ORIGINAL ARTICLE

WILEY · *Ecology of* FRESHWATER FISH

When alien catfish meet—Resource overlap between the North American *Ictalurus punctatus* and immature European *Silurus glanis* in the Arno River (Italy)

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Funding information
2020 Marie Sklodowska-Curie, Grant/Award Number: ITN-2014-ETN-642197

Abstract

Due to the increasing globalisation and ongoing introduction of alien species specifically regarding European freshwater ecosystems, native and already present alien species will be confronted with competitors with unknown outcomes. One such case is the situation of the European catfish *Silurus glanis* introduced in the Arno River (Central Italy), a species sought after by anglers, which is facing competition from the later introduced alien North American channel catfish *Ictalurus punctatus*. Large catfish species are highly valued among anglers, but their interspecific interactions and potential ecosystem-level impacts are still poorly known. We used stomach contents and stable isotope analyses to study niche partitioning between these two alien catfish species, coexisting in the Arno River. The results suggest partial niche segregation, with immature *S. glanis* showing a narrower dietary and isotopic niche and a slightly higher trophic position than *I. punctatus*. Monitoring the catfish population sizes, trophic niches and effects on lower trophic levels are essential for future management and mitigation of their potential impacts on invaded freshwater ecosystems.

KEYWORDS

alien species, dietary analysis, interactions, isotope analyses, niche overlap, niche partitioning

1 | INTRODUCTION

In some cases, introduced species served human well-being (Ewel et al., 1999) without significantly affecting the recipient environment (Jerscke & Strayer, 2005; Williamson & Fitter, 1996a,1996b). Nonetheless, many alien species become invasive and dominate native communities (Crooks, 2002; Kolar & Lodge, 2001), leading towards a homogenisation of ecosystems (Mack et al., 2000; Rahel, 2000). While interactions among alien and native species have recently received increasing attention (Balzani et al., 2016; Busst &

Britton, 2017; Strayer, 2010), the current issue is to understand interactions among alien species (Bissattini & Vignoli, 2017 ; Ricciardi, 2001). Particularly interesting, even if difficult to address, is the scenario of a top predator confronted with the introduction of another potential alien top predator that originates from a different area, and how relationships with other present species are affected (Griffen, Guy, & Buck, 2008; Wei, Wu, & Guo, 2012).

As in many Europeans countries (Gherardi, Gollasch, Minchin, Olenin, & Panov, 2009), alien fish rapidly increased over the past 25 years (e.g., Italy: 40 out of 105 species—38% are alien species;

Gherardi et al., 2008; Nocita & Zerunian, 2007). This process has re-shaped most freshwater communities. Although some introductions might have occurred accidentally, a significant proportion of species has been voluntarily introduced by anglers and sport fishing associations to improve recreational fishing.

One such species is the European or Wels catfish *Silurus glanis* (Linnaeus, 1758), a fish native to north-eastern Europe and Asia. It is known to be the largest freshwater Osteichthyes in Europe (max size 2.7 m and 130 kg; Stone, 2007; Boulêtreau & Santoul, 2016). In the last decades, *S. glanis* experienced a drastic increase in population size and distribution due to angling activities (Copp et al., 2009; Cunico & Vitule, 2014). It was introduced in Italy in the 1990s (Balma, Delmastro, & Forneris, 1989) and was subsequently spread throughout the Italian peninsula with diverse impacts on native and also newly introduced species (Castaldelli et al., 2013). In the Arno River Basin, it was most likely introduced to Bilancino Lake and then spread downstream towards the Sieve River (a tributary of the Arno River; Gualtieri, Mecatti, & Cecchi, 2010). In the Florentine stretch of the Arno River, *S. glanis* has been reported by anglers since 2004 (Gualtieri & Mecatti, 2005). In the course of a few years, this species has become the target of many anglers. The increased investigation into invasive *S. glanis* revealed considerable positive economic (Cucherousset et al.., 2017; Rees et al., 2017) but negative environmental impacts (Castaldelli et al., 2013; Copp et al., 2009).

At the same time, the North American channel catfish *Ictalurus punctatus* (Rafinesque, 1818) was also introduced to Italy. However, information on pathways and means of introduction remain scarce (Haubrock, Balzani, Johović, Inghilesi, & Tricarico, 2018a; Haubrock et al., 2017; Ligas, 2008). In the Arno River, according to catches by local authorities and anglers, it is likely that *I. punctatus* was introduced near Pisa for the purpose of angling and was subsequently transported upriver (G. Castaldelli pers. comm.) as it is increasingly favoured by anglers due to its high reproduction rate and catchability (T. Busatto pers. comm.). In the inner-Florence stretch of the Arno River, it first appeared in 2004 (A. Nocita pers. comm.).

Catfish such as *S. glanis* have specific functions in ecosystems, affecting various ecological groups with their presence. *S. glanis* is known to be a generalist that is capable of rapidly adapting to new prey sources (Vejřík et al., 2017). However, data about the diet of immature (<60–80 cm) *S. glanis* from alien populations (but see Gualtieri & Mecatti, 2005, and Syväranta et al., 2010, for a basic analysis of *S. glanis*' diet) and about interactions with other catfish species are scanty. Similarly, much more information is available about genetics and physiology of *I. punctatus* in regard to aquaculture usage, but most studies that investigated the behaviour of *I. punctatus* are considerably old, with a minority of studies focusing on its invasiveness and diet (Busbee, 1968; Haubrock, Balzani, Johović, et al., 2018a; Rosen, Schwalbe, Parizek, Holm, & Lowe, 1995).

Although these two catfish species are morphologically unequal, with *S. glanis* reaching larger sizes, they are highly tolerant to environmental factors and show high invasive capabilities (Copp et al., 2009; Hilge, 1985). Control activities on *S. glanis* have been carried out in countries such as Italy (see, e.g., Pascale et al., 2013; LIFE-Project

LIFE03NAT/IT/000113 and LIFE15 NAT/IT/000989). Furthermore, these two species of catfish have different feeding strategies. With a fast expansion of the mouth while keeping opercular valves closed in the beginning to maximise the sucked volume, *S. glanis* imbibes prey inside its oral opening (Bruton, 1996). In contrast, the exact morpho-dynamic prey mechanism of *I. punctatus* has not been studied, but a combination of sucking and pursuing-and-biting is possible (Pavlov & Kasumyan, 2002). Moreover, length–weight relationships and thus growth rates might differ between both species. However, they are ecosystem and factor depending. Moreover, information for both *I. punctatus* in Europe as well as *S. glanis* from the Arno River has not yet been assessed and remains anecdotal. Furthermore, such information is needed to better understand the impact these species have on recipient ecosystems (Haubrock, Balzani, Johovic, et al., 2018b). However, the diet of *I. punctatus* has been recently analysed by collecting stomach contents of specimens in the Arno River (Haubrock, Balzani, Johović, et al., 2018a; Haubrock et al., 2017). In contrast, recent and relevant data for *S. glanis'* feeding habit from Central Italy are preliminary or anecdotal (Gualtieri & Mecatti, 2005), making investigating facilitation processes or interfering competition processes difficult.

Interactions between alien top predators are very likely, because in fish communities, resource partitioning mainly occurs along the trophic dimensions, that is across trophic levels (Ross, 1986). According to the competitive exclusion principle (Hardin, 1960), coexistence can only be possible if utilised resources and occupied dimensions (activity time, habitat use) are different (Chase & Leibold, 2003; Schoener, 1986). Studies investigating dietary and, thus, dietary niche partitioning mostly focused on either mature life stages (Schulze, Dörner, Baade, & Hölker, 2012; Zaia Alves et al., 2017) or ontogenetic variations (Davis, Blanchette, Pusey, Jardine, & Pearson, 2012; Tarkan et al., 2018). However, immature life stages in catfish species can dominate an ecosystem and have a considerable impact on other species as well as the potential to become a target to manifold interaction with other species (Alp, Kara, & Büyükçapar, 2004; Alp, Kara, Üçkardeş, Carol, & García-Berthou, 2011; Elrod, 1974; Persson, 1988).

Stomach content analyses can provide a direct insight into recently consumed items and, consequently, feeding behaviour of different life stages, while stable isotope analysis (SIA) provides long-term dietary information. Both combined allow a reconstruction of the studied communities' trophic web and the investigation of niche partitioning (Boecklen, Yarnes, Cook, & James, 2011; Layman et al., 2012). This is possible because isotopic signatures relate with the trophic position (nitrogen, N) and with the main energy source (carbon, C) of a consumer (Layman et al., 2012). Additionally, SIA allows the estimation of trophic levels (Post, 2002) and quantification of feeding niches (Jackson, Parnell, Inger, & Bearhop, 2011; Newsome, Martinez del Rio, Bearhop, & Phillips, 2007; Swanson et al., 2015). The degree of overlap among isotopic niches of different species can therein be assessed to evaluate the potential food competition between species (Balzani et al., 2016; Layman et al., 2012) and niche partitioning (Barbour et al., 2009; Werner, 1979).
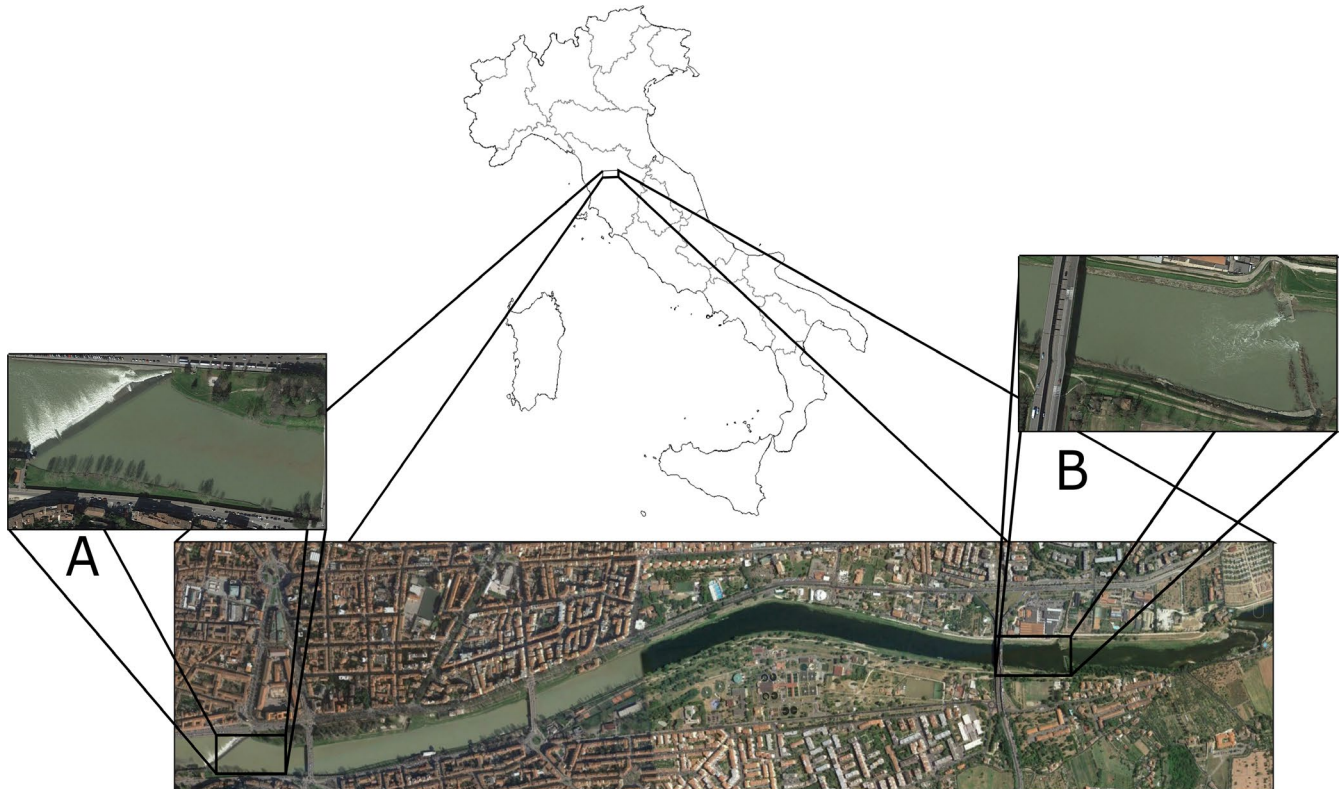
FIGURE 1 Sampling areas within the inner-city section of the Arno River in Tuscany (N43.7648903, E11.2697444)

Over the last years, many anglers and local authorities reported steadily decreasing catches of *S. glanis* (abundance and biomass) in the Arno River within Florence while simultaneously the amount of *I. punctatus* increased (Gherardi et al., 2008; Nocita, 2007; Nocita & Zerunian, 2007). Hence, the present work uses a combined approach of stomach content and stable isotope analyses from both co-occurring species (immature and mature *I. punctatus*, immature *S. glanis*) in order to investigate the degree of interspecific interactions (e.g. feeding competition or prey partitioning), thereby aiming to determine whether the presence of *I. punctatus* potentially affects the population of *S. glanis*.

2 | MATERIALS AND METHODS

2.1 | Sampling

Sampling was conducted twice a week, once in the morning (3–8 a.m.) and evening (4–11 p.m.) between May and June 2018, as these months are considered an ideal activity period for both species (samples were taken after the initial 2-month period of resumed activity, following the inactive winter months). These times were chosen because *S. glanis* shows its activity mostly during the night with peaks of activity before sunrise and after sunset (Carol, Zamora, & García-Berthou, 2007) while *I. punctatus* shows diurnal and nocturnal activity with highest feeding activity during dusk and dawn (Boujard & Leatherland, 1992). Moreover, February and March are typically periods of high water currents and strong

rains, negatively affecting the sampling. The far west end of the inner-Florence river stretch was chosen due to its accessibility for fishing and the low human activity on both riversides (Figure 1). The sampling area was characterised by high turbidity and no aquatic vegetation with scarce vegetation on river banks during the first half of the sampling period due to seasonal patterns and anthropogenic disturbance. Fish were caught using standard fishing rods (2.20–3.90 m), 0.30–0.44 mm monofilament line and size 2–26 fishing hooks baited with a variety of food (maggots, worms, and freshly cut liver or baitfish) placed (a) on the bottom, (b) in the middle water and (c) below the surface. Caught specimens were euthanised (gill cuts) and put on ice before being transported to the laboratory for further processing. In total, 40 individuals of *I. punctatus* were sampled and the stage of maturity was set according to Haubrock, Balzani, Johovic, et al. (2018b) as 31.9 cm, resulting in 20 "immature *I. punctatus*" and 20 "mature *I. punctatus*." Additionally, 39 individuals of "immature *S. glanis*," recognised by the lack of mature and visible gonads and size ranges for immature individuals in this species identified by Copp et al. (2009), were sampled and are referred to as "*S. glanis*." Older and bigger *S. glanis* were not sampled due to (a) their rarity in the sampled stretch and (b) local pressure by anglers.

2.2 | Sample preparation

For all specimens, total length (TL; cm) was measured with an accuracy of 1 mm and body weight (F_W) with an accuracy of 1 g. Values

reported in the text are average plus or minus the standard deviation. Specimens were stored in a freezer (–20°C) until stomach contents were extracted for dietary analyses. For SIA, a sample of dorsal muscle tissue was taken from each specimen, preserved without any chemicals and stored in a freezer (–20°C). Samples were dried in an oven at 60°C for 48 hr and ground into a fine and homogenised powder with an agate mortar and pestle. For each sample, approximately 0.25 mg of powder was weighed and packed into a tin capsule for isotopic analyses. Samples were analysed with an elemental analyser (FlashEA 1112) connected to an isotope ratio mass spectrometer (Thermo Finnigan Delta Plus Advantage) at the National Research Council in Montelibretti, Rome.

2.3 | Growth and dietary analyses

As fish length affects fish weight, examination of the length–weight relationship was achieved with a logarithmic transformation of fish weight and length. Applying a linear regression model, the slope of both linear models was used as a proxy to identify growth types (allometric vs. isometric; Karachle & Stergious, 2012). Thus, the species-specific growth was compared by testing for homogeneity of slopes in an analysis of covariance (ANCOVA; Dhillon & Fox, 2004) with the state "species" used as categorical independent variable. To compare the weight gained with increased length, weight was set as the dependent variable and length as covariate.

The weight of ingested food (ST_W) was expressed as the percental weight of the specimens total weight (F_W) following the approach of Hureau (1969): $F_I = (100*ST_W)/F_W$, where F_I is considered as the fullness index. Only cardiac, caecum and pyloric parts were considered without discarding contents of the intestine. The feeding intensity was calculated using the vacuity index (V_I), as the percentage of empty stomachs with respect to stomachs that contained prey items (Batistić et al., 2005). The diet breadth was estimated based on Levin's index formula (Whittaker, Levin, & Root, 1973): $B_i = \frac{1}{\sum p_i^2}$ where B_i is the standardised index of diet breadth for specimen i and p the sum of the squared proportion of each prey item of specimen I (Levins, 1968). For further analyses, the stomach content data were expressed as frequency of occurrence (F% = number of stomachs containing each food item in relation to total number of full stomachs) and abundance (N% = the number of individuals of each food item with respect to the total number of individuals). With these, the prominence value (PV) for each dietary component was estimated following the approach of Hickley, North, Muchiri, and Harper (1994): $PV = N\% * \sqrt{F\%}$ to estimate the diet overlap index α using the formula of Schoener (1986): $\alpha = 1 - 0.5 \left(\sum_{i=1}^{n} \left| PV_{x_i} - PV_{y_i} \right| \right)$, with n being the number of food items, PV_{x_i} the prominence value of food item i in species x_i and PV_{y_i} the prominence values of food item i in species y. The estimated index varies between 0, that is no overlap, and 1, when diets are identical (Wallace, 1981). Pianka's measure of diet-based niche overlap (Pianka, 1974) for species j and species k using the formula $O_{j\&k} = \frac{\sum_j^n p_j p_k}{\sqrt{\sum_i^n p_j^2 \sum_i^n p_k^2}}$ was calculated, where p_{ij} and p_{ik} are the proportions of the ith resource used by the jth and k^{th} species. Both estimates for diet overlap were used together, as Pianka's measure of niche overlap alone can be insufficient to identify a relation between niche overlap and competition, that is resource partitioning (Krebs, 1999). We utilised a permutational analysis of variance (PERMANOVA; S17 Bray–Curtis similarity, 3 fixed factor, three levels: "immature *I. punctatus*," "mature *I. punctatus*" and "*S. glanis*"; Type III (partial) sum of squares, unrestricted permutation of raw data, 1 dummy variable) and pairwise comparisons using the software PRIMER (Clarke & Warwick, 2001) to determine whether diets varied between species and life stages.

2.4 | Stable isotope analyses

The trophic position of every individual (TP_c) was calculated by applying the equation $TP_c = ((\delta^{15}N_c - \delta^{15}N_{base})/\Delta N) + \lambda$, where $\delta^{15}N_c$ is the mean $\delta^{15}N$ of the consumer, $\delta^{15}N_{base}$ the mean $\delta^{15}N$ of primary producer (*Potamogeton nodosus*, n = 5), ΔN the standard enrichment of 3.4 ‰ between trophic levels, and λ the basal trophic level (= 1 for plants) (Britton et al., 2018; Post, 2002). A primary producer was chosen rather than a primary consumer (e.g., molluscs) due to the lower variability of stable isotope values in plants (Bissattini, & Vignoli, 2017 ; McClelland, Valiela, & Michener, 1997) and the possibility of high as well as variable $\delta^{15}N$ values in primary consumers due to the nitrogen-accumulating nature of the also present *Phragmites australis*.

A linear regression model was applied to investigate potential relationships between TL of *S. glanis* as well as *I. punctatus* and stable isotope values, while the relationship between the two was analysed for potential correlations (Spearman, statistic: r_s). Additionally, to estimate and quantify intraspecific niche width and, thus, being able to compare species, Layman's metrics (Layman, 2007; Layman, Arrington, Montaña, & Post, 2007) were calculated with the R-package SIAR (Stable Isotope Analysis in R; Parnell, Inger, Bearhop, & Jackson, 2010).

$\delta^{15}N$ and $\delta^{15}C$ ranges (NR and CR) as well as the mean distance to the centroid (CD) are measurements of the extent of the $\delta^{15}N/\delta^{15}C$ bi-plot, reflecting the community niche width. The mean nearest neighbour distance (MNND) and the standard deviation of the nearest neighbour distance (SDNND) relate to the distance of species and indicated the degree of trophic redundancy. While Layman's metrics are usually employed in community-wide analyses, they can be used to compare species present within one ecosystem without consideration of the entire species community (Bissattini, & Vignoli, 2017; Jackson et al., 2011; Layman, 2007). Additionally, the corrected standard ellipse area (SEAc; considering 40% of central data points) and the corresponding 95% ellipse area (SEAb), which are convex hull areas encompassing a sampled population in a $\delta^{15}N/\delta^{15}C$ bi-plot space and serve as measures of total isotopic niche space occupied, were calculated for both species and life stages for *I. punctatus*. With these, the degree of isotopic niche overlap (which lays between 0, i.e., no overlapping, and 1, completely overlapping) can be estimated and subsequently used as a quantitative measure for similarity within the diet of
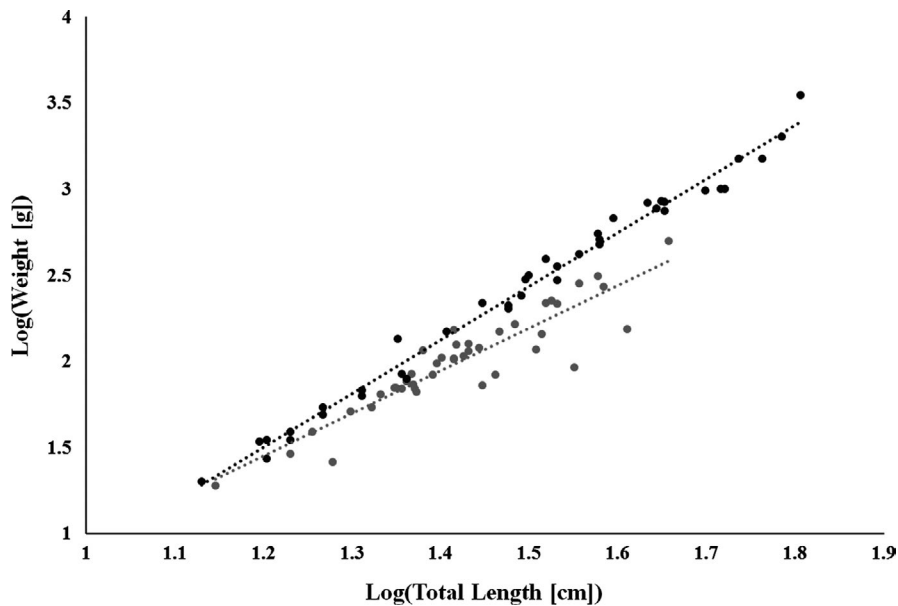
FIGURE 2 Log-transformed length–weight relationship of *Ictalurus punctatus* (black; $y = 3.1177x - 2.2405$; $R^2 = 0.9874$) and *Silurus glanis* (grey; $y = 2.4836x - 1.5297$; $R^2 = 0.84$)

different species (Jackson et al., 2012). Calculations were computed using the R package SIBER (Jackson et al., 2011). Furthermore, the percentual isotopic niche overlap between groups was calculated using the formula of Stasko, Johnston, and Gunn (2015).

The directional pairwise probability of species to exert overlapping niche width was estimated for *I. punctatus* and *S. glanis* using the R-package "nicheROVER," which applies a Monte Carlo estimation (chain length: 10,000 steps) on the potential overlap. Thus, the package computes the directional pairwise probability of the niche of one species (not either species) overlapping onto the niche of another to quantify trophic relationships (Swanson et al., 2015).

Lastly, a PERMANOVA (1 fixed factor, three levels: "immature *I. punctatus*," "mature *I. punctatus*" and "*S. glanis*"; Type III (partial) sum of squares, unrestricted permutation of raw data) was performed to test for significant differences in δ^{15}N and δ^{13}C levels among life stages as well as species and to eventually determine whether groups and/or species are clearly distinguishable by either isotope. Additionally, a canonical analysis of principal coordinates (CAP) for factors whose levels were identified by the PERMANOVA test to be significantly different was applied to identify how δ^{15}N and δ^{13}C contribute to differentiate the levels. Pearson correlations with CAP axis for each variable are reported. For all tests, the level of significance under which the null hypothesis was rejected is $\alpha = 0.05$.

3 | RESULTS

Overall, 40 individuals of *I. punctatus* (mean TL = 33.8 ± 2.2 cm; mean F_W = 538.5 ± 672.1 g) consisting of 20 immature (mean TL = 22.4 ± 1.4 cm; mean F_W = 117.8 ± 96.3 g) and 20 mature specimens (mean TL = 45.2 ± 2.1 cm; mean F_W = 959.2 ± 738.5 g) were collected. *S. glanis* (*n* = 39; mean TL ± SD = 27.1 ± 1.1 cm; mean F_W ± SD = 122.8 ± 89.9 g) matched the size range of sampled *I. punctatus*, enabling a direct comparison. The growth type of both species

was positive; however, growth type was significantly different among species (ANCOVA, $T = 74.376$; $df = 1$; $p < 0.001$; Figure 2). Resultant, *I. punctatus* growth type can be seen as nearly isometric (similar length–weight growth), while "*S. glanis*" grow slower in weight than in length.

3.1 | Dietary analyses

From the 40 sampled *I. punctatus*, all contained prey items (V_I = 100%), while from the collected *S. glanis*, 19 stomachs (V_I = 48.7%) were found empty. F_I of *I. punctatus* was 8.4 ± 3.3% (immature 8.2 ± 3.5; mature 8.7 ± 3.1) and 3.2 ± 1.8 for "*S. glanis*." The diet of both species as well as life stages of *I. punctatus* was significantly different (PERMANOVA, $F = 9.0434$; $df = 2$; $p < 0.05$; post hoc tests: $t = 1.4282$; $p < 0.05$). The most common food source for *I. punctatus* was the easily accessible prey items, detritus and plants ($F\% = 0.55$; $N\% = 0.28$), followed by *Palaemonetes* sp. ($F\% = 0.35$; $N\% = 0.20$), terrestrial ($F\% = 0.40$; $N\% = 0.18$) and aquatic insects ($F\% = 0.35$; $N\% = 0.09$), and lastly small cyprinids (juvenile *Cyprinus carpio* Linnaeus, 1758, *Alburnus alburnus* Linnaeus, 1758, *Pseudorasbora parva* Temminck & Schlegel, 1846; $F\% = 0.20$; $N\% = 0.05$). The occurrence of detergent in *I. punctatus*, potentially remnants from water cleaning plants or fishermen's bait, was previously discussed (Haubrock, Balzani, Johovic, et al., 2018b). Utilising the estimated prominence value (PV) as an indicator of the importance of a prey item indicated that *Palaemonetes* sp., terrestrial insects and plants were most important for the diet of *I. punctatus*. For *S. glanis*, small cyprinids and plant material were dominant food items (Table 1). The diet-based niche breadth for *I. punctatus* was 8.1 for immatures, 6.7 for mature specimens and 8.8 for the overall population, while *S. glanis* showed a lower niche breadth (*B* = 5.6) than *I. punctatus*. The niche overlap was moderately high between "immature *I. punctatus*" and "mature *I. punctatus*" as well as "mature *I. punctatus*" or between the total population of *I. punctatus* and "*S. glanis*." In contrast,

TABLE 1 Frequency of occurrence (%F), abundance (%N), and prominence value (PV) of food items analysed for *Ictalurus punctatus* and *Silurus glanis*

Prey items	*Ictalurus punctatus* (immature) [F%]	[N%]	[PV]	*Ictalurus punctatus* (mature) [F%]	[N%]	[PV]	*Ictalurus punctatus* (Total) [F%]	[N%]	[PV]	*Silurus glanis* (immature) [F%]	[N%]	[PV]
Detritus	0.30	0.08	0.05	0.25	0.04	0.02	0.30	0.06	0.03	0.10	0.09	0.03
Plants	0.45	0.09	0.05	0.60	0.14	0.11	0.45	0.12	0.08	0.13	0.11	0.04
Detergent	0.20	0.08	0.05	0.05	0.01	0.00	0.20	0.04	0.02	0.00	0.00	0.00
Palaemonetes sp.	0.25	0.18	0.11	0.15	0.04	0.02	0.25	0.10	0.05	0.03	0.02	0.00
Dikerogammarus villosus	0.18	0.14	0.05	0.20	0.03	0.02	0.18	0.08	0.03	0.05	0.07	0.02
Procambarus clarkii	0.10	0.01	0.00	0.15	0.03	0.01	0.10	0.02	0.01	na	na	na
unid. Crustaceans	0.08	0.14	0.05	na	na	na	0.08	0.06	0.02	0.03	0.02	0.00
Terr. insects	0.43	0.16	0.10	0.45	0.29	0.19	0.43	0.23	0.15	na	na	na
Aq. insects	0.13	0.00	0.00	0.25	0.06	0.03	0.13	0.03	0.01	0.03	0.02	0.00
Hirudinea	0.03	0.00	0.00	0.05	0.01	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Fish larvae	0.08	0.02	0.01	0.05	0.01	0.00	0.08	0.01	0.00	na	na	na
unid. fish	na	na	na	na	na	na	na	na	na	0.03	0.02	0.00
Small cyprinids	0.25	0.05	0.02	0.30	0.08	0.04	0.25	0.06	0.03	0.18	0.16	0.07
Large cyprinids	0.03	0.00	0.00	0.05	0.01	0.00	0.03	0.00	0.00	na	na	na
Ictalurus punctatus	na	na	na	na	na	na	na	na	na	0.08	0.09	0.03
Molluscs	0.05	0.00	0.00	0.10	0.04	0.01	0.05	0.02	0.01	na	na	na
Small mammals	0.03	0.00	0.00	0.05	0.01	0.00	0.03	0.00	0.00	0.03	0.02	0.00
Small birds	0.08	0.01	0.00	0.10	0.02	0.01	0.08	0.01	0.00	0.03	0.02	0.00
Testudines	0.03	0.00	0.00	0.05	0.01	0.00	0.03	0.00	0.00	na	na	na

Note. "0.00" indicates that the specific prey items in the fish's diet were considerably low; "na" indicates that respective prey item was not present.

all groups of *I. punctatus* expressed moderate-to-high diet overlap index with "*S. glanis*" (α range: 0.612–0.839; Table 2).

3.2 | Stable isotope analyses

With a trophic score of 3.3, *S. glanis* occupied a slightly higher trophic position than immature (3.1) and mature *I. punctatus* (2.9). *Silurus glanis*, however, had a lower variability in Layman's metrics and lower N range compared to both immature and mature

I. punctatus. In contrast, both *I. punctatus* showed a narrower C range (Table 3). The applied linear regression model for $\delta^{15}N$ and total length of both species indicated a decreasing trophic position with increasing size that was significant for *I. punctatus* ($p < 0.05$; Figure 3). Regarding TL and $\delta^{13}C$, statistically significant regressions ($p < 0.05$) as well as negative correlations were found for *S. glanis* ($r_s = -0.512$; $n = 39$; $p = 0.001$) and *I. punctatus* ($r_s = -0.665$; $n = 40$; $p < 0.001$). Calculating the overlap of SEAc and SEAb revealed different results (Table 3): while

TABLE 2 Estimated niche (Levins' Index) and diet overlap based on stomach content data

Index	*Ictalurus punctatus* (immature)	*Ictalurus punctatus* (mature)	*Ictalurus punctatus* (Total)	*Silurus glanis* (immature)
Pianka's measure of niche overlap				
Ictalurus punctatus (immature)	x	0.634	x	0.363
Ictalurus punctatus (mature)	0.634	x	x	0.591
Ictalurus punctatus (Total)	x	x	x	0.549
Silurus glanis (immature)	0.363	0.591	0.549	x
Diet overlap index a				
Ictalurus punctatus (immature)	x	0.740	x	0.779
Ictalurus punctatus (mature)	0.740	x	x	0.839
Ictalurus punctatus (Total)	x	x	x	0.612
Silurus glanis (immature)	0.779	0.839	0.612	x

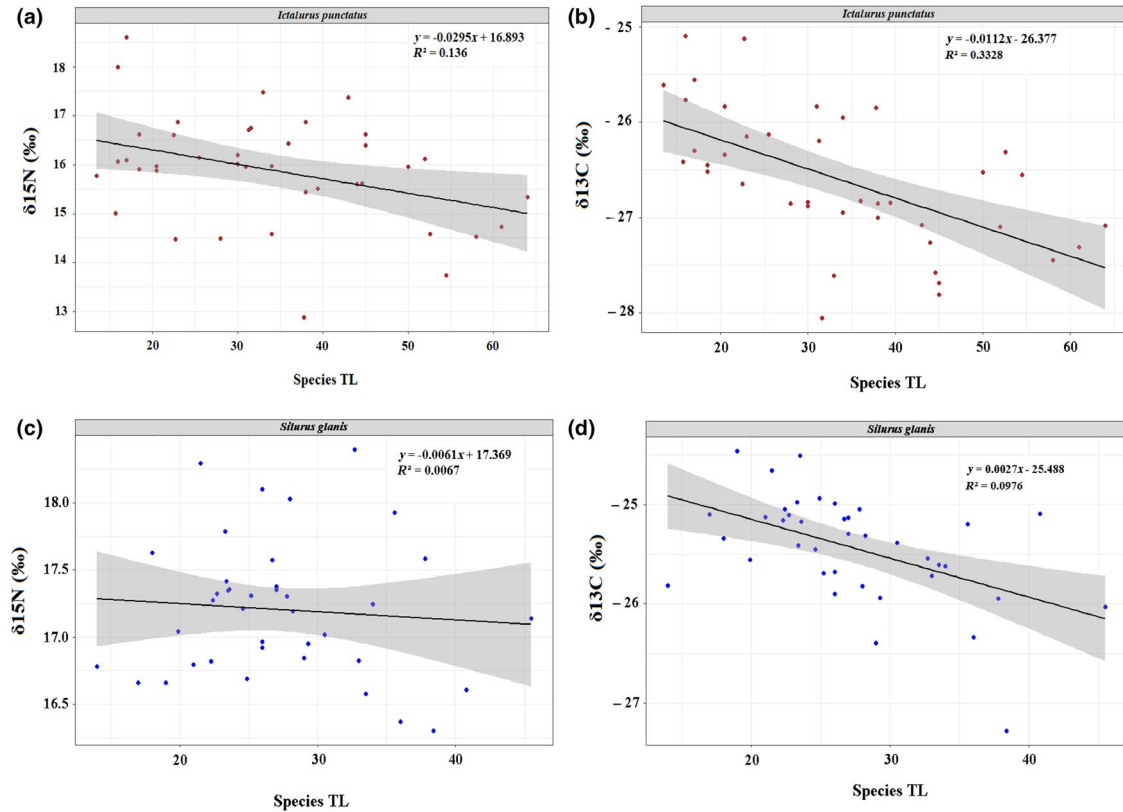**FIGURE 3** Linear regression between total length (TL) and $\delta^{15}N$ and $\delta^{13}C$ for *Ictalurus punctatus* (a, b) and *Silurus glanis* (c, d) from the inner-Florence section of the Arno River

"immature *I. punctatus*" and "*S. glanis*" showed a moderate overlap (SEAc = 0.22/SEAb = 0.28), "mature *I. punctatus*" overlap with "*S. glanis*" was very low (0.00/0.09). Overall, immature and mature *I. punctatus* presented a medium overlap (0.27/0.42), considerably higher than the SEAc overlap of the overall population of *I. punctatus* with "*S. glanis*" (0.01/0.19; Table 4; Figure 4).

Moreover, the percentual isotopic niche overlap was low between "immature *I. punctatus*" and "*S. glanis*" (14.3%) as well as between "immature *I. punctatus*" and "mature *I. punctatus*" (13.4%),

while no overlap was estimated between "mature *I. punctatus*" and "*S. glanis*" or the total population of *I. punctatus* and "*S. glanis*." Pairwise overlaps (95%) between groups indicated that "immature *I. punctatus*" showed the highest probability to occur in the niche of "mature *I. punctatus*" (95%) and "*S. glanis*" (97%), followed by the probability of "mature *I. punctatus*" to fall into the niche of "immature *I. punctatus*" (80%). However, *S. glanis* showed lower probabilities to fall in either niche of immature (68%) or mature (33%) *I. punctatus*.

TABLE 3 Estimated Layman's metrics and stable isotope results for $\delta^{15}N$ and $\delta^{13}C$ of all groups of *Ictalurus punctatus* and immature *Silurus glanis*

Group	Layman metrics and stable isotope analysis results									
	Mean $\delta^{15}N$ (±SD)	Mean $\delta^{13}C$ (±SD)	TP	NR	CR	TA	CD	MNND	SDNND	SEAc
Ictalurus punctatus (immature)	16.2 (±1.0)	−27.0 (±0.7)	3.1	4.1	3.0	8.76	0.93	0.45	0.49	2.20
Ictalurus punctatus (mature)	15.6 (±1.2)	−26.2 (±0.5)	2.9	4.1	2.0	5..39	0.91	0.29	0.24	1.84
Ictalurus punctatus (Total)	15.9 (±1.1)	−26.6 (±0.7)	3.0	5.7	3.0	11.55	1.11	0.34	0.35	2.59
Silurus glanis (immature)	17.1 (±0.6)	−25.5 (±0.6)	3.3	2.8	4.1	4.09	0.79	0.19	0.17	0.87

Note. CD: mean distance to centroid; CR: $\delta^{13}C$ range; MNND: mean nearest neighbour distance; NR: $\delta^{15}N$ range; SDNND: standard deviation of the nearest neighbour distance; SEAc: standard ellipse area; TA: convex hull area.

TABLE 4 Estimated niche overlap for all groups using the maximum likelihood fitted standard ellipse area (SEAc) and the overlap between the corresponding 95% ellipse area (SEAb)

Index	*Ictalurus punctatus* (immature) (SEAc/ SEAb overlap)	*Ictalurus punctatus* (mature) (SEAc/SEAb overlap)	*Ictalurus punctatus* (Total) (SEAc/SEAb overlap)	*Silurus glanis* (immature) (SEAc/SEAb overlap)
SEAc overlap				
Ictalurus punctatus (immature)	x	0.27/0.42	x	0.22/0.28
Ictalurus punctatus (mature)	0.27/0.42	x	x	0.00/0.09
Ictalurus punctatus (Total)	x	x	x	0.01/0.19
Silurus glanis (immature)	0.22/0.28	0.00/0.09	0.19	x

The PERMANOVA main test confirmed significant differences among groups, and the post hoc comparisons showed that the three levels are clearly different (Table 5). Considering the results from CAP analysis (Figure 5), group differences are well explained by the first axis (CAP1, squared canonical correlation of $\delta_1^2 = 0.5957$; CAP 2 $\delta_2^2 = 0.004$). Both $\delta^{13}C$ ($r_s = -0.926$) and $\delta^{15}N$ ($r_s = -0.771$) are highly inversely correlated to CAP1 and effectively contribute to the differentiation of the groups, suggesting in particular that *S. glanis* is clearly different to other two groups for higher values for $\delta^{15}N$ and $\delta^{13}C$. Overall, mature *I. punctatus* have lower values while immature *I. punctatus* lay in an intermediate position (see Figure 4).

4 | DISCUSSION

Interactions among alien fish species, especially with different life histories, are an understudied topic. More specifically, there is a lack of studies concerning trophic relationships among alien top predator's native to different geographic areas while co-occurring in a new region, making this, at least to our knowledge, the first study assessing this issue.

In this study, *S. glanis* was observed to mainly feed on small cyprinids and *Dikerogammarus villosus*, fitting to this species early developing piscivorous diet with generalist tendencies (Copp et al., 2009;

Syväranta et al., 2010). Moreover, *S. glanis* was identified to be less of a generalist than *I. punctatus*, which showed a more diverse diet including insects, plant material, crayfish and fish that was highly variable among life stages. Additionally, all specimens of *I. punctatus* contained prey in their stomach, while almost half of *S. glanis*' stomachs were empty. The observed high number of empty stomachs in immature *S. glanis* was unexpected as especially smaller fish feed every day (Ricker, 1946). However, this result could be linked to the utilised sampling methods, inducing a lot of stress on hooked specimens and potentially resulting in vomiting of previously ingested prey, rather than on the time of sampling. Moreover, the length-to-weight ratio of *I. punctatus* was higher than that of *S. glanis* and the fullness index estimated for *I. punctatus* was in all three cases (immature, mature and all specimens) more than twice than that measured for *S. glanis*. Concerning *I. punctatus*, omnivorous feeding with insectivorous tendency agrees with its diet and feeding behaviour from the native area (Busbee, 1968; Franssen & Gido, 2006). The high occurrence of plants (terrestrial as well as aquatic leaves) within the diet of sampled *S. glanis* is highly unusual (Carol, Benejam, Benito, & García-Berthou, 2009). However, alien species (and especially *S. glanis*) are known to adapt to new and easily accessible prey (Copp et al., 2009; Strayer, 2010). Abundant algae or plants could potentially be a response to either scarce animal prey or an adaptation to abundant vegetation as a replacement to avoid intra- as well as interspecific

TABLE 5 PERMANOVA main and post hoc tests results

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Gr	2	63.519	31.76	28.53	0.001	999
Res	80	89.057	1.1132			
Total	82	152.58				
Groups			*t*		P (perm)	Unique perms
"Immature *I. punctatus*"	"*S. glanis*"		4.3082		0.001	958
"Mature *I. punctatus*"	"*S. glanis*"		7.6838		0.001	969
"Immature *I. punctatus*"	"Mature *I. punctatus*"		2.4983		0.003	747

Note. Design: 1 fixed factor, three levels; resemblance matrix measure of distance: Euclidean distance; Type III (partial) sum of squares, unrestricted permutation of raw data.
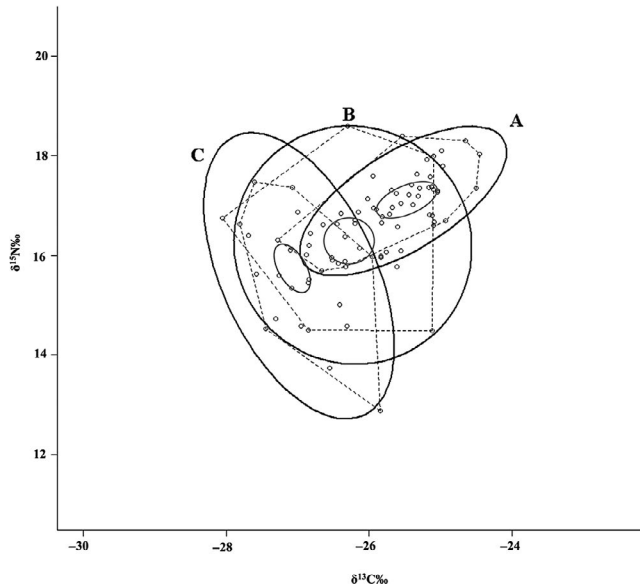
FIGURE 4 Standard ellipse area (SEAc; solid grey line); total convex hull area (TA; dashed black line) as well as 95% ellipse area (SEAb; solid black line) for Silurus glanis (A), immature (B) and mature (C) *Ictalurus punctatus*

FIGURE 5 Two-dimensional scatter plot of the first and second principal coordinate axis (after resemblance matrix with Euclidean distance, *n* samples = 83, *n* variables = 2,) for immature and mature *Ictalurus punctatus* and *Silurus glanis*. Vectors of the linear correlations (Pearson) between individual variables (i.e., δ^{15}N and δ^{13}C labelled in the graph as N and C isotopes) are superimposed on the graph

competition (Copp et al., 2009; Davidson, Jennions, & Nicotra, 2011; Haubrock, Balzani, Johovic, et al., 2018b). Nonetheless, the used fullness index is potentially affected by physiological or morphological differences, for example differing weight-to-length ratios, but since both species belong to the order Siluriformes, these can be considered of secondary importance. However, these results indicate an advantageous adaptation to the invaded ecosystem, more efficient predation by *I. punctatus* or a comparably higher growth rate commonly found in majorly produced aquaculture fish species.

4.1 | Diet and niche overlap

Schoener's diet overlap between all groups was considerably high (α > 0.6), but while Pianka's diet-based niche overlap was similar between "mature *I. punctatus*" and "*S. glanis*," "Immature *I. punctatus*" and "*S. glanis*" showed a lower diet-based niche overlap value (0.36) with respect to Schoener's diet overlap value. This difference can be due to the "prominence value" in the used formula, weighing the importance of prey items and, thus, being affected by the sample size. In contrast, SIA and the derived estimated ellipse overlay of SEAc indicated a higher similarity between niches occupied by "immature *I. punctatus*" and "*S. glanis*" than between "mature *I. punctatus*" and "*S. glanis*."

   Opposed to the narrow time-constrained information presented by stomach content analysis, SIA offers temporally integrated information on diet as well as, with SEAc and SEAb, occupied feeding niches. Thus, a moderate-to-high niche overlap can indicate that the compared species consume similar resources, while not stating if they can coexist over a longer time period nor whether they feed on similar prey resources due to limited interference competition. Hence, neither dietary similarity between groups estimated with
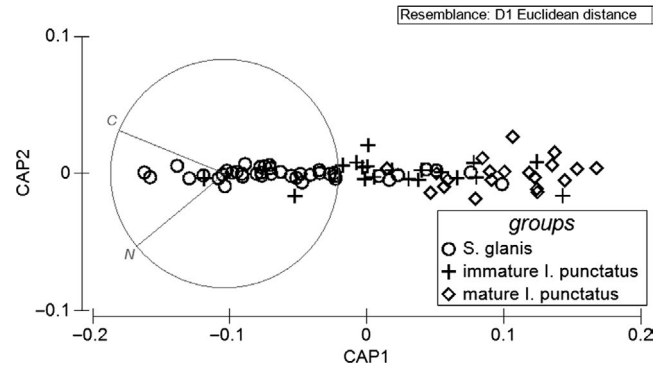
the overlap of SEAc, SEAb, nor percentual isotopic niche overlap reflected the results gained from direct dietary information. Analyses of diets are very focused and dependable on observable ingested items that can be affected by activity times or responses of species to being caught, while isotope analyses consider previously consumed and assimilated prey, thus a considerably longer time (Tarkan et al., 2018). Additionally, all three groups belong to approximately the same estimated trophic position as expected from *I. punctatus* and *S. glanis* (Gido & Franssen, 2007; Syväranta et al., 2010), but "*S. glanis*" had a slightly wider δ^{13}C range than the two life stages of *I. punctatus*. This observation reflects the consumption of a greater variety of carbon sources. A study on *S. glanis* in France found that *S. glanis* was considerably enriched and variable in δ^{13}C with respect to other fishes, explainable with the frequent predation on terrestrial birds and/or mammals (Syväranta et al., 2010). However, this study lacked large-bodied individuals. Nonetheless, it seems reasonable to expect similar results, as anglers' observations confirm the active predation on pigeons by large *S. glanis* in the Arno River (T. Busatto, pers. comm.; Cucherousset et al., 2012). Similarly, δ^{15}N values tend to increase with the length of catfish (Syväranta et al., 2010), reflecting an increased piscivorous or animal diet. While this might be true for *S. glanis* (Syväranta et al., 2010), our results show generally lower mean δ^{15}N values and lower trophic position of "mature *I. punctatus*" with respect to "immature *I. punctatus*." This can potentially be explained by the high level of eutrophication (Romero et al., 2013) and the natural accumulation of nutrients (i.e., dead matter) in the river bottom (Hansen & Kristensen, 1998; Hendrix et al., 1986). Immature *I. punctatus* are benthivorous and often detritivorous, while mature individuals exert increased offshore feeding (as indicated by the difference in δ^{13}C values; Gido, Franssen, & Propst, 2006). Additionally, the lower mean δ^{15}N values could be linked to a considerable competition for increasingly piscivorous mature *I. punctatus* with other species like mature *S. glanis* (Fry et al., 1999). Moreover, Fry et al. (1999) observed that especially δ^{15}N values of *I. punctatus* tend to remain constant with increasing size,

while sampling at several occasions resulted in two mature groups with clearly distinct niches; they linked this observation to varying feeding activities of different schools of *I. punctatus*. Furthermore, a higher $\delta^{15}N$ range was found in *I. punctatus*, underlying its generalist and opportunistic behaviour. Thus, it is possible that the relationship of shared niche space continues to weaken as larger age classes of *S. glanis* are included, because prey fish size increases with age and size of *S. glanis*. This seems to suggest that the difference in niche space may be exaggerated further by including larger size classes and that *S. glanis* prey preference and feeding strategy may change as they grow from immature to mature. Indeed, *S. glanis'* Layman's metrics showed a less variable niche occupation linked to a more specialised diet and niche placement compared to *I. punctatus*. The lower $\delta^{15}N$ values in "mature *I. punctatus*" could be due to the sample, other disturbances (lack of prey, competition, etc.) or the opportunistic feeding of individual "immature *I. punctatus*," therefore needing further investigations.

The results presented by SIA indicate that "mature *I. punctatus*" and "*S. glanis*" likely occupy different trophic niches with generally low similarity in their diet. However, both species show some degree of diet overlap for common prey items like small cyprinidae and Pianka's diet-based measure for niche overlap, an observation likely linked to gape size-limited predation in catfishes (Johnson, Martinez, Hawkins, & Bestgen, 2008). While some analyses indicated low probability of overlap (e.g., SEAc and SEAb), computing directional probabilities using the nicheROVER package reported high probabilities of overlap. This overlap could be related to the opportunistic nature of very generalist *I. punctatus* (Busbee, 1968; Rosen et al., 1995), while "*S. glanis*" showed a lower diet and diet-based niche overlap but a more similar isotopic niche occupation. Considering the estimation of higher probabilities for *I. punctatus* (immature and mature) to occur within the niche of each other as well as within the niche of *S. glanis* indicated that *I. punctatus* shows a higher plasticity in its niche occupation.

The high number of empty stomachs in *S. glanis* and high frequencies of certain prey items (e.g., detritus, plants, algae, small cyprinids) in the diet of *I. punctatus* result in an overall similar prey assortment for the diet analyses, while the associated energy intake and thus isotope assimilation might differ. However, the estimated overlap and thus potentially arising competitions (aside from competition for shelter) are only potential explanations for the observed decrease in *S. glanis*. Furthermore, it is possible that the feeding mechanism of "sucking-in" of small-sized *S. glanis* is less efficient compared to the more active predation mechanism used by *I. punctatus*. Also, Menzel (1945) observed that especially immature *I. punctatus* predate eggs and larvae or fish species, as they commonly share the same habitat, enabling this species to threaten entire populations in relative short time after its introduction (Lentsch, Converse, & Thompson, 1996; Marsh & Brooks, 1989; Nesler, 1995). In the case of the Arno River, *I. punctatus* is seemingly more efficient in its prey consumption and shows signs of an advantageous biology, making it better adapted to the non-native ecosystem that is slower-growing *S. glanis* of similar lengths. Furthermore,

this hypothesis is supported by the wider trophic niche occupation and a less specialised diet paired with the observed higher fullness index as well as a higher length–weight ratio in *I. punctatus*. Additionally, while both species are usually active during the night, *I. punctatus* (especially immatures) tend to extend their activity time into the day, thus giving it an advantage over *S. glanis* (Boujard, 1995; Boujard & Leatherland, 1992; Noeske-Hallin, Richard, Nick, & Suttle, 1985).

The observed differences in stomach content analyses and SIA, based on the different information they provide, underline the opportunistic feeding behaviour of *I. punctatus*. Moreover, this opportunistic feeding behaviour leads to diet and niche overlap. Additionally, the results also highlight the potential for those two species that share a common habitat and overlap in their activity time to compete for resources in the case they become limited. Moreover, this observed niche overlap likely affects the more specialised *S. glanis* and could increase in times when resources are increasingly limited. Therefore, the potential of both alien catfish species to compete could be among the main reasons why a decrease in the abundance of mature *S. glanis* was observed after the introduction of *I. punctatus*, but more long-term studies covering the entire year while also including mature *S. glanis* will be needed.

5 | CONCLUSION

The presence of the alien North American catfish *I. punctatus* was previously believed to have a negative impact on the population of *S. glanis*, indicated by the decreasing abundance of *S. glanis* and an increase in catchments of *I. punctatus* (Arno River: A. Nocita and T. Busatto pers. obs.; Po River: M. Fiedler, A. Battaglini and P. Haubrock pers. obs.). However, while results suggest partial niche segregation, they also indicate the possibility for competition that might be due to the potential for immature *I. punctatus*, which are the dominating life stage (Haubrock, Balzani, Johovic, et al., 2018b; Haubrock et al., 2017; Ligas, 2007), and immature *S. glanis*, a species that is more specialised in its niche occupation, to compete. Although both species are alien, *S. glanis* is a large body-sized fish (Copp et al., 2009) and cherished among "catch-and-release anglers" (Arlinghaus et al., 2007) as a trophy fish. However, with the increasing distribution of the fast-growing and comparably more generalist as well as opportunistic *I. punctatus* (Olden & Poff, 2005; Tucker & Hargreaves, 2004), the population of *S. glanis* could be negatively affected through competition. Further studies should focus on the degree of predation between big-sized *Silurus glanis* (>~70 cm) and the two life stages of the North American catfish under the consideration of differing age and length classes.

AUTHORS' CONTRIBUTION

PJH and ET conceived and designed the investigation. MA and PB performed field work. MA, PJH and AFI analysed the data. PJH, AFI and PB wrote the paper.

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