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Too many dams: habitat fragmentation threatens the future of the Japanese giant salamander

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ABSTRACT

Habitat fragmentation is a major driver of global biodiversity loss, and amphibians are particularly sensitive to this threat. In riverine ecosystems, dams cause longitudinal disconnection, especially affecting fully aquatic species. Across North America, China, and Japan, giant salamanders inhabit rivers where they exert key ecological roles. As strictly aquatic species, dams may severely reduce habitat connectivity and compromise their long-term population viability. In this context, we assessed the fragmentation risk faced by Japanese giant salamander (*Andrias japonicus*) populations in Japan by compiling a detailed inventory of dams in eight watersheds where the species occurs. We adapted a Dam Fragmentation Index (DFI), taking into account density and height of dams, and the presence of fishways, to quantify fragmentation levels. A total of 2,434 river barriers were identified, with only five percent equipped with fishways potentially usable by giant salamanders. DFI scores indicated moderate to very high fragmentation levels. Moreover, salamander locations were on average at 587 m from barriers. These findings suggest that river fragmentation represents a major threat to the long-term viability of *A. japonicus* populations by disrupting movements needed for breeding and gene flow. Conservation actions are urgently needed, including the implementation of suitable passage structures such as salamander-adapted ladderways, and the integration of this species' ecological needs into future river management plans. Our study provides a new framework to quantify barrier impact on amphibians and highlights the importance of addressing river connectivity for the conservation of freshwater biodiversity.

Keywords: Amphibian ecology, Conservation, Dams, Freshwater ecosystems, Habitat fragmentation, River connectivity

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1. Introduction

Habitat fragmentation is a commonly used umbrella term encompassing two distinct but interrelated processes: habitat loss and fragmentation per se (Fahrig, 2003, 2017; Lindenmayer & Fischer, 2007). While habitat loss refers to the reduction in total habitat area, fragmentation denotes the breaking up of continuous habitats into smaller, isolated patches. Together, these processes are among the primary drivers of global biodiversity decline (Haddad et al., 2015). Over the last decades, this issue has been a central focus in ecology and conservation biology, guiding efforts in protected area delineation, sustainable landscape management, and biodiversity conservation (Driscoll et al., 2013; Fardila et al., 2017; Lindenmayer et al., 2006; Tscharntke et al., 2012). Despite significant progress, the complexity of fragmentation effects — which often depend on spatial scale, landscape context, and species-specific traits — continues to challenge generalizations (Fahrig, 2017; Fischer & Lindenmayer, 2007). Furthermore, fragmentation increasingly interacts with other global pressures such as climate change and land-use intensification (Brook et al., 2008). In riverine systems, some degree of fragmentation occurs naturally (e.g., waterfalls or beaver dams), but human-built infrastructure has dramatically increased fragmentation intensity (Fuller et al., 2015). While much research has focused on terrestrial ecosystems, freshwater systems, especially riverine networks, are now recognized as particularly vulnerable to fragmentation, with dams and other instream barriers severely altering longitudinal connectivity (Fuller et al., 2015; Grill et al., 2019). The density of dams is often very high, resulting in a vast number of barriers for riverine species worldwide (Barbarossa et al., 2020; Carolli et al., 2023; Nilsson et al., 2005; Spinti et al., 2023). Despite growing recognition of these impacts, small and medium-sized dams remain understudied compared to large hydropower infrastructures, even though their cumulative ecological effects can be significant (Fencl et al., 2015; Grill et al., 2015).

Freshwater ecosystems, including riverine systems, are among the most biodiverse and ecologically valuable environments on Earth (Harrison et al., 2010; Strayer & Dudgeon, 2010; Wetzel, 2001). They provide essential ecosystem services such as water supply, nutrient cycling, flood regulation, and habitats for a wide array of aquatic and riparian species (Dudgeon et al., 2006). Currently, very few rivers remain free-flowing, especially in developed and densely populated regions (Baird et al., 2025; Grill et al., 2019; Spinti et al., 2023). Anthropogenic fragmentation developed rapidly and disrupts the natural flow regime, sediment transport, and connectivity essential for aquatic and riparian biodiversity (Fischer & Lindenmayer, 2007; Grill et al., 2019; Liermann et al., 2012) and more globally for biodiversity conservation (Correa Ayram et al., 2016). This disruption impedes species movement, isolates populations, reduces gene flow, and can ultimately lead to local extinctions, particularly for species with limited dispersal abilities over land or specialized habitat requirements, such as many amphibians and fish (Favaro & Moore, 2015; Fuller et al., 2015; Heggenes & Røed, 2006; Hermoso et al., 2011). Furthermore, dam height is a critical factor that strongly influences the degree of river fragmentation (Chan et al., 2025). Ultimately, longitudinal connectivity, i.e. the connection between upstream and downstream sections of river networks, is crucial for the persistence of populations (Fagan, 2002).

Amphibians are experiencing global population declines (Beebee & Griffiths, 2005; Bishop et al., 2012; Luedtke et al., 2023), with habitat loss and fragmentation among the principal drivers (Cushman, 2006; Dare et al., 2020; Hanski, 1998; MacArthur & Wilson, 2001). However, amphibians remain comparatively under-represented in habitat fragmentation research relative to other vertebrate groups (Bista et al., 2022; Liu et al., 2025; Tan et al., 2023). Much of the existing work has focused on terrestrial movements or migrations between aquatic and terrestrial habitats in biphasic species (DeMaynadier & Hunter Jr., 1995; Rothermel, 2004; Semlitsch, 2008; Todd et al., 2009). By contrast, fully aquatic amphibians depend entirely on longitudinal river connectivity, making them particularly vulnerable to fragmentation caused by instream barriers such as dams (Bjordahl et al., 2020; Takahashi et al., 2016). Among salamanders, all the members of four families (Cryptobranchidae, Amphiumidae, Sirenidae, and Proteidae) and some species or phenotypes in others can have an entire aquatic life cycle as a result of paedomorphosis, the retention of larval traits at the adult stage (Denoël et al., 2005). Within these groups, members of the family Cryptobranchidae (giant salamanders sensu stricto) are unique as strict specialists inhabiting flowing freshwater systems. Their strong dependence on river environments makes them especially relevant for studying the ecological consequences of dam-induced fragmentation on aquatic amphibians.

The Cryptobranchidae family represents one of the most ancient lineages of extant amphibians, with origins tracing back to the Middle Jurassic (Gao & Shubin, 2003). The large, fully aquatic species in this family belong to the genera *Cryptobranchus* in North America and *Andrias* in East Asia. The Japanese giant salamander (*Andrias japonicus*), endemic to Japan, is one of the largest amphibians in the world, capable of reaching lengths of up to 1.5 meters (Okada et al., 2008). It is an ambush predator that uses suction feeding to capture prey (Heiss et al., 2013; Matsumoto et al., 2024; Tago, 1931; Tochimoto, 2002) and is considered as a top predator in its ecosystem (Duret et al., 2026). This species lives in lotic habitats (i.e., running waters), ranging from small headwater streams to wider midstream sections of rivers, typically characterized by clear, cold water and moderate to strong flow (Tochimoto et al., 2007). These habitats provide essential conditions for its survival, including oxygen-rich water and coarse substrate that offers shelter and nesting sites. During the breeding season, individuals undertake localized upstream or downstream movements to reach suitable nesting sites, making longitudinal connectivity within river networks particularly important for successful reproduction (Kawamichi & Ueda, 1998; Taguchi, 2009; Wakabayashi et al., 1976). Over time, numerous dams have been constructed throughout Japanese river systems to support irrigation, drinking water supply, hydropower, and flood control (Fan & Huang, 2020; Itsukushima, 2023). In particular, the post–World War II boom in dam construction for hydroelectric, agricultural, flood-control, and water-storage purposes has resulted in widespread and severe habitat fragmentation across the country's rivers (Takemura, 2007). While dams have played a key role in Japan's water management history, they also contributed to biodiversity degradation (Fukushima et al., 2007). Despite the species' ecological importance and its designation as a "Special Natural Monument" under Japanese law since 1952 (Japanese Agency for Cultural Affairs 1952), no study has yet quantitatively assessed the extent to which dams fragment the habitat of the Japanese giant salamander (Fig. 1). This represents a major gap in conservation planning, particularly given the species reliance on longitudinal river connectivity.

To address the knowledge gap regarding the presence of dams in lotic amphibian habitats (i.e., running waters), particularly for fully aquatic species, this study aims to characterize river fragmentation within the distribution range of the Japanese giant salamander and assess its potential implications for habitat connectivity. The core objectives of this study were to (1) quantify dam density within river networks of watersheds inhabited by Japanese giant salamanders (expressed as number of dams per kilometre of river length) by identifying and describing manmade structures that may obstruct their movement; (2) assess the degree of habitat fragmentation caused by these dams using a barrier-based fragmentation index that incorporates dam height, density and presence of ladderways; (3) evaluate the proximity of dams to known Japanese giant salamander locations as an indicator of potential constraints on movement and longitudinal connectivity within occupied river networks.

We hypothesised that all studied watersheds would exhibit a high density of dams, with a wide range of dam sizes. This would result in high values of the proposed fragmentation index, reflecting heavily fragmented river networks. We expected the density and height of dams to be key drivers of fragmentation, due to their influence on the species' capacity to cross barriers. In addition, we hypothesized that high dam density would result in short distances between salamander occurrences and the nearest dam, thereby limiting dispersal and migration opportunities.

2. Material and methods

2.1. Study area and occurrence of Japanese giant salamanders

To explore and quantify the fragmentation of Japanese giant salamander habitat by dams, we selected eight watersheds within the species' distribution in Japan (Duret et al., 2025). We first compiled detailed occurrence records (i.e., georeferenced observations) of Japanese giant salamanders from field surveys as well as from previous studies conducted in eight prefectures where the species is actively monitored (Bjordahl et al., 2020; Duret et al., 2025; Kuwabara et al., 2005; Okada et al., 2008; Taguchi & Natuhara, 2009; Tochimoto et al., 2007). The compiled records span multiple years (2005–2025), a period shorter than the lifespan of giant salamanders, which can extend over several decades (Tochimoto, 2005). Based on these data, we selected the eight watersheds with the highest number of occurrences: Chikusa (Hyogo Prefecture, $n = 21$), Gono (Hiroshima Prefecture, $n = 31$), Ichi (Hyogo Prefecture, $n = 71$), Kiso (Gifu Prefecture, $n = 35$), Maruyama (Hyogo Prefecture, $n = 30$), Ota (Hiroshima Prefecture, $n = 64$), Yakkan (Oita Prefecture, $n = 81$), and Yodo (Hyogo, Mie and Nara Prefectures, $n = 43$). Within each watershed, we then identified and delineated the areas where salamander records were located, allowing us to focus the analyses on the places confirmed to host the species (Fig. 2). Seven of the selected watersheds are located on Honshu Island, and one on Kyushu Island. These islands are characterised by mountainous terrain, high precipitation, and dense river networks (Yoshimura et al., 2005). Rivers in Japan are typically short, flowing rapidly from mountainous headwaters to the coast, and traversing both agricultural and urban landscapes, making them particularly susceptible to fragmentation (Oguchi et al., 2001).

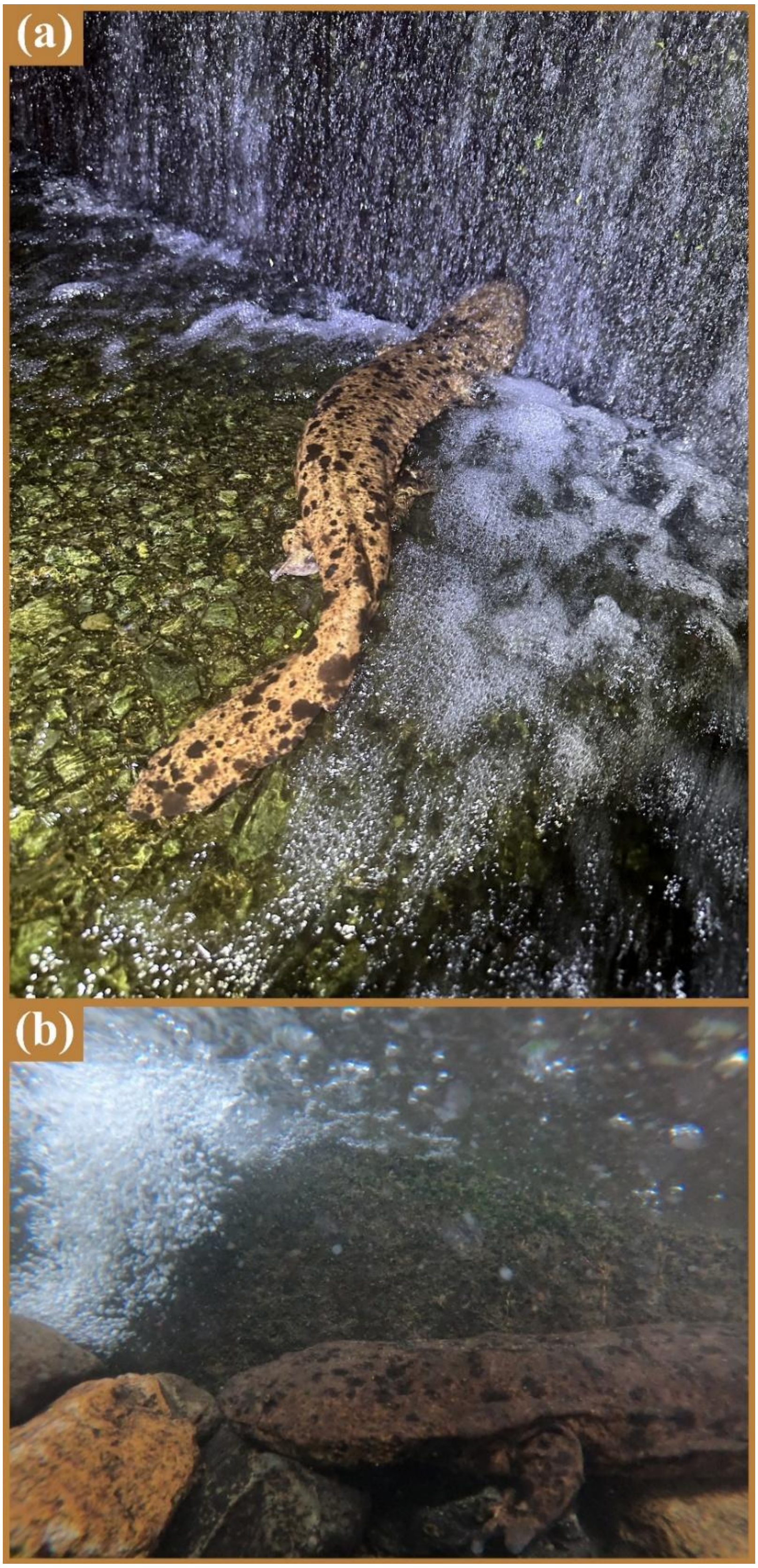

Fig. 1. Two photographs illustrating the problem posed by dams for Japanese giant salamanders. (a) An individual observed in front of a dam (photo by Yuki Taguchi). (b) Underwater view showing a giant salamander at the base of a dam (photo by Mathieu Denoël).

2.2. Dam identification and characterization

A comprehensive assessment of river barriers within the selected portions of the eight watersheds was conducted through detailed spatial analysis using high-resolution geospatial data (satellite images). All spatial data were processed using QGIS 3.26. River networks and watershed boundaries for the islands of Honshu and Kyushu were obtained from the National Land Numerical Information portal of the Ministry of Land, Infrastructure, Transport and Tourism (MLIT) of Japan. For each watershed, we selected river sections where Japanese giant salamanders occur, from their spring to the main confluence.

High resolution satellite imagery from Google Earth Pro (2016–2025) was used to visually and systematically inspect river sections to locate dams. When a dam was identified using aerial imagery, additional information was retrieved using Google Street View to assess structural characteristics. For each dam, we recorded height category (classified into four groups: 1: < 0.5 m; 2: 0.5–1 m; 3: 1–5 m; and 4: > 5 m), and presence or absence of fish passage infrastructure (fishways). Dam height was visually estimated from street-level imagery and used to assign each structure to one of the four height classes. Height estimation relied on comparison with nearby standardized structural elements of known or typical dimensions, including road safety guardrails, bridge parapets, concrete revetment blocks commonly used in Japanese river engineering, steps, and occasionally visible human figures. In addition, the measured dam width obtained from aerial imagery provided a complementary spatial reference through proportional comparison between horizontal and vertical dimensions. Measurements were supported by Google Earth Pro scale tools when applicable (see Supplementary Fig. S1 for an example of height category estimation of a dam). Because dam height was estimated from remote imagery, precise continuous measurement was not feasible. Dams were therefore assigned to broad categorical ranges, forming a functional classification designed to reduce uncertainty associated with visual estimation. Moderate estimation uncertainty was unlikely to affect class assignment except near category boundaries.

Height categories were intended to approximate broad differences in potential passability rather than represent strict ecological thresholds or equal physical intervals. Passability is expected to vary along a continuum. However, given the large body size of Japanese giant salamanders and their limited ability to overcome vertical drops, even relatively small barriers (≈0.5–1 m) are likely to substantially restrict their movement in the absence of passage structures, whereas structures exceeding 1 m are expected to act as strong or near-complete movement barriers. This categorical approach captures general differences in barrier severity while maintaining ecologically relevant distinctions.

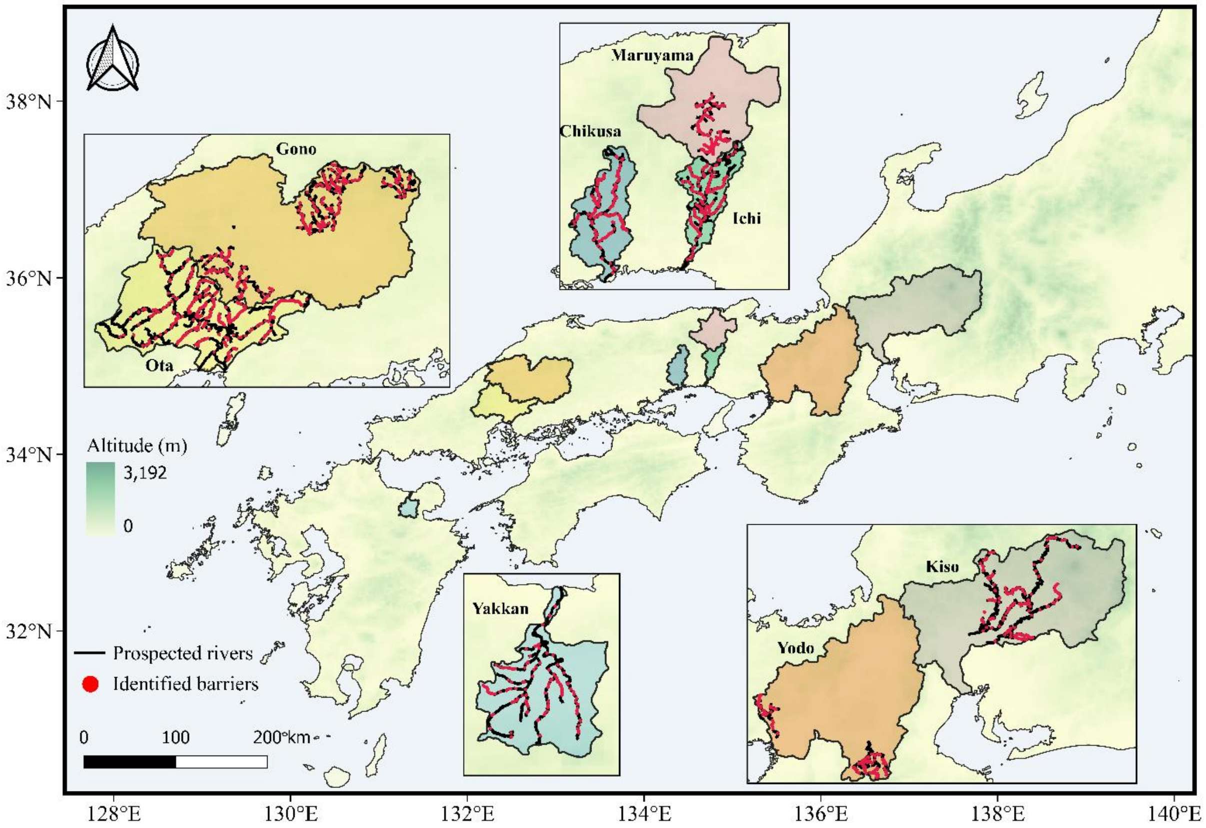

Fig. 2. Map of the study area showing the eight watersheds surveyed in Honshu and Kyushu Islands, Japan. Red dots in the submaps indicate identified barriers within the explored areas where Japanese giant salamanders occur. Background shading represents the mean elevation above sea level (Ministry of Land, Infrastructure, Transport and Tourism of Japan).

2.3. Dam Fragmentation Index (DFI): conceptual framework and calculation

2.3.1. Conceptual basis

For each watershed, dam density was calculated as the number of dams per kilometre of river. To evaluate the degree of river fragmentation and assess potential impacts on Japanese giant salamander habitats, we developed a Dam Fragmentation Index (DFI). Rather than representing a novel metric, the DFI constitutes an adaptation of existing approaches to the specific ecological context of a benthic and strictly aquatic amphibian with limited dispersal ability.

The DFI was calculated at the watershed scale and represents an integrated measure of longitudinal fragmentation across the entire river network within each watershed. Its design draws primarily from the Dendritic Connectivity Index for potamodromous fish (DCI_P, Cote et al., 2009) and the Population Connectivity Index (PCI, Rodeles et al., 2021), which both focus on barrier passability and the length of river segments between dams. We additionally considered conceptual and methodological elements from broader connectivity and river fragmentation frameworks, including the hydrological connectivity model proposed by Shao et al. (2020) and the synthesis of fragmentation and flow alteration metrics reviewed by Jumani et al. (2020). However, these existing indices were not fully suited to our focal species. In

Japanese giant salamanders, structural barrier characteristics are likely particularly important: dam height is expected to play a critical role in determining whether a structure is surmountable, and the presence of fishways may mitigate, but not fully eliminate, fragmentation effects. We therefore incorporated dam height as a weighted parameter combined with fishway presence or absence to better reflect fragmentation risk for this taxonomic group. Unlike connectivity metrics based solely on inter-dam segment length, the DFI emphasizes functional barrier permeability, which is likely more relevant for a benthic amphibian with limited dispersal ability in comparison to many fish species.

2.3.2. Mathematical formulation

The DFI combines structural, functional, and spatial components of fragmentation and can be expressed as:

$$DFI = \sum_{i=1}^{n} \left(w_i \cdot \frac{B_i \cdot (1 - F_i)}{L} \right) \times 10$$

where B_i is the number of dams in height category i, w_i is the weight assigned to each height category, F_i is the fraction of barriers in the category i with fishways, and L is the river length of the watershed. The DFI can be calculated for any size stream, river system or for the complete watershed. Passability parameters (height and presence or absence of fishways) were assigned at the individual dam level, whereas the resulting DFI represents an aggregated measure of fragmentation calculated at the watershed scale in this study. Including fishways in the index ensures that barriers with potential mitigation measures are weighted differently, providing a more ecologically realistic estimate of habitat fragmentation. Barrier slope was not included as a parameter in the DFI calculation because slope values showed very limited variation among structures, with 82.8% of dams presenting slopes exceeding 75°, and because this characteristic was largely homogeneous among watersheds. Steep slope alone does not necessarily determine passability, particularly for low-height structures. Dam height was considered the primary factor influencing the ability of Japanese giant salamanders to overcome obstacles.

2.3.3. Treatment of dams with uncertain height

For the DFI calculation, each dam had to be assigned to a height category. However, for a subset of dams, satellite and street imagery did not allow for a clear determination of dam height. To incorporate these uncertain cases in the DFI calculation, we first calculated the overall proportion of dams falling into height categories 1 to 3 across all watersheds, using only dams for which height could be confidently assessed. Category 4 dams were not included in this proportional redistribution because their height was consistently distinguishable from satellite imagery. The calculated proportions for categories 1 to 3 were then used to reassign dams with unknown height among these three categories, while all clearly identifiable category 4 dams were retained as such.

2.3.4. Weighting schemes and sensitivity scenarios

To calculate the DFI, each height category was assigned a relative weighting coefficient reflecting its assumed contribution to fragmentation severity (Fig. 3). These weights do not represent empirical probabilities of successful crossing but instead scale the relative influence of barrier classes within the index calculation. Because quantitative passability thresholds for Japanese giant salamanders are unavailable, we implemented a scenario-based sensitivity analysis to explore how alternative ecological assumptions regarding barrier severity influence DFI values. Lower weights indicate a higher likelihood of successful crossing by salamanders. Weights were normalized to sum to 1 within each scenario to preserve proportional relationships among barrier categories and maintain comparability across watersheds. This normalization ensures consistent scaling but does not imply that dams collectively share a fixed total contribution within a watershed.

We considered two scenarios to explore the sensitivity of the DFI to different ecological assumptions regarding barrier severity for Japanese giant salamanders. In Scenario 1 (DFI 1), the following weighing scheme was applied: category 1: 0.1; category 2: 0.3; category 3; 0.3; category 4: 0.3 (Fig. 3). This scenario represents a conservative assumption in which only the smallest dams (<0.5 m) may be passable, whereas all higher height classes are treated as similarly strong functional barriers. In Scenario 2 (DFI 2) weights were assigned as follows: category 1: 0.05; category 2: 0.2; category 3: 0.375; category 4: 0.375. This scenario assumes a more gradual increase in barrier severity, in which moderately-sized dams (0.5–1 m) may still be passable for large individuals, while taller structures (≥ 1m) are considered similarly severe barriers. These weighting schemes reflect the known or assumed physical capabilities of Japanese giant salamanders (Takahashi et al., 2016, S. Okada and Y. Taguchi, pers. obs.) and account for uncertainties in dam height classification. Importantly, these weights do not represent empirical probabilities of successful crossing. Rather, they function as relative scaling coefficients that modulate the contribution of each height class to overall fragmentation pressure. These scenarios are intended as sensitivity analyses that bracket plausible ecological conditions.

2.3.5. Interpretation of DFI values

Values of DFI can be interpreted as follows: a DFI of 0 indicates no fragmentation, meaning that the habitat is intact without any dam; values below 1 indicate a low fragmentation, suggesting minimal habitat fragmentation with barriers that still allow species dispersal across dams; values between 1 and 1.5 correspond to a moderate fragmentation; values between 1.5 and 2 show a high fragmentation, where barriers are considerably impeding connectivity between upstream and downstream populations. Finally, a DFI greater than 2 represents a very high fragmentation. The threshold values used to interpret DFI results were defined to provide an ecologically meaningful gradient of fragmentation intensity rather than to match a standardized numerical scale such as the DCI or PCI (which range from 0 to 100). While those indices quantify overall connectivity loss, the DFI expresses relative fragmentation pressure based on dam density and structural characteristics. These categories do not represent empirically validated biological tipping points but instead reflect relative increases in cumulative fragmentation pressure based on dam density and structural characteristics.

Threshold ranges were informed by theoretical index variation under contrasting fragmentation scenarios (e.g., absence of dams vs. high density of impermeable barriers).

2.4. Distance from Japanese giant salamanders to dams

Within the eight studied watersheds, we measured the distance from each Japanese giant salamander occurrence point to the nearest dam along the river network, using river line features in a GIS environment (QGIS 3.26). Distances were calculated along the river network to the closest barrier located either upstream or downstream. Distances to dams were interpreted as an indicator of dam configuration within occupied habitat. The height category of the closest dam was also recorded for each point, to evaluate potential differences in barrier intensity.

To explore how watershed-scale fragmentation relates to the spatial configuration of occupied river networks, we conducted a linear regression analysis between the DFI value of each watershed and the mean distance from salamander occurrences to the nearest dam. The DFI was calculated at the watershed scale as described above. Mean distances were computed based on all known georeferenced occurrence records within each watershed and represent a structural indicator of proximity between occupied habitat segments and instream barriers. This analysis does not infer species distribution limits or abundance patterns, but rather evaluates whether increasing fragmentation intensity is associated with reduced spatial separation between occupied sites and barriers. The analysis was performed using the ‘lm’ function in R version 4.3.2.

3. Results

3.1. Abundance and density of dams

We identified a total of 2,434 river barriers across the portions of the eight watersheds studied (Fig. 2). The distribution of dams in the eight watersheds is presented in Table 1. A total of 2,341 km of river segments were explored to locate and document dam structures. The overall dam density (± SE), calculated as the total number of dams divided by the total river length across all eight studied watersheds, was 1.23 ± 0.53 dams/km, and dam density varied across watersheds, ranging from 0.55 to 2.38 dams/km in Kiso and Maruyama watersheds, respectively (Table 1).

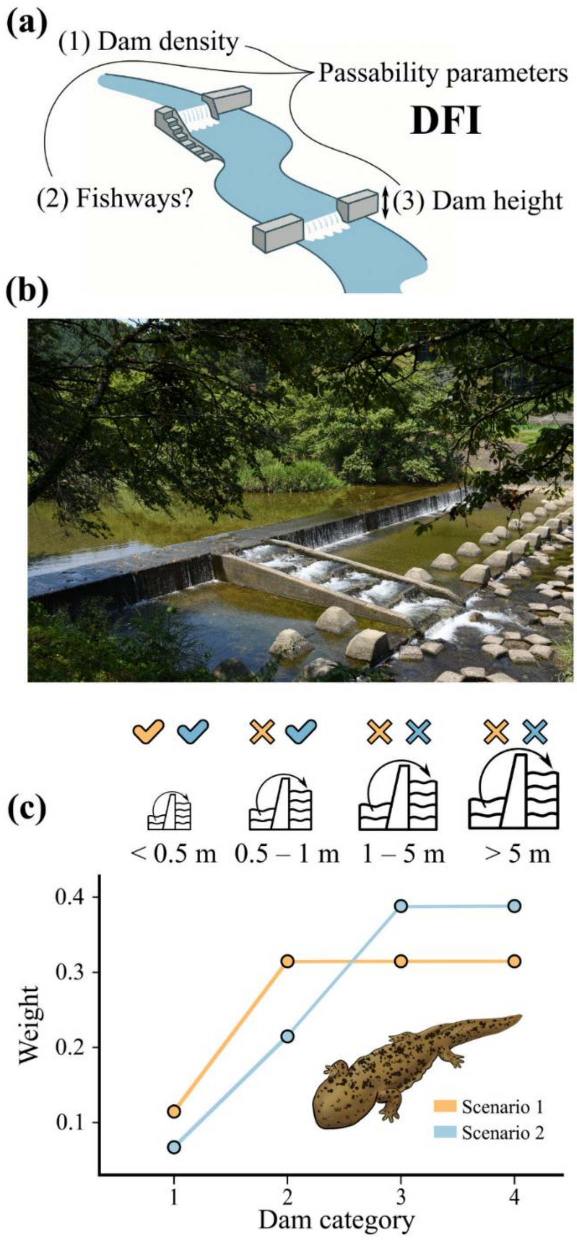

Fig. 3. (a) Example of impacted rivers and passability parameters included in the Dam Fragmentation Index (DFI). Passability parameters are assigned at the individual dam level based on structural characteristics (height category and "fishway” presence) and are subsequently integrated across the river network to produce a single DFI value at the watershed scale. (b) Example of a small dam equipped with a “fishway” (Gifu Prefecture, Japan; photo by Mathieu Denoël). (c) Visual representation of the two weighting scenarios used to calculate the Dam Fragmentation Index (DFI), illustrating assumptions about Japanese giant salamander permeability across four dam height categories. For each category, coloured symbols indicate whether salamanders are assumed able (tick symbols) or unable (cross symbols) to cross, depending on the scenario. Yellow symbols correspond to DFI Scenario 1, which assumes only the smallest dams (< 0.5 m) are permeable, while all larger dams are impassable. Blue symbols correspond to DFI Scenario 2, which assumes partial permeability for dams under 1 m and complete obstruction for larger structures.

3.2. Height of dams

Initial categorisation based on estimated dam height revealed that 967 barriers (39.7%) could not be reliably assigned to a specific height class. For the 1,467 barriers for which height could be determined, the distribution was: category 1 (<0.5 m): 580 barriers (39.6%); category 2 (0.5–1 m): 468 barriers (31.9%); category 3 (1–5 m): 364 barriers (24.8%); and category 4 (>5 m): 55 barriers (3.7%). Based on the relative distribution of height categories, the 967 unclassified dams were proportionally redistributed among the different categories, resulting in final estimated totals of: 984 dams in category 1, 813 in category 2, 582 in category 3, and 55 in category 4.

3.3. Fishways

A total of 120 fishways were identified, representing 4.93% of all dams (Table 1). Among these, 34 fishways were found on dams for which height categorisation was not possible. The distribution of the 86 remaining fishways by dam category was as follows: 22% on dams of category 1; 38% in category 2; 38% in category 3; 2% in category 4.

Table 1
Characteristics of dams in each studied watershed inhabited by the Japanese giant salamander, including each parameter used to calculate the dam fragmentation indexes (DFI 1, with weights from Scenario 1; DFI 2, with weights from Scenario 2). Height categories: 1: < 0.5 m; 2: 0.5–1 m; 3: 1–5 m; and 4: > 5 m).

Watershed (Prefecture)	Number of dams by height category					River length (km)	Dam density (dams/km)	Fishways	DFI 1	DFI 2
	1	2	3	4	Total					
Chikusa (Hyogo)	116	69	48	1	234	176.9	1.32	12	2.5	2
Gono (Hiroshima)	110	87	161	12	370	391.1	0.95	12	2.18	2.13
Ichi (Hyogo)	147	104	51	5	308	235.5	1.31	7	2.56	1.99
Kiso (Gifu)	124	82	61	14	280	510.5	0.55	29	1.05	0.9
Maruyama (Hyogo)	94	59	85	2	239	100.4	2.38	8	5.12	4.69
Ota (Hiroshima)	250	212	110	8	581	544.1	1.07	29	2.16	1.71
Yakkan (Oita)	42	89	23	9	164	141.1	1.16	16	2.53	2.02
Yodo (Hyogo - Mie - Nara)	101	111	43	4	259	240.9	1.08	7	2.3	1.8

3.4. Japanese giant salamanders and dams proximity

The mean distance ± SE between salamanders and the closest dam was 598 ± 40 m. Ten giant salamander locations were nearest to a dam with unidentified height (2.6%). Among the others, the distances to the nearest dam were distributed as follows: < 0.5 m (Category 1): 115 locations (29.8%); 0.5–1 m (Category 2): 159 locations (41.2%); 1–5 m (Category 3): 88 locations (22.8%); > 5 m (Category 4): 14 locations (3.6%). At the watershed level, mean salamander–dam distances ± SE were: Maruyama: 306 ± 63 m ($n = 30$); Gono: 465 ± 115 m ($n = 31$); Chikusa: 449 ± 104 m ($n = 21$); Yodo: 485 ± 71 m ($n = 43$); Yakkan: 500 ± 58 m ($n = 81$); Ichi: 614 ± 86 m ($n = 71$); Ota: 871 ± 128 m ($n = 64$); and Kiso: 893 ± 220 m ($n = 35$) (Fig. 4).

3.5. Dam fragmentation index (DFI)

In both scenarios, fragmentation levels were generally high across the eight watersheds, and the variation in weights had only a limited effect on overall DFI values. Under Scenario 1 (weights: 0.1 for category 1; 0.3 for categories 2–4), the mean ± SE DFI was 2.55 ± 0.41, indicating a high fragmentation, with disparities among watersheds (Table 1). DFI ranged from 1.05 in the Kiso watershed (Gifu Prefecture), indicating a moderate fragmentation, to 5.12 in the Maruyama watershed (Hyogo Prefecture), indicating a very high fragmentation. Under Scenario 2 (weights: 0.5 for category 1; 0.2 for category 2; 0.375 for categories 3 and 4), the mean ± SE DFI was 2.16 ± 0.39, and DFI values ranged from 0.9 (Kiso) to 4.69 (Maruyama). In both scenarios, seven out of eight watersheds exhibited a DFI greater than 1.5, confirming substantial global river fragmentation (Table 1).

A linear regression analysis revealed a significant negative relationship between the average salamander–dam distance and watershed-level DFI for the two scenarios tested (Scenario 1: $\beta = -0.0038 \pm 0.0015$ SE, $t_6 = -2.57$, $p = 0.042$; Scenario 2: $\beta = -0.0037 \pm 0.0014$ SE, $t_6 = -2.63$, $p = 0.039$). The model explained 52.4% of the variation in DFI in scenario 1 ($R^2 = 0.52$; adjusted $R^2 = 0.44$) (Fig. 5) and 53.6% in scenario 2 ($R^2 = 0.54$; adjusted $R^2 = 0.46$).

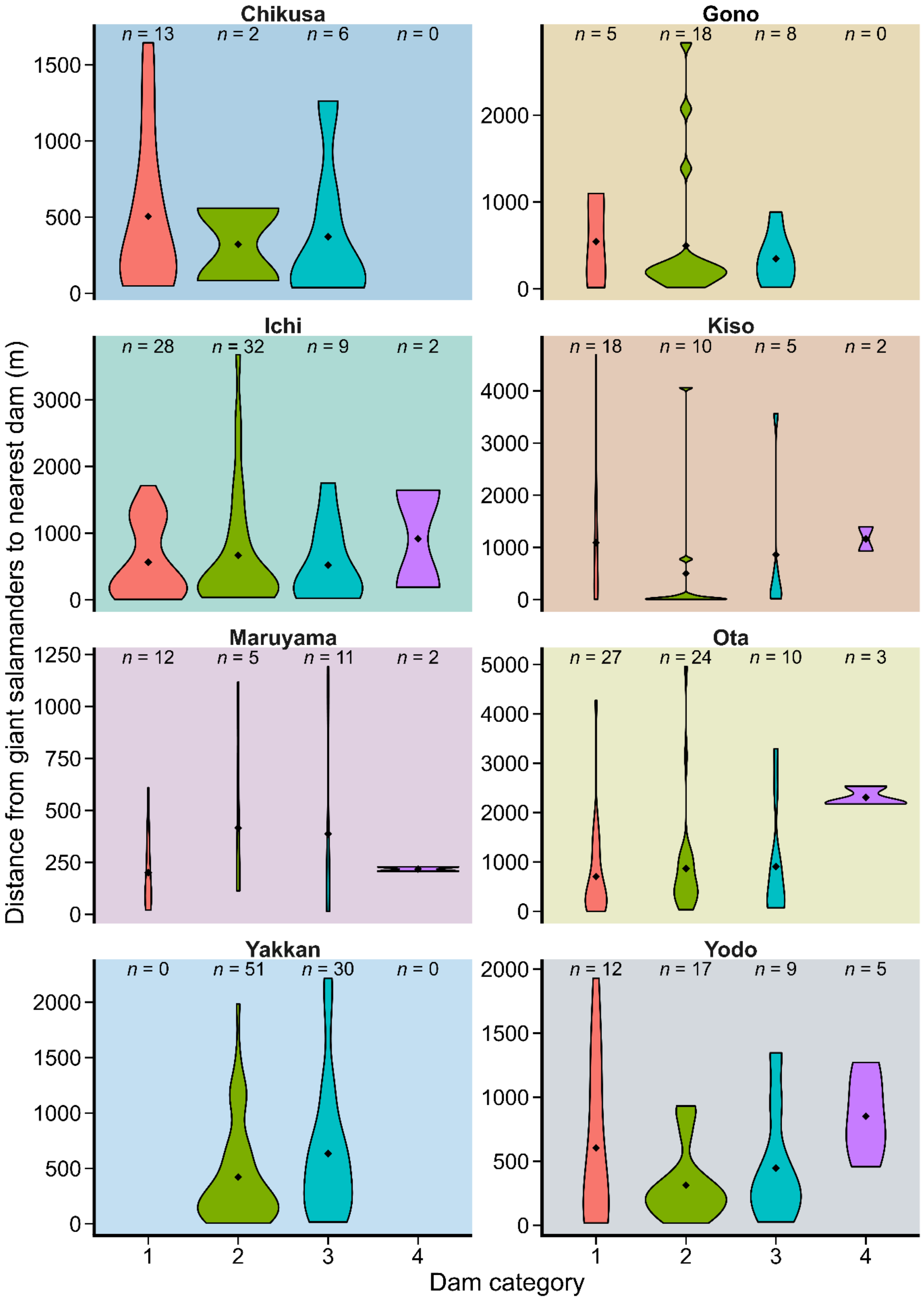

Fig. 4. Distances of the giant salamanders to the closest dam, across different dam types and watersheds. Each panel represents one watershed, and within each panel, violin plots display the distribution of salamander–dam distances for four dam height categories (1: < 0.5 m; 2: 0.5–1 m; 3: 1–5 m; 4: > 5 m). Mean distances are shown as black diamonds.

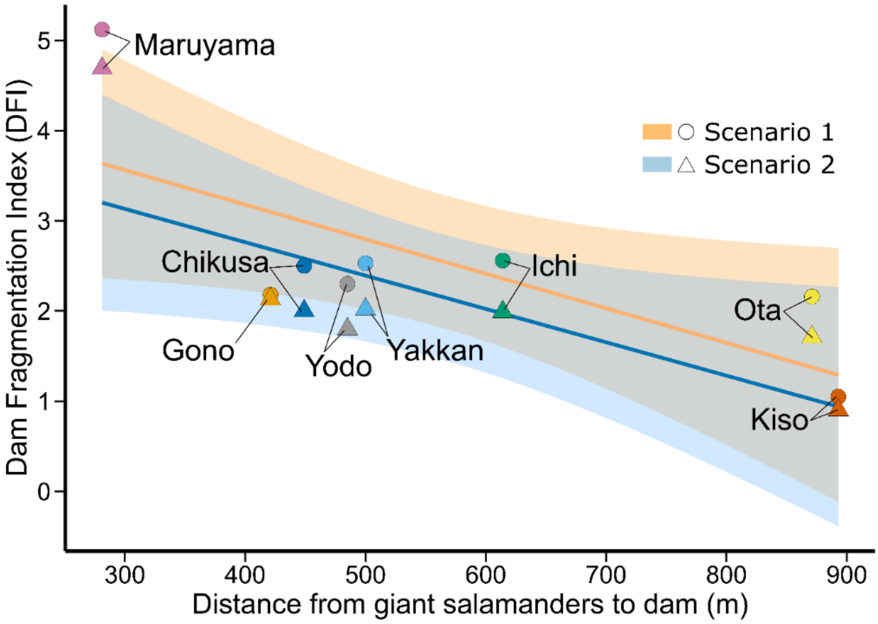

Fig. 5. Relationship between the distance from giant salamanders to the nearest dam and the Dam Fragmentation Index (DFI) for the two scenarios tested. Circles correspond to values for the scenario 1 and triangles to the scenario 2. The lines show the linear regressions, with shaded areas representing the 95% confidence interval.

4. Discussion

Our study provides the first large-scale quantification of riverine fragmentation in the habitat of the Japanese giant salamander, highlighting the pervasiveness and potential ecological consequences of anthropogenic barriers across eight major watersheds. More broadly, it highlights how artificial barriers can alter connectivity in the habitat of amphibians. We recorded dam densities of up to 2.38 dams per kilometre, ranging from small structures under 0.5 m height to large barriers over 5 m, creating repeated structural discontinuities along occupied river networks. Given the limited dispersal capacity of *Andrias japonicus*, dam densities observed in these watersheds may contribute to reduced connectivity along river networks. Using a Dam Fragmentation Index (DFI), we showed that most watersheds exhibited high to very high levels of fragmentation.

Different DFI weighting scenarios highlight variation in barrier impact, but in all cases, the index serves to illustrate the intensity of structural discontinuities that may limit salamander movement. While watersheds vary in dam density and barrier height, the DFI allows a standardized comparison of fragmentation levels, supporting interpretation of habitat connectivity across the species' range. Future studies could build on this framework to explore risks for local populations at local and global scales. Particularly, modelling the density of varied dam heights could serve as a proxy for background fragmentation intensity. Due to the high density of dams, also shown by the high DFI values, the majority of known Japanese giant salamander occurrences were located within a few hundred meters of a dam, suggesting that many occupied sites are located in close structural proximity to instream barriers, increasing the likelihood of movement constraints. Altogether, these findings point to a severe and widespread risk of habitat fragmentation (i.e., structural subdivision of river networks) and reduced longitudinal connectivity (i.e., functional limitation of movement among habitat patches) for the Japanese giant salamander, with implications for its movement, reproduction, and long-term persistence.

4.1. Vulnerability of Japanese giant salamanders to fragmentation by dams

Our observed average dam density of 1.23 dams per kilometre provides a concrete basis to examine how artificial barriers may influence Japanese giant salamander populations. Japan's topography, marked by steep mountainous terrain and frequent intense rainfall, expose rivers to periodic extreme flooding (Fan & Huang, 2020). In response, numerous artificial structures have been built including dams for flood control, hydropower generation, agriculture, and infrastructure development (Itsukushima, 2023). For species with complex life cycles, movements are necessary to access distinct habitats required at different life stages (Lucas & Baras, 2008; Taylor et al., 1993; Werner & Gilliam, 1984). In amphibians, these movements are often particularly evident during the breeding season, when individuals must reach suitable spawning sites. In Japanese giant salamanders, both males and females migrate through the rivers to spawn (Kawamichi & Ueda, 1998; Taguchi, 2009; Wakabayashi et al., 1976). One study tracking pre- and post-breeding movements showed that most individuals moved around 200 m, but some travelled much further, up to nearly 4,000 m (Taguchi, 2009). These findings suggest that a high density of dams, such as found in our study, may obstruct access to suitable breeding habitats for adults. Similarly, these structures likely prevent larvae, juveniles and adults from dispersing to new habitats, further limiting population longitudinal expansion in the main course of rivers and tributaries. In addition, larvae hatching upstream of dams may experience entrapment in upstream reaches, leading to confinement in dead-end habitat segments. This isolation constrains dispersal and recruitment into breeding populations but also to access favourable habitats with limited predation risk.

Beyond reproductive challenges, dams can lead to complete isolation of subpopulations, increasing the risk of local extinction. For example, the Chinese paddlefish (*Psephurus gladius*) was driven to extinction partly due to river fragmentation in the Yangtze River in China (Scarnecchia, 2023). Other examples among freshwater megafauna include the Gharial (*Gavialis gangeticus*) and the Chinese sturgeon (*Acipenser sinensis*), all of which are severely affected by dam-induced habitat fragmentation (He et al., 2017; Lang et al., 2019; Wu et al., 2015). Genetic diversity among populations, as well as its distribution, is strongly affected by habitat fragmentation (Keyghobadi, 2007). Population isolation promotes genetic divergence, which, combined with evolutionary processes, can undermine population persistence through loss of adaptative potential and accumulation of deleterious mutations. Studies on the North American giant salamander, also known as the hellbender (*Cryptobranchus alleganiensis*), revealed strong genetic differentiation between river sections, primarily explained by population isolation (Freake et al., 2018; Templeton et al., 1990). Like the hellbender, the Japanese giant salamander is fully aquatic and lacks the ability to disperse over land. However, individuals have occasionally been observed on land near dams, exploring the surrounding area for a suitable slope to cross the structure, which illustrates their need to access upstream habitats (Taguchi & Natuhara, 2009). Maintaining river connectivity remains therefore essential for sustaining gene flow and ensuring the long-term survival of the species.

While Japanese giant salamanders may occasionally be found near dams in water, this apparent proximity should not be interpreted as evidence that barriers are harmless. Given the high density of dams, giant salamanders are frequently confined near these barriers, restricting the movements essential for their breeding success. Moreover, the species is extremely long-lived, and such organisms typically display delayed demographic responses to habitat alteration (Kuussaari et al., 2009; Tilman et al., 1994). In amphibians, population declines may remain undetected for years because adults persist while recruitment progressively collapses (Cayuela et al., 2020; Schmidt et al., 2005). This means that the current presence of individuals near dams does not necessarily indicate population viability, functional dispersal, or long-term persistence. Robust predictive demographic modelling would require watershed-level data on population size, age structure, reproduction, and genetic connectivity, datasets that are not available for this species. For this reason, our study focused on quantifying structural fragmentation rather than forecasting population trajectories. Future work integrating demography, reproduction, and genetic connectivity will be essential to detect potential extinction debts and evaluate the long-term impacts of dams on giant salamander populations.

Dams do not only fragment river continuity but also contribute to habitat degradation (Taguchi & Natuhara, 2009; Tochimoto, 2005). Among the most affected features are stream banks, which are often modified or concreted. This is particularly detrimental during the breeding season (August–September), when males actively search for and defend nesting sites, typically consisting in concealed burrows along stream banks with narrow openings (Kuwabara et al., 2005; Kuwabara & Nakagoshi, 2009; Okada et al., 2015). The alteration or destruction of these banks can thus pose a direct threat to reproductive success and Japanese giant salamander populations viability. Future studies should assess the extent of watershed disturbance caused by artificial banks, in addition to the effects of dams presented here, in order to better evaluate the multiple risks of habitat alteration for giant salamanders.

4.2. Climate change and habitat fragmentation

Habitat fragmentation is one of the multiple threats currently affecting Japanese giant salamander populations. It adds to other pressures, such as climate change, as shown by a recent study predicting a substantial loss of suitable habitats under future climate scenarios, mainly due to shifts in temperature and precipitation patterns (Duret et al., 2025). Due to climate change, the frequency and intensity of extreme flood events are expected to increase across Japan (Hatsuzuka et al., 2021; Shakti et al., 2020), posing direct threats to the survival of Japanese giant salamanders by altering river dynamics and habitat stability. In response, future dam construction is likely to intensify, primarily targeting flood control and the management of extreme hydrological events (Fan & Huang, 2020). These structures may include both large flood-control dams, designed to store or divert massive water volumes, and smaller weirs or levees intended to regulate flows in tributaries or protect human settlements. Although different in size, both types can disrupt river connectivity, block dispersal pathways, and modify spawning or foraging habitats. At the same time, Japan's commitment to drastically reducing CO_2 emissions is expected to increase reliance on renewable energy sources, including hydropower (Cheng et al., 2022). Hydropower dams represent a strong incentive in a country with a dense hydrographic network and limited domestic energy production (Japan Commission on Large Dams, 2009). However, the ecological costs of such developments may be substantial. New dams, especially in upstream sections where giant salamanders are most abundant, could exacerbate habitat fragmentation and isolate populations. Without incorporating ecological considerations, future dam expansion risks compounding the already severe threats faced by this iconic species. In this context, habitat fragmentation and climate change are not only co-occurring threats but are also tightly interconnected. Together, they represent the primary challenges to the long-term survival of Japanese giant salamander populations (Borzée et al., 2024; Duret et al., 2025; Taguchi & Natuhara, 2009) and also for populations of the other species of giant salamanders (Freake & DePerno, 2017; Wang et al., 2004; Yan et al., 2018).

A further concern for Japanese giant salamander habitats is the alteration of river flow regimes, especially when combined with climate change, which may profoundly impact the physicochemical properties of water, most notably temperature and dissolved oxygen levels. Natural flow regimes are fundamental for maintaining riverine habitat integrity, hydrologic connectivity, water quality, and aquatic community composition (Grill et al., 2019; Poff et al., 1997), and their disruption, particularly by dams, is a leading cause of freshwater ecosystem degradation (Bunn & Arthington, 2002; Poff et al., 2010). Together, climate change and damming represent synergistic pressures on flow regimes and habitat structure (Chalise et al., 2021). Rising temperatures, coupled with hydrological fragmentation, may promote the formation of slow-flowing or stagnant upstream waters, which are often warmer and contain less dissolved oxygen, an especially concerning scenario for giant salamanders, which rely heavily on cutaneous respiration (Da Silva Neto et al., 2023; Kawamichi & Ueda, 1998; Okada et al., 2008). In Japanese giant salamanders, both water temperature and oxygen levels within nests are critical for embryonic development and survival (Okada et al., 2015). Consequently, shifts in thermal and oxygen conditions near dams, resulting from morphological modifications, and climate change could compromise reproductive success of giant salamanders. Therefore, combined impacts of warming and flow alteration pose severe risks to the survival and fitness of giant salamanders. The intensification of extreme flood events may also directly affect giant salamanders. Such floods can displace individuals downstream, sometimes over long distances, and the presence of dams can prevent them from migrating back to their upstream habitats. Consequently, increased flooding frequency combined with river fragmentation may further exacerbate population isolation and reduce habitat availability for the species.

4.3. Conservation perspectives

Japanese giant salamanders are facing multiple, connected threats that require active and adaptive conservation strategies across their range. In addition to protecting habitat directly, improving landscape connectivity should be a key goal in order to mitigate the effects of river fragmentation caused by dams.

Most research on crossing dams has focused on fish species, particularly migratory taxa such as salmonids and sturgeons, with the primary objective of improving the design and efficiency of fishways (Bunt et al., 2012; Noonan et al., 2012; Silva et al., 2018). However, these structures are often designed specifically for swimming species and are generally unsuitable for fully aquatic and benthic amphibians such as the Japanese and other giant salamanders, which lack swimming endurance. Only one study has evaluated the ability of Japanese giant salamanders to use artificial structures such as ladderways to cross dams (Takahashi et al., 2016). The results indicated that individuals were able to climb small dams using specially designed step-type or sloped ladderways, particularly when side walls were present to prevent falling. This suggests that specially designed sloped passages could provide a viable upstream migration route for salamanders. Future studies should test different slope angles, surface textures, and flow conditions, and assess the performance of individuals across size and age classes to optimize such structures. Tailoring these designs to the ecology and locomotor abilities of the Japanese giant salamander and other salamander species will be essential for improving their field effectiveness and long-term conservation outcomes.

A conservation tool with long-term impact is dam removal, which has been shown to trigger both short- and long-term ecological recovery in river systems (Bednarek, 2001; Bellmore et al., 2019). While large-scale dam removal may not be realistic in Japan given the socio-economic context, targeted removal of obsolete or redundant small dams could be a feasible strategy that would benefit not only giant salamanders but also entire riverine communities, especially in rural areas that experience significant human population declines.

In all cases, a balanced approach is needed, one that considers the real needs of human populations, such as flood control, irrigation, and energy production, while simultaneously securing viable habitats for native fauna. The proliferation of dams worldwide has already led to a critical reduction in free-flowing rivers, with severe ecological consequences (Grill et al., 2019; Zarfl et al., 2015). Given that additional dam construction will exacerbate habitat fragmentation and biodiversity loss, it is essential to slow down or stop their development and prioritize alternative strategies for flood control and energy production that are less harmful to riverine ecosystems. The Japanese giant salamander, and giant salamanders in general, can be considered as a key umbrella species whose protection could lead to the preservation of aquatic biodiversity (Branton & Richardson, 2011; Fleishman et al., 2000; Roberge & Angelstam, 2004). Indeed, their ecological requirements for clean, oxygen-rich, connected rivers reflect those of many co-occurring species.

A socio-demographic factor might unexpectedly play in favour of the conservation of Japanese giant salamanders: Japan’s population is decreasing and aging, particularly in rural areas. This demographic transition could reduce future anthropogenic pressure on rivers (e.g., lower demand for agricultural irrigation and hydropower infrastructure), potentially creating opportunities to restore river connectivity, remove obsolete dams, and rewild degraded river segments. In some upstream areas where depopulation has progressed, small irrigation dams are increasingly left unmanaged and, in some cases, collapse naturally due to aging and lack of maintenance. While such processes can occasionally promote partial restoration of river connectivity, they may also cause localized sediment release or instability, underscoring the need for monitoring and adaptive management in depopulating regions. Anticipating this demographic shift and incorporating it into long-term conservation planning will therefore be key to securing lasting benefits for Japanese giant salamanders and broader riverine biodiversity (Uchida et al., 2025).

5. Conclusions

Globally, amphibians inhabiting running waters remain largely overlooked in assessments of river fragmentation, despite their partial or complete dependence on continuous aquatic corridors and their limited dispersal capacities in comparison to more mobile taxa. While the impacts of dams on fish movement and connectivity have been widely documented (Fukushima et al., 2007; Grill et al., 2019; Liermann et al., 2012), comparable large-scale evaluations for amphibians are almost nonexistent. Global syntheses repeatedly highlight that amphibians are strongly underrepresented in fragmentation research, particularly in aquatic environments (Cushman, 2006; Fardila et al., 2017; Tan et al., 2023). This gap is notable for species inhabiting river ecosystems (Bohada-Murillo et al., 2021), particularly for paedomorphic salamander families (cryptobranchids, sirenids, amphiumids and proteids) which are fully aquatic and use entirely or partly river habitats, but also members of other salamander families which are facultatively paedomorphic or biphasic such as in plethodontids. In all cases, artificial barriers on the dendritic river systems can severely restrict movements, gene flow, and recolonization dynamics. Our study demonstrates how high-resolution mapping combined with a fragmentation index can provide a watershed-scale perspective on habitat fragmentation. Such approaches are most powerful when combined with detailed local field surveys, which allow precise characterization of individual barriers. Integrating broad-scale mapping with on-the-ground assessments would improve our ability to identify priority areas for conservation. Similar combined approaches are urgently needed worldwide, especially in regions experiencing rapid dam development (Zarfl et al., 2019), to identify amphibian species and populations most threatened by river infrastructure (Crnobrnja-Isailović et al., 2021).

CRediT authorship contribution statement

Clément Duret: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft. **Olivia A. Schulz Kumar:** Data curation, Formal analysis, Writing – review & editing. **Sumio Okada:** Data curation, Resources, Writing – review & editing. **Yuki Taguchi:** Data curation, Resources, Writing – review & editing. **Mizuki K. Takahashi:** Data curation, Resources, Writing – review & editing. **Osamu Kishida:** Funding acquisition, Writing – review & editing. **Mathieu Denoël:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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Data availability

The authors do not have permission to share data.

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