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Titel | Title

Diet composition and feeding strategies of early life stages of Danube fish species

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Abstract

Although early feeding patterns strongly influence larval fish survival and growth, detailed knowledge from large river systems remains limited. This thesis investigates species- and stage-specific diet compositions of larvae from eight fish species in the Austrian Danube to identify trophic interactions, feeding strategies, and ontogenetic dietary shifts. Larvae were collected from different inshore nursery habitats of the free-flowing Danube, downstream of Vienna, Austria, in May 2022. Individuals (n = 121) were identified to species level and developmental stage, and their gut contents were analyzed to the lowest feasible taxonomic level. Feeding intensity (gut fullness) varied among species, with *Chondrostoma nasus* showing higher gut fullness than *Abramis brama* and *Rutilus virgo* and later larval stages exhibiting higher gut fullness than earlier stages. Gut length increased with fish length, while no overall correlation was found between fish length and gut fullness. Diet composition differed among species, with mollusks, detritus, crustaceans, rotifers and insects as the most frequent prey. Notable patterns included high insect intake in *C. nasus* and sediment consumption in *Cyprinus carpio*. Multivariate analyses revealed partial dietary overlap among species and ontogenetic shifts in *C. nasus* and *Leuciscus aspius* toward larger, more mobile prey. Diet composition also showed subtle variation among mesohabitats, with the bay exhibiting greater diet variability, suggesting habitat structure may influence larval feeding opportunities. Feeding strategies ranged from generalist to opportunistic, with no species fully specialized. These findings highlight larval feeding flexibility and the role of complex habitats in supporting early fish development in large rivers.

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Introduction

Fishes play an important role in ecosystems due to their influence on food web structures and nutrient cycling (Radenković et al., 2024; Villéger et al., 2017). Moreover, their feeding traits can provide useful insights into ecosystem functioning and trophic dynamics (Radenković et al., 2024).

Feeding ecology is especially critical during early developmental stages, as fish larvae experience high mortality rates in the initial weeks after hatching, primarily due to starvation and predation (Cowan and Shaw, 2002; Wilson et al., 2018). Larvae survival, development and growth during this sensitive period are greatly influenced by their feeding success (Burns et al., 2020; Wilson et al., 2018). Slower-growing individuals have a higher risk of predation because their prolonged larval stage coincides with higher predation pressure (Wilson et al., 2018). Furthermore, their size constraints and limited mobility (Sánchez-Hernández et al., 2019) mean they have specialized feeding requirements. Disruptions in food sources and prey availability can influence fish larvae's recruitment success by leading to high mortality (Cowan and Shaw, 2002; Wilson et al., 2018), which can affect species abundance, population dynamics, and, consequently, ecosystem stability. Hence, understanding feeding patterns in larval stages is crucial for predicting recruitment success (the survival of an annual group of fish through its first year of life), as the year class strength of stock is often set during this time (Burns et al., 2021; Cowan and Shaw, 2002).

Even though prey abundance is often assumed to be high, significant food mechanisms in fish larvae also influence recruitment success (Burns et al., 2020). One such food mechanism is ontogenetic dietary shifts, which are the changes in diet that occur throughout an individual's lifespan (Sánchez-Hernández et al., 2019). These shifts typically reflect changes in morphology, physiology and behavior – such as increased swimming ability, mouth gape, gut length and visual capacity – and allow fish to handle larger or more mobile prey (Reckendorfer et al., 2001). Many fish species feed on zooplankton and phytoplankton as well as small macroinvertebrates in their larval stages, and they change their diet to bigger prey like larger macroinvertebrates, fish and plants or detritus in their later life stages (Sánchez-Hernández et al., 2019).

Another important aspect of feeding patterns is the degree of inter- and intraspecific dietary overlaps, which can be used as an indirect metric of overlapping food niches and potential feeding competition between different species (Uzunova and Dashinov, 2022). Such

overlapping trophic niches can shape trophic interactions, as they may lead individuals to change their foraging behavior to reduce inter- and intraspecific competition (Sánchez-Hernández et al., 2019).

The choice of prey is another significant food mechanism. Simply feeding does not entail the best growth performance, as several fish species larvae selectively feed on prey taxa that ensure optimal growth (and with that survival), indicating that different taxa fulfil different requirements related to energy and essential nutrients (Burns et al., 2021, 2020; Murphy et al., 2013; Robert et al., 2009). This selection is species-specific, and successful feeding on favored prey species typically leads to enhanced larval development and increased survival rates (Burns et al., 2020). Therefore, the variability in preferred prey availability is an important factor for larval survival, and the identification of preferred larval prey is critical for evaluating the connections between larval vital rates and fluctuations in the feeding environment (Wilson et al., 2018).

For a long time, the feeding patterns and prey selection of fish larvae have been the subject of many studies, most of which have been conducted in marine environments (Hunter, 1980; Miller et al., 2019; Østergaard et al., 2005), while few have been carried out in freshwater systems and very few have been conducted in rivers (Reckendorfer et al., 2001; Trochine et al., 2022). Nevertheless, freshwater and, particularly, riverine systems are highly dynamic and under increasing pressure from anthropogenic stressors such as habitat fragmentation, altered flow regimes, sedimentation and pollution – all of which can affect prey availability and habitat suitability for larval fish. In this context, the Austrian Danube, a heavily modified yet ecologically diverse river system, provides a valuable case study for examining early-stage feeding patterns across multiple fish species.

This thesis examines the gut contents and dietary composition of larvae from different early life stages of eight fish species collected in various inshore areas of the main stem of the River Danube. The gut contents, gut fullness and morphological attributes related to feeding are compared between the different species to determine their food spectrum, and the relationships between stage, size, the alimentary tract and food are analyzed. The gut contents are also analyzed to the lowest possible taxonomic level to determine prey composition and identify species- and stage-specific feeding patterns.

The overarching aim of this thesis is to enhance the current understanding of trophic interactions and feeding strategies in developing riverine fish. It provides new, more detailed insights into feeding patterns during a critical phase of the life cycles of fish,

thereby providing information about the quality of different habitats with regard to food accessibility, which is essential for the development of restoration measures in modified large rivers. Specifically, it is hypothesized that (1) gut content composition will differ between species with respect to different food categories and their proportions because different species vary in morphology, feeding behavior and trophic preference, which shape their diet; (2) There will be identifiable patterns of dietary overlap in gut content composition among species, as co-occurring larvae in the same habitats may exploit similar prey resources; (3) the diet composition of the same species will differ between mesohabitats, as prey availability and habitat structure can influence feeding opportunities and selectivity; and (4) the diet composition varies across different developmental stages within a species, as the ontogenetic development – including features such as vision, body size, swimming capabilities, maneuverability, mouth gape, and gut length – affects the food selection and the uptake of prey organisms. By elucidating these patterns, this study aims to provide a deeper understanding of the ecological interactions during the early life stages of Danube fish species.

Material and Methods

Sampling location

The Danube is the second-longest river in Europe, spanning over 2850 km from its source in Germany to its mouth at the Black Sea. Within Austria, the Danube covers 349 km and exhibits an average discharge of 1500 to 1900 m^3s^{-1} (average flow) and is characterized by high current velocities and high sediment transport capacities (Schiemer et al., 1999). Historically, a braided river with extensive floodplains, the Austrian Danube has since been heavily regulated for flood protection, navigation, shipping and energy production. Currently, 10 hydropower stations operate in the Austrian Danube. There are only two free-flowing sections remaining in Austria (Schiemer et al., 1999), one of which is protected by the Alluvial Zone National Park Donau-Auen, established in 1996 (“Nationalpark Donau Auen,” 2025). The other is the Wachau Valley west of Vienna, which has been a UNESCO World Heritage Site since 2000. The samples for this study were taken within the framework of the Integrated River Engineering Project (via donau - Österreichische Wasserstraßen-Gesellschaft mbH, 2025) in different inshore nursery habitats of the main

stem of the free-flowing Danube, downstream of Vienna, Austria, between river kilometers 1884.0 and 1886.7 (Figure 1).

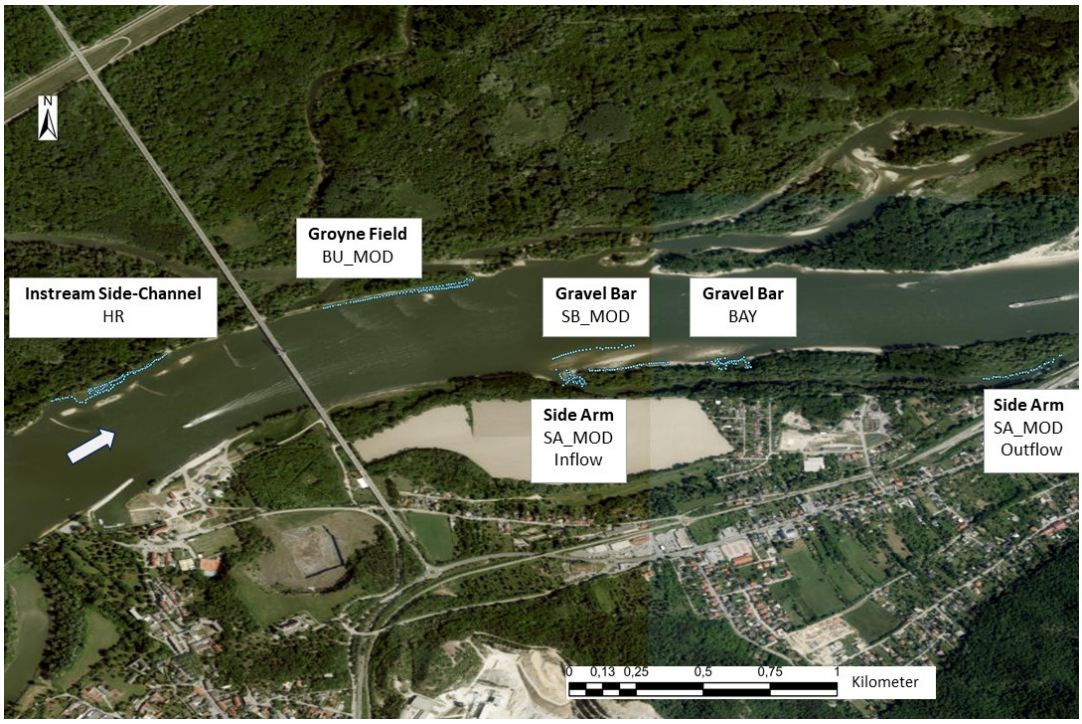


Figure 1: Location of sampling points at different mesohabitats (HR = instream side-channel, BU_MOD = groyne field, SB_MOD = gravel bar, SA_MOD = side arm) for early stages of fish in the Danube, between river kilometers 1884.0 and 1886.7 (Keckeis et al., 2025)

Field sampling method and species identification

The samples for the current study were taken on May 9 and 23, 2022, as part of the monitoring program for the Integrated River Engineering Project on the Danube East of Vienna (FGP) (via donau - Österreichische Wasserstraßen-Gesellschaft mbH, 2025). Point abundance sampling (Persat and Copp, 1989) was carried out to investigate the occurrence and habitat use of early-stage fish during their main season of occurrence. From the total catch, a subsample was taken for the genetic determination of the species and identification of the developmental stage (Wang, n.d.). The developmental stages were determined according to Peňáz (2001). The guts of the 121 individuals representing eight species were dissected under a binocular and fixed in 97% ethanol. The size (total length) of each individual and the length of its gut were measured to the nearest ± 0.1 mm.

Sample processing

First, each gut was examined to estimate the gut-fullness as a percentage. For the dissection, the gut was transferred to an object plate with a drop of water to prevent dehydration. Using dissecting needles, the gut was carefully opened longitudinally, and the contents were gently extracted by scraping, allowing the material to disperse into the surrounding water drop. The sample was then examined systematically under a Leica® (Type DM500) microscope to determine the gut content. This was done by scanning the entire sample from top to bottom and side to side. Microscopic resolutions of 10x and 40x were primarily used. The gut content was categorized into defined food categories: detritus, mucus, algae, plant material, mollusks, crustaceans, rotifers, insects, oligochaetes and fish larvae. The percentage contribution of each category was estimated based on its volume relative to the total gut content, with all categories summing to 100% per sample. The contents were identified at the lowest feasible taxonomic level.

Data analysis

Normal distribution of the variables for various comparisons was tested using the Shapiro-Wilks test. Kruskal-Wallis tests were performed using Past4® (Hammer et al., 2001) to compare gut fullness among species and between developmental stages, followed by Dunn's post hoc test with Bonferroni correction to account for multiple comparisons. The Kruskal-Wallis test was chosen because the data exhibited non-normal distribution. A linear regression analysis was performed in R to examine the relationship between fish length and gut length, as the assumptions for linear regression (normal distribution of residuals, homoscedasticity and linearity) were not violated, justifying the use of a parametric linear model. Gut fullness values were arcsine square-root transformed (McCune and Grace, 2002) beforehand to approximate normality. Non-metric multidimensional scaling (NMDS) analyses were conducted based on Bray-Curtis dissimilarities with the type 1 stress formula in Canoco5 (Šmilauer and Lepš, 2014) to further explore patterns in dietary composition among fish species and developmental stages, as well as between mesohabitats. NMDS was used to identify potential clustering of samples and to infer the influence of distinct prey groups on the trophic niche of each fish species and developmental stage.

Figures and tables were plotted in R using the tidyverse packages (Wickham et al., 2019) and ggplot2 (Wickham, 2016), as well as in Excel® (Microsoft Corporation, 2021).

Results

Of the 121 identified larvae, 43 individuals were nase (*Chondrostoma nasus*), 38 were asp (*Leuciscus aspius*), 20 were roach (*Rutilus rutilus*), five were freshwater bream (*Abramis brama*), four were chub (*Leuciscus cephalus*), four were cactus roach (*Rutilus virgo*), four were common carp (*Cyprinus carpio*), and three were ide (*Leuciscus idus*) (Table 1).

The degree of individual gut fullness varied considerably, ranging from 0% to 100%. Only one individual of *C. nasus* had an empty gut (0% gut fullness); all other individuals contained some food. On average, most species exhibited moderate gut fullness levels (30–50%), including common carp, asp, chub and roach. Freshwater bream and cactus roach showed lower average gut fullness values (<20%), while nase and ide displayed high average levels (>60%). This indicates notable interspecific variation in feeding intensity, which may reflect differences in prey availability, feeding strategies or developmental stages. *C. nasus* exhibited a significantly higher degree of gut fullness (63.3% ± 33.2) compared to *A. brama* (17.0% ± 24.1) and *R. virgo* (8.7% ± 7.5) (Kruskal-Wallis test, $p < 0.001$; Dunn´s post hoc with Bonferroni correction). No significant differences were found among the other species (Figure 2).

Table 1: Data set (individual numbers) for the gut analyses, with the sampling date, the mesohabitat and the developmental stage (Peňáz, 2001) of the analyzed individuals from different fish species. Mesohabitats: SA MOD = side arm; BUC = bay with gravel bar; BU_MOD = groyne field; HR = instream side-channel; SB = gravel bar; SB_MOD = modified gravel bar. L1 – L6 = larval stages one to six.

			Stages					
Species	**Date**	**Mesohabitat**	**L1**	**L2**	**L3**	**L4**	**L6**	**total**
Abramis brama	23.05.22	SA_MOD			1	4		5
Chondrostoma nasus	09.05.22	BU_MOD		5				5
		BUC	2	6				8
		HR		6	5			11
		SA_MOD	1	6				7
		SB		6				6
	23.05.22	BU_MOD		1		1		2
		BUC			1	1		2
		HR				1		1
		SB_MOD				1		1
Cyprinus carpio	23.05.22	BU_MOD				1		1
		BUC		1				1
		SA_MOD		2				2
Leuciscus aspius	09.05.22	BUC		1		2		3
		HR		5	1			6
		SA_MOD		6				6
		SB		11				11
		SB_MOD		1				1
	23.05.22	BU_MOD					1	1
		BUC				4		4
		HR				5		5
		SB_MOD				1		1
Leuciscus cephalus	23.05.22	BUC		3				3
		SA_MOD		1				1
Leuciscus idus	09.05.22	BUC		1				1
		HR		1				1
		SB			1			1
Rutilus rutilus	09.05.22	BUC		1				1
		SB				1		1
	23.05.22	BU_MOD			3	3		6
		BUC			1			1
		HR		1	4	1		6
		SA_MOD			2			2
		SB_MOD			3			3
Rutilus virgo	09.05.22	SA_MOD		3				3
	23.05.22	BU_MOD			1			1
total			3	67	23	26	1	121

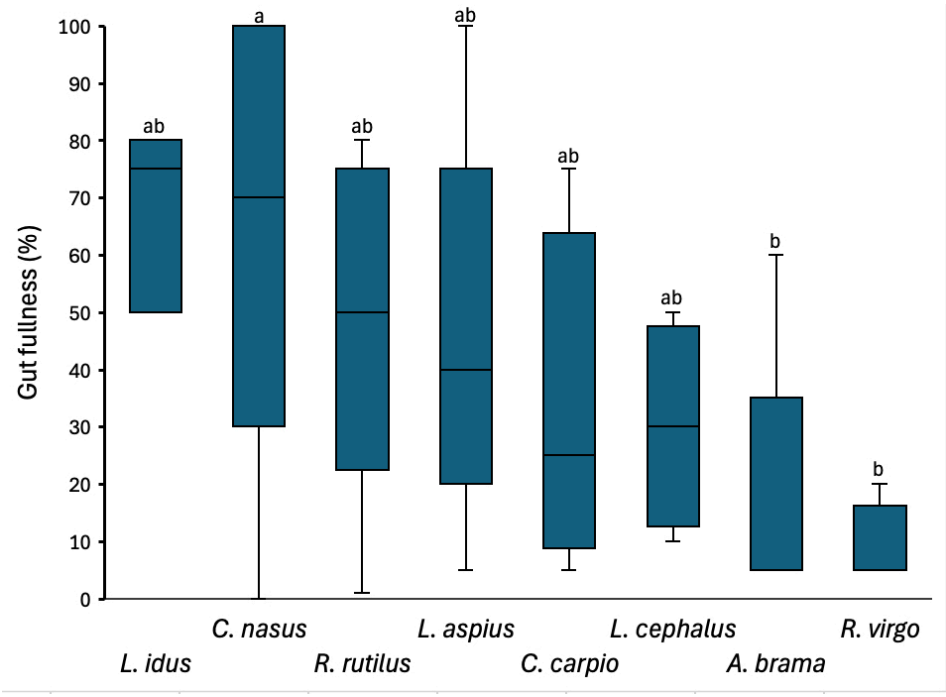


Figure 2: Boxplots of species-specific gut fullness. Species are sorted by median to allow for a better visual comparison. The letters indicate the post hoc test results (Dunn's post hoc with Bonferroni correction).

When considering gut fullness across the developmental stages of all species, a clear pattern emerged: the first larval stage (L1) generally exhibited lower gut fullness compared to later stages. Furthermore, the second larval stage (L2) showed a higher median and variation in gut fullness compared to L1, while L3 exhibited a significantly higher degree of gut fullness than L2 (Kruskal-Wallis test, $p = 0.007$; Dunn's post hoc with Bonferroni correction) (Figure 3).

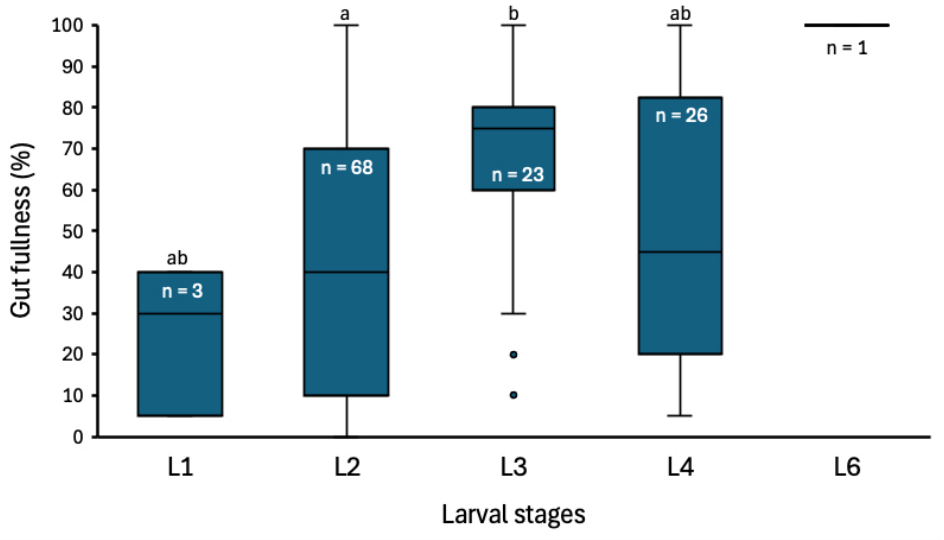


Figure 3: Boxplots of gut fullness across developmental stages for all examined fish species. L1–L6 represent developmental larval (L) stages. N(L1) = 3; n(L2) = 68; n(L3) = 23; n(L4) = 26; n(L6) = 1. L6 was not included in the analysis (n =1). The letters indicate the post hoc test results (Dunn's post hoc with Bonferroni correction).

A similar pattern was found when analyzing the species-specific stages of nase and asp. The L1 stage of nase had a significantly lower degree of gut fullness than L3 and L4 ($p = 0.001$), and in asp, the L2 larvae had significantly lower gut fullness than the L4 larvae ($p = 0.007$) (Figure 4). Since the L3 and L6 of asp consisted of only one individual, they were not tested against the other stages.

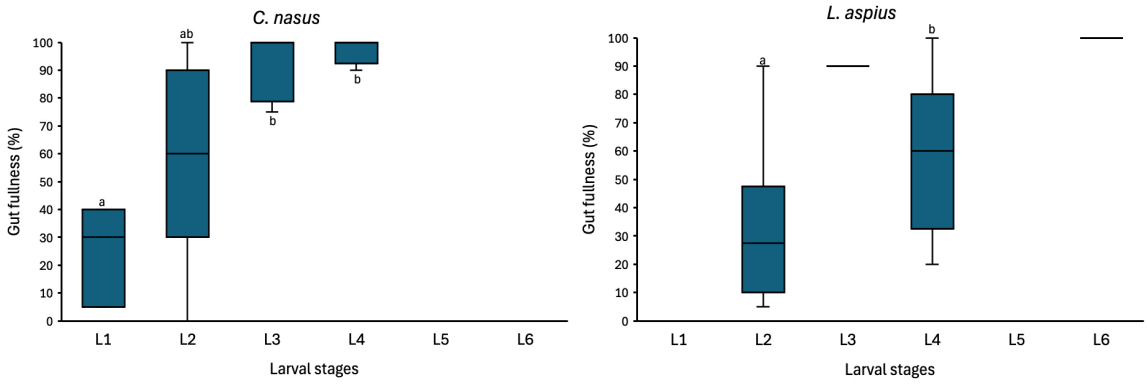


Figure 4: Boxplots of gut fullness across developmental stages for *C. nasus* and *L. aspius*. L1–L6 represent developmental larval (L) stages. N(L1 nase) = 3; n(L2 nase) = 30; n(L3 nase) = 6; n(L4 nase) = 4; n(L2 asp) = 24; n(L3 asp) = 1; n(L4 asp) = 12; n(L6 asp) = 1. The letters indicate the post hoc test results (Dunn's post hoc with Bonferroni correction).

Beyond the developmental stage, body size was also evaluated as a potential factor influencing gut fullness across all species. Overall, no strong correlation was observed between body length and gut fullness, suggesting that size alone does not explain much of the variation in gut fullness. However, the few observed largest individuals tended to exhibit fully filled guts, hinting at a possible threshold effect or size-related advantage in foraging efficiency (Figure 5).

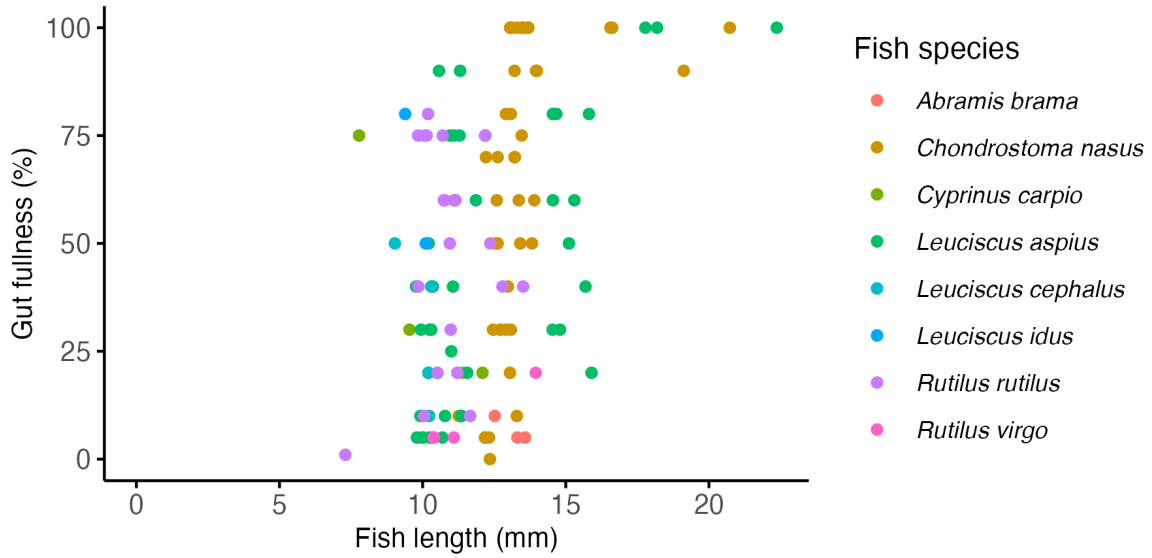


Figure 5: Relationship between fish length and gut fullness across all examined species: x-axis = total fish length, y-axis = arcsine square root-transformed (tr) percentage values of the gut fullness.

A generally strong and significant positive relationship ($p < 0.001$) between fish length and gut length was observed (Figure 6), with fish length explaining 76% of the variation in gut length. According to this model, gut length increases by approximately 0.47 mm for every 1 mm increase in fish length.

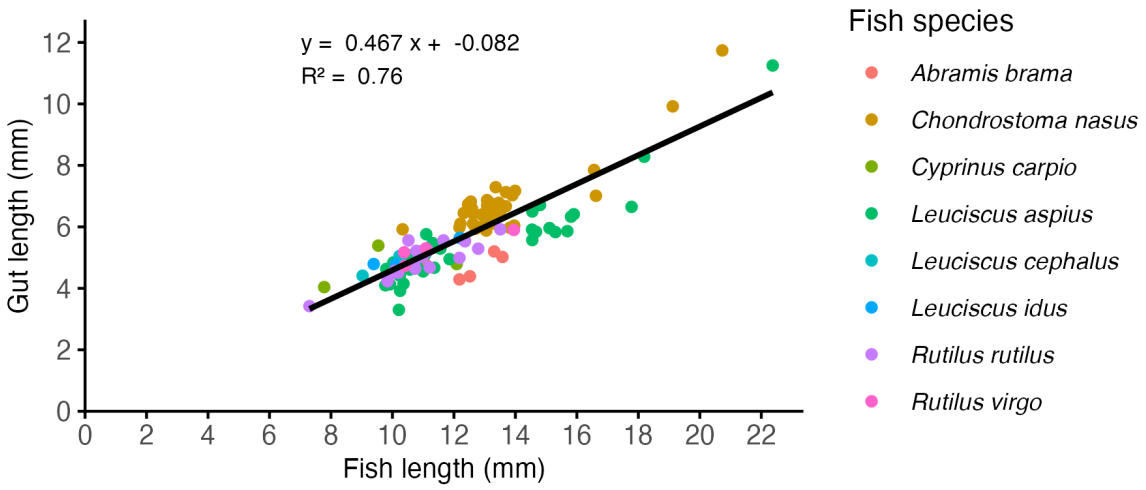


Figure 6: Relationship between fish length and gut length of the pooled data from all species (n = 121). The indicated formula represents the parameters of the fitted linear regression model (black line): y = gut length in mm; x = fish length in mm.

Diet composition

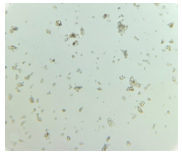
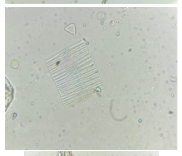
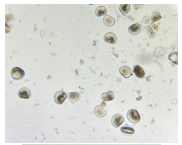
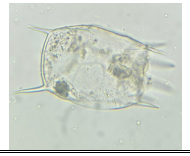
The diet composition differed among fish species, particularly in the proportions of the various food categories. A detailed overview of the proportional distribution of food categories across all examined species is provided in Table 2. Mollusks were the category with the highest percentage across all species, often in considerable quantities. In several cases, they occurred in dense aggregations within the gut content. The highest proportional number of mollusks was found in roaches. The second-most frequent category present in all examined fish species was detritus, referring to organic material that cannot be further identified under the microscope. The freshwater bream showed the highest proportion of detritus in its gut. In four of the six examined fish species (nase, asp, chub and roach), a variety of insects (both in their larval and adult stages) was found. The majority of larval insects belonged to Chironomidae, while among the adults, a few Thysanoptera and Diptera were detected. Overall, the insect composition was taxonomically diverse. Crustaceans were found in all examined fish species. Rotifers also occurred in all examined fish species except the common carp. All identified rotifers were Keratella sp. The identified crustaceans consisted mostly of copepods, naupliae and some cladocerans. Crustaceans were proportionally most abundant in the guts of common carps and rotifers in the guts of ides. Algae were found in all fish species albeit in small quantities. Most of the identified algae were diatoms. They were often distributed around other food items, like oligochaetes

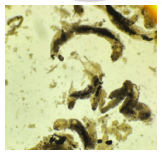
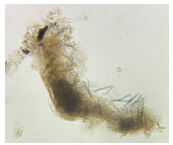
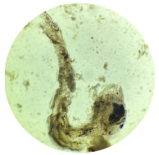
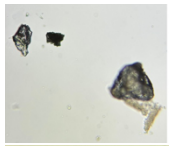
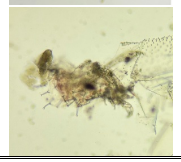
or insects, which could indicate that they are taken up together with those other food items. Several *Closterium* sp. and one *Pediastrum* sp. (in an L2 nase) were identified. The highest proportions of algae were found in the chub. In addition to algae, plant material was found in the guts of common carp, chub, roach and nase. These structures were identified as vascular bundles. The common carp had the most plant material in their guts proportionally. Oligochaetes represented a minor food category, observed in some guts of cactus roach, roach, nase and asp (see Table 2 for detailed proportions). Since the oligochaetes were already quite well digested or split up into pieces, they were identified mostly by their bristles. The findings of oligochaetes were always accompanied by diatoms. Oligochaetes were distinctly the most abundant in the guts of cactus roaches. Another smaller fish larva was found in the gut of one asp individual. Mucus was noticed in small quantities in the guts of nase, asp and roach. The category "other" comprises clearly visible but unidentified structures or prey items. Sediment particles were also included in this category. Table 3 shows exemplary images of characteristic items of the different food categories

Table 2: Average (± standard deviation) percentages of the different food categories of the gut content of examined fish species.

Fish species	Detritus	Mucus	Plant material	Algae	Mollusca	Crustacea	Rotifera	Insects	Fish larvae	Oligochaeta	Other
A. brama	56,6 ± 11,3	0,0 ± 0,0	0,0 ± 0,0	1,4 ± 2,1	36,0 ± 15,2	2,6 ± 5,8	3,4 ± 4,8	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
C. nasus	19,2 ± 30,2	0,2 ± 0,9	1,8 ± 5,8	3,5 ± 6,3	12,3 ± 16,9	7,1 ± 17,5	2,6 ± 4,6	47,3 ± 38,6	0,0 ± 0,0	3,4 ± 12,9	0,3 ± 1,7
C. carpio	28,0 ± 42,2	0,0 ± 0,0	25,0 ± 50,0	0,5 ± 0,6	2,8 ± 4,3	23,8 ± 47,5	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0	20,0 ± 40,0
L. aspius	17,7 ± 21,1	0,2 ± 0,9	0,5 ± 2,5	2,5 ± 4,1	33,2 ± 27,1	12,1 ± 13,9	8,1 ± 10,9	20,9 ± 29,0	2,4 ± 14,6	2,4 ± 8,8	0,1 ± 0,3
L. cephalus	25,0 ± 23,5	0,0 ± 0,0	12,5 ± 12,6	7,5 ± 5,0	36,3 ± 23,6	2,5 ± 5,0	3,8 ± 4,8	12,5 ± 25,0	0,0 ± 0,0	0,0 ± 0,0	0,0 ± 0,0
L. idus	13,0 ± 11,3	0,0 ± 0,0	0,0 ± 0,0	7,3 ± 5,5	42,3 ± 32,2	17,3 ± 25,8	15,0 ± 5,0	0,0 ± 0,0	0,0 ± 0,0	5,0 ± 8,7	0,0 ± 0,0
R. rutilus	22,2 ± 25,0	0,1 ± 0,4	2,4 ± 4,1	1,9 ± 3,0	46,8 ± 23,4	8,5 ± 8,3	8,0 ± 15,2	6,3 ± 13,7	0,0 ± 0,0	4,0 ± 12,2	0,0 ± 0,0
R. virgo	37,5 ± 40,9	0,0 ± 0,0	0,0 ± 0,0	6,3 ± 7,5	15,0 ± 23,5	12,5 ± 18,9	8,8 ± 8,5	0,0 ± 0,0	0,0 ± 0,0	20,0 ± 40,0	0,0 ± 0,0

Table 3: Example images of representative food categories with the associated image metadata. Objects' sizes were estimated based on their proportion within the field of view, calculated using the eyepiece field number (FN = 18) and the objective magnification (Field of View = FN / objective magnification).

Food Category	Image	Image Metadata		
		Description	Magnification	Est. object size
Detritus		particulate organic matter	10x	49µm
Algae		Fragilaria sp.	40x	28µm
Plant material		vascular bundles	40x	338µm
Molluscs		aggregation of small molluscs	10x	86µm per mollusc
Crustaceans		Cladocera sp.	10x	675µm
Rotifers		Keratella sp.	40x	150µm

Food Category	Image	Image Metadata		
		Description	Magnification	Est. object size
Insects		Adult Thysanoptera	10x	1,35mm
		several chironomid larvae	4x	1,13mm per larvae
Oligochaetes		Oligochaete with bundles of bristles	10x	1,08mm
Fish larvae		fish larvae as prey	4x	6,75mm
Other		small, transparent sediment	10x	225µm for the biggest
		not identified object	10x	360µm

The distribution of food categories among the eight fish species showed considerable variation (Figure 7). Across all studied species, the prey categories with the highest level of occurrence were predominantly composed of small-sized prey items such as detritus, mollusks, crustaceans and rotifers (except for the high abundance of insects in *C. nasus*). An exemplary overview of average prey sizes can be found in Table 3. *R. rutilus* contained the highest average proportion of mollusks, at 46.8%, followed by detritus (22.2%). Crustaceans and rotifers were present at very similar proportions of 8.5% and 8.0% respectively, making up over 75% of the average gut contents with the first two categories combined. Insects, oligochaetes, plant material, algae and mucus contributed to the diet in smaller amounts. At first glance, *L. idus* showed a similar pattern, with mollusks accounting for 42.3% and detritus comprising 13.0% of the average gut content. However, the relative numbers of crustaceans and rotifers were approximately twice those of *R. rutilus* (17.3% and 15.0%, respectively). *L. idus* had the highest average proportion of rotifers in their guts, while algae and oligochaetes contributed a smaller proportion. *L. cephalus* showed high proportions of mollusks, at 36.2% and detritus, at 25%, and more evenly distributed fractions of plant material, insects and algae (highest average proportion across species), followed by crustaceans and rotifers, which showed comparatively small proportions. The fish species showing the highest average proportion of detritus (56.6%) was *A. brama*. Meanwhile, mollusks accounted for 36.0%, and the remaining proportions were rotifers, crustaceans and algae. High average proportions of mollusks (33.2%) and detritus (17.7%) were also found in *L. aspius*, with an additional high amount of insects (20.9%). Crustaceans and rotifers contributed a distinct amount, followed by algae, oligochaetes, mucus, plant material and "other." A single individual in the sixth and final larval stage of *L. aspius* contained another fish larva in its gut.

R. virgo showed a different distribution of food categories compared to the other species. Although detritus remained a dominant component at 37.5%, oligochaetes represented the second-most abundant category and reached their highest relative proportion among all species examined (20%). Despite this difference, mollusks, crustaceans and rotifers made up a significant portion of the gut contents, followed by algae. *R. virgo* did not contain plant material. *C. nasus* had the highest proportion of insects of all examined species (48.4%). Detritus and mollusks were found in smaller quantities (19.6% and 12.6%, respectively), followed again by crustaceans, rotifers, algae, oligochaetes, plant material and mucus, as well as unidentified objects in the "other" category. *C. carpio* again contained a more even distribution of crustaceans (the highest proportional amount of all examined species at

23.7%), detritus (28%), plant material (also the highest proportional amount at 25%) and "other" (20%) than the other species, whereas the "other" category consisted of small, transparent sediment, probably quartz particles. Small proportions of mollusks and algae were also found. *C. carpio* was the only species with crustaceans but no rotifers in their guts. Figure 8 presents an overview comparison of the average diet composition between species.

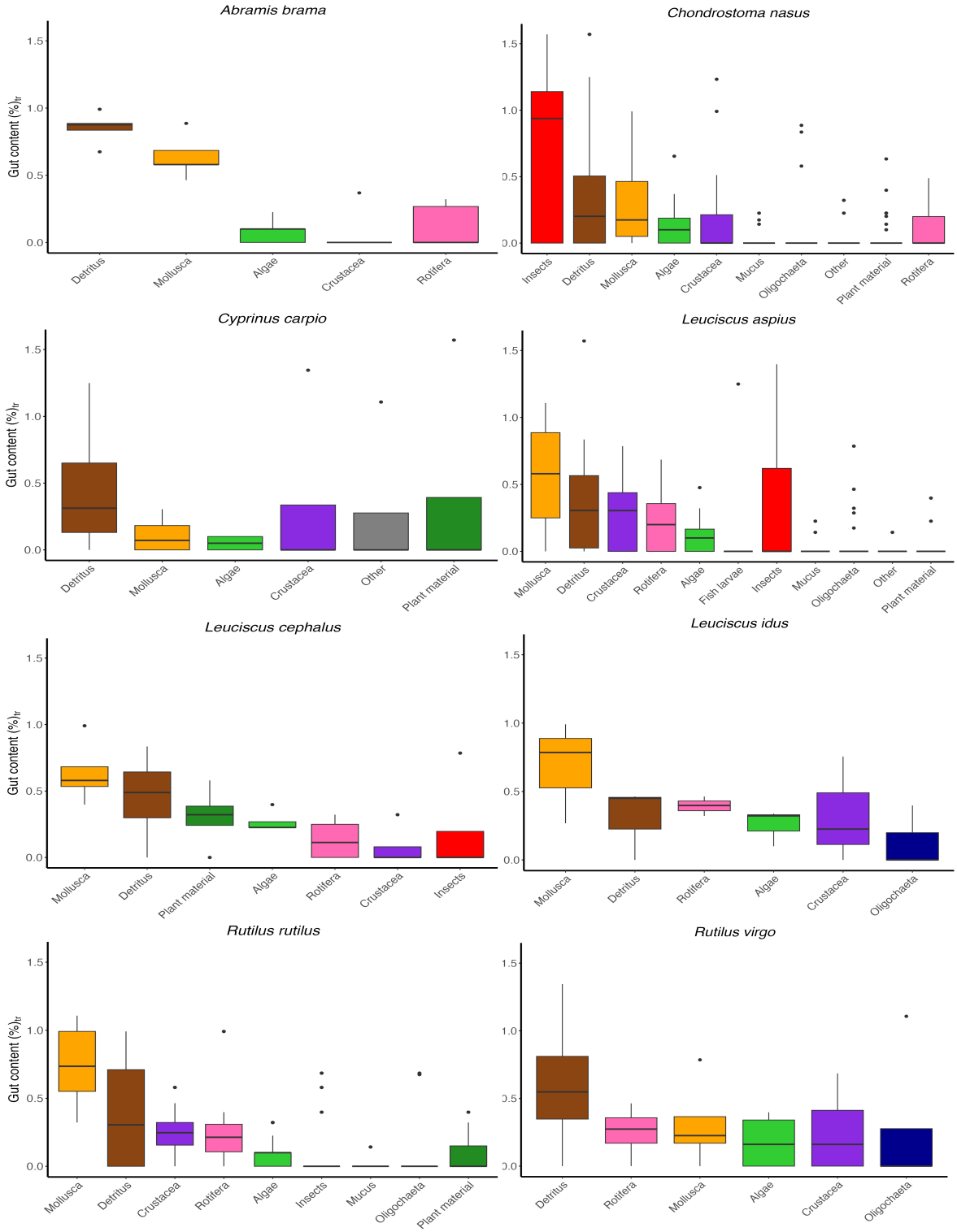


Figure 7: Boxplots of relative gut content composition of examined fish species. The y-axis represents the arcsine square root-transformed percentage values of gut content, while the x-axis shows the food categories. The categories for each species are sorted by median to allow for a better visual comparison.

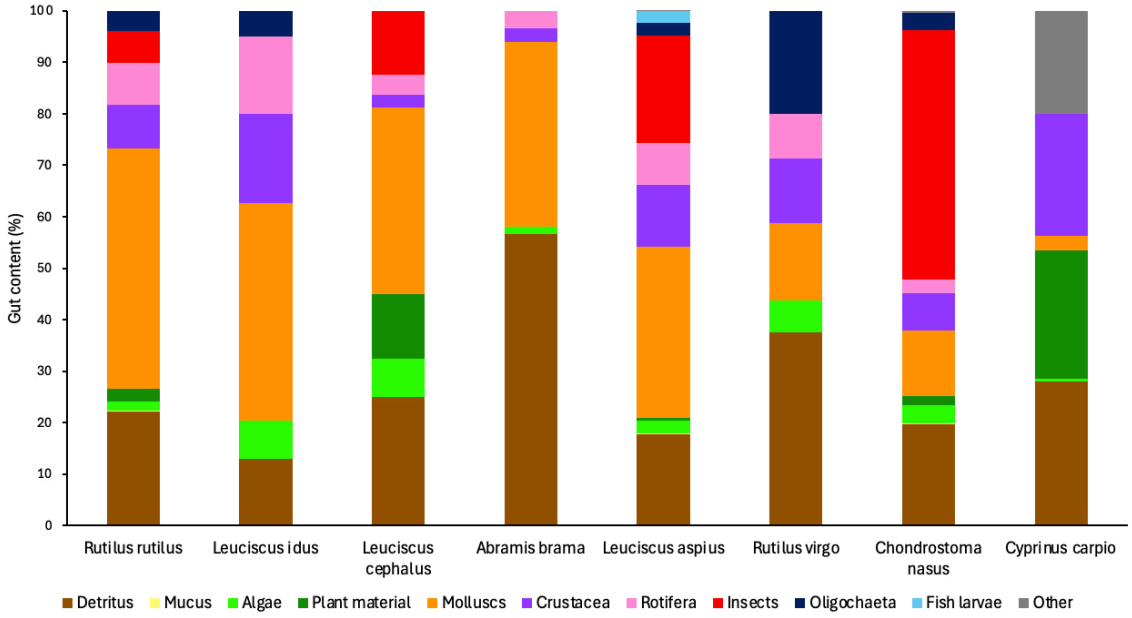


Figure 8: Average diet composition of the larvae from the different fish species observed, sorted by the largest portion (mollusks).

These compositional differences indicate distinct species-specific feeding patterns, which were further explored using NMDS analysis. This multivariate approach enabled the visualization of dietary variation across fish species based on the full spectrum of consumed prey items. The NMDS ordination (Figure 9) revealed some clustering tendencies by species, although notable overlaps in diet composition were observed across species. The most influential vectors were insects, detritus and mollusks, followed by oligochaetes and rotifers, as indicated by vector lengths. *C. nasus* individuals were broadly dispersed across the ordination space but tended to cluster toward the right side of the plot, aligning more strongly with the insect vector and, to a lesser extent, detritus. In contrast, they showed weaker associations with molluscs. *L. aspius* was the most widely spread across the ordination, showing no clear association with a specific food category, suggesting a more generalized feeding pattern. *L. cephalus* also showed broad dispersion, associating with multiple vectors. Meanwhile, *R. rutilus* exhibited a tighter cluster than *C. nasus*, *L. aspius* and *L. cephalus*, aligning more with the detritus and mollusk vectors. *R. virgo* and *C. carpio* showed somewhat similar patterns, though *R. virgo* appeared to have a broader niche. *C. carpio* aligned more closely with the vectors for oligochaetes, “other” and detritus, while *R. virgo* associated more with detritus, though not exclusively. *A. brama* and *L. idus* were the only two species that showed no overlap, which could indicate dietary differences despite their small sample size. Overall, the dietary vectors explained 98.44% of the total

variation in the NMDS, indicating a strong relationship between diet composition and fish species.

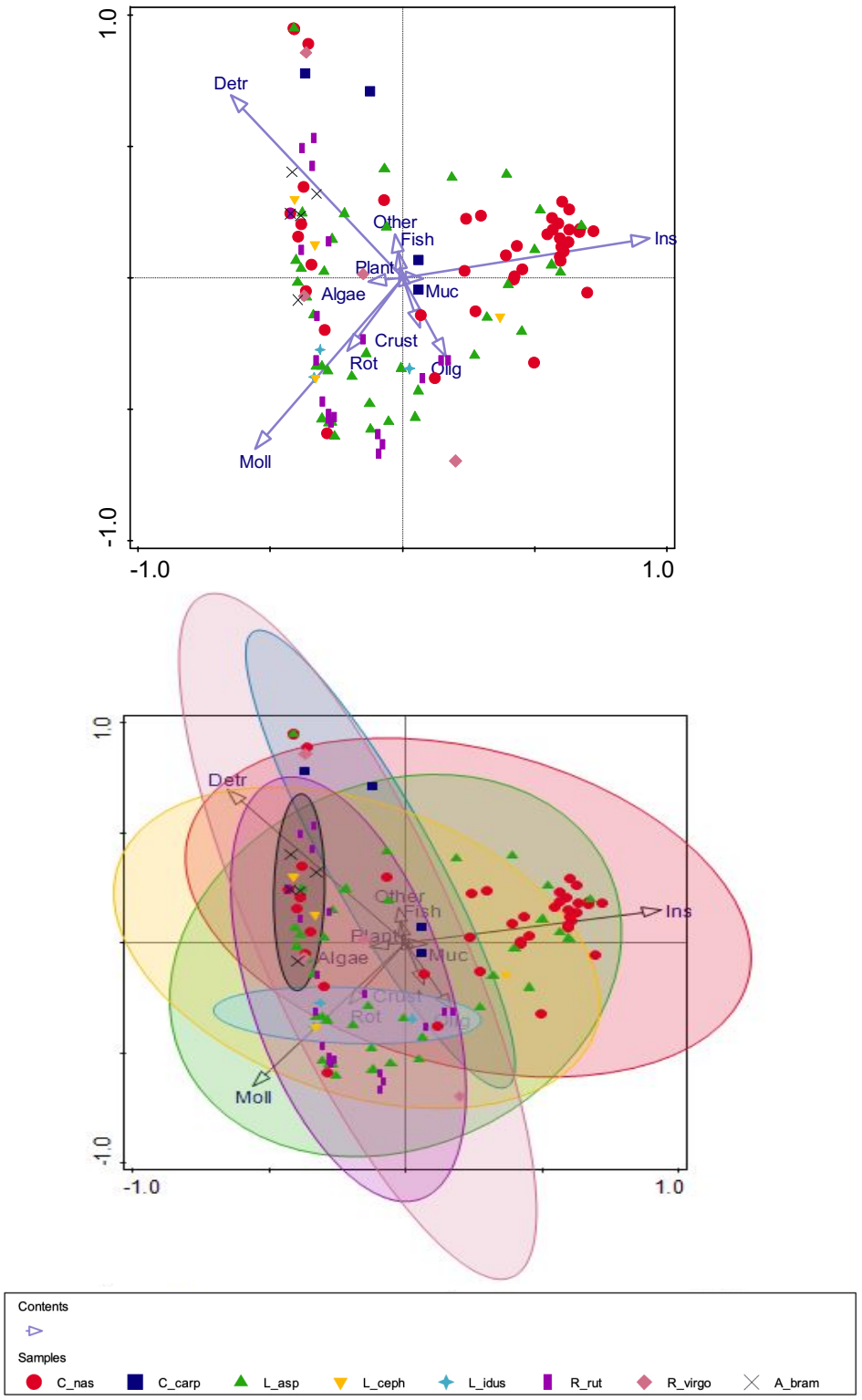


Figure 9: NMDS analysis based on Bray-Curtis dissimilarities across fish species. The stress level is 0.15. The first two NMDS axes account for approximately 72% of the variation. The upper panel shows the NMDS biplot with samples and fitted vectors, while the lower panel includes normal based ellipses at the 95% level to facilitate visual interpretation of diet overlaps.

Using the ellipses to guide interpretation clarifies the overlap between species. The ellipses also show a difference in group dispersion; the ellipses of *R. virgo* and *C. carpio* are noticeably more elongated and narrower than those of the other groups, with a higher influence of detritus, oligochaetes and zooplankton (crustaceans and rotifers).

Based on these findings, additional NMDS analyses were conducted focusing exclusively on the species with the highest numbers of individuals, namely *C. nasus* and *L. aspius*. These analyses assessed dietary variation in relation to developmental stage and mesohabitat, using the same set of dietary vectors, allowing for a more detailed examination of within-species trophic variation across ecological and ontogenetic gradients. Concerning *C. nasus*, the NMDS revealed differences in diet composition across developmental stages (Figure 10). L1 nase clustered distinctly from the other stages and aligned more strongly with the detritus and mollusk vectors, suggesting a greater reliance on these prey during early development. L2 individuals were more broadly distributed across the ordination space than individuals of the other stages, with a large and rounded ellipse, indicating greater dietary variability during the transition period between mixed feeding and exogenous feeding stages. In contrast, individuals from L3 and L4 clustered more closely together and occupied a different region of the ordination space, indicating similar dietary patterns. The ellipses of L3 and L4 nase were noticeably narrower and more elongated than those at the L2 stage, and both stages showed stronger associations with crustaceans, insects and oligochaetes. The most influential vectors were detritus, insects, mollusks and crustaceans, with detritus being particularly impactful for the L1 stage. The elongated shape of the L1 ellipse also suggests that mollusks have a substantial influence on the dietary composition at this stage. Overall, the ordination suggests ontogenetic shifts in diet within *C. nasus*, with increasing dietary specialization in later stages.

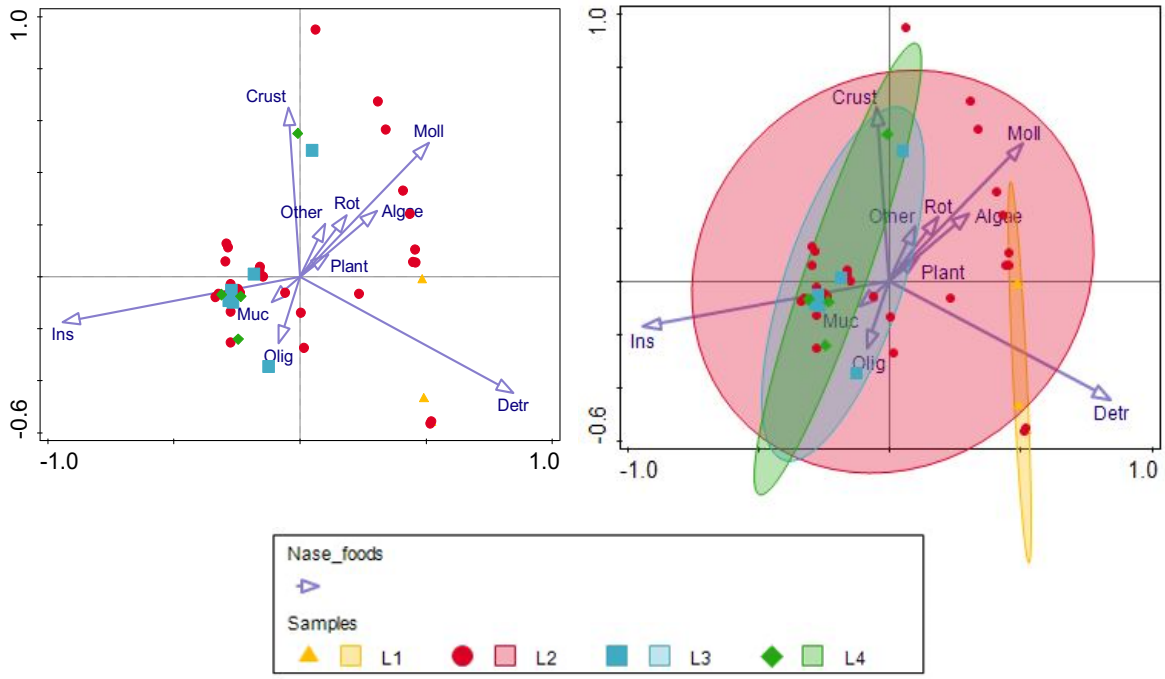


Figure 10: NMDS analysis based on Bray-Curtis dissimilarities across the developmental stages of C. nasus. The stress level is 0.11. The first two NMDS axes account for approximately 85% of the variation.

Following the analysis of developmental stages, dietary differences among mesohabitats were also assessed for *C. nasus*. This NMDS analysis revealed no strong overall patterns or separation between habitat types, with considerable overlap in diet composition across all groups (Figure 11). However, subtle patterns were observed. Individuals from the gravel bar (SB) formed a relatively tight cluster, as indicated by a narrower ellipse, suggesting that this mesohabitat was associated with more consistent feeding behavior than other mesohabitats. Some of these individuals showed a stronger association with insect prey. The gravel bar encompasses the bay (BUC) as a subelement with river-like characteristics, but samples from the bay exhibited a much broader dispersion in the ordination space than samples from the gravel bar. The corresponding ellipse for the bay was wider, reflecting greater dietary variability. Samples from the groyne field also displayed moderate clustering, with a slightly larger yet still narrow ellipse; these samples were also aligned closely with both the insect and detritus vectors. In contrast, individuals from other mesohabitats were more broadly scattered throughout the ordination space, indicating higher dietary variability. Overall, while no clear habitat-specific feeding patterns emerged, the ordination suggests that certain habitats – particularly, the gravel bar – are associated with slightly more homogeneous diets, and some differentiation may even exist among adjacent sites.

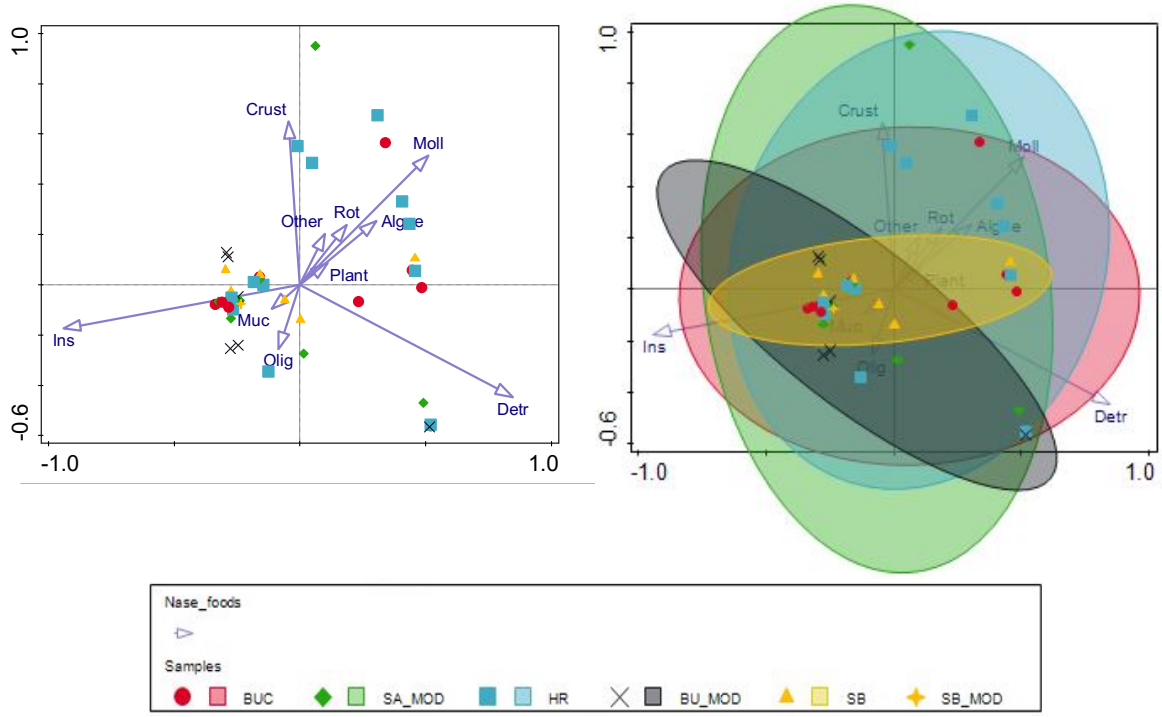


Figure 11: NMDS analysis based on Bray-Curtis dissimilarities across mesohabitats of C. nasus. The stress level is 0.11. The first two NMDS axes account for approximately 85% of the variation.

The NMDS also revealed differences in dietary composition among stages of *L. aspius* (Figure 12). Specifically, L2 and L4 asps clustered in distinct regions of the ordination space, with some overlap in the central area. The ellipses for L2 and L4 were similar in shape and size, indicating comparable dispersion, but they had different orientations. The L2 asps were closely associated with vectors for rotifers, detritus, mollusks and algae, while L4 asps aligned with insects and crustacean vectors. Only one sample each was available for L3 and L6. As with *C. nasus,* the ordination suggests ontogenetic shifts in diet within *L. aspius*, reflecting a transition toward different prey items as individuals develop.

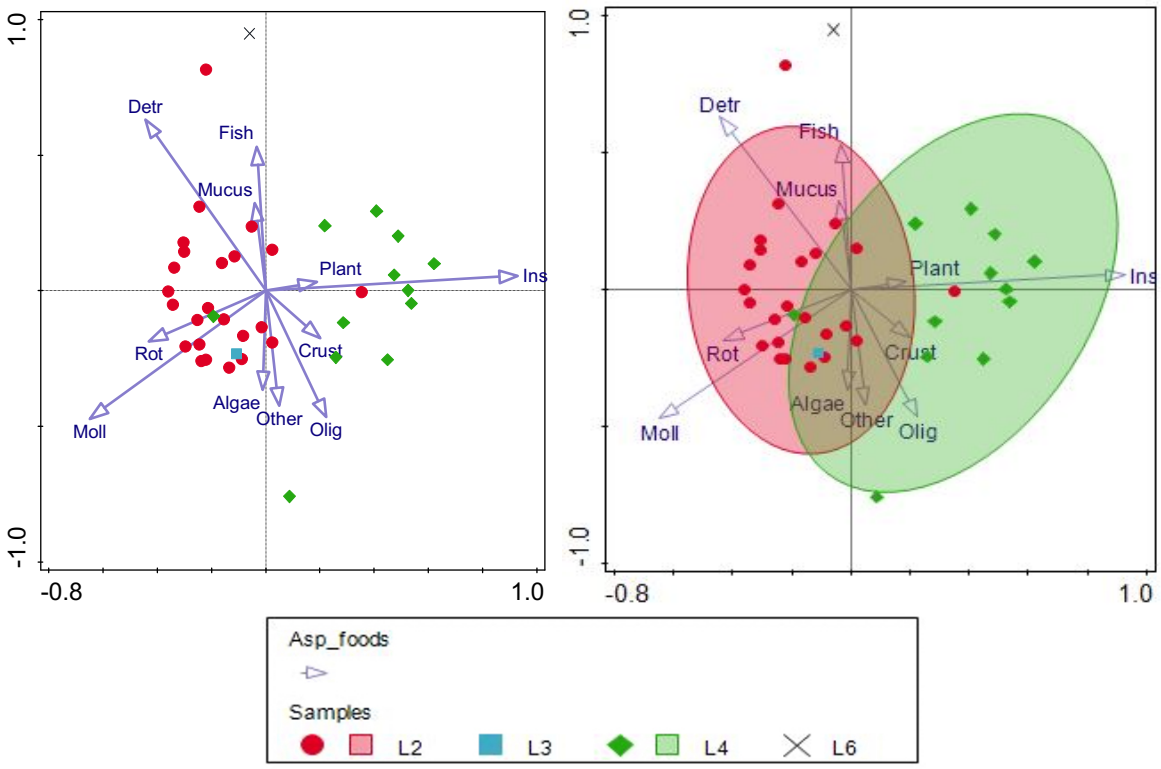


Figure 12: NMDS analysis based on Bray-Curtis dissimilarities across developmental stages of L. aspius. The stress level is 0.17. The first two NMDS axes account for approximately 79% of the variation.

In contrast to *C. nasus*, the NMDS ordination for *L. aspius* revealed more distinct differences in dietary composition among mesohabitats (Figure 13). Individuals from the bay (BUC) were widely scattered across the ordination space, indicating high dietary variability. In contrast, individuals from other habitats exhibited tighter clustering, suggesting more consistent feeding patterns. As observed with *C. nasus*, the bay showed much greater dispersion than the gravel bar (SB and SB_mod), despite being a subelement of it. Insects, oligochaetes and detritus vectors were most strongly associated with the bay. Notably, samples from the instream side-channel aligned with vectors for mollusks, insects, crustaceans and detritus, suggesting a diverse but cohesive feeding pattern. In comparison, individuals from the side arm showed a stronger association with detritus and rotifers.

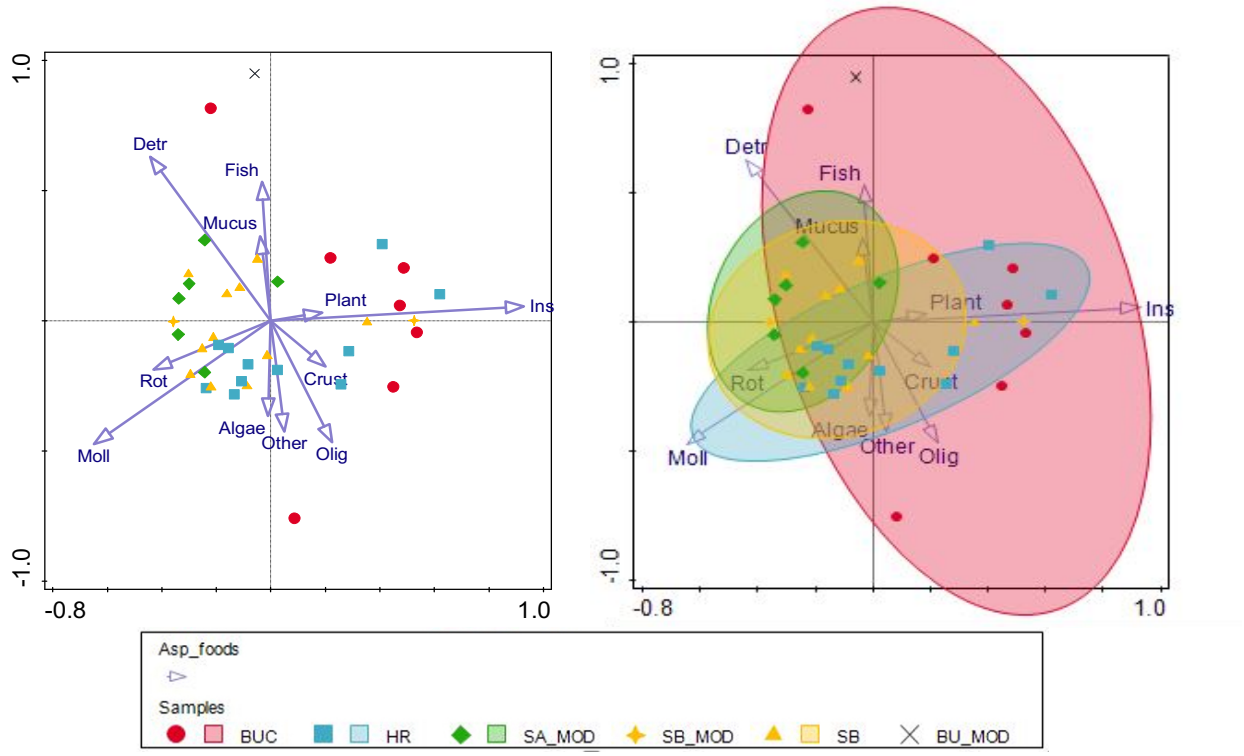


Figure 13: NMDS analysis based on Bray-Curtis dissimilarities across mesohabitats of L. aspius. The stress level is 0.17. The first two NMDS axes account for approximately 79% of the variation.

Feeding strategies

The feeding strategies of the examined fish species were analyzed with Amundsen et al.'s (1996) graphical method, which represents a modification of the original approach from Costello (1990) (Figure 14). This method distinguishes degrees of (individual) specialization and generalist traits as well as opportunistic, selective or supply-oriented feeding of a specific species or population. The method relates the portions of individuals of the population with the portions of prey categories found in their guts (i.e., prey items that occur in the upper left of the graph are consumed by few individuals of the population and they make up large proportions of the gut content, signaling a specialized individual diet). Prey items in the upper right are dominant food items found in most or all of the examined individuals, indicating that the whole population feeds on a single, probably highly abundant food type. Prey items in the lower left corner are rare and were seen in only a few individuals, indicating low overall importance. In contrast, prey items in the lower right corner were found in many individuals but in small proportions, signaling a generalized diet with a frequent but low-level consumption of these items.

The feeding strategies among the eight species varied considerably. Most species consumed a wide variety of prey items, with five to 11 food categories observed per species. Many food categories showed large error bars across all fish species, indicating high within-variability in prey-specific abundance between individuals.

The gut content of *A. brama* consisted of five food categories, two of which had an occurrence of 100%, meaning that all individuals included this category in their diet. Specifically, detritus had a high prey-specific abundance and mollusks had a slightly lower prey-specific abundance. The other three categories varied in occurrence but showed low prey-specific abundance. *A. brama* displayed the clearest example of preferential feeding on the most abundant food sources (opportunistic feeding strategy).

The feeding strategies of the larvae reveal many characteristics of generalization, which is indicated in low prey-specific abundance and occurrence in different portions of the individuals, and an orientation towards dominant prey, which is shown in relatively high values of occurrence and prey-specific abundance. Few species reveal a high within-phenotype component of niche width, which means that each individual utilizes a broad range of resources. That is, the population is composed of generalists, whereas the opposite pattern (a high between-phenotype component of niche width) was not found.

C. carpio differed notably from the other species regarding its occurrence. The six food categories display a V-shape pattern in the plot, with detritus having a high occurrence and mid prey-specific abundance, mollusks and algae having a medium occurrence and low abundance and the rest of the categories having a low occurrence but high abundance. The shape of the distribution suggests a unique feeding pattern involving frequently and rarely consumed prey categories. The sample consisted of individuals with a tendency toward specialization, as well as individuals showing a generalist feeding mode. *R. virgo* showed a strategy of generalization with a tendency to a high within-phenotype component of niche width. Several food categories – specifically, detritus, mollusks and rotifers – had high occurrence and medium to low abundance. Zooplankton and algae had a medium occurrence with low abundance, and oligochaetes had a slightly higher abundance and lower occurrence. *C. nasus* displayed a broader trophic niche, which points to a generalization strategy, utilizing several food categories with low prey-specific abundance. Mollusks and algae had a high occurrence but low abundance, which reflects a high within-phenotype component of niche width. Meanwhile, insects showed considerably high prey-specific abundance despite occurring in fewer individuals, indicating their role as a common, dominant prey source when present. *L aspius* also exhibited a wide niche breadth,

with several prey categories spread across the plot, which shows a predominantly generalized feeding strategy. One individual of *L. aspius* was the only fish with another fish larva in its gut. Like several other species, *L. idus* showed a wide spread of food categories across the plot but differed by having more categories with 100% occurrence.

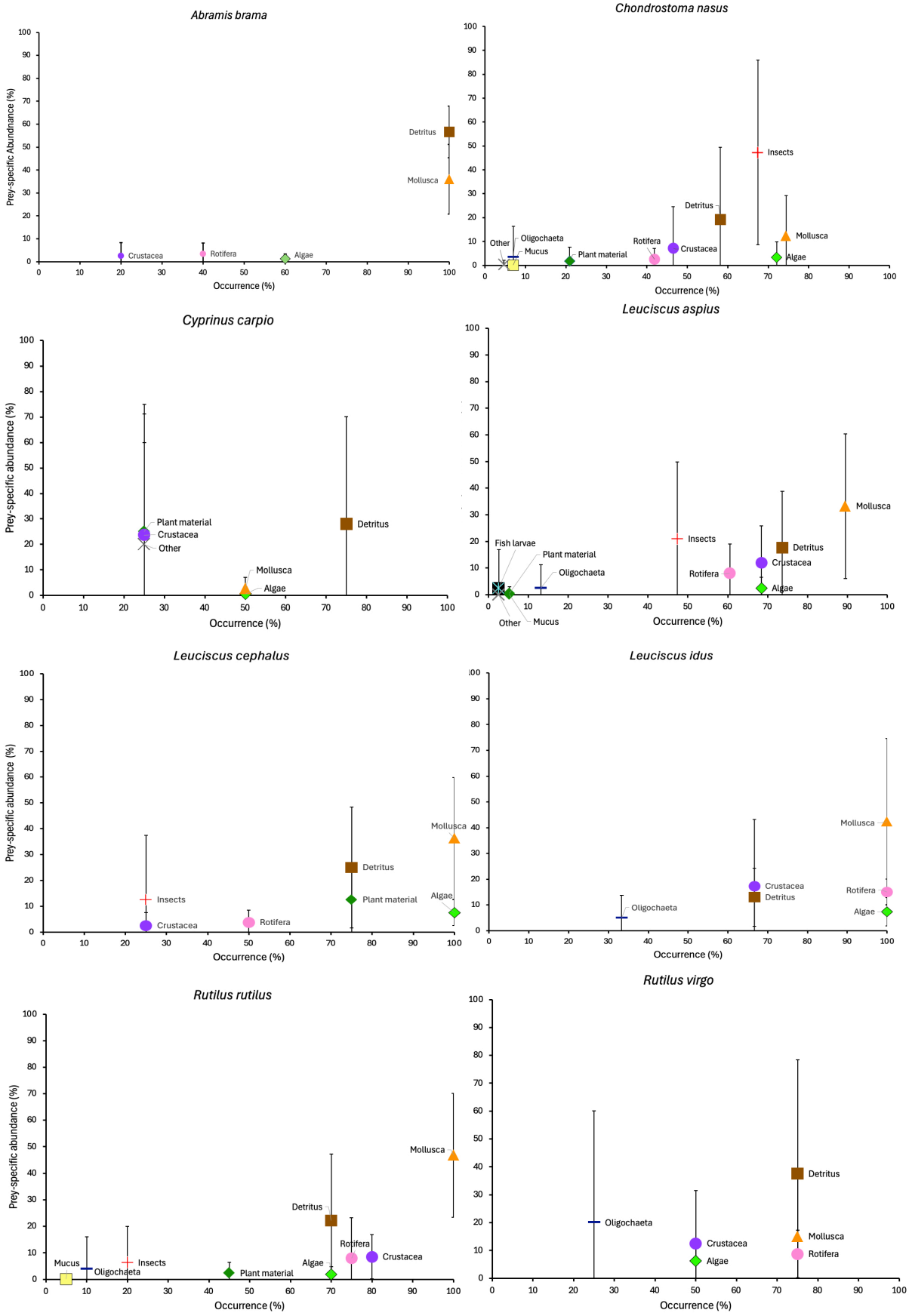


Figure 14: Feeding strategies in the examined fish species with frequency of occurrence of food categories and prey-specific abundance. The error indicators display the standard deviation.

C. nasus, C. carpio, L. aspius and *R. virgo* did not show a food category at 100% occurrence. None of the examined fish species had a clear specialized prey item positioned at high prey-specific abundance and low occurrence.

C. nasus and *L. aspius* were used for an intraspecific comparison between early (L1–L2) and later (L3–L6) larval stages to assess whether ontogenetic development influences diet composition and feeding strategies, as these species revealed a representative sample size (Figure 15).

A comparison of the feeding strategy plots of L1/L2 nase and L3/L4 nase revealed obvious differences. For one, insects have a 100% occurrence in later nase larvae and a high prey-specific abundance, while they occur in less than half of the early nase larvae. Moreover, detritus has a considerably higher occurrence and abundance in early nase larvae than in the later stages. The other categories also change their position in the plots between early and later larval stages. Notably, algae and rotifers maintain approximately the same abundance but exhibit changes in occurrence. The early and later stages exhibit the same food categories but with differences in their levels of importance. Visible differences were also found in the feeding strategies of asps, depending on whether they were in an early or later larval stage. Mollusks occur less often in later larval stages than in the early stages and exhibit a lower level of prey-specific abundance. Insects play a considerably more important role in the later stages. Zooplankton also occur more often in later stages, but their abundance remains roughly the same. Meanwhile, detritus is of greater importance in earlier stages. As was the case with nase, algae have a higher occurrence in later larval stages but keep about the same abundance. Oligochaetes and fish larvae only appear in the later stages, as well as the “other” category. There is also a visible change in the standard deviation for some categories between the early and later stages, showing a change in variability across larval development.

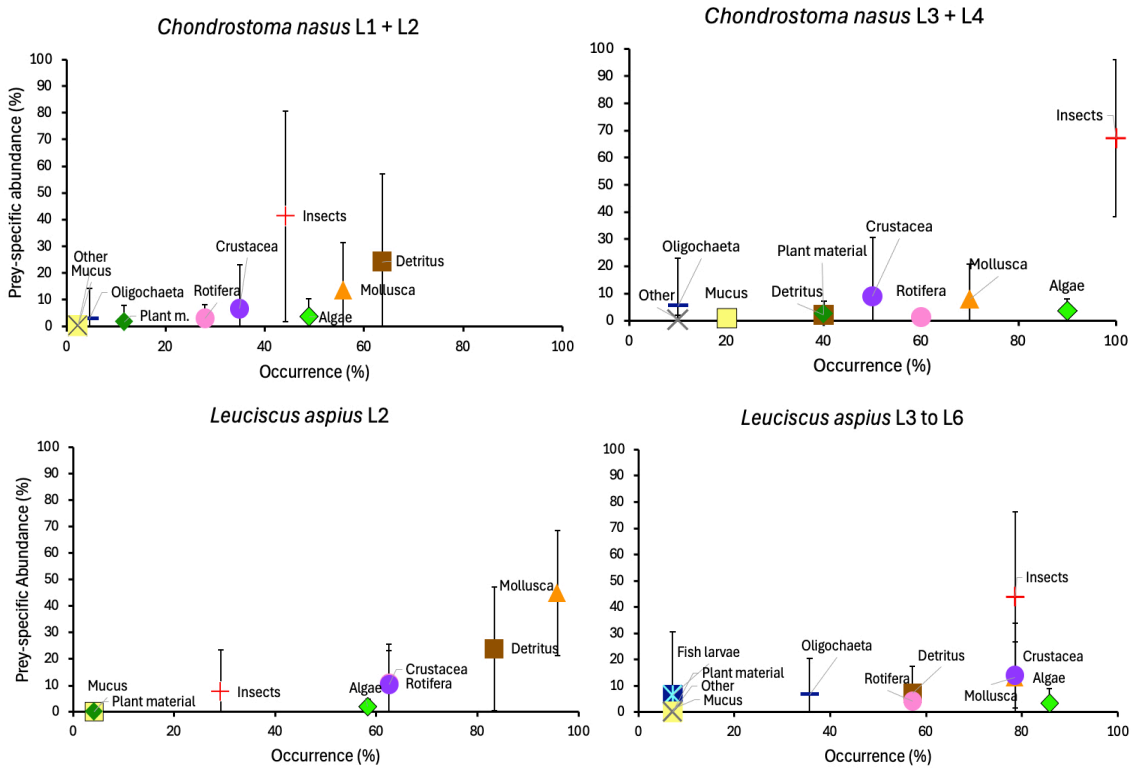


Figure 15: Feeding strategies of early (L1 and L2) fish larvae and later (L3 to L6) fish larvae of C. nasus and L. aspius, with standard deviation used as the error indicator.

Discussion

Gut fullness and length

Food availability was generally sufficient for all sampled mesohabitats, as reflected in the generally high values of gut fullness across all species and stages – only one of 121 fish larvae (0.82%) had an empty gut. The results indicate that the investigated sites within the main stem and in a side arm serve as nursery habitats, providing adequate quantities of food for all larval stages of several species. Previous studies support this interpretation, as highly diverse inshore structures are known to be important for fish larvae (Keckeis et al., 1997) and low-flow inshore mesohabitats support higher zooplankton densities, thereby enhancing their suitability as nurseries (Reckendorfer et al., 1999; Winkler et al., 1997). Optimal nurseries offer both shelter and high food availability while also promoting zooplankton production, further increasing food resources for fish larvae (Stoffers et al., 2022). Most of the observed species exhibited moderate gut fullness. The two species with

notably low gut fullness (freshwater bream and cactus roach) were represented by only a few individuals, preventing statistically robust conclusions.

When gut fullness was compared across developmental stages of all species, a (non-significant) pattern emerged, suggesting that gut fullness is higher in the two latest larval stages. Comparable findings were reported by Matzinger (2009), who observed significant increases in gut fullness between the larval stages L2 to L3 and L5. Such developmental patterns are likely related to the ontogenetic changes that occur during the early life stages of fish. The first larval stage of L1 cyprinids marks the start of exogenous feeding while still partially relying on yolk sac reserves (mixed feeding period) (Peňáz, 2001). By stage L2, the yolk sac is typically fully absorbed, and feeding becomes entirely exogenous (Peňáz, 2001). In stage L3, the posterior chamber of the swim bladder gets filled with gas in cyprinids, whereas only the anterior chamber is filled in stages L1 and L2 (Peňáz, 2001). These internal and external morphological developments, such as changes to the notochord, fins and mouth-width (Peňáz, 2001), improve maneuverability and allow later larval stages to increase capture efficiency and handle larger or more mobile prey (Reckendorfer et al., 2001). This likely explains why prey items such as mollusks and detritus, which are less mobile and more accessible to early-stage larvae due to their small size and passive nature, were more frequently consumed by L1 and L2 larvae. In contrast, insects – particularly more mobile or terrestrial ones – became more important in later larval stages, reflecting their increased foraging capabilities. However, L2 nase already showed high insect consumption, indicating species-specific deviations from this general pattern. Furthermore, this study found a strong positive correlation between gut length and fish length, supporting findings reported by Matzinger (2009). A longer gut not only increases gut volume but also allows the ingestion of larger or more numerous prey items. This trait may be particularly important in the context of prey selection, as the larvae of several fish species selectively consume prey taxa that ensure optimal growth (Burns et al., 2021, 2020; Murphy et al., 2013; Robert et al., 2009).

Diet composition

Diet studies of fish larvae in free-flowing sections of large rivers such as the Danube remain scarce. While extensive research has examined the early life history, hydrodynamics, and habitat use in such systems (Keckeis et al., 1997; Schiemer et al., 2003; Stoffers et al., 2022; Winkler et al., 1997), few studies have focused specifically on gut content and

feeding strategies of fish larvae in these dynamic environments. This gap is surprising given the critical role of larval feeding in survival and recruitment success (Burns et al., 2020; Wilson et al., 2018), especially under the dynamic flow and prey availability found in natural, unregulated river stretches.

In total, 11 different food categories were identified in the diets of the fish species observed in this study. Most food categories were used regularly, with only a few occurring rarely, suggesting a broad dietary base and resource use across species. While overall diet composition varied mainly in the proportions of the different food categories, several species shared similar dietary profiles. For example, mollusks made up roughly one-third to one-half of the gut contents of roach, ide, chub, freshwater bream and asp individuals. Similarly, roach, cactus roach and asp displayed comparable proportions of crustaceans and rotifers. Meanwhile, freshwater bream exhibited low dietary diversity with a clear dominance of detritus. Carp was the only species with sediment particles in the gut and showed relatively balanced proportions among food categories. Cactus roach also had a fairly balanced diet but had the highest proportions of oligochaetes among all species. However, the findings for these three species should be interpreted with caution due to the small sample sizes. Little is known about species-specific dietary preferences of riverine fish larvae in general, especially concerning rare and endangered species like the cactus roach. Nase larvae had more insects in their diet than other prey sources. This species also consumed more insects than any of the other observed species. Insects, which are a mobile and energetically rich prey, may reflect the improved foraging capacities of older larvae – though, as noted, even L2 nase consumed them in large proportions. One possible explanation is the tendency of nase larvae to forage near the surface of water, where terrestrial insects and drifting invertebrates are more abundant. This surface-oriented feeding behavior was documented by Schiemer and Spindler (1989), who described an ontogenetic shift from surface to benthic feeding during larval development. Similarly, Reckendorfer et al. (2001) observed this behavior in intermediate-sized classes, further supporting the idea that early developmental stages of nase utilize surface-oriented foraging strategies. Still, mollusks were the most abundant food category overall. Their passive nature and small size likely make them suitable prey for fish in their early life stages, which have limited mouth gape and poor swimming performance. Both larval and adult forms of insects were found, with the latter likely representing terrestrial insects captured on the water surface. Zooplankton was composed of crustaceans and rotifers, with only Keratella

sp. identified among the rotifers. Crustaceans (e.g., copepods and cladocerans) and rotifers have long been known as important live feed for rearing fish larvae due to their nutritional value (Ashaari et al., 2024). Many fish larvae consume these prey items nearly exclusively during ontogenetic periods (Reckendorfer et al., 2001; Zhang et al., 2017). However, in this study, crustaceans and rotifers contributed less than half of the total diet composition. Diatoms (which belong to the algae category) were often found near other food items and, thus, may not have been ingested deliberately. Similarly, the presence of plant material in some guts could reflect accidental ingestion during foraging or selective consumption.

The NMDS analysis across all species identified insects, detritus and mollusks as the most influential vectors, followed by oligochaetes and rotifers. While some distinct clusters were evident, considerable overlap between species was observed. Among species with larger sample sizes, differences became more apparent – namely, insects were a key dietary component for nase, although not exclusively, and asp individuals were widely dispersed across all food categories. Roach exhibited tighter clustering, with mollusks, detritus, algae and zooplankton being dominant vectors.

NMDS analyses also revealed differences between developmental stages among nase and asp. In nase, the few L1 individuals formed a separate cluster from later stages, only overlapping with L2 nase, which could indicate limited foraging ability. The broad scattering of L2 individuals may reflect opportunistic feeding behavior before more selective patterns emerge and or intraspecific specialization. Research has shown that fish improve their foraging skills through learning, both by sampling prey individually and by observing other foragers, suggesting that experience-based learning may shape dietary refinement (Warburton and Hughes, 2011). L3 and L4 stages showed tighter clustering and stronger association with crustaceans, insects and oligochaetes, hinting at a dietary shift with ontogenetic development. Although the small sample size of the later stages limits interpretation, this pattern aligns with the findings of Reckendorfer et al. (2001), who observed a shift in the diet of nase from rotifers in early larval stages to invertebrates and terrestrial insects in later larval stages, followed by another shift to benthic algae and detritus in juveniles and adults.

The examination of mesohabitats revealed both overlap and clustering. The bay (BUC), a subelement of the gravel bar (SB) with river-like characteristics, exhibited a broader prey spectrum than the gravel bar itself, indicating its potential role as an important nursery

habitat for nase. This is supported by Reckendorfer et al. (1999), who reported higher zooplankton densities in a bay within the free-flowing section of the Danube downstream of Vienna compared to adjacent gravel banks. Reckendorfer et al. (1999) also emphasized the ecological importance of low-flow storage zones for zooplankton reproduction and abundance. Notably, although the bay is not submerged when water levels are low, it had the highest larval density during sampling at average and higher water levels. Keckeis et al. (1997) also found that bays in this section of the Austrian Danube supported higher densities and diversity of fish larvae, along with greater food availability, compared to gravel banks. They emphasized that such habitats with favorable abiotic conditions and abundant food are critical for the successful recruitment of *C. nasus* in large river systems (Keckeis et al., 1997). Fish larvae are generally restricted to low-flow, sheltered habitats during early stages, and an ontogenetic shift from lentic bays to shallow gravel banks has been documented for *C. nasus* (Winkler et al., 1997). In contrast to the bay, the modified groyne field (BU_mod) and gravel bar (SB) showed narrower clustering in the ordination space, suggesting more homogenous food availability in those habitats.

The L2 and L4 stages of asp showed overlap as well as distinct differences. Specifically, L2 individuals were more associated with detritus, mollusks and rotifers, while L4 individuals were more linked to insects, oligochaetes, plant material and crustaceans. These findings are consistent with the findings of Specziár and Rezsu (2009), who reported the earliest life stages of asp as zooplanktivorous, which involves a transition to a facultative piscivorous lifestyle with large crustaceans and surface arthropods and then to obligatory piscivory in bigger asps. The diet composition of asp larvae in natural riverine habitats remains under-researched. Most studies have either focused on controlled environments or group larval data with juveniles and adults without differentiation. For example, Kujawa et al. (1998) found that asp larvae feed on rotifers and crustaceans, with bigger asp fry at 20 mm also consuming insects; however, these asps were initially reared in tanks and then in illuminated cages with zooplankton lures. The NMDS also revealed more pronounced mesohabitat-driven differences in asp compared to nase. Once again, the bay (BUC) provided a broader prey spectrum that was particularly rich in insects, reinforcing its role as a rearing habitat for both species. Other mesohabitats exhibited narrower clustering with substantial overlap, suggesting a more homogenous food availability. Notably, the instream side channel (HR) aligned strongly with the mollusk vector. This pattern indicates that the instream side channel may be a suitable habitat for mollusks, perhaps due to its favorable

substrate conditions, such as the presence of fine sediments or mixed grain sizes. Mollusks appear to be an important dietary component for early larval stages, given that L2 asps aligned more strongly with the mollusk vector than later stages did.

Feeding strategies

The Costello-Amundsen method (Amundsen et al., 1996) was applied to examine the feeding strategies of the observed fish larvae. This method plots prey-specific abundance against frequency of occurrence (Figure 16), providing a clear framework to assess dietary specialization at both the individual and population levels. Its two-axis format helps differentiate whether a species is primarily generalist or specialist, and whether generalization occurs when individuals exploit multiple prey types (high within-phenotype component) or when individuals display distinct specialization (high between-phenotype component). The x-axis represents the frequency of occurrence of each prey item across individuals (percentage of fish individuals that fed on the specific component), while the y-axis shows the prey-specific abundance (the proportion that the item contributes to the diet when present). This enables prey importance, niche width contribution and feeding strategy to be interpreted according to the position of the prey items in the graph. Prey items in the upper left are consumed in large proportions but by few individuals, indicating individual specialization and a high between-phenotype component (high BPC) by which individuals specialize on different resource types. Prey items in the upper right are frequently consumed and dominant in the diet, indicating a population-level specialization with a narrow niche width on the dominant prey. Prey items in the lower left have low prey-specific abundance and low occurrence; these are rare food items of low dietary importance. Finally, prey items in the lower right have low prey-specific abundance and high occurrence, meaning they appear in many individuals but only in small amounts. They contribute to the population diet at the same overall level as prey items in the upper left but characterize generalist feeding with a high within-phenotype component (high WPC), by which most individuals incorporate a wide range of resources.

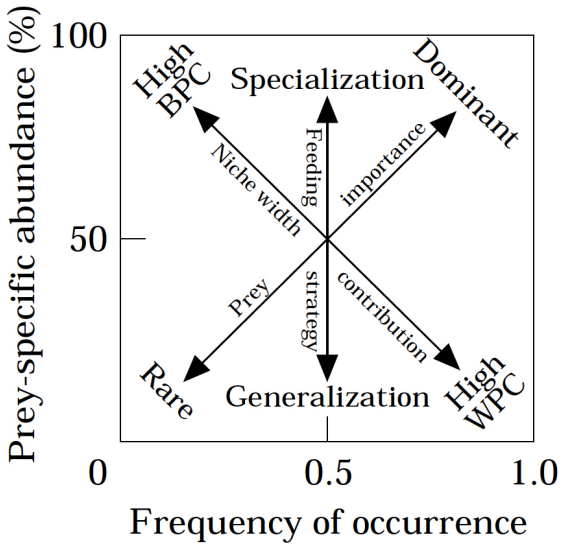


Figure 16: Predator feeding strategy, niche width contribution and importance of prey, modified from Costello (1990) (Amundsen et al., 1996)

The Costello-Amundsen plots highlight that none of the eight examined fish species exhibited strong specialization. Instead, they were predominantly generalists with a high WPC. However, several species, including the freshwater bream, ide, chub and roach, tended to consume dominant prey items with a high occurrence and medium prey-specific abundance. This pattern is characteristic of a supply-oriented feeding strategy, in which diet composition largely reflects the availability of prey in the environment rather than active prey selection.

Across all studied species, prey categories with the highest level of occurrence (molluscs, algae, detritus, crustaceans and rotifers) tended to be small. This pattern is consistent with functional morphological constraints in early developmental stages, like a smaller mouth gape and reduced maneuverability, which limit them to smaller, less mobile prey (Reckendorfer et al., 2001). These findings support the hypothesis that larval fish initially employ a generalized feeding strategy, focusing on readily available and easily handled prey, before transitioning to more selective feeding as they mature. An exception to this trend appears in the nase larvae, which frequently consume relatively large prey items (insects), albeit with considerable individual variation. This could indicate the early onset of dietary specialization.

Notably, freshwater bream and common carp displayed differences in their feeding strategies compared to the other observed species. The freshwater bream exhibiting a

tendency to dominant prey and exhibited a population-level specialization with a narrow niche width. In contrast, the carp exhibited a V-shape pattern in the Costello-Amundsen plot, with several food categories at nearly the same prey-specific abundance but highly different occurrences. This may reflect a mixed feeding strategy among individuals. Young carp have been observed to feed on crustaceans and rotifers as well as detritus and insects (Chakrabarti and Jana, 1990; Tesfaye et al., 2020). Khan (2003) observed an ontogenetic shift in carp, with individuals with a total length of <2 cm feeding exclusively on crustaceans, and those with a length of >2 cm incorporating benthic food into their diets while still preferring crustaceans. However, due to the limited number of carp individuals in the sample, conclusions remain tentative. The observed pattern might also indicate a lack of preferred prey items at the sampling sites, as no food category exceeded one-third in prey-specific abundance. Furthermore, resource availability and habitat structure can influence feeding patterns, as shown by Pease et al. (2006), who observed habitat-related differences in the diets of larval fish.

A clear ontogenetic niche shift was observed in both nase and asp larvae. In early stages (L1–L2), both species consumed more detritus and algae, while later stages (L3–L6) increasingly consumed insects, which then occurred in all examined nase individuals and approximately 80% of asp individuals. Additionally, nase larvae showed an increase in the occurrence of rotifers and algae, though algae remained consistently low in prey-specific abundance. Similarly, later-stage asp larvae consumed more crustaceans and algae, but less detritus and mollusks, with the latter occurring only slightly less frequently and with lower prey-specific abundance. These observations indicate a generalist feeding strategy with high WPC in both species, though nase may trend toward population-level specialization in later stages. Together, these results suggest that early-stage larvae exploit abundant, low-energy resources, switching to energetically richer (bigger) prey as efficiency and mobility increase. The detected within-phenotype generalization implies high plasticity, potentially enhancing resilience in dynamic environments; this is a key advantage for maintaining population stability under fluctuating resource conditions. In the Danube, for instance, fish fry associations have been shown to respond sensitively to hydromorphological changes, emphasizing the importance of adaptive capacities during early life stages (Schiemer et al., 1991). Notably, no previous studies were found that applied the Costello-Amundsen method to larval stages of *C. nasus* or *L. aspius,* underscoring the novelty of the present findings and the need for further research on trophic strategies during early ontogeny.

In summary, this study provides valuable insights into the dietary ecology and ontogenetic feeding dynamics of cyprinid fish larvae in the Austrian Danube. The findings underscore the importance of habitat heterogeneity and prey availability in supporting the early developmental stages of multiple species, including both generalists and emerging specialists. Most food categories identified in the samples were consistently present in the gut contents of the observed individuals, indicating a generalist feeding strategy among species, with some underlying species- and stage-specific preferences. These early dietary patterns reflect ontogenetic niche shifts and the gradual development of species- and stage-specific dietary specializations. The identification of the bay (BUC) as a key mesohabitat for both nase and asp – and probably for early stages of other cyprinid species – further underlines the ecological role of such structurally diverse zones in larval rearing. While this study offers important insights into species-specific larval feeding patterns, it is limited in its ability to account for potential shifts in food availability, as different prey densities can influence the diet spectrum of fish larvae (Reckendorfer et al., 2001).

Overall, this study contributes valuable data for understanding trophic ecology in early life stages of fish in large river systems. These insights can inform river management and conservation planning by highlighting the importance of maintaining a mosaic of mesohabitats that provide both physical refuge and access to diverse food sources. Ensuring the availability of varied prey types is particularly crucial for supporting the dietary requirements of different fish species during various developmental stages. Therefore, protecting structurally diverse, low-flow habitats such as bays is essential – not only for sustaining current fish populations but also for enhancing resilience against future challenges such as altered flow regimes, increasing temperatures, and changes in sedimentation caused by climate change and hydromorphological modifications. These stressors may threaten the persistence of such habitats and, by extension, limit the recruitment of native riverine fish species.

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Appendix

Zusammenfassung

Das Überleben und Wachstum von Fischlarven hängt in einem hohen Ausmaß von der Verfügbarkeit geeigneter Nahrung ab, doch aus großen Flusssystemen liegen bislang nur begrenzte Detailkenntnisse vor. In dieser Arbeit werden arts- und entwicklungsspezifische Nahrungszusammensetzungen von Larven von acht Fischarten in der österreichischen Donau untersucht, um trophische Interaktionen, Nahrungsstrategien und ontogenetische Nahrungswechsel zu identifizieren. Die Larven wurden im Mai 2022 in verschiedenen ufernahen Aufwuchsgebieten des frei fließenden Donauabschnitts flussabwärts von Wien gesammelt. Insgesamt wurden 121 Individuen auf Artniveau und Entwicklungsstadium bestimmt. Ihre Darminhalte wurden bis zur niedrigst möglichen taxonomischen Stufe mikroskopisch analysiert. Die Darmfüllung variierte zwischen den Arten, wobei *Chondrostoma nasus* höhere Werte als *Abramis brama* und *Rutilus virgo* aufwies. Zudem wiesen spätere Larvenstadien eine höhere Darmfüllung auf als frühere. Die Darmlänge nahm generell mit der Fischlänge zu, während zwischen Fischlänge und Darmfüllung kein signifikanter Zusammenhang festgestellt wurde. Die Nahrungszusammensetzung unterschied sich zwischen den Arten. Mollusken, Detritus, Krebstiere, Rädertierchen und Insekten waren die häufigsten Beutetiere. Auffällig waren ein hoher Insektenanteil bei *C. nasus* sowie Sedimentaufnahme bei *Cyprinus carpio*. Multivariate Analysen zeigten partielle Überschneidungen in der Nahrung verschiedener Arten sowie ontogenetische Verschiebungen bei *C. nasus* und *Leuciscus aspius* hin zu größerer, mobilerer Beute. Zwischen den Mesohabitaten zeigten sich subtile Unterschiede, wobei in der Bucht eine höhere Variabilität der Nahrung festgestellt wurde – ein Hinweis darauf, dass die Habitatstruktur die Nahrungsverfügbarkeit für Larven beeinflussen kann. Die untersuchten Arten wiesen Nahrungsstrategien von generalistisch bis opportunistisch auf, keine war vollständig spezialisiert. Die Ergebnisse unterstreichen die Ernährungsflexibilität von Fischlarven und die Bedeutung komplex strukturierter Lebensräume für die frühe Entwicklung und das Überleben von Fischen in großen Flusssystemen.