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Research Paper

Feeding Overlap among Co-existing Indigenous and Exotic Fish Species from the Freshwater Ecosystems of Pakistan

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Abstract

The invasion of exotic fish species threatens indigenous freshwater fish communities by modifying behavioral interactions, population processes, and overall community organization. Understanding feeding behavior is therefore essential for preventing ecological degradation. At the head Qadirabad (River Chenab), feeding habits of both native (*Labeo calbasu*, *Cirrhinus mrigala*, *Catla catla* and *Labeo rohita*) and exotic (*Hypophthalmichthys nobilis*, *Hypophthalmichthys molitrix*, *Ctenopharyngodon Idella*, *Cyprinus carpio*, *Carassius auratus*, and *Oreochromis niloticus*) species of fish were investigated from January to December 2019. A total of 36 mature fish specimens were used to investigate the feeding habits by gut content analysis. Results indicated that *Labeo rohita*, *Ctenophyaryngodon idella* and *Oreochromis niloticus* were herbivorous, while *Labeo calbasu*, *Cirrhinus mrigala*, *Hypophthalmichthys nobilis* and *Cyprinus carpio* were detritivores. *Catla catla* and *Hypophthalmichthys molitrix* behaved as planktivorous, whereas *Carassius auratus* were omnivorous fish species. Significant feeding overlap (Schoener's Index Value: 0.60-0.99) has been observed among coexisting native and exotic species. The current study presents astonishing results, showing that the *Hypophthalmichthys nobilis* diet was altered to become a detritivorous feeder, which may represent a leading step towards divergent evolution. Present data will help to investigate trophic niche overlap based on stable isotope analysis and further molecular studies. Amendment in the feeding behaviour of exotic fish is a strategy for becoming successful invaders, which aligns with the observations of the current study.

Introduction

Exotic fish species can induce substantial alterations in otherwise stable native ichthyofaunal communities. However, the ecological predictors driving invasion dynamics are limited and show inconsistent patterns of invasion success across different ecosystems (Ribeiro et al., 2008; Ayalew et al., 2025). It is therefore necessary to investigate species' food preferences to understand these phenomena. Changes in the abundance or behaviour of top predators indirectly affect lower trophic levels, including prey and primary producers. Ecological generalists exhibit strong physiological tolerances, making them powerful invaders in new populations (Marchetti et al., 2004; Erdoğan, 2025). Biological invasion imposes environmental and economic consequences worldwide (Gozlan, 2008; Imran et al., 2021).

The introduction of non-native fish species is increasingly common due to their close association with human activities. While some exotic species fail to establish self-sustaining populations, others thrive and integrate into new ecosystems (Khan et al., 2011; Ghia et al., 2025). Their impact on native fish populations spans the genetic, community, and ecosystem levels (Cucherousset & Olden, 2011), while others remain unreported. Fish introductions occur for various reasons, including recreational fishing, aquaculture development and ornamental trade (Gozlan, 2008). Generally, alien fish species are larger than indigenous species, which is a guarantee of their successful invasion. Body size measurement is a fundamental tool for determining an organism's trophic level within an ecosystem (Hildrew et al., 2007; Serra et al., 2024).

Introduction leads to interactions with co-existing animals, such as predators, prey, and other competitors. The feeding niche overlap among exotic and indigenous fish may affect the local food web and community structure (Lockwood et al., 2007). It was therefore necessary to investigate the aquatic ecosystems already disturbed by anthropogenic activities (Cucherousset & Olden, 2011). Resource partitioning plays a crucial role in structuring ecological communities (Molles, 2002; Stephens et al., 2008). The intra and interspecific feeding competition helps find the available ecosystem resources (Stephens et al., 2008; Araújo et al., 2011). Interpretation of trophic dynamics is necessary to predict the potential impact of invaders in newly invaded habitats. Kolar et al. (2005) concluded that exotic species possess broad dietary niches and are more successful in establishing new populations.

Water reservoirs are directly and indirectly subject to various anthropogenic disturbances (Leira & Cantonati, 2008). Freshwater reservoirs, particularly lakes, are highly susceptible to exotic fish invasions (Legler et al., 2010). Exotic fish species, i.e., *O. mozambicus*, *O. niloticus*, *H. nobilis*, *C. carpio* and *C. idella*, were introduced in 1985 (De Silva et al., 2004), 1954 (Naik et al., 2015), 1964 (FAO, 1970), 1975 (Mahboob, 2011) and 1964 (FishBase, 2003) from Egypt, Thailand/Egypt & Indonesia, China, China & Nepal and the United Kingdom & Thailand, respectively. However, the introduction of *H. molitrix* (FAO, 1970) and *C. auratus* (Mirza, 2003) into Pakistan is not documented. The introduction of these fish was aimed at promoting fish culture and controlling aquatic weeds in Pakistan (Khan et al., 2011). These introduced fish overlap with the feeding niches of native fish fauna. Exotic fish have ensured their breeding in shallow waters, modified their diet and stabilized them in an ecosystem with changing food resources (De Silva et al., 2004; Ghia et al., 2025). The present study is designed to report the occupied niche area of the exotic fish species in one of the disturbed aquatic ecosystems in Pakistan. Alien fishes are highly visible in disturbed ecosystems (Davias et al., 2014) and are driven by vacant feeding niches (Turetsky et al., 2017; Fridley & Sax, 2014; Lekevičius, 2009).

2. Materials and Methods

The samples were collected in the year 2019 from the River Chenab, Punjab province of Pakistan (Head Qadirabad 32.381039 N; 73.90753 E, Downstream 32.330105 N; 73.62942 E, Upstream 32.338904 N; 73.76585 E) (Figure 1). Sampling was conducted in January, April, August, and December to maximize specimen diversity. Cast nets, hand nets, drag nets, and gillnets were used with lengths and heights of 10 and 1.6 m, respectively, and mesh sizes ranging from 15 to 110 mm for fish collection.

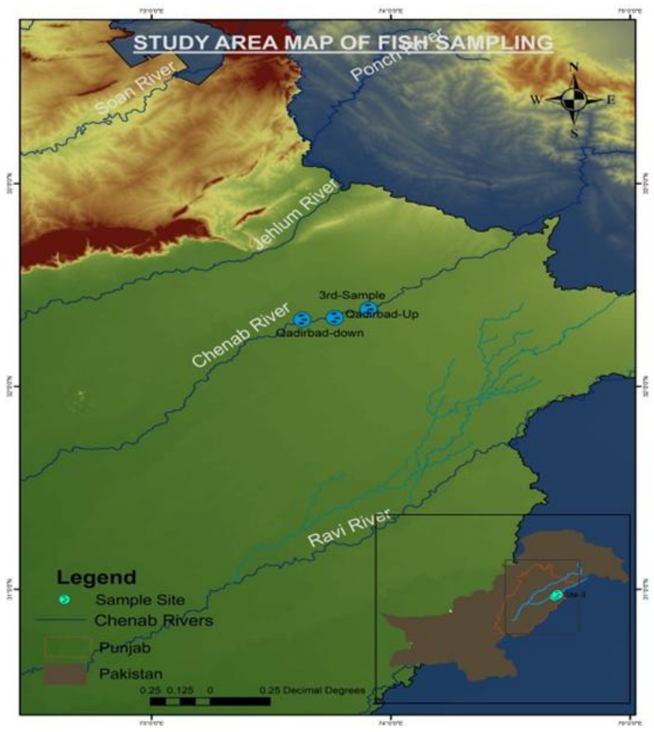

Figure 1. Cinematic presentation of the sampling area

Thirty-six mature samples were identified to species level using standard taxonomic keys (Talwar & Jhingran, 1991; Mirza & Sharif, 1996; Mirza, 1990). To prevent decomposition, large specimens were injected with 10% formalin. The encountered food was preserved in 70% alcohol (Sladky et al., 2001; Pervaiz et al., 2018). Diet composition was quantitatively analyzed using a metallurgical microscope (40X-1600X magnification) with Polarizing Darkfield and dual Lights following Hyslop's (1980) methodology.

2.1 Quantitative food analysis

2.1.1 Frequency of occurrence

Presence of food items in the fish gut was recorded and expressed as frequency of occurrence ($\%Oi$) proposed by Ahlbeck et al. (2012) and Baker et al. (2014) as $\%Oi = \frac{Ni}{N} \times 100$ (Ni is the number of stomachs that contained food, while N is the total number of stomachs that were examined.

2.1.2 Percentage of number

All of the stomachs having food were individually examined, and each food category was enumerated and expressed as a percentage of numbers ($\%Ni$) proposed by Hynes (1950) as $\%Ni = \frac{Ni}{Nt} \times 100$ (Ni is the number of particular food items in the stomach, while Nt is the total number of food items present in the stomach).

2.1.3 Index of relative importance

Relationship among different food items (IRI) in the stomach was expressed as an index of relative importance (IRI = $\%Ni \times \%Oi$) where %Ni is the percentage number, and %Oi is the percentage of frequency (Boughamou et al., 2016; Morote et al., 2010). Percentage comparison (%IRI) between different food items was calculated as %IRIi = 100 × $\frac{\text{IRIi}}{\Sigma\text{IRI}}$ (where IRIi and ΣIRI are the index of the relative importance of a particular food item and the sum of the index of relative importance, respectively.

2.1.4 Feeding overlap

The selection criteria of similar food items were calculated and expressed as $(D = 1 - 0.5(\Sigma_{i=1}^{s}|Xi - Yi|)$, where S is the number of food classes, X*i*= %IRI of food category *i* in one species, while Y*i*=%IRI of food category *i* in other species (Schoener, 1968). The Schoener's index ranges from 0 to 1, where 0.00 to 0.49, 0.50 to 0.59, 0.60 to 0.99, and 1.00 indicate no overlap, highly significant non-overlap, significant overlap, and complete overlap, respectively.

3. Results and discussion

A total of 36 fish samples, including 3 *L. rohita*; 3 *L. calbasu*; 4 *C. catla*; 3 *C. mrigala*; 4 *H. molitrix*; 3 *H. nobilis*; 3 *C. idella*; 3 *C. carpio*; 3 *C. auratus* and 7 *O. niloticus*. Among the collected, only mature fish were sacrificed to analyze their feeding behaviour, as mature fish exhibit consistent feeding behaviour. All of the processed individuals contained food in their alimentary canal. Information on stomach analysis in freshwater fishes of Pakistan is limited, except for a few studies on catfishes (Sandhu & Lone, 2017).

Zooplanktons (Z), Macrophytes (M), Phytoplanktons (P) and undifferentiated (U) matter were found from the processed *L. rohita* samples with different selection criteria (P>M>Z>U) and composition (Table 1). Its dietary habit slightly but non-significantly overlapped with those of other fish species, namely *C. catla* (0.59), *C. idella* (0.55), and *O. niloticus* (0.57) (Table 2). *L. calbasu* significantly overlapped (0.96) its diet with *H. nobilis*, while this overlap was highly non-significant with *C. mrigala* (0.53) and *C. carpio* (0.55), where its food was mainly comprised of detritus (90.50%) (Table 2). *C. catla* consumed a variety of food items at different frequencies, with a preference ranking of MS<F<U<D<H<M<Z<P, which was the preference policy (Table 1). Highly non-significant feeding overlap was observed among indigenous fish *C. catla* and exotic fish species *H. molitrix*, *C. mrigala* and *C. idella*, *C. carpio* and *O. niloticus* as 0.53, 0.52, 0.54 and 0.55, respectively (Table 2).

The feeding habits of *C. mrigala* and *C. carpio* significantly overlapped (0.96), while this overlap was non-significant with *H. nobilis* (0.56) and *C. auratus* (0.58) (Table 1). *H. molitrix* encountered Z & P with 100% while other food items encountered different frequencies. Its food selection criteria showed non-significant overlap with other species (Tables 1 & 2). The feeding habit of *H. nobilis* was preferably detritus-based, with different preferences as (MS<U<H<Z<M<P<D) (Table 1). Its feeding niche was significantly overlapped with the co-existing species *L. calbasu* (0.96) (Table 2). *C. idella* grasped P, Z and

M as 95.00, 4.00 and 1.00%, respectively, while other food items were not identified from its dissected guts (Table 1). Its feeding niche was significantly overlapped with *O. niloticus* (0.57) (Table 2). The feeding selection criteria of *C. carpio* were as follows (F<H<MS<U<M<Z<P<D) (Table 1). Its major food was animal, plant and detritus-based, significantly similar to *C. mrigala* (0.96) (Table 2). *C. auratus* encountered all food categories (Z, U, D, P, MS, M, H and F) with different compositions (Table 1). None of the other co-existing species encountered significantly similar food (Table 2). Plant matter was the major food in the processed guts of *O. niloticus*, which was significantly identical (0.79) to *C. idella* species.

Table 1: Quantitative food analysis of different freshwater fish species from the river Chenab, Pakistan

Food Type		**Q.V**	**Fish Species**									
Major Group	**Minor Group**		***L. rohita***	***L. calbasu***	***C. catla***	***C. mrigala***	***H. molitrix***	***H. nobilis***	***C. idella***	***C. carpio***	***C. auratus***	***O. niloticus***
			S.S									
			03	03	04	03	04	03	03	03	03	07
Plant Material	**P**	%O	100	100	100	100	100	100	100	100	100	100
		%N	50.67	5.00	43.75	21.33	11.00	6.00	95.00	21.50	9.30	73.00
		IRI	5067	500	4375	2133	1100	600	9500	2150	930	7300
		%IRI	50.86	5.00	47.01	22.04	11.37	6.00	95.32	22.63	9.30	75.82
	M	%O	100	100	100	100	75	100	66.67	100	100	71.43
		%N	44.33	2.50	7.00	5.00	2.00	4.00	1.00	5.25	16.10	4.00
		IRI	4430	250	700	500	150	400	66.67	525	1610	285.72
		%IRI	44.66	2.50	7.52	5.17	1.55	4.00	0.67	5.53	16.10	2.96
Animal Material	**Z**	%O	100	100	100	100	100	100	100	100	100	71.43
		%N	4.00	2.00	35.00	19.33	81.00	2.00	4.00	18.75	30.90	4.00
		IRI	400	200	3500	1933	8100	200	400	1875	3090	285.72
		%IRI	4.01	2.00	37.61	19.98	83.78	2.00	4.01	19.74	3.90	2.97
	H	%O	00	00	75	66.67	25	100	00	50	100	00
		%N	0.00	0.00	6.25	4.00	2.00	1.00	0.00	4.00	15.00	0.00
		IRI	00	00	468.75	266.68	50	100	00	200	1500	00
		%IRI	0.00	0.00	5.04	2.75	0.52	1.00	0.00	2.11	15.00	0.00
	F	%O	00	00	50	33.34	00	00	00	50	100	42.68
		%N	0.00	0.00	0.50	0.34	0.00	0.00	0.00	0.50	4.70	1.00
		IRI	00	00	25	11.34	00	00	00	25	470	42.68
		%IRI	0.00	0.00	0.27	0.12	0.00	0.00	0.00	0.26	4.70	0.45
Detritus	**U**	%O	66.67	100	50	66.67	75	100	00	100	100	57.14
		%N	1.00	1.00	2.00	5.00	3.00	1.00	0.00	5.00	4.20	1.00
		IRI	66.67	100	100	333.35	225	100	00	500	420	57.14
		%IRI	0.67	1.00	1.08	3.44	2.33	1.00	0.00	5.26	4.20	0.59
	MS	%O	00	100	25	100	25	100	00	50	100	57.14
		%N	0.00	1.50	0.50	6.00	0.25	1.00	0.00	5.50	4.80	1.00
		IRI	00	150	12.50	600	6.25	100	00	275	480	57.14
		%IRI	0.00	1.50	0.13	6.20	0.07	1.00	0.00	2.89	4.80	0.59
	D	%O	00	100	25	100	50	100	00	100	100	100
		%N	0.00	88.00	5.00	39.00	0.75	85.00	0.00	39.50	15.00	16.00
		IRI	00	8800	125	3900	37.50	8500	00	3950	1500	1600
		%IRI	0.00	88.00	1.34	40.30	0.38	85.00	0.00	41.58	15.00	16.62

Note: P, M, Z, H, F, U, MS, D, QV, %O, %N, IRI, %IRI and S.S are Phytoplanktons, Macrophytes, zooplanktons, Higher invertebrates, Fish/fish parts, Unidentified mater, Mud/sand, detritus, quantitative values, Percentage Frequency, Percentage Number, Index of Relative Importance, Percentage of Index of Relative Importance and Sample Size respectively.

Table 2: Feeding overlap among exotic and native ichthyofauna at River Chenab, Pakistan

Fish Species	*L. rohita*	*L. calbasu*	*C. catla*	*C. mrigala*	*H. molitrix*	*H. nobilis*	*C. idella*	*C. carpio*	*C. auratus*	*O. niloticus*
L. rohita	N.A	0.10	0.59	0.33	0.18	0.12	0.55	0.35	0.45	0.57
L. calbasu	0.10	N.A	0.12	0.53	0.10	0.96*	0.08	0.55	0.42	0.27
C. catla	0.59	0.12	N.A	0.53	0.53	0.15	0.52	0.54	0.43	0.55
C. mrigala	0.33	0.53	0.53	N.A	0.36	0.56	0.28	0.96*	0.58	0.47
H. molitrix	0.18	0.10	0.53	0.36	N.A	0.12	0.17	0.37	0.32	0.17
H. nobilis	0.12	0.96 *	0.15	0.56	0.12	N.A	0.09	0.58	0.45	0.28
C. idella	0.55	0.08	0.52	0.28	0.17	0.09	N.A	0.31	0.29	0.79*
C. carpio	0.35	0.55	0.54	0.96*	0.37	0.58	0.31	N.A	0.57	0.48
C auratus	0.45	0.42	0.43	0.58	0.32	0.45	0.29	0.57	N.A	0.47
O. niloticus	0.57	0.27	0.55	0.47	0.17	0.28	0.79*	0.48	0.47	N.A

* A value above 0.60 indicates significant dietary overlap

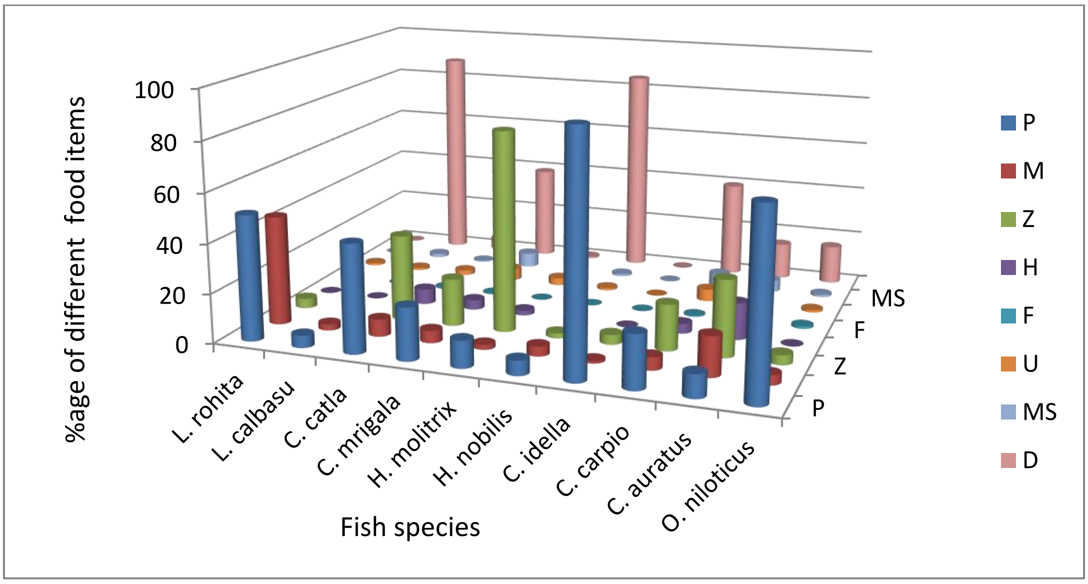

Figure 2. Food selection criteria of different Indigenous and exotic fish species

The *L. rohita* is considered a herbivorous fish that primarily feeds on plant-based food. In 2011, Mahboob reported phytoplankton as the main food (70-80%), followed by zooplankton (25-30%), corroborating the current findings. Majumder et al. (2018) supported the current observations that *L. rohita* primarily feeds on phytoplankton during its life. *L. calbasu* was observed as a pure detritus feeder, empowered by another study conducted by Kumar (2000), where it was a bottom dweller with detritus as a significant food component. Dasgupta (2001) reported that *L. calbasu* feeds on vegetable debris, *Vallisneria*'s leaves, insect larvae and various molluscs. In contrast, Khaing and Khaing (2020) declared it a planktivorous fish. The capacity of an animal to change its diet compared to others is determined by its inheritance and environmental conditions (Ivlev, 1961; Serra et al., 2024).

The *C. catla* is declared an omnivore (feeding on zooplankton and phytoplankton) fish with surface feeding behaviour, whereas other food items were less critical. Adults feed on vegetable debris, algae, and higher invertebrates (Khabade, 2015). The current study is corroborated by Mahboob (2011) and Lalit et al. (2015), both of which support its findings.

The *C. mrigala* is a generalist feeder that mainly takes zooplankton, phytoplankton and detritus as its food, while other food items were encountered in small quantities. Khabade (2015) provided the basis for the present investigations by observing that its food consisted of 32.9% plants and 66.5% detritus.

H. molitrix encountered primarily planktonic food (partially at phytoplanktons and mostly on zooplankton), while *H. nobilis* selected detritus as its major food component (exceeding 50%). Based on gill raker structure (20-25 µm for *H. molitrix* and 20-60 µm for *H. nobilis*), both Asian carps are adapted to consume phytoplankton and zooplankton and compete with filter-feeding indigenous fish species because of resilience in their feeding behaviour (Miura, 1990; Dong & Li, 1994; Xie, 2001). Offem et al. (2009) observed that *H. nobilis* consumed zooplankton (*Brachionus* and *Keratella* species) at about 76%, while *H. molitrix* (*Brachionus, Keratella* and *Trichocerca* species) about 92%. Both of these species are filter-feeders and intake major available plankton food (Dong & Li, 1994; Domaizon & Devaux, 1999). They inferred that availability and prey size are limiting factors influencing their diet composition. Their food was observed as algae in Mississippi, while detritus in the Missouri River, which suggests their plastic-feeding habit (Williamson & Garvey, 2005; Kolar et al., 2005; Erdoğan, 2025). Both of these species are generalist feeders. The unusual feeding behaviour of *H. nobilis* has been established in 24 countries (Kolar et al., 2005).

Results of the current study indicated that *C. idella* fed on planktons, preferably on plant matter, at the adult life stage. It principally feeds on phytoplankton (28-75%), trailed by zooplankton (25-45%), and occasionally detritus (Mahboob, 2011). Furthermore, it relies on variable diet composition, accounting for availability, interactions among coexisting species, and the availability of feeding sources (Milstein & Svirsky, 1996).

C. carpio behaved as a generalist that feeds on different food categories (benthic fauna and decaying floral matter) at the bottom of the freshwater reservoirs (Khan et al., 2016), which corroborates the present investigations. Mahboob (2011) reported that oligochaetes, insects (pupae/larvae), and a few zooplankton make their food, whereas consumption of detritus occasionally corroborates the current findings. High tolerability against temperature and turbidity, making it a persistent and successful exotic fish (Vilizzi & Tarkan, 2015). Spataru et al. (1983) reported that *C. carpio* mainly feeds on zooplankton and benthic macroinvertebrates, which is contrary to present investigations, in which zooplankton (5.7%) is present due to its opportunistic feeding behaviour. Detritus with animal and plant matter also contributed to its diet (Shafi et al., 2012; Ayalew et al., 2025). Its detri-omnivorous feeding nature was also confirmed by Shukla and Patel (2013), Naik et al. (2015), Brahmia (2016), and Imran et al. (2021), which supports the findings of the present study.

C. auratus is a generalist feeder with an omnivorous feeding behaviour, mainly encountering detritus, benthic vegetation, crustaceans, insect larvae, fish eggs/fry, and phytoplankton (Maitland, 2004; Nico et al., 2006). Imran et al. (2021) described it as an omnivorous fish that feeds on crustaceans, zooplankton, plant matter, mosquito larvae, and detritus. It mainly feeds on detritus (53.9 to 85.51%) in stony shorelines, while on open-water plankton (Specziár et al., 1998). Real et al. (2000), Bat and Akbulut (2001), and Titmus and Badcock (2006) reported its benthic omnivorous feeding habit, which is consistent with the current investigations. Its higher tolerance against temperature (Spotila et al., 1979), pollution (Abramenko et al., 1997), pH (Nowruzfashkhami & Bahmani, 2018), salinity (Nico et al., 2006) and low oxygen demand (Nilsson, 2001) help it to dwell in various freshwater ecosystems.

O. niloticus encountered phytoplankton as its major food component. Different morphologies in fluctuating environments are responsible for variable feeding habits among fish species (Wimberger, 1992; Houlihan et al., 2001). Teferi et al. (2000) reported that *O. niloticus* mainly fed on phytoplankton trailed by detritus, while zooplankton were negligible food contributors. Its basic diet was plant-based, while the presence of detritus and zooplankton confirmed its omnivorous feeding behaviour (Tesfahun & Temesgen, 2018). *O. niloticus* encounters food based on its ecosystem capacity (Tsegay et al., 2016; Temesgen, 2017). Crustaceans and insects could be its major food components (Northcott et al., 1991), which is contrary to the current findings, while gut food varies with plasticity to available food, water temperature, animal size, and light intensity (Piyasiri & Perera, 2001).

Conclusion

Gut content analysis provided clear evidence of ecological stress associated with the feeding strategies of co-occurring fish species. The study revealed substantial dietary overlap (Schoener's Index Value > 0.60) between native and exotic species at the Head Qadirabad site of the River Chenab in Punjab, Pakistan. Marked overlap among native-native, native-alien, and alien-alien groups reflects increasing trophic competition within Pakistan's rapidly changing freshwater ecosystem, where shifts in the key parameters such as water temperature, nutrient load, turbidity, and dissolved oxygen are reshaping species interactions due to anthropogenic disturbances. Pollution-driven habitat degradation further appears to contribute to heightened dietary overlap. Further research should incorporate a large sample size and integrate long-term monitoring of migration patterns, fecundity and physiological tolerance ranges, alongside environmental parameters assessment, to develop stronger predictive models and management strategies for Pakistan's freshwater ecosystem under continued ecological change.

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