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ORIGINAL ARTICLE

Trophic niche overlap investigation among native and alien fish species via Stable Isotope Analysis using Bayesian Inference

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Abstract
The introduction of alien invasive species is one of the major threats to the native fish fauna of aquatic ecosystems. Exotic species spread new diseases and parasites, reduce the number of native fish, and disrupt the natural balance of ecosystems. The present study utilized stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) to examine the feeding patterns of eight aliens (*Hypophthalmichthys nobilis*, *Hypophthalmichthys molitrix*, *Carassius auratus*, *Ctenopharyngodon idella*, *Cyprinus carpio*, *Oreochromis aureus*, *O. niloticus*, and *O. mossambicus*) and four native (*Labeo rohita*, *Cirrhinus mrigala*, *Catla catla*, and *Labeo calbasu*) fish species from Head Baloki and upstream (Ravi River), Punjab, Pakistan from January to December in 2020. Community-wide metrics in the $\delta^{13}C$-$\delta^{15}N$ bi-plot space, which reflect the important components of the trophic structure, were also calculated. The results demonstrate that there is trophic niche overlap and potential nutritional competition among co-existing species. The alien species cover greater trophic diversity and niche size than native fish species. This indicates that alien species are opportunistic feeders and consume various food items with multiple basal resources (wide range of $\delta^{13}C$ values). Among the native fish, *L. rohita* with had lower $\delta^{15}N$ and $\delta^{13}C$ values displayed a slightly isolated dietary niche and no direct feeding competition with other species. This niche partitioning might be due to the feeding pressure imposed by the alien fishes in fastly changing aquatic ecosystem of Pakistan. The current study provides baseline data to aquaculturists, land managers, and researchers for the management of aliens and the conservation of native fish species.

Keywords: Native species, Fish, Trophic niche, Stable Isotopic

INTRODUCTION

The introduction of alien fish species changes the composition, relative abundance, and resource utilization of native fish fauna (Imran et al. 2021; Said et al. 2022; Abideen et al. 2023). Risk assessments have consistently predicted that alien fish are likely to cause ecological problems in newly invaded habitats (Wang et al. 2018). Alien fishes reduce the fitness of native ichthyofauna (Douglas et al. 1994) through feeding competition (Sharma & Borgstrom 2008; Ke et al. 2008; Zambrano et al. 2010) and promote algal growth by increasing the availability of free nitrogen and phosphorus which alters the trophic structure (Figueredo & Giani 2005). The introduction of fish species across the globe, including Pakistan, has shifted different aspects of plankton communities such as declines in crustacean zooplanktons and changes in size of phytoplankton towards nano- and picophytoplankton community (Sass et al., 2014; Milardi et al., 2019). Undoubtedly, the rapid introduction of exotic species like *Hypophthalmichthys molitrix, H. nobilis, Oreochromis niloticus, O. mossambicus, O. aureus, Carassius auratus, Ctenopharyngodon idella,* and *Cyprinus carpio* in the freshwater ecosystems of Pakistan has reduced the population of many economically important native fishes including *Cirrhinus mrigala, Labeo rohita, L. calbasu, Tor putitora,* and *Catla catla* (Khan et al. 2011; Imran et al. 2021; Said et al. 2022). Alien fishes have a high fecundity rate and may prey on small co-existing native fishes in the scarcity of feeding resources, increasing alien success and decreasing native species (Said et al. 2022). In many countries like the USA, Brazil, and India millions of dollars are spent every year on the control and management of invasive

species. Invasion science helps comprehend, perceive and mitigate the impact of invasion on the native community (Marks et al. 2010; Ullah et al. 2021; Richardson 2011). Invasion ecologists try to protect the ecosystem's health and economy at the national and international level (Hulme et al. 2008; Pysˇek & Richardson 2010).

To determine their effect under anthropogenic perturbations and normal setups, it is important to assess both conventional and cutting-edge techniques such as stable isotope analysis (Montoya et al. 2006; Wang et al. 2018; Ullah et al. 2023). Differences in photosynthetic pathways (C3/C4) and growth patterns affect the carbon isotope signatures of organisms (Kohn & Cerling 2002). $\delta^{13}C$ analysis is used to measure the resource diversity at the base of the food chain (Fry et al. 2003) while the consumer's trophic level is determined through $\delta^{15}N$ stable isotopic signature (Minagawa and Wada 1984; Polis and Strong 1996). Additionally, $\delta^{13}C$ and $\delta^{15}N$ values provide information regarding consumer's predatory feeding behavior and its assimilation power (Post 2002), providing more accurate, significant, and integrated evidence of the resource connections between different trophic levels (both temporally and spatially) (Haubrock et al. 2021).

Earlier, stable isotope analysis was confined to tracing the flow of carbon in the food chain (Peterson & Fry 1987; Fry 1991). Later, its application evolved into a variety of different functions, including food chain length measurement (Post 2002; Jackson et al. 2016), trophic niche overlap determination (Haubrock et al. 2020a; Balzani et al. 2020), and investigation of alien impacts on an ecosystem. Consumers' stable isotopic signature values have been regularly analyzed to estimate the trophic niche, eating habits and trophic interactions using modern statistical tools (Newsome et al. 2007; Boecklen et al. 2011; Guzzo et al. 2013; Jackson et al. 2016). A set of metrics for trophic niches proposed by Layman et al. (2007) are being used to describe the trophic ecology and community structures. The results of hydrological fluctuations, ecosystem fragmentation (Lockwood et al. 2007), and alien introduction (Hulme 2006; Córdova-Tapia et al. 2015; Haubrock et al. 2020b) have already been evaluated through this numerical approach. According to Jackson et al. (2011), a Bayesian technique is currently used to evaluate trophic interactions at the species and community levels. Since the last decade, stable isotope analysis, especially of ecosystem stability, has increased because their ratio calculates the animal's feeding habits (Szepanski et al. 1999; Kurle & Worthy 2002). A reasonable clear picture can be presented only if large amounts of data are available to understand the fractionation variations among different body parts (Gannes et al. 1997). The trophic shift for the $\delta^{15}N$ ranges from 1.3-5.3% (Minagawa & Wada 1984) while in routine exercise 3.4% value is used to find the consumers' food in reverse calculation (Herrera et al. 2002). Based on consumed food and physiological processes, the stable isotopic signature value ($\delta^{13}C$/ $\delta^{15}N$) is the product of heavy to light isotopes (Marshall et al. 2007). Carbon fixation during photosynthesis is a marker for tracing the feeding habits of consumers from herbivores to predators in a food chain.

The ability to quantify and compare trophic niches has advanced with the integration of stable isotope analysis and Bayesian inference (Erhardt & Wilson 2022), particularly in invasion ecology (Quintana et al. 2023). Tools like SIBER (Cybulski et al. 2022), nicheROVER (Dillon et al. 2021), and MixSIAR allow for estimating isotopic niche width, directional niche overlap, source contributions, and isotopic niche overlap with uncertainty propagation (Yang et al. 2025). These methods have been applied to assess dietary overlap and competition displacement among invasive species, such as tilapia (Shuai et al. 2023), silver carp (Seghers et al. 2025) and common carp (Lackmann et al. 2025). Studies show that invasive fish species often have broader or more variable trophic niches than natives, indicating adaptability and competitive dominance in unstable resource environments (Diallo & Olden 2025).

It is evident that Pakistan's freshwater ecosystems, particularly the River Ravi, have not been extensively studied using stable isotope analysis (SIA) to examine

Table 1. Coordinates of Study area.

Site	East	North
I	73.859 E	73.859 E
II	73.955 E	31.298 N
II	74.042 E	31.368 N

trophic niche overlap. Additionally, the effects of invasive species on native fish communities are largely overlooked in the existing literature. Current research in this region primarily focuses on species richness, diversity (Muhammad et al. 2024), dietary preferences (Ali et al. 2024; Shabir et al. 2025), and pollution (Ilyas et al. 2023), rather than on the complex trophic interactions that occur within these ecosystems. In addition, the extent to which alien fish species change food webs and competition for resources in various degraded rivers, such as Head Balloki, is poorly understood which calls for better systems to make clearer ecological evaluations. Utilizing stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), the current research goals were to study the feeding ecology of native and alien fish species and to determine the trophic niche overlap betweennative and alien fish species residing in the sampling site, Head Balloki located on River Ravi, in the Punjab province of Pakistan.

MATERIALS AND METHODS

Study site: The samples were collected for one year (2020) in January, April, August and December (twice each of the month) from the river Ravi at Head Baloki and its upstream regions as Site I, Site II and Site III (Table 1).

Samples collection, preservation and processing: Local contractors and fishermen assisted in sample collection, with nets having different mesh sizes (12m long, 1.8m high, and mesh ranging from 20-115mm knot-knot) (Khan et al. 2011). Immediately after collection, samples were identified up to the species level using proper identification keys (Mirza & Javed 2003; Mirza & Sharif 1996), preserved in ice packs, and further processed in the Paleo-ecology and Environmental Biology Laboratory (PEEBL), Institute of Zoology, University of the Punjab Lahore,

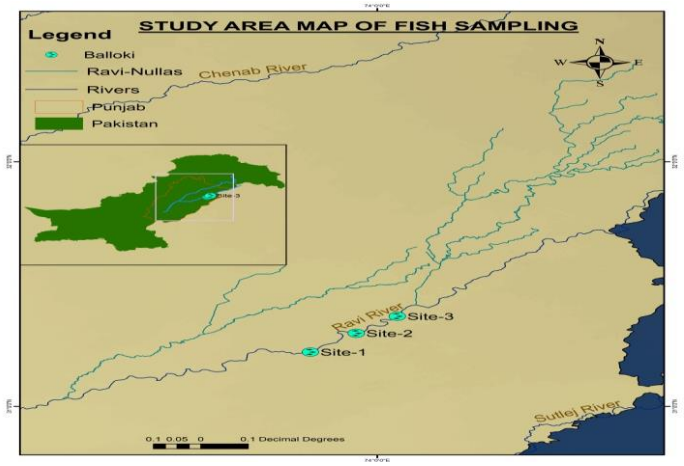

Fig.1. Pictographic presentation of the sampling sites.

Pakistan. Dorsal muscles of each specimen were used for the stable isotope analysis. These tissues have the lowest variations in $\delta^{13}C$ and $\delta^{15}N$ values compared to other body tissues which increases the accuracy of the results (Pinneggar & Polunin 1999). Muscle samples were oven-dried (for 72 hours at 60°C), and ground using a grinder (Moulinex Company) to make a homogeneous powder (Said et al. 2022). The acid fumigation technique was applied to remove inorganic carbon (Lorrain et al. 2003). Lipid extraction/correction (Folch et al., 1957) of pre-treated samples was done to reduce results bias (Peterson & Fry 1987; Ryan et al. 2012; Yurkowski et al. 2015). The powdered samples were sent to the Isotope Application Division (IAD) of Pakistan Institute of Nuclear Sciences and Technology (PINSTECH), Nilore, Islamabad, in air-tight labeled tubes for $\delta^{13}C$ and $\delta^{15}N$ analyses.

Stable isotope ($\delta^{15}N$ & $\delta^{13}C$) analysis: The Delta Plus Advantage Isotope Ratio Mass Spectrometer (IRMS, Thermo Finnigan) utilized carbon dioxide (CO2) and nitrogen gas (N2) as inlet sources for δ13C and δ15N, respectively. CO2 was prepared following the method outlined by Sajjad et al. (1993), while N2 was prepared according to Kjeldahl (1883). The δ13C and

δ15N values were measured against international standards, using atmospheric nitrogen (AIR) for nitrogen and Vienna Pee Dee Belemnite (V-PDB) for carbon (Eq. 1). The machine's precision was ±0.1% for δ13C and ±0.5% for δ15N.

$$\delta^{13}C \text{ or } \delta^{15}N = \{(R_{sample} - R_{standard})/ (R_{standard})\} x\ 1000 \quad (1)$$

Where $R = {}^{13}CO_2/{}^{12}CO_2$ for $\delta^{13}C$

$R = {}^{15}N_2/{}^{14}N_2$ for $\delta^{15}N$

Population niche metrics: Layman et al. (2007) introduced population niche metrics for species' niche overlap and trophic structure examination. These community-wide metrics reflect key elements of the trophic structure and assess the entire degree of spacing and trophic redundancy inside a $\delta^{13}C$–$\delta^{15}N$ bi-plot.

1. **$\delta^{15}N$ range (NR)**, is the difference between the specimen with the most enriched and depleted $\delta^{15}N$ values. A bigger NR among consumers shows more trophic levels and greater trophic niche diversity, and providesa concrete illustration of a vertical structure and a trophic length index for a population.

2. $\delta^{13}C$ range (CR), is the difference between individuals with the highest and lowest $\delta^{13}C$ values. When numerous diverse food supplies with various $\delta^{13}C$ levels are at the base of the food web, higher CR in food webs is to be expected.

Statistical Analysis: Observed stable isotope data were used to determine the trophic niche and possible resource overlap. The normality of the $\delta^{13}C$ and $\delta^{15}N$ data was determined using the Shapiro-Wilk test (α=0.05 in all cases). Kruskal-Wallis one-way ANOVA on ranks was used to compare the mean values of $\delta^{13}C$ and $\delta^{15}N$ using IBM SPSS Statistics 26. The present study opted for SIBER to analyze the data, as it allows for greater flexibility in modeling isotopic niches and provides valuable statistical inferences. This method is accessible to researchers through the SIAR package. All analyses were executed using the R statistical computing package, and the assumption of multivariate normality was validated using the Shapiro test. The validity of this assumption is confirmed by a test statistic value (MVW= 0.92893) with a *P*-value of 6.014e-09. To apply SIBER, a three-step algorithm was followed:

1. Stable isotopic signature data (e.g., $\delta^{13}C$ and $\delta^{15}N$ values) from native and alien fishes was collected.
2. Bayesian statistics to estimate the mean and variance for each group of samples was applied.
3. Bayesian ellipses to represent each group's statistical uncertainty around the mean isotope values were created. These ellipses were plotted on a graph, forming a confidence region that accounts for data variability. Further editing of figures and graphs was done through Microsoft Excel 2019 and COREL DRAW X7.

RESULTS

A total 117 samples of 12 species (4 natives i-e *Labeo rohita*, *Labeo calbasu*, *Cirrhinus mrigala*, and *Catla catla* and 8 aliens i-e *Ctenopharyngodon idella*, *Hypophthalmichthys molitrix*, *H. nobilis*, *Cyprinus carpio, Carassius auratus*, *Oreochromis aureus*, *O. niloticus,* and *O. mossambicus)* were analyzed for $\delta^{15}N$ % and $\delta^{13}C$ % to explore their trophic niche and overlap in terms of their dietary competition. The mean $\delta^{15}N$ value was highest for *O. niloticus* (i.e., 8.72±0.42) and the lowest for *L. rohita* (i.e., 5.36±0.42), while the mean $\delta^{13}C$ value was highest for *C. idella* (i.e., -18.1±0.68) and lowest for *L. rohita* (i.e., -30.73±0.64) (Table 2).

The $\delta^{15}N$ and $\delta^{13}C$ signature values of the fish species collected on different sampling occasions did not exhibit any significant differences. Therefore, the data for the same species were combined for further analysis. The results of the Shapiro-Wilk test (values <0.05) showed that all data were non-normality distributed. The Kruskal-Wallis one-way ANOVA on Ranks revealed that there are statistically significant differences among the $\delta^{15}N$ and $\delta^{13}C$ values (for $\delta^{15}N$ Kruskal-Wallis One-way ANOVA, sig. = 0.00, df= 11, P<0.01 and for $\delta^{13}C$ Kruskal-Wallis One-way ANOVA, Asymptomatic sig. = 0.00, df= 11, P<0.01).

NR values indicated that all the species are feeding at a single trophic level, as the values of their NRs are lower than the degree of average isotopic fractionation (3.4%) for each trophic transfer, except for *H. nobilis* and *C. auratus* (greater than 3.4%), which depict that

Table 2. Means±standard deviation values of $\delta^{13}C$ % (V-PDB) and $\delta^{15}N$ % (AIR) of the fish species.

Species	N	$\delta^{15}N$ % (AIR)			$\delta^{13}C$ % (V-PDB)		
		Mean ± SD	Min	Max	Mean ± SD	Min	Max
L. rohita	6	5.36±0.42	4.88	5.89	-30.73±0.64	-31.67	-29.69
L. calbasu	9	8.67±0.61	8	9.78	-23.7±0.84	-25.14	-23.13
C. catla	6	6.45±0.06	6.39	6.51	-23.8±0.1	-23.9	-23.71
C. mrigala	6	6.13±0.99	5.02	7.14	-25.13±0.84	-26.18	-23.59
H. molitrix	9	5.75±0.22	5.14	5.99	-26.44±0.41	-27.21	-25.61
H. nobilis	16	5.54±1.79	3.96	8.73	24.14±1.37	-25.66	-22.85
C. idella	8	8.54±0.31	7.97	9.11	-18.1±0.68	-18.98	-17.28
C. carpio	8	6.15±0.27	5.85	6.59	-24.8±0.91	-25.84	-22.91
C. auratus	22	5.5±1.26	4.06	8.78	-23.95±0.96	-25.34	-22.65
O. niloticus	8	8.72±0.42	7.99	9.12	-22.85±0.45	-23.47	-22.03
O. aureus	12	8.12±1.14	6.29	8.99	-23.24±0.93	-25.24	-22.71
O. mossambicus	7	7.77±1.29	6.31	8.98	-22.85±0.08	-22.98	-22.76

Table 3. Trophic niche metrics showing the NR, CR, TA & SEA values of the selected fish species.

Species	*L. rohita*	*L. calbasu*	*C. catla*	*C. mrigala*	*H. molitrix*	*H. nobilis*	*C. Idella*	*C. carpio*	*C. auratus*	*O. niloticus*	*O. aureus*	*O. mossambicus*
N	6	9	3	6	9	16	8	8	22	8	12	7
CR	1.98	2.01	0.19	2.59	1.6	2.94	1.7	2.93	2.69	1.44	2.53	0.22
NR	1.01	1.78	0.12	2.12	0.85	4.77	1.14	0.74	4.72	1.13	2.7	2.67
TA	0.69	2.3	0.06	0.9	0.68	4.78	0.96	1.13	5.36	0.97	3.65	0.45
SEA	0.58	1.47	0.05	0.73	0.28	2.06	0.58	0.64	3.22	0.56	2.81	0.31
SEAc	0.77	1.68	0.06	0.91	0.32	2.20	0.68	0.75	3.38	0.66	3.09	0.37
SEA.B	0.83	2.02	0.06	3.48	0.32	2.18	0.68	0.77	3.45	0.66	3.14	0.37

both of these species feed on more than one trophic level. The NR value was the highest in *H. nobilis* and lowest in *C. catla*. The values of the CRs among species spanned a range from 0.19 to 2.94, with the smallest in *C. catla* and the highest in *H. nobilis* (Table 3). Small NR and CR values indicate that *C. catla* has the lowest trophic diversity and occupies the smallest niche space (Fig. 2), whereas *H. nobilis* had the highest CR and NR values and thus occupied the largest niche space and had the highest trophic diversity among the species. Total Convex Hull Area (TA) in indigenous fishes ranges from 2.3 (maximum in *L. calbasu*) to 0.06 (minimum in C. catla), while its value among the alien fish's ranges from 5.36 (maximum in *C. auratus*) to 0.45 (minimum in *O. mozambicus*). Standardized Ellipses Area (SEA), Standardized Ellipses with its corrected version (SEAc), and Standardized Ellipses Area via Bayesian analysis (SEA.B) have the lowest values of 0.05, 0.06, and 0.06, respectively, in *C. catla* and the highest in *L. calbasu* (SEA 1.47, SEAc 1.68), while SEA.B is maximum (3.48) in *C. mrigala* among native fish species. Among alien fish species, the lowest values were recorded in *H. molitrix* (SEA 0.28, SEAc & SEA.B 0.32), and the highest were recorded as 3.22, 3.38, and 3.45, similarly in the case of *C. auratus*.

As shown in Fig. 2, *L. rohita* exhibits a slightly isolated trophic niche, with less direct feeding competition and potential influence from alien fish. The other native species, *C. mrigala* and *C. catla*, show greater trophic niche overlap with *C. carpio*, *H. molitrix*, *H. nobilis*, and *Carassius auratus*, but

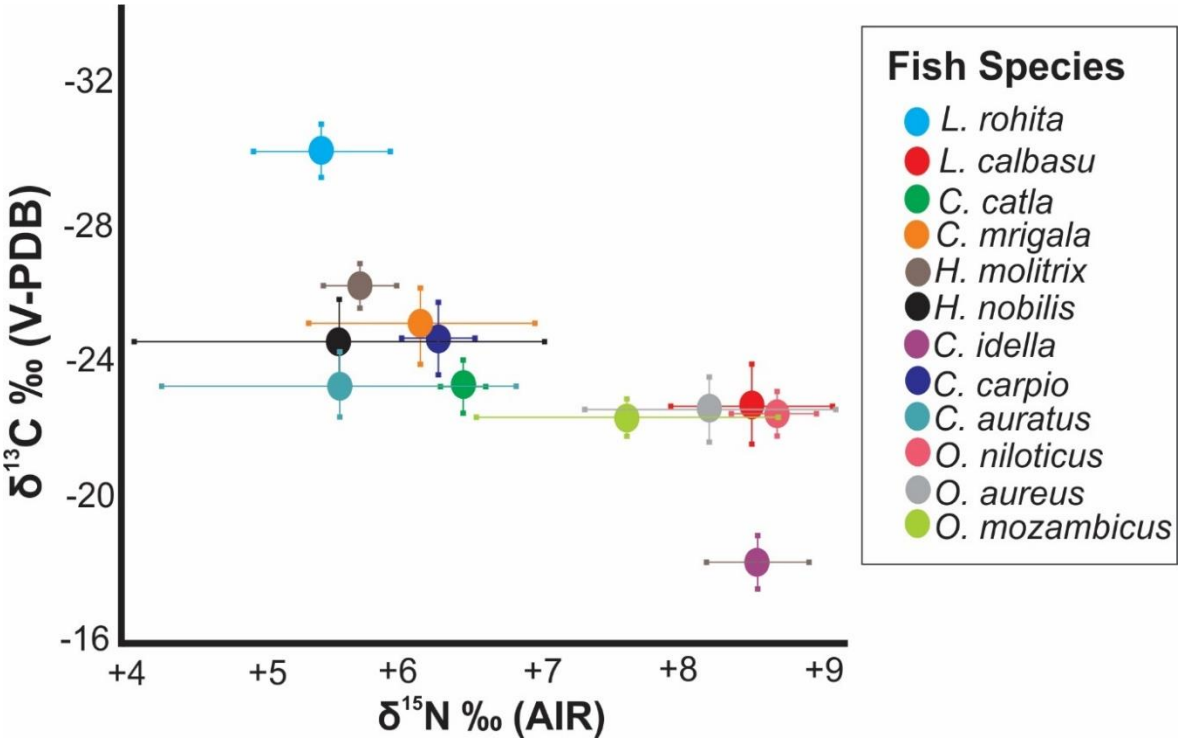

Fig.2. Means±standard deviation values of $\delta^{13}C$ % (V-PDB) and $\delta^{15}N$ % (AIR) in fish species.

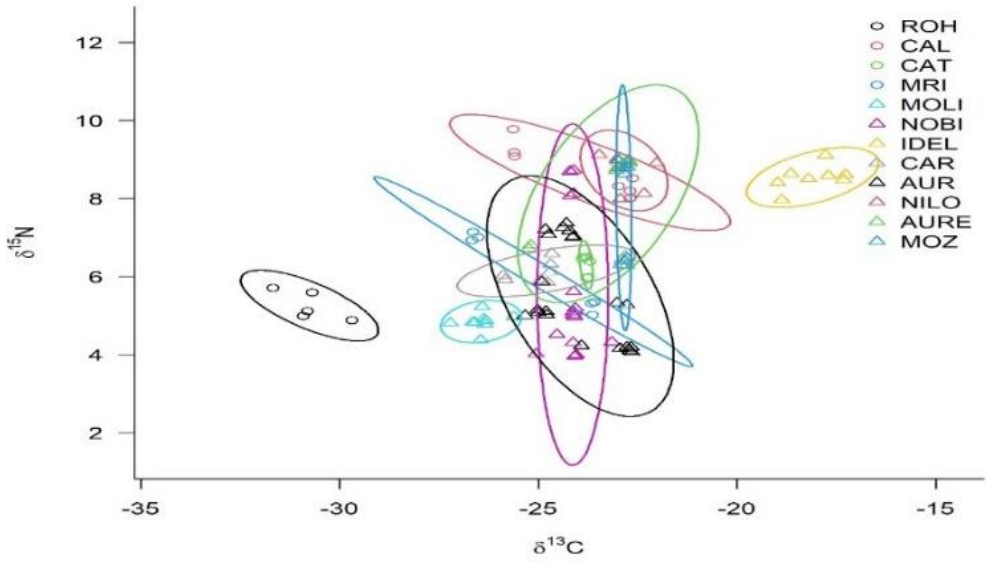

Fig.3. Pictographic presentation of the size and shape of Bayesian ellipses of the fish species.

lower overlap with *C. idella* and tilapia species (*O. aureus*, *O. niloticus*, and *O. mossambicus*). *L. calbasu* also shows higher overlap with *O. aureus*, *O. niloticus*, and *O. mossambicus*. Due to its higher δ13C values, *C. idella* occupies a slightly isolated position in the trophic niche.

Figure 3 shows the size and shape of Bayesian ellipses, providing insights into isotope value variability within native and alien fish species. Wider and more elongated ellipses indicate greater variation, while smaller and more circular ellipses suggest less variation. Overlapping ellipses indicate shared ecological space between these groups. In Figure 4, credible interval ellipses are constructed to represent the uncertainty associated with stable isotope data visually. The center of the ellipse represents the

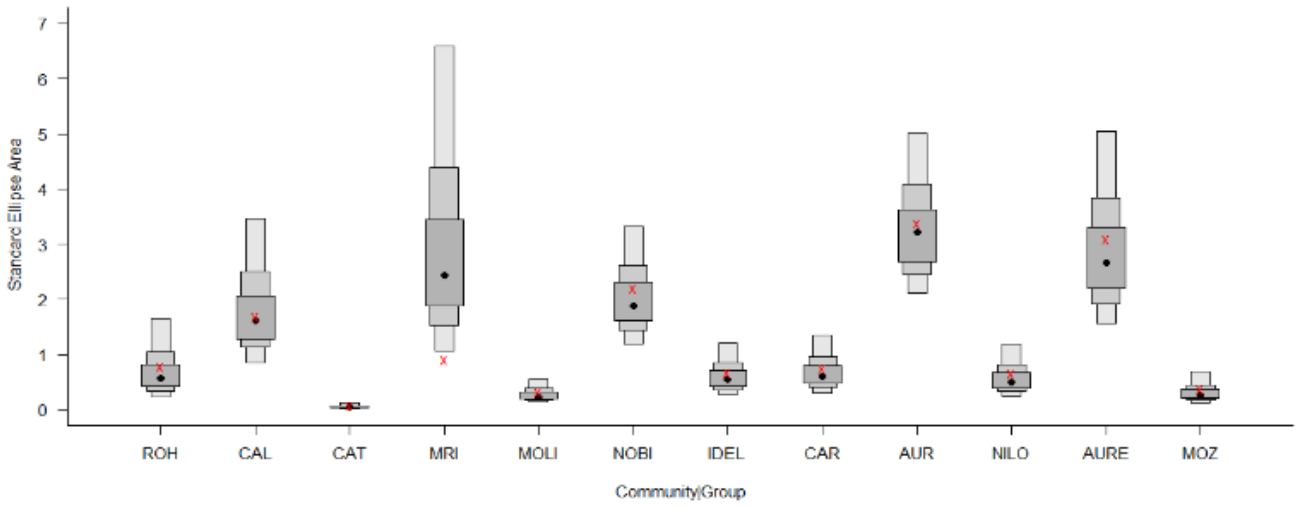

Fig.4. Credible interval ellipses, black dot represents their mode, red crosses as true population value and the shaded boxes representing the 50% 75% and 95% credible intervals from dark to light grey.

estimated mean of stable isotope values, while the shaded region around it represents credible intervals (e.g., 50%, 75%, and 95%), indicating the level of uncertainty. Researchers use these ellipses to compare stable isotope values and their uncertainty between different groups, identifying significant differences in mean isotopic values, which may suggest dietary differentiation between species.

This study also explored the trophic niche overlap of alien species among themselves. *C. carpio*, *H. molitrix*, *H.nobilis*, and *C. auratus* are in direct competition with each other while all the tilapia species; *O.aureus*, *O. niloticus*, and *O. mossambicus* are in higher competition with each other (Fig. 2).

DISCUSSION

The application of stable isotopes (e.g. $\delta^{15}N$ and δ^{13}) has become more popular in ecological studies in recent decades , and it is unblemished that some more multifaceted tools (Bearhop et al. 2004; Layman et al. 2007a; Newsome et al. 2007) have the potential to revolutionize the way for investigating different hypothesis related to niche occupancy and community structure. In the present study, the original metrics proposed by Layman et al., (2007a) using Bayesian methodology and standard ellipses were developed to demonstrate more honest and robust community structure. Podani (2009) eluded that the application of a convex hull area for the isotopic niche width description should be engaged with due caution for sample sizes.

Invasive alien fish species may reduce the abundance and diversity of native fishes in numerous ways; their effects on the food chain may pose a serious threat (Zambrano et al. 2010; Khan et al. 2011). Exotic fish species also have different secondary impacts. For example, *O. aureus* (Tilapia) enhances nitrogen and phosphorus levels, leading to fast algal growth and ultimately causing a trophic cascade (Figueredo & Giani 2005), whereas *C. carpio* increases water turbidity (sediment re-suspension that is harmful to macrophytes), causing foraging trouble for generalist feeding fishes (Miller & Crowl 2006; Scheffer et al. 2006). To comprehend the influence of alien species on native fishes, a proper understanding of resource partitioning and possible (direct and indirect) feeding overlap among different fish species (Johnson et al. 2002; Nahon et al. 2020).

Stable carbon isotopic signatures (δ13C) provide information about feeding resources, as different sources of organic carbon have distinct δ13C values at the base of the food chain, such as phytoplankton and zooplankton. The trophic position within the food web is revealed through nitrogen isotopic signatures

(δ15N) (Peterson & Fry 1987). The combined analysis of δ15N and δ13C enhances our understanding of niche overlap and partitioning among coexisting native and alien fish species (Pilger et al. 2010). For instance, native fishes exhibit constrained nutritional roles, characterized by very low δ15N values, in the presence of alien fishes that have higher δ15N values and intensively utilize available food resources (Zambrano et al. 2010). This study presents the trophic niche overlap between native and alien fishes in the Ravi River, Punjab, Pakistan. A variety of exotic fish species, including Chinese carp and tilapia, have been introduced into the rivers of Pakistan, and the Ravi River is no exception (Khan et al. 2011). The presence of these species is intensifying due to increasing pollution pressure in the river (Mahboob et al. 2015). To assess their influence on trophic niche overlap, we evaluated the stable isotopic signatures (δ15N and δ13C) of indigenous and exotic fish species.

The primary objective of the study is the characterization and identification of the feeding habits of both exotic and indigenous fishes. Furthermore, niche overlap and breadth were calculated by Lyman et al. (2007). The dietary niche overlap clarifies the decline in indigenous fish populations from the freshwater ecosystem of Pakistan. Current investigations will additionally support to restore and rehabilitation of indigenous fish species along the management of exotic ichthyofauna.

L. rohita is a column feeder that primarily consumes phytoplankton (Pervaiz et al., 2018). Its low carbon isotope values (-30.73%± 0.64%) compared to other fish indicate its herbivorous diet. The species exhibits an isolated dietary niche, as evidenced by its low nitrogen values in conjunction with its carbon isotopic values. Additionally, the diversity of *L. rohita* is declining, as noted by Imran et al. (2021) and Khan et al. (2011). Although this species does not directly compete for food with others, the evidence suggests that its restricted trophic niche is primarily a result of feeding pressure from exotic fish species.

In contrast to *L. rohita*, all of the other native fishes, i.e., *C. mrigala*, *C. catla*, and *L. calbasu*, showed both direct and indirect feeding overlap with alien fishes. Gut content analysis (Imran et al. 2021) declared *L. calbasu* a detritus feeder (macrophytes were found in higher proportions), while *C. catla* and *C. mrigala* were preferentially omnivores. The average δ13C value for *L. calbasu* (-23.7%±0.84) indicated that the diet of this species is composed of zooplankton and macrophytes rather than phytoplankton, having less than 40mm size based on gill rakers' anatomy (Jayasinghe et al. 2015). Peterson et al. (2020) declared it an omnivorous, preferentially zooplankton feeder; the higher δ15N values (8.67%±0.61) depict that this fish species feeds at a higher trophic position compared to other contemporary fishes, indicating its zooplankton feeding behavior.

C. mrigala and *C. catla*, two native species, showed average δ13C values of -25.13% ± 0.84 and -23.8%±0.1, respectively. The latter is observed to be omnivorous, feeding on phytoplankton and macrophytes as preferred food, with sizes greater than 40 mm (Pervaiz et al. 2018). However, the enriched δ13C values of *C. catla* compared to *L. rohita* contradict the former assumption regarding its omnivorous trophic niche; rather, we suppose that its diet is mainly composed of macrophytes, with zooplankton also present but in small amounts. Conversely, this species is an opportunistic omnivore, where phytoplankton acts as the main feeding category. The carbon isotopic signature suggests that its trophic niche mainly relies on phytoplankton, while it opportunistically shifts to omnivorous feeding behavior. The average δ15N and δ13C values of *C. catla* showed a higher degree of feeding overlap with *C. carpio* and *H. molitrix* (Table 1). Their overlapping trophic niche is due to feeding on zooplankton. *C. catla* was presumed to be omnivorous in feeding behavior (Pervaiz et al. 2018), changing its diet based on phytoplankton availability and the feeding pressure imposed by *H. molitrix*. Conversely, zooplankton is the preferred diet for *C. catla* at higher trophic levels, where *H. molitrix* rarely exists (Bostock et al. 2010; Jayasinghe et al. 2015), as shown by lower δ15N values. This is possibly due to changes in gill anatomy in both fish species that mark *C. catla* as a weak competitor to *H. molitrix* (Ke et al. 2008). The superior competitive

feeding nature of *H. molitrix* is due to the capacity of its gill rakers, which can hold tiny particles (4.5-10 mm). The introduction of *H. molitrix* may be considered a threat to the native *C. mrigala* and *C. catla*, as indicated by recent reports of a sharp decline in their populations (Mahboob et al. 2015; Khan et al. 2016; Imran et al. 2021). Generalized niche overlap among different indigenous and exotic fishes is demonstrated in Figure 2.

Average δ15N and δ13C values of *C. mrigala* were 6.13±0.99% and -25.13±0.84%, respectively, which classifies it as an opportunistic omnivore, equally relying on zooplankton and phytoplankton (Cordovo-Tapia et al. 2015), compared to *C. catla* and probably positions it in the center of the food web. *C. mrigala* displays a higher degree of competition with *H. molitrix*, *C. carpio*, *H. nobilis*, and *C. auratus* as indicated in Figure 2 and Table 1. C. *carpio* behaves as an omnivore that preferably feeds at the bottom, while *C. auratus* is an opportunistic omnivore in addition to having a detritivore nature (Khan et al. 2011; Ullah et al. 2021). Among the species, *C. carpio* and *C. mrigala* exhibit direct and the highest degree of direct feeding competition (Fig. 2) due to having the same trophic position. *C. auratus* and *H. nobilis* have moderate dietary overlap with both *C. mrigala* and *C. carpio* because of low-protein food (lower δ15N values). *C. mrigala* is declining as the *C. carpio* population has increased over the last decade (Mahboob et al. 2015).

Though the alien species compete with indigenous species as prescribed by Khan et al. (2011), Imran et al. (2021), Said et al. (2022), and Afzala et al. (2023), stable isotopic values of nitrogen and carbon reveal that invasive fish species are also competing with each other (Fig. 2; Table 1). For example, the average δ15N and δ13C values show that *C. carpio*, *C. auratus*, *H. nobilis*, and *H. molitrix* have an intense feeding niche overlap. All the tilapia species (*O. aureus*, *O. niloticus*, and *O. mossambicus*) have relatively similar δ15N and δ13C values, present in the same region of the δ15N-δ13C biplot area (Fig. 2), showing trophic niche overlap. This is a new finding of the current study, contrary to previous thoughts. However, the circumstances remain the same; alien invasive fishes continue to be one of the main reasons for the native population's decline.

Why are alien fish, despite their intense dietary overlap, not a threat to each other? Several plausible considerations provide insight into this phenomenon. Alien fish that successfully establish populations tend to exhibit rapid growth rates, shorter generation times, and higher densities in their native ranges, enhanced dispersal capabilities, broader environmental tolerances, and greater reproductive potential (Chen et al. 2009; Di Donato et al. 1993; Afzala et al. 2023). The alien fish species in the Head Balloki region of the River Ravi display many of these characteristics, which make them superior competitors to native fish species, allowing them to mitigate the challenges posed by competition.

However, alien fish species can also have several negative impacts, including disease transmission, alterations to spatial and habitat dynamics, trophic changes, and gene pool modification in newly occupied ecosystems (Cordovo-Tapia et al. 2015; Jessen et al. 2019; Jayasinghe et al. 2015; Imran et al. 2022). This study suggests that the indigenous fish fauna of the River Ravi, particularly at the Head Balloki site and its upstream areas, has been adversely affected. This could lead to a bottleneck effect, ultimately resulting in a loss of the gene pool and biodiversity of native fish due to the introduction of nonnative fish species in a rapidly changing aquatic ecosystem.

CONCLUSION

The results of the $\delta^{15}N$ and $\delta^{13}C$ values demonstrate trophic niche overlap and probable feeding competition among exotic and native fish species in River Ravi, Punjab, Pakistan. The alien fish species being aggressive and highly opportunistic feeders with greater trophic niche areas may outcompete the native fish species under limited available resources.

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مقاله کامل

بررسی همپوشانی جایگاه تغذیه‌ای میان گونه‌های بومی و غیربومی ماهیان با استفاده از آنالیز ایزوتوپ‌های پایدار و استنباط بیزی

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چکیده: ورود گونه‌های مهاجم غیربومی یکی از مهم‌ترین تهدیدها برای تنوع زیستی ماهیان بومی در اکوسیستم‌های آبی محسوب می‌شود. این گونه‌ها با انتقال بیماری‌ها و انگل‌های جدید، کاهش جمعیت گونه‌های بومی و برهم زدن تعادل طبیعی اکوسیستم‌ها، پیامدهای زیست‌محیطی گسترده‌ای ایجاد می‌کنند. در پژوهش حاضر، از ایزوتوپ‌های پایدار نیتروژن ($\delta^{15}N$) و کربن ($\delta^{13}C$) برای بررسی الگوهای تغذیه‌ای هشت گونه غیربومی شامل *Hypophthalmichthys nobilis*، *H. molitrix*، *Carassius auratus*، *Ctenopharyngodon idella*، *Cyprinus carpio*، *Oreochromis aureus*، *O. niloticus* و *O. mossambicus* و چهار گونه بومی شامل *Labeo rohita*، *L.calbasu*، *Cirrhinus mrigala*، *Catla catla* و صیدشده از منطقه هد بالوکی و بخش بالادست رودخانه راوی، ایالت پنجاب پاکستان، طی دوره ژانویه تا دسامبر سال ۲۰۲۰ استفاده شد. همچنین، شاخص‌های جامعه‌محور در فضای دوبعدی $\delta^{13}C$–$\delta^{15}N$ که مؤلفه‌های مهم ساختار تروفیکی جامعه را نشان می‌کنند، محاسبه شدند. نتایج نشان داد که میان گونه‌های همزیست، هم‌پوشانی قابل‌توجهی در جایگاه تغذیه‌ای وجود دارد که بیانگر احتمال بروز رقابت بر سر منابع غذایی است. گونه‌های غیربومی نسبت به گونه‌های بومی، تنوع تروفیکی و وسعت جایگاه تغذیه‌ای بیشتری را اشغال کردند. این یافته نشان می‌دهد که گونه‌های غیربومی دارای رفتار تغذیه‌ای فرصت‌طلب بوده و با بهره‌گیری از منابع پایه غذایی متنوع، طیف گسترده‌ای از اقلام غذایی را مصرف می‌کنند؛ موضوعی که با دامنه وسیع‌تر مقادیر $\delta^{13}C$ تأیید می‌شود. در میان گونه‌های بومی، *Labeo rohita* با داشتن مقادیر پایین‌تر $\delta^{15}N$ و $\delta^{13}C$، جایگاه تغذیه‌ای نسبتاً مجزایی را اشغال کرده و هم‌پوشانی اندکی با سایر گونه‌ها نشان داد؛ بنابراین، رقابت مستقیم غذایی این گونه با سایر ماهیان محدود به‌نظر می‌رسد. این تفکیک جایگاه تغذیه‌ای احتمالاً در نتیجه فشار تغذیه‌ای ناشی از حضور گونه‌های غیربومی در اکوسیستم‌های آبی در حال تغییر سریع پاکستان ایجاد شده است. نتایج این مطالعه اطلاعات پایه ارزشمندی را برای متخصصان آبزی‌پروری، مدیران منابع طبیعی و پژوهشگران فراهم می‌آورد و می‌تواند در تدوین راهبردهای مدیریت گونه‌های غیربومی مهاجم و حفاظت از گونه‌های بومی ماهیان مورد استفاده قرار گیرد.

کلمات‌کلیدی: گونه‌های بومی، ماهیان، همپوشانی جایگاه، ایزوتوپ‌های پایدار