

When giant amphibians rule the river: Community trophic structure of Japanese giant salamander ecosystems

Clément Duret^{1, *} | Benjamin Lejeune¹ | Gilles Lepoint² | Tiphane Bartet¹ | Sumio Okada³ | Keitaro Fukushima⁴ | Osamu Kishida⁵ | Mathieu Denoël¹

¹Laboratory of Ecology and Conservation of Amphibians (LECA), Freshwater and Oceanic science Unit of reSearch (FOCUS), University of Liège, Liège, Belgium

²Laboratory of Trophic and Isotope Ecology (LETIS), Freshwater and Oceanic science Unit of reSearch (FOCUS), University of Liège, Liège, Belgium

³The Hanzaki Research Institute of Japan, Asago, Hyogo, Japan

⁴Faculty of Food and Agricultural Sciences, Fukushima University, Fukushima city, Fukushima, Japan

⁵Wakayama Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Hokkaido, Japan

Correspondence: Clément Duret; E-mail address: clement.duret@uliege.be

Abstract

Top predators strongly influence food webs, often because they reach large body sizes. Amphibians are typically regarded as prey in such systems, but giant salamanders are a rare exception. Because gigantism entails extreme ontogenetic body size variation, it is expected to drive strong trophic niche shifts and reshape interactions within and among species as individuals grow. However, such trophic shifts in giant amphibians and relationships with other consumers remain largely unexplored, limiting our understanding of the contribution of this flagship species to river food web structure. Here, we used stable isotope analysis ($\delta^{13}\text{C}$ – $\delta^{15}\text{N}$) to investigate the trophic structure of a freshwater community dominated by the Japanese giant salamander (*Andrias japonicus*). We assessed how extreme ontogenetic body size variation modifies intra- and interspecific interactions and contributes to overall community structure. We also quantified the dominant carbon sources fueling the community, and modeled trophic positions (TPs), niche metrics, and relationships of all major consumer species. By sampling 161 giant salamanders and approximately 700 other consumers for stable isotope analysis, we provide the first comprehensive characterization of food web structure in a freshwater community dominated by *A. japonicus*. We found clear trophic shifts: smaller individuals overlapped with mesopredators (fish, prawns, turtles), suggesting potential competition, whereas TP increased with size, placing larger individuals above other predators, at the top of the food web. Large salamanders broadened the community $\delta^{15}\text{N}$ range, contributing significantly to the trophic evenness and total community niche space. Basal source tracing revealed that both aquatic and terrestrial energy pathways sustained the food web. Overall, these findings show that gigantism in *A. japonicus* shapes trophic hierarchies, contributing significantly to vertical complexity and trophic diversity of the community, and highlighting

how ontogenetic shifts in giant predators can structure riverine food webs. By integrating isotopic niches, TP, and basal source contributions at the whole-community scale, this study provides a generalisable framework for linking predator ontogeny to food web structure, with direct relevance for conserving vulnerable freshwater ecosystems; endangered top predators such as *A. japonicus* may contribute disproportionately to food web resilience and community structure.

KEYWORDS

food web structure, freshwater ecosystems, gigantism, isotopic niche, rivers, stable isotope analysis, top predator, trophic interactions

INTRODUCTION

Body size is a key trait determinant of species interactions within food webs, because it constrains prey size, foraging mode, energetic demand, and vulnerability to predation (Werner & Gilliam, 1984; Woodward et al., 2005). Across ecosystems, body size is strongly linked to trophic position (TP) of consumers and interaction strength, making it a central dimension for understanding food web architecture (Brose, 2010; Cohen et al., 2003). Among large-bodied predators, many serve as top predators, that is, species occupying the highest TPs in ecosystems. In many ecosystems, including freshwater systems, size-dependent predation and competitive asymmetries can modify trophic interactions by enabling access to larger or otherwise less accessible prey, and by shifting competitive relationships among consumers (Claessen et al., 2002). Because large-bodied predators typically grow through ontogeny, body size variation within a species can generate pronounced niche shifts and alter its role in the community over time (Nakazawa, 2015; Wilbur, 1980). Such ontogenetic shifts can influence both intra- and interspecific trophic interactions, thereby affecting community structure and food web dynamics (de Roos & Persson, 2013; Kopf et al., 2025).

Gigantism represents an extreme case of body size variation, typically defined as the evolution or occurrence of exceptionally large body sizes relative to other species or conspecifics within a given ecological context (Vermeij, 2016). Gigantic consumers frequently occupy top trophic levels, facing reduced predation risk but increased vulnerability to extinction during environmental crises (Heim et al., 2015; Vermeij, 2012). In freshwater ecosystems, gigantism has been particularly studied in several large predators (e.g., large teleosts and crocodilians) (Echeverria et al., 2022; Rejas et al., 2023). Although amphibians are typically considered prey of top predators in large freshwater ecosystems worldwide, the clade of giant salamanders (Cryptobranchidae family) occurring in East Asia and North America (Gao & Shubin, 2003), may represent an exception. Beyond their large size, these species are ecologically unique predators, retaining paedomorphic traits and using suction feeding (Bonett et al., 2022; Matsumoto et al., 2024; Tago, 1931; Tochimoto, 2002). Previous work has shown pronounced ontogenetic dietary shifts in Japanese giant salamanders (JGSs) (Duret et al., 2026a) as well as in other giant salamander species (Hecht et al., 2017; Unger et al., 2020). However, by contrast to giant predators in other taxa, it remains unclear what the

trophic relationships are between giant salamanders and other predators in rivers, and how their important ontogenetic size variation may structure trophic interactions in river food webs. The JGS (*Andrias japonicus*), endemic to Japan (Duret et al., 2025), can reach 1.5 m in total length, making it a particularly relevant model for assessing how extreme body size in predators may shape trophic interactions and food web structure (Duret et al., 2026a; Okada et al., 2008). Understanding the ecological implications of such a large-bodied predator in a riverine ecosystem requires examining how trophic interactions shift across its extensive growth trajectory. Because large predators can function as keystone species, clarifying their trophic role is also important from a conservation perspective, especially for threatened taxa used as flagship species (Hammerschlag et al., 2019).

Lotic food webs are typically supported by a mixture of aquatic production (often periphyton) and terrestrial subsidies (leaf litter), but their relative importance varies with environmental context (Polis et al., 1997; Vannote et al., 1980). Increasing evidence suggests that consumer body size is a key determinant of how these basal energy pathways are exploited and integrated within food webs. Larger consumers generally have broader home ranges, higher energetic demands, and the ability to capture larger prey, allowing them to couple resources originating from multiple habitats and trophic pathways (Jardine et al., 2017; McCauley et al., 2012; Rooney et al., 2006; Woodward et al., 2005). Consequently, body size may strongly influence the degree to which aquatic versus terrestrial carbon sources are channeled through food webs. Whether and how such size-dependent integration of basal energy pathways occurs in food webs dominated by giant salamanders, and ultimately supports their populations, remains unknown. Quantifying these contributions is therefore key to understanding energy flow and community structure in such systems (Chételat et al., 1999; Finlay & Kendall, 2007).

Here, we investigated the trophic structure of a riverine community dominated by the JGS, with a focus on trophic niche variation of giant salamanders with size and relationships with other consumers and predators within the community (Figure 1). Our objectives were (1) to evaluate how extreme ontogenetic body size variation modifies trophic interactions of salamanders at the intra- and interspecific levels, including how different size classes contribute to the whole aquatic community trophic structure, and (2) to quantify basal carbon sources sustaining the community by contrasting terrestrial and aquatic production pathways. To this end, we used stable isotope analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) (McCutchan et al., 2003; Parnell et al., 2010; Post, 2002), which offers a robust, time-integrated approach to characterize consumer diet and resource use through stable isotope niche modeling (Belouard et al., 2024; Bissattini et al., 2021).

We formulated hypotheses at three ecological levels. At the intraspecific level, we predicted that the ontogenetic niche shift along the food chain in salamanders would lead to decreasing niche overlap among size classes as body size increases. In line with previous findings from the same population (Duret et al., 2026a), which identified a marked dietary shift at a snout–vent length (SVL) of 39 cm, we further expected this transition to be reflected in trophic niche structure, with individuals above this threshold showing more distinct trophic niches and reduced overlap with other consumers. At the interspecific level, we expected large

salamanders to occupy higher and more distinct trophic niches with limited overlap with other consumers, while smaller salamanders would overlap substantially with mesopredators, reflecting higher potential for competition. This pattern would indicate reduced competition with other taxa for larger salamanders, suggesting an ecological advantage of gigantism. The same patterns were expected for TP. At the community level, we hypothesized that larger salamanders would make a significant contribution to the overall trophic structure of the community, including key aspects of food web organization such as food chain length and trophic evenness. Finally, we expected that most species in the community primarily depend on aquatic carbon sources, reflecting a food web largely based on aquatic primary production (periphyton).

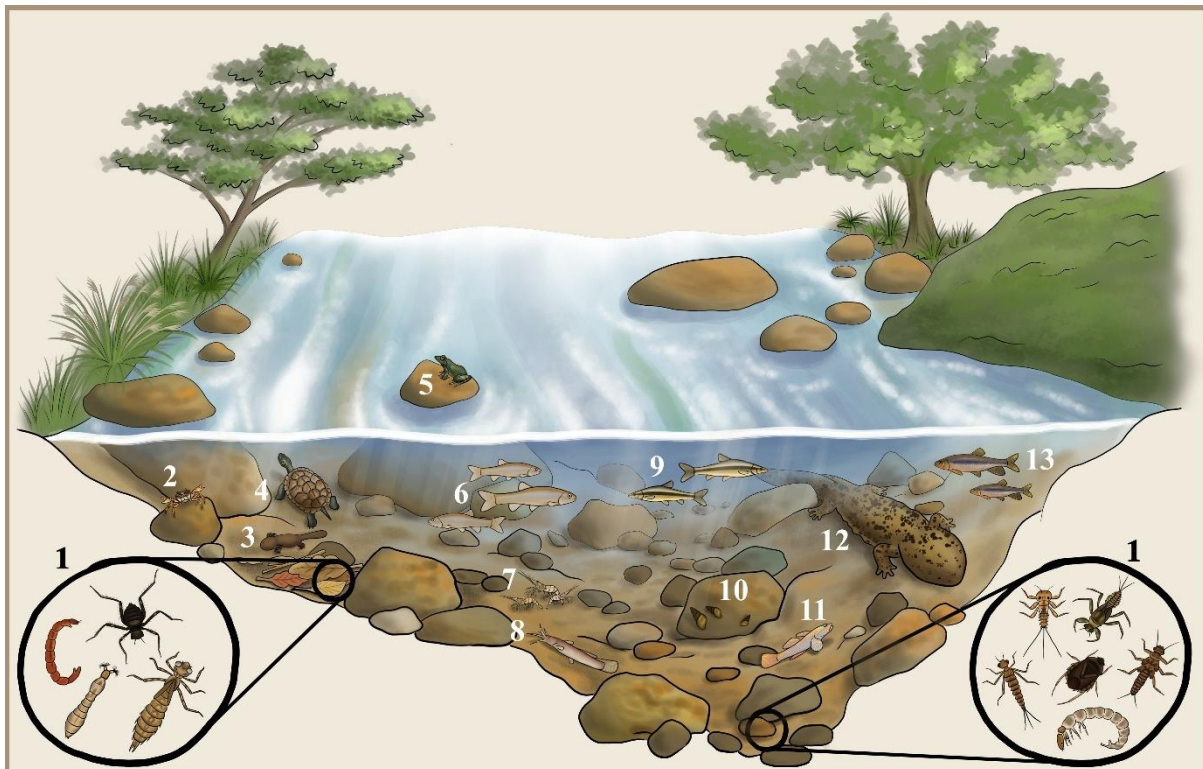


FIGURE 1 Schematic representation of the aquatic community studied, dominated by the Japanese giant salamander. The illustration depicts a river cross-section and the main species present, identified by a number: (1) aquatic insects (larvae); (2) freshwater crab (*Geothelphusa dehaani*); (3) juvenile Japanese giant salamander (*Andrias japonicus*); (4) turtle (*Mauremys* sp.); (5) frog (*Buergeria buergeri*); (6) Chinese minnow (*Rhynchocypris oxycephala*); (7) prawns (*Palaemon paucidens*); (8) catfish (*Liobagrus reinii*); (9) gudgeons (*Pungtungia* sp.); (10) aquatic gastropods (*Semisulcospira* spp.); (11) lizard goby (*Rhinogobius flumineus*); (12) Japanese giant salamander (adult); (13) dark chub (*Nipponocypris temminckii*). Aquatic insects on the left are associated with leaf litter, whereas those on the right are associated with mineral substrates. Illustrations created by Juliette Vallin.

MATERIALS AND METHODS

Study area

This study was conducted in the headwaters of the Ichi River and in its tributary, the Nagano River, located in Ikunochō Kurokawa, Hyogo Prefecture, Japan (35.21° N–134.88° E). These river sections represent typical upstream environments with clear, oligotrophic waters and little aquatic vegetation, and a riverbed dominated by coarse substrates including large boulders, cobbles, and gravel (Vannote et al., 1980).

Sampling

To conduct stable isotope analysis, we aimed to sample a broad range of animal species representing the aquatic community dominated by JGSs. Fieldwork was carried out between April and June 2023 across the entire study area.

Japanese giant salamanders

JGS isotope data used in this study are the same as in a previous study (Duret et al., 2026a) which focused solely on intraspecific sources of isotope variation, notably to characterize the ontogenetic shift of TP in this species. By contrast, the present study uses these data within a community-wide framework, incorporating all main consumer taxa and basal resources to address the implications of extreme body size variation in giant salamanders. Specifically, it focuses on characterizing changes in interspecific trophic relationships along ontogeny, the contribution of different giant salamanders size classes to food web structure and basal energy pathways. The sampling was based on a total of 32 surveys to capture JGSs across a wide range of body sizes. For each captured individual ($n = 161$), we measured the SVL, from the tip of the snout to the end of the cloaca and the individuals were identified using 12-mm microchips (Biolog-ID, 134.2 kHz) except five individuals due to small size that were identified based on unique skin patterns. For stable isotope analysis, a small noninvasive sample of caudal tail muscle was collected from each individual.

Other consumers: sampling and identification

Daytime sampling sessions were conducted to collect and identify the other consumer species present in the study area. These included a wide range of taxa (Appendix S1: Table S1): fish, crustaceans (freshwater crabs and prawns), turtles, anurans (including tadpoles), aquatic insects, and aquatic gastropods. In different sections of the river, fishing traps (50 × 25 × 25 cm; mesh size: 5 mm) were used to capture fish and freshwater crabs, and dip nets (50 × 25 × 25 cm; mesh size: 1 mm) to collect aquatic insects, prawns, tadpoles, and freshwater crabs, which were also hand-collected by overturning rocks. Hand collection was also employed for aquatic insects and gastropods. All species were identified to the lowest taxonomic level possible prior to tissue sampling (Appendix S1: Table S1). The group “aquatic insects” encompassed larvae of several orders and families, including: Plecoptera (e.g., Perlidae), Megaloptera (Corydalidae), Odonata–Anisoptera (Aeshnidae, Macromiidae, and Gomphidae), Odonata–Zygoptera (Calopterygidae), Diptera (Chironomidae and Simuliidae), Ephemeroptera (e.g., Ephemerellidae and Heptageniidae), and Trichoptera (e.g., Stenopsychidae) (Kawai &

Tanida, 2018). It also included adult Hemiptera (Aphelocheiridae). The studied river sections correspond to upstream habitats where fish communities are dominated by small- to medium-bodied species and where no other large-bodied top predators are known to occur. Our sampling methods were designed to effectively capture the dominant consumer taxa, including the largest fish species present. For stable isotope analysis, muscle samples from all fish species, freshwater crabs, prawns, and gastropods were collected. Whole bodies of aquatic insects were collected to have sufficient quantity of tissue. Using sterilized scissors, hind legs interdigital membranes were collected on frogs, tail fin tissue on tadpoles, and small pieces of claw tips on turtles.

Baselines

We sampled baselines of the aquatic community, focusing on two key sources: the terrestrial baseline, represented by leaf litter collected from the streambed, and the aquatic baseline, represented by periphyton scraped from submerged surfaces. In addition, aquatic gastropods (*Semisulcospira* spp.), which feed primarily on periphyton, were hand-collected and used as an additional proxy for the aquatic baseline. Throughout the manuscript, references to “terrestrial carbon sources” specifically denote carbon derived from the decomposition of leaf litter deposited within the stream channel.

Stable isotope samples processing

All tissue samples were dried in an oven at 60 °C for 72 h (Mktrshy incubator) and then finely ground into a uniform powder. Because JGS material could not be transported outside Japan, their carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios were determined locally at Fukushima University (Faculty of Food and Agricultural Sciences) using an isotope ratio mass spectrometer (Delta-V Advantage coupled to a Flash Elemental Analyzer, Thermo Fisher Scientific). Isotope analyses for all other consumer and baseline samples were conducted in Belgium at the Laboratory of Trophic and Isotope Ecology (LETIS, University of Liège), with a continuous-flow isotope ratio mass spectrometer connected to an elemental analyzer (PrecisION, Vario MICRO cube, Elementar, Germany). Isotopic values are reported in conventional δ notation in ‰ (Coplen, 2011). The details of reference standards used are presented in Appendix S1: Table S2.

Modelling and statistical analysis

For further analyses, we used a clustering approach to assign JGSs to different size classes (SVL related) to investigate variations in isotopic niche width, trophic overlap with other consumer species, and community-wide metrics. We first calculated a distance matrix between SVL of salamanders and their $\delta^{15}\text{N}$ values and then applied a clustering procedure to this matrix using the package “NbClust” with a “ward.D2” method, which minimizes the total within-cluster variance (Charrad et al., 2014) in an R environment (version 4.3.2). Then, each individual was assigned to one of the four size classes obtained through clustering: JGS Group 1: 4–16.7 cm SVL ($n = 9$); JGS Group 2: 16.8–41.5 cm SVL ($n = 74$); JGS Group 3: 41.6–52.7 cm SVL ($n = 67$); JGS Group 4: 52.8–67.3 cm SVL ($n = 11$). This clustering approach was chosen to identify data-driven groupings that reflect both body size and TP simultaneously,

rather than relying solely on arbitrary or predefined size thresholds. However, previous work on the same population (Duret et al., 2026a) identified a dietary shift at 39 cm SVL. We therefore evaluated how this biologically meaningful threshold relates to the clusters obtained here and considered its implications when interpreting our results. The largest individual sampled (67.3 cm SVL) corresponds to a large adult (106 cm total length). The stable isotope analyses described below were conducted on the following consumer groups: JGS (four size classes), fish (six species), turtles, frogs, tadpoles, freshwater crabs, prawns, aquatic insects, and aquatic gastropods (Appendix S1: Table S1).

Stable isotope Bayesian ellipses approach

Isotopic niches were quantified using Bayesian standard ellipses (SEAB) implemented in the SIBER (2.1.9) package (Jackson et al., 2011) in R (version 4.3.2). SEAB provides a bivariate estimate of the core isotopic niche while accounting for unequal sample size. Pairwise comparisons of niche widths were based on posterior distributions (10^5 iterations), and differences were considered robust when posterior probabilities $\geq 95\%$. Niche overlap among groups was assessed using standard ellipse area corrected for small sample sizes (SEAC), and total convex hull area (TA) was calculated following Layman et al. (2007).

To compare isotopic niche characteristics among consumer groups, we used three Layman's metrics: the carbon range (CR), the nitrogen range (NR), and the mean nearest neighbor distance (NND), representing basal carbon-source diversity, vertical trophic structure, and trophic redundancy, respectively. Metrics were estimated using nonparametric bootstrap resampling (10,000 iterations), standardized to the smallest sample size in the dataset ($n = 9$). Groups with insufficient sample size (catfish, tadpoles) were excluded from comparisons. Posterior probabilities from bootstrap distributions were used to evaluate differences between groups, with $\geq 95\%$ indicating robust contrasts.

Because the “aquatic insects” category pooled taxa with heterogeneous trophic ecology, we tested whether this grouping obscured potential overlap with salamanders by subdividing insect samples according to $\delta^{13}\text{C}$ values. Both subsets remained isotopically distinct from salamanders, confirming the robustness of group-level comparisons (Appendix S1: Figure S2).

Trophic position and carbon fluxes across the community

The TP of organisms composing the studied community was calculated using the tRophicPosition package (Quezada-Romegialli et al., 2018). TP was estimated using a dual baseline Bayesian approach, considering two isotopic baselines (aquatic with periphyton and terrestrial with leaf litter) and trophic discrimination factors (TDFs) from muscle tissues of $\delta^{15}\text{N}$ (2.9 ± 0.32) and $\delta^{13}\text{C}$ (1.3 ± 0.3) (McCutchan et al., 2003). The parameter λ , corresponding to the TP of the baselines, was set to 1. In addition, the model estimates the proportional contribution of the terrestrial baseline (α) to each consumer by partitioning their $\delta^{13}\text{C}$ values between the two sources, while accounting for trophic discrimination. Thus, α represents the estimated fraction of carbon derived from terrestrial organic matter in each consumer's diet.

Contribution of Japanese giant salamanders to food web structure along ontogeny

To explore the global contribution of JGSs of different sizes to the community structure, we quantified their contribution to emergent community-level trophic structure by evaluating how key isotopic metrics proposed by Layman et al. (2007) change under different community configurations. The metrics were calculated for four community scenarios: all salamander groups included (All), exclusion of only the largest salamanders (JGS Group 4; NL), inclusion of only smaller salamanders (Groups 1 and 2; OS), and no salamanders (NS). Metrics were calculated using a Bayesian approach with the SIBER package (Jackson et al., 2011). Within $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space, NR and CR quantify vertical trophic structure and basal carbon-source diversity, respectively; TA is the convex hull area encompassing all points and reflects overall trophic niche width; and centroid distance (CD) is the mean Euclidean distance to the community centroid, indexing trophic diversity. Two additional metrics characterize niche packing and redundancy: mean NND, which measures how closely species are grouped in isotopic space, and the SD of NND (SDNND), which describes the evenness of species spacing and is less sensitive to sample size than NND alone.

RESULTS

Isotopic niche width and shape

Niche comparison among size classes in Japanese giant salamanders

The isotopic niche width comparison among the four size groups of JGSs revealed that all groups had similar isotopic niche width (Figure 2; Appendix S1: Figure S1 and Table S3). Niche areas estimated using alternative metrics were similar for the four groups (SEA , SEA_C , SEA_B , and TA ; Appendix S1: Tables S3 and S7). Group 1 tended to show a slightly wider niche than Groups 2 and 3, but with posterior probabilities below the robustness threshold (90.9% and 88.2% of the posterior draws, respectively). CR values declined with increasing body size of giant salamanders, with only the contrast between Groups 1 and 4 reaching a significant difference (97.5% probability) (Figure 3a; Appendix S1: Table S8). By contrast, NR values were similar among groups, and no pairwise comparison indicated significant differences (Figure 3b; Appendix S1: Tables S4 and S9).

Interspecific niche width comparison

Across all consumer groups, giant salamander size classes consistently had larger isotopic niches than dark chubs, catfish and tadpoles (>95.9%). Groups 1 and 3 had larger niches than Chinese minnows (98.3% and 95.3%, respectively). Freshwater crabs and turtles displayed broader niches than most taxa, while prawns exceeded all groups except aquatic insects and turtles (Appendix S1: Table S7).

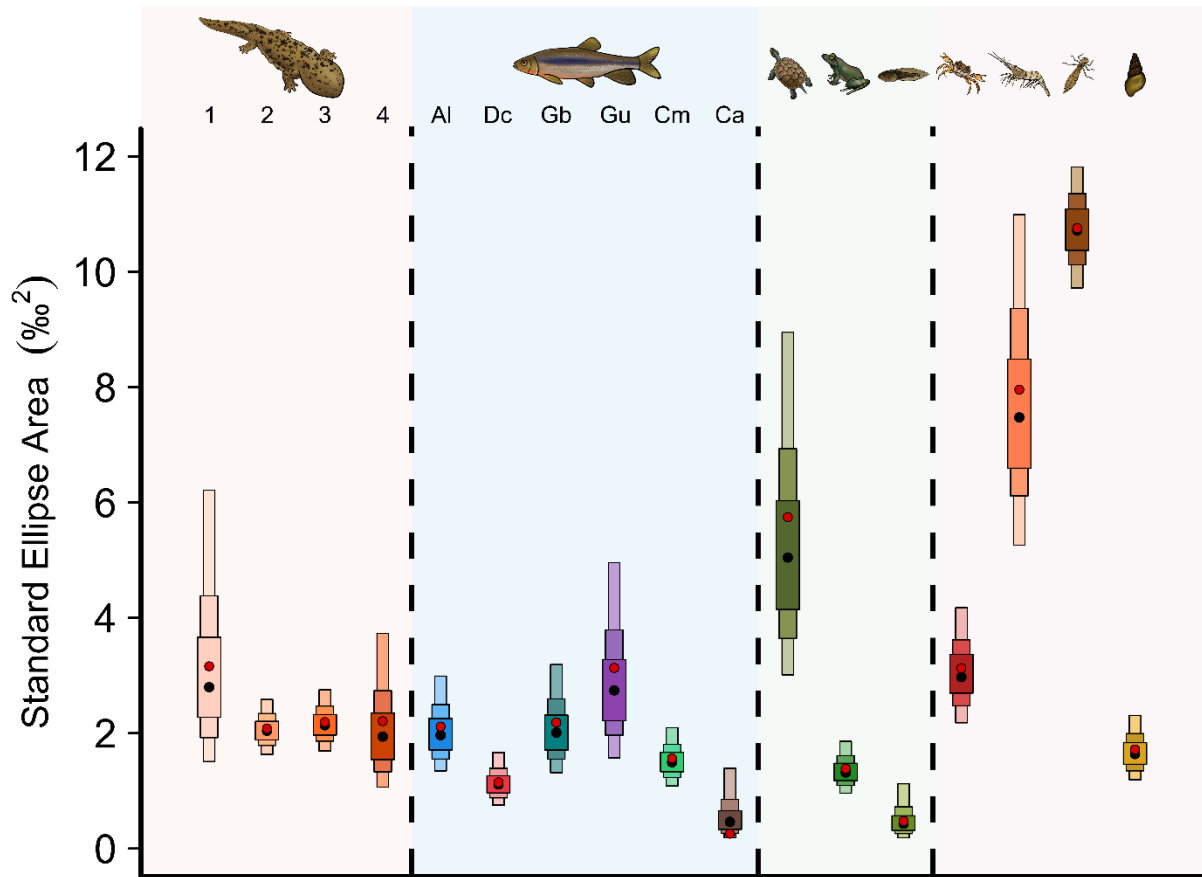


FIGURE 2 Standard ellipse area estimated for all consumers with the Bayesian models (SEA_B). Black dots represent the mode and red dots the standard ellipse area corrected for small sample sizes (SEA_C). Organism groups are arranged from left to right as follows: four Japanese giant salamander size classes (from smallest to largest), six fish groups (Al, alevins; Dc, dark chubs; Gb, lizard gobies; Gu, gudgeons; Cm, Chinese minnows; Ca, catfish), turtles, frogs, tadpoles, freshwater crabs, prawns, aquatic insects, and gastropods. Vertical dashed lines delineate different organism groups: Japanese giant salamanders (light orange background), fish (light blue), other vertebrate consumers (light green), and invertebrates (light gray). For each group, colored rectangles indicate the 50%, 75%, and 95% Bayesian credible intervals. Illustrations created by Juliette Vallin.

Isotopic niche overlaps

Among Japanese giant salamander size classes

Patterns of isotopic niche overlaps among the four groups of giant salamanders, assessed using SEA_C , indicated low overlaps. Group 1 of JGSs (the smallest) shared only 5.6% of their niche with Group 2, and Group 2 shared 13.7% of their niche with Group 3 (Appendix S1: Figure S2 and Table S5). There was no overlap among the other groups of JGSs.

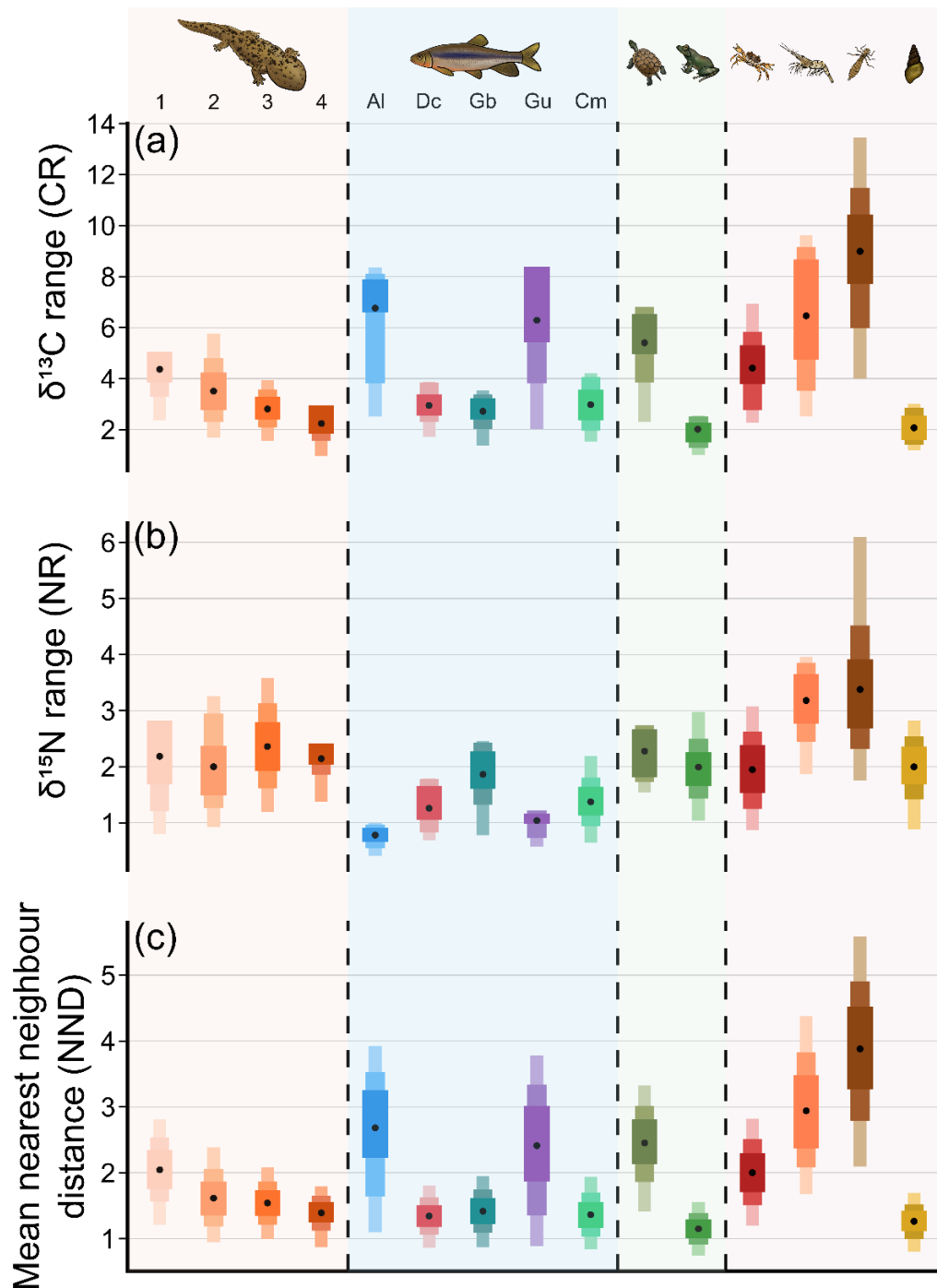


FIGURE 3 Results of three Layman's metrics estimated through bootstrapping for each group found in the community. (a) CR = $\delta^{13}\text{C}$ range (%); (b) NR = $\delta^{15}\text{N}$ range (%); (c) NND = mean nearest neighbor distance (Euclidean distance). In each graph, organism groups are arranged from left to right as follows: four Japanese giant salamander size classes (from smallest to largest), five fish groups (Al, alevins; Dc, dark chubs; Gb, lizard gobies; Gu, gudgeons; Cm, Chinese minnows), turtles, frogs, freshwater crabs, prawns, aquatic insects, and gastropods. Vertical dashed lines delineate different organism groups: Japanese giant salamanders (light orange background), fish (light blue), other vertebrate consumers (light green), and invertebrates (light grey). Illustrations created by Juliette Vallin.

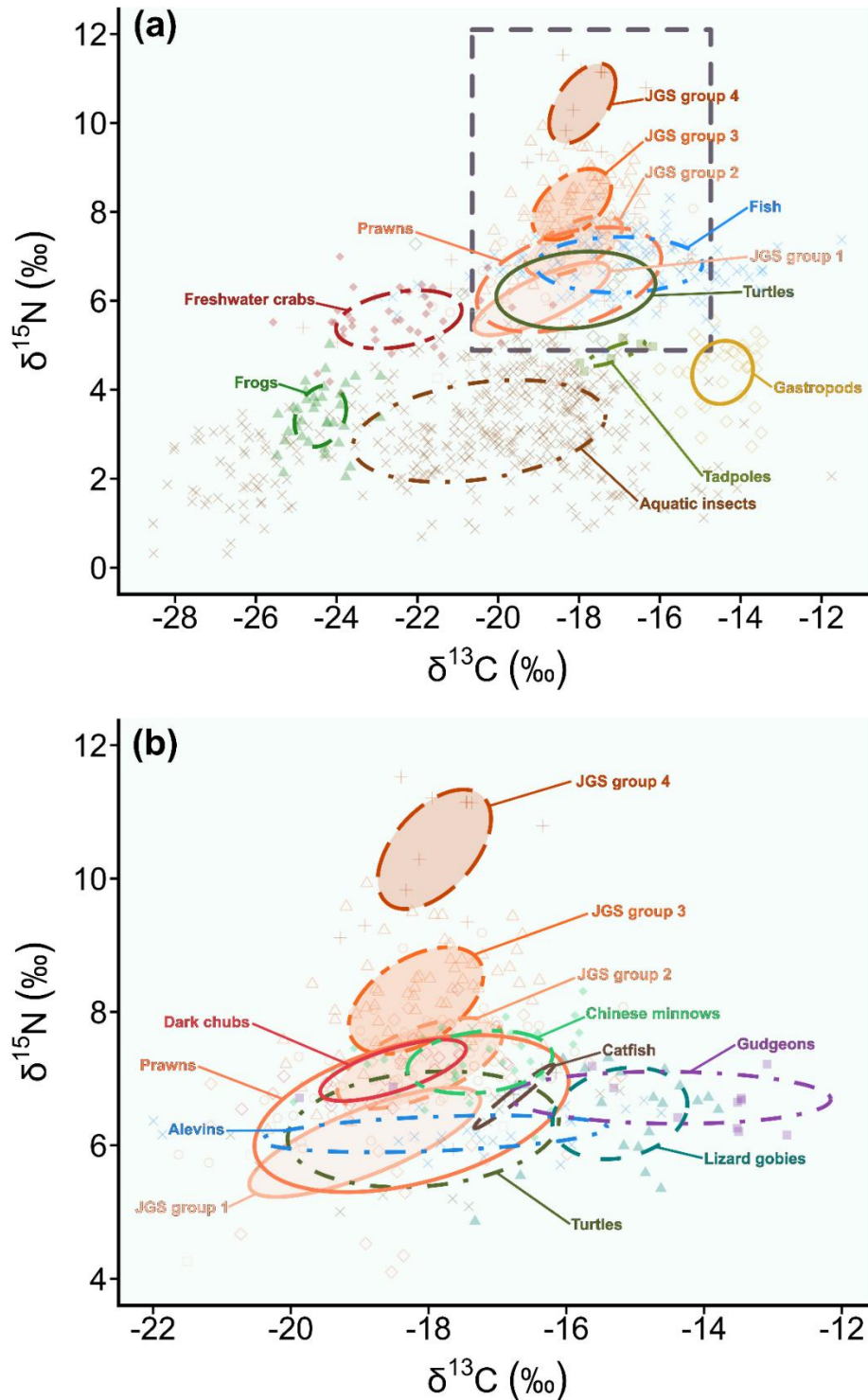


FIGURE 4 Stable isotope bi-plot illustrating the isotopic niches of consumers within the food web dominated by Japanese giant salamanders. (a) Isotopic niches of all consumer groups, where the category “fish” includes all fish species found in the system. (b) Zoom on the area where isotopic niches overlap (gray dashed rectangle), with the “fish” category subdivided into all constituent species for finer resolution. The lines represent the standard ellipse areas corrected for small sample size (SEAC), providing a measure of the isotopic niche width for each group.

Niche overlap between Japanese giant salamanders and other consumers

Isotopic niche overlap between salamanders and other consumers decreased markedly with increasing salamander body size, with a particularly marked effect in larger salamanders (Groups 3 and 4). Giant salamander Group 1 shared 90.7%, 79.4%, 35.2%, and 3.1% of their isotopic niche with the prawns, turtles, alevins, and Chinese minnows, respectively. Giant salamander Group 2 shared 83.5%, 50.3%, 38.9%, and 35.6% of their niche with prawns, dark chubs, Chinese minnows, and turtles, respectively. Giant salamander Group 3 overlapped only with prawns (4.4%), and Group 4 showed no overlap with any other consumer (Figure 4; Appendix S1: Table S5).

Trophic similarities among individuals within each group

Mean NND varied widely among taxa, reflecting differences in trophic redundancy, that is, individuals sharing more similar trophic ecology (Figure 3c; Appendix S1: Table S4). Apart from aquatic insects, prawns and alevins showed the highest NND values, indicating low redundancy and greater trophic distinctiveness among individuals. By contrast, gastropods, frogs, and several fish species exhibited the lowest NND values, consistent with more homogeneous trophic ecology. Salamander groups showed intermediate values, with NND gradually decreasing from the smallest to the largest size classes, but without significant differences (Appendix S1: Table S10).

Contribution of the Japanese giant salamander to community-level food web characteristics

JGSs had a strong and progressive contribution to all community-wide metrics, with each size group contributing to changes in trophic structure (Appendix S1: Figure S3). All groups consistently increased TA and expanded the $\delta^{15}\text{N}$ range (NR), whereas their presence reduced the community CD, indicating shifts in the relative positioning of taxa within isotopic space.

Communities including all salamander size classes exhibited the largest TA (39.70) and NR (7.35), and these values declined stepwise when large individuals were removed (Appendix S1: Figure S3 and Table S4), highlighting the disproportionate contribution of larger size classes to vertical trophic structure. Excluding only the largest group produced a moderate reduction, whereas removing both large groups resulted in TA and NR values similar to communities without salamanders. Conversely, CD remained consistently lower when salamanders were present, even after excluding larger size classes. No significant differences were detected among the remaining Layman metrics.

Trophic position and contribution of carbon sources

Trophic position

TP increased consistently with salamander body size (Figure 5a; Appendix S1: Table S6). Pairwise comparisons showed that Group 1 had a significantly lower TP than both Groups 3 and 4 (95% and 99.6% probability, respectively), and that Group 2 also had a significantly lower TP than Group 4 (99% probability) (Appendix S1: Table S11). At the top of the food web, the largest group of giant salamanders (Group 4) exhibited a significantly higher TP than

all other groups and species, with the exception of JGS Group 3 (94.2% probability). Gastropods had significantly lower TP values than most species, differing only nonsignificantly from frogs, tadpoles, and aquatic insects.

Contribution of carbon sources to consumers in the food web

The α values (representing the contribution of terrestrial versus aquatic carbon sources) indicated a slightly higher contribution from aquatic sources to the isotopic carbon composition of JGSs. However, α values did not differ significantly among giant salamander groups. Only two groups (frogs and freshwater crabs) had $\alpha > 0.5$ (Figure 5b; Appendix S1: Table S6). Gastropods had significantly lower α values than all other species, except gudgeons, while frogs had significantly higher α values than all species, except tadpoles, prawns, and aquatic insects (Appendix S1: Table S12).

DISCUSSION

Using carbon and nitrogen stable isotope analysis, we provide for the first time a whole-community characterization of trophic structure in a freshwater food web dominated by giant salamanders, unusual amphibian top predators. Our results support the central hypothesis that extreme body size variation in giant salamanders is likely a key structuring factor of food webs' architecture, emphasizing the importance of "giant" predators in terms of conservation. As salamanders grow, their niche gradually shifts from substantial overlap with mesopredators to a distinct top predator role, reshaping trophic hierarchies and the distribution of interactions across the community. This highlights the functional importance of large-bodied amphibian predators in river ecosystems and aligns with broader evidence that large individuals of long-lived species can structure food webs and generate ecosystem-wide effects (Kopf et al., 2024). This aligns with results supporting a key functional role of top predators on other major groups in marine and freshwater environments (Villamarín et al., 2017; Williams et al., 2004). Beyond system-specific insights, our findings underscore the conservation relevance of maintaining threatened top predators because their impact through ontogeny can scale up from individual niche shifts to community-level organization and trophic integrity (Rodríguez-Lozano et al., 2015).

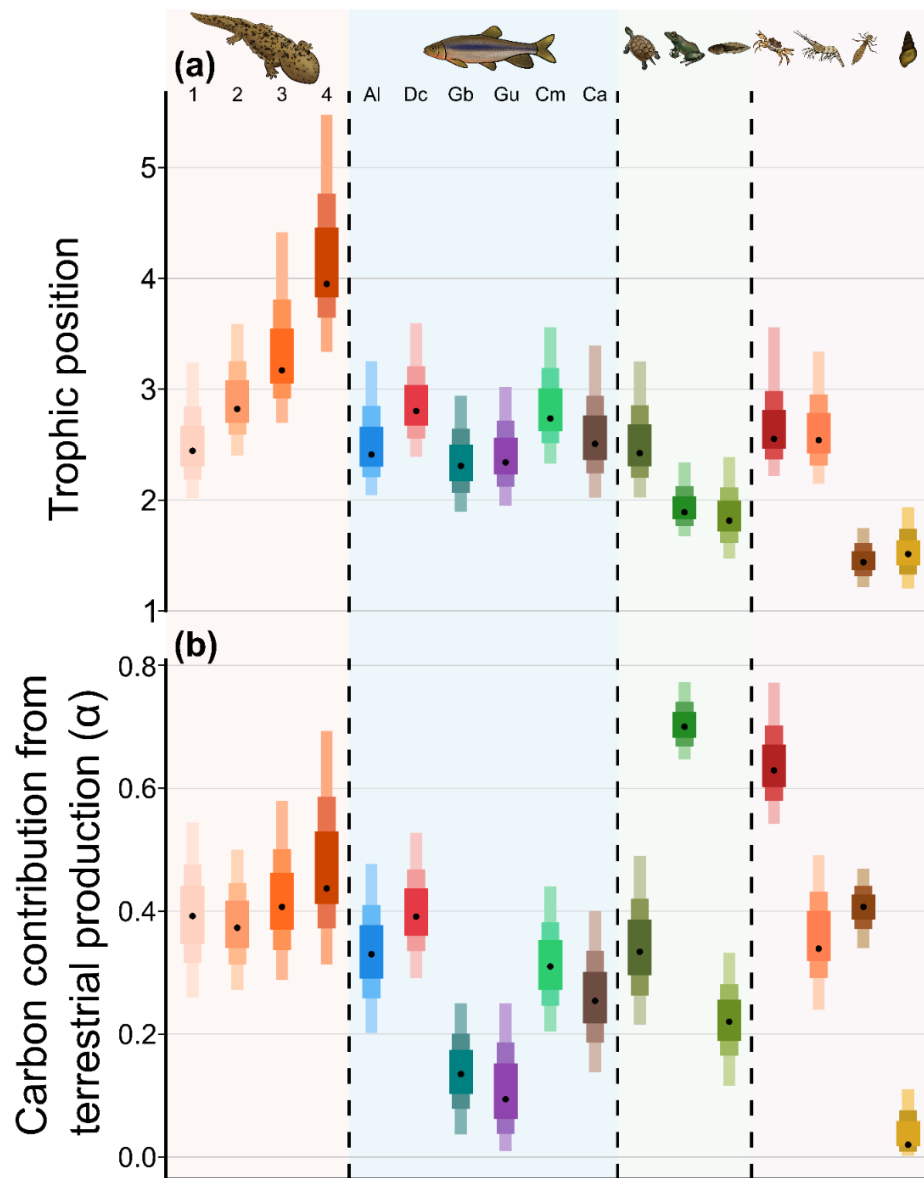


FIGURE 5 Bayesian estimates of trophic position (a) and the proportional contribution of terrestrial carbon sources (α) (b) for all organism groups in the community. An α value of 0 indicates complete reliance on aquatic carbon (periphyton), while $\alpha = 1$ indicates complete reliance on carbon from terrestrial origin (i.e., terrestrial subsidies such as leaf litter feeding the benthic compartment of the river). In each graph, organism groups are arranged from left to right as follows: four Japanese giant salamander size classes (from smallest to largest), six fish groups (Al, alevins; Dc, dark chubs; Gb, lizard gobies; Gu, gudgeons; Cm, Chinese minnows; Ca, catfish), turtles, frogs, tadpoles, freshwater crabs, prawns, aquatic insects, and gastropods. Vertical dashed lines delineate major consumer categories: Japanese giant salamanders (light orange background), fishes (light blue), other vertebrate consumers (light green), and invertebrates (light gray). For each group, colored rectangles indicate the 50%, 75%, and 95% Bayesian credible intervals, while black dots represent the posterior mode. Illustrations created by Juliette Vallin.

Ontogenetic shifts in trophic interactions in the Japanese giant salamander

Like many ectothermic top predators (Radloff et al., 2012; Villamarín et al., 2024), the JGS exhibits substantial ontogenetic body size variation and our results indicate that this translates into clear shifts in isotopic niches, in line with their increase in TP. Smaller individuals overlapped isotopically with mesopredators and fed at similar trophic levels, consistent with stronger potential for competitive interactions. By contrast, larger salamanders occupied distinct niches at the highest trophic levels. This ontogenetic shift, from mesopredator to dominant predator, aligns with patterns found in crocodilians (Villamarín et al., 2018), freshwater fish (Kopf et al., 2025; Ou et al., 2017), and also in other giant salamander species such as the hellbender (*Cryptobranchus alleganiensis*) in North America (Hecht et al., 2017). Such ontogenetic shifts imply both increased variability in resource use (Duret et al., 2026a) and reduced predation risk with growth (Werner & Gilliam, 1984; Wilbur, 1980). Like other traits that promote intraspecific niche differentiation, such as facultative paedomorphosis in amphibians (Denoël & Joly, 2001; Lejeune et al., 2018, 2021), gigantism in JGSs represents a factor of ecological opportunity, allowing individuals to reduce niche overlap with other consumers and to establish themselves as top predators.

Importantly, the pattern we observed reflects niche reconfiguration rather than progressive niche expansion (Nakazawa, 2015; van Leeuwen et al., 2014). In JGSs, prey turnover across size classes appears to dominate, with aquatic insects central in smaller size groups but progressively replaced by larger prey such as fish, freshwater crabs, and frogs (Duret et al., 2026a), with a marked transition occurring around 39 cm SVL. Consistent with this turnover, salamander size groups showed a marked upward shift in $\delta^{15}\text{N}$ with body size, which is in line with the dietary transition previously identified around 39 cm SVL, while isotopic niche breadth at the group level did not increase (i.e., no clear isotopic niche expansion). This pattern is consistent with broader observations in riverine food webs, where trophic niche breadth often does not increase with body size despite shifts in resource use (Keppeler et al., 2026). This suggests that ontogenetic dietary shifts may frequently involve niche reorganization rather than expansion across freshwater taxa. Rather than broadening, resource use appears to be reconfigured across ontogeny: early size groups integrate a taxonomically diverse insect prey base associated with a wide range of $\delta^{13}\text{C}$ values, whereas larger size groups rely more strongly on fish, whose isotopic variability is more constrained. This provides a mechanistic explanation for the observed decline in $\delta^{13}\text{C}$ range (CR) with size (Figure 3a), despite the strong trophic shift in $\delta^{15}\text{N}$. Comparable ontogenetic changes in isotopic position have been reported for other large ectothermic predators, including crocodilians (Santos et al., 2018).

Interspecific competitive trophic interactions

Before reaching large body sizes, JGSs exhibited substantial isotopic niche overlap with other consumers, particularly fishes, turtles, and prawns. Among fishes, overlap with smaller salamanders was mainly restricted to the adults of two species, the Chinese minnow and the dark chub, as well as all alevins of the community. These species rely mainly on aquatic invertebrates (Katano, 1996; Lei et al., 2018), consistent with diets expected for juvenile

salamanders (Duret et al., 2026a), suggesting potential trophic competition through shared prey and similar TPs. Such competition in early life stages may constrain resource availability and influence their ecological performance. Given the central role of both predation and competition in shaping food web structure (Woodward & Hildrew, 2002), our findings support the idea that gigantism may provide an adaptive route to reduce competitive overlap as salamanders grow (Anaya-Rojas et al., 2023).

Contribution of large Japanese giant salamanders to food web structure

Our results suggest that JGSs contribute significantly to the trophic architecture of the aquatic community. All size groups except the smallest significantly and progressively influenced each Layman metric chosen to depict key attributes of food web structure, with the largest individuals driving most of the effects. In particular, salamanders increased total isotopic niche area and NR, consistent with access to higher-trophic-level resources (e.g., fish, frogs, freshwater crabs), and increased food web complexity along its vertical axis, amplified by gigantism (Estes et al., 2011; Rooney et al., 2006). Salamanders also contributed to lowering the mean distance to the centroid among consumers within the food web, indicating a shift in the relative positioning of taxa within isotopic space. Together, the strong contributions to total isotopic niche area, NR, and mean distance to centroid suggest that salamander loss would reduce overall trophic diversity and effectively remove a trophic level from the food web, with potential negative consequences for food web stability and consequently community structure (Pace et al., 1999; Ripple et al., 2014). We therefore suggest that gigantism in this species has effects beyond individual foraging: by enabling the largest giant salamanders to occupy and add an upper trophic layer, it expands community isotopic space and strengthens vertical trophic structure, which can contribute to food web stability and functional integrity (Bascompte et al., 2005). In this context, the largest and oldest individuals play disproportionately important ecological roles. These individuals not only access higher-trophic-level resources but also help maintain food web complexity and vertical structure. Importantly, they may also be particularly vulnerable to anthropogenic pressures, such as habitat degradation or climate change (Duret et al., 2025), which could disproportionately affect the functional integrity of the community. This aligns with the concept of Longevity Conservation, emphasizing the ecological and conservation value of maintaining populations of long-lived and large-bodied organisms within ecosystems (Kopf et al., 2024).

In many river systems, the role of large-bodied top predators is typically fulfilled by fish (Kopf et al., 2025; Ou et al., 2017). By contrast, the studied headwater sections lack such predators, suggesting the presence of an unoccupied trophic niche. Our results indicate that JGSs likely fill this role, acting as dominant apex consumers and structuring trophic interactions across the community. This highlights how taxonomically atypical predators can functionally replace more commonly studied groups, reinforcing the importance of considering functional roles rather than taxonomic identity when examining food web structure. However, this interpretation should be considered in light of the spatial scope of our study. This study was conducted at a single study site, and caution is therefore needed when extrapolating these results to other systems. While JGSs often function as apex predators in freshwater ecosystems, variation in local community composition may influence the strength and structure of trophic

interactions. Future multisite studies would help assess the generality of the patterns observed here.

Carbon sources in the community

Freshwater food webs often rely on a mix of aquatic and terrestrial carbon sources, with the relative importance of each varying across ecosystems (Finlay & Kendall, 2007; Jardine et al., 2017; Polis et al., 1997). In our study system, stable isotope data indicate that most taxa (except frogs and freshwater crabs) relied primarily on aquatic-derived carbon source, highlighting that periphyton is the dominant basal source supporting higher-level consumers, including fish and giant salamanders, and reinforcing its key role in riverine food webs (Chételat et al., 1999). Terrestrial carbon nonetheless contributed through detrital subsidies (leaf litter) feeding benthic detritivores, as well as via frogs which exploit terrestrial prey but may act themselves as a terrestrial subsidy to larger aquatic predators. Interestingly, the terrestrial contribution slightly increased with salamander body size, likely reflecting increased predation on frogs with growth. This ontogenetic expansion toward terrestrial prey underscores the ecological importance of the aquatic-terrestrial habitat connectivity and highlights the conservation value of both riverine and riparian habitats to maintain functional integrity in giant salamander-dominated food webs (Cole et al., 2011). Headwater streams are often characterized by substantial allochthonous inputs, which can contribute to consumer diets through detrital and trophic pathways (Brett et al., 2017; Jardine et al., 2017). Although terrestrial sources contribute notably to the diet of some consumers, their overall contribution remains lower than that of aquatic-derived carbon (generally $\alpha < 0.4$). However, the maintenance of riparian vegetation is still important to sustain these energy subsidies and the functional integrity of food webs dominated by JGSs. Previous studies have shown that large-bodied consumers can rely substantially on terrestrial carbon sources, sometimes to a greater extent than observed here (Jardine et al., 2017). By contrast, although terrestrial contributions increased with salamander body size in our study, aquatic sources remained dominant, suggesting that autochthonous production may remain sufficient to support even large predators in this system.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the Hanzaki Research Institute of Japan and the Wakayama Experimental Forest of Hokkaido University for their invaluable support during fieldwork in Japan. Thanks are also given to the Asago City Board of Education and Japan's Agency for Cultural Affairs for granting the necessary research permits. Special thanks go to M. K. Takahashi for his logistical support and assistance in the field. We sincerely thank Juliette Vallin for her outstanding artwork illustrating the community and all species involved in this study. We sincerely thank the two anonymous reviewers and the handling editor for their constructive comments and insightful suggestions, which helped improve the manuscript. Mathieu Denoël and Gilles Lepoint are Research Directors of Fonds de la Recherche Scientifique—FNRS, and Benjamin Lejeune is a Postdoctoral Researcher of Fonds de la Recherche Scientifique – FNRS. Clément Duret is supported by a FRIA doctoral fellowship from the same institution. This work was supported by the “Topsalamander” and “Freshwater

Predator” Fonds spéciaux pour la recherche grants (FOCUS, ULiège) to Mathieu Denoël and Gilles Lepoint, by Fonds de la Recherche Scientifique—FNRS, by Fonds pour la Formation à la Recherche dans l’Industrie et dans l’Agriculture (1.E.058.22F, to Clément Duret) and by the Ministry of Education, Culture, Sports, Science and Technology, Japan Society for the Promotion of Science (JSPS KAKENHI Grant Number 22H04983, 22H05644, and 23K23957 to Osamu Kishida).

AUTHOR CONTRIBUTIONS

Clément Duret, Benjamin Lejeune, and Mathieu Denoël conceived the study and designed the conceptual framework. Mathieu Denoël and Osamu Kishida secured funding. Osamu Kishida and Sumio Okada provided logistical support for field sampling. Clément Duret and Tiphane Bartet conducted the fieldwork. Gilles Lepoint and Keitaro Fukushima supported the processing of stable isotope samples. Clément Duret performed the statistical analyses, wrote the initial draft, and coordinated manuscript revisions. Mathieu Denoël and Benjamin Lejeune contributed to manuscript review and editing. All authors reviewed and approved the final version of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Duret et al., 2026b) are available in Dryad at <https://doi.org/10.5061/dryad.fn2z34v89>.

ORCID

Mathieu Denoël: <https://orcid.org/0000-0002-3586-8323>;

Clément Duret: <https://orcid.org/0000-0002-5809-4826>;

Keitaro Fukushima: <https://orcid.org/0000-0001-5968-5938>;

Osamu Kishida: <https://orcid.org/0000-0002-2663-8155>;

Benjamin Lejeune: <https://orcid.org/0000-0001-6881-8931>;

Gilles Lepoint: <https://orcid.org/0000-0003-4375-0357>

References

- Anaya-Rojas, J. M., R. D. Bassar, B. Matthews, J. F. Goldberg, L. King, D. Reznick, and J. Travis. 2023. “Does the Evolution of Ontogenetic Niche Shifts Favour Species Coexistence? An Empirical Test in Trinidadian Streams.” *Journal of Animal Ecology* 92: 1601–12. <https://doi.org/10.1111/1365-2656.13912>.
- Bascompte, J., C. J. Meli_an, and E. Sala. 2005. “Interaction Strength Combinations and the Overfishing of a Marine Food Web.” *Proceedings of the National Academy of Sciences* 102: 5443–47. <https://doi.org/10.1073/pnas.0501562102>.
- Belouard, N., E. J. Petit, J. Cucherousset, and J.-M. Paillisson. 2024. “Variation of the Stable Isotope Niches of Native Amphibians in Ponds Invaded by the Red Swamp Crayfish.” *NeoBiota* 93: 245–262. <https://doi.org/10.3897/neobiota.93.120477>.
- Bissattini, A. M., P. J. Haubrock, V. Buono, P. Balzani, N. Borgianni, L. Stellati, A. F. Inghilesi, et al. 2021. “Trophic Structure of a Pond Community Dominated by an Invasive Alien Species: Insights from Stomach Content and Stable Isotope Analyses.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 948–963. <https://doi.org/10.1002/aqc.3530>.
- Bonett, R. M., N. M. Ledbetter, A. J. Hess, M. A. Herrboldt, and M. Denoël. 2022. “Repeated Ecological and Life Cycle Transitions Make Salamanders an Ideal Model for Evolution and Development.” *Developmental Dynamics* 251: 957–972. <https://doi.org/10.1002/dvdy.373>.
- Brett, M. T., S. E. Bunn, S. Chandra, A. W. E. Galloway, F. Guo, M. J. Kainz, P. Kankaala, et al. 2017. “How Important Are Terrestrial Organic Carbon Inputs for Secondary Production in Freshwater Ecosystems?” *Freshwater Biology* 62: 833–853. <https://doi.org/10.1111/fwb.12909>.
- Brose, U. 2010. “Body-Mass Constraints on Foraging Behaviour Determine Population and Food-Web Dynamics.” *Functional Ecology* 24: 28–34. <https://doi.org/10.1111/j.1365-2435.2009.01618.x>.
- Charrad, M., N. Ghazzali, V. Boiteau, and A. Niknafs. 2014. “NbClust: An R Package for Determining the Relevant Number of Clusters in a Data Set.” *Journal of Statistical Software* 61: 1–36. <https://doi.org/10.18637/jss.v061.i06>.
- Chételat, J., F. R. Pick, A. Morin, and P. B. Hamilton. 1999. “Periphyton Biomass and Community Composition in Rivers of Different Nutrient Status.” *Canadian Journal of Fisheries and Aquatic Sciences* 56: 560–69. <https://doi.org/10.1139/f98-197>.
- Claessen, D., C. Van Oss, A. M. de Roos, and L. Persson. 2002. “The Impact of Size-Dependent Predation on Population Dynamics and Individual Life History.” *Ecology* 83: 1660–75. [https://doi.org/10.1890/0012-9658\(2002\)083\[1660:TIOSDP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1660:TIOSDP]2.0.CO;2).

- Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. "Ecological Community Description Using the Food Web, Species Abundance, and Body Size." *Proceedings of the National Academy of Sciences* 100: 1781–86. <https://doi.org/10.1073/pnas.232715699>.
- Cole, J. J., S. R. Carpenter, J. Kitchell, M. L. Pace, C. T. Solomon, and B. Weidel. 2011. "Strong Evidence for Terrestrial Support of Zooplankton in Small Lakes Based on Stable Isotopes of Carbon, Nitrogen, and Hydrogen." *Proceedings of the National Academy of Sciences* 108: 1975–80. <https://doi.org/10.1073/pnas.1012807108>.
- Coplen, T. B. 2011. "Guidelines and Recommended Terms for Expression of Stable-Isotope-Ratio and Gas-Ratio Measurement Results." *Rapid Communications in Mass Spectrometry* 25: 2538–60. <https://doi.org/10.1002/rcm.5129>.
- de Roos, A. M., and L. Persson. 2013. *Population and Community Ecology of Ontogenetic Development*. Princeton: Princeton University Press.
- Denoël, M., and P. Joly. 2001. "Adaptive Significance of Facultative Paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): Resource Partitioning in an Alpine Lake." *Freshwater Biology* 46: 1387–96. <https://doi.org/10.1046/j.1365-2427.2001.00762.x>.
- Duret, C., T. Bartet, A. Hambuckers, O. Kishida, S. Okada, Y. Taguchi, M. K. Takahashi, and M. Denoël. 2025. "Loss of Habitat Suitability and Distribution Range of the Endangered Japanese Giant Salamander under Climate Change." *Frontiers of Biogeography* 18: e133105. <https://doi.org/10.21425/fob.18.133105>.
- Duret, C., B. Lejeune, G. Lepoint, T. Bartet, S. Okada, K. Fukushima, O. Kishida, and M. Denoël. 2026a. "A Giant's Appetite: How Body Size Drives the Diet and Trophic Position of the Japanese Giant Salamander." *Oikos* 2026: e11831. <https://doi.org/10.1002/oik.11831>.
- Duret, C., B. Lejeune, G. Lepoint, T. Bartet, S. Okada, K. Fukushima, O. Kishida, and M. Denoël. 2026b. "Data and Code for: When Giant Amphibians Rule the River: Community Trophic Structure of Japanese Giant Salamander Ecosystems [Dataset]." Dryad. <https://doi.org/10.5061/dryad.fn2z34v89>.
- Echeverria, A., S. Botta, M. Marmontel, G. Melo-Santos, P. Fruet, M. Oliveira-da-Costa, M. Pouilly, J. Di Tullio, and P. A. Van Damme. 2022. "Trophic Ecology of Amazonian River Dolphins from Three Rivers in Brazil and Bolivia." *Mammalian Biology* 102: 1687–96. <https://doi.org/10.1007/s42991-022-00267-x>.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333: 301–6. <https://doi.org/10.1126/science.1205106>.
- Finlay, J. C., and C. Kendall. 2007. "Stable Isotope Tracing of Temporal and Spatial Variability in Organic Matter Sources to Freshwater Ecosystems." In *Stable Isotopes in Ecology and Environmental Science*, 2nd ed., edited by R. Michener and K. Lajtha, 283–333. Oxford: Blackwell Publishing Ltd.

- Gao, K.-Q., and N. H. Shubin. 2003. "Earliest Known Crown-Group Salamanders." *Nature* 422: 424–28. <https://doi.org/10.1038/nature01491>.
- Hammerschlag, N., O. J. Schmitz, A. S. Flecker, K. D. Lafferty, A. Sih, T. B. Atwood, A. J. Gallagher, D. J. Irschick, R. Skubel, and S. J. Cooke. 2019. "Ecosystem Function and Services of Aquatic Predators in the Anthropocene." *Trends in Ecology & Evolution* 34: 369–383. <https://doi.org/10.1016/j.tree.2019.01.005>.
- Hecht, K. A., M. A. Nickerson, and P. B. Colclough. 2017. "Hellbenders (*Cryptobranchus alleganiensis*) May Exhibit an Ontogenetic Dietary Shift." *Southeastern Naturalist* 16: 157–162. <https://doi.org/10.1656/058.016.0204>.
- Heim, N. A., M. L. Knope, E. K. Schaal, S. C. Wang, and J. L. Payne. 2015. "Cope's Rule in the Evolution of Marine Animals." *Science* 347: 867–870. <https://doi.org/10.1126/science.1260065>.
- Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. "Comparing Isotopic Niche Widths Among and Within Communities: SIBER – Stable Isotope Bayesian Ellipses in R." *Journal of Animal Ecology* 80: 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>.
- Jardine, T. D., T. S. Rayner, N. E. Pettit, D. Valdez, D. P. Ward, G. Lindner, M. M. Douglas, and S. E. Bunn. 2017. "Body Size Drives Allochthony in Food Webs of Tropical Rivers." *Oecologia* 183: 505–517. <https://doi.org/10.1007/s00442-016-3786-z>.
- Katano, O. 1996. "Foraging Tactics and Home Range of Dark Chub in a Japanese River." *Oecologia* 106: 199–205. <https://doi.org/10.1007/BF00328599>.
- Kawai, T., and K. Tanida. 2018. *Aquatic Insects of Japan: Manual with Keys and Illustrations*, 2nd ed. Kanagawa: Tokai University Press.
- Keppeler, F. W., T. Giarrizzo, C. G. Montaña, A. Adite, Ş. Akın, R. Angelini, C. C. Arantes, et al. 2026. "What Determines Trophic Niche Breadth? A Global Analysis of Freshwater Fishes Using Isospaces." *Reviews in Fish Biology and Fisheries* 36: 13. <https://doi.org/10.1007/s11160-025-10023-2>.
- Kopf, R. K., S. Banks, L. J. N. Brent, P. Humphries, C. J. Jolly, P. C. Lee, O. J. Luiz, D. Nimmo, and K. O. Winemiller. 2024. "Loss of Earth's Old, Wise, and Large Animals." *Science* 387(6729):eado2705. <https://doi.org/10.1126/science.ado2705>.
- Kopf, R. K., L. McPhan, P. J. McInerney, B. Zampatti, J. Thiem, W. Koster, G. L. Butler, N. Bond, and R. M. Thompson. 2025. "Intraspecific Body Size Determines Isotopic Trophic Structure of a Large River Fish Community." *Journal of Animal Ecology* 94: 1435–48. <https://doi.org/10.1111/1365-2656.70069>.
- Layman, C. A., D. A. Arrington, C. G. Montaña, and D. M. Post. 2007. "Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure?" *Ecology* 88: 42–48. [https://doi.org/10.1890/0012-9658\(2007\)88\[42:CSIRPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2).

- Lei, J., W. Xiong, X.-Y. Sui, and Y. F. Chen. 2018. "Feeding Habits of the Chinese Minnow *Rhynchocypris oxycephalus* (Sauvage & Dabry de Thiersant, 1874) from the Upper Yangtze River, China." *Journal of Applied Ichthyology* 34: 550–55. <https://doi.org/10.1111/jai.13597>.
- Lejeune, B., L. Bissey, E. A. Didaskalou, N. Sturaro, G. Lepoint, and M. Denoël. 2021. "Progenesis as an Intrinsic Factor of Ecological Opportunity in a Polyphenic Amphibian." *Functional Ecology* 35: 546–560. <https://doi.org/10.1111/1365-2435.13708>.
- Lejeune, B., N. Sturaro, G. Lepoint, and M. Denoël. 2018. "Facultative Paedomorphosis as a Mechanism Promoting Intraspecific Niche Differentiation." *Oikos* 127: 427–439. <https://doi.org/10.1111/oik.04714>.
- Matsumoto, R., S.-i. Fujiwara, and S. E. Evans. 2024. "The Anatomy and Feeding Mechanism of the Japanese Giant Salamander (*Andrias japonicus*)." *Journal of Anatomy* 244: 679–707. <https://doi.org/10.1111/joa.14004>.
- McCauley, D. J., H. S. Young, R. B. Dunbar, J. A. Estes, B. X. Semmens, and F. Micheli. 2012. "Assessing the Effects of Large Mobile Predators on Ecosystem Connectivity." *Ecological Applications* 22: 1711–17. <https://doi.org/10.1890/11-1653.1>.
- McCutchan, J. H., W. M. Lewis, Jr., C. Kendall, and C. C. McGrath. 2003. "Variation in Trophic Shift for Stable Isotope Ratios of Carbon, Nitrogen, and Sulfur." *Oikos* 102: 378–390. <https://doi.org/10.1034/j.1600-0706.2003.12098.x>.
- Nakazawa, T. 2015. "Ontogenetic Niche Shifts Matter in Community Ecology: A Review and Future Perspectives." *Population Ecology* 57: 347–354. <https://doi.org/10.1007/s10144-014-0448-z>.
- Okada, S., T. Utsunomiya, T. Okada, Z. I. Felix, and F. Ito. 2008. "Characteristics of Japanese Giant Salamander (*Andrias japonicus*) Populations in Two Small Tributary Streams in Hiroshima Prefecture, Western Honshu, Japan." *Herpetological Conservation and Biology* 3: 192–202.
- Ou, C., C. G. Montaña, and K. O. Winemiller. 2017. "Body Size–Trophic Position Relationships among Fishes of the Lower Mekong Basin." *Royal Society Open Science* 4: 160645. <https://doi.org/10.1098/rsos.160645>.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. "Trophic Cascades Revealed in Diverse Ecosystems." *Trends in Ecology & Evolution* 14: 483–88. [https://doi.org/10.1016/S0169-5347\(99\)01723-1](https://doi.org/10.1016/S0169-5347(99)01723-1).
- Parnell, A. C., R. Inger, S. Bearhop, and A. L. Jackson. 2010. "Source Partitioning Using Stable Isotopes: Coping with Too Much Variation." *PLoS One* 5: e9672. <https://doi.org/10.1371/journal.pone.0009672>.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. "Toward an Integration of Landscape and Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs." *Annual Review*

- of Ecology, Evolution, and Systematics* 28: 289–316.
<https://doi.org/10.1146/annurev.ecolsys.28.1.289>.
- Post, D. M. 2002. “Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions.” *Ecology* 83: 703–718. [https://doi.org/10.1890/0012-9658\(2002\)29083%5B0703%3AUSITET%5D2.0.CO%3B2](https://doi.org/10.1890/0012-9658(2002)29083%5B0703%3AUSITET%5D2.0.CO%3B2).
- Quezada-Romegialli, C., A. L. Jackson, B. Hayden, K. K. Kahilainen, C. Lopes, and C. Harrod. 2018. “tRophicPosition, an R Package for the Bayesian Estimation of Trophic Position from Consumer Stable Isotope Ratios.” *Methods in Ecology and Evolution* 9: 1592–99. <https://doi.org/10.1111/2041-210X.13009>.
- Radloff, F. G. T., K. A. Hobson, and A. J. Leslie. 2012. “Characterising Ontogenetic Niche Shifts in Nile Crocodile Using Stable Isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) Analyses of Scute Keratin.” *Isotopes in Environmental and Health Studies* 48: 439–456. <https://doi.org/10.1080/10256016.2012.667808>.
- Rejas, D., T. Oberdorff, S. A. J. Declerck, and M. Winder. 2023. “The Introduced *Arapaima gigas* in the Bolivian Amazon: Trophic Position and Isotopic Niche Overlap with Native Species.” *Ecology of Freshwater Fish* 32: 926–937. <https://doi.org/10.1111/eff.12734>.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, et al. 2014. “Status and Ecological Effects of the World’s Largest Carnivores.” *Science* 343: 1241484. <https://doi.org/10.1126/science.1241484>.
- Rodríguez-Lozano, P., I. Verkaik, M. Rieradevall, and N. Prat. 2015. “Small but Powerful: Top Predator Local Extinction Affects Ecosystem Structure and Function in an Intermittent Stream.” *PLoS One* 10: e0117630. <https://doi.org/10.1371/journal.pone.0117630>.
- Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. “Structural Asymmetry and the Stability of Diverse Food Webs.” *Nature* 442: 265–69. <https://doi.org/10.1038/nature04887>.
- Santos, X., S. Navarro, J. C. Campos, C. Sanpera, and J. C. Brito. 2018. “Stable Isotopes Uncover Trophic Ecology of the West African Crocodile (*Crocodylus suchus*).” *Journal of Arid Environments* 148: 6–13. <https://doi.org/10.1016/j.jaridenv.2017.09.008>.
- Tago, K. 1931. “The Salamanders of Japan.” Geisho-Do (in Japanese).
- Tochimoto, T. 2002. “Studies of the Japanese Giant Salamanders. X. Food Habits I.” *Hyogo Biology* 12: 134–39 (in Japanese).
- Unger, S. D., L. A. Williams, L. Diaz, and C. B. Jachowski. 2020. “DNA Barcoding to Assess Diet of Larval Eastern Hellbenders in North Carolina.” *Food Webs* 22: e00134. <https://doi.org/10.1016/j.fooweb.2019.e00134>.
- van Leeuwen, A., M. Huss, A. Gårdmark, and A. M. de Roos. 2014. “Ontogenetic Specialism in Predators with Multiple Niche Shifts Prevents Predator Population Recovery and Establishment.” *Ecology* 95: 2409–22. <https://doi.org/10.1890/13-0843.1>.

- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. "The River Continuum Concept." *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–37. <https://doi.org/10.1139/f80-017>.
- Vermeij, G. J. 2012. "The Evolution of Gigantism on Temperate Seashores." *Biological Journal of the Linnean Society* 106: 776–793. <https://doi.org/10.1111/j.1095-8312.2012.01897.x>.
- Vermeij, G. J. 2016. "Gigantism and Its Implications for the History of Life." *PLoS One* 11: e0146092. <https://doi.org/10.1371/journal.pone.0146092>.
- Villamarín, F., T. D. Jardine, S. E. Bunn, A. Malvasio, C. I. Piña, C. M. Jacobi, D. D. Araújo, et al. 2024. "Body Size Predicts Ontogenetic Nitrogen Stable-Isotope ($\delta^{15}\text{N}$) Variation, but Has Little Relationship with Trophic Level in Ectotherm Vertebrate Predators." *Scientific Reports* 14: 14102. <https://doi.org/10.1038/s41598-024-61969-5>.
- Villamarín, F., T. D. Jardine, S. E. Bunn, B. Marioni, and W. E. Magnusson. 2017. "Opportunistic Top Predators Partition Food Resources in a Tropical Freshwater Ecosystem." *Freshwater Biology* 62: 1389–1400. <https://doi.org/10.1111/fwb.12952>.
- Villamarín, F., T. D. Jardine, S. E. Bunn, B. Marioni, and W. E. Magnusson. 2018. "Body Size Is More Important than Diet in Determining Stable-Isotope Estimates of Trophic Position in Crocodilians." *Scientific Reports* 8: 2020. <https://doi.org/10.1038/s41598-018-19918-6>.
- Werner, E. E., and J. F. Gilliam. 1984. "The Ontogenetic Niche and Species Interactions in Size-Structured Populations." *Annual Review of Ecology and Systematics* 15: 393–425.
- Wilbur, H. M. 1980. "Complex Life Cycles." *Annual Review of Ecology and Systematics* 11: 67–93.
- Williams, T. M., J. A. Estes, D. F. Doak, and A. M. Springer. 2004. "Killer Appetites: Assessing the Role of Predators in Ecological Communities." *Ecology* 85: 3373–84. <https://doi.org/10.1890/03-0696>.
- Woodward, G., B. Ebenman, M. C. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, P. H. Warren, P. C. de Ruiter, V. Wolters, and J. C. Moore. 2005. "Body Size Determinants of the Structure of and Dynamics of Ecological Networks: Scaling from the Individual to the Ecosystem." In *Dynamic Food Webs – Multispecies Assemblages, Ecosystem Development and Environmental Change*, edited by P. C. de Ruiter, V. Wolters, and J. C. Moore, 179–197. Amsterdam: Elsevier.
- Woodward, G., and A. G. Hildrew. 2002. "Food Web Structure in Riverine Landscapes" *Freshwater Biology* 47: 777–798. <https://doi.org/10.1046/j.1365-2427.2002.00908.x>.