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# The opportunistic trophic behaviour of the European catfish (*Silurus glanis*) in a recently colonised large peri-alpine lake

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## Abstract

The European catfish (*Silurus glanis*) recently colonised large peri-alpine lakes where its exploitation of the different lake habitats (i.e. littoral, pelagic and deep benthic) may be supported by interindividual trophic variations fostering its establishment. We investigated the prey and lake habitats supporting *S. glanis* diet in the largest French peri-alpine lake (Lake Bourget) based on the contents of 231 stomachs combined with 217 individual stable isotope measurements ($\delta^{13}C$ and $\delta^{15}N$). The interindividual diet variations in stomachs and isotopes were quantified to identify individual specialisation within the population. The effects of body size on trophic characteristics were also explored. For most individuals, a major reliance on littoral resources was determined based on both stomach contents (86% of prey items) and stable isotopes using Bayesian mixing models (BMMs; 70.3 ± 9.6% contributions of the littoral resources). However, pelagic and deep benthic prey (e.g. whitefish and burbot) were also identified, and BMMs indicated significant contributions of pelagic and deep benthic resources to *S. glanis* diets (15.8 ± 5.3% and 13.9 ± 5.2% respectively). Interindividual variations based on stomach contents were much higher than those estimated from stable isotopes, supporting an opportunistic trophic behaviour; although the population strongly relied on crayfish, perch and roach. Body size explained a minor fraction of *S. glanis* trophic characteristics, suggesting that ontogeny does not strongly structure the current population diet. Our results underscore the feeding plasticity of *S. glanis*, revealing that besides the littoral habitat, this invader exploits resources from all habitats in large peri-alpine lakes (deep benthic and pelagic). Therefore, its establishment in these ecosystems may represent a growing threat to resident species, especially if the population and individual body size increase in the near future.

**KEYWORDS**
individual specialisation, invasive species, ontogeny, stable isotopes, stomach contents

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## 1 | INTRODUCTION

The trophic characteristics of invasive species are one of the main drivers of their invasion success and are often directly related to their impacts on resident communities (Gallardo et al., 2015). In particular, invasive fishes have received growing interest regarding their ability to modify food web structures and prey communities (David et al., 2017; Sagouis et al., 2015). For instance, introduced rainbow trout (*Oncorhynchus mykiss*) altered the whole trophic structures of naturally fishless Canadian lakes by eliminating the top invertebrate predator (MacLennan et al., 2015). Characterising the feeding habits of invasive fishes is fundamental to understand their trophic interactions with resident species and to provide a basis for assessing their invasiveness.

Invasive fishes are usually generalist consumers (i.e. with large diet breadths) and can rapidly adapt their diets to available prey in newly colonised ecosystems (García-Berthou, 2007). However, the large diet breadth of generalist populations often involves heterogeneous individual diets that can originate from diverse factors such as prey preferences, sex, available microhabitats and ontogeny (Alofs & Polivka, 2004; Araujo et al., 2011; Rossman et al., 2015; Sanchez-Hernandez et al., 2019). These interindividual diet variations compared to the diet of the average population provide information on individual specialisation within the population (Bolnick et al., 2002; Rosenblatt et al., 2015; Salvidio et al., 2015; Smith et al., 2011). Individual dietary specialisation can cause strong constraints on population dynamics, as it decreases intraspecific and/or interspecific competition (Swanson et al., 2003) and thus appears advantageous for the sustainability of invasive populations in newly colonised ecosystems (Jackson et al., 2017; Layman & Allgeier, 2012).

One of the most frequently introduced fish in Europe is the European catfish (*Silurus glanis*), a long-lived species (i.e. >30 years, sexual maturity at ~3 years and 80 cm; Copp et al., 2009), that can reach body sizes and weights higher than 270 cm and 130 kg respectively (Boulêtreau & Santoul, 2016). Over the past decades, *S. glanis* has dramatically expanded its geographical range in Western Europe by the increasing rate of voluntary introductions for aquaculture and recreational angling purposes, but also through its active colonisation via the hydrographic network (Cucherousset et al., 2017; Guillaume, 2012). Over the past 10 years, *S. glanis* has colonised large peri-alpine lakes connected to the Rhône River (Lake Geneva and Lake Bourget; Jacquet et al., 2020; Périat et al., 2014). These lakes are deep (maximum depth > 100 m) and can thus be compartmentalised into three main habitats (i.e. littoral, pelagic and deep benthic) in which the trophic characteristics of *S. glanis* have not yet been investigated. In large rivers and reservoirs, this species is a generalist and is known to rapidly adjust its diet to available resources (i.e. opportunistic species; Copp et al., 2009). The trophic behaviour of *S. glanis* was described as site (Ferreira et al., 2019; Syväranta et al., 2010) and size-dependent (i.e. ontogenetic diet shift from invertebrates to fish; Alp, 2017; Carol et al., 2009; Copp et al., 2009). Moreover, individual specialisation has been identified among populations in various ecosystems. *S. glanis* specialised on prey such as waterfowl (Carol et al., 2009; Vejřík et al., 2017a), terrestrial birds (Cucherousset et al., 2012), small mammals (Copp et al., 2009), amphibians (Vejřík et al., 2017a), migratory fish (e.g. lamprey *Petromyzon marinus*, salmon *Salmo salar* and allis shad *Alosa alosa*; Boulêtreau et al., 2018; Boulêtreau et al., 2020; Boulêtreau et al., 2021) and also perch (*Perca fluviatilis*) egg strands (Vejřík et al., 2017b).

In this study, we investigated the trophic characteristics of *S. glanis* in Lake Bourget (a large peri-alpine lake) at both the population and individual level for assessing its predation on the resident species. We combined stomach content and stable isotope analyses to: (i) determine the prey composition and the lake habitats supporting the diet of *S. glanis*, (ii) measure the interindividual diet and isotopic variations supporting potential individual specialisation within the population and (iii) test the influence of ontogeny (i.e. body size) on these different trophic characteristics. We expected that most *S. glanis* diet would be derived from the littoral habitat while a smaller proportion of its diet would be acquired from the other lake habitats due to its benthic-adapted morphology and its thermal ecological requirements (i.e. warmer temperatures in the littoral habitat than in other lake habitats). We also hypothesised stronger interindividual trophic variations inferred from stomach contents than from stable isotopes as the wide variety of prey that *S. glanis* can consume may exhibit similar isotopic compositions (e.g. littoral invertebrates) being fuelled by similar basal resources. Ontogenetic diet transition from invertebrates to fish was also expected because large *S. glanis* in other ecosystems can exploit larger-sized prey.

## 2 | MATERIAL AND METHODS

### 2.1 | Study site and *S. glanis* sampling

Lake Bourget is the largest natural French lake (45° 43' 46.842" N, 5° 52' 10.484" E) created following the retreat of the Alpine glaciers. This lake experiences a temperate climate, with annual precipitations ~300 mm year$^{-1}$ and seasonal air temperatures between 0°C and 28°C. Lake Bourget covers an area of 44.5 km² and has a mean depth and maximum depth of 85 m and 145 m respectively. *S. glanis* catches started in 2013 in Lake Bourget representing ~9 kg of fish per year, concomitantly with the restoration of the fish ladder connecting the lake to the Rhône River, where *S. glanis* is established since more than 30 years (Faure & Tanzilli, 2016). Currently, >300 kg year$^{-1}$ of *S. glanis* are captured in the lake considering all the fisheries (i.e. commercial, scientific survey and angling; unpublished data CISALB).

*S. glanis* analysed in this study were collected in Lake Bourget during their active period (feeding activity) from February to October between 2017 and 2019. Fish were caught with 100-m long bottom lines equipped with single hook baited with dead sardines every 10 m. The bottom lines were installed at depths ranging from 3 to 15 m at dusk and retrieved at dawn the following day. Complementarily, *S. glanis* individuals were recovered from both

littoral (3–15 m of depth, water column <20 m, shore distance ~500 m) and pelagic nets (10–40 m of depth, water column = 60–100 m, shore distance >500 m) by commercial fishermen. This sampling strategy allowed the coverage of pelagic and littoral habitats in the whole lake and led to the capture of 283 individuals measuring from 12 to 135 cm (mean length ± SD = 63.5 ± 25.9 cm). A total of 20% of individuals were captured using bottom lines in the littoral habitats, 32% of individuals were caught with littoral nets, 12% using pelagic nets while capture methods and/or location data were not available for 36% of the sampled individuals mainly when fishermen did not provide information due to a large amount of fish collected in few days apart.

## 2.2 | Stomach contents

We dissected stomachs of 231 individuals measuring between 12 and 135 cm (mean length ± SD = 62.5 ± 26.5 cm). Prey found in stomachs were measured (to the nearest 1 mm), weighed (to the nearest 0.1 g), identified at the highest possible taxonomic level (abbreviated species names are provided in Table 1) and classified as pelagic, littoral or deep benthic using the classification keys of Tachet et al. (2010), Boismartel et al. (2011) and Keith et al. (2011). The body masses (g) of partially digested prey were obtained from empirical mass–length relationships (Table S1, Figure S1) determined from the annual scientific survey in Lake Bourget (© SOERE OLA-IS, INRAE Thonon-les-Bains, CISALB; Rimet et al., 2020). Biomasses (sum of prey weight for each species), occurrence numbers (percent of stomachs containing each species), abundances (sum of prey corresponding to each identified species), prey richness (sum of the different prey species) and number of prey were used to characterise the diet of the population. The prey assemblages found in stomach contents were investigated via a principal component analysis (PCA, Pearson, 1901) based on Hellinger-transformed prey abundances (Legendre & Gallagher, 2001). We kept rare prey (i.e. with low occurrence) in the PCA analysis as they represented the dominant fraction of diets (63.6% of prey species had occurrences below 5%), hence contributed significantly to the diet of the population.

## 2.3 | Stable isotopes

The caudal fins of 217 *S. glanis* individuals (including 165 individuals analysed for stomach contents), measuring between 12 and 135 cm (mean length ± SD = 64.5 ± 25.4 cm), were sampled as a muscle substitute in accordance with Syväranta et al. (2010) who showed strong correlations between isotopic values from *S. glanis* fins and muscles for both stable isotopes (1:1 fit, $r^2 = 0.95$ for carbon and $r^2 = 0.98$ for nitrogen). The isotopic compositions of the resource pools characterising the three lake habitats were obtained from the stable isotope values of representative species of each lake habitat sampled from 2015 to 2018. Specifically, chironomids sampled in surficial sediment at different depths (i.e. 20 m, 40 m and 80 m) using an Ekman grab represented the deep benthic resource pool ($n = 23$). Whitefish (*Coregonus lavaretus*) sampled by volunteer anglers and zooplankton (*Bythotrephes longimanus*, *Daphnia longispina* and *Leptodora kindtii*) collected using a 100-µm mesh net were used to characterise the pelagic resource pool ($n = 118$). The littoral resource pool ($n = 148$) was characterised using crayfish (*Orconectes limosus* and *Pacifastacus leniusculus*) and other invertebrates (*Asellus aquaticus*, *Ephemera* sp., oligochaetes and chironomids), sampled with Surber nets of 500-µm mesh size, and by two fish species (*Salaria fluviatilis* and *Ameiurus melas*) sampled with nets of 100-mm mesh size. All littoral resources were sampled from 2 to 4 m depths. Species that may be found in different lake habitats, such as perch (*Perca fluviatilis*) or roach (*Rutilus rutilus*), were not considered in the characterisation of the resource pools, and consequently in lake habitat contributions for supporting *S. glanis*, even though they may contribute to the population diet.

The fish fins, crayfish muscle and macroinvertebrates were gently washed in a 2% HCl bath to remove carbonate prior to being dried at 40°C for 48 h, and 1–1.5 mg dry weight of each sample was

**TABLE 1** Prey abbreviations used in the different figures and in the main text based on species scientific name

| Abbreviation | Common name | Scientific name |
|---|---|---|
| Invertebrates | | |
| Bthy | Bithynia | *Bithynia*sp. |
| Chrn | Chironomid | *Chironomus*sp. |
| Drsp | Zebra mussel | *Dresseina polymorpha* |
| Ephm | Ephemerid | *Ephemera*sp. |
| Lcnc | Stag beetle | *Lucanus cervus* |
| Odnt | Odonata | *Libellulidae*sp. |
| Orcl | Spiny-cheek crayfish | *Orconectes limosus* |
| Pscc | Piscicolidae | *Piscicola*sp. |
| Fish | | |
| Crgl | Whitefish | *Coregonus lavaretus* |
| Esxl | Northern pike | *Esox lucius* |
| Lpmg | Pumpkinseed sunfish | *Lepomis gibbosus* |
| Ltlt | Burbot | *Lota lota* |
| NniF | Unidentified fish | / |
| Prcf | Perch | *Perca fluviatilis* |
| Rtlr | Roach | *Rutilus rutilus* |
| Slrf | Blenny | *Salaria fluviatilis* |
| Slrg | European catfish | *Silurus glanis* |
| Tnct | Tench | *Tinca tinca* |
| Other | | |
| Mmml | Unidentified vertebrate | / |
| Mnrm | Mineral matter (gravel) | / |
| Ntrm | Viperine snake | *Natrix maura* |
| Vgtl | Vegetal matter | / |

placed into a tin cup after being ground using a mortar. Analyses of the carbon and nitrogen isotopes in the samples were performed at the Technical Platform of Functional Ecology (OC 081, UMR 1137 EEF, Champenoux) using an isotope ratio mass spectrometer coupled to an elemental analyser (EA-IRMS). International isotope standards were used to calibrate the stable isotope values for carbon (IAEA-CH-7 = 31.8‰) and nitrogen (IEAEA-N-1 = 0.4‰, IEAEA-N-2 = 20.3‰, IEAEA-NO-3 = 4.8‰). The internal precision expressed as the standard deviation of replicate analyses of internal standards ($n$ = 21), were ±0.08 for carbon and ±0.26 for nitrogen isotopes. The stable isotopic ratios were expressed as follows:

$$\delta^{13}C \text{ or } \delta^{15}N\,(‰) = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000 \quad (1)$$

where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

The isotope values for whitefish were corrected from fin to muscle following Hanisch et al. (2009), where $\delta^{13}C_{muscle} = 0.8677\ \delta^{13}C_{fin} - 4.64$ and $\delta^{15}N_{muscle} = 0.8574\ \delta^{15}N_{fin} + 0.94$. The isotope values for the other fish were corrected from fin to muscle following the method of Hette-Tronquart et al. (2012) where $\delta^{13}C_{muscle} = 0.82\ \delta^{13}C_{fin} - 5.89$ and $\delta^{15}N_{muscle} = 1.01\ \delta^{15}N_{fin} + 0.74$.

The contribution of lake habitats supporting *S. glanis* diet was investigated using Bayesian mixing models (BMMs; Parnell et al., 2012). We assumed that the stable isotope composition of each individual represented a mixture of the isotope compositions from the resource pools of the three lake habitats. The BMMs were parameterised with a burn-in duration of $10^3$, $10^4$ iterations, using four Markov chain Monte Carlo simulation techniques. The average carbon and nitrogen concentrations of resources and an isotopic fractionation of 0.8 ± 1 for $\delta^{13}C$ and 3.4 ± 1 for $\delta^{15}N$ (Post, 2002; Vander Zanden & Rasmussen, 2001) were incorporated in the BMMs. These models returned density distributions of the relative contributions of each resource pool to the assimilated diet of each *S. glanis* individual, and their average values were retained as the proportion of assimilated resources originating from each lake habitat.

Preliminary analyses did not indicate seasonal variations in *S. glanis* stable isotope compositions. Furthermore, the isotopic turnover rate would be around 130 days for a 2.6 kg fish (i.e. the average population body mass) according to Weidel et al. (2011), suggesting that if seasonal diet variations occurred, those would be intricate to reveal using stable isotopes. Therefore, all individuals from summer (21%), autumn (6%) and late winter (6%) were pooled with those from spring (67%) in further analyses.

## 2.4 | Interindividual diet variations

Interindividual diet variations were estimated from the diet matrix of prey abundances based on the method of Bolnick et al. (2002) to support the identification of possible individual specialisation. Although this method would optimally be applied on repeated estimates of individual diets, it can still provide insights on individual diet departure from the average population diet using non-repeated measures (Araujo et al., 2009; Cusa et al., 2019; Frédérich et al., 2010). In our case, the recapture of individuals was unrealistic considering the large size of Lake Bourget. Therefore, we applied the method of Bolnick et al. to obtain a proxy of the interindividual dietary variations while being aware of the possible overestimation of individual specialisation.

Specifically, interindividual diet variations were estimated using $V_{i_SC}$ to represent the diet departure of individual $i$ from the average population diet $q$ (Araujo et al., 2009) as follows:

$$V_{i_{SC}} = 1 - PS_i \quad (2)$$

with

$$PS_i = 1 - 0.5 \sum_j \left|p_{ij} - q_j\right| \quad (3)$$

where $p_{ij}$ is the proportion of resource $j$ in the observed diet of *S. glanis* $i$ and $q_j$ is the proportion of resource $j$ found in the average population diet.

The extent of interindividual variations in the population ($V_{POP_SC}$) was complementarily estimated by averaging all $V_{i_SC}$. The significance of $V_{POP_SC}$ was tested under the null hypothesis that each individual diet was randomly distributed from the average population diet (Bolnick & Paull, 2009). A null model was built following Bolnick et al. (2002) by simulating 100 populations, each using the same number of individuals ($n$ = 115) and prey per individual as the empirical population with functions, specifically elaborated for our study, inspired from the R package "RInSp" (Zaccarelli et al., 2013). We simulated individual diets using a multinomial distribution where the prey probability to be sampled corresponded to the prey proportions in the empirical population diet ($q$) and the number of random draws was equal to the number of prey. The simulated $V_{POP_SC}$ could hence be compared to the empirical $V_{POP_SC}$ to obtain a statistical significance estimate of interindividual diet variations in the population (i.e. the proportion of simulated $V_{POP_SC}$ values higher than the empirical $V_{POP_SC}$ value).

## 2.5 | Interindividual isotopic variations

The extent of interindividual isotopic variations in the population was complementarily estimated ($V_{POP_SI}$). We used the method of Araujo et al. (2007) based on the relationship between the isotopic variances ($Var_{ISO}$) of both $\delta^{13}C$ and $\delta^{15}N$ of a population and its $V_{POP_SI}$. Specifically, we simulated 100 populations using the same previously described null model, with the prey number varying from 1 to 100 (i.e. the number of random draws in the multinomial distribution) to simulate individual diets in each population. The stable isotope values and the body masses of prey items assigned to each hypothetical individual diet (Table S2) while the predicted isotope

values of simulated catfish individuals (*S. glanis i*) were estimated using the method of Araujo et al. (2007) as follows:

$$\delta X_{i\,(estimated)} = \sum_j \frac{p_{ij} m_j}{\sum_j p_{ij} m_j} \delta X_j \quad (4)$$

where $\delta X_i = \delta^{13}C$ or $\delta\,^{15}N$ of *S. glanis i*, $m_j$ = average dry mass of prey *j*, $p_i$ = proportion of prey *j* in the diet of *S. glanis i* and $\delta X_j = \delta^{13}C$ or $\delta\,^{15}N$ of prey *j*.

$Var_{ISO}$ and the corresponding $V_{POP_SI}$ could hence be calculated for each simulated population, and their relationships were fitted using generalised additive models (GAM; Wood, 2017). The empirical $V_{POP_SI}$ values were then retrieved from the $Var_{ISO}$-$V_{POP_SI}$ relationships established for both carbon and nitrogen.

At the individual level, interindividual isotopic variations ($V_{i_SI}$) were quantified as the normalised Euclidian isotope distance of *S. glanis i* from the centroid of the isotope convex hull of the population as follows:

$$V_i = \frac{\sqrt{\left(\delta^{13}C_{centroid} - \delta^{13}C_i\right)^2 + \left(\delta^{15}N_{centroid} - \delta^{15}N_i\right)^2}}{\max(V_i)} \quad (5)$$

$V_{i_SI}$ does not discriminate identity of consumed prey as different prey items can have variable distances on the isotopic space. However, $V_{i_SI}$ provides information regarding individual isotopic departure from the mean population isotopic signature expected to originate from the exploitation of variable proportions of the resource pools from the different lake habitats. Hence, $V_{i_SI}$ provides a complementary index for examining interindividual variations at a coarser scale (i.e. lake habitat) than $V_{i_SC}$ (i.e. prey identity).

### 2.6 | Body size constraints on *S. glanis* trophic characteristics

GAMs were used to explore the relationships between *S. glanis* body sizes (i.e. ontogeny) and the prey richness, the individual scores on the two first PCA axes, the contributions of resource pools of lake habitats and the interindividual trophic variations ($V_{i_SC}$ and $V_{i_SI}$). A gamma distribution (suitable for right-skewed continuous data) was used to fit the GAMs when using the first two PCA axis scores (transformed by adding the minimal PCA axis scores to make them positive), the resource pool contributions, $V_{i_SC,}$ and $V_{i_SI}$ as response variables. A negative binomial distribution was used to fit a GAM with prey richness (right-skewed counts) as the response variable. All GAMs were checked to ensure their validity (i.e. the model residuals had no trend over the explanatory and response variable; Faraway, 2006).

All statistical analyses were performed using R.3.5.1 (R Core Team, 2018) with the packages ggplot2 (Wickham, 2016), mgcv (Wood, 2017), raster (Hijmans, 2020) and simmr (Parnell, 2019). R codes for reproducing analyses are available at https://github.com/chloevagnon/Feeding_Behavior.

## 3 | RESULTS

### 3.1 | Stomach contents

Among the 231 analysed stomachs, 115 of them (i.e. 49.8%) contained at least one prey item, and only 2.4% were not identifiable (mostly fish bones). The 494 prey items identified from the 115 non-empty stomachs belonged to 22 different items that were mainly invertebrates (seven taxa) and fishes (nine taxa; Figure 1, Table 1). Four prey species clearly dominated *S. glanis* diets and represented 83% of the relative abundance of prey items: the spiny-cheek crayfish (*Orconectes limosus*, $n$ = 198), the perch (*Perca fluviatilis*, $n$ = 100), the roach (*Rutilus rutilus*, $n$ = 56) and the zebra mussel (*Dreissena polymorpha*, $n$ = 56) (Figure 1a). The roach, spiny-cheek crayfish and perch represented 89.4% of the total biomass (65.5%, 16.7% and 7.2%, respectively), while other prey biomass contributed little to diets (i.e. <5%; Figure 1b). These three prey were also found most frequently in non-empty stomachs (i.e. total relative occurrence >60%; Figure 1c). Rare prey (occurrence <5%) belonged to different lake habitats and covered a wide taxonomic range, including invertebrates (e.g. *Ephemera* sp., Ephm, $n$ = 1), littoral fish (e.g. *Salaria fluviatilis*, Slrf, $n$ = 5), pelagic fish (*Coregonus lavaretus*, Crgl, $n$ = 1) and deep-benthic related fish (*Lota lota*, Ltlt, $n$ = 10). Gravel and plant material were also identified. The prey richness was generally low, as a single prey item was present in 30.4% of non-empty stomachs, and 33.0% of stomachs contained more than a single prey corresponding to only one species (Figure 1d).

The dietary composition was not strongly structured by the different prey species, as shown by the two first PCA axes that captured a restricted fraction of the overall *S. glanis* diet variability (16.3% of the total variance) yet permitted the visualisation of different prey assemblages (Figure 2). A crayfish-based diet was negatively correlated with PCA axis 1 (30% contribution), while burbot, perch and pumpkinseed sunfish (*Lepomis gibbosus*) were positively correlated with PCA axis 1, contributing 25%, 20% and 17% respectively, to the axis. Odonates, blenny (*Salaria fluviatilis*), and roach mainly influenced PCA axis 2. Rare prey (e.g. pike, whitefish) were not discriminated in the PCA biplot, and their rare occurrences led most *S. glanis* individuals that consumed them to lie close to the biplot centre.

### 3.2 | Stable isotopes

The stable isotope compositions of the resource pools from the different lake habitats were distinct and clearly delineated different isotopic spaces (Figure 3a). The littoral resource pool was $^{13}C$-enriched, contrary to the deep benthic pool that was characterised by $^{13}C$-depleted isotope values. Both pools had similar $\delta^{15}N$ values, although the deep benthic pool exhibited a higher variability (Table 2). The pelagic resource pool had enriched $\delta^{15}N$ values that slightly varied and intermediate $\delta^{13}C$ values compared to the two other pools.

There was substantial variation in both the $\delta^{13}C$ and $\delta^{15}N$ values of *S. glanis*, where most $\delta^{13}C$ values tended to be similar to those of the littoral resource pool, while the $\delta^{15}N$ values were highly variable (Table 2, Figure 3a). The variability in individual isotopic compositions reflected different contributions of the three lake resource pools according to the BMM inferences (Figure 3b). The littoral resource pool mainly contributed to the assimilated diets of *S. glanis* (70.3 ± 9.6%), while the two other pools had lower but significant and similar contributions (pelagic = 15.8 ± 5.3% and deep benthic = 13.9 ± 5.2%). It is worth noting that the pelagic and deep benthic contributions largely varied among individuals, with maximum values of 35.9% and 51.5% for the pelagic and deep benthic pools respectively.

## 3.3 | Interindividual trophic variations

The interindividual diet variation index ($V_{i_SC}$) varied among individuals. Most *S. glanis* individuals had $V_{i_SC}$ values above 0.5 (87%), where 43% of individuals ranged from 0.5 to 0.6 and 23% were above 0.9, indicating high interindividual variations (Figure 4a). In contrast, the $V_{i_SI}$ values were more evenly distributed, with 91% of the $V_{i_SI}$ values being below 0.5 (Figure 4b), suggesting low interindividual isotopic variations at the individual level. Nonetheless, a few individuals presented clear departures in their isotopic compositions from the mean population isotopic composition (5% of individuals with $V_{i_SI} > 0.6$), suggesting effective differences in habitat exploitation, as seen through assimilated diets, compared to the average population.

The extent of interindividual diet variations ($V_{POP_SC}$) was high and significant ($V_{POP_SC} = 0.67$; $p$-value < .001), while the $V_{POP_SI}$ values derived from the fitted relationships $Var_{ISO}$-$V_{POP_SI}$ (Figure S2) were notably lower and insignificant ($V_{POP_SI}$ from $Var_{\delta 13C} = 0.23$ and $V_{POP_SI}$ from $Var_{\delta 15N} = 0.15$; $p$-value > .05).

## 3.4 | Body size and trophic characteristics

Body size explained less than 10% of *S. glanis* trophic characteristics (Table 3). However, the significant increase in individual PCA axis 1 scores (characterised by a crayfish-to-fish diet) could indicate a possible ontogenetic dietary change, that is consistent with increased and decreased contributions from the littoral and deep-benthic resource pools, respectively to assimilated diets with increasing body size. The significant increase in $V_{i_SI}$ values may also support an ontogenetic diet change with larger individuals that tend to exhibit more distinct isotopic compositions than the mean population isotopic value.

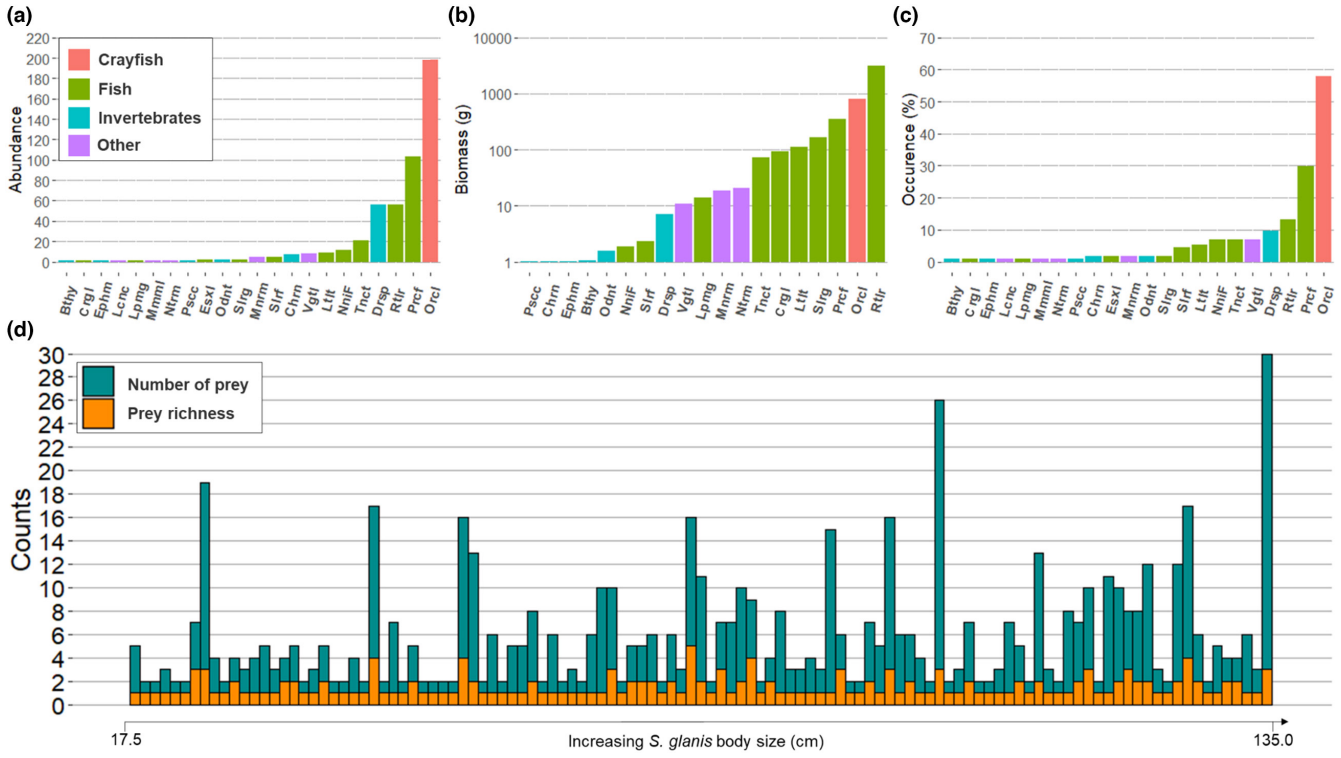


FIGURE 1 Summary of *S. glanis* non-empty stomach contents ($n$ = 115) from Lake Bourget: cumulative abundance (a), cumulative biomass (note the log-scale) (b) and occurrence (c) of prey items. Barplots showing the number of prey and prey richness for each individual are ranked by increasing body size (d). In (a), (b) and (c): Orcl, Orconectes *limosus*; Prcf, Perca *fluviatilis*; Rltr, Rutilus *rutilus*; Drsp, Dreissena *polymorpha*; Crgl, *Coregonus lavaretus*; and Ltlt, Lota *lota*. Abbreviations for other prey names are reported in Table 1

## 4 | DISCUSSION

This study provides original insights on *S. glanis* trophic ecology in a large deep peri-alpine lake. It confirmed the high littoral reliance of this species while identifying significant contributions of both pelagic and deep benthic habitats to the population diet. The population appears opportunist and generalist, with high short-term interindividual dietary variations and lower interindividual isotopic

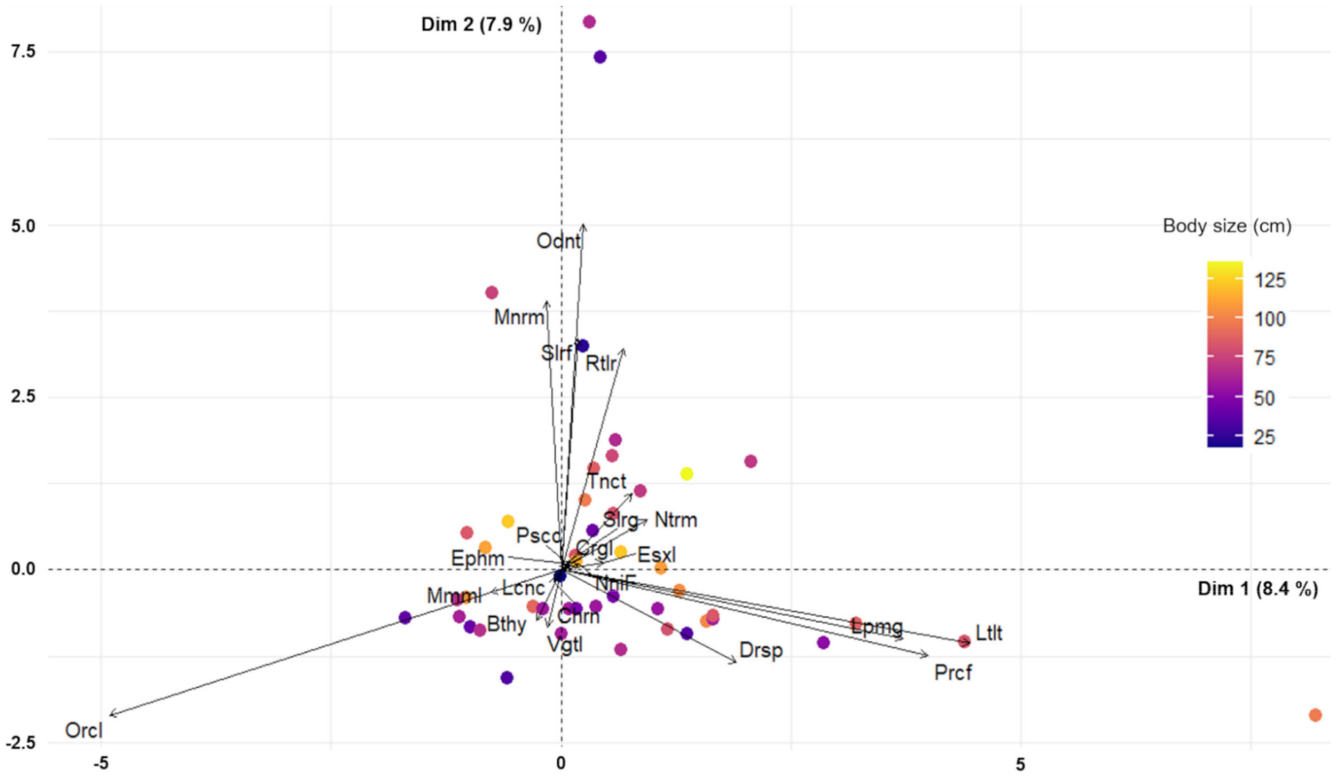


FIGURE 2 PCA of prey assemblages based on prey abundances in *S. glanis* stomach contents from Lake Bourget. A colour gradient from purple to yellow represents *S. glanis* body sizes. On PCA axis 1, Orcl, Orconectes *limosus*; Prcf, Perca *fluviatilis*; Ltlt, Lota *lota*; Lpmg, Lepomis *gibbosus*; Drsp, Dreissena *polymorpha*. On PCA axis 2, Odnt, odonate; Mnrm, mineral matters (gravel); Slrf, Salaria *fluviatilis*; and Rltr, Rutilus *rutilus*. Abbreviations for other prey names are reported in Table 1

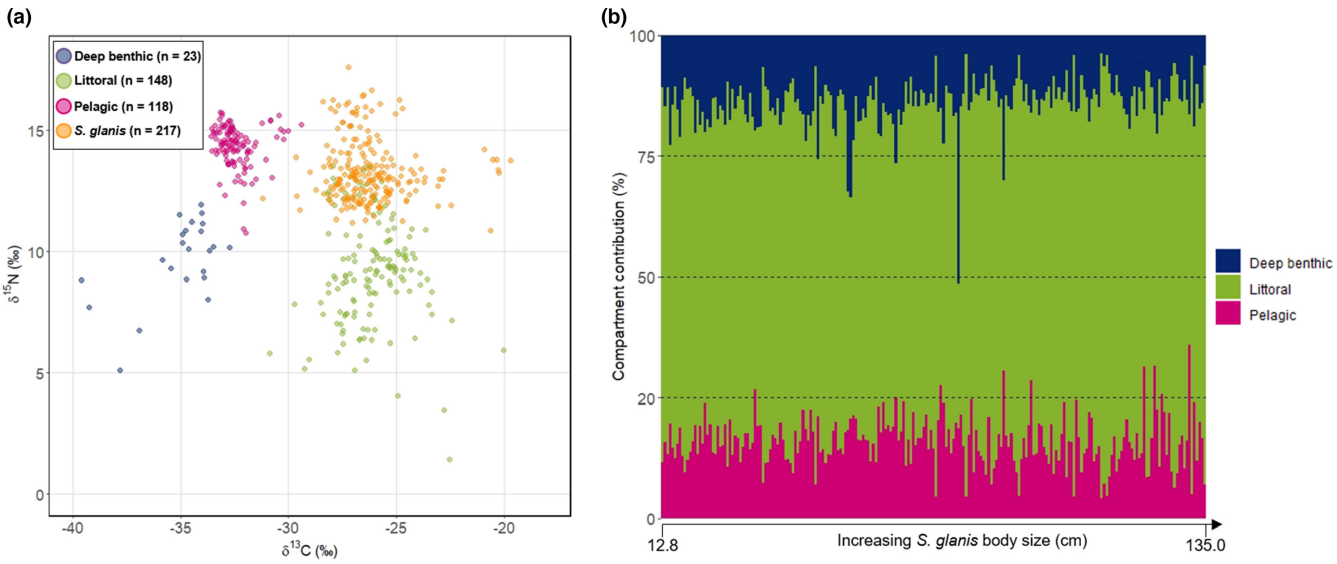


FIGURE 3 Biplot of isotope values for *S. glanis* (orange) and for the three resource pools related deep benthic, littoral and pelagic habitats from Lake Bourget (a). Relative contribution of each resource pool to the assimilated diet for *S. glanis* individuals from Lake Bourget inferred with Bayesian mixing models and ranked by increasing body sizes from left to right (b)

variations. Contrary to our first expectations, body size does not structure *S. glanis* trophic characteristics in Lake Bourget.

## 4.1 | Diet of *S. glanis* in Lake Bourget

The population diet mostly relied on three core prey: crayfish, roach and perch; although a wide diversity of prey was highlighted. Most prey species were consistent with those frequently described in studies conducted in large rivers and reservoirs (Carol et al., 2009; Copp et al., 2009; Ferreira et al., 2019; Guillerault et al., 2015; Haubrock et al., 2020; Vejřík et al., 2017a) and mainly belonged to the littoral habitat (i.e. 86% of the prey species). Infrequently detected items such as vegetation, gravel and zebra mussels were likely unintentionally ingested during predation on littoral species such as crayfish and littoral fish (Ptatscheck et al., 2020).

The reliance on the littoral habitat was further supported by the major contribution of the littoral resource pool to *S. glanis* assimilated diets inferred with BMM, confirming our expectation that *S. glanis* would preferentially exploit the littoral lake habitat. The structural complexity of this habitat (e.g. macrophytes and immersed trees) and the warmer water temperature are likely most suited to the ecological requirements of this invader compared to pelagic and deep benthic habitats (Copp et al., 2009; Cucherousset et al., 2017). Nonetheless, our results revealed significant contributions of the deep benthic and pelagic resource pools to *S. glanis* diet, based on the stable isotope analysis. A few of the prey found in stomachs supported the exploitation of these habitats by *S. glanis* (e.g. burbot is a deep-benthic fish species while European whitefish is associated with the pelagic habitat), which are typical of large peri-alpine lakes. The foraging of *S. glanis* in the pelagic habitat was supported by regular catches by commercial and recreational fishermen up to 1 km from the shore, from between 5 and 15 m in depths to >100 m depths. This result is further supported by whitefish predation by *S. glanis* reported in Most Lake (Czech Republic) (Vejřík et al., 2017a) and in Maggiore Lake (Italy) (De Santis & Volta, 2021). Although *S. glanis* body shape (i.e. round head and thick body) may not be particularly suited for hunting in the pelagic habitat, its non-visual predation technique based on its lateral line sensitivity (Pohlmann et al., 2004) predisposes it to be an effective nocturnal pelagic predator. Nonetheless, the pelagic habitat may appear attractive for *S. glanis* by providing various fish resources (e.g. whitefish, roach and perch regularly detected during scientific surveys; Jacquet et al., 2020) and serving as a resting place when the littoral habitat is affected by summer recreational activities (e.g. boating).

The significant exploitation of pelagic and deep benthic habitats by *S. glanis* appeared much lower based on the stomach contents compared to stable isotopes. Prey often exhibit intraspecific variations in their diet and foraging habitats (Eloranta et al., 2017). Consequently, stomach content analyses may have underestimated the contribution of these habitats to subsidise *S. glanis* diet. For instance, in Lake Bourget, perch demonstrate high interindividual $\delta^{13}C$ variations (Table S2), ranging from −37‰ (suggesting a significant contribution of the deep benthic habitat) to −24‰ (suggesting a major reliance on the littoral habitat). These isotopic signatures would then be transmitted to *S. glanis*, which may hence derive their energy from different lake habitats despite consuming the same prey species. The encounters between *S. glanis* and deep benthic or pelagic resources can also be fostered by the behavioural characteristics of pelagic and deep benthic species that can experience diel migrations, often leading to the time-limited occupancy of littoral habitats at night (e.g. burbot; Cott et al., 2015). These periodic behaviours both increase the spatial matching of prey with *S. glanis* and with its preferential feeding times at dusk and dawn (Cucherousset et al., 2017).

## 4.2 | Interindividual trophic variations

Potential individual specialisation within the population was only suggested based on stomach content analyses that revealed significant interindividual diet variations, even though no individual specialisation was identified using stable isotopes (i.e. low and non-significant interindividual isotopic variations). This discrepancy may emerge due to two main reasons. First, individual specialisation inferred from stomach contents may be overestimated due to the high proportion of rare species present in diets (i.e. high occurrence of 0 in the diet matrix; Bolnick et al., 2002) and the non-repeated measure on diets. These limitations may inflate $V_{i_SC}$ and thus the significance of individual specialisation ($V_{POP_SC}$). Second, individual specialisation assessed using stable isotopes may be underestimated considering a different diet integration time and variations in the prey isotope values (Araujo et al., 2009). High prey intraspecific isotopic differences can inflate consumer $Var_{ISO}$ and the corresponding $V_{POP_SI}$, while low prey interspecific isotopic differences may dampen $Var_{ISO}$ and the corresponding $V_{POP_SI}$ (Bond et al., 2016; Matthews &

**TABLE 2** Characteristics of isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of *S. glanis* and for each resource pool associated to deep benthic, littoral and pelagic habitats in Lake Bourget

| | $\delta^{13}C$ | $\delta^{15}N$ |
|---|---|---|
| | Mean value ± SD (‰) (min; max) | Mean value ± SD (‰) (min; max) |
| *S. glanis* ($n$ = 217) | −26.3 ± 1.7 (−32.1; −19.7) | 13.3 ± 1.3 (10.9; 17.6) |
| Deep benthic ($n$ = 23) | −35.0 ± 1.8 (−39.6; −32.7) | 9.7 ± 1.7 (5.1; 11.9) |
| Littoral ($n$ = 148) | −26.1 ± 1.5 (−30.9; −20) | 9.3 ± 2.2 (1.4; 13.5) |
| Pelagic ($n$ = 118) | −32.4 ± 0.8 (−33.6; −29.3) | 14.4 ± 0.9 (10.8; 17.7) |

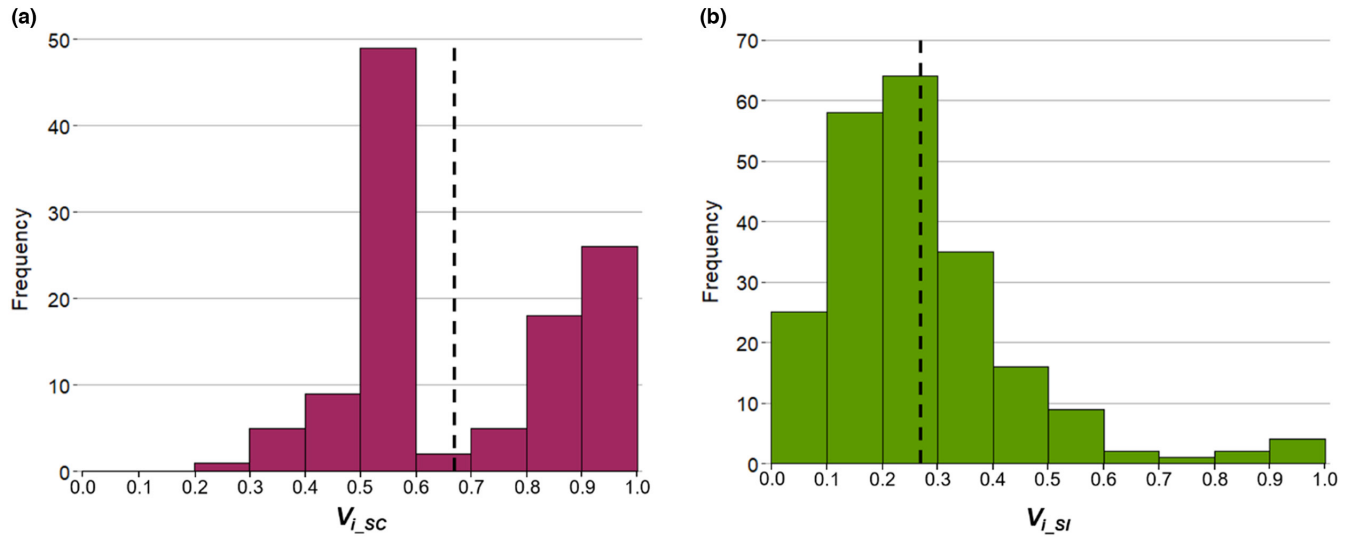


FIGURE 4 Histograms of interindividual dietary variations $V_{i_SC}$ (a) and interindividual isotopic variations $V_{i_SI}$ (b) of *S. glanis* from Lake Bourget. The vertical dashed lines correspond to the mean of $V_{i_SC}$ and $V_{i_SI}$

TABLE 3 Summary statistics of generalised additive models used to assess the influence of body size (i.e. ontogeny) on trophic characteristics of *S. glanis*

| | edf | Deviance explained (%) | *p*-value |
|---|---|---|---|
| Prey richness | 1.0 | 2.22 | .311 |
| Individual scores on PCA axis 1 | 1.0 | 4.39 | **.029**[a] |
| Individual scores on PCA axis 2 | 1.0 | 0.40 | .603 |
| Littoral compartment contribution | 1.0 | 2.15 | **.023**[a] |
| Pelagic compartment contribution | 1.0 | 0.17 | .531 |
| Benthic compartment contribution | 2.6 | 8.16 | **.003**[b] |
| Interindividual diet variations | 2.7 | 5.65 | .264 |
| Interindividual isotopic variations | 1.5 | 3.10 | **.044**[a] |

*Note:* Significant relationships between body size and the different variables are identified in bold.

Abbreviation: edf, estimated degree of freedom.

[a]Significant relationship at $p < .05$.

[b]Significant relationship at $p < .005$.

Mazumder, 2004). Regardless of the divergence between the two approaches, our results are consistent with the findings of Vejřík et al. (2017a) that highlighted short-term specialisation and long-term generalism within *S. glanis* populations in Czech lakes using repeated measures on diets.

However, several individuals clearly differed in their diets and stable isotope compositions compared to the average population estimates, likely indicating a highly opportunistic trophic behaviour and a large trophic plasticity. Additionally, the stable isotope analyses displayed the temporal consistency of individual specialisation (i.e. specialisation considering few months) and underscored the generalist feeding behaviour of the population. Indeed, individuals with high $V_{i_SI}$ values presented less mixed isotopic compositions (contribution of one resource pool >90%), while most individuals were characterised by a mixed contribution of resource pools, strengthening the opportunistic feeding behaviour in the different lake habitats and reflecting a generalist diet (Lopezosa et al., 2019).

### 4.3 | Ontogenetic diet changes

Contrary to our expectations, individual body size had a minor influence on the trophic characteristics of *S. glanis*. Therefore, ontogeny currently seems to poorly constrain the trophic characteristics of *S. glanis* in Lake Bourget, contrary to results obtained in other ecosystems (Alp, 2017; Carol et al., 2009; Copp et al., 2009). This result may be partly due to the limited body size range found in the current population, with most individuals measuring less than 80 cm and the absence of large individuals (>140 cm) consistent with the recent colonisation of the species in this lake (~10 years). Indeed, ontogenetic trophic variations were highlighted within older *S. glanis* populations established for a longer time (>30 years) and including several individuals larger than 140 cm. The probable future change in the population body size structure, expected to include larger individuals in line with the aging of the population, may result in a stronger ontogenetic pattern in diet divergence between small and large individuals, which are expected to become increasingly piscivorous (Alp, 2017; Carol et al., 2009; De Santis & Volta, 2021).

## 5 | CONCLUSIONS

This study provides an overview of the trophic ecology of *S. glanis* in a large peri-alpine lake and underscores its high reliance on the littoral habitats. The individual diets of *S. glanis* appear to be heterogeneous and characterised by a diversified set of rare prey, highlighting individual opportunism. This trophic opportunism may be a key driver of its establishment in peri-alpine lakes by exploiting a large

diversity of available resources, although crayfish, roach and perch were the three main prey of the *S. glanis* population. The survey of their stocks could thus be required in further management plans.

The significant exploitation of pelagic and deep benthic habitats, typical habitats of large peri-alpine lakes, is a novel observation of *S. glanis* trophic ecology in its non-endemic geographic distribution, particularly on its adaptive behaviour to new ecosystems. Our results raise concerns on the potential impacts of *S. glanis*, not only on the littoral habitat, but on all lake habitats; particularly ones occupied by pelagic fishes such as European whitefish that are targeted in commercial fisheries. *S. glanis* may thus represent a risk not only for resident species but also for ecosystems services (e.g. commercial fisheries), especially if its abundance rapidly increases in the future as expected from invasive species during their first colonisation phases and observed at the moment for the population in Lake Bourget.

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## CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

## AUTHOR CONTRIBUTION

Conceived and designed the investigation: CV, VF, JG, FC. Performed field and/or laboratory work: CV, SB, VF. Analysed the data: CV. Contributed materials, reagents and/or analysis tools: CG. Wrote the paper: CV, VF.

## DATA AVAILABILITY STATEMENT

A part of data is provided in Supplementary Information and the other part is accessible in open-access at https://github.com/chloevagnon.

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