to orchestrate maximum packaging of elements.

balanced diet (Roy et al., 2022, 2024a, b; Mraz et al., 2025). It is, by nature, a deliberate error to keep primary productivity running on free nutrients leaked/spilled by consumers. Nutritionists have been able to address those natural flaws while understanding physiology and fulfilling the commercial interests of animal production science. Thanks to that, we are now farming animals at much lower nutritional requirements and maximized digestible and metabolic nutrient use efficiencies (e.g., poultry, fish, pig) than what they used to be in the past (Kaushik and Schrama, 2022; Kim et al., 2019; You et al., 2024; Turchini et al., 2019; Glencross et al., 2023). It is not the elemental C, N, or P that ecologists traditionally see, but specific biomolecules (aka rings) that ecologists can use to understand C, N, and P flows (or even manage C, N, and P cycles) in ecosystems. It is not the C, N, or P in the food web but the package in which they come (aka Rings of Power) to animal systems that decides the fate of nutrient cycles in higher trophic levels (Roy et al., 2022; Roy et al., 2024a). Total N in seston or algae may be meaningless for zooplankton or fish food web calculations; it is the essential-amino-acid-bound N that matters. Likewise, total C in seston or algae could be meaningless for zooplankton or fish; it is the non-protein-fraction-bound C that is easily assimilated (and not part of fibers/non-starch polysaccharides, polyunsaturated fatty acids, or cholesterol) that matters. Total P in seston or algae could also be meaningless, as the non-apatite-, non-phytate-, and phospholipid-bound P is what matters for zooplankton or fish. For example,

rings of power for fish and crustaceans (including zooplankton) in aquatic systems could be ratios of starch/glycogen–fatty acid–cholesterol-bound C, lysine–methionine–arginine-bound N, and phospholipid-bound P or orthophosphates in water absorbed by integuments. Even for terrestrial mammals or humans, the rings of power could be ratios of starch–triglyceride-bound C, leucine-bound N, and organic P in food. Here, it is important to note that nutritionists emphasize not the quantity alone, but the relative proportion of these rings of power that rule the Liebig’s law of the minimum in animal systems (Konnert et al., 2022; Rombenso et al., 2022; Roy et al., 2022, 2023, 2024a). These rings of power, when sufficient, could abolish nutrient–energy transfer barriers between food and the body and suppress nutrient leakage or spillover from the ecosystem’s consumers. When these rings of power are insufficient in the food webs, they do the opposite – ecosystems turn into a soup of free nutrients, overshooting primary productivity (but no effect on secondary and tertiary productivity), and the chain of trophic transfer efficiency is broken (“kaput”). The mechanism of rings of power is conceptually described in Fig. 1.

Recent efforts by fish nutritionists to balance seasonal imbalances or natural stoichiometric errors in aquatic ecosystems are an excellent example of the potential of the rings of power to manage nutrient cycles (Roy et al., 2022; Kabir et al., 2020). For example, nutrients from human settlements, land, runoff, and farming end up in standing water bodies like a shower sink. In contrast, rings of power in aquatic

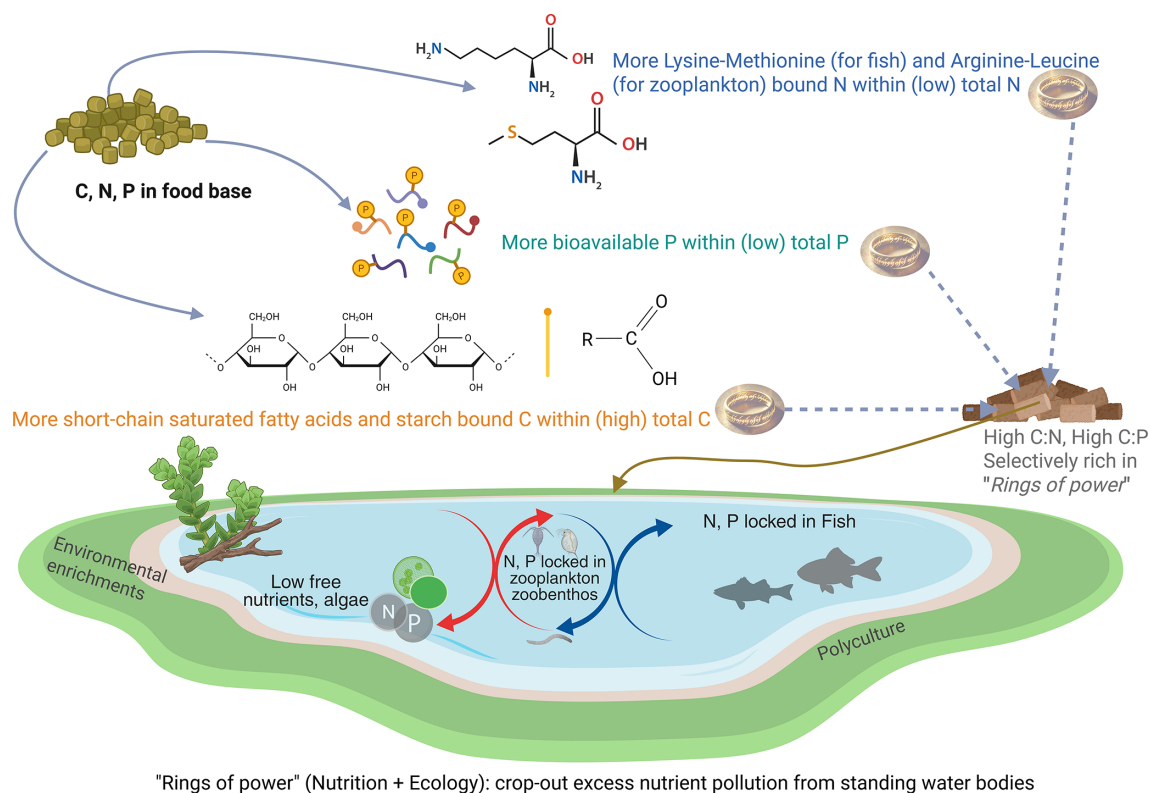


Figure 2. Rings of power in action to slow down nutrient flows from tipping points in standing freshwater bodies. By providing “rings-of-power feeds” (e.g., spring/autumn-time digestible non-protein energy or C-rich feed, summer-time essential-amino-acid- and non-protein-energy-balanced feed), one can periodically stock and harvest fish stocks to remove anthropogenic nutrients loaded into these waterbodies. Detailed specifications of such rings-of-power-spiked aquatic feeds, but low in overall N and P content, can be found elsewhere (Roy et al., 2025).

food webs, such as specific amino acids (lysine) and fatty acids (saturated fatty acids), go missing over the vegetative season (Roy et al., 2024b; Mraz et al., 2025), or remain missing throughout the season, e.g. specific carbohydrate (starch/ glycogen) (Roy et al., 2023, 2024a). Their absence impedes the assimilation of nutrients (C, N, P) into the bodies of aquatic consumers (Bureau et al., 2003; Kaushik et al., 1995; Kim and Kaushik, 1992; Roy et al., 2022, 2023, 2024a; Ruohonen et al., 1999; Watanabe et al., 1987). As a result, free nutrient pollution in water and harmful algal blooms may take precedence (Sharitt et al., 2021; Brabrand et al., 1990; Vileger et al., 2012). By designing “stoichiometric feeds” combining principles of ecological stoichiometry theory, ecological plankton modeling (PEG model), and fish nutritional bioenergetics, scientists are turning nutrient pollution into a solution (biomass) (Roy et al., 2025; Kabir et al., 2020). It is possible to control freely available nutrients (N, P) and suppress eutrophication processes (Roy et al., 2022, 2023, 2024a, 2025; Kabir et al., 2020).

It is now known that fish can directly absorb orthophosphateP from water into the body, in addition to P from the dietary pathway (Roy et al., 2024a; Drábiková, 2023; Sarker et al., 2011; Sugiura, 2024). It is also known that fish can

retain more N and P per unit of body mass under a balanced diet, under the influences of the rings of power, e.g., lysine–methionine-bound N and digestible “non-protein” energy or C (Heinitz et al., 2018; Kaushik et al., 1995; Kaushik and Seiliez, 2010; Kim and Kaushik, 1992; Roy et al., 2023; Ruohonen et al., 1999; Watanabe et al., 1987). Besides, the planktonic food web, dominated by zooplankton, can keep C, N, and P from being freely available in the water under low fish grazing pressure (Sommer et al., 2012; Fott et al., 1980; Scheffer and van Nes, 2007; Scheffer, 1998). There is an indirect pathway to cause high metabolic satiety of fish stocks and gut fullness via balanced feeds (Holt et al., 1995; Yamamoto et al., 2003; Harter et al., 2015) that relieves some grazing pressure (active gill filtering, not passive) on zooplankton or reduces homing range in search for benthic macrozoobenthos (Mehner et al., 2019; Jurajda et al., 2016; Říha et al., 2026). Besides the effect of nutrition, providing substrates or refugia in water can also enhance consumer biomass, which can further lock in nutrients (Kajgrova et al., 2021; Šetlíková et al., 2024; van Dam et al., 2002).

Given the global problem of eutrophication and the reliance on chemical- or plant/algae/microbial-based remedial measures to abate nutrient pollution (Kakade et al., 2021),

the poor metabolic assimilation of C, N, and P in aquatic consumers may also need to be addressed. Combining the above knowledge or pathways, what if we could maximize the overall efficiency of aquatic consumers (zooplankton and fish) to store more C, N, and P in their bodies? By applying stoichiometrically corrective seasonal feeds spiked with the “rings of power”, we can crop out nutrients via fish and plankton harvests. We have thought of such regenerative agriculture before (Newton et al., 2020), but are the “rings of power” a means to realize it? It can be done in focus locations, such as the inland freshwater standing water bodies that naturally collect anthropogenic and agricultural nutrients from the landscape (like the sink of a shower) – converting them from points of pollution into solutions. A conceptual diagram of the approach is shown in Fig. 2. It is time to establish the field of nutritional ecology within educational and research organizations, where animal nutritionists should be trained and tasked with working on applications in ecology.

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