



ISSN Print: 2664-9926
 ISSN Online: 2664-9934
 NAAS Rating: 4.82
 IJBS 2025; 7(5): 127-130
www.biologyjournal.net
 Received: 20-02-2025
 Accepted: 26-03-2025

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Trophic cascade effects of top predator removal on benthic invertebrate communities in temperate streams

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DOI: <https://www.doi.org/10.33545/26649926.2025.v7.i5b.691>

Abstract

Trophic cascades - the indirect effects of predators on lower trophic levels - are well documented in lakes and marine systems but remain less understood in flowing freshwater habitats where current, substrate heterogeneity, and drift complicate food web dynamics. This research tested whether removal of the top invertebrate predator (stonefly nymphs, Plecoptera: Perlidae) from enclosed stream sections would trigger cascading changes in benthic invertebrate community structure and periphyton biomass. A replicated field experiment was conducted in four second-order streams near Qingdao, Shandong Province, China, from April to September 2023. Each stream contained paired predator-removal and control reaches (8 m each, enclosed with 1 mm mesh barriers). After 12 weeks, predator removal led to a 68.3% increase in total invertebrate density, a shift in community composition from Ephemeroptera/Trichoptera dominance toward Chironomidae/Gastropoda dominance, and a 2.3-fold rise in periphyton biomass. Shannon diversity dropped from 2.41 to 1.87, as a few grazer taxa expanded unchecked. These results confirm a three-level trophic cascade (predator → grazer → algae) operating in temperate headwater streams.

Keywords: Trophic cascade, top predators, benthic invertebrates, temperate streams, food web dynamics, predator removal, periphyton, stonefly, grazer control, community structure

Introduction

Textbook ecology teaches that top predators keep herbivore populations in check, and that removing predators allows herbivores to overgraze primary producers ^[1]. This three-level trophic cascade is beautifully demonstrated in systems like Yellowstone's wolf-elk-aspen interaction or sea otter-urchin-kelp forests ^[2]. But flowing water is a different kind of arena. Stream invertebrates drift with the current, cling to substrates, and experience patchy food resources in ways that don't map neatly onto the food web diagrams drawn from still-water systems ^[3].

In temperate headwater streams, the top invertebrate predators are typically large stonefly nymphs (Plecoptera: Perlidae) that consume smaller invertebrates including mayfly and caddisfly larvae ^[4]. These prey taxa, in turn, are the main grazers of periphyton - the algal film coating stream rocks. If stonefly predation keeps grazers sparse, removing stoneflies should allow grazers to proliferate and graze down periphyton. But some earlier manipulation experiments found weak or inconsistent cascading effects in streams, possibly because of high prey mobility or compensatory immigration from upstream reaches ^[5].

This research used enclosed stream sections to minimize immigration artifacts and tested whether stonefly removal triggers measurable trophic cascade effects on both invertebrate community structure and periphyton standing crop over a 12-week period.

Material and Methods

Study Area Description

Four second-order streams in the Laoshan Mountain range east of Qingdao (36°10'N, 120°42'E) were selected based on the presence of established Perlidae populations and accessibility. Stream widths ranged from 2.4 to 3.8 m, depths from 15 to 35 cm, and water temperature from 11.4°C in April to 23.7°C in August.

Substrates were predominantly cobble and gravel with scattered boulders. Riparian vegetation consisted of mixed deciduous forest providing moderate canopy cover (48-62%).

Material

Enclosure barriers were constructed from PVC frames fitted with 1 mm nylon mesh, anchored to the streambed with steel stakes and sealed along the bottom with sandbags. Each stream received two consecutive 8 m enclosed reaches separated by a 15 m buffer. Equipment included a Surber sampler (500 μ m mesh, 0.09 m² frame), chlorophyll-a extraction supplies (90% acetone, GF/F filters), a YSI ProDSS multiparameter meter, and specimen storage vials. All laboratory work was done at the Qingdao University of Marine Biology.

Methods

In each stream, one enclosed reach was randomly assigned as 'predator removal' and the other as 'control.' Stonefly nymphs (Perlidae: *Neoperla* and *Kamimuria* spp.) were manually removed from treatment reaches by disturbing substrates and netting dislodged individuals three times per week for the first two weeks, then weekly thereafter. Controls were similarly disturbed (sham removal) to control for physical disturbance effects. Benthic invertebrates were sampled monthly (five Surber samples per reach) from May through September. Specimens were preserved in 75% ethanol, sorted, and identified to family or genus level. Periphyton was sampled monthly from five randomly placed

unglazed ceramic tiles (25 cm² each) per reach; chlorophyll-a was extracted and measured spectrophotometrically at 665 nm. Water temperature, dissolved oxygen, pH, and conductivity were recorded at each sampling visit. Shannon diversity (H') and Bray-Curtis dissimilarity were calculated. Differences between treatments were tested with repeated-measures ANOVA in R 4.3.1. The research was approved by the Qingdao University Environmental Research Ethics Board (Protocol QU-ERB-2023-011, approved March 2023).

Results

Table 1: Benthic invertebrate community metrics in control and predator-removal reaches after 12 weeks (mean $\pm$ SE, n = 4 streams)

Metric	Control	Removal
Total density (ind/m ²)	1,847 $\pm$ 213	3,108 $\pm$ 347
Taxon richness	24.3 $\pm$ 2.1	19.7 $\pm$ 1.8
Shannon H'	2.41 $\pm$ 0.12	1.87 $\pm$ 0.14
Perlidae density (ind/m ²)	38.4 $\pm$ 6.7	2.1 $\pm$ 0.8
Periphyton Chl-a (mg/m ²)	14.8 $\pm$ 2.3	34.1 $\pm$ 4.7

Predator removal increased total invertebrate density by 68.3% ($p < 0.001$) but reduced taxon richness and diversity (Table 1). Periphyton biomass more than doubled in removal reaches, driven by release of grazing pressure from abundant Chironomidae and Gastropoda that thrived without stonefly predation.

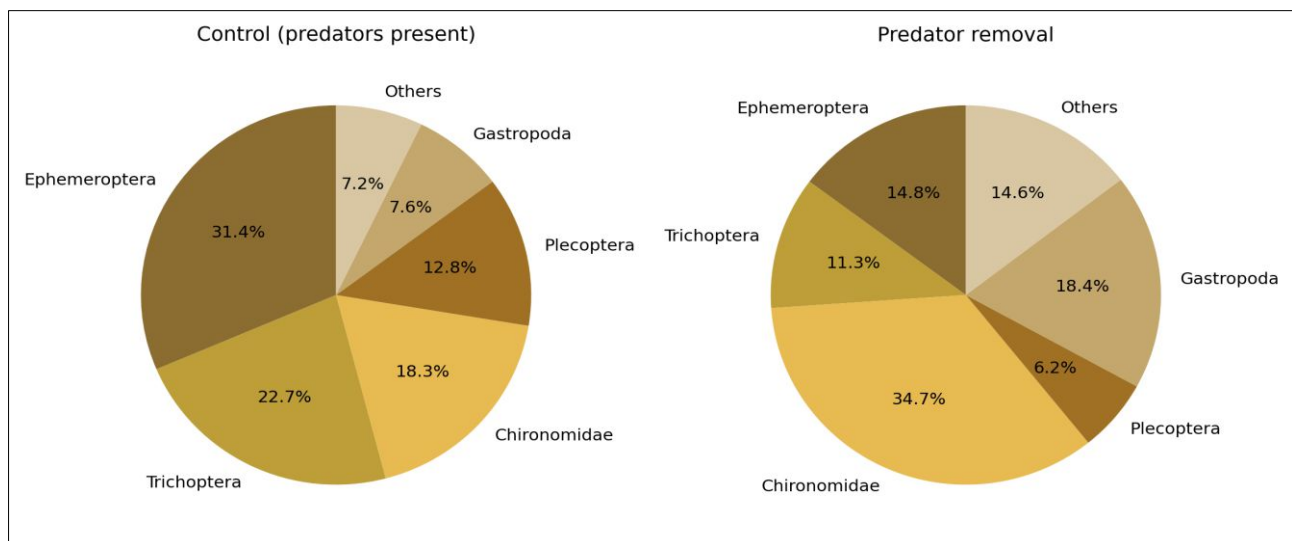


Fig 1: Benthic invertebrate community composition (% relative abundance) in control reaches with predators present (left) and predator-removal reaches (right) after 12 weeks

Community composition shifted markedly (Figure 1). In control reaches, Ephemeroptera (31.4%) and Trichoptera (22.7%) dominated, reflecting predator-maintained balance. In removal reaches, Chironomidae expanded from 18.3% to

34.7% and Gastropoda from 7.6% to 18.4%, while Ephemeroptera and Trichoptera declined. Bray-Curtis dissimilarity between treatments was 0.52, indicating substantial community restructuring.

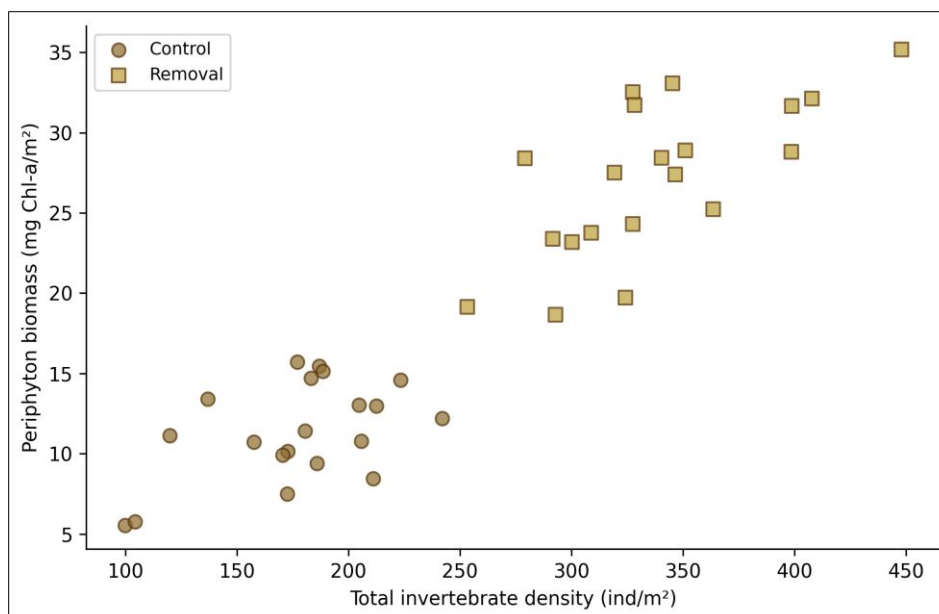


Fig 2: Relationship between total invertebrate density and periphyton biomass (chlorophyll-a) in control and predator-removal stream reaches

The scatter plot (Figure 2) shows that removal reaches occupied a distinct cluster at higher invertebrate density and higher periphyton biomass. While this may seem counterintuitive - more grazers should mean less algae - the pattern reflects the compositional shift: the expanding taxa (Chironomidae, Gastropoda) are less efficient periphyton grazers than the declining Ephemeroptera, and some chironomid taxa are deposit-feeders rather than scrapers [6].

Discussion

The trophic cascade detected in these streams was clear and consistent across all four replicates. Removing stonefly predators led to more invertebrates, fewer taxa, lower diversity, and - somewhat paradoxically - more periphyton. The paradox dissolves when community composition is considered: the dominant taxa that expanded after predator release were not the most efficient grazers [7]. This compositional mediation of the cascade adds a layer of complexity missing from simple three-level food chain models.

The strength of the cascade observed here may partly reflect the enclosed design, which prevented immigration from compensating for predator removal. In open stream reaches, drift from upstream sections could buffer the effects of local predator loss, potentially explaining the weak cascades reported by some earlier field experiments [5, 8]. Our enclosures traded some realism for experimental control, and the 12-week duration was long enough to detect community-level shifts.

From a management perspective, the results caution against assuming that predator loss in streams will simply increase prey abundance. The quality of the invertebrate community changed in ways that could affect ecosystem services - reduced Ephemeroptera and Trichoptera populations mean fewer drift-feeding prey items for fish, while elevated chironomid biomass could alter nutrient processing rates [9, 10].

Conclusion

Top predator removal triggered a three-level trophic cascade in temperate headwater streams, increasing total invertebrate

density by 68.3% and periphyton biomass by 130% over 12 weeks. But the cascade was mediated by community composition shifts rather than simple numerical changes: efficient grazers declined while less efficient taxa expanded, weakening top-down control of algae. Shannon diversity fell from 2.41 to 1.87, and community composition diverged substantially between treatments. These findings confirm that trophic cascades operate in flowing freshwater systems but warn that their effects depend on which species fill the niches left by absent predators [11, 12].

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