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Modeling trophic webs in freshwater fishpond systems using Ecopath: towards better polyculture management

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ABSTRACT: Freshwater pond polyculture faces many challenges in Europe. Appropriate tools must be developed to better understand and manage trophic interactions in pond ecosystems. The objective of our study was to understand the trophic interactions and make inference on the fish diet in common carp polyculture through a combination of experiments and trophic web modeling. We conducted an experiment in small fishponds of common carp polyculture reared with roach and perch and used Ecopath with Ecosim software to characterize the food web. Two replicates of 3 treatments were performed: a semi-extensive pond with low fish density and no formulated feed, an intensive pond with twice the fish density and formulated feed and an intensive pond coupled with a planted lagoon. Ten trophic groups were defined to describe the food web. The modeling procedure enabled us to estimate the diets of each trophic group. The fish diet in fed and non-fed treatments differed greatly since the carp fed mainly on formulated feed when available. The roach exhibited trophic plasticity by adapting their diet to the available resources. The benthic macroinvertebrates and zooplankton were preyed upon intensively; they became the limiting factors for fish production and depended on phytoplankton availability. Detritus and phytoplankton were the main sources of nutrients in all treatments but were not used efficiently. These results provide several insights for improving polyculture. In particular, they promote better management of zooplankton and macroinvertebrates as food sources for target species and a better balance in fish assemblages for more efficient use of resources.

KEY WORDS: Food web · Pond aquaculture · Ecological modeling · Ecopath with Ecosim · Common carp

1. INTRODUCTION

Freshwater pond aquaculture is decreasing in Europe due to increasing environmental restrictions, little appreciation for the taste of pond fish and the abandonment of fish farming for more profitable ventures such as hunting or other recreational activities. Nonetheless, the demand for aquatic products, as well as more local and natural food, is increasing. In this context, pond systems face many challenges to become sustainable: being productive, robust, resilient and environmentally friendly; having natural and cultural value; and using more local and natural resources (Aubin et al. 2017). Pond systems which have a close relationship between natural and managed ecosystems promote more intensive use of ecological functions (i.e. 'ecological intensification') (Aubin et al. 2019). Ecological intensification is also applied in integrated multi-trophic aquaculture (IMTA) (Troell et al. 2003, Neori et al. 2004, Soto 2009), which uses assemblages of species to increase nutrient recycling and decrease environmental im-

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pacts. This approach is considered a promising way to improve aquaculture systems and design new ones (Neori et al. 2004, Granada et al. 2016).

The reference model of species assemblage in freshwater pond systems is carp polyculture, which has been established in China since the Tang dynasty (Milstein 1992). This system combines cyprinid species of different trophic levels that feed on the varied nutritional resources in the pond. It has a high fish yield and its principles have been adapted to multiple ecological, economic and pedoclimatic contexts in Asia and South America. However, pond polyculture focuses on the fish assemblage and does not explicitly consider the plant or invertebrate compartments of the ecosystem. Thus, sustainability of pond polyculture systems may be improved by using a larger range of adapted (and approved) species. This requires an understanding of the complex trophic interactions in pond ecosystems in order to adapt the species assemblage as a function of the natural productivity of the pond and its biodiversity. Among the many ways to intensify pond systems, using formulated feed can sustain fish productivity but may cause changes in the trophic web and an overload of nutrients (nitrogen, phosphorus) and organic matter. This is a major trend in fish farming throughout the world (Tacon et al. 2010), especially in Asia, where non-fed polyculture systems have been abandoned in favor of fed monoculture systems (FAO 2018). In this context, most new systems use additional technical facilities (filters, planted lagoons, algae tanks) to mitigate the environmental impacts of emitted nutrients and occasionally to co-produce commercial products (Marques et al. 2017). Plant production is becoming increasingly popular in this domain, especially varieties developed for aquaponics (Love et al. 2015), and reintroduces ancient concepts of nutrient recycling (Diab et al. 1992, Gál et al. 2013). For instance, ecological intensification can be achieved by adding a planted pond, which may regulate nutrient cycles and support biodiversity (Jaeger & Aubin 2018). The combination of species requires a previous understanding of complex interactions, which may only be feasible with the application of ecological modeling (Reid et al. 2020).

Ecopath with Ecosim (EwE) is one of the most popular tools for modeling trophic interactions in aquatic ecosystems, especially in fishery science (Christensen & Pauly 1992). It has been used mainly in the context of ecosystem-based management but is not limited to this subject. EwE is composed of several modules permitting static or dynamic simulations; the Ecopath component provides a mass-balanced snapshot over a time step of the ecosystem (Christensen & Walters 2004). It has been applied to many ecosystems, but rarely to pond aquaculture despite its successful application in a Chinese polyculture system in 1993 by Ruddle & Christensen (1993). We identified 4 additional studies that used Ecopath to model aquaculture systems, 3 of them specific to Asia. Xu et al. (2011) developed a trophic web model of tilapia culture in a mangrove system. Zhou et al. (2015) used Ecopath to understand the trophic web in a grass carp culture pond, and Feng et al. (2017) analyzed the trophic structure of a crab polyculture system. Gamito et al. (2020) analyzed the trophic structure of IMTA systems in a coastal area of southern Portugal. To date, no models of freshwater European polyculture systems have been published in scientific journals.

In this study, our objective was to better understand the processes underlying different management practices of pond polyculture, combining experimental work with an Ecopath modeling exercise. Based on the experimental results, our knowledge and the Ecopath model simulations, we expected to infer the fish diets and resource use. This framework is proposed as a basis for the more efficient and environmentally friendly management of a freshwater pond system in a European context.

2. MATERIALS AND METHODS

2.1. Experiment

The experiment was performed on an experimental fishpond farm (U3E) located in Le Rheu (France), from 1 March to 8 December 2016 (280 d). The experimental design consisted of 3 treatments — semi-extensive (SE), intensive (I) and intensive coupled (IC) — that were performed in six 500 m^2 freshwater ponds (2 replicates) with a mean depth of 0.8 m. Nets protected the ponds from bird predation. No water renewal system was used, but water was added to compensate for seepage and evaporation. The fish assemblage consisted of a polyculture of common carp *Cyprinus carpio* as the main species, roach *Rutilus rutilus* and rudd *Scardinius erythrophthalmus* for their omnivorous and pelagic habit, and Eurasian perch *Perca fluviatilis* as a carnivore. Given the similar feeding habits of roach and rudd and the difficulty in identifying their offspring, we merged the 2 species into the 'roach' group for the model construction. At the beginning of the experiment, all ponds were stocked with the same ratio of species, but the SE treatment had half the fish density (per m^2) of the other 2 treatments (Table 1).

Table 1. Initial composition of the fish assemblage in semi-extensive (SE), intensive (I) and intensive-coupled (IC) ponds

Species	Mean wet weight (g)	Individuals pond^{-1} SE	I	IC
Common carp	7.5	330	660	660
Roach	40.7	25	50	50
Rudd	43.2	5	10	10
Eurasian perch	11.0	5	10	10

Fish in the I and IC ponds were fed a formulated feed (32% protein, 9% fat, with 15% of ingredients from marine fish) at the same rate (ca. 3% of carp live weight d^{-1}). In the IC treatment, the fish-rearing pond was coupled with a planted pond of the same area; thus, its overall initial fish density (including the planted pond) equaled that of the SE treatment. Pumping and overflow maintained the water level. The main macrophyte species in the planted ponds were watercress *Nasturtium officinale*, water lily *Nuphar lutea*, manna grass *Glyceria aquatica* and pickerel weed *Pondeteria cordata*.

Physical parameters of water quality (i.e. oxygen concentration, temperature, pH, turbidity) were measured once per week, and water was sampled and analyzed once per month to determine concentrations of nitrogen and phosphorus compounds. Sediments in each pond were sampled at the beginning and end of the experiment to analyze their nitrogen, phosphorus and carbon concentrations. Chlorophyll concentrations, which represented blue-green algae (Cyanophyceae), green algae (Chlorophyceae, Tebrouxiophyceae and Zygophyceae) and brown algae (Dinophyceae and Bacillariophyta), were measured once per month using a fluorometer phytoplankton analyzer (PHYTO-PAM, Walz). Biodiversity and production of benthic macroinvertebrates were assessed in May and September by sampling the ponds' biotopes using the PLOCH protocol (Oertli et al. 2005). Zooplankton production was also assessed once per month by sampling the water column, using a method previously adapted to ponds (Hanson et al. 2007, Roucaute & Quemeneur 2007). At the end of the experiment, the ponds were drained and the fish were collected and measured for length and mass. Water quality was also tested. Except for the monitoring of biodiversity and the fish species in the assemblage, the experimental design was similar to that of Jaeger & Aubin (2018).

2.2. Modeling

Ecopath assumes a mass-balance of the ecosystem over a large time frame (usually 1 yr), based on the conservation of energy in which the energy or mass entering each trophic group (or species) equals the energy or mass leaving it (Christensen 2009). This mass-balance assumption supports the equations for production (P) and consumption (C) (Christensen et al. 2005):

$$P = \text{catches} + \text{predation mortality} + \text{biomass accumulation} + \text{net migration} + \text{other mortality} \quad (1)$$

$$C = \text{production} + \text{respiration} + \text{unassimilated food} \quad (2)$$

Once applied to each trophic group (or species) that is considered essential for the ecosystem, these equations determine the contribution of each group to ecosystem productivity. Several parameters must be defined to run the model, such as the average biomass (B) and the P:B and C:B ratios.

The following points describe the methodology for model input estimations:

• Trophic groups, each of which contains one or more species with similar feeding habits. We defined groups for perch, carp, adult roach, juvenile roach, crayfish *Procambarus clarkii* (which grew spontaneously in the ponds), macroinvertebrates, zooplankton, phytoplankton, detritus/organic matter and formulated feed (Table 2). Each trophic group was classified as either detritus, a producer or a consumer. Formulated feed, as an inert input, was classified as detritus (having a trophic level [TL] of 1) as proposed by Bayle-Sempere et al. (2013).

• In our study, B and P were calculated in g of dry matter m^{-2} over a rearing period of 280 d.

Table 2. Trophic groups considered in the food web model of ponds

Trophic class	Trophic group	Note
Consumer	Eurasian perch	Single species
Consumer	Common carp	Single species
Consumer	Roach	Roach and rudd combined
Consumer	Juvenile roach	Spontaneous spawning of roachand rudd
Consumer	Crayfish	Exotic species
Consumer	Macroinvertebrate	Group of species (benthic invertebrates >2 mm)
Consumer	Zooplankton	Group of species
Producer	Phytoplankton	Group of species
Detritus	Detritus, organic matter	Multiple origins
Detritus	Formulated feed	Considered as detritus by convention

• B and the P:B ratio of stocked fish: the average B of fish was estimated as the average number (N) × average weight (W). Average W was estimated as the average individual W, i.e. (W_{final} + $W_{initial}$) / 2. Average N was estimated as (N_{end} − N_{start}) / Z, where Z is natural mortality, estimated as $Z = -\ln(N_{end} / N_{start})$, according to Pauly & Yáñez-Arancibia (1994) and Gamito (1998); N_{end} is the number of individuals at harvesting and N_{start} the number of individuals at seeding. The P:B ratio was calculated from data recorded during the experiment. Since no predators or migration occurred in the ponds, the P:B ratio of the fish groups was estimated, based on Christensen & Walters (2004) and Heymans et al. (2016) production equation, as: P:B = BA / B + Z, where BA / B is equal to biomass accumulation (BA = B_{end} − B_{start}) divided by the average B.

All wet weights were converted into dry weights using the conversion factors indicated in Table S1 in the Supplement at www.int-res.com/articles/suppl/q013p311_supp.pdf. Estimates of B were extrapolated to m^{-2} by dividing the estimated B by the pond area (500 m^2).

• B and the P:B ratio of the other trophic groups: for crayfish, macroinvertebrates, phytoplankton and zooplankton, initial B was considered as null, as the experiment started from drained ponds in February. For crayfish and juvenile roach, B was estimated as the average individual weight at harvest divided by 2 and multiplied by the number of individuals at harvest since we did not have detailed information on the population dynamics of these 2 species. For macroinvertebrates and zooplankton, B was calculated from invertebrate samples taken at different points of the ponds, as described by Bayona et al. (2014) and Bayona et al. (2015). For phytoplankton, B was calculated from the measured chlorophyll concentrations, assuming a fixed carbon content (50 mg carbon mg^{-1} chlorophyll) (Zhou et al. 2010) and the Redfield ratio (106:16:1) (Redfield 1934). For detritus, B was calculated from the carbon concentration in the upper 2 cm of sediments in each pond, using the conversion ratio of 1.74 from C to organic B (Nelson & Sommers 1996). For the formulated feed (considered as an import), B was calculated from the mean amount of feed fed daily.

For crayfish, the P:B ratio used the value proposed by Anastácio & Marques (1995). For invertebrates, the P:B ratio was estimated from models of macroinvertebrates (Morin & Dumont 1994) and zooplankton (Zhou et al. 2010). For phytoplankton, the P:B ratio was estimated by assuming absorption of 3.7 g of carbon g^{-1} of chlorophyll h^{-1} of daylight (3772 h in our study) (Cloern et al. 1995).

• The C:B ratio of each trophic group: for fish groups, C:B ratio was calculated using the equation of Palomares & Pauly (1998). For crayfish, an estimate of the C:B ratio came from Croll & Watts (2004); for other invertebrates (zooplankton and macroinvertebrates), C was estimated as 30% of P (Feng et al. 2017).

• Ecotrophic efficiency (EE), the fraction of P that is accumulated or utilized within the system for predation or export (Christensen & Pauly 1998), was estimated by EwE from the B and P:B and C:B ratios introduced and from the diet relationships. The proportion of unassimilated food was defined as 0.2 and 0.4 of C for fish and invertebrates, respectively (Winberg 1980).

• The diet composition of each consumer trophic group. We used a 3 step method (1) initial estimates from the literature, especially FishBase (Froese & Pauly 2020) for fish and Tachet et al. (2010) for macroinvertebrates; (2) after balancing the model, by comparing the results to those of other Ecopath models of aquaculture systems, to check the consistency of the main indicators (EE and respiration) (Ruddle & Christensen 1993, Xu et al. 2011, Zhou et al. 2015, Feng et al. 2017) and (3) by increasing EE by stepwise adjustments of the consumers' diets based on the availability of food sources in the ponds and our knowledge of pond food webs and species behavior. From this diet composition, the software calculated a theoretical TL for each trophic group.

Other indicators permitting us to evaluate the performance of the ecosystem are calculated by EwE. Among them, we selected 3 that are commonly used in the literature:

• The System Omnivory Index (Libralato 2013), which quantifies the distribution of the feeding interactions among TLs of the food web

• The Connectance Index (Christensen & Pauly 1993), which is the ratio of observed connections to potential connections in the food web

• Finn's Cycling Index (Finn 1976), which describes the percentage of ecosystem throughput that was recycled.

Moreover, the pedigree index was calculated based on an estimate of the degree of confidence in each parameter to evaluate the overall quality of the Ecopath model (Christensen & Walters 2004, Morissette 2007).

3. RESULTS

3.1. Fish productivity

Fish productivity at harvest was calculated by subtracting the initial B at stocking from the final B at harvest measured in the experiment. This varied among treatments: mean of 29.5 kg in SE (590 kg ha^{-1}), 104.2 kg in IC (2045 kg ha^{-1}) and 120.2 kg in I (2401 kg ha^{-1}) (Fig. 1, Table S2). Productivity appeared to be influenced by the use of feed (i.e. the large difference between SE vs. I and IC) and the addition of the planted pond, which decreased mean productivity by 13%. Fish B was mainly from common carp, which contributed 73, 91 and 94% of total harvested fish weight in SE, IC and I, respectively. Therefore, fish productivity depended greatly on the final mean weight of individual carp observed at harvest (101.4 g in SE, 186.3 g in IC, 236.5 g in I) and on fish density at stocking (SE density half that of IC and I). Treatment had no influence on the mean weight of individual roach, which ranged from 85.4–114.7 g at harvest. As expected, roach spawned spontaneously during the experiment, and the number of juvenile roach at harvest varied greatly among ponds (7–1138), regardless of the treatment. At harvest, the mean weight of individual Eurasian perch ranged from 72.6–126.2 g among ponds, and 0–289 exotic crayfish had settled and spawned in each pond, regardless of the treatment.

3.2. Ecological performances

Flow diagrams of the food web varied among treatments (Fig. 2). They provide a picture of the size of the different trophic groups in the ecosystem and the intensity of the trophic links among them. In particular, we can observe the dominance of the detritus

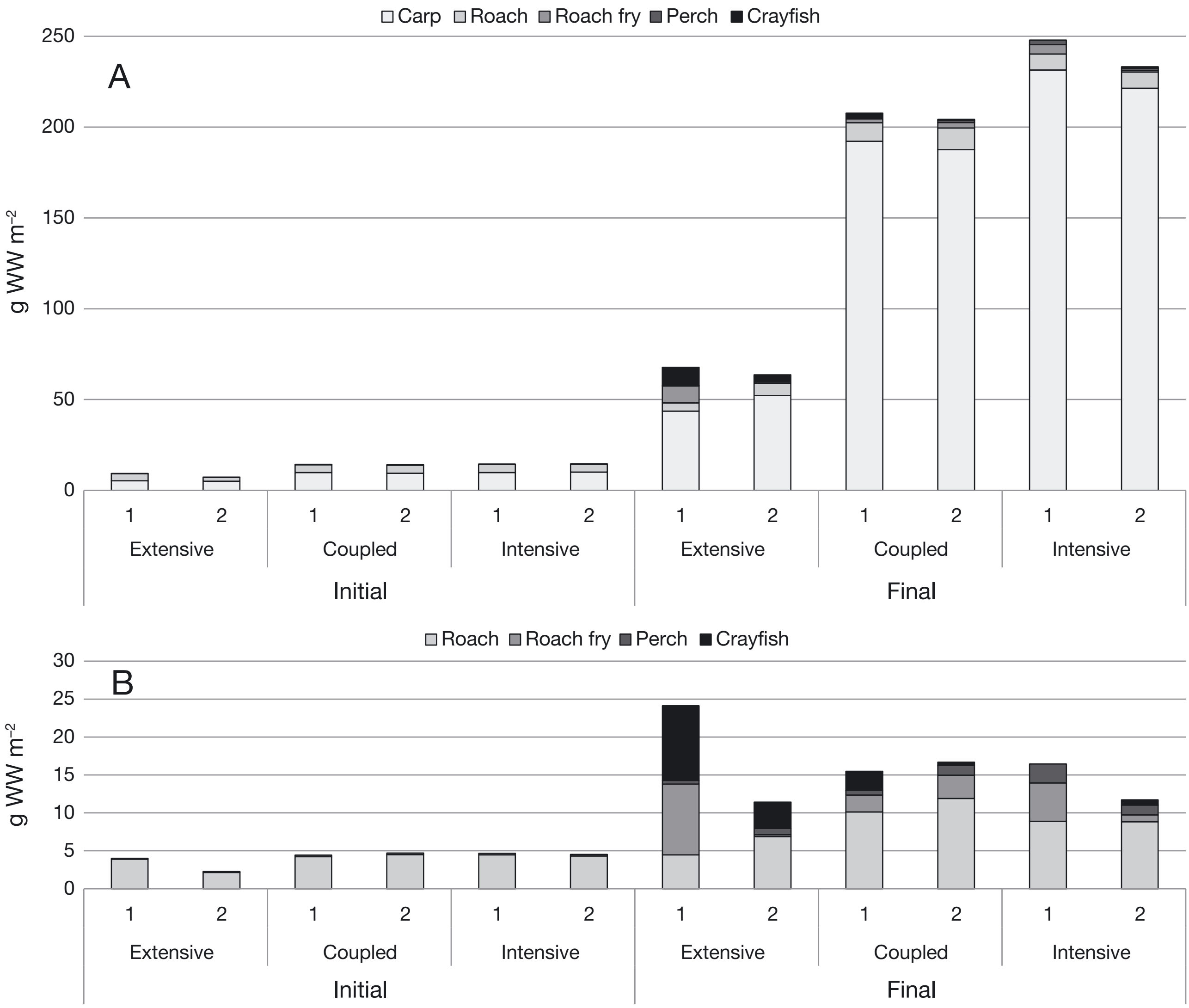

Fig. 1. Fresh biomass per surface unit (g wet weight m^{-2}) of the different reared species at stocking (initial) and harvesting (final). (A) all reared species; (B) all species without common carp

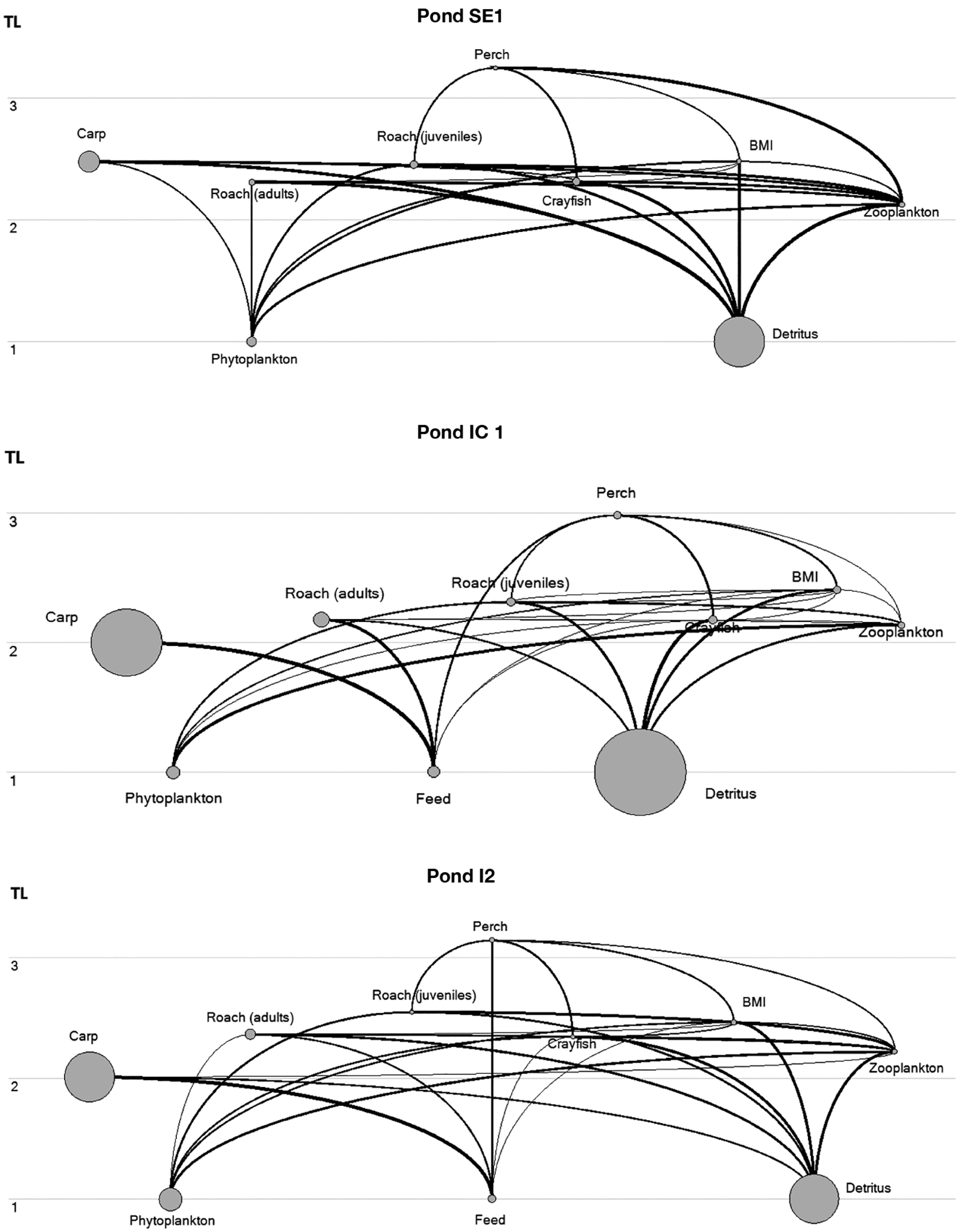

Fig. 2. Flow diagram of the food web as a function of trophic level (TL) in the 3 treatments: Pond SE1: semi-extensive pond no. 1; Pond IC1: intensive pond coupled with a planted lagoon no. 1; Pond I2: intensive pond no. 2. BMI: benthic macroinvertebrates. Circles are proportional to the biomass on a logarithmic scale

group and the fundamental role of phytoplankton in supporting the trophic web. Carp was the dominant fish species, but fed mainly on formulated feed, while roach had a more diversified diet. Despite their moderate size, the zooplankton and benthic macroinvertebrate groups appear to play an important role in the different fish group diet. These observations are supported by the input values of estimated B and the P:B ratio for each pond (Table 3). The mean B in each pond was dominated by detritus (33.84–72.2 g m^{-2}), which represented a large potential food source. The P:B ratio in each pond was dominated by phytoplankton (118.6 g m^{-2}). Phytoplankton B was lower in the IC ponds, probably due to competition for dissolved nutrients between phytoplankton and macrophytes in the planted lagoon. Zooplankton B was highest in SE ponds (0.54–0.58 g m^{-2}), 50% lower in I ponds (0.27 g m^{-2}) and more than 80% lower in IC ponds (0.03–0.09 g m^{-2}). As observed for fish productivity, fish B was dominated by common carp (78–95%), with a large difference between the fed ponds (I and IC) and non-fed (SE) ponds. Nevertheless, the P:B ratio of carp (1.70– 1.91 for 280 d) was lower than that of the roach juveniles and crayfish (2 and 5 for 280 d, respectively).

The trophic groups presented different ecological performances (Table 4). Carp and roach (adults and juveniles) had similar EE among the treatments (0.80–0.95). The EE of perch varied between 0.44 and 1.00. The lowest value is related to the higher observed mortality in the IC1 pond, while the highest value reflects the lack of mortality in the I1 pond. The EE in crayfish was more variable (0.59–0.94), highlighting the difficulty in optimizing their C by other trophic groups by the modeling process. Regardless of treatment, macroinvertebrates and zooplankton had an EE of nearly 1 (0.89–1.00), which indicates that they were intensively preyed upon by other species. Formulated feed also had high EE (0.95–0.99) in all ponds, indicating that it was fully used in the ponds. Phytoplankton and detritus had the lowest EE (0.04–0.23) in the IC and I, which mirrored their inefficient use in the fed ponds. Their EE was higher in SE (0.25–0.59), where they represent a more exploited food resource.

Table 3. Estimated average biomass (B, g m^{-2}) and production:biomass ratios (P:B) for a 280 d rearing period of the trophic groups in replicates 1 and 2 of the semi-extensive (SE), intensive-coupled (IC) and intensive (I) ponds, based on experimental observations

	SE1		SE2		IC1		IC2		I1		I2	
	B	P:B	B	P:B	B	P:B	B	P:B	B	P:B	B	P:B
Eurasian perch	0.09	1.56	0.13	1.63	0.15	1.62	0.22	1.60	0.34	1.68	0.20	1.48
Common carp	7.40	1.70	8.96	1.77	30.36	1.85	30.01	1.86	38.64	1.91	35.12	1.88
Roach	0.84	0.74	1.11	0.99	1.79	0.76	2.06	0.97	1.67	0.74	1.66	0.73
Juvenile roach	1.16	2.00	0.03	2.00	0.35	2.00	0.89	2.00	0.63	2.00	0.11	2.00
Crayfish	1.16	5.00	0.41	5.00	0.30	5.00	0.10	5.00			0.08	5.00
Macroinvertebrate	0.25	14.50	0.20	17.64	0.19	13.29	0.30	15.37	0.58	10.79	0.37	13.36
Zooplankton	0.54	92.43	0.58	83.58	0.09	53.71	0.03	87.14	0.27	72.84	0.27	80.37
Phytoplankton	1.92	118.66	2.66	118.62	1.31	118.62	0.61	118.66	2.26	118.62	6.41	118.62
Detritus	48.81		41.76		56.48		72.20		43.67		33.84	
Feed					0.87		0.87		0.87		0.87	

Table 4. Ecological performances calculated by Ecopath. EE: ecotrophic efficiency; TL: trophic level of the trophic groups in replicates 1 and 2 of the semi-extensive (SE), intensive-coupled (IC) and intensive (I) ponds

	SE1		SE2		IC1		IC2		I1		I2	
	EE	TL	EE	TL	EE	TL	EE	TL	EE	TL	EE	TL
Eurasian perch	0.67	3.24	0.86	3.20	0.44	2.98	0.78	2.93	1.00	3.02	0.93	3.14
Common carp	0.82	2.48	0.80	2.31	0.87	2.00	0.85	2.00	0.80	2.01	0.86	2.01
Roach	0.81	2.31	0.95	2.31	0.96	2.18	0.87	2.07	0.81	2.30	0.80	2.36
Juvenile roach	0.82	2.45	0.93	2.44	0.90	2.31	0.87	2.11	0.84	2.51	0.86	2.55
Crayfish	0.94	2.31	0.86	2.21	0.59	2.17	0.94	2.14			0.82	2.34
Macroinvertebrate	0.95	2.48	0.89	2.20	0.98	2.41	0.91	2.39	1.00	2.31	0.97	2.46
Zooplankton	0.92	2.12	0.94	2.18	0.96	2.14	0.94	2.11	0.89	2.16	0.98	2.22
Phytoplankton	0.25	1.00	0.25	1.00	0.07	1.00	0.14	1.00	0.15	1.00	0.04	1.00
Detritus	0.59	1.00	0.41	1.00	0.08	1.00	0.16	1.00	0.23	1.00	0.11	1.00
Feed	–		–		0.95	1.00	0.95	1.00	0.99	1.00	0.99	1.00

Given the observed size of the trophic groups and the stepwise modeling procedure, we obtained resulting diets of fish and other consumer groups, which varied among ponds (Fig. 3, Table S3). We obtained differences among treatments but similar patterns between the 2 replicates of each treatment. Fed and non-fed treatments differed greatly. In non-fed treatments, common carp and roach (adults and juveniles) are expected to feed mainly on detritus and zooplankton. In fed treatments, common carp are expected to feed mainly on formulated feed — more so in IC (100 %) than in I (85 %) ponds — and adult roach are expected to feed more on formulated feed and detritus. Roach (adults and juveniles) are expected to adapt their diet to the resources available in each treatment, especially the zooplankton in the I ponds. When zooplankton are available (in I and SE), they can be a major food source for juvenile roach, along with detritus. Phytoplankton could be a secondary food source for juvenile roach. Eurasian perch are expected to feed mostly on zooplankton in the SE ponds, and more on macroinvertebrates and crayfish in the IC and I ponds, when they are available. Perch are also expected to feed on juvenile roach and, in the IC and I ponds, on formulated feed. This specific diet resulted in the highest TL among the trophic groups (2.93–3.24) (Table 4). The resulting TL of roach ranged from 2.07–2.55, depending on the availability of zooplankton and macroinvertebrates, with higher TL values for the juveniles due to the higher inclusion of zooplankton in the diet. The resulting TL of common carp ranged from 2.31–2.48 in the SE ponds and 2.00–2.01 in the IC and I ponds due to their dependence on formulated feed (considered detritus by convention in Ecopath).

Complementary indicators qualifying the balance and quality of the ecosystem are provided in Table S4. The System Omnivory Index was higher in the SE ponds (0.21–0.27) than in the I and IC ponds (0.11–0.21). The Connectance Index ranged from 0.39–0.49 in our study, which was higher than those in studies by Xu et al. (2011) (0.24), Bayle-Sempere et al. (2013) and Feng et al. (2017) (0.24, 0.19 and 0.27, respectively). Finn's Cycling Index ranged from 12–17 % for SE and 1–4 % for I and CI, which indicates more recycling in the non-fed ponds.

4. DISCUSSION

The observed fish yields (580–2478 kg ha^{-1}) were particularly high for traditional freshwater polyculture ponds in France, which are usually extensive and usually yield ca. 200 kg ha^{-1} (A. Toqueville pers. comm.). These positive results were due to the relatively small size of the ponds (which tend to be more productive), the relatively high level of fish stocking and the protection from bird predation (nets). Nonetheless, these yields are lower than those of intensive pond systems in tropical countries, which can reach several 10s of t ha^{-1} yr^{-1} (Phan et al. 2009).

Total fish P came mainly (64–95 %) from common carp B, due to the use of formulated feed. Nahon et al. (2020) used stable carbon and nitrogen isotopes to demonstrate that carp feed almost exclusively on formulated feed when it is not limiting. The decrease in carp P in the IC ponds compared to that of the I ponds (ca. 15 %) is not explained by the use of formulated feed but by the limited availability of other sources of food in the ecosystem (zooplankton and invertebrates), especially during early stages of carp growth (i.e. the beginning of the experiment). The B of invertebrates and zooplankton was more abundant in the I ponds than in the IC ponds during the important early stage of fish growth. Roach also fed on formulated feed when it was available. Nahon et al. (2020) discussed the plasticity of the roach diet, which adapted well to zooplankton and invertebrate availability. As indicated by their high EE, zooplankton and macroinvertebrates played a major role in fish nutrition, especially in non-fed ponds; they can thus be considered factors that limit system productivity. In the SE ponds, we observed that the zooplankton population shifted towards smaller sizes with a higher P potential, which is a likely consequence of intense predation by fish (M. Roucaute et al. unpubl. data). In the fed ponds (I and IC), differences in phytoplankton P may have regulated the zooplankton P.

Conversely, phytoplankton and detritus seemed underused given their high P and low EE. Thus, the pond ecosystems tended to stock organic matter, which accumulated in the sediments. Sediments, which were not included in the food web, can become a major source of nutrients in ponds, depending on management practices and species combinations (Edwards 2015). They were underexploited in this polyculture system. This observation is in accordance with the level of Finn's Cycling index, especially in fed ponds (I and IC).

Phytoplankton had complex interactions in the studied ponds. Adding a planted lagoon to the system improved water quality, buffered daily variations in oxygen and pH and supported biodiversity (Jaeger & Aubin 2018). However, the macrophytes competed with the phytoplankton for nutrients; consequently, the IC ponds had lower phytoplankton

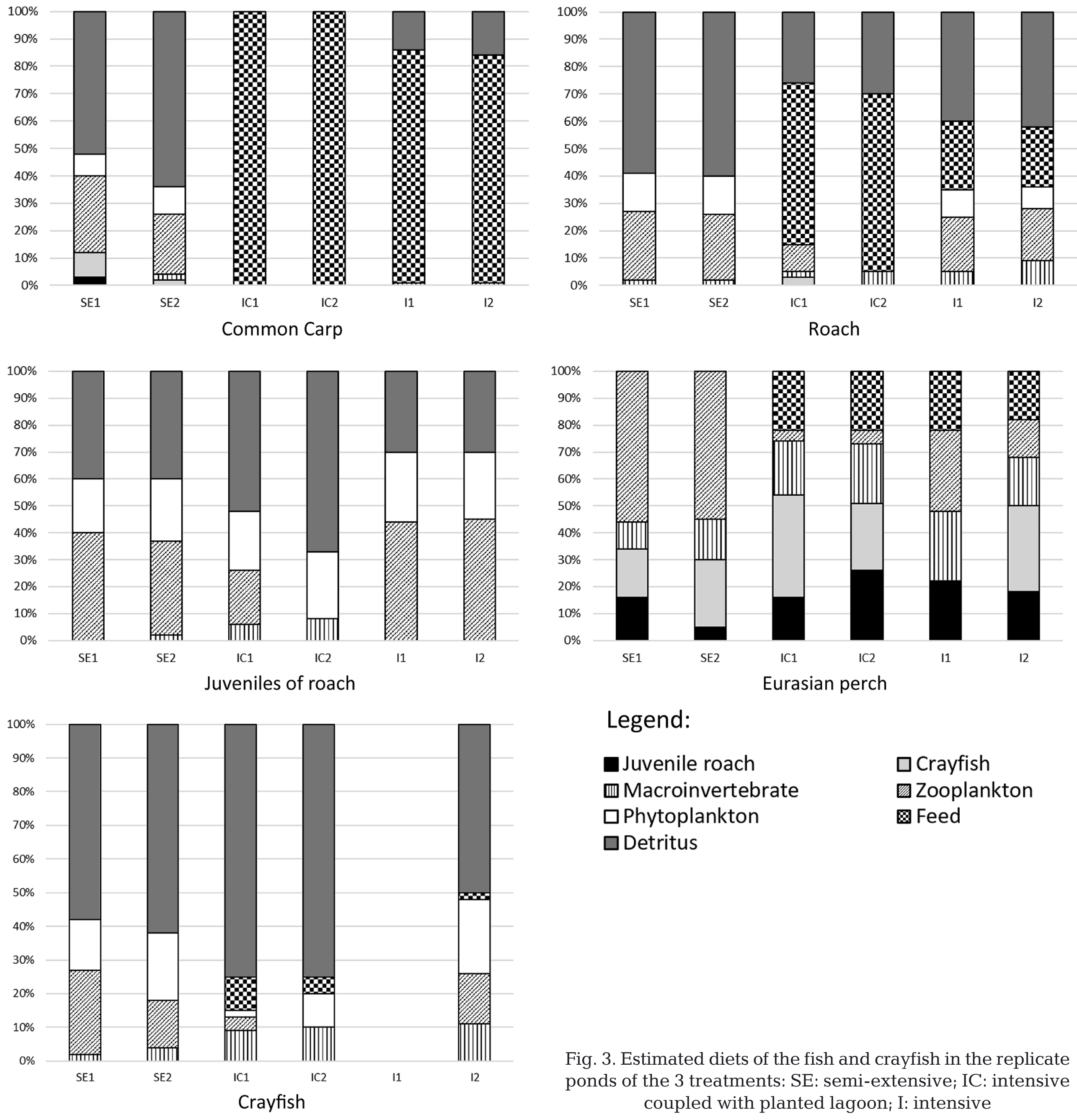

Fig. 3. Estimated diets of the fish and crayfish in the replicate ponds of the 3 treatments: SE: semi-extensive; IC: intensive coupled with planted lagoon; I: intensive

concentrations than the I ponds. This lower concentration did not seem sufficient to support a zooplankton population large enough for the latter's intense predation by fish. Therefore, we did not introduce zooplankton in the modeled diet for roach in replicate 2 of the IC pond due to its low availability. Maintaining a sufficiently large zooplankton population may be useful to sustain overall fish productivity. The inclusion of macrophytes as a functional group could have helped to better characterize the competition between macrophytes and phytoplankton, especially in the IC ponds; however, this was not possible due to the lack of robust data on macrophyte productivity in the planted pond.

In our experiment, we stocked a simplified fish assemblage and mobilized the natural resources of the pond for only one production season. Thus, we induced a limited number of TLs, and the low values of the System Omnivory Index are characteristic of developing ecosystems with a low level of maturity. The values were in the same range as those in other fed polyculture systems (0.08 in Feng et al. 2017 and

0.19 in Xu et al. 2011) or ecosystems modified by formulated feed import (0.129 in Bayle-Sempere et al. 2013). Nonetheless, the Connectance Index indicated more interconnections and fewer linear systems than in those same studies, despite having fewer trophic groups.

The high stocking of carp and the low inclusion of detritus in the diets seemed to decrease the polyculture's recycling potential, which was also degraded by the use of formulated feed. The low level of Finn's Cycling Index seems to corroborate this idea, especially in the fed ponds (I and CI). These values are far lower than those in natural ecosystems, as indicated by Gamito et al. (2020), who compared IMTA systems (2.48%) to a local natural ecosystem (30%). In our ponds, there were few detritus-feeding organisms to consume and recycle the large amounts of organic matter produced. In fact, the detritus EE was low in fed ponds, varying from 0.08–0.23, which indicates that the trophic groups consumed a low quantity of detritus compared to the amount accumulated from several sources such as fish feces and other unassimilated food. Furthermore, the B of phytoplankton was not being consumed, as denoted by the EE varying between 0.04 and 0.25, and flowed into the detritus group. More balanced stocking of fish species could increase the recycling of energy and nutrients and support production of more diversified ecosystem services (Mathe & Rey-Valette 2015, Willot et al. 2019).

Because little of the pond's B was Eurasian perch, this species played a small role in the polyculture and its P varied among the ponds. Nonetheless, the modeled diets of perch suggests its ability to adapt to different food sources, from zooplankton and crayfish to juvenile roach.

According to the model results and the stepwise adjustments of the diets, the spontaneous appearance of crayfish in the ecosystem did not substantially modify the food web. However, crayfish may have contributed to the diet of several species (especially perch) and fed on detritus, which was an underused trophic group. Consequently, although it is an exotic species, crayfish may provide a useful link in the food web and function as a valuable resource for stocked fish predators.

Based on experimental data, expert knowledge and optimization of consumers' diets, the use of Ecopath permitted us to build a quantitative description of trophic flows in freshwater pond polyculture and their potential adaptations to different treatments. However, the modeling procedure has some limitations. When establishing the diets, we maintained the balance between resources and C while also maintaining homogeneity within the treatments and the overall biological requirements of the species. Since the diets of the trophic groups were based on the literature and expert knowledge, stepwise optimization of the diets in each pond may have yielded inaccurate results. This observation agrees with the pedigree index of 0.4 that Ecopath calculated, which indicates a medium-low quality of the model due to the lack of local data (Morissette 2007).

In our experiment, the dominance of one species (common carp) and slight variations in its diet changed the resources available for other trophic groups greatly. Therefore, Ecopath, integrating the mass-balance over a long time scale, likely underestimated the diversity of the diets and their dynamics during the experiment. In particular, due to the high B of carp and the low availability of zooplankton and invertebrates in the fed ponds, it was not possible to represent these groups in the carp diet despite their potential contribution, especially in the early stages.

As suggested in previous studies (Ramsvatn 2013, Nahon et al. 2020), concentrations of natural carbon and nitrogen isotopes among food web compartments could corroborate the estimated diets (Ramsvatn 2013, Nahon et al. 2020). However, the isotopes can only indicate food sources that a given species consumed within a few weeks of sampling. In addition, we were not able to use traditional methods of stomach content analysis due to the small number of individuals in certain fish groups and the fact that analyzing stomach contents would have decreased fish B during the experiment. Moreover, the dynamics of populations of food sources, especially phytoplankton and zooplankton, would have provided only snapshots of the diets rather than an overall understanding of them. Therefore, there is no fully satisfactory option for increasing our confidence in the trophic relationships among the different groups.

One of Ecopath's assumptions is the mass-balance of the ecosystem over a large time scale. Our fish-production system had no equilibrium per se since fish populations grew continually during the rearing period, and therefore we considered the B accumulation.

As a simplification in Ecopath, formulated feed is classified as detritus (TL = 1; Bayle-Sempere et al. 2013); however, feed with fish meal and oil ingredients has a theoretical TL greater than 1. Therefore, although common carp had a TL of only 2 in the IC and I pond models, this species has a TL of 3.1 in FishBase (Froese & Pauly 2020) based on diet studies in natural ecosystems.

5. CONCLUSIONS

Ecopath models successfully described snapshots of the food web of each treatment and helped us to estimate the diets of the key species. The models highlighted the influence of feed on the food web (especially for carp and roach) and the key role of zooplankton and macroinvertebrates in the fish diet. They also helped to identify the consequences of competition for nutrients between phytoplankton and macrophytes in the planted lagoon through the differences in fish diets and the levels in production of the different trophic groups.

The Ecopath model results provided guidance to develop polyculture rearing practices, such as reusing nutrients stocked in sediments, improving phytoplankton use, supporting zooplankton and invertebrate production, managing macrophytes and phytoplankton for better water quality, biodiversity support and overall productivity and emerging new fish assemblages as a tool to balance sustainable polyculture ecosystems. In this study, new knowledge was built on pond polyculture in temperate areas. From this information, it will be possible to draw new experimental designs using Ecopath modeling as a guide to better adapt stocking densities and select species assemblages for the sustainable use of natural resources and to rationalize artificial inputs like feed.

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