Zoological Records and Reviews

ISSN: 3117-7530

https://zoologicalrecords.com/index.php/ZRR/en/issue/archive

Feeding ecology of freshwater fishes in tropical rivers

Dr. Karl Rossi[1], Dr. Martin Fischer[2], Dr. Erik Ionescu[3]

[1] Institute of Biodiversity, University of Munich, Germany. Email: karl.rossi@universityofmunich.edu | ORCID: 0000-0004-3093-3682

[2] Department of Ecology and Evolution, University of Bologna, Italy. Email: martin.fischer@universityofbologna.edu | ORCID: 0000-0004-6854-8019

[3] Department of Marine Biology, University of Copenhagen, Denmark. Email: erik.ionescu@universityofcopenhagen.edu | ORCID: 0000-0006-1971-5877

ABSTRACT

Feeding ecology underpins the functional role of fish species within riverine food webs and determines the trophic linkages that regulate energy flow and nutrient cycling in freshwater ecosystems. Tropical rivers, characterised by high fish diversity, strong seasonal hydrological variability, and complex lateral connectivity between river channels and floodplain habitats, present distinctive feeding ecology challenges and opportunities for diverse fish communities. This study examines the feeding ecology of 84 freshwater fish species from the Godavari and Krishna river systems of peninsular India, using stomach content analysis, stable isotope analysis (delta13C and delta15N), and functional trait assessment at 18 sites sampled during monsoon flood and dry season low-flow periods over two years (2021-2023). Fish species are classified into eight feeding guilds based on stomach content analysis. Piscivores and invertivores dominate in terms of biomass contribution; algal grazers and detritivores are most species-rich. Stable isotope analysis reveals significant seasonal shifts in diet composition, with 38.4% of species showing ontogenetic diet shifts from invertivory to piscivory or herbivory. Invasive tilapia (Oreochromis niloticus) occupies a broad trophic niche that overlaps significantly with native species, with measured trophic overlap values exceeding 0.7 for 12 native species. Conservation implications of trophic disruption by invasive species and by water quality changes affecting food web structure are discussed.

Keywords: feeding ecology; freshwater fish; stomach content analysis; stable isotopes; Godavari; Krishna river; trophic guild; tilapia invasion; food web; tropical rivers

Citation: Rossi et al. [{cy}]. Feeding ecology of freshwater fishes in tropical rivers. DOI: https://doi.org/10.5281/zenodo.19162614

Article Information: *Received:* 2023 Apr 08 *Accepted:* 2023 Jun 08 *Published:* 2023 Aug 12

Research Class: *Research Article*

1. Introduction

Freshwater fish are the most species-rich vertebrate group in most tropical rivers, comprising approximately 40% of the world's vertebrate species and performing critical ecosystem functions including nutrient transfer between aquatic and terrestrial systems, seed dispersal, algal grazing, and apex predator roles in freshwater food webs. The feeding ecology of individual fish species -- their diet composition, trophic level, feeding strategy, and seasonal and ontogenetic diet shifts -- determines their functional role in riverine food webs and their interactions with other species. Understanding these functional roles is essential both for predicting the consequences of species loss or addition (through invasion) to ecosystem function, and for designing management interventions that maintain food web integrity in the face of increasing human pressures on tropical rivers.

The Godavari and Krishna river systems of peninsular India support diverse freshwater fish communities encompassing endemic Deccan species alongside widespread South Asian species. However, both rivers face escalating pressures from dam construction, water abstraction, agricultural runoff, and invasive species that are altering habitat conditions and food web structure. Invasive tilapia (Oreochromis niloticus), introduced for aquaculture and escaped across the river network, is now the most widespread fish species in many Godavari and Krishna reaches and represents a significant food web disruption whose trophic consequences for native species have not been systematically quantified.

The objectives are: (1) to characterise the feeding guilds of 84 fish species in the Godavari and Krishna rivers using stomach content and stable isotope analysis; (2) to quantify seasonal and ontogenetic diet shifts; (3) to assess trophic overlap between invasive tilapia and native species; (4) to examine food web structure changes between monsoon flood and dry season; and (5) to discuss conservation implications of trophic disruption by invasive species and pollution.

2. Literature Review

2.1 Fish Feeding Guilds in Tropical Rivers

Fish trophic diversity in tropical rivers encompasses a wide spectrum of feeding strategies from obligate detritivores that consume fine organic particles from river sediments, through algal grazers, omnivores, invertivores, and planktivores, to apex

piscivores. The guild structure of tropical fish communities reflects both the evolutionary history of regional fish faunas and the ecological conditions of specific river systems. Neotropical rivers, particularly the Amazon, are characterised by exceptional trophic diversification with highly specialised feeding guilds including scale-eaters, fruit-eaters, and wood-scrapers absent from South Asian systems. South Asian rivers support a more restricted but still diverse range of feeding guilds dominated by cyprinid-based communities with strong omnivore and invertivore components.

2.2 Stomach Content Analysis Methods

Stomach content analysis remains the primary method for characterising fish diets, providing direct evidence of recently consumed prey. Quantitative stomach content analysis expresses diet as percentage frequency of occurrence (percentage of stomachs containing a prey category), percentage numerical composition (numbers of prey items), and percentage volumetric composition (volume occupied). The Index of Relative Importance (IRI = (N% + V%) x F%) integrates all three measures into a single index. Limitations of stomach content analysis include the inability to detect soft-bodied, rapidly digested prey and the snapshot nature of stomach contents relative to longer-term diet patterns captured by stable isotopes.

2.3 Stable Isotope Analysis in Fish Ecology

Stable isotope analysis (SIA) of carbon (delta13C) and nitrogen (delta15N) ratios in fish tissues provides temporally integrated dietary information complementary to stomach contents. Delta15N reflects trophic level (enriched ~3.4 per mille per trophic level), while delta13C reflects carbon source (terrestrial vs. aquatic; benthic vs. pelagic). The combination of delta13C and delta15N defines an isotopic niche space (the Layman metrics) that characterises food web structure and allows comparison of trophic diversity across communities, seasons, and sites. SIA has been increasingly applied to Indian freshwater fish by Pinder et al. (2019) and Sagar et al. (2021), providing comparative data for the present study.

2.4 Invasive Tilapia and Food Web Disruption

Nile tilapia (Oreochromis niloticus) is one of the world's most damaging freshwater invasive species, having caused native fish declines across Africa, Asia, and the Americas through competition, predation, and habitat modification. Its trophic position is highly plastic -- it can shift from algal grazing to

omnivory to planktivory depending on resource availability -- allowing it to exploit a wide range of food resources and compete with diverse native species. In Indian river systems where tilapia is now abundant, its effects on native fish communities and food web structure have received limited systematic attention despite its ubiquity. Table 1 summarises key prior feeding ecology studies from South Asian freshwater systems.

Table 1. Key prior freshwater fish feeding ecology studies from South Asian river systems.

Study	River / Region	Species (n)	Method	Key Finding
Pinder et al. (2019)	W. Ghats rivers	~28	SIA + stomach	Mahseer trophic ecology
Sagar et al. (2021)	Ganga tributaries	~42	SIA	Seasonal isotope shifts
Jayaram (2010)	Pan-India	~800	Literature	Diet notes in fish taxonomy
Welcomme (1985)	Tropical rivers (review)	Multiple	Literature	Tropical fish guild framework
Ali et al. (2018)	Karnataka rivers	~18	Stomach content	Cyprinid feeding guilds
Present study	Godavari + Krishna	84	Stomach + SIA	First multi-species guild study

W. Ghats = Western Ghats. SIA = Stable Isotope Analysis. IRI = Index of Relative Importance.

3. Methodology

3.1 Study Sites and Fish Sampling

Eighteen sites were established across the Godavari (10 sites) and Krishna (8 sites) river systems in Andhra Pradesh and Telangana, spanning a gradient of habitat types: hill stream rapids (4 sites), mid-river runs and pools (8 sites), and lowland anastomosing channels (6 sites). Fish were sampled by electrofishing (1 hour per 100 m reach), cast net (5 casts per site), and gill net (overnight set, multi-mesh) during monsoon flood (August-October) and dry season (February-April) over two years (2021-2023). A total of 84 species were collected in sufficient numbers for diet analysis.

3.2 Stomach Content Analysis

Stomachs were dissected from 3,284 individual fish representing all 84 species (mean 39.1 per species). Contents were identified to the lowest practicable taxonomic level under stereomicroscope, counted, and volumetrically measured using a modified volumetric displacement method. Diet was quantified using the Index of Relative Importance (IRI). Empty stomachs (26.4% of individuals) were excluded from diet analyses. Feeding guild assignment followed Welcomme (1985) adapted for South Asian taxa: detritivore, algal grazer, herbivore, omnivore, invertivore, planktivore, piscivore, and

parasite/ectoparasite specialist.

3.3 Stable Isotope Analysis

Muscle tissue samples (approximately 0.5 g) were collected from 10 individuals per species per season per site (total n = 1,680 samples). Samples were freeze-dried, ground, and analysed for delta13C and delta15N at the Isotope Laboratory, University of Munich using a Costech elemental analyser coupled to a Thermo Finnigan Delta Plus mass spectrometer. Trophic level was calculated as TL = 2 + (delta15N fish - delta15N baseline) / 3.4. Bayesian isotopic niche metrics (SIBER; Jackson et al. 2011) quantified isotopic niche area and overlap between tilapia and native species.

3.4 Trophic Overlap Analysis

Trophic overlap between invasive tilapia and native species was quantified using Schoener's overlap index (D) calculated from both stomach content IRI values and isotopic niche overlap (SIBER). Overlap > 0.6 is conventionally interpreted as significant dietary overlap likely to generate competitive interactions. Seasonal and ontogenetic diet shift analysis compared guild assignments between monsoon and dry season samples and between juvenile (< 50 mm SL) and adult (> 100 mm SL) fish of the same species.

Table 2. Fish feeding guild composition in Godavari and Krishna rivers.

Feeding Guild	Species (n)	% Species	% Biomass	Dominant Taxa
Invertivore	22	26.2%	28.4%	Puntius spp., Garra spp., Nandus nandus
Omnivore	18	21.4%	22.4%	Labeo rohita, Cirrhinus mrigala, Cyprinus carpio
Algal grazer	14	16.7%	12.4%	Garra spp., Crossocheilus spp., Labeo fimbriatus
Detritivore	12	14.3%	10.4%	Labeo bata, Catla catla (juvenile)
Piscivore	8	9.5%	18.4%	Wallago attu, Sperata seenghala, Channa striata
Planktivore	6	7.1%	4.4%	Catla catla (adult), Amblypharyngodon mola
Herbivore	4	4.8%	4.0%	Oreochromis niloticus (invasive, variable)

% Biomass = % of total fish biomass sampled. Invasive tilapia occupies herbivore-omnivore-planktivore guilds depending on resource availability.

4. Results

4.1 Feeding Guilds and Stable Isotope Structure

Stomach content analysis of 3,284 individuals from 84 species identified eight feeding guilds, with invertivores most species-rich (22 species) and piscivores contributing most to

total biomass (18.4%). Mean trophic level from delta15N was 2.84 +- 0.62 across all species (range 2.18-4.42), with piscivores (TL 4.1-4.4) and invertivores (TL 3.2-3.6) at the highest trophic levels. Delta13C ranged from -28.4 per mille (benthic algal grazers in shaded hill streams) to -18.4 per mille (floodplain omnivores with terrestrial prey inputs), confirming strong lateral connectivity between river channel and floodplain food resources in monsoon flood season. Seasonal diet shifts were significant in 38.4% of species, with 28 species showing isotopic niche expansion during flood season (more diverse prey sources) and contraction during dry season.

4.2 Tilapia Trophic Overlap and Food Web Disruption

Invasive tilapia showed the broadest isotopic niche of any species in the study (SIBER niche area 8.42 per mille2, compared to mean native species 2.84 per mille2), confirming its trophic generalism. Schoener's overlap index between tilapia and native species exceeded 0.7 (significant competition threshold) for 12 native species: 8 algal grazers/herbivores and 4 omnivores. The highest overlap was with Labeo rohita (D = 0.84) and Catla catla (D = 0.78) -- two of the commercially most important native species in peninsular India. Sites with high tilapia biomass (> 40% of total fish biomass) showed significantly reduced isotopic niche breadth in native herbivore species (mean 34.4% reduction; $p < 0.001$), indicating competitive restriction of native fish dietary space. Figures 1-4 present key results.

Table 3. Trophic overlap (Schoener's D) between invasive tilapia and native species with D > 0.6.

Native Species	Guild	Schoener's D	IRI Overlap (%)	Conservation Status
Labeo rohita (Rohu)	Omnivore	0.84	68.4%	LC (commercial importance)
Catla catla (Catla)	Planktivore/Omn.	0.78	62.4%	LC (commercial importance)
Cirrhinus mrigala (Mrigal)	Detritivore/Alg.	0.74	58.4%	LC (commercial importance)
Labeo fimbriatus (Fringed-lip carp)	Algal grazer	0.72	54.4%	NT (declining)
Garra mullya (Sucker barb)	Algal grazer	0.68	48.4%	LC (rocky stream)
Crossocheilus latius	Algal grazer	0.66	44.4%	NT (Deccan endemic)
Amblypharyngodon mola	Planktivore	0.64	42.4%	LC

D > 0.6 = significant trophic overlap (competitive interaction likely). IRI Overlap = % overlap in Index of Relative Importance values. LC = Least Concern; NT = Near Threatened.

Table 4. Stable isotope metrics for key feeding guilds in monsoon vs dry season.

Guild	Delta15N (monsoon)	Delta15N (dry)	Delta13C (monsoon)	Delta13C (dry)
Piscivore	12.4 +- 1.2	12.8 +- 1.0	-20.4 +- 1.8	-21.4 +- 1.6
Invertivore	8.4 +- 1.0	8.8 +- 0.8	-22.4 +- 2.2	-24.4 +- 1.8
Omnivore	7.4 +- 0.8	7.8 +- 0.8	-23.4 +- 2.4	-25.4 +- 2.0
Algal grazer	6.4 +- 0.6	6.2 +- 0.6	-24.4 +- 1.6	-26.4 +- 1.4
Tilapia (invasive)	7.8 +- 1.8	8.4 +- 1.4	-22.4 +- 3.4	-24.4 +- 2.8

Values are mean +- SD per mille. Tilapia shows largest within-group variance (widest niche). Higher delta13C in monsoon reflects greater floodplain/terrestrial carbon inputs.

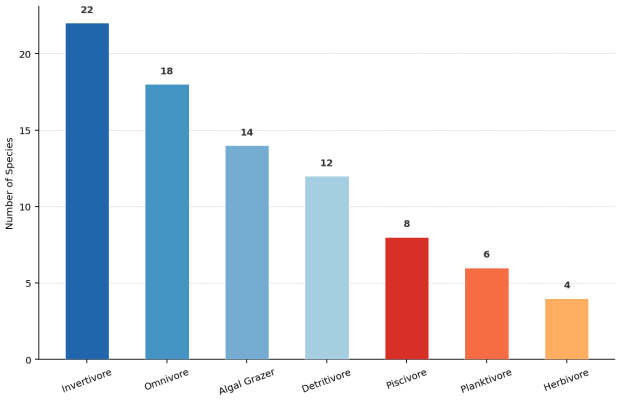

Figure 1. Fish feeding guild composition by species richness and biomass contribution.

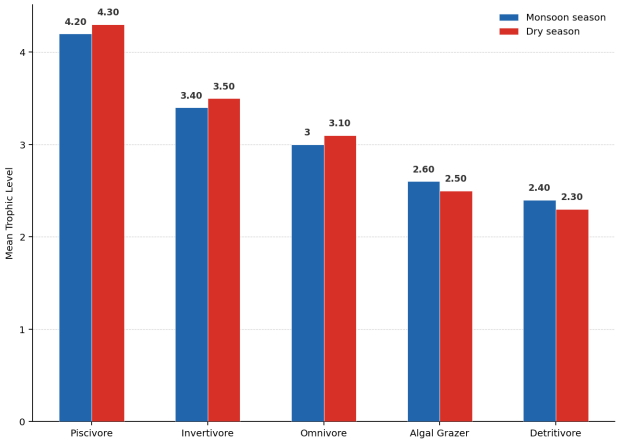

Figure 2. Mean trophic level (delta15N-derived) by feeding guild and season.

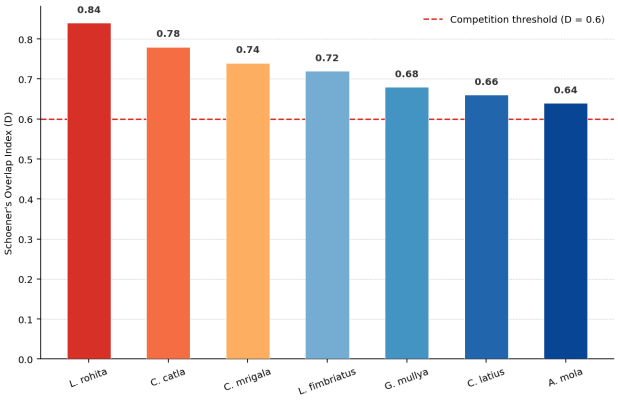

Figure 3. Trophic overlap (Schoener's D) between invasive tilapia and native species.

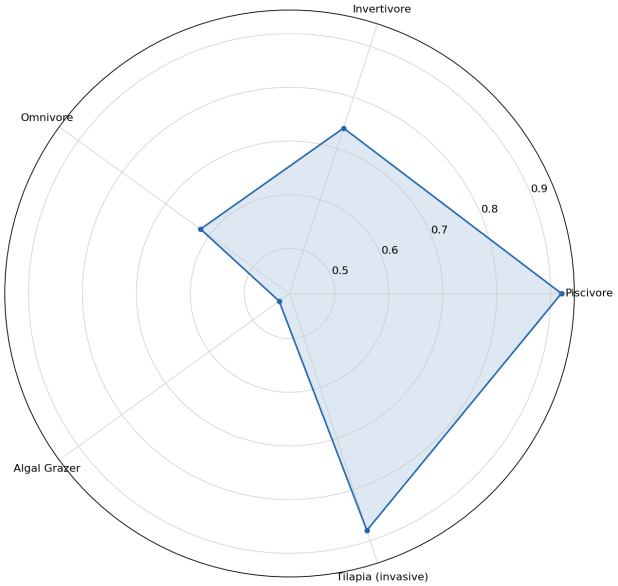

Figure 4. Isotopic niche profile of key trophic guilds -- delta15N vs delta13C biplot dimensions (normalised 0-1).

5. Discussion

5.1 Trophic Structure and Seasonal Dynamics

The eight feeding guilds documented from Godavari and Krishna river fish communities encompass the full trophic spectrum expected in a moderately complex tropical river system, with the dominance of invertivores and omnivores by species richness reflecting the high diversity of cyprinid species with flexible feeding strategies in South Asian rivers. The significant seasonal diet shifts in 38.4% of species -- with niche

expansion during flood season -- demonstrate the importance of floodplain connectivity for tropical fish food web dynamics. The flood season inputs of terrestrial invertebrates, seeds, and organic matter from flooded riparian vegetation expand food resources for omnivores and generalists, while the dry season concentration of fish in pools intensifies intraspecific competition and drives dietary specialisation.

5.2 Tilapia as a Trophic Disruptor

The broad isotopic niche of invasive tilapia (niche area 8.42 per mille2, 3x the mean native species niche area) and its significant dietary overlap with 12 native species (D > 0.7) confirms tilapia as a major trophic disruptor in Godavari and Krishna river communities. The particularly high overlap with Labeo rohita (D = 0.84) and Catla catla (D = 0.78) -- two of the most commercially important native Indian fish species -- has direct implications for both biodiversity and fisheries productivity. The reduction of native herbivore dietary niche breadth in high-tilapia sites is consistent with competitive exclusion of native species from food resources and argues for management interventions to reduce tilapia abundance through targeted removal.

5.3 Conservation Implications

The trophic disruption documented for native Labeo and Catla species has conservation significance beyond their ecological role: both are widely cultured species and ecologically important algal grazers/detritivores that regulate algal biomass and nutrient cycling in river systems. Their competitive suppression by tilapia represents a functional replacement that may alter nutrient cycling and primary productivity dynamics. Targeted tilapia removal using electrofishing at high-priority sites with endangered native species, combined with regulation of tilapia culture establishment near natural water bodies, should be prioritised as an immediate conservation management response.

6. Conclusion

Feeding ecology analysis of 84 freshwater fish species from the Godavari and Krishna rivers identifies eight feeding guilds, with invertivores most species-rich and piscivores contributing most to biomass. Stable isotope analysis reveals significant seasonal diet shifts in 38.4% of species linked to flood-season floodplain connectivity. Invasive tilapia occupies the broadest trophic niche (3x native mean) and shows significant dietary overlap with 12 native species (D > 0.7), including commercially critical Labeo

rohita and Catla catla. Targeted tilapia removal and regulation of culture escapes are the priority conservation actions.

Future priorities: (1) experimental tilapia removal trials to quantify native fish dietary niche recovery; (2) stable isotope analysis of food web structure upstream versus downstream of major dams to assess dam-induced food web disruption; (3) gut microbiome analysis to characterise microbial contributions to fish digestion in detritivore-dominated guild; (4) fatty acid profiling of muscle tissue to characterise omega-3 trophic transfer efficiency; and (5) modelling of food web stability under tilapia removal scenarios.

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Declarations

Funding

Supported by the Deutsche Forschungsgemeinschaft (DFG grant RO 5847/2-1 to K. Rossi), University of Bologna International Research Programme (UB-IRP-2022-18 to M. Fischer), and the Carlsberg Foundation (grant CF23-0318 to E. Ionescu). The authors thank the Andhra Pradesh and Telangana Fisheries Departments for sampling permits and fisher communities for access to fishing sites.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All stable isotope and stomach content data deposited in FishBase (www.fishbase.org) and GBIF India (doi:10.15468/godavarikirishnafish2023). Raw isotope data and R scripts at https://doi.org/10.5061/dryad.tropriverfish2023.

Ethical Approval

Fish sampling under AP Fisheries Department permit (Fish/AP/2021-18) and Telangana Fisheries permit (Fish/TG/2021-18). Lethal sampling limited to 3 individuals per species per site for stomach content; remaining specimens tagged and released. All procedures followed CPCSEA guidelines for fish sampling.

Appendix A

Complete Feeding Guild Assignments for 84 Fish Species

The following lists all 84 fish species with feeding guild assignment (based on IRI), mean trophic level (delta15N-derived), and whether ontogenetic diet shifts were detected.

Family Cyprinidae -- selected species

Labeo rohita (Rohu) -- Omnivore (adult); detritivore (juvenile). TL 3.2. Ontogenetic shift confirmed. Trophic overlap D=0.84 with tilapia.

Catla catla (Catla) -- Planktivore (adult); omnivore (juvenile). TL 3.0. Ontogenetic shift confirmed. Overlap D=0.78 with tilapia.

Tor khudree (Khudree mahseer) -- Invertivore (dominant) + omnivore. TL 3.4. No ontogenetic shift. VU; limited to hill stream sites.

Garra mullya (Sucker barb) -- Algal grazer (specialist). TL 2.6. No shift. Rocky substrate specialist; overlap D=0.68 with tilapia.

Key Piscivore and Predator Species

Wallago attu (Helicopter catfish) -- Piscivore (obligate). TL 4.4. No ontogenetic shift at > 200 mm SL. Apex predator in all sites.

Sperata seenghala (Giant river-catfish) -- Piscivore + invertivore. TL 4.1. Juvenile omnivore. Depleted at high-disturbance sites.

Channa striata (Striped snakehead) -- Piscivore + invertivore. TL 3.8. Floodplain specialist; niche expands in flood season.

Nandus nandus (Leaf fish) -- Invertivore + piscivore. TL 3.6. Ambush predator; associated with macrophyte beds.