

University of South Bohemia in Ceske Budejovice

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Habilitation Thesis

Nutritional ecology of European carp ponds for
ecosystem, food system, and nutrient-sensitive
aquaculture

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Declaration

I hereby declare that I prepared the submitted habilitation thesis, entitled “*Nutritional ecology of European carp ponds for ecosystem, food system, and nutrient-sensitive aquaculture*”, independently, using the publications listed in the references. In compiling the habilitation thesis, I used selected original results obtained during my scientific work jointly with the co-authors named in the respective publications.

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1. DEFINITIONS

Term	Definition and operational context in the thesis
Ecosystem-friendly aquaculture	Aquaculture that maintains or supports water quality, biodiversity, food-web functioning, and other ecosystem processes while minimizing ecological disturbance. Especially in terms of respecting the EU water framework directive on N, P concentration thresholds for good ecological quality, maintaining keystone species such as large-bodied daphniids in pond food webs, and suppressing algal bloom.
Fed aquaculture	Aquaculture in which cultured organisms receive externally supplied feed to support production, either as the main food source or as a supplement to naturally available food. Especially supplementary feedstuffs and supplementary feeding strategy of ponds, which constitutes a significant allochthonous organic matter input into ecosystem.
Food-system-friendly aquaculture	Aquaculture that contributes nutritious food while using resources efficiently, supporting circularity, and complementing rather than disproportionately burdening the wider food system. Especially lowered ReCiPe Midpoint or Endpoint category impact values per unit of functional unit (edible fish/ nutrients) under life cycle assessment. For example, lower nutrient footprint, land use or greenhouse gas emissions per unit edible fish/ nutrients net yield from pond.
Nutrient-sensitive aquaculture	Aquaculture that manages nutrient inputs, transformations, retention, and losses to maximize their conversion into harvested biomass while minimizing nitrogen and phosphorus release to the environment.

	Especially focusing on improving retention efficiency of essential amino acids and fatty acids in fish biomass leading to voluminous and more nutritious edible fish respectively. Rather than focusing on improving crude productivity alone at the expense of man-made eutrophication, the focus is shifted to maximizing input use efficiency, producing more nutritiously dense products and maintaining cleaner production.
Nutritional ecology	The study of how the quantity, quality, balance, and ecological availability of nutrients influence organism nutrition, food-web interactions, and nutrient cycling within ecosystems. Especially how plankton ecology group model (PEG model), ecological stoichiometry theory (ES theory), top-down and bottom-up effect scenarios of planktonic and microbial food web translates to nutritional requirement of pond fish and efficiency of nutritional bioenergetics <i>in-vivo</i> leading to fish stocks storing away N, P (as food) or recycling N, P into water (as fertilizer).
Regenerative aquaculture	It is defined as a commercial or subsistence aquaculture performed with focus on social, economic, and ecological responsibility and stability, with minimal external input and impact to the environment. Especially it happens in an aquatic system that is otherwise prone to aquatic pollution. Examples are semi-intensive pond aquaculture, hybrid ponds in the integrated multi-trophic aquaculture (IMTA) model that are low to moderately fed.

2. PREFACE

My academic journey began in 2008 in West Bengal, India, a region where freshwater fish is deeply embedded in culture, diets, and livelihoods. I grew up beside two extensively managed carp ponds at my ancestral home and spent much of my childhood fishing for Indian major carps. This early exposure fostered a lasting interest in fish, ponds, and aquatic ecosystems, although I did not initially expect it to become my profession.

My education has remained entirely within fisheries and aquaculture: a BSc in Fish & Fisheries (2008–2011), MSc in Aquaculture (2011–2014), and PhD in Fishery (2018–2022). Across nearly two decades of academic and research experience combined, I have worked with tropical Asian ponds and wetlands, temperate European fishponds and shallow lakes, recirculating aquaculture systems, and aquaponics. I therefore consider myself primarily an aquaculture nutritionist with strong training in freshwater food-web ecology and aquaculture–environment interactions.

My MSc research on urban and rural ponds in Central India taught me a fundamental lesson: standing waterbodies act as sinks for nutrients originating from human activities, agriculture, and land runoff. From 2015 to 2018, while working under the Government of India's NICRA programme at ICAR-CIFRI, I studied climate-change effects on inland waters of the lower Gangetic plains, including water quality, carbon sequestration, and fish reproduction. This work showed me how climate change can accelerate eutrophication and alter biogeochemical processes. I also came to recognize that fed aquaculture commonly introduces more nutrients into aquatic systems than it removes through harvest.

In 2018, I moved to the Czech Republic for a PhD focused on fish feeding and water quality. I investigated nutrient flows from supplementary feeds and natural food webs through fish and into the aquatic environment, gradually moving from elemental nutrient flows to the role of specific biomolecules in animal nutrition. This work led me to develop the balanced pond feeding concept, in which supplementary nutrition is synchronized with the natural food web to improve nutrient use efficiency and reduce eutrophication. It also convinced me that aquaculture, when nutritionally and ecologically designed, can contribute to environmental improvement without necessarily sacrificing production.

Having experienced both highly productive tropical pond aquaculture and intentionally constrained European pond aquaculture later in my career gave me a valuable perspective on their contrasting strengths and limitations. As a postdoctoral researcher, I continued integrating fish nutrition with pond food-web ecology. This habilitation thesis represents the post-PhD development of that scientific trajectory, during which I established my own niche field 'nutritional ecology of aquatic production systems'. I have tried to develop a distinct interdisciplinary profile at the interface of aquaculture nutrition, food-web ecology, nutrient cycling, and food systems thereby defining my academic and research identity.

3. INTRODUCTION

3.1. *Environment, food systems and fishponds*

A recent assessment by EEA-FOEN agency ¹ showed the European limit for biogeochemical flows of nitrogen (N) and phosphorus (P) is exceeded; the major contributor of which is land-based food system (agriculture, livestock). Land use for sustaining human food chain is expanding at unsustainable rates ¹⁻³. Agriculture's role in losing biosphere integrity (biodiversity) is also estimated to be ~80% ². Freshwater use in Europe is perhaps a planetary health boundary which is not exceeded, although globally it has been exceeded ¹. Developed economies such as Europe have accountability for global greenhouse gas emissions (GHG) ⁴, considering its luxurious food system ⁵⁻⁷. Degrowth is proposed as a solution ⁵ for animal sourced protein and lipids (ASPL) in EU diet ⁸. Although, it is unrealistic to eliminate ASPL from human food ⁹. Rather, the problematic ones (*i.e.*, more impactful ASPL) are replaced by the other (*i.e.*, less impactful ASPL) ⁷. If future Europe is to live within planetary health boundaries limits ¹, key prerequisites would be redistributed cropland (*i.e.*, aquatic food production zones"), improved water–nutrient management (*i.e.*, nature-based solutions), food waste reduction (*i.e.*, circular bioeconomy"), and dietary changes (*i.e.*, aquatic foods) ⁶. In general, animal-based foods are more resource intensive than plant-based foods. Aquatic animal products potentially use fewer resources than terrestrial meat products (egg, pork, poultry, dairy, beef). Sustainably farmed fish may be as low resource intensive as some plant-based foods. Data in this regard can be found ¹⁰⁻¹². Aquatic foods are expected to nourish future nations ^{13,14}, a key component of planetary and healthy diet ⁷. It is being increasingly understood that there is potential of farming more food from water ¹⁵.

Systems thinking surrounding fishponds is gaining traction ¹⁶. As land-based food production is overburdened, the 'pondscapes' remain branded for nature-based solutions or ecosystem services ¹⁷. The thought that European pondscapes could be transformed to eco-friendly, OneHealth and regenerative food production systems is largely ignored/ disputed. In Central European Pond farming, we have developed supplementary feeding concepts ¹⁸⁻²¹ that can upcycle local circular resources in an efficient or carbon-neutral manner to produce nutritious food from the ponds. In harmony with the natural food web ^{18,22}. Also, with a special emphasis on improving farmed pond fish biomass use efficiency from farm-to-fork ²³ and ecological engineering of fishponds ²⁴. We have also demonstrated that pond ecosystem components (such as enzymes from water,

microbiota, natural food ²⁵) and free-ranging consumers itself (feeding on stoichiometrically balanced diet ²²) augment fish stocks' capabilities to first digest and then metabolically assimilate nutrients and energy and deliver it to the human food chain with minimum losses/ spillage. It does not mean more intensive monoculture of common carp in European fishponds; like it happened in the past ²⁶. Rather it is the application of practices such as polyculture ²⁷, environmental enrichments (littoral macrophyte vegetation ²⁸; artificial periphyton beds ²⁹), and ecosystem-sensed feeding strategies ^{18,21} that complement harmoniously with natural food web dynamics ^{18,24,28,30}. Also, the aquatic food production can nicely complement land-based production system, without necessarily competing for the resources or land that can be otherwise utilized for humans directly ³. Without competing for resources that are having feed-food competition, ponds can solely thrive on absorbing the waste streams of terrestrial food system ^{31,32}. It does not mean dumping agri-food wastes to pond or increasing feeding in ponds. Rather changing the perspective of feeding; strategically feeding selected set of agri-food system by-products (called LOCBs or low-opportunity-cost-biomass) to either supplement missing energy or nutrients in pond ecosystem during specific windows in vegetative season (Figure 1).

The predominantly land-locked Central Eastern European Region (CEER) has a long tradition of large, often medieval-origin fishponds, where semi-intensive carp farming remains the backbone of inland aquaculture ^{16,33,34}. These pond systems account for most EU carp production and combine food production with important ecosystem services. Their environmental footprint is relatively low compared with many terrestrial food-production systems, particularly in terms of nitrogen, phosphorus, and greenhouse-gas emissions. At the same time, fishpond aquaculture is subject to increasing environmental regulation and scrutiny. Fertilization, manuring, and supplementary feeding are restricted or closely controlled in several countries, creating a need to balance production, profitability, water quality, and ecosystem functioning. Consequently, improving supplementary feeding has become a central management challenge: feeds must support fish growth and product quality while minimizing nutrient losses and preserving the ecological functions of pond ecosystems ^{18,21,35}. For carp culture waters, EU Directive 2006/44/EC (Articles 3 and 5, Annex I) specifies upper permissible concentrations of 0.4 mg L⁻¹ for PO₄ and 1 mg L⁻¹ for NH₄.

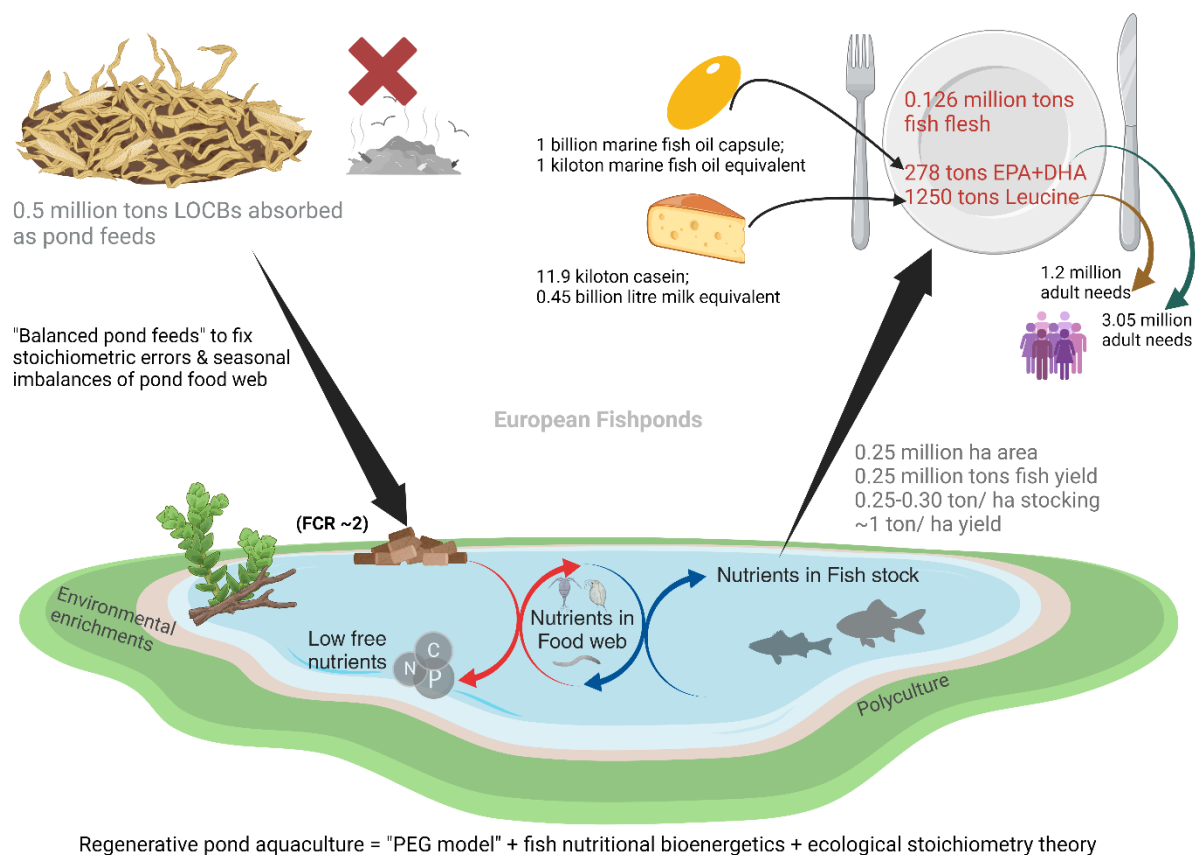


Figure 1: A mind map of the potential of ecological pond aquaculture in European inland waters to fix food system problems and respect water protection ³⁶. Created using BioRender premium.

European fishponds, an over-regulated yet important component of European aquaculture ^{16,33}, largely remain in a hypereutrophic state. It is mainly due to synergistic top-down and bottom-up effects of fish stock and nutrient legacy ³⁷, or over-stocking and poor feeding management ³⁵. Managing eutrophication and optimizing N/P cycles in these water bodies needs to be prioritized in the European union to keep living safely within Europe's safe operating space for future generations ^{1,38}. By limiting point source of nutrient emissions (N, P pollutions), reducing or stopping aquaculture activities, and lake biomanipulation projects, many European shallow-lake ecosystems have fulfilled mixed expectations ³⁷. Climate change is expected to further cause eutrophication, by increased carbon sequestration, primary productivity, nutrient cycling, nitrogen or phosphorus loadings from sediment, watershed or higher feed intake/ respiration, growth and excretion of the aquatic biota including fish in ponds ^{39,40}. Under natural or man-made increase of primary productivity ⁴¹, 'pondscapes' in Europe, despite their multifunctionality ¹⁷, may not

function or sustain without fish biomass (secondary consumers) in it and without excavation (harvesting) of such fish biomass periodically to remove the bioremediated nutrients ⁴². It brings us to extensive or semi-intensive mode of aquaculture in European ponds as a long-term solution. But such an ecosystem-restorative or regenerative form of aquaculture has to be as organic or as ecological as possible; unlike Asian fishponds where farmers overuse some inputs to 'inefficiently' maximize productivity ⁴³ and cause pollution ⁴⁴. Reduction in fish stock (aquaculture) is an option to lower nitrogen and phosphorus emissions *in-situ* ⁴⁴, but a balanced pond feeding aiming to improve natural food base nutrient bioeconomy or nutrient use efficiency by fish stocks is solution too ^{18,21} or selectively supplying carbon to pond ecosystem ^{45,46}.

3.2. State of European pond carp aquaculture

Fed carp aquaculture in ponds is one of the oldest and among the most dominant aquaculture systems of the world amounting 14.69 million tons in 2023, which is one-quarter of global fed aquaculture production. Pond carp aquaculture, primarily concentrated in Asia followed by Europe, have an estimated aquaculture feed consumption of 15.73 Mt in 2023 (using an economic feed conversion ratio). This amount is ~23% of the total global aquaculture feed demand ^{47,48}. Among pond-cultured fishes, cyprinids represent the dominant production group and account for approximately 23% of global aquafeed demand. Globally, carp production in ponds increased steadily from 1983 to around 2015 and subsequently stagnated, whereas European production declined over the same period. Fishponds have been integral to European landscapes since the Middle Ages, supporting food production, recreation, and rural livelihoods. Today, many Central European fishponds remain large, shallow waterbodies, typically covering 2–300 ha with depths of about 1–4 m, and continue to serve as important sites for inland aquaculture ^{16,33,34}. European carp production come from the fishponds of CEER: Poland (21600 ton carp; 44700 ha fishponds; ~484 kg ha⁻¹ yield), Czech Republic (20401 ton; 40595 ha; ~500 kg ha⁻¹), Hungary (12300 ton; 26000 ha; ~473 kg ha⁻¹), and Germany (10000 ton; 40000 ha; ~250 kg ha⁻¹). Semi-intensive carp ponds continue to be the backbone of inland aquaculture in CEER ¹⁹. Within Europe, Czechia, Poland, and Hungary have increasingly concentrated production, together accounting for 74% in 2023. Czechia and Poland have alternated as Europe's largest pond carp producers ^{47,49}. Despite this production importance, the economic position of European carp farming remains challenging. Farm-gate prices have generally remained low, at approximately €2.0–2.5 kg⁻¹ live weight in Czechia and Germany and around €1.9 kg⁻¹ in Hungary ⁵⁰⁻⁵². Beyond food production, carp ponds

generate direct farm income of up to approximately €1,123 ha⁻¹ and ecosystem services valued at around €1,257 ha⁻¹ ^{19,53}. However, domestic demand remains weak. Czech consumers eat only about 1 kg of carp per person annually within an overall fish consumption of approximately 4 kg per capita. Across the Central and Eastern European Region, apparent carp consumption remains similarly low at approximately 0.6–1.2 kg per capita annually ⁵⁴⁻⁵⁶. Thus, European carp aquaculture combines substantial cultural, ecological, and food-production value with stagnating production, low farm-gate prices, and limited domestic consumption ^{50,51}.

Supplementary feeding in European fishponds are built on decades of valuable knowledge and practical experience. This practice is generally well understood and clearly illustrated through various regional feeding tables and charts. Notable examples can be found in several sources ⁵⁷⁻⁶⁰. Present-day management practices are characterized by semi-intensive systems that operate with low to moderate stocking densities (0.2–0.4 tons ha⁻¹), achieving production levels of approximately 0.5 to 1 ton ha⁻¹, partially sustained by supplementary feed inputs ^{19,33}. In most of these systems, it is estimated that natural food sources support about 50–60% of carp growth, particularly protein accretion, while cereals—primarily energy-rich—serve as the supplementary feed component ^{16,33}. This dual feeding strategy, where carp consume both natural prey and cereals, typically requires at least two growing seasons under temperate climatic conditions in Western and Central Europe to reach marketable sizes exceeding 1.5 to 2 kg ^{16,19,33}. The grains that are applied as supplementary feed in European fishponds cannot replace ‘nutritionally’ the natural food in terms of essential amino and fatty acids, including bioavailable phosphorus ⁶¹. Most European standing waterbodies including fishponds are now hypereutrophic ³⁰, and aquatic consumers are finding it hard to contain the algal growth, unlike in the past ⁶². In these ecosystems, nutrient and plankton dynamics exhibit well-defined seasonal rhythms, largely following the Plankton Ecology Group (PEG) model ^{63,64}. However, biochemical cycles remain largely unexplored.

Unlike tropical ponds, the European fishponds resemble temperate shallow-lake like ecosystems that have an alternating pattern ⁶³. In one part, zooplankton dominate (e.g., clear-water phase) while in the other part algae dominate (e.g., turbid-state) ⁶⁵. Such perturbations in food base in a pond have generally known implications on nutrient ingestion and excretion by fish stocks ⁶⁶⁻⁶⁸. Aquatic consumers consume food ineffectively resulting in poor food to biomass conversion due to nutritional deficiency ⁶⁷⁻⁶⁹. Under nutritional over-sufficiency, they may grow efficiently but also excrete large amounts of nutrients in the process ^{67,68,70,71}. Ultimately, the

interplay of ingestion-excretion processes of fish stocks may determine whether a waterbody functions as a nutrient sink or a nutrient source ⁷²⁻⁷⁴. The zooplankton and zoobenthos are considered key source of essential amino acids and fatty acids for carp in ponds ⁷⁵⁻⁷⁷, whereas phytoplankton is a relatively poorer source of those essential nutrients in ponds ^{78,79} as well as higher in indigestible fractions such as fibrous carbohydrates as fillers in the food ^{80,81}. Nutritionally depleted zooplankton such as the lean (low-fat) ones could also possess a relatively high indigestible carbohydrate fraction such as chitin in their dry matter ⁸²⁻⁸⁴. Under future climate change associated warming of water temperatures and alterations of seasonality in the Northern hemisphere ⁸⁵⁻⁸⁷, pond feeding management may need to take care of the following: (a) suppressing or slowing down of consumer-driven nutrients recycling to suppress algal blooms ⁷⁴; (b) fulfill increased nutrient-energy demand of fish having higher food intake or growth or elevated bioenergetics ⁴⁰; (c) not burden the carrying capacity of ecosystem by allochthonous feed input during heatwaves, hypoxia, etc. ⁸⁸. Such improved feeding strategies require nutritional ecology of ponds to be deeply understood in tandem with food web ecology and fish nutritional bioenergetics seasonally in temperate European conditions.

3.3. Nutritional ecology of temperate European fishponds

Nutritional ecology of temperate shallow-lake ecosystems requires integration of classic ecological theories with animal nutrition principles. Globally, biogeochemical flows of nitrogen and phosphorus are at tipping points. Especially the aquatic systems are now key to pull them back within safe operating space of Earth system⁸⁹. For example, most Czech standing waterbodies are now hypereutrophic³⁰, and aquatic consumers are finding it hard to contain the algal growth, unlike in the past⁶². Traditional aquatic ecology examines food webs through an elemental perspective, plankton community structure, emphasizing nutrient cycles and ecological stoichiometry, while aquatic animal nutrition focuses on indispensable biomolecules, nutritional bioenergetics, growth and metabolism. However, no existing framework links these perspectives to describe the biochemical dynamics of the aquatic food web, particularly in shallow temperate lakes. In these ecosystems, nutrient and plankton dynamics exhibit well-defined seasonal rhythms, largely following the Plankton Ecology Group (PEG) model^{63,64}. However, biochemical cycles remain largely unexplored. How do key biomolecules of aquatic animal nutrition and bioenergetics significance fluctuate in response to seasonal and ecological drivers? How do these molecular fluxes relate to eutrophication events and algal blooms? Addressing these questions requires an

interdisciplinary approach, merging ecological theory (PEG model + ecological stoichiometry, ES theory⁹⁰) with nutritional sciences (nutrient requirements⁶⁸, metabolism^{21,91}, and bioenergetics¹⁸).

There is a growing realization that traditional ecological models based solely on elemental ratios (C:N:P)/ ecological stoichiometry theory (ES theory)^{92,93} or plankton community dynamics/ PEG model^{63,65} are insufficient for understanding ecosystem functioning, necessitating the integration of animal nutrition principles into ecology^{18,21,36,68,91,94}. Despite their interconnected nature, ecology and nutrition remain largely separate disciplines, with minimal cross-disciplinary exchange⁹⁵⁻⁹⁹. While ecologists have taken initial steps to incorporate nutritional perspectives, these efforts have been fragmented, often focusing on isolated biomolecules rather than their interactions, proportions, and bioenergetic implications within food webs. Existing studies emphasize single biomolecules, such as fatty acids, while neglecting amino acids, despite their essential role in protein synthesis and metabolism. Additionally, discussions on food web biochemistry frequently analyze lipid dynamics in isolation, disregarding complex bioenergetic principles such as protein-lipid sparing effects, the role of protein quality in tissue synthesis, and the metabolic preferences of mitochondria for different fuel sources (e.g., starch and saturated fatty acids vs. complex-to-metabolize long-chain polyunsaturated fatty acids). This narrow focus limits our understanding of trophic bioenergetics and nutrient assimilation. These gaps highlight the need for a nutritional ecology¹⁰⁰ perspective in aquatic food-web research. Primary producers (plants, algae) rely on elemental nutrients (C, N, P) for growth, whereas consumers (animals) require complex biomolecules (proteins, carbohydrates, lipids, phospholipids) both as sources of these elements and as functional macromolecules^{92,101}.

Higher trophic levels such as consumers (e.g., fish) have lost key metabolic abilities, such as indispensable amino acid biosynthesis, necessitating dietary intake rather than *de-novo* synthesis. Furthermore, consumer homeostasis prevents direct reflection of food composition in their body⁹², and unlike plants, animals require metabolic energy and catabolism to synthesize and store new biomass. These aspects of consumer-driven nutrient cycling^{73,102-104} and bioenergetics^{21,67,68,91} are best understood by animal nutritionists, whose expertise extends beyond elemental fluxes to biomolecule transformations and metabolic pathways^{18,21,46,68,91,94,101,105-108}. In natural ecosystems, food webs facilitate nutrient digestion⁹¹, yet metabolic assimilation of digested nutrients is constrained by stoichiometric mismatches and consumer homeostasis⁶⁸. This inherent inefficiency ensures continuous nutrient leakage, sustaining primary productivity through

consumer excretion. However, certain biochemical limitations dictate Liebig's law of the minimum in animal systems^{18,21,68}, where key limiting biomolecules—when sufficient—enhance nutrient-energy transfer efficiency, reducing losses between food and body tissues while suppressing nutrient leakage from consumers. When these biomolecules are insufficient, unassimilated nutrients accumulate, triggering excessive primary productivity without supporting higher trophic levels. This results in a breakdown of trophic transfer efficiency^{109,110} and ecosystem instability^{30,73}.

Current understanding of pond fish nutrition^{18,30,57,75,78,111,112} shows a pronounced seasonal imbalance in Central European carp ponds. At the beginning of the vegetative season, carp rely mainly on zooplankton and zoobenthos, which provide highly digestible protein and amino acids, bioavailable phosphorus, and high-quality fatty acids, but relatively little non-protein energy. Their high P:N and low C:N and C:P ratios can exceed the metabolic capacity of fish to retain absorbed nutrients, promoting homeostatic excretion of soluble reactive N and P back to the water and thereby supporting eutrophication. By mid- to late season, natural food declines and cereals become the dominant supplementary feed. Nutrition then shifts toward abundant carbohydrate energy but insufficient protein, particularly lysine and methionine, together with low bioavailable P and poor-quality fatty-acid supply. Although cereals provide high C:N and C:P ratios, much of their phosphorus is phytate-bound and lost in faeces, while amino-acid imbalance limits protein deposition and promotes metabolic losses of both N and P. Thus, neither seasonal nutritional extreme is optimal: early-season natural food supplies excess protein and P relative to energy, whereas late-season cereal feeding supplies excess energy relative to essential nutrients. Both result in poor nutrient retention and elevated faecal or metabolic N and P losses. The solution is therefore to supplement what is nutritionally missing, when it is missing, in synchrony with natural-food dynamics and the bioenergetic constraints governing nutrient retention and recycling in fish.

3.4. Aim and objectives of the work

The overarching aim of this habilitation thesis is to develop a nutritional ecology framework for European fishponds that integrates fish nutrition, natural food-web ecology, nutrient cycling, and food-system considerations to support nutrient-sensitive, ecosystem-friendly, and food-system-friendly fed aquaculture. This aim is addressed through four interconnected objectives:

1. To characterize the nutritional role of the pond food web, including its contribution to nutrient digestion and the seasonal and spatial availability of protein, indispensable amino acids, phosphorus, and long-chain polyunsaturated fatty acids to pond fish.
2. To determine how nutritional quality and balance regulate nutrient retention and recycling by aquatic consumers, particularly how specific biomolecules and non-protein energy influence the metabolic fate of nitrogen and phosphorus beyond predictions based solely on elemental C:N:P stoichiometry.
3. To translate nutritional ecology into feeding and ecosystem-management strategies that complement seasonal changes in natural food, improve nutrient-use efficiency and fish nutritional quality, and reduce nutrient recycling, eutrophication, and external feed inputs.
4. To evaluate the wider role of European fishpond aquaculture in sustainable food systems, particularly its capacity to produce nutritionally valuable aquatic food, utilize circular resources, provide ecosystem services, and reduce dependence on more resource-intensive or externally sourced foods and nutrients.

The results addressing these objectives are presented in the following chapters and described in detail in the ten publications included as part of this habilitation thesis.

3.5. Justification of the studies included and the mind map of inclusion

I have included a total of ten post-PhD publications that are either first authored or supervised and corresponded by me, demonstrating my leadership in the area. The study numbers are assigned chronologically from 1 to 10 based on the recency or year-month of publication.

Study number	Full bibliography (IF: impact factor; FWCI: field-weighted citation impact)
1.	Roy, K., Dvořák, P., Machová, Z., Mráz, J., 2023. Nutrient footprint versus EPA +DHA security in land-locked regions—more of local pond farmed, imported marine fish or fish oil capsules? <i>npj Science of Food</i> 7: 48. https://doi.org/10.1038/s41538-023-00224-z (IF 2022 = 6.400; FWCI = 1.58)
2.	Roy, K., Kajgrová, L., Capkova, L., Zabransky, L., Petraskova, E., Dvořák, P., Náhlík, V., Kuebutornye, F.K.A., Blabolil, P., Bláha, M., Vrba, J., Mráz, J., 2024a. Synergistic digestibility effect by planktonic natural food and habitat renders high digestion efficiency in agastric aquatic consumers. <i>Science of the Total Environment</i> 927:

	172105. https://doi.org/10.1016/j.scitotenv.2024.172105 (IF 2022 = 9.800; FWCI= 1.01)
3.	Roy, K. , Vrba, J., Kuebutornye, F.K., Dvorak, P., Kajgrova, L. and Mraz, J., 2024b. Fish stocks as phosphorus sources or sinks: Influenced by nutritional and metabolic variations, not solely by dietary content and stoichiometry. <i>Science of The Total Environment</i> , 938: 173611. https://doi.org/10.1016/j.scitotenv.2024.173611 (IF 2022 = 9.800; FWCI= 1.01)
4.	Roy, K. , Verdegem, M.C.J., Mráz, J., 2025. Ecological Restoration of Inland Aquaculture in Land-Locked Europe: The Role of Semi-Intensive Fishponds and Multitrophic Technologies in Transforming Food Systems. <i>Reviews in Aquaculture</i> 17: e12999. https://doi.org/10.1111/raq.12999 (IF 2023 = 8.800; FWCI= 0.80)
5.	Mráz, J., Mandal, B., Vrba, J., Kajgrova, L., Bláha, M., Kuebutornye, F.K.A., Zábranský, L., Náhlík, V., Lepič, P., Roy, K. , 2026. Nutritional requirement of European fishponds to achieve low and efficient feed use avoiding eutrophication. <i>Aquaculture</i> 613: 743389. https://doi.org/10.1016/j.aquaculture.2025.743389 (IF 2024 = 3.9; FWCI= 11.4)
6.	Roy, K. , Mraz, J., 2026a. The Rings of Power: managing nutrient cycles in aquatic food webs above and beyond primary producers. <i>Web Ecology</i> , 26: 27-33. https://doi.org/10.5194/we-26-27-2026 (IF 2024 = 2.4; FWCI= 2.61)
7.	Roy, K. , Mandal, B., Hossain, M.F., Nahlik, V., Regenda, J., Rahi Roy, D, Penka, T., Kucera, V., Malinovskyi, O., Lepic, P., Policar, T. and Mraz, J., 2026b. Ecological stoichiometry and nutrient reduction strategies for intensive yet sustainable hybrid pond systems: Concepts for regenerative aquaculture. <i>Aquacultural Engineering</i> 115: 102796. https://doi.org/10.1016/j.aquaeng.2026.102796 (IF 2025 = 4.8; FWCI= 0)
8.	Hossain, M.F., Sezimova, K., Mraz, J., Gebauer, R., Zabransky, L., Roy, K. , 2026. Amino acids in the natural food web of global fishponds: way forward for precision protein feeding in pond cyprinid aquaculture. <i>Reviews in Aquaculture</i> , 18(4): e70195. https://doi.org/10.1111/raq.70195 (IF 2025 = 13.8; FWCI= 0)
9.	Mandal, B., Gebauer, R., Mraz, J., Roy, K. , 2026. Spatiotemporal distribution of long-chain polyunsaturated fatty acids (LC-PUFA) in gill filterable fish food webs of European freshwater lakes and ponds: a systematic review. <i>Environmental Sciences</i>

	<i>Europe</i> , 38: 158. https://doi.org/10.1186/s12302-026-01464-y (IF 2025 = 7.1; FWCI= 0)
10.	Mandal, B., Tomcala, A., Rahi Roy, D., Mraz, J., Roy, K. , 2026. Why pond farmed carp remain poor in EPA+DHA despite rich food and genetic repertoire: evidence from pond food-web and fatty acid supply dynamics. <i>Animal Feed Science and Technology</i> , 335: 116678. https://doi.org/10.1016/j.anifeedsci.2026.116678 (IF 2024 = 2.7; FWCI= 6.40)

Conceptually, the ten selected studies answer the following knowledge gaps existing in the nutritional ecology of temperate European carp ponds under semi-intensive aquaculture:

- *What does the food web provide?* → Studies 2, 8, 9
- *Why are those nutrients sometimes poorly retained?* → Studies 3, 6
- *How can we manage the system better?* → Studies 5, 7, 10
- *Why does this matter beyond the pond?* → Studies 1, 4

A mind map of the ten studies included in the thesis, clustered under the four objectives, is graphically represented in Figure 2.

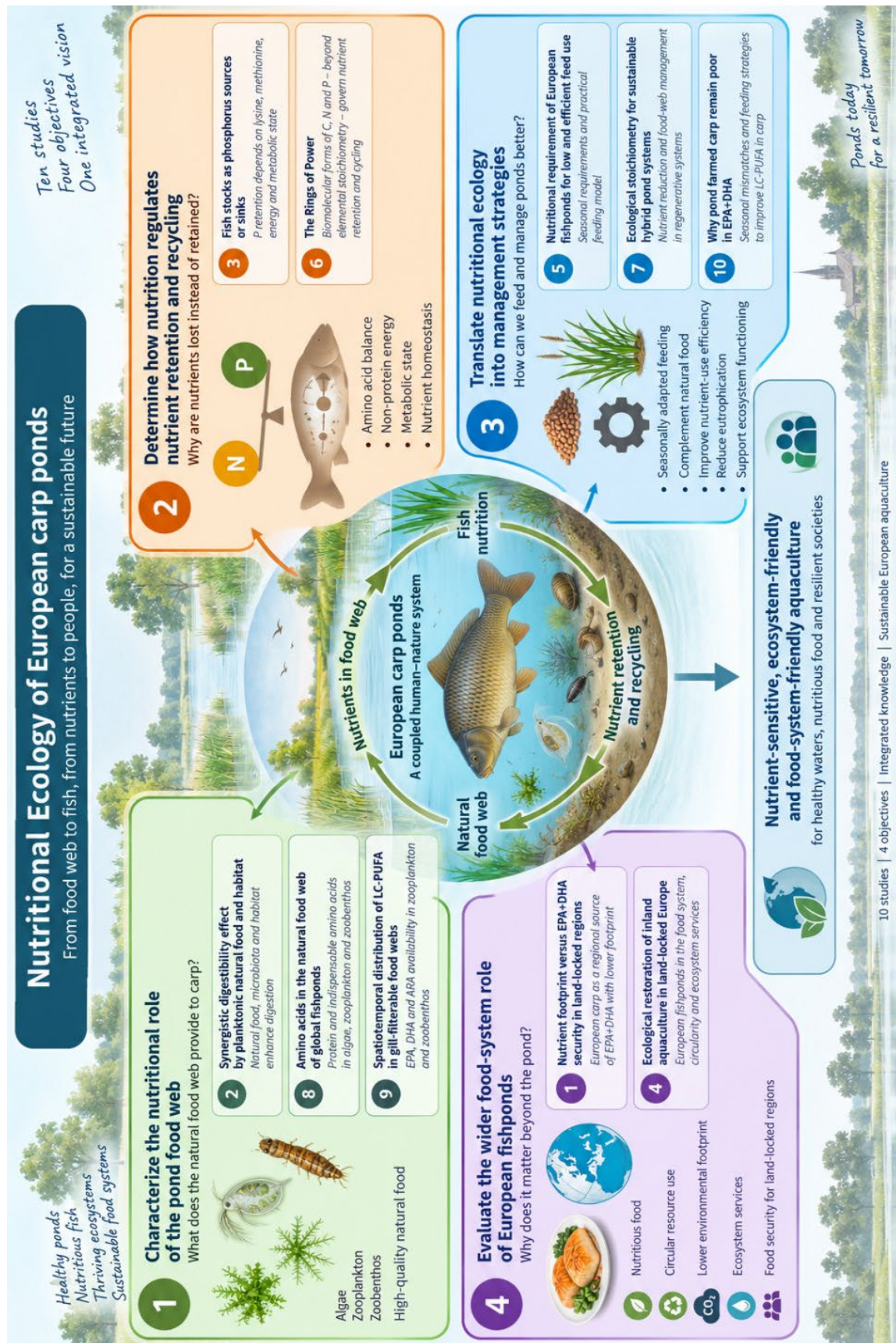


Figure 2: Mind map of how the ten included studies fit into the topic of the habilitation thesis, its overarching aim, and the four objectives. Created using OpenAI GPT-5.6 sol.

4. EXECUTIVE SUMMARY OF SELECTED PUBLICATIONS

The studies are chronologically arranged from 1 to 10 based on the recency of publication.

Study (year ↓)	Primary objective	Why it fits
1. Nutrient footprint versus EPA + DHA security in land-locked regions (2023)	<i>Objective 4</i> – Food-system role	Evaluates pond carp as a regional source of EPA+DHA relative to imported marine fish, salmon, and fish-oil capsules, integrating nutrient footprint, GHG emissions, resource-use efficiency, and food-system security.
2. Synergistic digestibility effect by planktonic natural food and habitat (2024)	<i>Objective 1</i> – Nutritional role of the pond food web	Demonstrates that natural food, microbiota, and pond habitat can enhance digestion of proteins, carbohydrates, phosphorus compounds, and complex polymers by carp.
3. Fish stocks as phosphorus sources or sinks (2024)	<i>Objective 2</i> – Nutritional regulation of nutrient retention/recycling	Shows that P retention and excretion depend not only on dietary P or N:P stoichiometry, but also on lysine, methionine, non-protein energy, and metabolic state.
4. Ecological Restoration of Inland Aquaculture in Land-Locked Europe (2025)	<i>Objective 4</i> – Food-system role	Places European fishponds and freshwater multitrophic aquaculture within the wider European food system, circularity, ecosystem services, and low-impact aquatic food production.
5. Nutritional requirement of European fishponds to achieve low and efficient feed use avoiding eutrophication (2026)	<i>Objective 3</i> – Feeding and ecosystem-management strategies	Converts seasonal natural-food dynamics and fish nutrient requirements into a practical feeding model, identifying when protein, lysine, and methionine become limiting and when supplementary feeds should change.

6. The Rings of Power: managing nutrient cycles in aquatic food webs above and beyond primary producers (2026)	<i>Objective 2 –</i> Nutritional regulation of nutrient retention/recycling	Provides the conceptual framework that specific biomolecular forms of C, N, and P—not elemental stoichiometry alone—govern nutrient retention, excretion, and cycling in consumers.
7. Ecological stoichiometry and nutrient reduction strategies for intensive yet sustainable hybrid pond systems (2026)	<i>Objective 3 –</i> Feeding and ecosystem-management strategies	Tests ecological-stoichiometric and food-web management principles for controlling algal production, nutrient availability, and zooplankton quality in regenerative hybrid ponds.
8. Amino Acids in the Natural Food Web of Global Fishponds (2026)	<i>Objective 1 –</i> Nutritional role of the pond food web	Characterizes protein and indispensable amino-acid quality across algae, zooplankton, and zoobenthos and translates this information toward precision protein feeding.
9. Spatiotemporal distribution of LC-PUFA in gill-filterable fish food webs of European freshwater lakes and ponds (2026)	<i>Objective 1 –</i> Nutritional role of the pond food web	Defines spatial, seasonal, and environmental variation in EPA, DHA, and ARA availability in zooplankton and zoobenthos and identifies nutritional hotspots and constraints.
10. Why pond farmed carp remain poor in EPA+DHA despite rich food and genetic repertoire (2026)	<i>Objective 3 –</i> Feeding and ecosystem-management strategies	Identifies seasonal mismatches between food-web LC-PUFA supply and carp requirements and uses these findings to propose alternative feeding strategies for improving EPA+DHA accumulation.

5. RESULTS AND DISCUSSIONS

4.1. *Nutritional role of the pond food web: What does the food web provide?* (Study 2, 8, 9)

In study-2⁹¹, natural food and the pond environment enhanced digestion in agastric common carp. Pond carp showed higher or comparable digestive enzyme activities than tank-reared carp and tilapia, while planktonic food exhibited exceptionally high enzymatic activity. Zooplankton-rich, clear-water periods were associated with increased cellulolytic and chitinolytic activity in the carp gut, supporting a 'synergistic digestibility effect'. Thus, natural food, microbiota, and pond habitat can improve the breakdown of C-, N-, and P-containing macromolecules, including complex polymers such as cellulose, chitin, and potentially phytate. Laboratory estimates may therefore underestimate the digestive capacity of free-ranging pond fish, with implications for more efficient pond feeding management. Usually, the digestibility of food and feedstuffs under pond settings could be higher than what is measured in laboratory. For example, P digestibility in carp gut may be 1.5x stronger in pond settings than what is observed in RAS settings (Figure 3).

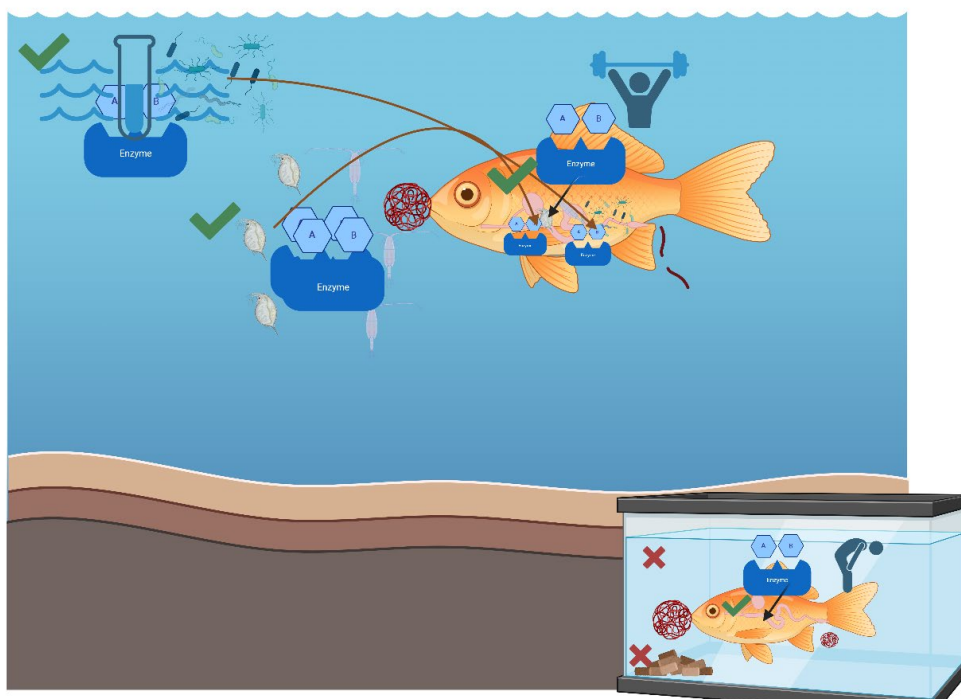


Figure 3: Graphical abstract of the synergistic digestibility effect phenomenon in pond fish not encountered in tank carp⁹¹. The study showed evidence of enhanced digestive function of the agastric carp free-ranging and grazing natural food in the ponds. Created using Biorender.

In study-8 ¹¹³, the systematic synthesis of amino acids adds a complementary food-web pattern: zooplankton generally exceeded zoobenthos and algae in protein and indispensable-amino-acid quality; lysine increased strongly with trophic position, whereas methionine was comparatively conserved and difficult to source. Across 30 studies systematically analysed, protein quantity and indispensable amino-acid quality followed the pattern zooplankton > zoobenthos > algae. Zooplankton and zoobenthos generally met or exceeded common carp amino-acid requirements, whereas algae were more likely to be deficient, particularly in lysine and methionine. The positive relationship between trophic position and indispensable amino acids supports trophic upgrading within pond food webs. These findings support precision pond feeding: supplementary feeds should compensate for seasonal nutritional gaps, especially lysine and methionine during algae-dominated periods, while non-protein energy may help spare amino acids when zooplankton is abundant. Synchronizing feed composition and timing with food-web dynamics can improve protein utilization, fish growth, and nutrient-use efficiency while reducing environmental impacts. Freshwater pond food webs provide an important protein and amino-acid resource for cyprinid aquaculture. However, the finding supports a methionine-centered supplementary-feed hypothesis and requires prospective pond tests. I have converted the synthesis into an applied digital tool for pond aquaculture (<https://zerofishcarpfeed.shinyapps.io/PondAmino/>)¹¹⁴.

In study-9 ¹¹⁵, the systematic LC-PUFA review broadens the spatial and temporal frame of LC-PUFA availability in fish gill-filterable food webs by correlations with latitude, dissolved organic carbon and total phosphorus, identifying 'hotspots' for exploitation, and possible detrimental effects of eutrophication and climate change. Across 48 studies systematically reviewed, zooplankton generally contained more DHA than zoobenthos, while EPA and ARA varied with latitude and habitat. EPA and DHA availability was favored by moderate dissolved organic carbon and low phosphorus, whereas eutrophication and climate-related changes were associated with declining n-3 LC-PUFA availability. Zooplankton and zoobenthos supplied about 600–1050 mg EPA+DHA 100 g⁻¹ dry matter, supporting their role as key vectors of omega-3 transfer to freshwater fish. These findings highlight European freshwater as potential inland sources of EPA and DHA, but also show that this nutritional resource is vulnerable to eutrophication and climate change. Management approaches such as polyculture, regulated feeding, finishing feeds (not necessarily by fish oil), and selective breeding may improve trophic transfer and retention of n-3 LC-PUFAs in farmed fish. Temperate European lakes and fishponds are important but underused sources of

nutritionally valuable LC-PUFAs. I have converted the synthesis into an applied digital tool for pond aquaculture (<https://zerofishcarpfeed.shinyapps.io/OmegaPonds/>)¹¹⁶.

4.2. *Nutritional regulation of nutrient retention/recycling: Why are those nutrients sometimes poorly retained?* (Study 3, 6)

In study-3⁶⁸, the series of four experiments showed fish can act as either phosphorus sources or sinks depending not only on dietary P and N:P stoichiometry, but also on the nutritional form of nitrogen and carbon. In common carp, dissolved reactive P losses increased with excess bioavailable P, low digestible N:P ratios, lysine–methionine deficiency, or insufficient non-protein energy. When lysine, methionine, and non-protein energy were adequate, P retention increased markedly and reactive P excretion could approach zero. Thus, identical food N:P ratios can produce very different P-retention outcomes because specific biomolecules—not elemental ratios alone—govern consumer P homeostasis. Metabolic state and phenotype also matter, with basal metabolism greatly reducing P recycling and scaly carp showing some advantage over scaleless fish. These findings argue for integrating ecological stoichiometry with fish nutritional bioenergetics to better understand and manage eutrophication. The study sharpened the mechanism of fish-driven P recycling (internal loading, eutrophication) in pond ecosystems. Dissolved algal-reactive P fractions loss depended not only on bioavailable dietary P intake, but also on lysine, methionine and non-protein energy supply from the food web; scaly and scaleless phenotypes differed; and recycling changed between feeding and basal metabolic states. Under sufficient amino-acid and energy conditions, dissolved P release approached zero and net uptake of P from water was even observed in the experimental system (Figure 4).

In study-6¹¹⁷, the “rings of power” concept proposes that nutrient cycling in aquatic consumers is governed less by bulk C:N:P ratios than by the specific biomolecular forms in which carbon, nitrogen, and phosphorus are supplied. Key dietary components—such as indispensable amino acids, non-protein energy, and selected lipid classes—can improve nutrient–energy transfer from food to biomass, increase N and P retention, and reduce metabolic nutrient leakage (Figure 5). Applied seasonally, stoichiometrically corrective feeds could therefore slow nutrient recycling in hypertrophic freshwater systems. Energy-rich feeds may complement spring and autumn food webs, while amino-acid- and energy-balanced feeds may correct summer deficiencies. By improving retention in fish and other consumers, nutrients can be captured in biomass and

subsequently removed through harvest rather than recycled to fuel excessive primary production. The concept links animal nutrition with food-web ecology as a potential basis for regenerative aquaculture: using targeted nutrition to convert nutrient-accumulating waterbodies from sources of eutrophication into systems that retain, recover, and export nutrients as aquatic biomass (Figure 6). My unpublished data⁹⁴ shows that European ponds experience disappearance of some rings of power from the food base of fish during certain seasonal windows quite predictably (as a signature of the ecotype and climatic conditions of the region), and they could be balanced by supplementing externally.

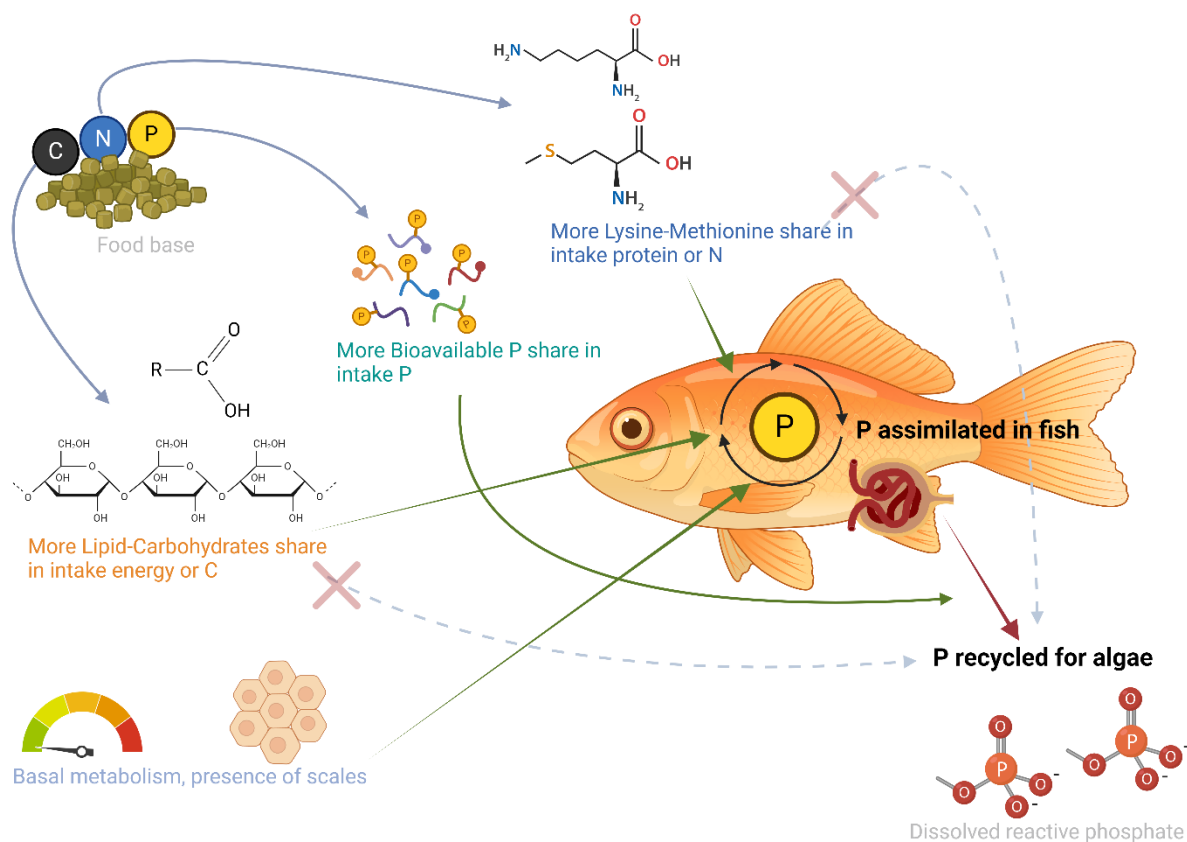


Figure 4: Graphical abstract of fish stocks acting as P source or sinks in ponds under nutritional and metabolic variations⁶⁸. Shows that P retention and excretion depend not only on dietary P or N:P stoichiometry, but also on lysine, methionine, non-protein energy, and metabolic state. Created using Biorender.

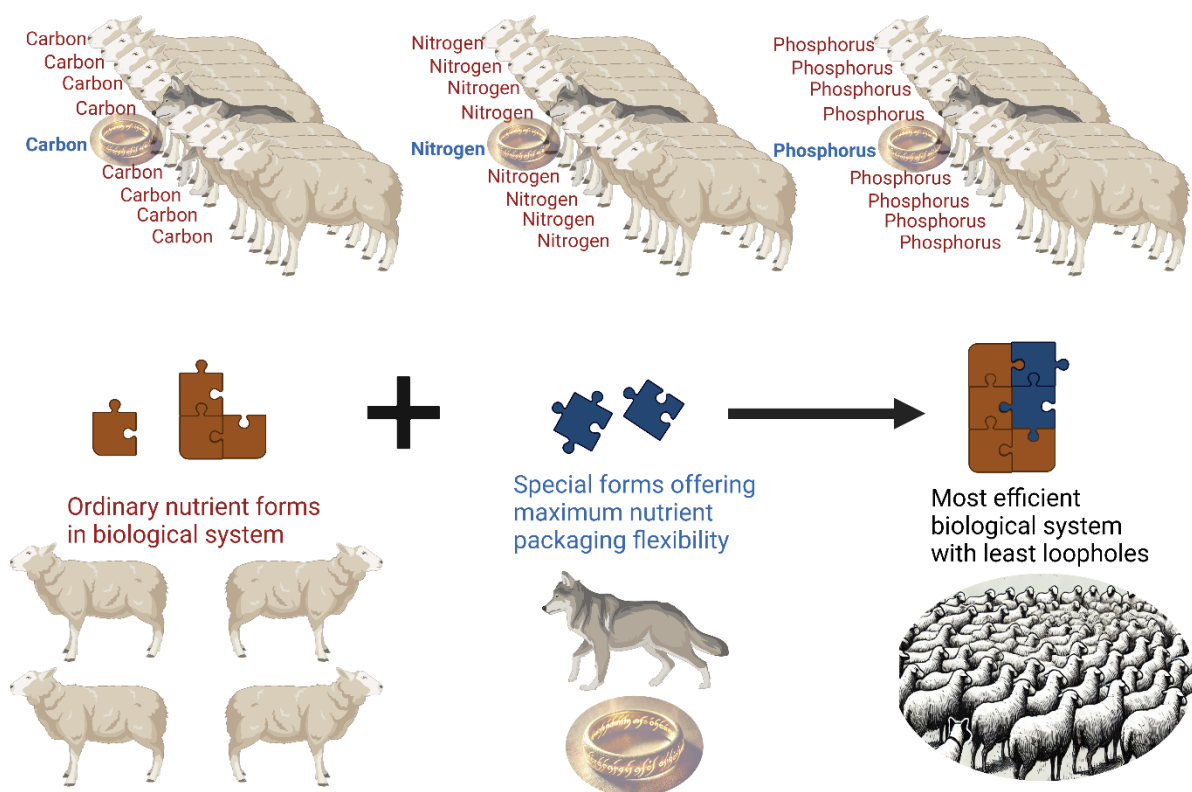


Figure 5: Graphical abstract of the Rings of Power philosophy in fish body ¹¹⁷. Portrayed metaphorically as a sheepdog (special biomolecules containing C, N, P) among sheep (average biomolecules containing C, N, P), holding the power to orchestrate maximum packaging of elements (C, N, P) into the fish body. Provides the conceptual framework that specific biomolecular forms of C, N, and P—not elemental stoichiometry alone—govern nutrient retention, excretion, and cycling in consumers. Created using Biorender.

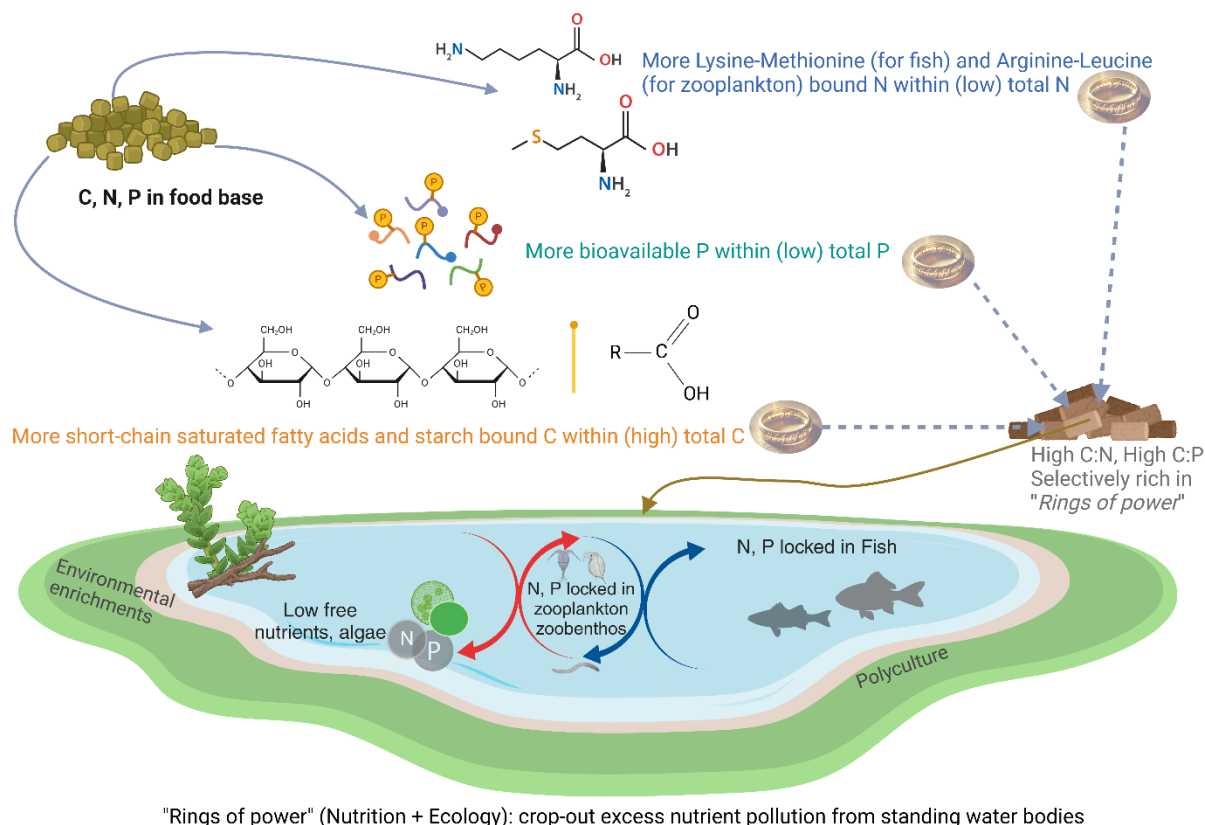


Figure 6: Graphical abstract of the Rings of power in action to slow down nutrient flows from tipping points in pond aquaculture¹¹⁷. By providing “rings-of-power feeds” (e.g., spring-/autumn-time digestible non-protein energy or C-rich feed, summer-time essential-amino-acid- and non-protein-energy-balanced feed), one can periodically stock and harvest fish stocks to manage nutrients loaded into these waterbodies.

4.3. Feeding and ecosystem management: How can we manage the system better? (Study 5, 7, 10)

The study-5⁶¹ integrated seasonal pond nutrient status, natural-food supply and feeding requirements at a system level. Seasonal food-web dynamics create a clear nutritional mismatch in European carp ponds. Early-season natural food is abundant and nutrient-rich, but from mid-summer zooplankton quality declines, zoobenthos is depleted, and carp growth slows by 30–40%. From July onward, lysine and methionine become limiting, followed by digestible protein, while cereal-based feeds continue to provide sufficient or excess non-protein energy. These results show that fertilization or continued cereal feeding cannot correct late-season nutritional deficiencies. A

practical solution is to switch from energy-rich cereals to balanced supplementary feeds from July onward, supplying limiting amino acids and other missing nutrients. The resulting nutritional requirement model integrates limnology and fish nutrition to indicate what, how much, and when to supplement in European carp ponds, with the aim of improving growth, feed efficiency, nutrient retention, and water quality. The study converted seasonal natural-food dynamics and fish nutrient requirements into a practical feeding model, identifying when protein, lysine, and methionine become limiting and when supplementary feeds should change. Thus, bridging and advancing my earlier innovation during PhD, *i.e.*, balanced pond feeding concept published in 2022¹¹⁸. I have compiled them together into a certified methodology for innovative and improved feeding of European fishponds (Figure 7), thus converting the basic research to applied outcomes¹¹⁸. However, such calculations are quite complex and need comprehensive data of the system (Figure 8). Using such knowledgebase, I have co-developed some precision pond feeds for seasonal applications in European carp ponds and the improved feeding model including their specifications and performance indicators protected under a utility model (CZ 39011 U1). They include spring/autumn time energy feeds and summertime balanced protein-energy feeds for pond carp¹¹⁹.

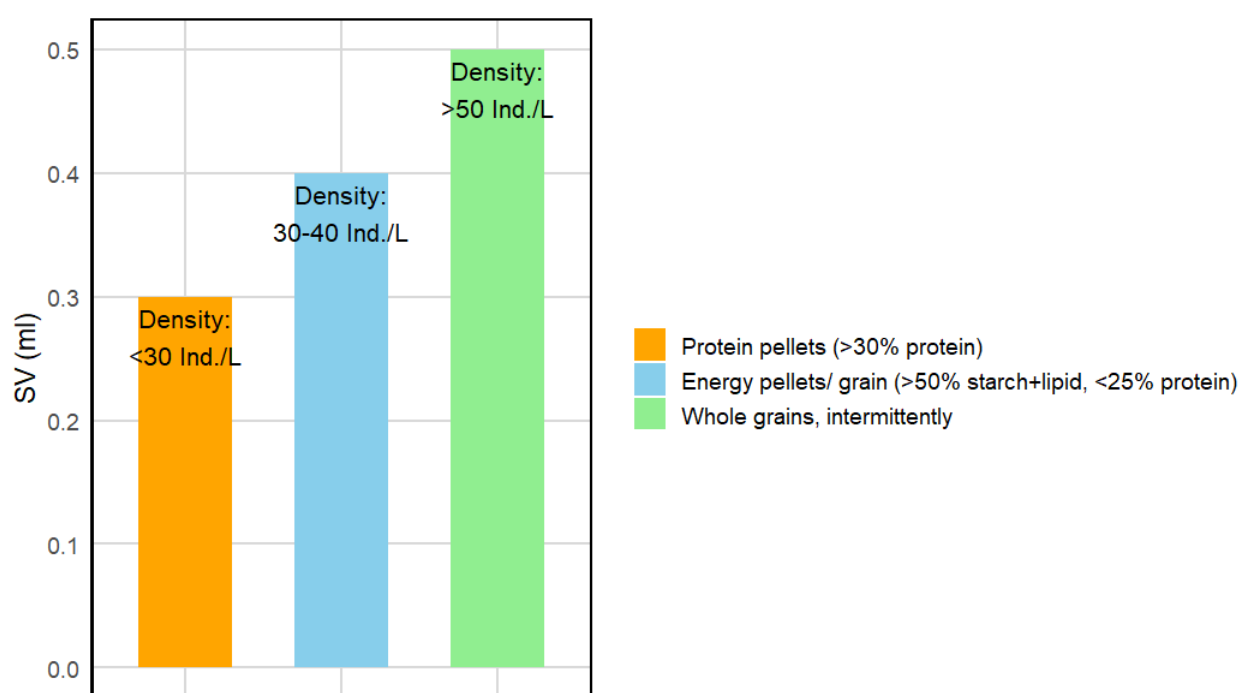


Figure 7: Decision tree for sedimentation volume (SV) of $\geq 500 \mu\text{m}$ mesh plankton consortia (from 20 L pond water) and corresponding pond feed type to be applied¹¹⁸. The SV of $>500 \mu\text{m}$ zooplankton fraction (in ml) is quite easy to determine according to open-access protocol of

Schlott and colleagues, pp. 25-26 pictorial guide ⁵⁹. The $>500\ \mu\text{m}$ mesh zooplankton abundance (individuals L^{-1}) can be then re-calculated multiplying SV in ml by 10. Thus, measuring directly on-site and decide on the type of pond feed to be used as supplementary feed accordingly.

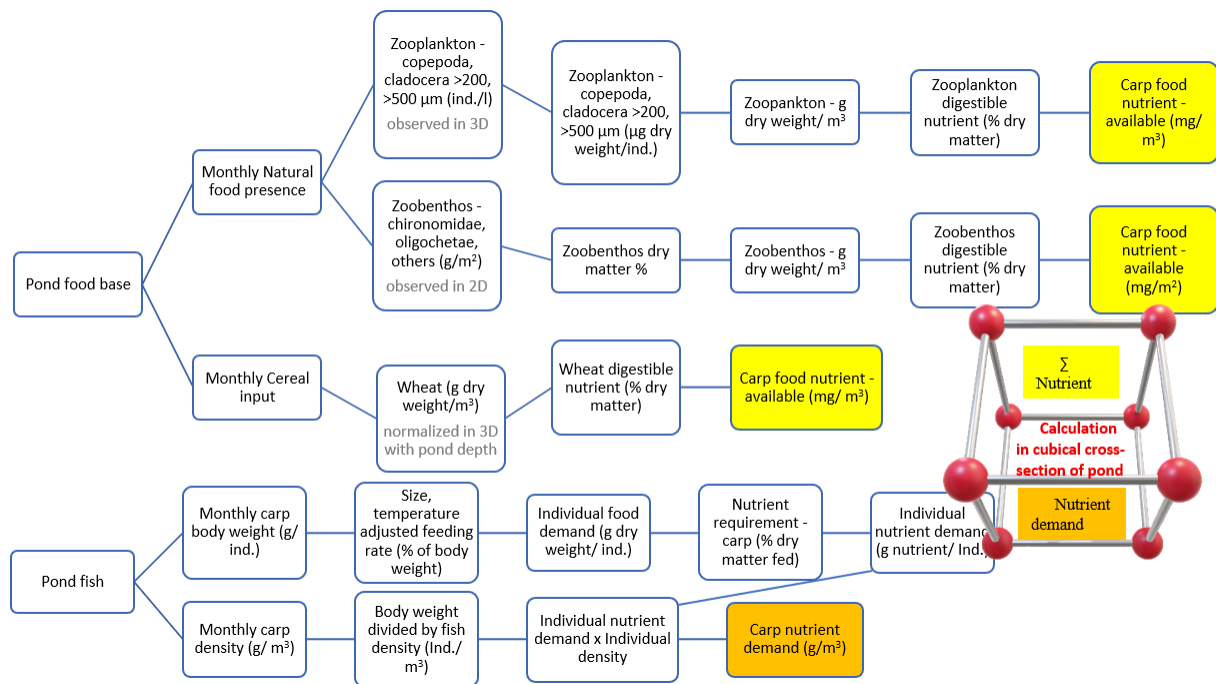


Figure 8: Monthly fish nutrition supply-demand gap modelling framework for semi-intensive aquaculture ponds ^{61,118}.

In study-7 ¹²⁰, a series of three experiments tested the ecological-stoichiometric and food-web management principles for controlling algal production, nutrient availability, and zooplankton quality in pond ecosystems. Fish-free pond-water mesocosms manipulated faecal nutrients and carbon under dilution scenarios, while pond living labs examined zooplankton nutritional ecology (amino- and fatty-acid composition) under bottom-up and top-down proxies. The study explored how ecological stoichiometry (ES theory) and plankton ecology (PEG model) could inform regenerative pond aquaculture. Mesocosm experiments showed that P enrichment promoted algal growth, while higher organic C inputs could partly suppress it, although excessive C under low-P conditions may increase brownification and oxygen risks. Lower C:P and N:P ratios favored algal responses, with N:P appearing more influential under the tested conditions. In pond living labs, cladoceran amino-acid composition was relatively stable, whereas key fatty acids such as arachidonic acid (ARA, 20:4n-6), eicosapentaenoic acid (EPA, 20:5n-3), and docosahexaenoic acid

(DHA, 22:6n-3) varied more strongly and coincided with seasonal changes in zooplankton condition factor (body fitness). Under variable top-down and bottom-up effects, zooplankton amino acids were comparatively stable while reproduction-related LC-PUFA were largely sensitive. Overall, the findings suggest that combining C amendment and P reduction with fish–zooplankton management may offer a pathway toward more regenerative pond aquaculture but requires careful control of carbon-related trade-offs (Figure 9).

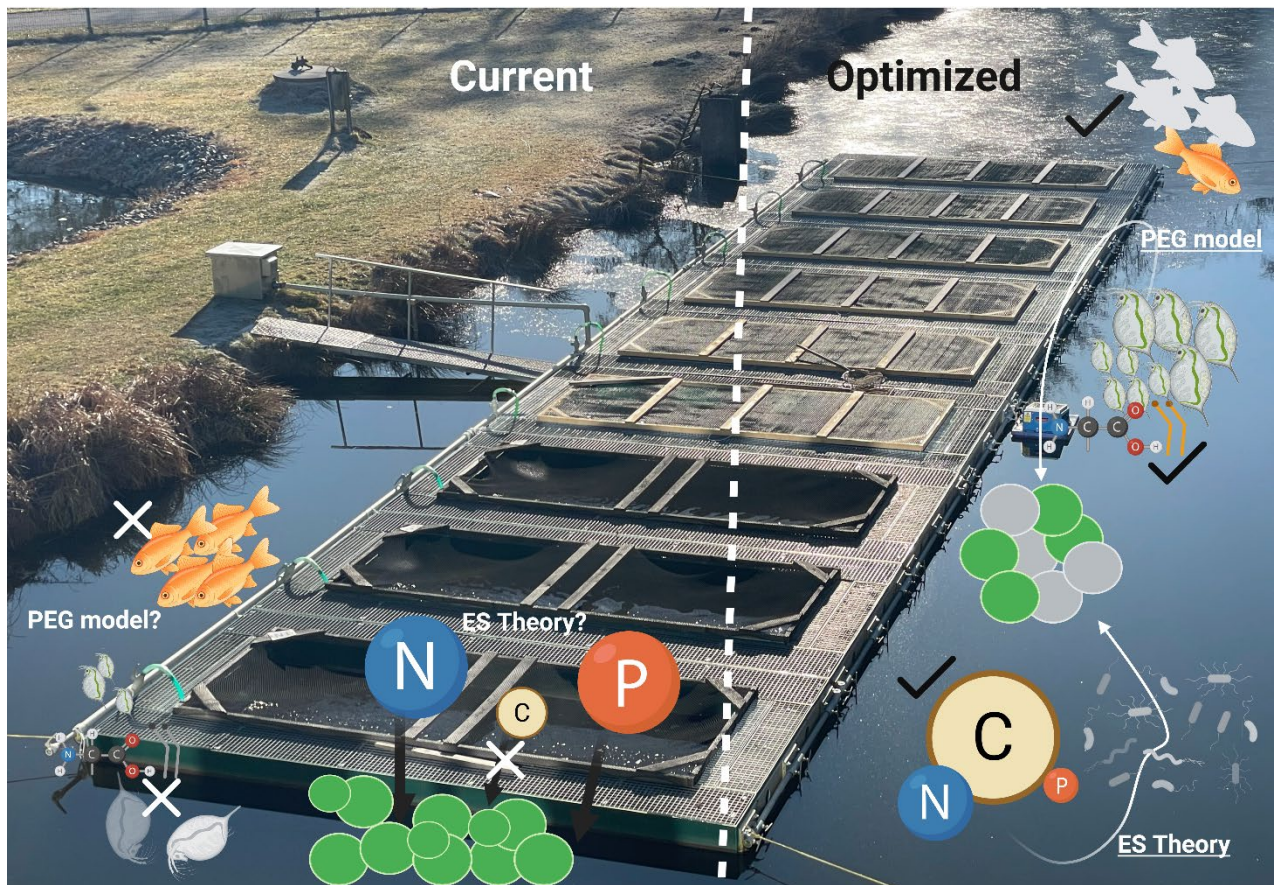


Figure 9: Graphical abstract of a regenerative pond aquaculture management ¹²⁰. It requires integration of ecological stoichiometry theory (ES theory), plankton ecology group model (PEG model) and zooplankton nutritional ecology under optimized top-down and bottom-up controls into pond management for enabling the regenerative functions.

The study-10 ¹²¹ identified seasonal mismatches between food-web LC-PUFA supply and carp requirements and uses these findings to propose alternative feeding strategies for improving EPA+DHA accumulation in edible portion of pond-reared carp. European carp ponds contain substantial omega-3 LC-PUFA resources, but their availability and transfer to fish decline strongly late in the growing season. EPA+DHA were abundant in plankton and zoobenthos, peaking during

May–July and declining sharply from August to October as cladocerans decreased, chlorophyll-a and fish biomass increased, and eutrophication intensified. During the final three months before harvest, both dietary EPA+DHA and their precursor α -linolenic acid (ALA, 18:3n-3) became deficient in the pond food base, limiting direct accumulation and even synthesis of EPA+DHA in carp. Thus, poor EPA+DHA content in harvested carp reflects a seasonal nutritional bottleneck rather than limited pond-food potential. Maintaining zooplankton–benthos resources, reducing eutrophication, and introducing ALA- or EPA+DHA-rich finishing feeds during the final months before harvest could improve omega-3 fatty acids retention and nutritional quality of pond-reared carp. This has been successfully demonstrated in pond trials (unpublished data from vegetative seasons 2023 in Czechia, 2025 in Czechia and Germany).

4.4. Food-system role: Why does this matter beyond the pond? (Study 1, 4)

The study-1²⁰ used a human-nutrition functional unit and showed that pond carp can have a low production footprint yet perform poorly per milligram of EPA+DHA compared with salmon unless its tissue concentration is improved. The study is a scenario and footprint analysis. Central European EPA+DHA intake remains low and depends largely on imported marine fish, farmed salmonids, and fish-oil supplements. Pond carp has a lower overall production footprint but currently provides much less EPA+DHA than salmon, resulting in a higher environmental footprint per unit of EPA+DHA supplied. However, if carp EPA+DHA content could be increased above ~300 mg 100 g⁻¹, this disadvantage could largely disappear. European fishponds nevertheless have strong potential because of their ecosystem services and high EPA+DHA output-to-input efficiency. Improved bioaccumulation, finishing feeds, polyculture, and circular feeding strategies could make pond fish a more important net source of EPA+DHA. Thus, pond-reared fish should complement rather than replace marine fish and salmonids in land-locked European diets, helping improve omega-3 security with lower pressure on global resources. It is an extension of my earlier work during PhD¹⁹ that resulted in the following perspective: environmental efficiency should be judged per useful edible nutrient²⁰ as well as per kilogram of fish¹⁹. For food systems, the conclusions drawn by either of these approaches may not necessarily agree and this means that nutrient-sensitive aquaculture in ponds focusing on product quality is equally important as productivity.

In study-4³⁶, the European fishponds and freshwater multitrophic aquaculture is imagined as a 'sleeping giant' within the wider European food system, circularity, ecosystem services, and

low-impact aquatic food production. European inland freshwater aquaculture remains underused in regional food-system strategies despite its potential to provide low-impact aquatic food. This review argues that semi-intensive fishponds and freshwater multitrophic systems could contribute through circular feeds, ecosystem services, and nature-based management. Central and Eastern European fishponds currently produce about 0.12 Mt of carp from 0.25 million ha. With balanced pond feeds based on low-opportunity-cost biomasses and better integration with natural food webs, production could potentially increase while reducing feed inputs and feed–food competition. At this scale, fishponds could supply substantial amounts of EPA+DHA and leucine, helping meet the annual requirements of roughly 1.2–3 million adults while reducing dependence on marine fish oil and dairy-derived protein sources. Overall, the study positions European fishponds as an overlooked component of a more circular, resource-efficient, and nutritionally valuable freshwater food system (Figure 1). The findings were incorporated into an European Commission policy document jointly by European Climate, Infrastructure and Environment Executive Agency, European Maritime, Fisheries and Aquaculture Fund (EMFAF) ¹²².

6. CONCLUSION AND ONGOING/ FUTURE RESEARCH

I found that natural food webs can enhance nutrient digestion, while metabolic assimilation remains constrained by nutritional imbalance, ecological stoichiometry, and consumer homeostasis. This led me to a broader research idea: if nutritional limitations in aquatic consumers can be corrected, more nitrogen and phosphorus can be retained in animal biomass rather than recycled into the water and subsequently removed through harvest.

My unpublished proof-of-concept studies performed in experimental ponds during vegetative seasons 2023-2025 reinforce the above points with data. For example, balanced pond feeding with plant-based (WP) or mixed-protein (PP) diets (switched during summer from the energy feed or grains) improved carp production from July onward without increasing eutrophication. Compared with traditional cereal feeding (NP), WP/PP increased final fish size, yield ($\sim 1.5 \text{ t ha}^{-1}$), feed efficiency (FCR ~ 2.5 vs. ~ 4), and edible yield, while water quality, sediment nutrients, chlorophyll-a, dissolved oxygen, and overall food-web structure remained comparable. Much of the additional dietary N and P appeared to be retained in higher consumer biomass rather than accumulating in water, sediment, or algae. Balanced feeding preserved sensory and protein quality while improving lipid quality, particularly EPA+DHA and vitamin B12, with WP showing the highest nutritional performance. WP also had the lowest estimated human-health and ecosystem impacts and was the only treatment achieving net-positive human-edible protein conversion. Overall, seasonally balanced plant-based feeding can make European carp ponds more productive, nutrient-efficient, nutritionally valuable, and food-system-friendly without compromising ecosystem quality. In another example (unpublished), replacing 55% of human-edible wheat with low-opportunity-cost biomass (LOCB) did not reduce carp survival, yield, market size, fillet yield, protein, EPA+DHA, or feed efficiency. Pond ecological indicators, including chlorophyll-a, zooplankton, dissolved oxygen, and C/N/P in water and sediment, also remained unchanged, indicating no added eutrophication risk. LOCB substitution reduced the overall ReCiPe endpoint environmental impact by 28.8%, mainly through lower human-health and ecosystem damage, although resource use increased. It also shifted human-edible protein conversion from net consumption to near net production, improved EPA+DHA output per unit of human-edible input, and reduced input-associated arable land use by about 46%. Overall, European fishponds can act as circular biorefineries, converting local low-value by-products into nutritious fish while reducing

feed–food competition, land demand, and overall environmental impact without compromising pond production or ecosystem function.

My research now seeks to develop this interface between nutrition, ecology, and nutrient cycling into a framework for nature-based and regenerative aquaculture. I envisage aquatic animals not only as food-production organisms, but also as active regulators of nutrient flows whose ecosystem and food system functions can be directed through carefully designed nutrition. For this goal, I am increasingly approaching experimental fishponds, recirculating aquaculture systems, and aquaponic systems as ‘living labs’ in which ecological and nutritional hypotheses could be tested across different production contexts and later integrated to establish the niche field called nutritional ecology of aquatic production systems. That is my long-term goal.

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8. ENGLISH ABSTRACT

Roy, K., 2026. Nutritional ecology of European carp ponds for ecosystem, food system, and nutrient-sensitive aquaculture. Habilitation thesis, University of South Bohemia in Ceske Budejovice, Faculty of Fisheries and Protection of Waters, Institute of Aquaculture and Protection of Waters. Ceske Budejovice, Czech Republic: 49 p. doi: xxxxxxxxxx

European carp ponds are semi-intensive food-production ecosystems in which fish nutrition, natural food-web dynamics, nutrient cycling, water quality, and food-system performance are tightly interconnected. This habilitation thesis develops a nutritional ecology framework for European fishponds by integrating principles of animal nutrition, ecological stoichiometry, plankton ecology, nutritional bioenergetics, and food-system sustainability. The central premise is that effective pond management requires understanding not only elemental carbon, nitrogen, and phosphorus flows, but also the specific biomolecular forms in which nutrients are supplied, assimilated, retained, or recycled by aquatic consumers. The ten studies collectively demonstrate that natural pond food webs provide substantially more than feed biomass. Plankton, benthos, microorganisms, and the pond environment enhance digestive capacity and supply high-quality protein, indispensable amino acids, bioavailable phosphorus, and long-chain polyunsaturated fatty acids. However, this nutritional supply changes markedly over the vegetative season. Early-season natural food is rich in protein, phosphorus, amino acids, and high-quality fatty acids but relatively poor in non-protein energy, whereas declining natural food later in the season coincides with increasing dependence on carbohydrate-rich cereals deficient in lysine, methionine, bioavailable phosphorus, and nutritionally valuable fatty acids. Both nutritional extremes can reduce nutrient-retention efficiency and promote nitrogen and phosphorus recycling. The work further shows that fish can function as either nutrient sinks or nutrient sources depending on nutritional and metabolic conditions. Nutrient retention cannot therefore be predicted from dietary C:N:P stoichiometry alone; specific amino acids, energy substrates, lipid fractions, digestibility, and consumer homeostasis regulate the transfer of nutrients from food into biomass. This understanding provides the mechanistic basis for seasonally adaptive feeding: supplementing what is nutritionally missing, when it is missing, in synchrony with natural-food dynamics. At the food-system level, European fishponds combine aquatic food production with ecosystem services and offer opportunities to improve nutrient recovery, circular resource use, and the supply of nutritionally valuable fish without simply intensifying production. The thesis therefore positions nutritional ecology as a framework for developing nutrient-sensitive, ecosystem-friendly, and food-system-friendly aquaculture, in which nutrition is used not only to promote fish growth but also to regulate nutrient cycling, reduce eutrophication, enhance nutritional quality, and strengthen the role of European fishponds in sustainable food systems.

Keywords: Nutritional ecology; European fishponds; Common carp; Nutrient cycling; Balanced pond feeding; Sustainable aquaculture

9. ČESKÝ ABSTRAKT

Roy, K., 2026. Nutriční ekologie evropských kaprových rybníků pro akvakulturu šetrnou k ekosystému, potravinovému systému a citlivou k živinovému zatížení. Habilitační práce, Jihočeská univerzita v Českých Budějovicích, Fakulta rybářství a ochrany vod, Ústav akvakultury a ochrany vod. České Budějovice, Česká republika: 49 s. doi: xxxxxxxxxx

Evropské kaprové rybníky představují polointenzivní produkční ekosystémy, v nichž jsou výživa ryb, dynamika přirozené potravní sítě, koloběh živin, kvalita vody a fungování potravinového systému úzce propojeny. Tato habilitační práce rozvíjí rámec nutriční ekologie evropských rybníků prostřednictvím propojení principů výživy živočichů, ekologické stochiometrie, planktonní ekologie, nutriční bioenergetiky a udržitelnosti potravinových systémů. Základní premisou je, že účinný management rybníků vyžaduje porozumění nejen tokům uhlíku, dusíku a fosforu, ale také konkrétním biomolekulárním formám, ve kterých jsou živiny přijímány, asimilovány, zadržovány nebo recyklovány vodními konzumenty. Soubor deseti studií ukazuje, že přirozené potravní sítě rybníků představují podstatně více než jen zdroj potravy. Plankton, bentos, mikroorganismy a samotné rybníční prostředí podporují trávicí schopnosti ryb a poskytují vysoce kvalitní bílkoviny, esenciální aminokyseliny, biologicky dostupný fosfor a dlouhořetězcové polynenasycené mastné kyseliny. Tato nutriční nabídka se však během vegetační sezóny výrazně mění. Přirozená potrava na začátku sezóny je bohatá na bílkoviny, fosfor, aminokyseliny a kvalitní mastné kyseliny, avšak relativně chudá na neproteinovou energii. V pozdější části sezóny přirozené potravy ubývá a roste závislost na sacharidově bohatých obilovinách s nedostatkem lysinu, methioninu, biologicky dostupného fosforu a nutričně hodnotných mastných kyselin. Oba tyto nutriční extrémy mohou snižovat účinnost retence živin a podporovat recyklaci dusíku a fosforu. Práce dále ukazuje, že ryby mohou v závislosti na nutričních a metabolických podmínkách fungovat buď jako zásobárna, nebo jako zdroj živin. Retenci živin proto nelze předpovídat pouze na základě stochiometrie C:N:P v potravě; přenos živin z potravy do biomasy regulují specifické aminokyseliny, zdroje energie, lipidové frakce, stravitelnost a homeostáza konzumenta. Toto poznání tvoří mechanistický základ pro sezónně adaptivní krmení: doplňovat to, co z nutričního hlediska chybí, v době, kdy to chybí, a to v souladu s dynamikou přirozené potravy. Z hlediska potravinového systému evropské rybníky spojují produkci vodních potravin s poskytováním ekosystémových služeb a nabízejí možnosti, jak zlepšit využití živin, cirkularitu zdrojů a produkci nutričně hodnotných ryb bez prostého zvyšování intenzity chovu. Habilitační práce proto představuje nutriční ekologii jako rámec pro rozvoj akvakultury citlivé k živinovému zatížení, šetrné k ekosystému a příznivé pro potravinový systém, v níž výživa neslouží pouze k podpoře růstu ryb, ale také k regulaci koloběhu živin, omezení eutrofizace, zlepšení nutriční kvality produkce a posílení role evropských rybníků v udržitelných potravinových systémech.

Klíčová slova: Nutriční ekologie; Evropské rybníky; Kapr obecný; Koloběh živin; Vyvážené krmení v rybnících; Udržitelná akvakultura

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11. ATTACHMENTS

Attachment code	Description
Study 1	Roy, K., Dvořák, P., Machová, Z., Mráz, J., 2023. Nutrient footprint versus EPA +DHA security in land-locked regions—more of local pond farmed, imported marine fish or fish oil capsules? <i>npj Science of Food</i> 7: 48. https://doi.org/10.1038/s41538-023-00224-z (IF 2022 = 6.400; FWCI = 1.58)
Study 2	Roy, K., Kajgrová, L., Capkova, L., Zabransky, L., Petraskova, E., Dvořák, P., Náhlík, V., Kuebutornye, F.K.A., Blabolil, P., Bláha, M., Vrba, J., Mráz, J., 2024a. Synergistic digestibility effect by planktonic natural food and habitat renders high digestion efficiency in agastric aquatic consumers. <i>Science of the Total Environment</i> 927: 172105. https://doi.org/10.1016/j.scitotenv.2024.172105 (IF 2022 = 9.800; FWCI= 1.01)
Study 3	Roy, K., Vrba, J., Kuebutornye, F.K., Dvorak, P., Kajgrova, L. and Mraz, J., 2024b. Fish stocks as phosphorus sources or sinks: Influenced by nutritional and metabolic variations, not solely by dietary content and stoichiometry. <i>Science of The Total Environment</i> , 938: 173611. https://doi.org/10.1016/j.scitotenv.2024.173611 (IF 2022 = 9.800; FWCI= 1.01)
Study 4	Roy, K., Verdegem, M.C.J., Mráz, J., 2025. Ecological Restoration of Inland Aquaculture in Land-Locked Europe: The Role of Semi-Intensive Fishponds and Multitrophic Technologies in Transforming Food Systems. <i>Reviews in Aquaculture</i> 17: e12999. https://doi.org/10.1111/raq.12999 (IF 2023 = 8.800; FWCI= 0.80)
Study 5	Mráz, J., Mandal, B., Vrba, J., Kajgrová, L., Bláha, M., Kuebutornye, F.K.A., Zábranský, L., Náhlík, V., Lepič, P., Roy, K. , 2026. Nutritional requirement of European fishponds to achieve low and efficient feed use avoiding eutrophication. <i>Aquaculture</i> 613: 743389. https://doi.org/10.1016/j.aquaculture.2025.743389 (IF 2024 = 3.9; FWCI= 11.4)
Study 6	Roy, K., Mraz, J., 2026a. The Rings of Power: managing nutrient cycles in aquatic food webs above and beyond primary producers. <i>Web Ecology</i> , 26: 27-33. https://doi.org/10.5194/we-26-27-2026 (IF 2024 = 2.4; FWCI= 2.61)
Study 7	Roy, K., Mandal, B., Hossain, M.F., Nahlik, V., Regenda, J., Rahi Roy, D, Penka, T., Kucera, V., Malinovskiy, O., Lepic, P., Policar, T. and Mraz, J., 2026b. Ecological stoichiometry and nutrient reduction strategies for intensive yet sustainable hybrid pond systems: Concepts for regenerative aquaculture. <i>Aquacultural Engineering</i> 115: 102796. https://doi.org/10.1016/j.aquaeng.2026.102796 (IF 2025 = 4.8; FWCI= 0)
Study 8	Hossain, M.F., Sezimova, K., Mraz, J., Gebauer, R., Zabransky, L., Roy, K. , 2026. Amino acids in the natural food web of global fishponds: way forward for precision protein feeding in pond cyprinid aquaculture. <i>Reviews in Aquaculture</i> , 18(4): e70195. https://doi.org/10.1111/raq.70195 (IF 2025 = 13.8; FWCI= 0)
Study 9	Mandal, B., Gebauer, R., Mraz, J., Roy, K. , 2026. Spatiotemporal distribution of long-chain polyunsaturated fatty acids (LC-PUFA) in gill filterable fish food webs of European freshwater lakes and ponds: a systematic review. <i>Environmental Sciences Europe</i> , 38: 158. https://doi.org/10.1186/s12302-026-01464-y (IF 2025 = 7.1; FWCI= 0)
Study 10	Mandal, B., Tomcala, A., Rahi Roy, D., Mraz, J., Roy, K. , 2026. Why pond farmed carp remain poor in EPA+DHA despite rich food and genetic repertoire: evidence from pond food-web and fatty acid supply dynamics. <i>Animal Feed Science and Technology</i> , 335: 116678. https://doi.org/10.1016/j.anifeedsci.2026.116678 (IF 2024 = 2.7; FWCI= 6.40)