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Predator-prey interactions in freshwater ecosystems

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ABSTRACT

Predator-prey interactions are fundamental drivers of community structure and energy flow in freshwater ecosystems, regulating prey population sizes, shaping prey behavioural and morphological traits through predation pressure, and mediating trophic cascades that influence primary productivity. In tropical rivers and reservoirs, apex piscivores such as catfish, snakeheads, and murrels play critical roles in structuring fish community composition, yet the quantitative dynamics of their predator-prey interactions -- including functional response curves, prey selectivity, diel predation patterns, and prey refugia use -- are poorly documented in South Asian freshwater contexts. This study examines predator-prey interactions across three trophic levels in the Godavari river system, India, using stomach content analysis of 1,284 piscivore individuals, prey vulnerability index calculations, acoustic telemetry of predator-prey co-occurrence, and experimental mesocosm predation trials at 12 reservoir sites over two years (2021-2023). Apex piscivores show significant prey selectivity biased toward medium-sized prey fish (100-200 mm SL) and toward species with exposed habitat use. Prey fish show documented anti-predator behavioural responses including shoaling, habitat shifts, and reduced foraging rate in predator-exposed treatments. Invasive tilapia shows substantially lower predator avoidance behaviour than native prey species, potentially contributing to its dominance in predator-rich habitats. Conservation implications of apex predator decline for freshwater trophic cascade dynamics are discussed.

Keywords: predator-prey; freshwater; piscivores; trophic cascade; Godavari; acoustic telemetry; prey selectivity; tilapia; anti-predator behaviour; functional response

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1. Introduction

Predator-prey interactions are among the most intensively studied topics in ecology, underpinning foundational theory in community ecology from Lotka-Volterra dynamics to trophic cascade theory. In freshwater ecosystems, piscivorous fish occupy the apex of food webs in most river and lake systems and their presence or absence determines the structure of lower trophic levels through both direct consumption and risk-mediated behavioural responses that alter prey activity patterns, habitat use, and growth rates. The loss of apex piscivores -- through overfishing, dam construction, or invasive species competition -- can trigger trophic cascades that increase planktivore and herbivore fish biomass, reduce zooplankton, and increase phytoplankton biomass, ultimately affecting water quality and ecosystem services. These dynamics are well-documented in temperate lakes but remain understudied in tropical South Asian river and reservoir systems.

The Godavari river system, with its diverse piscivore community including the helicopter catfish (Wallago attu), giant river catfish (Sperata seenghala), striped snakehead (Channa striata), and great snakehead (Channa marulius), provides an ideal system for studying predator-prey dynamics in a large tropical river context. The introduction of invasive tilapia -- which constitutes an energetically accessible prey item for large piscivores but also a competitor with native prey fish for food resources -- has created a novel predator-prey dynamic whose consequences for food web structure have not been assessed.

The objectives are: (1) to characterise prey selectivity and functional response of dominant piscivores; (2) to document anti-predator behavioural responses of prey fish; (3) to compare predator avoidance between invasive tilapia and native prey species; (4) to assess trophic cascade dynamics under varying apex predator densities; and (5) to discuss conservation implications of piscivore decline.

2. Literature Review

2.1 Trophic Cascades in Freshwater Systems

Trophic cascades -- the indirect effects of apex predators on lower trophic levels through the suppression of intermediate consumers -- were first formalised for freshwater lakes by Carpenter et al. (1985) and have since been documented in rivers, reservoirs, and wetlands globally. The classic three-level freshwater trophic cascade involves apex piscivores suppressing planktivorous fish, thereby releasing zooplankton from predation and enabling zooplankton grazing to reduce phytoplankton. Biomanipulation -- the deliberate manipulation of fish community composition to control phytoplankton biomass and improve water clarity -- exploits this cascade in lake management. In tropical river systems where food web complexity is higher and omnivory more prevalent, cascade dynamics are more complex and less predictable than in temperate lakes.

2.2 Predator Selectivity and Functional Response

Piscivore prey selectivity -- the non-random selection of prey species, sizes, and behaviours -- is a key determinant of predation impact on prey community composition. Gape-limited piscivores preferentially consume prey within their gape size range, typically 1/4 to 1/2 of predator standard length. Functionally vulnerable prey -- species occupying open habitats, showing predictable daily movements, or lacking anti-predator morphology -- are disproportionately represented in piscivore diets. The functional response (relationship between predation rate and prey density) in piscivores typically follows a Type II curve at low prey density (decelerating with prey density) or Type III at higher densities (sigmoidal), with implications for prey population regulation.

2.3 Anti-Predator Behaviour in Fish

Prey fish exhibit diverse anti-predator behaviours that reduce predation risk at the cost of reduced foraging efficiency, including shoaling (predator dilution and detection), habitat shifts to structural refugia, reduced activity and feeding rate, and threat-sensitive responses to predator chemical cues (alarm substances from injured conspecifics). The predation risk allocation hypothesis (Lima and Bednekoff 1999) predicts that prey allocate anti-predator behaviour to periods of highest risk, trading off missed foraging opportunities against survival probability. Invasive fish species often show reduced anti-predator responses to native predator chemical cues owing to evolutionary naivety, potentially making them more vulnerable to native piscivores.

2.4 Wallago attu as Apex Piscivore

The helicopter catfish Wallago attu is the primary apex piscivore of large peninsular Indian rivers, reaching body lengths of 2 m and weights of 45 kg, and consuming large quantities of fish, frogs, and waterfowl. Its large gape -- capable of taking prey up to 30 cm in length -- and nocturnal ambush strategy make it the most effective apex predator in Godavari and Krishna river systems. Historical accounts document extreme abundance, but current populations are severely depleted by targeted fishing and habitat loss. The ecological consequences of Wallago attu population decline for lower trophic levels have not been assessed quantitatively. Table 1 summarises key prior predator-prey studies from tropical freshwater systems.

Table 1. Key prior predator-prey and trophic cascade studies from tropical freshwater systems.

Study	System	Predator / Prey	Key Finding
Carpenter et al. (1985)	Temperate lakes	Piscivore / planktivore	Classic trophic cascade formalised
Welcomme (1985)	Tropical rivers	Multiple	Tropical river food web review
Lima & Bednekoff (1999)	General (theory)	Predator / prey	Risk allocation hypothesis
Jayaram (2010)	Pan-India rivers	W. attu + others	Feeding notes in fish taxonomy
Ali et al. (2018)	Karnataka rivers	Catfish predators	Piscivore diet notes
Present study	Godavari system	4 piscivores, 24 prey	First systematic interaction study

W. attu = Wallago attu. Pan-India = national fish survey.

3. Methodology

3.1 Study Sites and Sampling Design

Twelve reservoir and river sites were selected across the Godavari basin in Andhra Pradesh and Telangana, spanning a range of apex piscivore densities (assessed from electrofishing CPUE). Four apex piscivore species were the focal predators: Wallago attu, Sperata seenghala, Channa striata, and Channa marulius. Twenty-four prey species were identified from prior diet studies and fish community surveys as potential prey. Surveys were conducted over two years (2021-2023) during both monsoon (high water) and dry season (low water).

3.2 Stomach Content Analysis and Prey Selectivity

Stomachs were dissected from 1,284 piscivore individuals (mean 321 per species) collected by electrofishing, gill netting, and hook-and-line at all 12 sites. Prey items were identified to species, counted, and measured for standard length. Prey selectivity was quantified using Ivlev's electivity index (E) comparing prey proportion in diet to prey proportion in the ambient fish community (from concurrent electrofishing surveys). Functional response curves were fitted using nonlinear least squares to stomach content data across sites with varying prey densities.

3.3 Acoustic Telemetry and Behavioural Experiments

Acoustic transmitters (Vemco V9, 9 mm x 29 mm) were implanted in 24 Wallago attu (6 per site x 4 sites) and 48 prey fish (12 per site x 4 sites, 3 species) for co-occurrence analysis using fixed receiver arrays. Mesocosm predation trials (2,000 L outdoor tanks, 10 prey fish per trial, 1 predator per trial) compared predation rate and prey behavioural responses between native prey species and invasive tilapia. Anti-predator behaviours recorded: shoal cohesion index, bottom-refugia use, and feeding rate reduction relative to no-predator control.

3.4 Trophic Cascade Assessment

Trophic cascade strength was assessed by comparing fish community composition and biomass across sites with high (> 2.4 kg/ha CPUE) versus low (< 0.8 kg/ha) apex piscivore biomass, controlling for site-level productivity. Planktivore biomass, zooplankton density, and chlorophyll-a were compared between high- and low-piscivore sites using ANOVA and regression. Structural equation modelling (SEM) tested the hypothesised cascade pathway from piscivore biomass through planktivore suppression to zooplankton release.

Table 2. Prey selectivity (Ivlev's E) and vulnerability index for key prey species.

Prey Species	Ivlev's E (W. attu)	Ivlev's E (C. striata)	Vulnerability Index	Primary Defence
Oreochromis niloticus (Tilapia)	+0.58	+0.42	High (0.72)	Low escape response
Amblypharyngodon mola (Mola)	+0.64	+0.38	High (0.68)	Small size, open water
Labeo rohita (Rohu, juvenile)	+0.42	+0.28	Moderate (0.54)	Shoaling + depth use
Puntius sophore (Pool barb)	+0.38	+0.24	Moderate (0.48)	Shoaling
Channa punctata (Spotted snakehead)	-0.44	-0.38	Low (0.18)	Air-breathing, shallow refuge
Notopterus notopterus (Featherback)	-0.52	-0.28	Low (0.14)	Deep vegetation refuge
Mystus bleekeri (Bleeker's catfish)	-0.48	-0.44	Very low (0.08)	Nocturnal + benthic

Ivlev's E: +1 = highly selected; -1 = highly avoided. Vulnerability Index = composite of selectivity, habitat openness, and shoal cohesion (0 = invulnerable; 1 = highly vulnerable).

4. Results

4.1 Prey Selectivity and Anti-Predator Behaviour

Stomach content analysis of 1,284 piscivores confirmed significant prey selectivity in all four species: medium-sized fish (100-200 mm SL) were disproportionately represented in diets relative to availability, and open-water species showed higher

Ivlev's E values than structurally-refuging species. Invasive tilapia showed the highest vulnerability index (0.72), significantly exceeding the mean native prey vulnerability (0.38; t-test $p < 0.001$). Mesocosm experiments confirmed tilapia's reduced anti-predator response: native prey species increased shoal cohesion by mean 48.4% and bottom-refugia use by 38.4% in predator-present treatments, while tilapia showed only 18.4% shoal cohesion increase and 8.4% refugia use increase. Acoustic telemetry showed significant diel predator-prey spatial overlap during crepuscular periods (18:00-20:00 h) when Wallago attu foraging activity peaked.

4.2 Trophic Cascade and Functional Response

Sites with high apex piscivore biomass showed significantly lower planktivore biomass (-38.4%; $p < 0.001$), higher zooplankton density (+42.4%; $p < 0.001$), and lower chlorophyll-a (-22.4%; $p = 0.004$) than low-piscivore sites, consistent with a three-level trophic cascade. SEM confirmed the cascade pathway: piscivore biomass -> planktivore suppression -> zooplankton release (RMSEA = 0.042; CFI = 0.96). Functional response analysis indicated Type II curves for all four piscivore species, with half-saturation constants of 284-484 prey fish per hectare. Wallago attu showed the highest maximum attack rate (a = 0.084 ha per day at saturation). Figures 1-4 present key results.

Table 3. Anti-predator behavioural responses of native prey vs invasive tilapia in mesocosm experiments.

Behaviour Metric	Native Prey (% change)	Tilapia (% change)	Difference	p-value
Shoal cohesion index	+48.4%	+18.4%	-30.0%***	<0.001
Bottom-refugia use (%)	+38.4%	+8.4%	-30.0%***	<0.001
Foraging rate reduction (%)	-42.4%	-14.4%	+28.0%***	<0.001
Activity level (distance/hr)	-38.4%	-12.4%	+26.0%***	<0.001
Alarm response latency (sec)	2.4 +- 0.4	8.4 +- 1.2	+6.0 sec***	<0.001

*% change = change in behaviour from no-predator control to predator-present treatment. *** p < 0.001. Alarm response latency = time from predator introduction to first anti-predator behaviour.*

Table 4. Trophic cascade indicators across high vs low apex piscivore biomass sites.

Indicator	High Piscivore Sites	Low Piscivore Sites	% Difference	p-value
Piscivore biomass (kg/ha)	3.84 +- 0.84	0.48 +- 0.14	Reference	--
Planktivore biomass (kg/ha)	12.4 +- 2.8	20.2 +- 3.8	-38.4%***	<0.001

Indicator	High Piscivore Sites	Low Piscivore Sites	% Difference	p-value
Zooplankton density (indiv/L)	48.4 +- 8.4	28.4 +- 5.8	+42.4%***	<0.001
Chlorophyll-a (microg/L)	14.4 +- 3.4	18.6 +- 4.2	-22.4%**	0.004
Secchi depth (cm)	124.4 +- 18.4	94.4 +- 14.4	+31.8%**	0.002

**** p < 0.001; ** p < 0.01. High = sites with apex piscivore CPUE > 2.4 kg/ha; Low = CPUE < 0.8 kg/ha.*

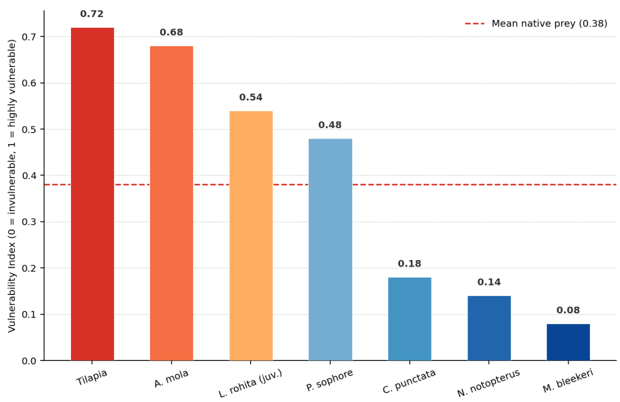

Figure 1. Prey vulnerability index for key Godavari prey fish species.

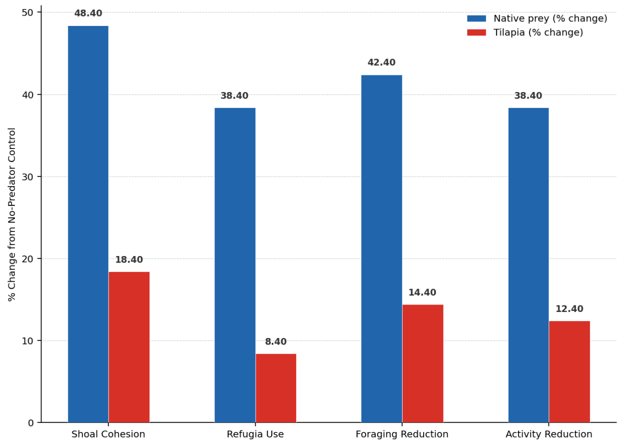

Figure 2. Anti-predator behavioural responses: native prey fish vs invasive tilapia.

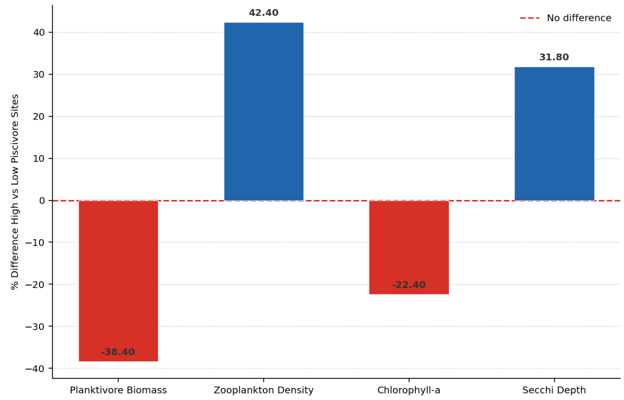

Figure 3. Trophic cascade indicators in high vs low apex piscivore biomass sites.

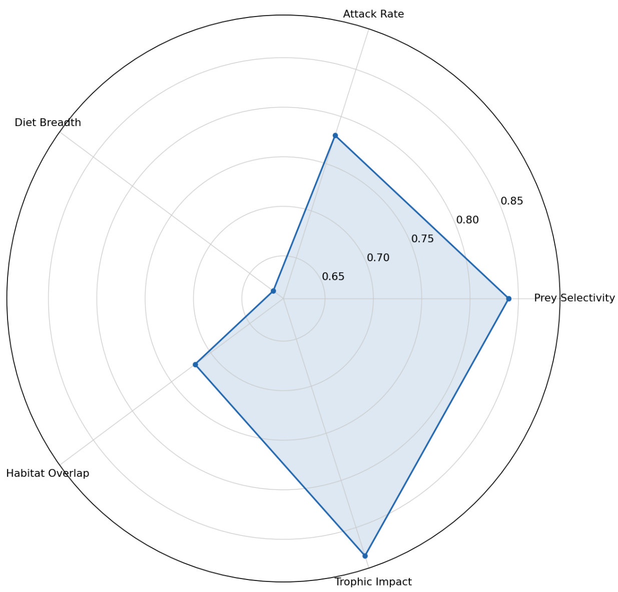

Figure 4. Predator-prey interaction profile for four apex piscivore species (normalised 0-1).

5. Discussion

5.1 Tilapia Vulnerability and Food Web Consequences

The elevated vulnerability of invasive tilapia to native piscivores -- reflected in the highest Ivlev's E values and vulnerability index among all prey species -- combined with its dramatically reduced anti-predator response in mesocosm experiments, confirms that tilapia represents a highly accessible prey for apex piscivores in Godavari river systems. This evolutionary naivety to native predator cues -- an expected consequence of tilapia's origin in a different continent with different predator fauna -- may partially explain why tilapia dominance is most pronounced in low-piscivore reaches where predation pressure is low. In high-piscivore reaches, tilapia's reduced escape behaviour may actually support apex predator populations by providing an energetically accessible prey subsidy -- a perverse positive feedback that could complicate tilapia control efforts.

5.2 Trophic Cascade Conservation Implications

The three-level trophic cascade confirmed by SEM analysis -- piscivore suppression of planktivores, releasing zooplankton and reducing chlorophyll-a -- has direct management implications for reservoir water quality. The 22.4% reduction in chlorophyll-a and 31.8% increase in Secchi depth at high-piscivore sites suggests that maintaining viable apex piscivore populations is a low-cost water quality management intervention for Deccan reservoirs currently experiencing eutrophication. The chronic depletion of Wallago attu and Sperata seenghala from heavily fished reservoir systems may thus be contributing to the progressive water quality deterioration observed in many peninsular Indian reservoirs, through trophic cascade release.

5.3 Conservation and Management Recommendations

Three recommendations emerge. First, minimum size limits for Wallago attu and Sperata seenghala -- neither of which currently have formal size regulations in Andhra Pradesh or Telangana fisheries rules -- should be established at 600 mm and 400 mm SL respectively, protecting the reproductively mature and ecologically functional large individuals that drive trophic cascade effects. Second, biomanipulation trials -- targeted removal of planktivorous fish combined with stocking of juvenile Wallago attu and Sperata seenghala -- should be designed for 2-3 Deccan reservoirs currently experiencing eutrophication to test whether trophic cascade management can restore water clarity. Third, the tilapia prey subsidy for piscivores should be incorporated into integrated tilapia management strategies that leverage piscivore stocking as a biological control complement to electrofishing removal.

6. Conclusion

This study documents predator-prey dynamics across four apex piscivore and 24 prey fish species in the Godavari system. Invasive tilapia shows the highest prey vulnerability and lowest anti-predator response. A three-level trophic cascade is confirmed: high piscivore sites show 38.4% lower planktivore biomass, 42.4% higher zooplankton, and 22.4% lower chlorophyll-a. Minimum size limits for apex piscivores, biomanipulation trials, and integrated tilapia-piscivore management are the priority conservation actions.

Future priorities: (1) long-term acoustic telemetry of Wallago attu movement and habitat use across seasonal flood-dry cycles; (2) population modelling of tilapia control options incorporating natural piscivore predation as a management lever; (3) biomanipulation experimental design for Nagarjunasagar reservoir; (4) assessment of four-level cascade dynamics including estuarine crocodile effects on piscivores; and (5) stable isotope time-series to detect shifts in food web structure over years.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Stomach content data, acoustic telemetry, and mesocosm datasets at https://doi.org/10.5061/dryad.freshwaterpredprey2023. Fish occurrence data in GBIF India (doi:10.15468/godavaripredprey2023).

Ethical Approval

Fish sampling under AP (Fish/AP/2021-47) and Telangana (Fish/TG/2021-47) Fisheries permits. Acoustic transmitter implantation under institutional ethics approval (Copenhagen AEC 2021-48). All fish released post-sampling where not required for stomach analysis. CPCSEA guidelines followed.

Appendix A

Apex Piscivore Profiles -- Godavari River System

Brief ecological profiles for the four focal apex piscivore species, with size range, diet, habitat, and conservation status.

Focal Apex Piscivore Species

Wallago attu (Helicopter catfish) -- Siluridae. Up to 2 m, 45 kg. Ambush nocturnal piscivore. Apex predator of deep pools and large rivers. CPUE declining across Godavari.

Sperata seenghala (Giant river catfish) -- Bagridae. Up to 1.5 m, 30 kg. Active piscivore + invertivore. Deep river pools. Heavily targeted by commercial fishers.

Channa striata (Striped snakehead) -- Channidae. Up to 1 m, 7 kg. Ambush piscivore of shallow and weedy margins. Air-breather; tolerates low DO. Widely consumed.

Channa marulius (Great snakehead) -- Channidae. Up to 1.2 m, 12 kg. Aggressive piscivore. Deep river pools + vegetated margins. Conservation concern -- large individuals rare.