Ontogenetic Carnivory Drives Secondary Production Across a Productivity Gradient

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ABSTRACT

1. Ontogenetic size shifts and omnivory are central to understanding consumer-resource interactions and energy flow in aquatic ecosystems. However, how these shifts and feeding behavior influence secondary production and organic matter flow remains poorly understood.
2. Here, we quantified the relationship between body size, carnivory (i.e., animal tissue consumption), secondary production, and organic matter flow across a primary productivity gradient in Brazilian Atlantic Forest streams. Using gut content analyses combined with estimates of secondary production for an overabundant net-spinning caddisfly with filter-feeding behavior (*Leptonema* sp.), we evaluated how body size influences feeding behavior and ecosystem fluxes.
3. Carnivory consistently increased with body size across the primary productivity gradient, with higher average animal tissue consumption at low-productivity sites. Carnivory was positively associated with secondary production but showed no relationship with overall organic matter flow, suggesting a decoupling between consumer-level production and energy throughput. This decoupling may reflect constraints related to resource quality and assimilation efficiency. Additionally, potential prey flux measured with drift nets did not predict carnivory, suggesting that resource quality, as described by the productivity gradient may outweigh prey availability in driving trophic behavior.
4. Our results provide novel evidence that omnivory depicted by size-enhanced carnivory is an adaptive strategy contributing to population-level production, but not necessarily to increased energy throughput at the ecosystem level. Our findings highlight the importance of considering consumer traits, such as

body size and trophic flexibility, in understanding energy flow and ecosystem functioning along productivity gradients in riverine networks.

KEYWORDS

Biomass turnover, Body size, Omnivory, River continuum concept.

1 | INTRODUCTION

Resource availability in river networks is shaped by variation in the origin, quality, and quantity of basal energy sources (Vannote et al., 1980), reflecting changes in canopy cover and light availability from headwaters to mainstem reaches (Leal et al., 2023). These patterns are further influenced by lateral and vertical connectivity across the river corridor (Thorp et al., 2006), resulting in changes in community composition following the basal resources available across the continuum. While allochthonous, low-quality detrital inputs typically dominate the upstream sections, the downstream sites show increasing rates of high-quality autochthonous resources such as algae and periphyton (Vannote et al., 1980). This productivity gradient influences consumer-resource interactions, as shifts in basal resource availability may alter consumer energy assimilation efficiency, diet breadth, and trophic position (Sánchez-Hernández, 2023; Leal et al., 2023).

Energy acquisition and storage by consumers have long been recognized as central components of organismal performance and success (Lindeman, 1942). Expanding on this view, Optimal Foraging Theory posits that consumer feeding behavior is shaped by energetic and nutritional demands (MacArthur & Pianka, 1966). More recent studies have emphasized the role of ontogeny and life-history strategies in determining these demands, ultimately influencing foraging behavior throughout an organism’s development (Cross et al., 2003; 2015). Omnivory is a foraging behavior defined as the consumption of food from multiple trophic levels (Pimm, 1982; Garvey & Whiles, 2016), and is widespread across ecosystems, including freshwater environments. In such systems, variation in resource availability may promote omnivory as an adaptive strategy in response to changing energetic constraints (Vannote et al., 1980; Sánchez-Hernández, 2023).

Filter feeding represents a foraging strategy in rivers and streams in which individuals capture food particles suspended in the water column as they flow through or overspecialized filtering structures (Jeschke et al., 2004). This feeding behavior is strongly associated with a type I functional response (Holling, 1965), characterized by a linear increase in ingestion rate with rising resource availability, due to negligible handling time and a sustained foraging effort even under high food concentrations (Jeschke et al., 2004). Among filter feeders, net-spinning caddisflies (Trichoptera), particularly those from the Hydropsychidae family, are a remarkable example of passive filter feeders (Wallace & Merritt, 1980). These individuals act as ecosystem engineers by altering substrate structure and local hydrodynamics (Tumolo et al., 2020). These modifications enhance nutrient retention and influence community assembly, thereby contributing to key ecosystem functions in stream environments (Bertagnoli et al., 2023; Tumolo et al., 2024). In addition to structural roles, their feeding behavior also contributes to ecosystem-level processes. As aquatic immatures, these insects construct silk nets to capture organic matter, algae, and small invertebrates, contributing significantly to the productivity and energy flow of freshwater ecosystems (Benke & Wallace, 1980, Benke 2018).

In Atlantic Forest streams, net-spinning caddisflies are among the most abundant and dominant taxa, contributing substantially to total energy flow and disproportionately shaping ecosystem functioning, despite their intermediate body size (Saito et al., 2024). Robert et al. (2024) showed that these insects can include overabundant large-bodied individuals that exhibit an omnivorous diet, characterized by high levels of carnivory. By capturing prey in addition to suspended material, net-spinning caddisflies display feeding strategies adapted to high metabolic demands and variable resource availability. These behaviors strongly contribute to the total energy flow within stream food webs (Saito et al., 2024) and enhance their dietary flexibility and individual body size (Robert et al., 2024).

Body size is a major trait that determines metabolic rate, which in turn influences key biological processes such as respiration, lifespan, and ultimately organismal energetic demands (Brown et al., 2004; White et al., 2007). At broader scales, the metabolic theory of ecology offers a comprehensive framework for understanding how these size-related processes affect biomass turnover and energy flow within and across ecosystems (Brown et al., 2004). At the ecosystem level, secondary production refers to the formation of heterotrophic biomass over time and is directly related to organic matter flow in ecosystems (Benke & Huryn, 2017). Frequently referred to as the ultimate variable in animal ecology (Benke, 1993), this dynamic metric is influenced by several factors, including body size and energy sources (Huryn & Benke, 2007; Junker et al., 2020), and environmental conditions such as temperature and light (Benke, 1993; Huryn & Benstead, 2019). In Neotropical aquatic systems, stable thermal and hydrologic regimes tend to support high rates of biomass turnover (Bottová et al., 2013), with individuals acquiring food resources to meet elevated energetic demands (Saito et al., 2021). At higher temperatures, organisms exhibit faster biomass turnover due to shorter lifespans, potentially leading to increased food consumption rates (Saito et al., 2021).

In freshwater systems, where many species undergo substantial ontogenetic growth, dietary shifts over the life cycle are common as a means to meet increasing consumption rates and nutritional demands (Woodward et al., 2005). These dietary shifts can be influenced by environmental conditions. For example, in detritus-dominated systems, limited nutritional quality may lead to increased carnivory as a compensatory strategy, whereas in autotrophy-rich environments, higher resource quality may reduce the reliance on animal prey (Cross et al., 2005; Marcarelli et al., 2011). This trophic plasticity could be especially advantageous in environments with high temporal or spatial variability in resource availability, such as Atlantic forest streams, reinforcing the idea that size-related shifts in feeding behavior have important implications for understanding energy flow, consumer-resource interactions (Brown & Gillooly, 2003; Trebilco et al., 2013), and ultimately biomass turnover and secondary production in freshwater ecosystems (Frauendorf et al., 2013).

The combined effects of resource quality and consumer traits, such as body size and feeding behavior, on ecosystem processes like secondary production and organic matter flow remain poorly understood, particularly across productivity gradients in tropical systems. We addressed this knowledge gap by combining gut content analyses with secondary production estimates of a large, abundant, and ubiquitous net-spinning caddisfly from Atlantic Forest streams (*Leptonema* sp.), thereby assessing how the interplay between body size and resource use shapes ecosystem functioning across a river continuum. This integrative approach is rare and allows us to clarify how body size and resource use interact to influence ecosystem-level processes.

Two central questions guided our research. First, we investigated whether ontogenetic size shifts result in increased carnivory along a productivity gradient. We hypothesized that carnivory would increase over the course of ontogenetic development, particularly at low-productivity sites, such as headwater streams. We predicted that larger individuals would consistently exhibit higher levels of carnivory than smaller ones, with the steepest increase in carnivory occurring at low-productivity sites, and weaker increases as basal resource quality improved along the productivity gradient (Figure 1A). Our second question was how carnivory influences secondary production and organic matter flow along productivity gradients. We hypothesized that carnivory and basal resource quality would interact, producing opposing effects on secondary production and organic matter flow across the gradient. We predicted high secondary production at sites with moderate primary productivity, where resource quality and carnivory together optimize growth and biomass turnover (Figure 1B). Thus, the effect of carnivory on secondary production and organic matter flow would depend on variations in basal resource quality along the riverine continuum. Greater carnivory would increase secondary production but reduce overall organic matter flow, as dietary shifts from low-quality basal resources to high-quality resources (i.e., prey and autochthonous resources) would lower total ingestion of material.

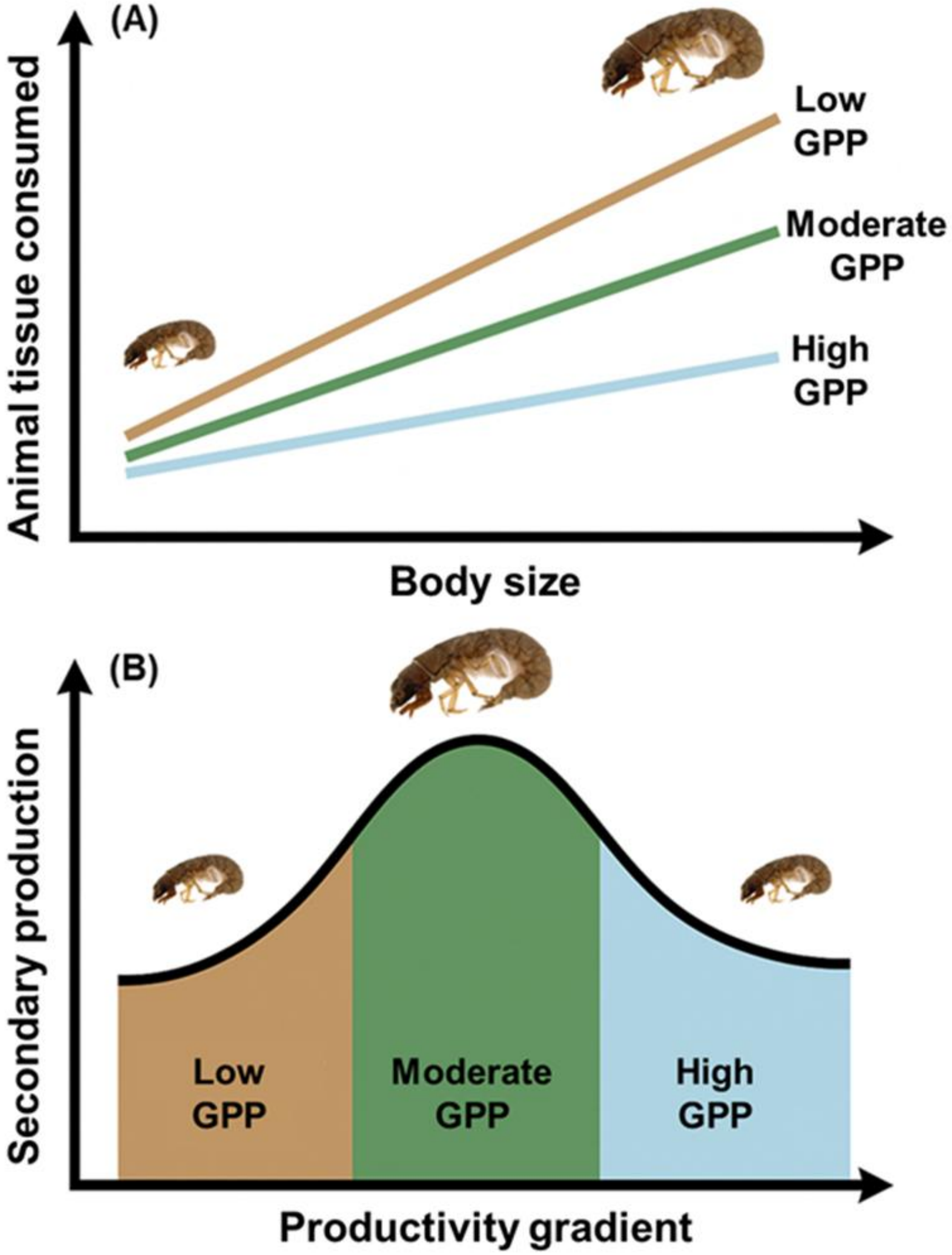


Figure 1. Conceptual framework illustrating the expected relationships between (A) body size and carnivory, and (B) carnivory and secondary production along a gradient of primary productivity in stream ecosystems. (A) Represents the predicted ontogenetic increase in carnivory, with stronger shifts expected at low-productivity sites due to limited basal resource quality. As primary productivity increases, the

reliance on animal prey is expected to decline due to the availability of high-quality autochthonous resources. (B) Shows the hypothesized interaction between carnivory and basal resource quality in shaping secondary production, with peak production expected at intermediate productivity levels where high-quality resources and increased carnivory converge to optimize growth and biomass turnover.

2 | METHODS

2.1 Study sites and field protocols

We conducted field sampling and experiments along a river continuum in the Intervales State Park (ISP), São Paulo, Brazil. ISP is a protected area and one of the few remaining undisturbed regions of the Atlantic Forest biome, where all study sites are in well-preserved condition. The region has a humid subtropical climate, with a mean annual air temperature of 20°C and an average annual precipitation of 2,000 mm (Fenton et al., 1999). We selected eight study sites - three headwater streams (wet width = 3.78 ± 0.879m), two in intermediate sections (5.68 ± 0.717m), and three in the mainstem (10.20 ± 0.908m) - forming a longitudinal continuum within the Carmo River basin. At each site, we monitored key environmental characteristics, including canopy cover (%), depth (m), width (m), and discharge (L s^{-1}) (see Supporting Information – Figure S1).

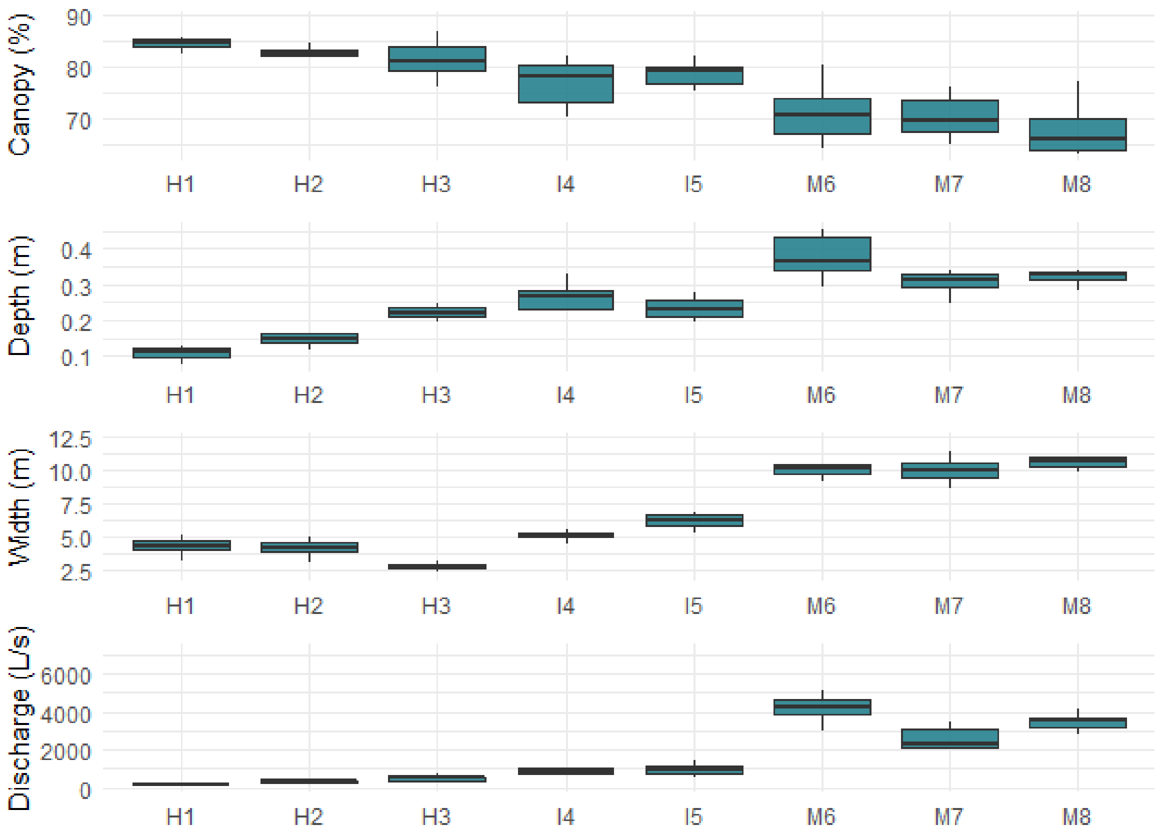
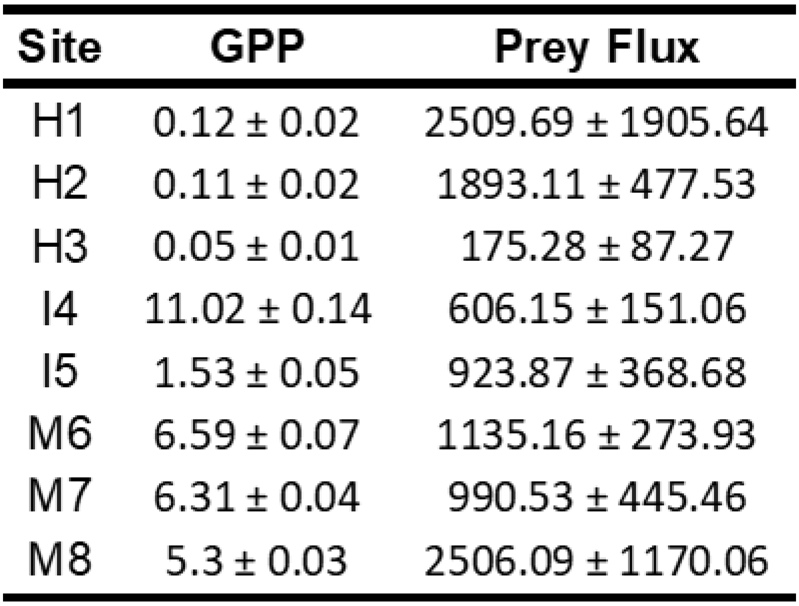


FIGURE S1. Environmental characteristics of the study sites in Intervales State Park from monthly measurements between August 2023 and July 2024.

To evaluate the resource availability along the productivity gradient, we estimated the stream metabolism at the study sites under base-flow conditions using a single-station method (Hall & Hotchkiss, 2017). The single-station method provides an integrated measure of metabolic rates over a stream reach, enabling continuous in situ monitoring of oxygen dynamics and capturing diel variations in stream metabolism (Grace et al., 2015). Gross primary production at the study sites was estimated using measurements of dissolved oxygen and water temperature (PME miniDOT loggers) along with photosynthetically active radiation (HOBO model UA-002-64 loggers). Daily GPP rates (in mg O_2 L^{-1} d^{-1}) were converted to annual rates in g ADFM m^{-2} y^{-1} by applying several sequential conversion factors: the conversion factor of 0.7 (Dodds et al., 2000), followed by the atomic ratio of C to O_2 (12:32) and the respiratory quotient for algae (1:1.2). The resulting values were then multiplied by 365 to obtain annual GPP rates in mg C m^{-2} y^{-1}, which were subsequently converted to ash-free dry mass values by applying a conversion factor of 0.53 (Steinman & Duhamel, 2017) (see Supporting Information – Table S1).



Site	GPP	Prey Flux
H1	0.12 ± 0.02	2509.69 ± 1905.64
H2	0.11 ± 0.02	1893.11 ± 477.53
H3	0.05 ± 0.01	175.28 ± 87.27
I4	11.02 ± 0.14	606.15 ± 151.06
I5	1.53 ± 0.05	923.87 ± 368.68
M6	6.59 ± 0.07	1135.16 ± 273.93
M7	6.31 ± 0.04	990.53 ± 445.46
M8	5.3 ± 0.03	2506.09 ± 1170.06

Table S1. Resource availability of the study sites in Intervales State Park in the forms of primary productivity (GPP) and prey flux, both in g AFDM m^{-2} y^{-1}.

To collect *Leptonema* individuals, we conducted monthly sampling from August 2023 to July 2024. At each stream, we took five Surber (0.09 m^2) samples, resulting in a total of 480 samples collected over the study period. We took a subsample of 144 individuals covering a range of body sizes and evenly distributed across the eight study sites (18 individuals per site) and preserved them for subsequent gut content analysis in the laboratory.

2.2. How do ontogenetic size shifts increase carnivory along a productivity gradient?

We defined eight size classes ranging from 2.5 to 32.0 mm, representing the minimum and maximum sizes of the *Leptonema* individuals collected. Following the procedures described by Rosi-Marshall et al. (2016), we assessed the degree of carnivory by analyzing the gut contents of the 144 *Leptonema* individuals of different body sizes, measuring the relative area of particles corresponding to each resource type. We quantified the percentage area of different resources, classifying them into the following categories: detritus, fungi, diatoms, algae, plant tissue, and animal tissue. To assess how both body size and primary productivity influence carnivory, we applied a beta regression model using a logit link function, including the interaction term between body size and GPP. The beta regression is appropriate for modeling continuous proportion data bounded between 0 and 1 (Cribari-Neto & Zeileis, 2010). This modeling approach accounts for the heteroscedasticity and skewness commonly present in proportion data, providing more reliable and interpretable estimates than linear models. Beta regression models were conducted in R using the betareg package (Cribari-Neto & Zeileis, 2010).

2.3. How does carnivory affect secondary production and organic matter flow along productivity gradients?

Related to the question of how carnivory influences secondary production and overall organic matter flow along a productivity gradient, we first estimated annual secondary production (g AFDM m^{-2} y^{-1}) using the size-frequency method (Benke & Huryn, 2017), adjusted for a cohort production interval of 103 days based on Jackson & Sweeney (1995), and applying an appropriate genus-level length-mass relationship (Coelho et al., 2023). Estimating secondary production requires precise measurements of population density and size structure (Benke, 1993). To achieve this, adequate replication is essential to account for the irregular distribution of individual sizes in aquatic environments. The size-frequency method is a non-cohort approach that assumes a specific distribution of individuals throughout the year, approximating a mortality curve for a mean cohort (Benke & Huryn, 2017). We selected this method because it is particularly useful when direct cohort tracking is unfeasible (e.g., multiple overlapping cohorts). We constructed 90% confidence intervals (CIs) for secondary production estimates using the bootstrap technique (Efron & Tibshirani, 1994). All analyses related to secondary production were performed in R.

In addition to primary productivity, we also estimated the prey flux available to *Leptonema* individuals using drift samplers. Drifts were installed for 24-hour periods at each study site to quantify prey availability. Each individual collected in the drifts was measured and identified to the lowest feasible taxonomic level (Hamada et al., 2018), and body mass was estimated using appropriate length-mass relationships (Benke et al., 1999). Clogged drifts were excluded from the study. We adapted the method described by Whiting et al. (2011) to estimate average annual prey flux (g AFDM m^{-2} y^{-1}) at our sites (see Supporting Information – Table S1), replacing seston concentrations with drift concentrations (g L^{-1}) and incorporating discharge values (L s^{-1}) and streambed area (m^2). Once again, beta regression models were performed to assess the effects of prey flux on carnivory across the productivity gradient. Frequent heavy rains made the estimation of allochthonous organic matter inputs (both vertical and lateral) unfeasible due to flash floods, which could wash away the traps.

To evaluate the effects of carnivory on secondary production and overall organic matter flow across the productivity gradient, we combined the data obtained from gut content analyses with estimates of secondary productivity and the principles of the trophic basis of production. Following the procedures described by Benke & Wallace (1980), we used the dietary composition percentages of the collected individuals to determine the proportion of production attributed to each resource category. Briefly, we quantified overall organic matter flow (g AFDM m^{-2} y^{-1}) by evaluating the trophic basis of *Leptonema* production, using published information on assimilation efficiency (AE) and net production efficiency (NPE). In ecological studies, AE refers to the proportion of ingested resources absorbed by a consumer, while NPE indicates the efficiency of energy conversion into new biomass (Benke, 2010). We assumed an NPE of 0.5 for all resources and an AE of 0.1 for detritus, fungi, and plant tissue; 0.3 for diatoms and algae; and 0.7 for animal tissue (Benke, 2018). We combined dietary composition data with production values obtained through the bootstrap technique, generating 1,000 values per study site, which allowed us to estimate mean values and 90% CIs for organic matter flow.

To assess the effects of carnivory and primary productivity on both secondary production and overall organic matter flow, we applied robust regression models using the MM estimator (Maechler et al., 2024). The MM estimator is a type of M-estimator that combines a robust location estimator (e.g., the Huber loss function) to minimize the influence of outliers, with a robust scale estimator to account for variability in the data. This approach provides efficient estimates even in the presence of outliers or deviations from normality. We assigned lower weights to observations with larger confidence intervals for both production and organic matter flow estimates. To test for unimodal responses as predicted, we included the proportion of animal tissue consumed, gross primary productivity (GPP), and the quadratic term for GPP (GPP^2) as predictors. Robust regression models were conducted in R using the lmrob() function from the robustbase package (Maechler et al., 2024).

3 | RESULTS

Dietary composition varied consistently across *Leptonema* size classes. Smaller individuals (size classes 1 and 2; 2.50 to 9.90 mm) fed mainly on basal resources, while medium to large individuals (size classes 3 to 8; 13.6 to 32.00 mm) consumed a substantial amount of animal tissue (see Supporting Information – Figure S2). Carnivory showed the highest average value at headwaters (59.0%), followed by intermediate sections (46.0%) and mainstems (37.3%).

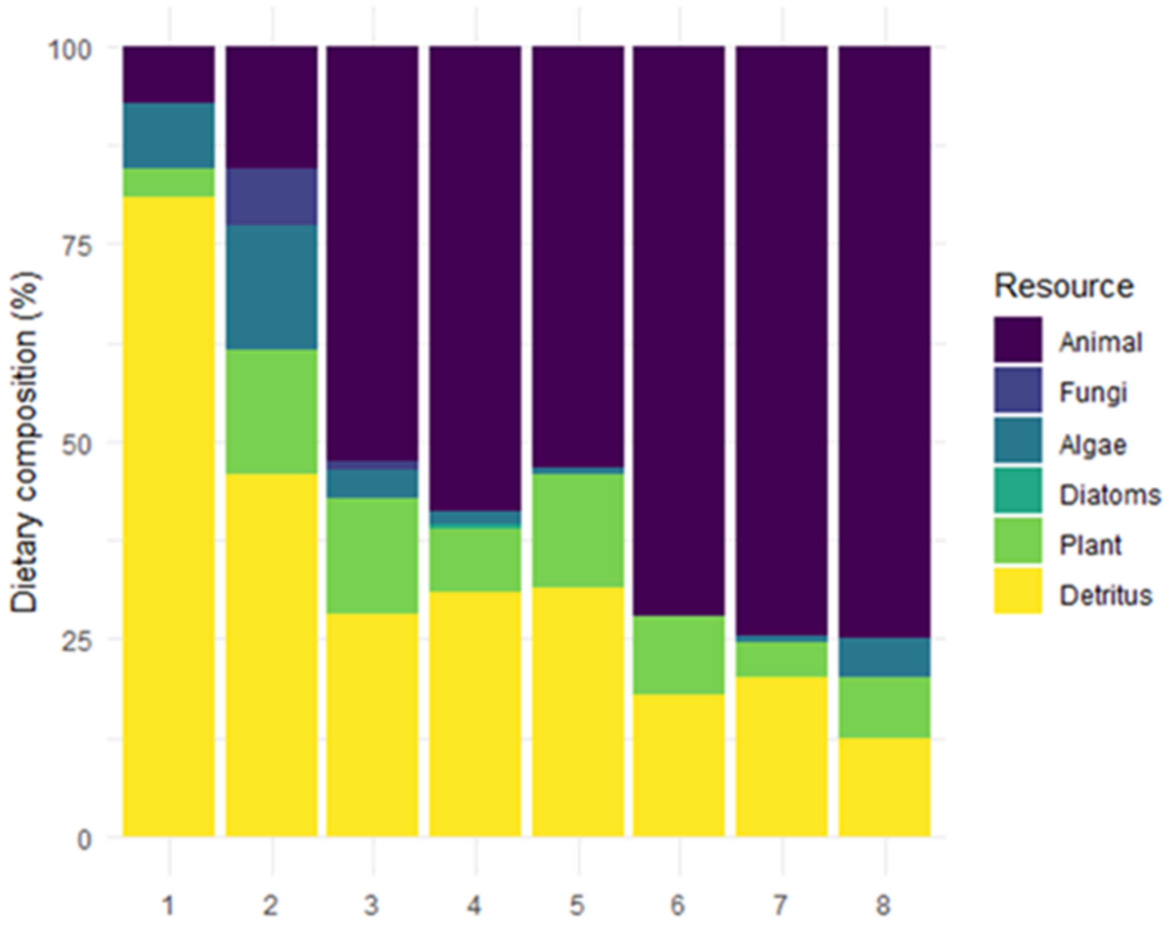


Figure S2. Dietary composition of *Leptonema* individuals across the size classes.

The beta regression model including body size, GPP, and their interaction explained a moderate proportion of the variation in carnivory (pseudo $R^2 = 0.39$). Body size had a positive effect on carnivory (coefficient = 0.087, $p < 0.001$), while GPP had a marginal negative effect (coefficient = -0.101, $p = 0.089$). There was no interaction between body size and GPP (coefficient = 0.003, $p = 0.321$), suggesting that the influence of body size on carnivory did not vary along the productivity gradient (Figure 2).

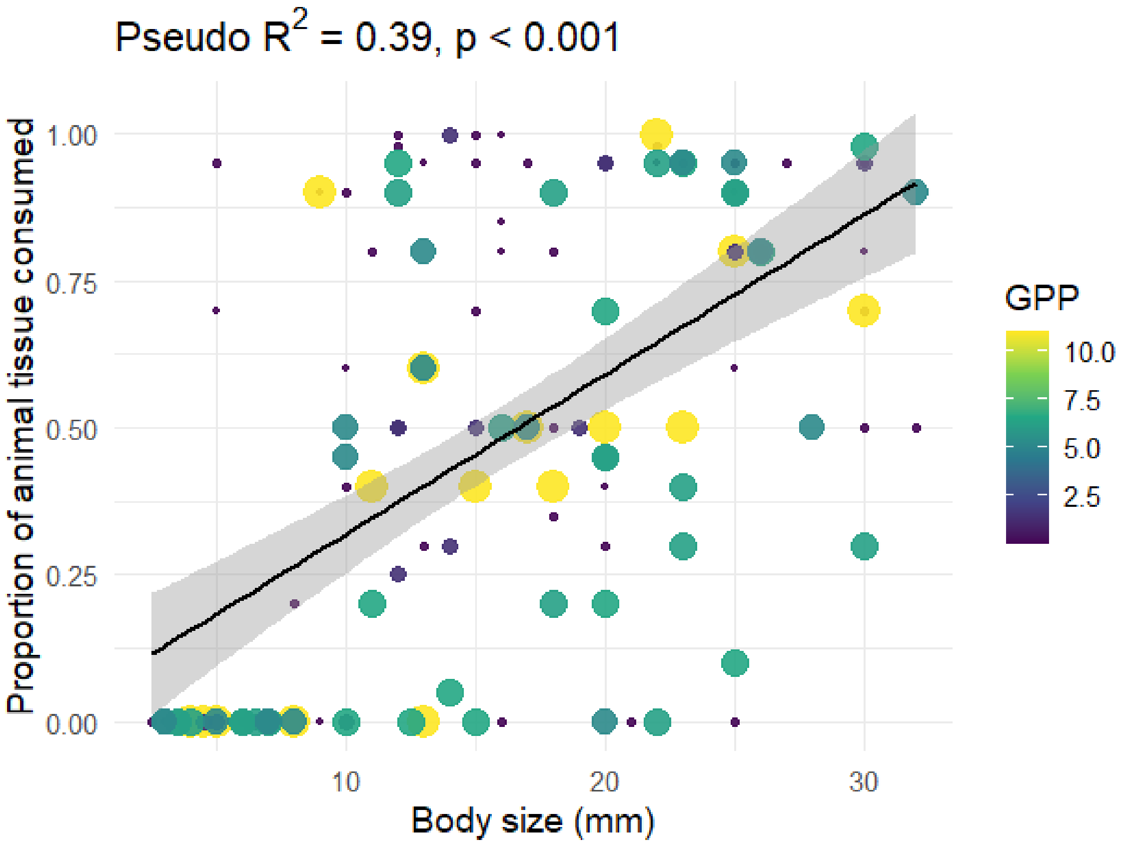


Figure 2. Relationship between *Leptonema* body size (mm) and proportion of animal tissue consumed across the productivity gradient, with GPP (g AFDM m^{-2} y^{-1}) as a covariate.

The beta regression model assessing the effect of prey flux on carnivory indicated no relationship (p = 0.725) (Figure 3). The model exhibited a low fit (pseudo R^2 = 0.016), indicating that variation in prey flux does not explain variation in carnivory.

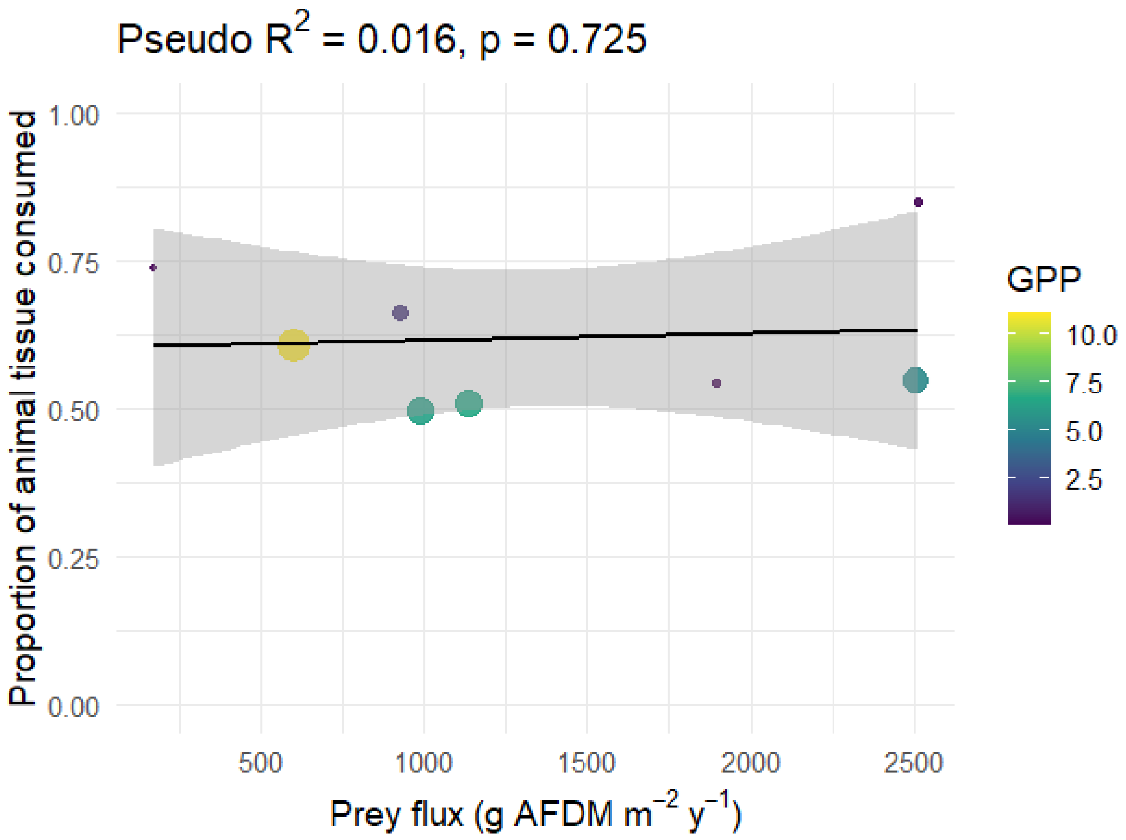


Figure 3. Relationship between prey flux (g AFDM m^{-2} y^{-1}) and proportion of animal tissue consumed across the productivity gradient, with GPP (g AFDM m^{-2} y^{-1}) as a covariate.

A linear regression between secondary production and organic matter flow indicated a marginal positive association ($p = 0.075$), explaining 43% of the variation in overall organic matter flow. The robust regression model evaluating secondary production as a function of mean carnivory and GPP revealed a positive effect of carnivory ($p = 0.049$), while both linear and quadratic GPP terms played no role ($p = 0.591$ and $p = 0.480$, respectively). This model explained 44% of the variation in *Leptonema* secondary production, but the adjusted R^2 was low (0.02). In contrast, the robust model for organic matter flow as the response variable showed no relationship with predictors. Although the GPP^2 term showed a marginal positive trend ($p = 0.139$), neither carnivory ($p = 0.270$) nor the linear GPP term ($p = 0.191$) influenced organic matter flow. A simplified robust model excluding GPP showed a positive relationship between secondary production and carnivory ($p = 0.039$; Figure 4A), explaining about 34% of the variation (adjusted $R^2 = 0.34$). Meanwhile, the relationship between carnivory and organic matter flow remained non-significant in the simplified model ($p = 0.841$; Figure 4B).

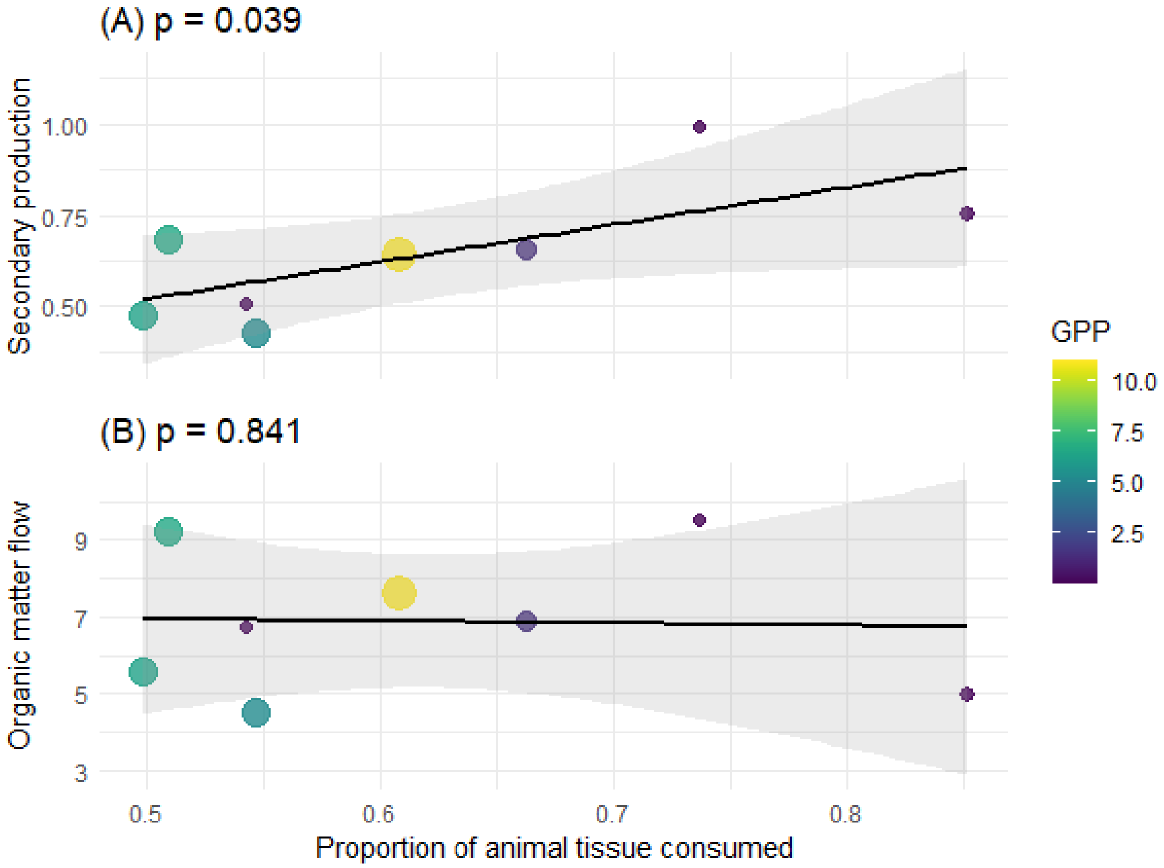


Figure 4. Relationships between the proportion of animal tissue consumed and *Leptonema* secondary production (A), and overall organic matter flow (B), both expressed in g AFDM m^{-2} y^{-1}, across the productivity gradient, , with GPP (g AFDM m^{-2} y^{-1}) as a covariate.

4 | DISCUSSION

By combining gut content analyses with estimates of secondary production for a dominant and overabundant net-spinning caddisfly (*Leptonema* sp.), we demonstrated that carnivory consistently increases with body size across different productivity levels. Our results indicate that carnivory remains a prevalent component of the diet of this omnivorous genus, regardless of primary productivity, suggesting that this feeding strategy is maintained across the gradient. Conversely, while carnivory was positively associated with *Leptonema* secondary production, it did not predict overall population consumption flows. Our findings provide new and valuable insights into the interplay between body size, omnivory, and ecosystem functioning, particularly within the context of riverine ecosystems.

Previous studies have documented high levels of body size-related carnivory by net-spinning caddisflies in tropical headwater streams (Robert et al., 2024), suggesting that this feeding behavior is a response to energetic constraints in resource-poor habitats, where consumers supplement low-quality basal resources with energy-rich animal prey to meet their metabolic demands (Saito et al., 2021). Since both the quantity and quality of basal resources are critical determinants of consumer foraging strategies and trophic interactions (Marcarelli et al., 2011; Leal et al., 2023), the predominance of low-quality detritus in resource-limited headwater streams may drive increased carnivory as a compensatory mechanism. Our results expand this understanding to broader spatial and ecological scales, including the riverine continuum and ecosystem-level processes, and show that consumer traits like body size and trophic flexibility may influence ecosystem functioning across productivity levels.

At more productive sites, consumers are expected to rely less on animal prey due to the greater availability of high-quality basal resources. For example, autochthonous resources such as algae, which are considered high-quality due to their low C:N:P ratios and known to enhance consumer growth and assimilation efficiency (Guo et al., 2018), become more abundant at productive sites, reducing the need for animal-derived energy (Sánchez-Hernández et al., 2018). A dietary shift toward basal resources at productive sites supports the broader view that omnivory is not merely a trait of individual species, but an adaptive response to spatial variation in resource availability along productivity gradients (Cross et al., 2015; Kratina et al., 2012). However, our results indicate that carnivory remains widespread across the productivity gradient, suggesting that for *Leptonema* and similar taxa, the degree of omnivory is likely an adaptive strategy that persists even in resource-rich environments, with consumers relying more on prey than on basal resources of varying quality. This result illustrates that, in riverine landscapes, understanding the structure and dynamics of food webs requires moving beyond simplistic descriptions of basal resource shifts to explicitly consider consumer-level traits and trophic interactions, thereby fully addressing the complexity of omnivory (Sánchez-Hernández, 2023).

Another key and intriguing finding of our study was the absence of a relationship between prey flux and carnivory, suggesting that resource availability does not necessarily determine trophic behavior, particularly in organisms with high metabolic demands. Instead, resource quality and consumer physiological needs may play a more pivotal role in shaping feeding strategies than sheer prey abundance (Sterner & Elser, 2002; Boersma et al., 2008). This result is consistent with broader evidence showing that nutritional quality determines food preferences and assimilation efficiency across diverse taxa, with consumers in resource-limited environments relying on energetically or nutritionally superior prey, regardless of its relative abundance (Boersma et al., 2008; Vanni & McIntyre, 2016; Neres-Lima et al., 2016). As predicted by optimal foraging theory, consumers may favor energetically richer prey in low-quality environments, even at the cost of longer handling times (MacArthur & Pianka, 1966). Our results suggest that for larger individuals, the metabolic gains from consuming animal prey likely offset these costs, making carnivory a beneficial strategy. Consequently, shifts toward carnivory with increasing body size reflect an adaptive foraging response driven by resource quality rather than abundance (Jeschke et al., 2004).

We observed a positive relationship between carnivory and secondary production, supporting the idea that dietary shifts toward higher trophic levels can enhance growth efficiency and biomass turnover (Polis & Strong, 1996; Benke & Huryn, 2017). However, carnivory did not predict overall organic matter flow across the productivity gradient, nor was there a relationship between secondary production and organic matter flow. Although this decoupling may reflect limitations of conventional energy flow metrics or gut content analysis, which may not fully capture the complexity of resource assimilation and trophic pathways (Nielsen et al., 2018), our findings align with previous evidence that variations in trophic efficiency and consumer traits can decouple secondary production from overall organic matter flow.

Davis et al. (2010) showed that increased resource availability does not necessarily lead to higher predator production due to prey traits limiting energy transfer to higher trophic levels. In our study, despite increased consumer-level production, energy throughput may be constrained by factors such as resource quality, assimilation efficiency, and trophic pathways shifts. While the assimilation efficiency of basal resources often require large ingestion volumes for assimilation, high-quality animal prey can meet energetic demands with lower intake rates, resulting in distinct energy flux dynamics (Cross et al., 2015). While our results provide a quantitative basis for understanding ecosystem functioning across productivity gradients, they also indicate that increased carnivory, although beneficial for population-level production, does not necessarily translate into higher energy throughput at the ecosystem level. To advance this understanding, future studies should move beyond taxon-specific estimates and incorporate broader, integrative approaches, such as stable isotope analyses (Saito et al., 2014), stoichiometric frameworks (Cross et al., 2015), and fatty acid profiling (Nielsen et al., 2018) to better elucidate the effects of resource use on energy flow in complex food webs.

Our findings highlight omnivory as a key strategy that allows consumers to adjust their foraging across life stages and resource conditions, providing resilience to fluctuations in basal resources and environmental variability (Kratina et al., 2012), particularly in Neotropical streams, where hydrological regimes and resource inputs are highly dynamic (Valente-Neto et al., 2024). To our knowledge, this study provides the first quantification of the interactions between body size and omnivory on ecosystem functioning across a productivity gradient within a riverine network. While most investigations of secondary production are restricted to headwater streams, ours encompasses a broader spatial scale (i.e., river continuum), engaging with classical theory and predictions (Vannote et al., 1980; Doretto et al., 2020) and refining our understanding of freshwater ecosystem functioning. Nonetheless, our reliance on gut content analysis may underestimate assimilation pathways and overlook temporal variation in resource use and energy flow. Future research should adopt more integrative and multiscale temporal approaches to better elucidate the complexity of trophic interactions and energy transfer in freshwater ecosystems.

AUTHOR CONTRIBUTIONS

José LS Mello and Victor S Saito conceptualized the study. José LS Mello and Victor S Saito developed methods. José LS Mello, Laura J Venuso, Julia M Braga, Pedro B Guerra, Erika M Shimabukuro and Victor S Saito conducted field work and lab analyses. José LS Mello conducted data analysis with inputs from Victor S Saito, T Siqueira and Jim R Junker. All authors contributed equally to the drafts and gave final approval for submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Not applicable.

STATEMENT ON INCLUSION

Our study is a collaboration between researchers from Brazil and the USA, led by a researcher based in the country where the research was conducted. It includes undergraduate, graduate, and senior researchers from the study region, all actively involved in the research design and execution, ensuring diverse perspectives were integrated.

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