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ORIGINAL ARTICLE

Flow and plankton availability control young-of-the-year fish diet in two floodplain nurseries

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Abstract

In large river floodplains, the availability of trophic resources to the fish fauna is highly variable as a consequence of seasonal environmental change and habitat diversity. Young-of-the-year fishes (YOY) must find suitable habitats to settle, feed and survive. However, very few in-depth studies are available about the food preferences of the young fishes during their first growing season. Here, we investigated the composition of planktonic assemblages and the YOY diet of three generalist fish species *Alburnus alburnus* (Linnaeus, 1758), *Squalius cephalus* (Linnaeus, 1758) and *Pseudorasbora parva* (Temminck & Schlegel, 1846) from four floodplain sites of the French Upper Rhône River. More specifically, we studied their temporal and spatial variations in relation to five environmental variables: hydrology, dissolved oxygen, primary production, water temperature and conductivity. Stable flow conditions and the associated temperature and conductivity strongly structured the phytoplankton community in the floodplain channels, whereas water movements within channels and dissolved oxygen concentrations were significantly correlated to the zooplankton composition. A zooplankton density above $\approx 100 \text{ ind L}^{-1}$ allowed the initiation of a YOY diet mainly based upon zooplankton for the three fish species. When zooplankton densities were insufficient, all three species used phytoplankton as their main food resource. Finally, the diet overlaps between species, differed significantly between sites. The study highlights the need to examine the diet of juvenile fishes and environmental variables in the floodplains.

KEYWORDS

diet overlap, environmental change, hydropeaking, juvenile fish, life-history traits, plankton

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1 | INTRODUCTION

Large rivers are inhabited by a diversity of fishes that exhibit a variety of life-history traits related to floodplain habitats and resources for their growth and reproduction (Dolédéc et al., 2015; Persat et al., 1994; Welcomme et al., 2006; Winemiller & Rose, 1992). In a natural context, floodplain habitats provide abundant small-sized food resources (Hein et al., 1999), suitable thermal conditions and moderate hydraulic constraints that offer optimal habitat conditions and shelters (Garner et al., 1996; Grenouillet et al., 2001) during the early development period of fish. However, as a consequence of river regulation, presence of dams, especially for hydroelectricity production, only a limited number of natural or near-natural floodplain sectors remain along large European rivers such as the Rhine, the Rhône or the Danube (Bravard, 1987).

In channelized rivers, small areas of stagnant waters in the riparian zone or excavations in levees often offer local zones of low current velocity and high prey densities favourable for the development of young-of-the-year (YOY; Ramler & Keckeis, 2019; Reckendorfer et al., 1999; Schiemer et al., 2001). Even if they provide feeding opportunities compared with the main channel, such stagnant waters represent only few patches of suitable habitats along river corridors (Scharbert & Borcherding, 2013) that do not possess the necessary retention time to allow for the development of high densities of zooplankton (Schiemer et al., 2001). Under limiting food conditions, inshore zones may act as fish traps where YOY do not find suitable habitat to settle, feed and survive. While flow regime influences floodplain accessibility for fish, but also biological processes such as planktonic production—the main food source for juvenile fish—in floodplains (Houser et al., 2015; Lehman et al., 2008; Reynolds & Descy, 1996; Roach et al., 2014; Tockner et al., 1999), the effects of hydrology on the functions of these nurseries remain rarely documented.

While previous restoration efforts have focused on physical aspects of habitats and hydrological connectivity (Stoffers et al., 2022), a more functional approach is required to sustain fish diversity and abundance (Decker et al., 2017; Palmer & Ruhi, 2019; Polvi et al., 2020). This approach should identify ecologically appropriate conditions for maintaining trophic resources and accessibility of fish nurseries, as well as key biological features to enhance their carrying capacity (i.e. total number of YOY that a nursery can host; del Monte-Luna et al., 2004). Today, this science has never been more needed to support floodplain restoration (Palmer & Ruhi, 2019; Wohl et al., 2015).

The main goals of this study are (i) to evaluate the relative influence of environmental conditions on the YOY food availability and quality in a large river floodplain and (ii) to investigate YOY fish diet in relation with environmental conditions and food availability. Study was carried out in the French Upper Rhône River in two restored floodplain channels connected to the main channel by their downstream end most of the time (except during large floods). YOY belonging to three species were chosen, the eurytopic natives, chub *Squalius cephalus* (Linnaeus, 1758) and bleak *Alburnus alburnus*

(Linnaeus, 1758) and the lenitophilic introduced topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel, 1846). Environmental factors, phyto- and zooplankton abundance and diversity were measured from July to October in four floodplain sites. YOY fishes of the three species were sampled to reconstruct their diet using carbon and nitrogen stable isotope ratios of fish tissues and of their principal sources of food. We hypothesized that seasonal and spatial variations in food production would be affected by environmental conditions and hydrological variations (Devetter, 1998; Illyová, 2006; Vadadi-Fülöp et al., 2009). Specifically, more stable hydrological conditions would result in enhanced plankton productivity and food availability for juvenile fishes (Humphries et al., 1999; King et al., 2003; Wieser et al., 1988). Theoretically, greater food production and availability should increase the selectivity of species (Roughgarden, 1972), and this prediction was tested in the field over a large gradient of resource availability (Francois et al., 2020). In floodplains, we hypothesized that the importance of phytoplankton and zooplankton (over other food resources) in diet composition should increase with higher food production (Latli et al., 2019). Subsequently, the trophic selectivity and the diet overlap between the three species should be higher in conditions of high availability of plankton.

2 | MATERIALS AND METHODS

2.1 | Sampling sites

In the restored reaches of the Rhone River, electrofishing surveys were carried out in more than 30 floodplain channels and during 50 years after restoration (Lamouroux et al., 2015; Lamouroux & Olivier, 2015). The results of these surveys illustrated the high potential as nursery habitats of two physically restored floodplain channels (i.e. widened, deepened and reconnected to the main channel), called Ponton and Molottes ('PONT' and 'MOLO' respectively hereafter). These two floodplain channels, geographically close, located in Brégnier-Brangues floodplain (French Upper Rhône River; Figure 1). Two sites, one upstream and one downstream (called 'UP' and 'DO' hereafter), offering suitable conditions for YOY fish in terms of habitat were selected in each of the two channels. Samples were collected in the four floodplain sites over 5 months in 2018: May 16 (phytoplankton), June 6 (phytoplankton), June 26 (phytoplankton+zooplankton), July 11-17 (phytoplankton+zooplankton+YOY), August 21-31 (phytoplankton+zooplankton+YOY) and October 5-16 (phytoplankton+zooplankton+YOY).

2.2 | Description of floodplain channels

2.2.1 | Hydrology

The two former floodplain channels, MOLO and PONT channels, are presently fully connected downstream with the main river channel. In this sector of the French Upper Rhône, the mean summer

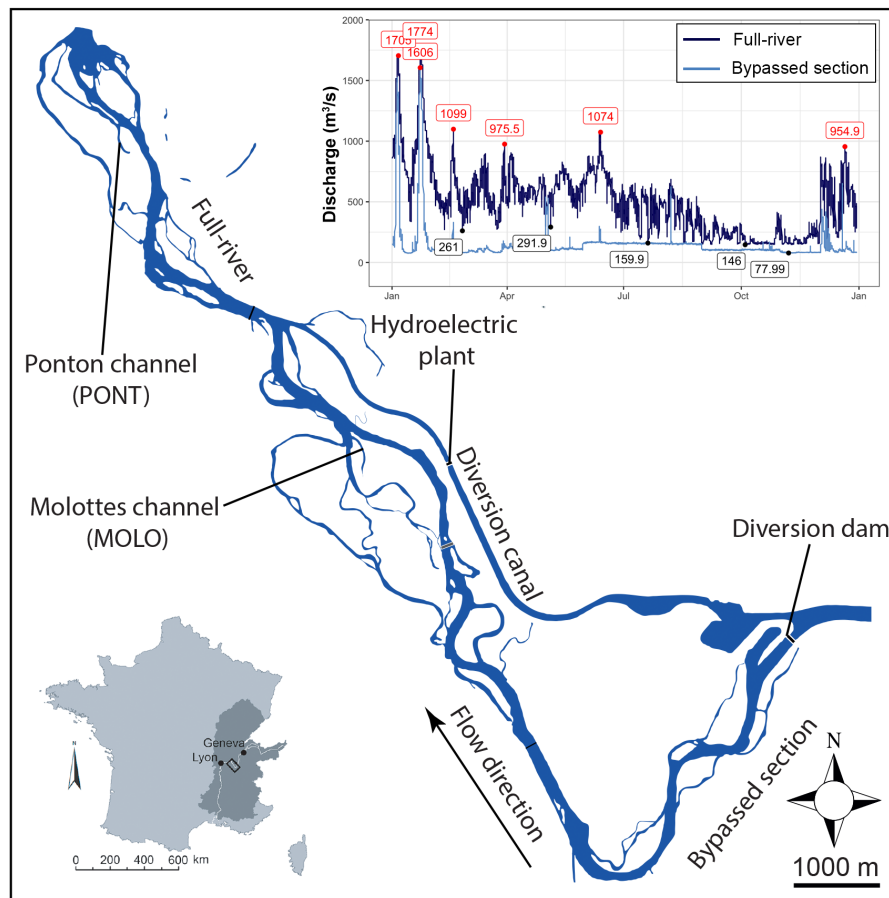


FIGURE 1 Rhône River in the Brégnier-Cordon sector (France) and locations of the two studied floodplain channels MOLO and PONT. At the top-right, the flow regimes of the studied sector in 2018. The hydrograph labels refer to the maximum (red) or minimum (black) flows recorded in the flow time series of the full river (i.e. diversion canal + bypassed section; dark blue) and the bypassed section (light blue) (discharge values provided by the Compagnie Nationale du Rhône).

discharge is about $\approx 700 \text{ m}^3 \text{ s}^{-1}$. Because of the construction of a hydroelectric power plant in 1982, the hydrological conditions of the two selected floodplain channels are different. The water levels in MOLO are dependent on a dam that stabilizes the flow. The water level can be impacted by backflow entries caused by changes in water levels and discharge variations in the main channel. In contrast, PONT is subjected to more variable hydrological conditions. It is located downstream of the hydroelectric scheme and experiences daily discharge fluctuations (between 200 and $500 \text{ m}^3 \text{ s}^{-1}$) and water level changes due to hydropeaking which occurs usually from Monday to Friday. The upstream flow connection (i.e. connectivity metric described in Riquier et al., 2015) occurs during important floods for less than 1 day per year on average for both floodplain channels. This very low upstream hydrological connectivity has important implications for abiotic conditions in the two floodplain channels, making them potential fish nurseries (Lamouroux & Olivier, 2015).

If the surface hydraulic connectivity is well defined, the vertical connection with groundwaters is poorly investigated. However, regarding nutrient concentrations (Table S1), we considered water flowing into the MOLO channel as derived from a combination of surface and groundwaters. While PONT channel appeared to be less influenced by groundwater supplies. As described by Juget et al. (1979), there was an upstream-downstream gradient along the channels in the relative importance of surface versus groundwaters.

2.3 | Environmental variables

We collected abiotic environmental variables at site and channel levels (Table 1). Abiotic variables related to seasonal changes in conductivity, dissolved oxygen and water temperature were recorded hourly using Onset HOBO data loggers installed at different depths (top and bottom layers) in each of the four sites. Water level data loggers (Onset HOBO) were used to monitor the water level in the channels. A total of nine loggers: 2 (two sites) \times 2 (two layers) for conductivity/temperature, 2 \times 2 for dissolved oxygen/temperature and 1 for water levels were installed in each floodplain channel. The coefficient of variation of the water level (cv_depth as a surrogate of water movements) in each channel was calculated using the colcv function from the Rfast R package. Following Needoba et al. (2012), diel oxygen curve methods using the single-station approach were applied to estimate rates of production and respiration in each site (Odum, 1956). Net ecosystem metabolism ('NEM' hereafter) was defined as:

$$\text{NEM}(t) = z \frac{dC}{dt} - k(C_s - C) \quad (1)$$

where C is the dissolved oxygen concentration (mg L^{-1}), C_s is the concentration at saturation, k is the reaeration coefficient, and z is the mean depth of the reach. Ecosystem respiration (ER) was estimated by calculating the mean hourly rate of NEM at night. Gross primary production (called 'GPP' hereafter) integrated during daylight hours was the

TABLE 1 Environmental variables included in the ordination analyses.

	Variable	Scale	Description
Abiotic	O ₂	S	Dissolved oxygen (mgL ⁻¹) at the top layer averaged over 14 days before plankton sampling
	conduc	S	Conductivity (microS cm ⁻¹) averaged over 14 days before plankton sampling
	temp	S	Water temperature (°C) averaged over 14 days before plankton sampling
	cv_depth	C	Water movements—Coefficient of variation of water depth (in cm) averaged over 14 days before plankton sampling
Biotic	gpp	S	Macrophyte production – GPP (gO ₂ m ⁻² h ⁻¹) at the bottom layer, averaged over 14 days before plankton sampling

Note: Variables were measured at two spatial scales: C = channel scale and S = site scale.

sum of hourly rates of NEM and ER. As many lentic floodplain channels show vertical stratification of oxygen concentration (Bini et al., 2001), we assumed that the quantification of GPP at the bottom layer allows predominantly the quantification of macrophyte growth. Hence, we applied the Equation (1) on the diel oxygen concentration from the bottom layer only and we neglected the exchange flux between both layers following Coloso et al. (2008). The O'Conner Dobbins method was used in a separate function ODobbins to calculate *k*. All functions are from the StreamMetabolism R package (Sefick, 2015).

To facilitate statistical relations between the environment and the planktonic communities, the five environmental variables were averaged over the 14 days preceding each plankton sampling date. This duration is considered as the time needed for a planktonic community to respond to an environmental change (Duarte et al., 2000).

2.4 | Planktonic community composition

A fluoroprobe (bbe-Moldaenke) was used to measure in situ four spectral algal groups: diatoms, cyanobacteria, green algae and cryptophyta. It used five light-emitting diodes (at 470, 525, 570, 590 and 610nm) for sequential light excitation of accessory pigments and the relative fluorescence intensity of chl *a* was measured between 690 and 710nm. The excitation spectrum obtained was compared by linear unmixing to a library of four fingerprints stored in the probe and the relative concentration of each algal group expressed in terms of the equivalent amount of chl *a* per liter (eq. µgL⁻¹) as well as the total chl *a* concentration. For a detailed description of the fluoroprobe (see Beutler et al., 2002).

The fluoroprobe was calibrated with 35 phytoplankton cultures by the manufacturer, and 25 mL of the ultrafiltered (0.2 µm) floodplain channel water was measured to obtain a 'natural background'. In each site, three sampling points were measured. The fluoroprobe sensor was lowered 50 cm below the surface at each measurement.

Zooplankton was collected at the same sampling points within sites by bottle sampler (volume of 1.4 L) at mid-depth. Water samples were filtered through a 80 µm mesh net to concentrate zooplankton that was then preserved in Lugol's solution and kept cool until identification and enumeration at the laboratory. Ultimately, zooplankton

were counted in separate groups: copepods, cladocerans, rotifers and ostracods under a binocular microscope and following Błędzki and Rybak (2016).

2.5 | Food resources, fish sampling and isotope measurements

Biofilm, aquatic vegetation, phytoplankton, zooplankton, fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM) were sampled as potential food sources for YOY. They were sampled at the four sites at the beginning (July 10) and at the end (October 5) of the fish sampling period. For phytoplankton, approximately 30 L of the floodplain channel water was filtered onto a 25-mm Whatman GF/F or GF/C glass-fibre filters (previously burned at 550°C) with a vacuum pump. Foreign materials as, for example zooplankton and debris were removed from filters under a binocular microscope. Then, filters were placed and agitated in 5 mL Eppendorf tubes to take over and re-suspend the phytoplankton in milliQ water before freeze-drying.

Zooplankton were sampled with a plankton net (mesh size 80 µm) along the bank of the two floodplain channels. Debris were removed under a binocular microscope. FPOM and CPOM were randomly taken using a Surber sampler (0.02 m² area and 500-µm mesh) placed on habitats representative of the whole site. We separated FPOM and CPOM according to their size, from 100 to 1000 µm for the fine and above 1000 µm for the coarse particulate organic matter by successive sieve filtrations. Efficiency of the filtration method was checked under a binocular microscope prior to zooplankton freeze-drying.

With a toothbrush, we scraped the biofilm over large submerged macrophyte leaves such as *Potamogeton* sp. L. Biofilm was sampled only once in each site in the middle of the fish sampling period. All samples were washed with distilled water and tested with hydrochloric acid (HCl) in order to prevent any contamination by sediment carbonates (Kharlamenko et al., 2001). Then, food samples were frozen individually at -20°C before freeze-drying. Each dried sample was then ground to obtain a homogeneous powder.

Fish samplings started in July 2018 as YOY would have been too small for isotope analysis prior to that date. Sampling points were randomly selected in the two sites of each channel where potential food sources were collected. YOY were caught using the 'point abundance sampling' by electrofishing from a boat along the banks as detailed in Copp (1987), Copp and Garner (1995), Garner (1997) and Persat and Copp (1990) with a EFKO FEG 5000 generator delivering a continuous current and a 10cm diameter anode for greater efficiency with fish larvae and juveniles. Twenty-five points were samples in each site; thus, a total of 300-point samples were collected over the study period (i.e. 4 sites \times 25 sampling points \times 3 sampling dates).

For each site date, we selected a maximum of 10 specimens per species and per site. In this way, a total of 321 YOY individuals (91 bleaks, 120 chubs and 110 topmouth gudgeons) were caught, identified at species level and measured to the nearest mm. Cold anaesthesia was used; then, fishes were rinsed with deionized water and frozen in an Eppendorf tube. Fishes were then individually dried at 60°C for at least 48 h. Dried fishes were weighted and cut into small pieces in a glass vial. As lipids are ^{13}C depleted compared with proteins (Post et al., 2007), lipids were extracted following the method described in Folch et al. (1957). Whole bodies of the fishes were homogenized in a 2:1 chloroform: methanol (v/v) mixture and kept in the fridge during 24 h. Then, the mixture with the fish fragments was pooled with a cone filter and the mixture from the cone filter was let to evaporate during 2 h. The filtered solution containing the lipids was removed.

Stable isotope ratio measurements were performed on the filtrate via continuous flow-elemental analysis-isotope ratio mass spectrometry using an elemental analyser (Flash EA1112; Thermo Scientific, and VarioPyrocube; Elementar) coupled to an Isoprime100 mass spectrometer (Isoprime Ltd). Isotopic ratios were expressed using the widespread δ notation (Coplen, 2011). Sucrose and cellulose (IAEA-CH3 and IAEA-CH6 respectively) for $\delta^{13}\text{C}$ and ammonium sulphate (IAEA-N1 and IAEA-N2) for $\delta^{15}\text{N}$ were used as certified reference materials. Both of these reference materials are calibrated against the international isotopic references, that is Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen. Standard deviations on multi-batch replicate measurements of in-house standards (aspartic acid and casein) were 0.1‰ for $\delta^{13}\text{C}$ and 0.3 ‰ for $\delta^{15}\text{N}$.

We calculated the contributions of potential food sources for each species for each date of sampling with the R-software (R 3.6.2 version, R Development Core Team, 2016) using the package MixSIAR (Stock et al., 2018). The MixSIAR models were constructed using trophic enrichment factor (TEF) determined previously by Latli et al. (2017) that concerned chub fish larvae (TEF = 2.1‰ \pm 0.03 for $\delta^{13}\text{C}$ and 2.3‰ \pm 0.8 for $\delta^{15}\text{N}$). Standard error of the $\delta^{13}\text{C}$ was finally increased until 0.5 ‰ giving a better accuracy of the models. To reduce the number of potential food sources in the model, we pooled FPOM and CPOM as POM because their isotope compositions were not statistically different.

2.6 | Fish feeding selectivity

We evaluated fish feeding selectivity by comparing the contributions of potential food sources among fish diet composition and prey availability. Planktonic concentration data were previously transformed into carbon biomass per litter following the conversion factor 1:28 (Chl *a*: C factor) from Cloern et al. (1995) for phytoplankton and the Equation (2) from Kerkar et al. (2020) for zooplankton. The conversion factor C_{zoo} was estimated following the equation:

$$C_{\text{zoo}} = 3e - 11x^{3.5922}, \quad (2)$$

with $x = 1200 \mu\text{m}$ as the averaged size of zooplankton defined according to the planktonic communities described in Jurasz and Amoros (1991) that were derived from a cut-off meander located in the same floodplain as the present study. The conversion factor C_{zoo} obtained was 3.45.

The Ivlev Selectivity (IS) Index (Ivlev, 1961) was used to evaluate the prey selectivity of species for each sampling date. IS was selected because it is simple and has been reported to be comparable with more complex indices (Strauss, 1979). The Ivlev Selectivity Index is expressed as:

$$E = \frac{ri - pi}{ri + pi}, \quad (3)$$

where ri is the contribution of food category i (as proportion of all food sources) and pi is the proportion (i.e. availability) of the prey in the site. E takes a value of zero for random feeding and deviates symmetrically from zero between plus and minus one as an item is, respectively, preferred or avoided. Given that the POM and biofilm food sources constitute a tertiary resource for the studied YOY, E and the proportion of the prey (ri) in the site were calculated considering the planktonic resources exclusively.

2.7 | Feeding overlap

Feeding overlap was measured for each fish pairs in August and October using the Pianka Index (Pianka, 1973):

$$O_{jk} = \frac{\sum_i^n p_{ij}p_{ik}}{\sum_i^n p_{ij}2 \sum_i^n p_{ik}2}, \quad (4)$$

where: O_{jk} = Pianka's measure of niche overlap index between j and k species; p_{ij} = proportion of resource i in the total resources used by species j ; p_{ik} = proportion of resource i in the total resources used by species k ; n = total number of resource states. The Index ranges from 0 (no overlap) to 1 (complete overlap). July was not retained in the analysis because of the quasi-systematic absence of one of the three fish species in the samples.

2.8 | Statistical analyses

Planktonic community composition was analysed at the channel and site levels for each date. We combined the phytoplankton measurements and zooplankton sample replicates taken within each site date by averaging across the three sampling points to reduce sample variability and to avoid pseudoreplication. Similarity among planktonic community composition was visualized using a principal coordinates analysis (PCoA, i.e. Multidimensional scaling, MDS). Then, to disentangle the roles of environmental variables in determining plankton community composition, a distance-based redundancy analysis (db-RDA) was performed. The db-RDA was carried out using the `capscale` function from the `vegan` R package (Oksanen et al., 2018) and based on Bray–Curtis similarity matrices following Borcard et al. (2011). Environmental variables were tested for correlation and collinearity [`vif.step` function from `usdm` R package (Naimi, 2015)] before being included in the PCoA. C_v and O_2 variables averaged over the 2 weeks before sampling were the highest correlated variables (0.54). GPP and O_2 were less correlated (0.48). Therefore, considering the correlation between variables as relatively low (<0.6), all the above-mentioned variables were retained for the analyses. Associations between the plankton communities and the environmental variables were assessed using environmental fits with the `envfit` function in the `vegan` package in R (Oksanen et al., 2018). We also used permutation analyses that generated p -values by pairwise comparison using the function `pairwise.factorfit` from `RVAideMemoire` R package (Herve, 2018) to specifically assess which sites differed significantly from the others in terms of planktonic community composition. We nested each fit test by channel, site and date.

The Ivlev's (prey selectivity) and Pianka's (feeding overlap) indices were obtained for each of the three fish species for statistical tests and modelling. Different relations (e.g. fish selectivity vs. resource availability and Pianka index vs. productivity gradient) were tested and quantified using a linear model. The significance of terms of the fixed effects of the linear models was tested with the chi-squared test using the `ANOVA` function. The departure from a null expectation of zero in the difference in selectivity values between species was tested with a Wilcoxon test. We used the `ggplot2` R package (Wickham, 2009) for all graphics within the R statistical environment (R 3.6.2 version, R Development Core Team, 2016).

3 | RESULTS

3.1 | Hydrological conditions in floodplain channels

Two hydrological conditions could be distinguished during the study period. The first period, from April to August, was characterized by two to three spring floods, whereas the second period, from September to November, displayed low and stable flow conditions. For both channels, the spring floods ('F', Figure 2) were periods of in-channel inundations; however, the magnitude and duration of these

events differed markedly between the two floodplain channels. In MOLO, the water level rise was not due to discharge increase in the main channel of the bypassed section but likely to prolonged return flows related to hydropeaking (Figure 2a,c). Compared with PONT, MOLO experienced neither prolonged inundation nor frequent water level fluctuations. In PONT, the hourly water level fluctuations closely followed the discharge variations in the main channel. Their amplitude varied between 40 and 60 cm and correlated with hydropeaking operations (Figure 2e).

3.2 | Planktonic community structure

The phytoplankton community was dominated by green algae and diatoms, making up to 70%–100% of the total chl a concentration at all dates and sites (Table S2). The upstream site in PONT (PONT UP) displayed a community composition highly similar to the downstream site in MOLO (MOLO DO; permutation test $p=.8$). Slight differences between both sites only concerned the proportions of green algae and diatom. In PONT, diatoms comprised $\approx 40\%$ of the total chl a concentration in August and October while they represented $\approx 70\%$ of the total chl a concentration in MOLO earlier in May and June. Diatoms were especially more abundant in MOLO UP reaching chl a concentrations six times higher than green algae in the same site in May and June (Table S2). Phytoplankton community composition was more variable through time in the downstream than in the upstream sites of both channels (Figure 3b).

The zooplankton community was dominated by copepods (especially in MOLO) making up $\approx 75\%$ – 85% of the total densities at all dates and sites. Cladocerans represented 7%–15% and other groups, that is rotifers and ostracods <5% of the total densities (Table S3).

3.3 | Spatial variations of planktonic concentrations

The quantity of planktonic resources varied between channels and sites. Higher plankton concentrations were on average measured in MOLO (total chl a : Wilcoxon test $p<.05$ and zooplankton densities: Wilcoxon test $p=.083$; Figure 2 and Tables S2 and S3). Higher values were also measured in the upstream sites of both channels (total chl a : Wilcoxon test $p<.01$ and zooplankton densities: Wilcoxon test $p=.48$ and $.68$ for MOLO and PONT respectively; Tables S2 and S3).

3.4 | Planktonic concentrations in relation to hydrology

The planktonic concentrations (Figure 2) indicated that peaks in chl a concentrations occurred in early May 2018 in MOLO (average chl a concentration $\approx 120 \mu\text{g L}^{-1}$ and $\approx 20 \mu\text{g L}^{-1}$ in the upstream and downstream sites respectively; Table S2) and in July for the zooplankton (average densities $\approx 180 \text{ ind L}^{-1}$ and $\approx 88 \text{ ind L}^{-1}$ for the upstream and

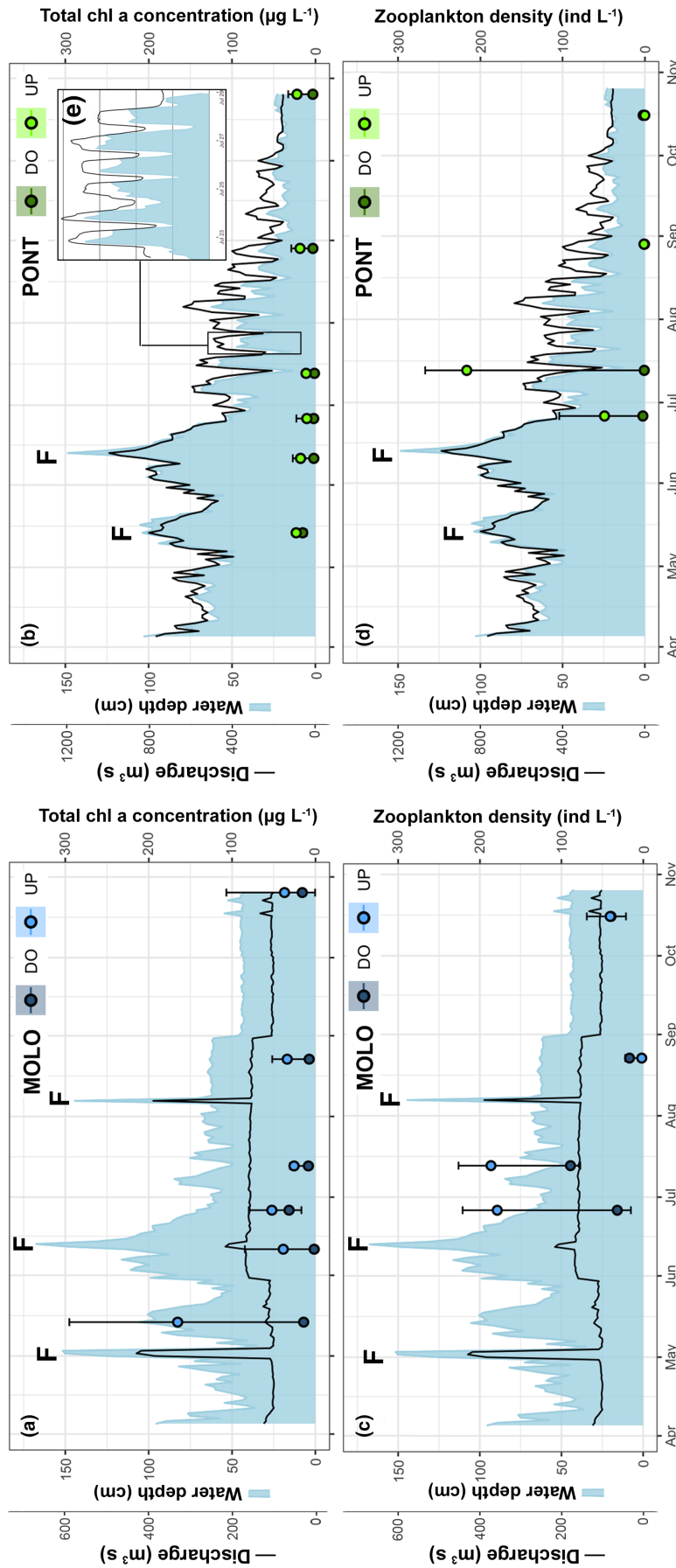
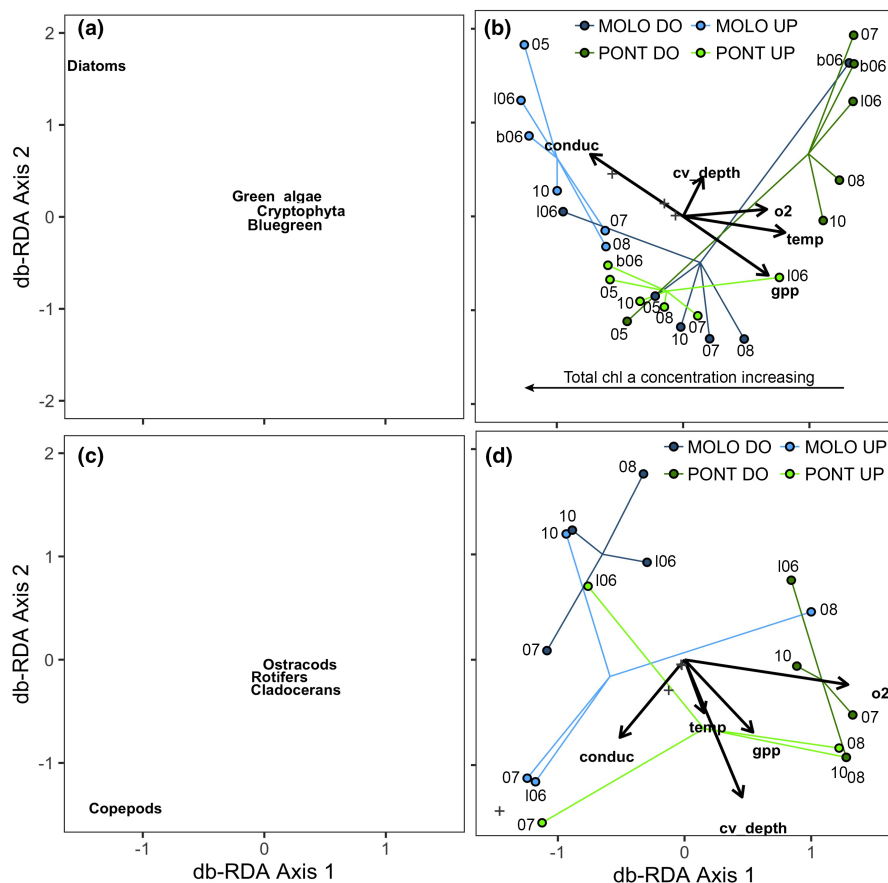


FIGURE 2 Water depth in the floodplain channels (cm; blue areas), discharge in the main channel ($m^3 s^{-1}$; black line) and temporal development of plankton (coloured points). Phytoplankton is expressed as total chl *a* concentration ($\mu g L^{-1}$; A, B) and zooplankton density as number of individuals per litre (ind L^{-1} ; C, D) from May to October 2018 at MOLO UP and DO (A–C) and PONT UP and DO (B–D) channel sites. **Figure 2E** gives an example of sub-daily water level fluctuations recorded at PONT (from July 22 to 29) caused by hydropeaking. Coloured points refer to the mean of a site and error bars to the min-max range of the channel. (F) Periods of potential downstream entry of river water during high flow events.

FIGURE 3 Distance-based RDA (db-RDA) ordination of phytoplankton (a – taxonomic group scores and b – date-site scores) and zooplankton (c – taxonomic group scores and d – date-site scores) community composition related to environmental variables. Each dot represents a month of sampling from May ('05'; for phytoplankton) or late June ('106'; for zooplankton) to October ('10'). 'b06', '07' and '08' refer to the beginning of June, July and August, respectively. Vectors are gradients of environmental variables. The arrow displayed at the bottom of the plot (b) indicates a relationship of phytoplankton composition with increasing total chl *a* concentration ('planktonic algae productivity gradient').



downstream sites respectively; Table S3). Peak chl *a* concentration and zooplankton density reached a maximum of almost $300\mu\text{gL}^{-1}$ and 230indL^{-1} , respectively, in MOLO UP, whereas downstream values in the same channel were below $25\mu\text{gL}^{-1}$ from July to October for chl *a* concentration (Table S2) and below 50indL^{-1} from August to October for zooplankton densities (Table S3). In PONT, chl *a* concentrations showed no apparent peak in early May at the upstream site (upstream chl *a* concentrations $\approx 20\mu\text{gL}^{-1}$ in May and June; Table S2 and Figure 2). Moreover, chl *a* concentrations in PONT were relatively low and stable over time at both upstream and downstream sites. However, in the same channel, the zooplankton density peaked in July at the upstream site (288indL^{-1} ; Table S3), at the beginning of the water level fluctuation period (Figure 2e). The downstream site in PONT differed markedly, providing the lowest zooplankton density ($<3\text{indL}^{-1}$; Table S3) and also the lowest phytoplankton concentrations ($<15\mu\text{gL}^{-1}$; Table S3 and Figure 2) among the four studied sites. Generally, the late summer period (after August) without flooding, reflected low chl *a* concentrations and zooplanktonic densities in the four sites (Tables S2 and S3 and Figure 2).

It is striking that for both phyto and zooplankton, high concentrations tightly coincided with the periods of more stable discharge (solid lines in Figure 2), as observed in MOLO from May to July (Figure 2a,c). However, in the case of PONT, the highest zooplankton density approaching 300indL^{-1} was also recorded during discharge fluctuations, in early July (Figure 2d).

3.5 | Planktonic composition in relation to environmental variables

The five environmental variables significantly explained 37.4% of the variability of the phytoplanktonic composition across channel sites and dates (db-RDA ANOVA $p=.02$; Figure 3a,b). Although high conductivity was significantly related to phytoplankton composition between channels and dates, we also observed a significant relationship of temperature with community composition between dates and sites (Figure 3a,b and Table 2). Ordering of the date sites along the first db-RDA axis reflected the gradient in chl *a* concentration (arrow on Figure 3b). Given the high proportion of the variance explained by the first db-RDA axis (24%; ANOVA $p=.013$), the scores of the date sites along the first db-RDA axis were used as a surrogate for the planktonic algae production (called 'planktonic algae productivity gradient' hereafter).

Although the five environmental variables explained 40.6% of the variations in zooplanktonic community composition, the model was not significant (db-RDA ANOVA $p=.21$; Figures 2d and 3c). In the ordination, date sites were split into two groups: (i) the highly productive site dates (mainly due to copepods) on the left, related to high conductivity, and (ii) the low productivity site dates (Figure 3d). Dissolved oxygen and water level variations were significantly related to changes in zooplankton composition between dates (Table 2).

TABLE 2 Goodness of fit statistics[†] and squared correlation coefficients for environmental variables fitted to the distance-based RDA (db-RDA) ordination space of the phytoplankton and zooplankton communities.

	Phytoplankton community				Zooplankton community			
	R ²	Pr(>r)			R ²	Pr(>r)		
		Ch. ^a	Sites ^b	Date ^c		Ch. ^a	Sites ^b	Date ^c
Dissolved oxygen	.11	.628	.987	.283	.43	.208	.197	.037*
Conductivity	.25	.044*	.743	.033*	.20	.203	.203	.204
Temperature	.17	.133	.043*	.002**	.07	.568	.593	.671
Water movements	.05	.664	.626	.448	.48	.091	.095	.008**
Growth primary production	.17	.186	.425	.093	.19	.514	.271	.206

Note: Channels: Molottes and Ponton; Sites: Upstream and Downstream; Date: Months from May (for phytoplankton) or late June (for zooplankton) to October (September is missing).

[†]Significant correlations are presented in bold (* $p < .05$, ** $p < .01$, *** $p < .001$).

^aThe effect of environmental variables on community composition regardless of the channels.

^bThe effect of environmental variables on community composition regardless of the channel sites.

^cThe effect of environmental variables on community composition regardless of sampling dates.

3.6 | Fish diet composition

In the four floodplain sites, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fishes were highly variable, ranging from -34.6 to -18.7‰ and from 6.5 to 14.2‰ , respectively. The fish isotope compositions were significantly different across channels, with $\delta^{13}\text{C}$ values of $-30.7 \pm 2.1\text{‰}$ and $-23.7 \pm 1.8\text{‰}$ (Kruskal Wallis test $p < .001$) and $\delta^{15}\text{N}$ values of $9.8 \pm 1\text{‰}$ to $11.5 \pm 0.8\text{‰}$ (Kruskal Wallis test $p < .001$). Within floodplain channels, zooplankton (ranging from -34.6 to -31.2‰) was generally depleted in ^{13}C compared with seston (ranging from -28.5 to -21.7‰ ; Wilcoxon test $p < .05$). The $\delta^{15}\text{N}$ values of seston and zooplankton were higher (ranging from 5.3 to 7.5‰) than $\delta^{15}\text{N}$ of benthic resources, that is POM and biofilm (ranging from 0.7 to 6.7‰ ; Wilcoxon test $p < .05$).

Fish diet was estimated with MixSIAR models for each site during July, August and October (Table S5). Plankton contributions in fish diets varied in a similar way to the seasonal and inter-sites variations of the planktonic resources in the environment. Indeed, zooplankton dominated the fish diets in July (>50% of the diet composition in PONT DO and MOLO) and August (>50% of the diet composition for MOLO except for the topmouth gudgeon). This resource decreased through time in favour of phytoplankton (MOLO and PONT) and biofilm (PONT) that both dominated the diets in August and October (Figure 4). Particulate organic matter (POM) and biofilm were marginal components of YOY diets except at PONT DO, where planktonic production was lower than in other sites (Figure 3), and where biofilm exceeded on average half of the diet composition of YOY chub in August and October. In this same site, bleak fed mainly on phytoplankton (>60% of the diet composition; Figure 4) while, for the topmouth gudgeon, the proportions of planktonic resources and biofilm were more equilibrated (<40% of the diet composition; Figure 4).

Comparison of selectivity index between planktonic resources highlighted zooplankton as more broadly selected than

phytoplankton by YOY (Figure 5a). This trend was generally similar and significant (Wilcoxon test $p < .01$ for topmouth gudgeon and $< .001$ for chub) or close to the significance level (Wilcoxon test $p = .06$ for bleak) among the three species.

According to the linear model, no interaction between seston biomass and prey selectivity was observed ($p = .1$, adjusted $r^2 = .06$; Figure 5b) but a negative interaction between prey selectivity and zooplankton density was significant ($p < .001$, adjusted $r^2 = .6$; Figure 5b). Zooplankton selectivity became negative for zooplankton densities above $\approx 100 \text{ ind L}^{-1}$ (Figure 5b). Independently of linear models, seston selectivity was maximal (≈ 0.5) at intermediate seston biomass ($\approx 10 \mu\text{g chl } a \text{ L}^{-1}$), whereas zooplankton selectivity peaked (≈ 1) at zooplankton density close to 0.

3.7 | Feeding overlap

The average dietary overlap was higher (Pianka's indices above 0.8; Figure 6) in the most productive sites (MOLO sites and PONT UP; Figure 3). The model indicated that increasing productivity in planktonic algae increased the diet overlap between the three fish species. Conversely, diet overlap decreased to 0.53 on average (ranging from 0.13 to 0.88) in PONT DO (Figure 6), the less productive site (Figure 3). Lower diet overlaps were observed between the two native species (average 0.76 ± 0.35), while the topmouth gudgeon had higher dietary overlaps with the chub (average 0.89 ± 0.15) and the bleak (average 0.87 ± 0.13).

4 | DISCUSSION

The composition of planktonic assemblages and the YOY diet of three fish species, bleak, chub and topmouth gudgeon, were investigated in two floodplain channels of the French Upper Rhône River.

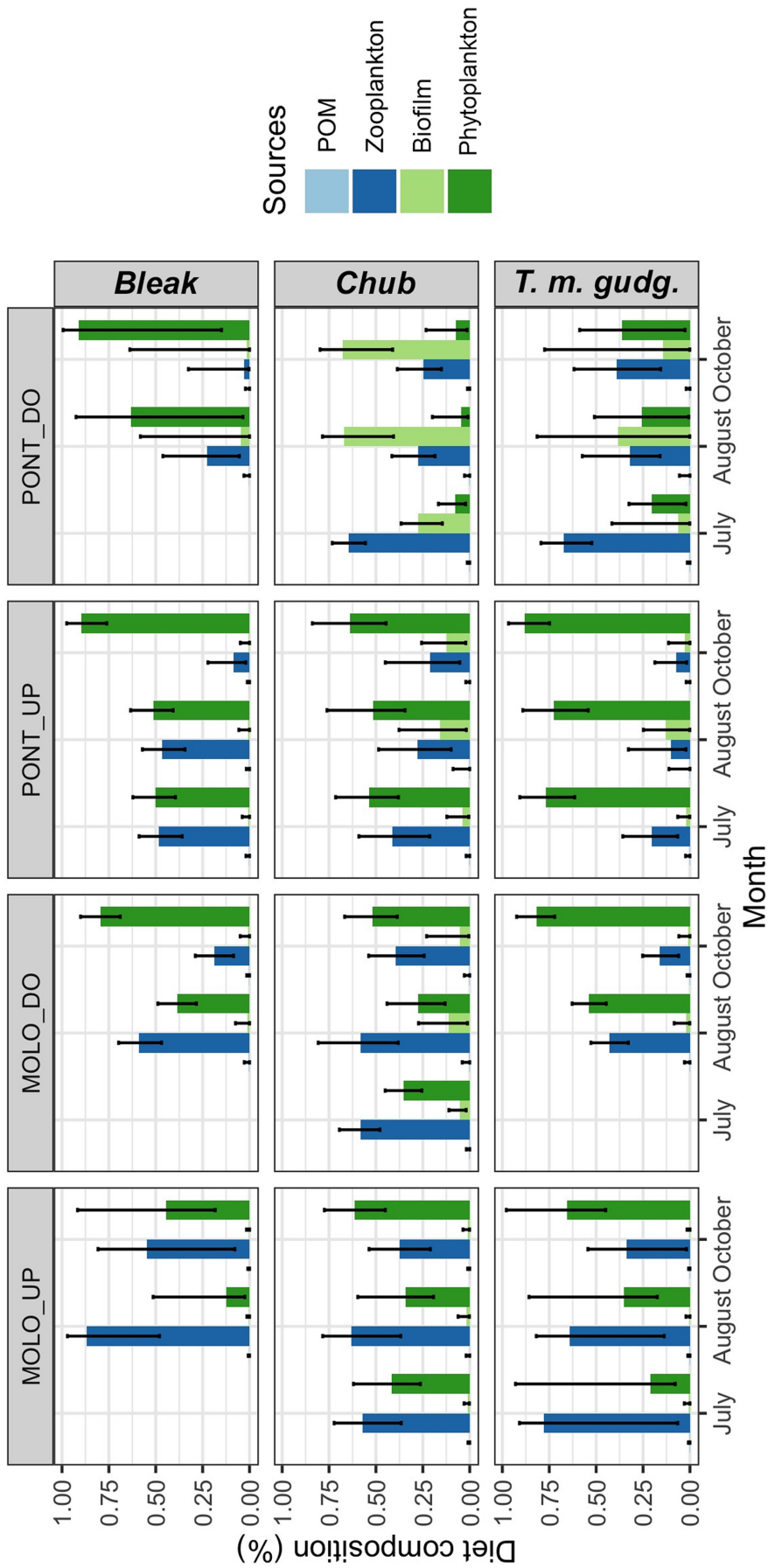


FIGURE 4 Estimated diet composition of three YOY fish species (rows) in the four channel sites (columns) in July, August and October. Diet compositions based on stable isotope analysis were estimated using MixSIAR multi-source Bayesian mixing models (Stock et al., 2018) and are presented as median estimates with 95% credibility intervals (error bars).

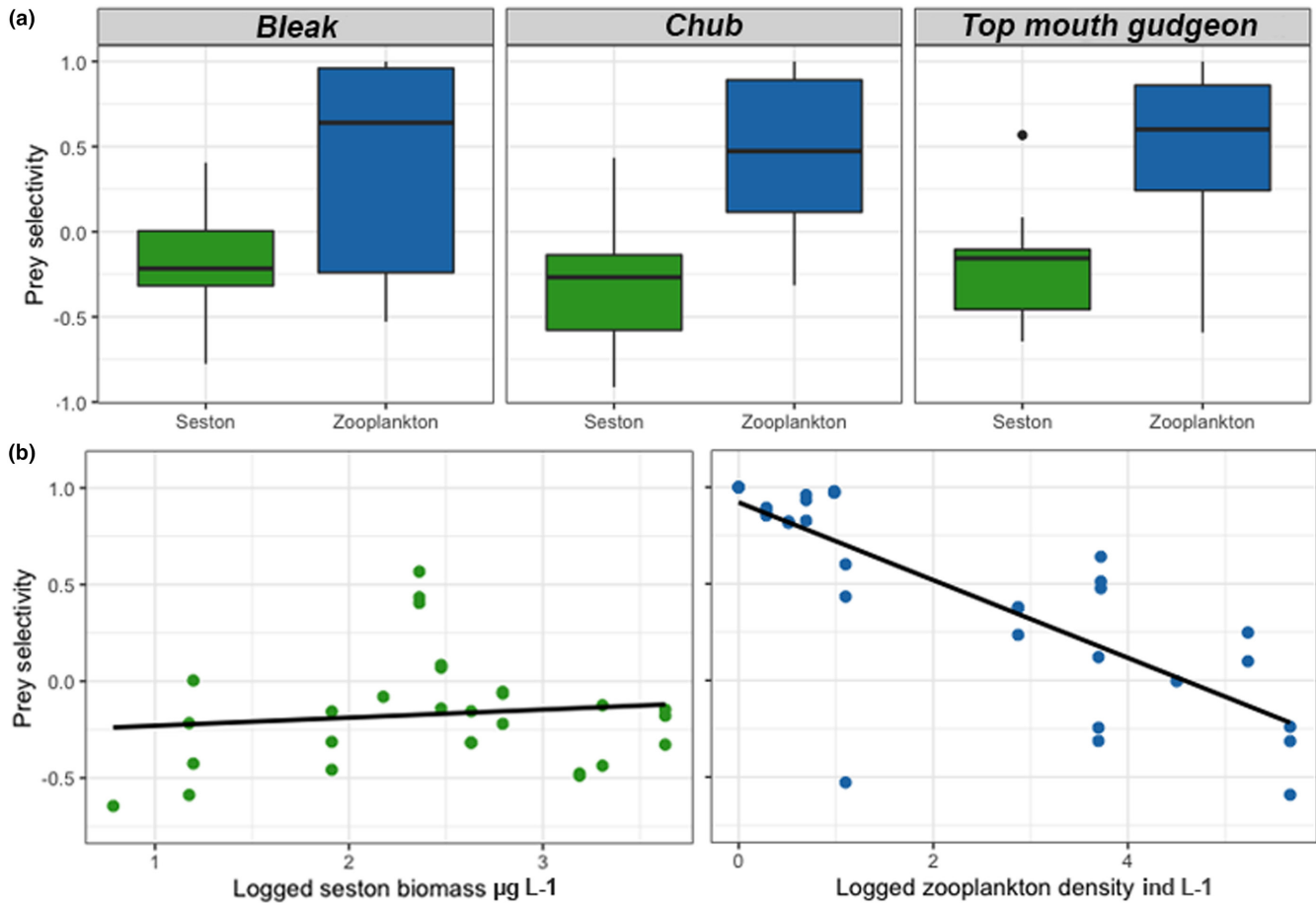


FIGURE 5 Prey selectivity (Ivlev's index) (a) for three YOY fish species towards phytoplankton and zooplankton and (b) in function of plankton availability (for the three species combined) in the four channel sites in July, August and October. Solid lines are least-square linear fits.

The temporal and spatial variations of the YOY diet was analysed in relation to plankton resource availability and phytoplanktonic algae productivity gradient. The results showed that (i) the diet of juveniles was dependent upon the availability of plankton, the dynamics of which was tightly linked with flow conditions and (ii) the food resources actually used by YOY, as well as the diet overlap between species, differed markedly along the planktonic algae productivity gradient.

4.1 | Food availability for YOY in relation to environmental variables

4.1.1 | Relation with hydrology

The development of plankton in the upstream part of the MOLO channel can be explained by more stable water level offering favourable conditions for their growth. At the beginning of the growing season (i.e. May), phytoplankton is mainly represented by diatoms and green algae, particularly used as an early trophic resource by fish larvae (Reynolds & Descy, 1996). The early development of these two groups can be explained by their reduced respiration at low

light and water temperature, compared with other algae (Lehman et al., 2008). Later, in MOLO (late June and July), zooplankton density reached a production peak (up to 180 ind L⁻¹), typical for the seasonal dynamics of zooplankton in freshwater ecosystems including floodplains (Illyová, 2006).

The presence of another hydroelectric scheme downstream of the study reach induces water level fluctuations propagating upstream as far as the MOLO channel during hydropeaking operations. The associated backflow entries by return flows (i.e. backwater conditions in mid-May and June) in MOLO are likely to increase nutrient content of the water in the floodplain channel and, in turn, to benefit phytoplankton and zooplankton growths. Numerous studies demonstrated the effects of backwater conditions limiting discharge and causing water level elevation in upstream areas (Amarnath & Thatikonda, 2020; Costabile et al., 2015; Teo, 2010). Therefore, we consider the plankton development in MOLO can also be supported by this backwater effect that favoured plankton development in floodplains because of the associated reduction in hydraulic shear stress. Later in September, because of the decrease in water level, floodplain channels changed into shallower pools, concentrating macrophytes (which also take up nutrients), reducing light penetration, dissolved oxygen and ultimately plankton production.

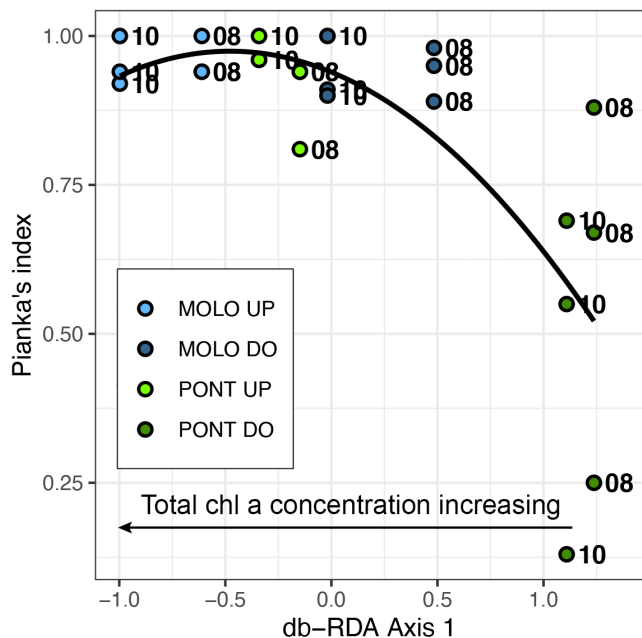


FIGURE 6 Relationship between feeding overlap index (Pianka's index) and the site scores of the first db-RDA axis that summarized the planktonic algae productivity gradient. Feeding overlap index was calculated for each pairwise comparison among the three species (three pairs per date) for the four channel sites sampled once in August ('08' for 2008) and once in October ('10' for 2010). Relationship between the overlap values and the db-RDA site scores was best fitted by a significant second-order curve ($b = -0.15$ and $p = .008$ and $b^2 = -0.15$ and $p = .031$; adjusted $R^2 = .53$). July was not retained in the analysis because of the frequent absence of one of the three species in the samples.

In contrast, the hydrological instability was more pronounced in PONT where water levels and flow conditions were mainly influenced by hydrological variations in the main channel. In PONT, water level fluctuated sub-daily between 40 and 60 cm (i.e. hydropeakings) from July to August, limiting phytoplanktonic production (Chaparro et al., 2018; Schagerl et al., 2009) but also potentially that of macrophytes (Wang et al., 2016). The reduced amount of macrophytes in PONT facilitates the downstream entry of river water during hydropeakings and could therefore accentuate the dilution of plankton within the floodplain channel. Plankton retention by macrophytes was documented in floodplain lakes of the Orinoco River (Hamilton et al., 1990).

These findings demonstrate that continuous supply of water caused by dam hydropeakings has a negative impact on plankton development in a partially connected floodplain channel. But, the observed hydrology had at least two important links with zooplanktonic productions. First, PONT UP underwent frequent and alternated periods of drought and high water during water level fluctuation periods that likely resulted in zooplankton recolonization from the sediment egg bank (Cáceres & Tessier, 2003; Cromel & Carpenter, 1988; Medley & Havel, 2007). This process might explain high zooplankton densities observed (288 ind L^{-1}). Despite the artificialized flow regime, YOY food production can still be achieved.

The second effect of hydrology on zooplankton was related to the stable flow conditions. A high concentration of chl *a* was recorded in May, followed by a peak in zooplankton in June–July, which is typical for the seasonal dynamics of plankton in a lentic floodplain channel (Illyová, 2006; Simões et al., 2012). In the present study, such a pattern was observed at MOLO UP where the zooplankton concentration was up to 180 ind L^{-1} in July. Other studies also reported that plankton production was the dominant energy source in fish nurseries of large rivers during low-flow conditions (Houser, 2016; King et al., 2003). Therefore, we posit that during high water levels, plankton production from recently inundated areas (i.e. PONT UP) represents an increased subsidy for larval and juvenile riverine fishes (Roach et al., 2014). Then, during low flows, channels permanently connected downstream with the river (e.g. MOLO) might be the most profitable floodplain habitat for YOY feeding. In addition, fish predation could be an important driving factor for zooplankton communities (as shown in the floodplain of River Ichilo, by Rejas et al. (2005)). These results also highlight the difficulty to explain compositional variations in YOY assemblages with abiotic variables only.

4.1.2 | Relations with groundwater supply

In MOLO, high phytoplankton concentrations led to a rapid nutrient assimilation. Generally, nutrient concentrations appeared low to bring about an increase in phytoplankton concentrations. Significant relationships between high conductivity, low temperature and increasing phytoplankton productivity suggest that groundwater supply may have a key role in phytoplankton growth and composition. Indeed, groundwater inputs are a potential source of $\text{N} - \text{NO}_3^-$ in floodplain systems (Boissier et al., 1996). In a tidal system, Welti et al. (2015) showed that extra nitrogen could cause local blooms in a nearshore marine zone, affecting diatom assemblages in terms of both numbers and species composition. In floodplains, this additional source of nitrogen is important to consider, as phytoplankton development is generally nutrient limited during low-flow periods (Reynolds & Descy, 1996; Tockner et al., 1999). Therefore, groundwater supply can count among the cues enhancing phytoplanktonic production in floodplain channels. It can partly counterbalance the influence of an anterior flood and rapid warming of water in early spring, as identified in the Ourthe River (Philippart, 1981).

4.2 | YOY response to the dynamics and interactions in floodplain food webs

In the Rhône River, the reproduction success of river fishes fluctuates largely from year to year: species that depend upon the floodplain for food and spawning are at the mercy of hydrological conditions (Bischoff & Wolter, 2001; Fruget et al., 2001; Pont & Nicolas, 2001). Hydrological variations undoubtedly affect the food availability in temperate river floodplains especially when channelization and dams strongly altered the hydromorphological

characteristics and the sediment transport (Chaparro et al., 2018; Cromel & Carpenter, 1988; Grift et al., 2003). Under natural conditions, fishes evolved life-history strategies to ensure successful breeding and viable offsprings (Mims & Olden, 2012; Welcomme et al., 2006). Our results showed that, regarding diet, YOY of the three species display a large trophic plasticity related to the variability in food availability. Overall, we observed differences in diets largely occurring between sites but not necessarily in relation with the established feeding preferences of the species (Figure 4 and Table 3). Spatially, YOY adopted different diets because they tend to feed on organisms that give the maximum nutritional return for the minimum expenditure of energy (i.e. 'optimal foraging'; Nunn et al., 2012). Indeed, YOY are generally visual predators and can only chase size-specific prey (Wanzenböck, 1995) in a limited space (Nunn et al., 2007). In this way, high planktonic production is highly profitable for YOY because the aggregation of food resources may reduce the energy needed for food collection as individuals move through floodplain habitats (Lehman et al., 2008). These observations are in line with the observations of Röpke et al. (2014) and Pereira et al. (2017) in Brazilian floodplains, Almeida et al. (2017) and Latorre et al. (2016) in Iberian reservoirs and rivers, Garner (1996) in the River Great Ouse (England) and Winemiller et al. (2000), Zeug et al. (2005) in the Brazos River floodplain.

In the present study, YOY fed mainly on two trophic sources: zooplankton and, secondarily, on phytoplankton. The ability to switch between these two alternative resources received little attention (Bone et al., 1995; Mann et al., 1997). In the present study, the diet compositions among species showed that prey switching occurred as a coordinated response to environmental changes. Indeed, if the factors inducing zooplanktonic production occurred, the diet switched afterwards to zooplankton, likely because it provides an energetic benefit for YOY development (Nunn et al., 2012). Even if the absolute abundance of a food item in the environment is not directly related to its availability for fishes (Uieda & Pinto, 2011; Wootton, 1999), we could evaluate that zooplanktonic densities above 100 indL⁻¹ appeared sufficient to allow initiation of a diet mainly (for more than 50%) based upon zooplankton. This threshold confirmed the estimates of Bone et al. (1995) who proposed zooplanktonic densities between 100 and 1000 indL⁻¹ as necessary for the development of freshwater and marine fish larvae in general.

Diet switches were especially conspicuous in MOLO UP, the most productive site, where chub and topmouth gudgeon fed more efficiently on zooplankton instead of phytoplankton during July and August, the latter being more often selected during October. For

these omnivorous species, switching diet to ingest resources of lower energetic value (phytoplankton or biofilm in the present case) may allow fishes to survive during suboptimal and disturbed periods, for example extreme low flow, and to stay longer in floodplain habitats until reconnection with the main channel (Zeug & Winemiller, 2007) that may not occur until the next winter (as described in Scharbert & Borcherding, 2013). This assumption is also further supported by the low diet overlap in less productive systems (PONT DO), which was previously identified as a mechanism facilitating diet partitioning and the coexistence of species (i.e. reduced competition) in species-rich systems during low food availability (Abrams, 2010; Correa & Winemiller, 2014; Keckeis & Schiemer, 1992; Poisot et al., 2011; Tewson, 2012). Hence, diet opportunism could be viewed as an evolutionary adaptation to variable conditions in a system with spatially and seasonally fluctuating food sources (Grandmottet, 1983; Humphries et al., 2002; King et al., 2003; Puckridge et al., 1998). By adopting this strategy, these species are able to coexist and to feed in a variety of habitats and under a range of environmental conditions in large river floodplains (Wolter et al., 2016). In turn, this represents a stabilizing effect in a generally disturbed system (DeAngelis et al., 2005; Mims & Olden, 2012).

5 | CONCLUSION

The present study showed seasonal and spatial variations in prey availability had important implications for the diet composition of YOY fishes in a large river floodplain. The results revealed that flow-induced changes in dominant resources (e.g. phytoplankton, zooplankton, POM and biofilm) and resource quantity (concentration and density) controlled YOY diets. More specifically, water level variations in the order of 30–100 cm can alter key ecosystem processes such as planktonic production and energy transfer through food webs. This illustrates the importance of hydrology, season and lateral hydrological connectivity for resource-consumer linkages and shows that not just plankton stocks, but also fish diet, may fluctuate over time in response to flow and seasonal variations.

In the French Upper Rhône River, the first goal of the restoration was to physically rehabilitate damaged floodplain habitats by, for example lateral flow reconnection, morphological and topographic manipulation (Lamouroux et al., 2015). These restoration works led to the recovery of a set of different floodplain channel types supporting ecological processes. As the hydrological features, biogeochemical

Species	Habitat/feeding preferences	Side-channel fidelity	Current preference	Reproductive strategy
<i>Chub</i>	Midwater/Omnivorous	Transient	Rheophilic	Periodic
<i>Bleak</i>	Surface/Omnivorous and zooplanktivorous	Transient	Eurytopic	Opportunistic
<i>Topmouth gudgeon</i>	Midwater/Omnivorous	Resident	Limnophilic	Opportunistic

TABLE 3 Studied fish species with their respective feeding and habitat preferences and floodplain channel fidelity (juvenile + adult stages), adapted from Copp (1987) and Balon (1992).

processes, thermal regimes differed from one floodplain channel to another. The structure of the food webs in each restored floodplain channel also greatly differed from one site to the other. Therefore, the way YOY can use trophic resources could also potentially vary, determining growth rate and survival between the cohorts of a given year. Basically, juvenile fishes were found to be abundant between the beginning of May and the end of July, at high temperature (at least 14°C; Table S4), under low flow velocity within the floodplain channels associated with facilitated larvae and juvenile access. The interaction of these factors provided for juvenile fishes to exploit a high primary and secondary planktonic production within restored floodplain nurseries. However, research into (i) variation in diet composition and resource availability with an estimation of threshold densities of key resources, that is that have implications for the growth or the survival rates of fish, and (ii) the interplay between the environmental conditions and the flow-dependent biological mechanisms that allow YOY to forage these key resources, needs to be further identified. Application of this research to juvenile fishes of different life-history traits and under a variety of environmental conditions (e.g. along a gradient of anthropogenic pressures) is also central for a better implication in the maintenance of diverse populations under different degrees of floodplain degradation. We also encourage the exploration of the correlations between spawning periods, flow regime and planktonic production in floodplains that incorporate greater details in fish recruitment potential in large alluvial rivers. Such information has functional and applied implications in the optimization of floodplain fish nursery restoration.

AUTHOR CONTRIBUTIONS

P.M. and J.-M.O. conceived the original idea and were in charge of overall direction and planning. P.M., L.S., A.R. and J.-M.O. conceived the experiments. P.M., A.R., P.G., N.G., H.M. and J.-M.O. contributed to field works and sample preparation. P.M., L.S., A.R. and C.G. designed the models and analysed the data. L.S. verified the numerical results of the models. P.M., L.S. and J.-M.O. contributed to the interpretation of the results. P.M. took the lead in writing the manuscript. E.C., V.I.S. and J.-M.O. contributed to the final version of the manuscript and supervised the project. All authors provided critical feedback and helped shape the research analysis and manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have not competing interest.

DATA AVAILABILITY STATEMENT

Data created during and/or analysed during the current study are available from the corresponding author Pierre Marle on reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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