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# Angling bait consumption and stable isotope niche of two cyprinids in different lake fisheries

Alexis Imbert<sup>1</sup>  | Jean-Nicolas Beisel<sup>2,3</sup>  | Stéphanie Boulêtreau<sup>1</sup>  | Julien Cucherousset<sup>1</sup> 

<sup>1</sup>Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS, IRD, Toulouse INP, Université Toulouse 3 – Paul Sabatier (UT3), Toulouse, France

<sup>2</sup>Laboratoire Image Ville et Environnement – UMR 7362 CNRS/ENGEEES, Université de Strasbourg, Strasbourg Cedex, France

<sup>3</sup>Ecole Nationale du Génie de l'Eau et de l'Environnement de Strasbourg (ENGEEES), Strasbourg Cedex, France

## Correspondence

Alexis Imbert, Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS, IRD, Toulouse INP, Université Toulouse 3 – Paul Sabatier (UT3), Toulouse, France.  
Email: [alex.imbert24@gmail.com](mailto:alex.imbert24@gmail.com)

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## Abstract

1. Terrestrial subsidies are important for freshwater ecosystems and, in lakes supporting recreational fisheries, angling baits can represent an important allochthonous input. This resource can directly contribute to fish diet but its consumption may be influenced by fish body size and the type of angling baits used in different fisheries. In this study, we evaluated angling baits consumption by two common cyprinid species, *Cyprinus carpio* and *Rutilus rutilus*, in three fishery types (specialised carp, specialised roach, and put-and-take fisheries).
2. We used stable isotope analyses ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of cyprinids, their natural prey and different angling baits in 16 gravel pit lakes located in south-western France, including four lakes without angling.
3. Angling baits were significantly  $\delta^{13}\text{C}$ -enriched and  $\delta^{15}\text{N}$ -depleted compared to natural prey. Overall, angling bait consumption was highly variable between individuals. For *C. carpio*, angling bait consumption averaged 30.5% ( $\pm 17.0$  SD) and was higher in specialised carp fisheries ( $40.0\% \pm 16.7$  SD) than in put-and-take fisheries ( $15.9\% \pm 9.0$  SD) and was not related to body size. For *R. rutilus*, angling bait consumption averaged 41.3% ( $\pm 15.7$  SD), did not differ significantly among fishery types, but increased with body size. The niche width of *C. carpio* was six times larger in specialised carp fisheries than in lakes without angling. For *R. rutilus*, niche width was two times larger in specialised carp and put-and-take fisheries compared to lakes without angling and specialised roach fisheries.
4. These results indicate that angling bait subsidies represent a novel and substantial resource opportunity for fishes in angling lakes, with trophic consequences for the targeted species through increase of their stable isotope niche size. These impacts are partly influenced by the type of angling baits used by anglers and the characteristics of the fisheries, suggesting the need for improved quantification

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of the temporal dynamics of this type of subsidy to better understand its consequences on freshwater fish and recipient ecosystems.

**KEYWORDS**

allochthonous subsidies, freshwater fish, recreational fisheries, stable isotopes

## 1 | INTRODUCTION

Freshwater ecosystems receive important external inputs of nutrients, matter, and energy due to their spatial distribution within catchments and their morphological characteristics (Leroux & Loreau, 2008). These inputs represent allochthonous subsidies that can influence food web dynamics by enhancing primary and secondary productivity (Polis et al., 1997). In lakes, subsidies substantially contribute to the pool of organic carbon used by each trophic level, and largely support energy transfer within the food web (Cole et al., 2006). While terrestrial organic carbon (t-OC) is mainly used for bacterial respiration, it is also an important subsidy that directly supports higher trophic levels under certain forms (Karlsson, 2007; Kritzberg et al., 2005). The contribution of t-OC to fish, constituted by particulate organic matter from upland and riparian ecosystems, can range from 30% to 50% in eutrophic temperate lakes and may exceed 60% in certain boreal lakes (Carpenter et al., 2005; Karlsson et al., 2012). However, human activities can disrupt these natural fluxes, particularly through the intentional or accidental inputs of anthropogenic subsidies (Oro et al., 2013).

Recreational fishing can result in significant inputs of anthropogenic t-OC into lakes that experience high fishing pressure (Arlinghaus & Mehner, 2003; Arlinghaus & Niesar, 2005). In such lakes, angling baits are a widespread fishing technique, especially for targeting cyprinids (Amaral et al., 2013; Arlinghaus, 2004). The quantities of angling baits used are highly variable, and averaged around 14.2 kg/year for cyprinid anglers with maximum values exceeding 200 kg/year for specialised carp anglers in Germany (Arlinghaus, 2004; Arlinghaus & Mehner, 2003). In general, angling baits have higher nitrogen (N) and phosphorous (P) contents than natural t-OC, making them significant contributors of nutrients to lakes (Elser et al., 2000; Imbert et al., 2022; Wenzel et al., 2012).

The consumption of angling bait by freshwater consumers can be quantified through stable isotope analyses (SIAs) (Bašić et al., 2015), as it can cause significant shifts in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values due to the terrestrial and/or marine origins of angling baits and subsequently increase trophic niche size (Britton et al., 2022; De Santis et al., 2019; Gutmann et al., 2017). The contribution of angling bait to the diet of fish has been reported to average 50% for *Barbus barbus* in English rivers experiencing high angling pressure (Bašić et al., 2015). While the consumption of angling baits can increase with fish body size (De Santis et al., 2019; Mehner et al., 2019), it is also highly variable among individuals going up to 80% for some individuals (Bašić et al., 2015; Gutmann et al., 2017). To date, however, most

investigations have focused on single fisheries, despite the potential influence of different types of fisheries on the types and quantities of angling baits used.

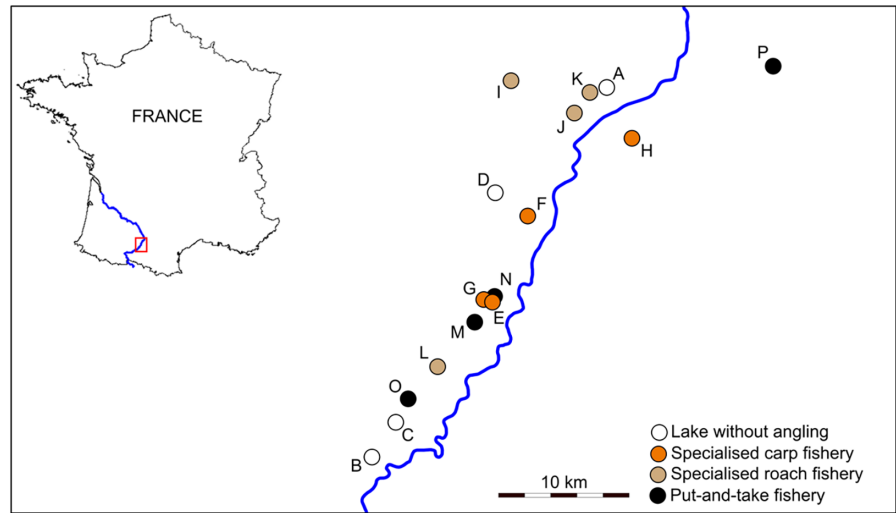
We used SIAs ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) to assess the consumption of angling baits by two omnivorous cyprinid species, namely carp and roach, (respectively *Cyprinus carpio* and *Rutilus rutilus*) across three different fishery types in gravel pit lakes. First, we compared the stable isotope values between the main angling baits used by anglers and the natural resources consumed by the two species. We hypothesised angling baits and natural prey differ in stable isotope values due to differences in their origins and composition. Second, we quantified the dietary contribution of angling baits to the two species using stable isotope mixing models. We hypothesised that the contribution of angling baits for both fish species differ among fishery types because targeted fisheries use specialised angling baits and consumption of specialised bait is positively correlated with body size. We then examined whether the stable isotope niche of the two species differed among fishery types. We hypothesised that the stable isotope niche size of fish in lakes supporting fisheries increased compared to lakes without angling, where only natural subsidies are present.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

The study was conducted in 16 gravel pit lakes located in the Garonne floodplain in south-western France (Zhao et al., 2016). These lakes were selected to represent four distinct fishery types: lakes without angling where angling is prohibited and no baiting occurs ( $n=4$ ), specialised carp fisheries ( $n=4$ ), specialised roach fisheries ( $n=4$ ), and put-and-take fisheries specialised in rainbow trout (*Onchorynchus mykiss*,  $n=4$ ). While specialised carp and roach fisheries systematically release fish after capture (catch-and-release fisheries), put-and-take fisheries involve stocking and rapid harvesting of fish (Arlinghaus & Cooke, 2009; Cowx, 2015). Gravel pit lakes are understudied compared to other freshwater ecosystems, but are abundant across the globe because of the excavation of billions of tons of gravel and sand per year (Mollema & Antonellini, 2016). They are typically located in the floodplains of large riverine systems, which usually correspond to areas with high levels of human activities such as recreational angling (Matern et al., 2019; Meyerhoff et al., 2019; Zhao et al., 2016). The studied gravel pit lakes were relatively small and shallow, with an average maximum depth of 3.3 m ( $\pm 1.4$  SD) and an average size

**FIGURE 1** Geographical distribution of the 16 studied gravel pit lakes located in south-western France (labelled A–P) in the floodplain of the Garonne River (indicated by the blue line) and between 2013 and 2021. Colours represent the different fishery types.



of 10.9 ha ( $\pm 6.8$  SD). All lakes were located within 35 km of each other (Figure 1). A principal component analysis based on the hydro-morphological characteristics and the spatial distribution of the gravel pit lakes was performed and revealed no significant differences in environmental conditions among the fishery types (PERMANOVA,  $p=0.344$ , Figure SI.1). Angling baits can be rich in nutrients (Imbert et al., 2022) and potentially impact water quality where they are used. Therefore, variables related to water quality were not included in these analyses. The average fish species richness in the studied gravel pit lakes was 9.75 ( $\pm 2.44$ ), with a range of eight to 14 species. The fish communities were dominated by Cyprinidae and Percidae (further details available in Zhao et al., 2016) and, overall, fish communities were not significantly different among the different fishery types (PERMANOVA,  $p=0.743$ , Figure SI.2).

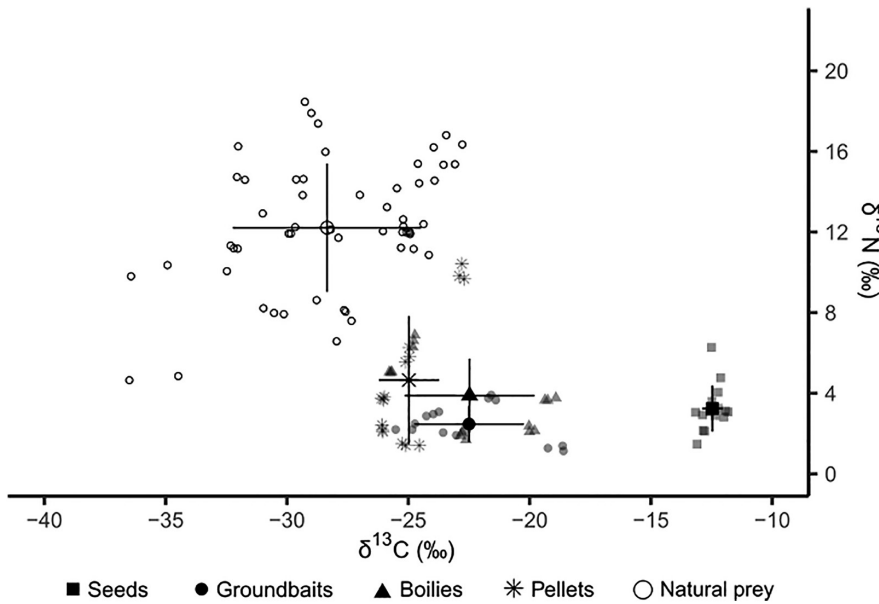
## 2.2 | Fish and invertebrate sampling

Fish and invertebrate sampling occurred simultaneously between 2013 and 2021, always between mid-September and early October. *C. carpio* and *R. rutilus* specimens were collected using gillnetting and electrofishing (Zhao et al., 2016). These species have been selected because they were ubiquitous and targeted by anglers. All individuals were measured for fork length to the nearest mm, and a sample was taken from the pelvic fin tip of each individual for SIAs. Stable isotope analyses were selected instead of stomach content analyses because diets of cyprinids are particularly difficult to assess because their pharyngeal teeth damage consumed prey, preventing precise diet identification and quantification. Fin sampling was selected as it represents a robust non-lethal alternative to muscle sampling for SIAs (McIntosh & Reid, 2021). The subsequent analyses focused on 99 *C. carpio* (ranging in size from 200 to 1300 mm) and 144 *R. rutilus* (50–320 mm; Table SI.3 for detailed information). In addition, the main natural prey items for the two fish species were collected during fish sampling in each studied gravel pit lake (Table SI.3 for details). For *R. rutilus*, putative preys consumed by all age classes included Ephemeroptera,

Chironomidae, molluscs (Gasteropoda and Bivalvia), and zooplankton (Cryer et al., 1986). For *C. carpio*, an omnivorous bottom-feeder fish (Keith et al., 2011), putative prey included chironomidae, molluscs, and crayfish (*Procambarus clarkii*). The natural preys were sampled at three locations in the littoral zone using a 500- $\mu$ m hand net, while Chironomidae were collected from the central part of each lake using an Ekman grab because Chironomidae abundance was very limited in the littoral zone. Each sample of macroinvertebrates included multiple whole individuals and guts were not removed prior to SIAs (Euclide & Stockwell, 2015). For crayfish, muscle samples were analysed. All samples were rinsed with distilled water before being oven-dried at 60°C for 48 h. Stable isotope analyses were performed at the Cornell Isotope Laboratory (Ithaca, USA).

## 2.3 | Angling baits

A field survey was conducted to identify the main angling bait types used by anglers. We then analysed the stable isotope values of the main angling bait types used by anglers in the four fishery types studied, which included seeds (maize and tiger nuts boiled in water), groundbaits (vegetal and animal flours compacted with water), boilies (animal or vegetal flours boiled with eggs and dairy products, aggregated with plant or fish oils and compacted into small balls), and pellets (compact animal flours blended with fish oil in cylinders) (De Carvalho et al., 2021; Imbert et al., 2022). For all bait types, especially the most industrialised ones (groundbaits, boilies, and pellets), spices, sugar, flavourings, preservatives, and additives could be added. SIAs were performed for a total of 20 angling bait models. An angling bait model was defined as a unique commercial product and manufacturers usually produce several models. For each angling bait type, models from several manufacturers were analysed to account for potential variability. Each angling bait model was analysed in triplicate. Angling baits were purchased between 2016 and 2020. In addition, the same angling bait model belonging to the groundbaits type was purchased and analysed twice in 2016 and 2019. Although the number of samples analysed was limited ( $n=3$  and 3 in 2016



**FIGURE 2** Stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of the main angling bait types (seeds, groundbaits, boilies, and pellets) and the main natural prey of *Cyprinus carpio* and *Rutilus rutilus* in lakes without angling ( $n=4$ ). The large points represent the mean values with their standard deviations.

and 2019, respectively), analyses revealed that stable isotope values were similar ( $\delta^{15}\text{N}=1.8\text{‰}\pm 0.5$  and  $\delta^{13}\text{C}=-23.6\text{‰}\pm 0.1$  in 2016 and  $\delta^{15}\text{N}=2.3\text{‰}\pm 0.3$  and  $\delta^{13}\text{C}=-23.2\text{‰}\pm 1.4$  in 2019). These limited differences are within the range of analytic errors (0.4‰ for  $\delta^{15}\text{N}$  and 0.2‰ for  $\delta^{13}\text{C}$ ), indicating that temporal change in the stable isotope values of angling baits was probably limited.

## 2.4 | Data analyses

First, we compared the stable isotope values of natural prey from lakes without angling with those of the four main angling bait types. We tested differences in stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  tested independently) between natural prey and angling baits using Linear Mixed-Effects Models with the *lme4* package (Bates et al., 2015). The fixed factor in the analysis was the origin (natural prey vs. angling baits) and the random factors were lake ID and angling bait model. Next, we compared the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between the four angling bait types using angling bait model as a random effect.

Second, we quantified the relative contribution of different trophic resources to the diet of individual *C. carpio* and *R. rutilus* in each fishery type using Bayesian mixing models in the *simmr* package (Parnell & Inger, 2016). We considered two types of natural prey for *C. carpio*, namely small benthic invertebrates (i.e. Chironomidae and molluscs) and crayfish. For *R. rutilus*, the natural prey consisted of small benthic invertebrates (Chironomidae, Ephemeroptera and Molluscs) and zooplankton. In lakes supporting a fishery, angling baits were added as potential prey items in the mixing models. Field observations indicated that pellets were predominantly used in put-and-take fisheries, groundbaits were used by specialised roach anglers, and a similar proportion of boilies and seeds was used by specialised carp anglers. The stable isotope values of angling baits for each fishery type were calculated

as the average value of all the angling bait models used by anglers. A trophic enrichment factor of 3.4‰ ( $\pm 1.0$  SD) for  $\delta^{15}\text{N}$  and 0.4‰ ( $\pm 1.3$  SD) for  $\delta^{13}\text{C}$  was applied (Post, 2002). Variability in trophic enrichment factor was included in the mixing models to account for potential differences between consumers, both within- and between-species. We conducted further analyses to examine the effects of fishery type and fish body size on angling bait contribution to the diet of each species, using the *lmer* function from *lme4* package. The full model included a two-term interaction with lake as a random effect. Non-significant interaction terms were subsequently removed from the models.

Third, we compared stable isotope niche of *C. carpio* and *R. rutilus* individuals among fisheries. To allow comparisons among lakes,  $\delta^{13}\text{C}$  values were corrected into  $\delta^{13}\text{C}_{\text{corrected}}$  using the following formula (Olsson et al., 2009):

$$\delta^{13}\text{C}_{\text{corrected}} = \frac{\delta^{13}\text{C} - \delta^{13}\text{C}_{\text{I}_{\text{mean}}}}{\delta^{13}\text{C}_{\text{I}_{\text{max}}} - \delta^{13}\text{C}_{\text{I}_{\text{min}}}}$$

where  $\delta^{13}\text{C}$  is the carbon stable isotope value of fish,  $\delta^{13}\text{C}_{\text{I}_{\text{mean}}}$  the mean carbon stable isotope value of invertebrates, ranging from the minimum value ( $\delta^{13}\text{C}_{\text{I}_{\text{min}}}$ ) to the maximum value ( $\delta^{13}\text{C}_{\text{I}_{\text{max}}}$ ) observed in each of the studied lakes.  $\delta^{15}\text{N}$  was converted into trophic position (TP) using the following formula (Anderson & Cabana, 2007):

$$\text{TP} = \frac{\delta^{15}\text{N} - \delta^{15}\text{N}_{\text{baseline}}}{3.4} + 2$$

where  $\delta^{15}\text{N}$  is the nitrogen stable isotope value of the fish and  $\delta^{15}\text{N}_{\text{baseline}}$  is the average of  $\delta^{15}\text{N}$  values of the baseline organisms (namely molluscs and Ephemeroptera, with a trophic position of 2).

Stable isotope niche size was estimated using the *SIBER* package (Jackson et al., 2011) by calculating the estimated standard Bayesian ellipse area ( $\text{SEA}_b$ , 20,000 iterations) and associated credibility intervals at 50%, 75%, and 95%, for each lake and species. All statistical analyses were performed using R v.4.0.3 (RStudio Team, 2020).

### 3 | RESULTS

Angling baits (mean  $\delta^{13}\text{C} = -20.60\text{‰} \pm 5.18$  and mean  $\delta^{15}\text{N} = 3.56\text{‰} \pm 2.08$  SD) was significantly  $\delta^{13}\text{C}$  enriched (lmer,  $\chi^2 = 8.86$ ,  $p = 0.003$ ) and  $\delta^{15}\text{N}$  depleted (lmer,  $\chi^2 = 54.30$ ,  $p < 0.001$ ) compared to natural prey (mean  $\delta^{13}\text{C} = -28.35\text{‰} \pm 3.88$  and mean  $\delta^{15}\text{N} = 12.22\text{‰} \pm 3.19$  SD; Figure 2).  $\delta^{15}\text{N}$  values did not differ among angling bait types (lmer,  $\chi^2 = 2.93$ ,  $p = 0.40$ ), whereas  $\delta^{13}\text{C}$  values did differ (lmer,  $\chi^2 = 114.89$ ,  $p < 0.001$ ). Seeds exhibited significant  $\delta^{13}\text{C}$  enrichment compared to the three other bait types (post hoc test,  $p < 0.001$ ) while no significant differences were observed in  $\delta^{13}\text{C}$  values among the three other bait types (Figure 2).

In lakes without angling, the diet of *C. carpio* primarily consisted of crayfish (58.4%  $\pm$  11.7 SD) followed by small benthic invertebrates (41.6%  $\pm$  11.7 SD). In lakes supporting fisheries, the contribution of angling baits to the diet of *C. carpio* averaged 30.5% ( $\pm$  17.0 SD) and ranged from 5.1% (lake O) to 76.5% (lake F, Figure 3a, Figures SI.4.1 and SI.4.2, Tables SI.5.1 and SI.5.2). For *R. rutilus*, small benthic invertebrates were the main prey consumed in lakes without angling (72.3%  $\pm$  14.7 SD), followed by zooplankton (27.7%  $\pm$  14.7 SD). In lakes supporting fisheries, angling baits contribution to *R. rutilus* diet averaged 41.3% ( $\pm$  15.7 SD) and ranged from 9.4% (Lake N) to 80.5% (Lake L, Figure 3b).

The contribution of angling baits to the diet of *C. carpio* was significantly different among fishery types (lmer,  $\chi^2 = 6.949$ ,  $p = 0.031$ , Figure 4a), with significantly higher contributions observed in specialised carp fisheries (40.0%  $\pm$  16.7 SD) compared to put-and-take fisheries (15.9%  $\pm$  9.0 SD). In the case of *R. rutilus* no difference among fishery types were observed (lmer,  $\chi^2 = 0.022$ ,  $p = 0.99$ , Figure 4b).

The effect of *C. carpio* body size on the contribution of angling baits to their diet was not significant (lmer,  $\chi^2 = 1.152$ ,  $p = 0.28$ , Figure 4c), whereas body size and contribution of angling baits were positively correlated for *R. rutilus* (lmer,  $\chi^2 = 4.753$ ,  $p = 0.029$ , Figure 4d).

The stable isotope niche size ( $\text{SEA}_b$ ) of *C. carpio* in specialised carp fisheries (95% confidence interval [CI] = 0.92–1.97‰) was six times greater than in lakes without angling (95% CI = 0.16–0.31‰) and more than three times greater than in specialised roach (95% CI = 0.23–0.75‰) and put-and-take (95% CI = 0.27–0.68‰) fisheries (Figure 5a–c). For *R. rutilus* populations, stable isotope niche size ( $\text{SEA}_b$ ) was similar between specialised carp (95% CI = 0.56–1.10‰) and put-and-take fisheries (95% CI = 0.42–0.85‰), which were more than two times greater than in lakes without angling (95% CI = 0.20–0.37‰) and specialised roach fisheries (95% CI = 0.20–0.43‰; Figure 5b–d).

### 4 | DISCUSSION

Terrestrial subsidies represent an important trophic resource for many freshwater organisms including fishes (Carpenter et al., 2005; Nakano & Murakami, 2001). In gravel pit lakes hosting fisheries, we observed that angling baits, whose stable isotope values significantly differed from natural prey, can have a substantial contribution to the diet of two common cyprinid species (30.5% ( $\pm$  17.0 SD) for *C. carpio* and 41.3% ( $\pm$  15.7 SD) for *R. rutilus*, respectively). These contributions were also highly variable among individuals as they ranged from 5.1% to 76.5% for *C. carpio* and 9.4% to 80.5% for *R. rutilus*. The consumption of angling baits by *C. carpio* differed between fishery types, with higher proportion observed in specialised carp

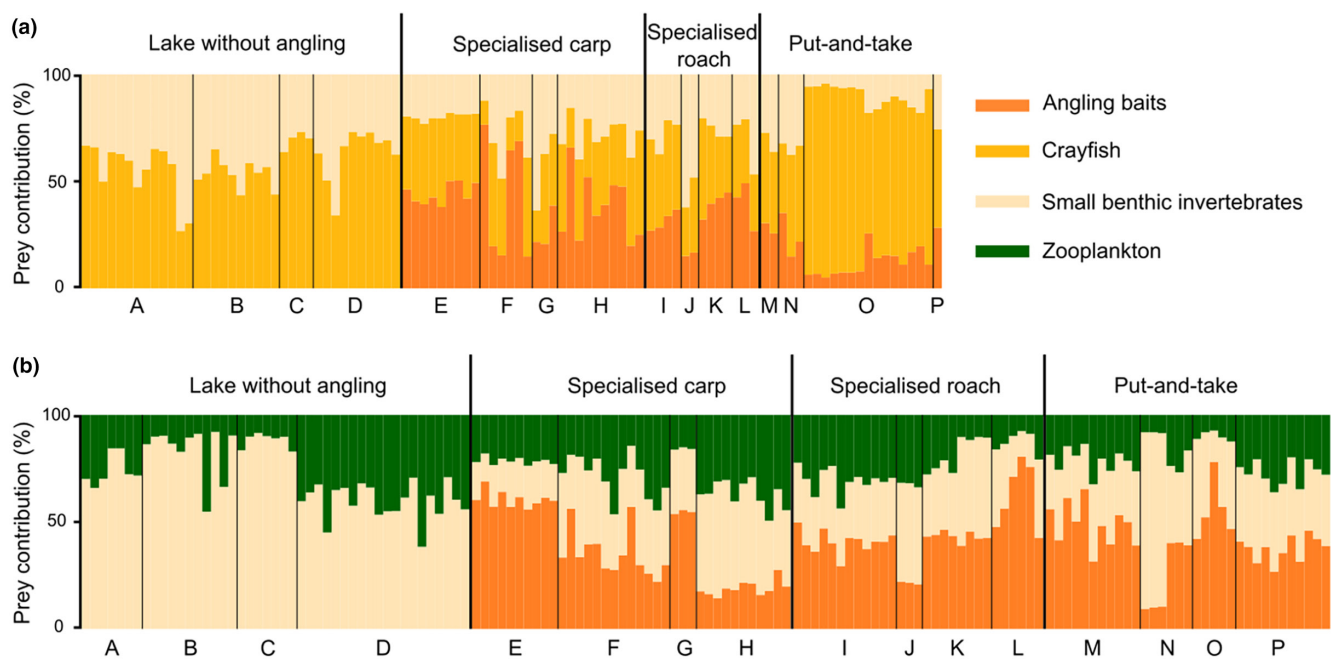
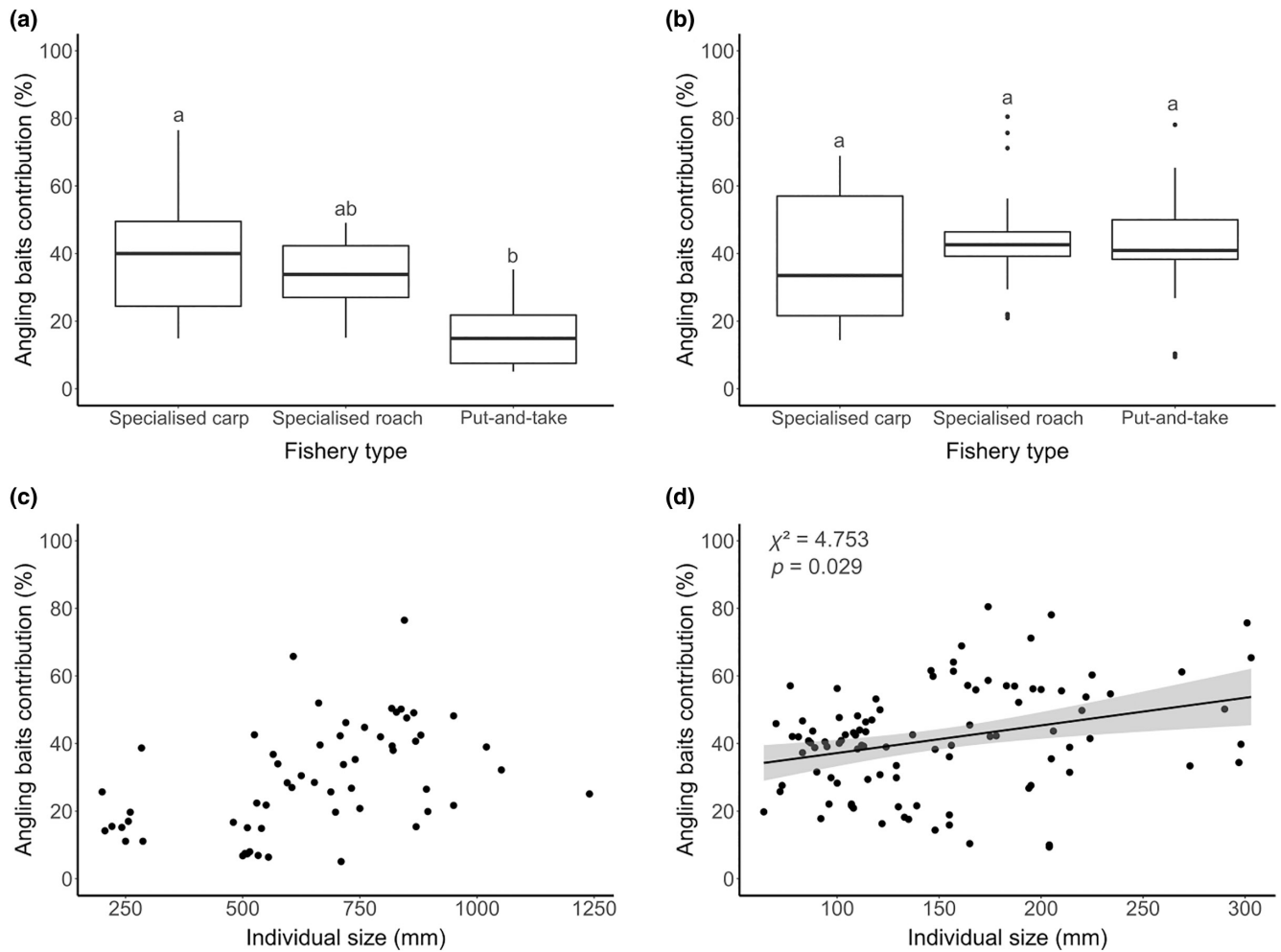


FIGURE 3 Estimated contribution of putative prey to the diet of (a) *Cyprinus carpio* and (b) *Rutilus rutilus* individuals in the 16 studied gravel pit lakes in south-western France: lakes without angling (A–D), specialised carp fisheries (E–H), specialised roach fisheries (I–L) and put-and-take fisheries (M–P). Each histogram represents the diet composition of an individual fish.





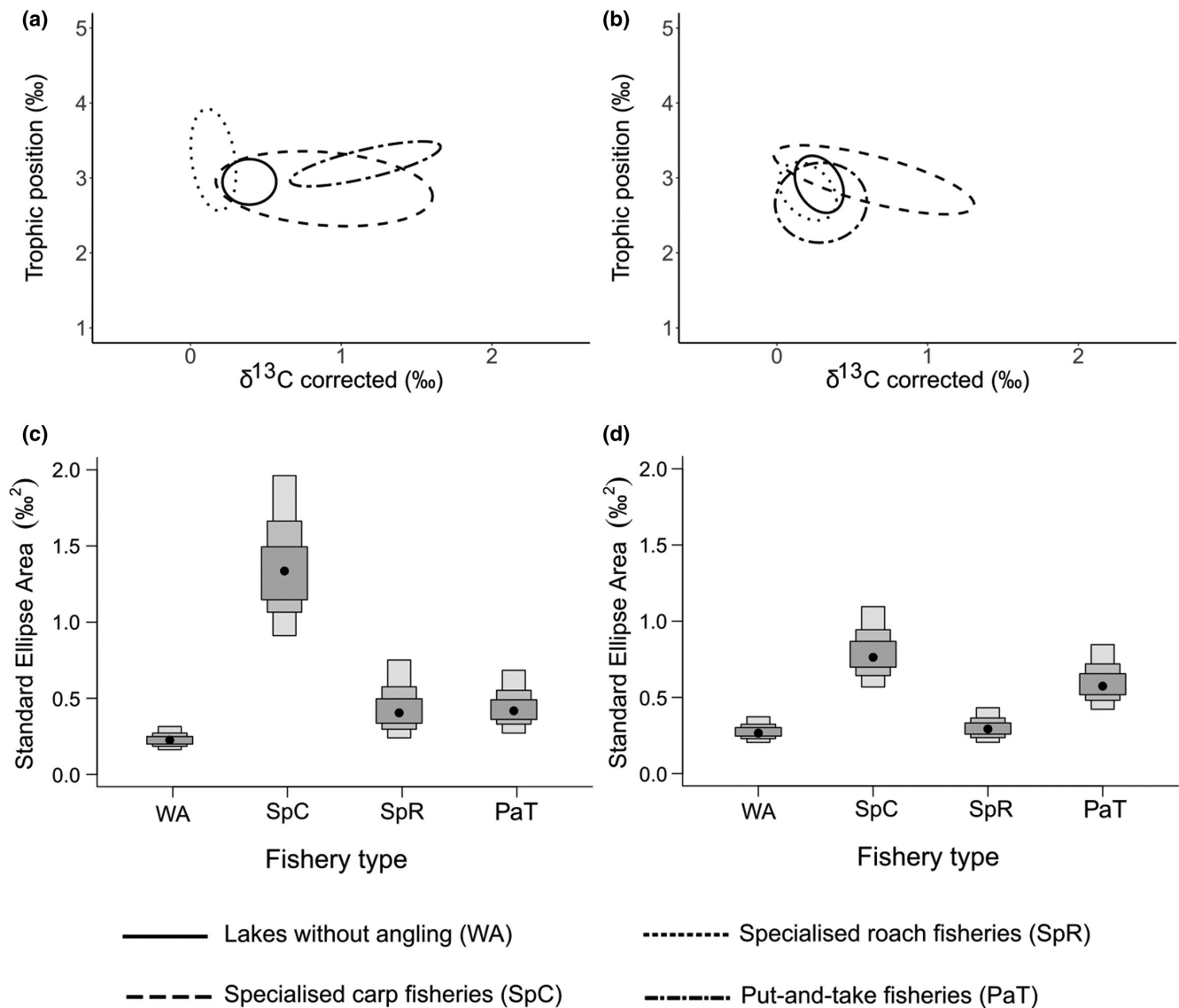
**FIGURE 4** Estimated contribution of angling baits to the diet of *Cyprinus carpio* (left,  $n=62$ ) and *Rutilus rutilus* (right,  $n=99$ ) for each fishery type (a, b) and relationship with fish body size (c, d). Different letters indicate significant difference between fishery types (a, b). A regression line is displayed when the relationship is significant.

fisheries. For *R. rutilus*, the consumption of angling baits was driven by individual body size, with larger individuals consuming a higher proportion of angling baits and did not differ between fisheries. Our first hypothesis that fishery type and fish body size can modulate the consumption of angling baits was therefore partially validated. The stable isotope niche assessed of *C. carpio* was six times larger in specialised carp fisheries compared to lakes without angling. For *R. rutilus*, the stable isotope niches were two times larger for specialised carp fisheries and put-and-take fisheries compared to lakes without angling and specialised roach fisheries, partially validating our second hypothesis of a wider stable isotope niche in lakes with fishing activities.

Given that angling bait components mainly constituted terrestrial oil and flours, a  $\delta^{13}\text{C}$  contrast with natural prey was expected as  $\delta^{13}\text{C}$  values allow to discriminate resources with a terrestrial or an aquatic origin (France, 1995). The differences in  $\delta^{13}\text{C}$  values between angling bait types can be partially explained by differences in the type of photosynthesis (Nonogaki et al., 2006). Seeds, such as corn and tiger nuts, rely on the C4 carbon fixation pathway, resulting

in  $\delta^{13}\text{C}$  values ranging between  $-12$  and  $-14\text{‰}$  (Wickman, 1952). Groundbaits, boilies and pellets are composed of a mixture of C4 (e.g. corn) and C3 (e.g. wheat) plants, leading to intermediate  $\delta^{13}\text{C}$  values falling between C4 plants and C3 plants ( $-25$  to  $-28\text{‰}$ ) (Nonogaki et al., 2006). The absence of information about the exact composition of commercially available and industrialised angling baits strongly limits our ability to fully understand the drivers of the variability in their stable isotope values, particularly regarding the  $\delta^{15}\text{N}$  values. The use of additional stable isotopes such as hydrogen ( $\delta^2\text{H}$ ) and sulfur ( $\delta^{34}\text{S}$ ) could improve the discrimination between allochthonous and autochthonous resources or between freshwater and marine-derived resources, respectively (Doucett et al., 2007; Gutmann et al., 2017; Privat et al., 2007), and represent opportunities to better evaluate the composition and importance of angling baits.

The range of angling bait contribution to fish diet was similar to the values measured for *B. barbus* in English rivers, where some individuals do not consume baits while others consume baits as main food item (Bašić et al., 2015; Britton et al., 2022; De Santis et al., 2019). Although our results were consistent with other studies,



**FIGURE 5** Stable isotope niche size (standard ellipse area, SEA<sub>b</sub>) calculated for *Cyprinus carpio* (a) and *Rutilus rutilus* (b) in each fishery type (lakes without angling, specialised carp fisheries, put-and-take fisheries and specialised roach fisheries). The associated confidence intervals of SEA<sub>b</sub> for *C. carpio* (c) and *R. rutilus* (d) are shown, with threshold values of 50%, 75%, and 95% and mode values are displayed with a black dot.

the characteristics of lakes (e.g. size, shape and depth) and fisheries (e.g. angling pressure, regulation) probably modulate the contribution of angling bait to the diet of fish. In the present study, each fishery type was replicated to limit the effects of these characteristics. In the case of *C. carpio* populations, we found that the fishery type strongly modulated the contribution of angling baits, with higher proportions observed in lakes specifically targeting this species. These differences could be explained by the preferential use of certain angling bait types for *C. carpio* such as seeds and boilies that are the preferred bait types by *C. carpio* compared to others cyprinids (Mehner et al., 2019). The amount of angling bait subsidies used by anglers and introduced in lakes, which strongly vary depending on fishery type, could have also influenced the contrasting consumption patterns observed in the present study. Indeed, the quantity of baits used and the period when these baits are introduced into a

given lake could be important drivers of their consumption by fish, but this remains to be quantified. Bait consumption by *R. rutilus* did not significantly differ between fishery types, suggesting that this species may have a more opportunistic consumption of angling baits. For roach, our results are consistent with findings demonstrating positive correlations between body size and bait contribution in other systems (De Santis et al., 2019). Further investigations are needed to understand the drivers of this relationship, notably to determine whether the energetic benefits provided by angling baits (Bašić et al., 2015; Mehner et al., 2019; Naylor et al., 2000) promote fish growth and/or if larger body size allows a higher consumption of baits by limiting gap size limitation and allowing the consumption of larger baits such as boilies and pellets.

Regarding *C. carpio* stable isotope niche size, our findings support the idea that a new feeding opportunity can result in a broader



stable isotope niche (Araújo et al., 2011). These results are consistent with previous studies conducted in English ponds, which reported a four-fold increase of stable isotope niche size ( $SEA_p$ ) for *C. carpio* in lakes receiving bait subsidies (Britton et al., 2022). However, for *R. rutilus* populations, we did not observe this pattern and instead we found a smaller stable isotope niche in fisheries where they were targeted. To explain this, we found that an increase of stable isotope niche size was not linearly correlated with the fishing pressure, as stable isotope niche size of cyprinid populations from high fished lakes was smaller than values observed for intermediate fishing intensities (Gutmann et al., 2017). Intermediate fishing intensities may induce only a subset of individuals to specialise in angling bait consumption due to limited availability of this subsidy, in contrast to high fished lakes where baits are abundant and more individuals can specialise in their consumption, leading to a diet homogenisation and subsequently a niche restriction. Therefore, quantitative assessment of fishing pressure and angling bait inputs are needed to understand how they can modulate the consumption of angling bait subsidies.

The inputs of angling baits can alter water quality through the increase of ammonium and phosphorus release from sediments (Lewin et al., 2006) and sulfide production (Koel et al., 2019), potentially contributing to lake eutrophication (Amaral et al., 2013). Our study emphasises the importance of considering the characteristics of angling baits and their consumption by fish that strongly differ among fishery types. These findings have important implication for ecosystem management and further investigations are needed to determine the quantity of angling baits, their nutrient concentration, and the timing of introduction in each fishery type to better understand how they affect recipient ecosystems. The use of angling baits could be perceived as a form of intentional pollution (Arlinghaus & Cooke, 2009) that is not regulated. Indeed, current fishery management practices primary focus on the regulation of fish harvesting and stocking practices (Cowx & Gerdeaux, 2004; Cucherousset et al., 2021); we argue here that more consideration should be given to the different types of angling baits in fishery management.

In conclusion, we found that angling bait subsidies can represent a significant trophic resource for two cyprinid species in different fisheries. Understanding how changes in the stable isotope niche of individuals are associated with physiological and/or behavioural changes is now needed to full appreciate their impacts on fish ecology and how they can subsequently affect water quality and the functioning of lake ecosystems. These results can also help to improve fishery management and maintain freshwater biodiversity by accounting for the role of fishery type on the impacts of angling practices.

#### AUTHOR CONTRIBUTIONS

Conceptualisation: A.I., J.N.B., S.B., J.C. Developing methods: A.I., J.N.B., S.B., J.C. Conducting the research: A.I., S.B., J.C. Data analyses: A.I., J.C. Data interpretation: A.I., J.C. Preparation of figures: A.I. Writing: A.I. Review and editing: J.N.B., S.B., J.C.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

#### ORCID

Alexis Imbert  <https://orcid.org/0000-0001-5377-9546>

Jean-Nicolas Beisel  <https://orcid.org/0000-0002-1935-7689>

Stéphanie Boulêtreau  <https://orcid.org/0000-0002-0094-0196>

Julien Cucherousset  <https://orcid.org/0000-0003-0533-9479>

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