

Ecology and conservation of snow trout (*Schizothorax* Heckel, 1838): a review



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ABSTRACT. Snow trout (*Schizothorax* Heckel, 1838) represent a diverse genus of cyprinid fishes of ecological and socio-economic significance in mountainous and sub-mountainous freshwater ecosystems throughout Asia, inhabiting major river systems from the Himalayas and Tibetan Plateau to Central Asia, often with high basin-level endemism. This review synthesizes current knowledge on their taxonomy, biogeography, ecology, and conservation, highlighting a complex taxonomic landscape shaped by ancient polyploidy and regional evolutionary processes. *Schizothorax* fishes display a wide spectrum of feeding strategies, from herbivory to omnivory, and are characterized by slow growth, late maturation, and low to moderate fecundity – life-history traits that limit demographic recovery and render many species vulnerable when combined with potamodromous migrations to spawning habitats. *Schizothorax* populations face pervasive threats, including overexploitation, habitat degradation and fragmentation, pollution, invasive species, and climate change, which have collectively resulted in population declines, one confirmed extinction, and numerous Red List listings across the genus. Significant knowledge gaps remain a barrier to effective management, particularly concerning taxonomy, the fundamental ecology of poorly studied species, the quantitative impacts of cumulative stressors, and species' physiological capacity to adapt to environmental change. Resolving these gaps through targeted research, coupled with robust habitat protection, ecological restoration, and sustainable fisheries management, is essential for the long-term conservation of these fishes and the fragile aquatic ecosystems they inhabit.

Keywords: Cyprinidae, marinka, snowtrout, snow barbel, rheophilic, spawning, life cycle

For citation: Karimov E., Schletterer M., Hayes D.S. Ecology and conservation of snow trout (*Schizothorax* Heckel, 1838): a review // Limnology and Freshwater Biology. 2026. — No. 5. — P. 669–692. DOI: [10.31951/2658-3518-2026-A-5-669](https://doi.org/10.31951/2658-3518-2026-A-5-669)

1. Introduction

The genus *Schizothorax* Heckel, 1838, commonly known as snow trout or snow barbel, comprises a species-rich group of cyprinid fishes predominantly inhabiting the cold, mountainous and sub-mountainous, often fast-flowing freshwater ecosystems of Asia, including the Himalayan region, the Qinghai-Tibetan Plateau, Pamir, Indo-Gangetic plain, Sistan basin and Central Asia (Coad and De Ville, 2004; Regmi et al., 2023; Rozimov et al., 2025). Snow trout are ecologically important to these river systems, serving as a crucial link in lotic and lentic food webs (Bhatt and Manish, 2023; Regmi et al., 2023). Their specific habi-

tat requirements and sensitivity to environmental alterations make them suitable bioindicators for aquatic ecosystem health and anthropogenic impacts (Ali and Khan, 2019). Socio-economically, many *Schizothorax* species represent a valuable resource, supporting local livelihoods and food security through fisheries (Pandey et al., 2023) and, increasingly, aquaculture (Gu et al., 2023).

Despite their ecological and socio-economic importance, *Schizothorax* populations are under increasing anthropogenic pressures, resulting in population declines and conservation concerns (Wang et al., 2009; Sun et al., 2023a; IUCN, 2025). Habitat degrada-

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Received: May 12, 2026;

Accepted after revised: June 16, 2026;

Available online: October 29, 2026

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tion and fragmentation resulting from dam construction, water abstraction, and pollution are widespread (Qureshi et al., 2007; IUCN, 2025). Overexploitation through unsustainable fishing practices, including the use of illegal methods, has led to significant declines in many areas (Bharti et al., 2023; IUCN, 2025). Furthermore, the introduction of invasive alien species such as *Oncorhynchus mykiss* and *Salmo trutta*, presents competitive and predatory threats (Bhatt and Manish, 2023; Jan et al., 2023a; IUCN, 2025). Additionally, climate change, including altered hydrological regimes and water temperatures, is projected to further exacerbate species vulnerabilities (Sharma et al., 2021a; IUCN, 2025).

Effective conservation and management strategies for *Schizothorax* spp. are, however, often hampered by incomplete or fragmented knowledge. The taxonomy and systematics of the genus, for instance, remain complex, with ongoing debates regarding species delimitation, the status of subspecies, and the presence of cryptic diversity (He and Chen, 2006; Bhatt and Manish, 2023; Purohit et al., 2023; Rozimov et al., 2025). While significant research has been conducted on certain well-studied species, comprehensive information on the fundamental life-history traits, population dynamics, physiological tolerances, and adaptive capacities of many *Schizothorax* species, particularly those inhabiting remote areas, is lacking. This knowledge deficit restricts our ability to predict species responses to environmental change and to formulate robust, evidence-based conservation strategies.

This article synthesizes the current state of knowledge regarding the ecology and conservation of snow trout. Specifically, the objectives are: (1) to present the taxonomy, systematics, and distribution patterns of *Schizothorax* spp.; (2) to summarize key aspects of the genus' ecological characteristics, including habitat preferences, feeding, reproductive biology, and physiological adaptations; (3) to evaluate the pri-

mary threats impacting snow trout populations; and (4) to identify critical knowledge gaps and highlight priorities for future research. By consolidating existing information from the literature and relevant databases, this review provides a scientific foundation to inform conservation efforts.

2. Materials and methods

Information was synthesized from articles retrieved from the Scopus literature database. The following search string (title, abstract, keywords) was used on 19 May 2025 to search for relevant papers: “snow-trout” OR “snow trout” OR “snowtrout” OR “Schizothorax”. This query yielded 827 records. The titles and abstracts of these records were subsequently screened, and articles containing relevant information on the ecology and conservation of *Schizothorax* spp. were selected for detailed review.

In addition, relevant grey literature was identified through the reference lists of retrieved articles. Information was also sourced from online ichthyological databases, specifically Eschmeyer's Catalog of Fishes (Fricke et al., 2025) for taxonomic and distributional data, and the IUCN Red List of Threatened Species (IUCN, 2025) for conservation status assessments.

3. Results

Research on *Schizothorax* spp. was scarce until the early twenty-first century, with the first indexed article published in 1922. Only 45 of the 827 articles (5%) retrieved were published before 2009. A significant increase in publications is evident from 2009 onwards (Fig. 1). Most of the published papers are written by authors affiliated with Chinese institutions (51%), followed by authors from India (25%), Pakistan (5%), and the United States (2%).

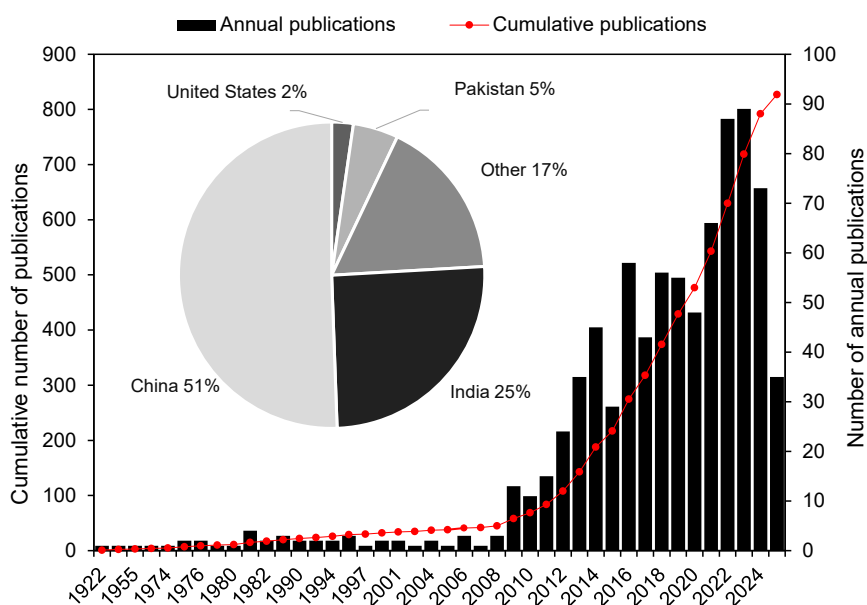


Fig. 1. Publication trends for *Schizothorax* in Scopus (n = 827). The bar chart illustrates the annual publication count and cumulative total (red line). The pie chart illustrates institutional affiliation by country, including collaborative contributions. The search was conducted on 19 May 2025 using the string: “snow-trout” OR “snow trout” OR “snowtrout” OR “Schizothorax” (data for 2025 represent a partial year until 19 May 2025).

3.1. Taxonomy, systematics, and species diversity

The genus *Schizothorax* Heckel, 1838, assigned to the family Cyprinidae and subfamily Schizothoracinae, constitutes a diverse group of freshwater fishes. Species richness estimates vary considerably, reflecting ongoing taxonomic uncertainties (He and Chen, 2006; Rozimov et al., 2025). Reported numbers range from 45 species (Sarma et al., 2024), 55 species (IUCN, 2025), and 62 species (Bhat et al., 2024), up to 68 species and subspecies (He and Chen, 2006). New species continue to be described, including *Schizothorax leukus*, *S. heteri* (Yang et al., 2013), and *S. gulinensis* (Wang et al., 2023b). This fluidity, coupled with historical misidentifications and the misapplication of names, complicates efforts to establish a definitive species count for *Schizothorax* (Bhatt and Manish, 2023; Purohit et al., 2023).

3.1.1. Morphological characterization

The genus *Schizothorax* (“cloven-breast”, from the Greek words *schízein* [to cleave] and *thorax* [breast]) exhibits a remarkable range of morphological diversity, sharing several core traits. Snow trout have an elongated body shape, adapted for benthic or near-benthic lifestyles. They have barbels (usually two pairs), triserial pharyngeal teeth (Berg, 1948), small scales covering the body, and a distinctive sheath of enlarged scales bordering the anus and anal fin base, frequently referred to as the anal cleft (Berg, 1948; Bharti et al., 2023). Mouth position is inferior or sub-inferior, facilitating bottom feeding (Berg, 1948).

Variations in body form are evident, often linked to habitat and life history characteristics. Many species exhibit a streamlined, laterally compressed body suitable for fast-flowing waters, such as *S. eurystomus* (Niu et al., 2022), *S. longibarbus* (Yan and Cao, 2013), and *S. prenanti* (Sun et al., 2023b). Head morphology is also diverse, ranging from pointed snouts, as seen in *S. bidulphi* (Liu and Hu, 2009), to blunter profiles observed in species like *S. nudiventris*, *S. heterophysallidos* (Yang et al., 2009), and *S. niger* (Gul and Rashid, 2025). An elongated snout, in contrast, is characteristic of *S. esocinus* (Gul and Rashid, 2025). A wide flat interorbital space is noted in *S. richardsonii* (Bharti et al., 2023). The genus encompasses a considerable size range: *S. niger* reaches standard lengths of ~30–33 cm (Mir et al., 2013c) and total lengths up to 39 cm (Yousuf et al., 2024), while *S. zarudnyi* and *S. richardsonii* can attain 60 cm and 2 kg (Shahriari Moghadam et al., 2014; Bhatt and Manish, 2023). *S. pseudoaksaiensis* can reach up to 90 cm and 5 kg (Wang et al., 2023a). Sexual dimorphism in size, with females often larger than males, is apparent in *S. waltoni* (Xu et al., 2023a) and *S. oconnori* (Ma et al., 2014). Additionally, mature *S. richardsonii* males may be brighter in coloration with a straight ventral profile, while females have distended bellies (Ciji et al., 2021; Bharti et al., 2023). Body coloration is frequently variable, with intraspecific differences linked to habitat. For instance, *S. argentatus* can range from silvery-white in juveniles to dark olive or black in larger specimens,

depending on the environment (Amirbekova et al., 2022). Specific markings, such as the black spots on *S. esocinus* (Kullander et al., 1999; Gul and Rashid, 2025) or the irregular spots on *S. griseus* (Yang et al., 2009), serve as distinct diagnostic characters, while other species, including *S. leukus* and *S. heteri*, lack such prominent spotting (Yang et al., 2013).

The oral region exhibits striking morphological diversity within *Schizothorax*. *S. curvifrons* has a crescent-shaped mouth (Gul and Rashid, 2025) while terminal mouths are also recorded, e.g., in *S. taliensis* (Wang et al., 2009). A pivotal adaptation in many species is the modification of the lower jaw, which is often reinforced with cartilage and covered with a sharp, keratinized horny sheath (Berg, 1948). This sheath is well-developed in species such as *S. grahami* (Jiao et al., 2023a), *S. wangchiachii* (Gu et al., 2022), and *S. leukus* (Yang et al., 2013), serving as an efficient tool for scraping algae, periphyton, and detritus from firm substrates. Notably, the lower jaw of *S. niger* is covered by a deciduous cartilaginous layer (Gul and Rashid, 2025). The absence of a horny sheath in species such as *S. davidi* (Gu et al., 2022), *S. griseus*, *S. nudiventris*, and *S. heterophysallidos* (Yang et al., 2009) serves as a key diagnostic feature.

Lip structure shows considerable variation. *S. niger* possesses thick lips with prominent lip folds and a raised pad between the upper and lower jaws (Gul and Rashid, 2025). In contrast, *S. curvifrons* has relatively thin lips without such expanded folds (Gul and Rashid, 2025). The lower lip, in particular, displays a remarkable variety of forms: it can be developed only at the corners or be continuous and uninterrupted (Berg, 1948), smooth, or covered with papillae, as in *S. leukus* (Yang et al., 2013). It may also be modified into distinct lobes, commonly bilobed, as in *S. taliensis* and *S. lissolabiatius* (Wang et al., 2009; Yang et al., 2009), or trilobed, as seen in *S. griseus*, *S. nudiventris*, and *S. heteri* (Yang et al., 2009, 2013), with the median lobe size varying. One of the most specialized labial adaptations is the development of an adhesive organ or a hard, papillated structure on the chin, documented in *S. richardsonii*, *S. plagiostomus*, *S. sinuatus* (Bharti et al., 2023; Sarma et al., 2024), and *S. lissolabiatius* (Sun et al., 2023a). This structure, composed of keratinized epidermal cells with complex micro-ornamentations, is crucial for adhesion to rocky substrates in swift currents. The nature of the postlabial groove, whether continuous or interrupted, also serves as a distinguishing character among species (Yang et al., 2009). The two pairs of barbels, characteristic of the genus, vary significantly in length. Some species, like *S. curvifrons*, possess relatively smaller barbels (Gul and Rashid, 2025), while others, such as *S. esocinus*, have long barbels (Kullander et al., 1999). Exceptionally long barbels are found in *S. longibarbus*, where their length can exceed twice the eye diameter (Yan and Cao, 2013).

Fin morphology and squamation patterns provide important taxonomic and functional information. The last unbranched ray of the dorsal fin is often a key diagnostic character: it can be a robust, ossified spine, either smooth or bearing distinct posterior serrations,

as in *S. taliensis*, *S. richardsonii*, and *S. heteri* (Wang et al., 2009; Yang et al., 2013; Bharti et al., 2023), or it can be relatively soft and flexible, as in *S. yunnanensis* (Yang et al., 2009), or only weakly ossified with small teeth or weak basal serrations, as seen in *S. pelzami iranicus* (Coad and De Ville, 2004), *S. dulongensis*, and *S. oligolepis* (Yang et al., 2013). The degree of denticulation on this spine can also diminish with age in some species (Berg, 1948). The position of the dorsal fin's origin relative to the pelvic fins, or to the snout and caudal fin base, is another variable trait (Akhtar et al., 2021). Squamation is generally characterized by small scales, for instance, as in *S. kozlovi* (Berg, 1948; Qin et al., 2024). Lateral line scale counts vary, for example, 95–109 in *S. taliensis* (Wang et al., 2009) and 110–118 in *S. biddulphi* (Liu and Hu, 2009). The extent of scalelessness on the ventral surface, particularly the thorax and belly, is a notable feature for distinguishing species. This is noted in *S. taliensis*, *S. biddulphi*, *S. leukus*, and *S. nudiventris* (Liu and Hu, 2009; Wang et al., 2009; Yang et al., 2009, 2013), with some species showing ontogenetic changes in this regard, such as *S. griseus* (Yang et al., 2009).

Internal anatomical structures also vary. The triserial pharyngeal teeth (e.g., 2,3,5–5,3,2 or 2,3,4–4,3,2) are adapted for processing various food items (Berg, 1948; Wang et al., 2009; Bharti et al., 2023). Gill raker morphology and number are linked to diet. For example, *S. biddulphi* possesses numerous (19–23) long, slender gill rakers, suggesting an adaptation for filtering planktonic or suspended particles (Liu and Hu, 2009; Wang et al., 2024b). *Schizothorax* species typically have an elongated intestinal tract, with gut length to body length ratios reported as high as 3:1 for Central Asian species (Berg, 1948) and 8:1 for *S. oconnori* (Ma et al., 2014). This intestinal length, coupled with lip thickness, has been identified as a key morphological variable associated with feeding specialization (Zhao et al., 2022). Unique internal features include the distinctively elongated posterior chamber of the air bladder (three to six times longer than the anterior one), e.g., noted in *S. heterophysallidos* (Yang et al., 2009).

Significant morphometric variation exists both within and among populations, often influenced by environmental factors and geographic isolation (Mir et al., 2013a, 2013c, 2014b; Gul et al., 2019). For example, landmark-based geometric morphometrics identified four heterogeneous populations of *S. richardsonii* in the Indian Himalayas based on body shape (Dwivedi, 2022). Truss network analysis has been used to differentiate populations, such as those of *S. plagiostomus* (Mir et al., 2013b) and *S. curvifrons* (Mir et al., 2014a). Advanced tools, such as the 3DPhenoFish software, facilitate high-throughput 3D morphological phenotyping, offering new avenues for studying intra-specific variation (Liao et al., 2021). Length-weight relationships, indicative of growth patterns (isometric or allometric) and condition, vary among *Schizothorax* species and populations. Such relationships have been documented, e.g., for *S. richardsonii* (Malik et al., 2021; Mehmood et al., 2021), *S. niger* (Yousuf et al., 2023; Karthik et al., 2025), *S. lissolabiatus* (Pan et al., 2018;

Tang et al., 2022), *S. eurycephalus* (Azamov et al., 2024; Karimov et al., 2024), *S. nukiangensis* (Liu et al., 2024), and *S. prenanti* (Shi et al., 2023), often reflecting local differences in body form and environmental conditions.

3.1.2. Molecular phylogenetics and genetic relationships

Molecular data, primarily from mitochondrial genes such as COI and Cytb, alongside nuclear markers and chromosome studies (see Supplementary Table S1 on genetic information, accession numbers, and references for selected studies), have been used to investigate *Schizothorax* systematics (Ganai et al., 2011; Zhang et al., 2022b). These approaches have helped to clarify interspecific relationships, distinguish closely related species, and identify distinct evolutionary clades within the genus (Barat et al., 2012; Bashir et al., 2016; Niu et al., 2022). Phylogenetic analyses consistently point to a complex evolutionary history, with some studies suggesting the 'Tarim-Central Asia' clade to represent an ancestral lineage (Gu et al., 2024; Rozimov et al., 2025). Furthermore, molecular techniques have been instrumental in uncovering instances of natural hybridization (Cheng et al., 2022) and highlighting the potential for significant diversity within morphologically defined species, particularly across the genus's extensive and fragmented range (Regmi et al., 2023). While the Schizothoracinae subfamily has been broadly classified into evolutionary groups based on morphology (e.g., primitive, specialized, highly specialized groups *sensu* Cao et al., 1981), molecular data continue to refine these classifications and reveal deeper phylogenetic patterns.

3.1.3. Polyploidy and karyological characteristics

A significant genomic feature of the genus *Schizothorax* is the widespread occurrence of polyploidy, with both tetraploid and hexaploid species identified. Diploid and triploid individuals of *S. richardsonii* were also identified using erythrocyte indices (Rani et al., 2023). These polyploidization events are thought to be ancient, likely linked to major climatic shifts during geological transitions (Eocene to Oligocene, 33.9 Ma; Pliocene to Pleistocene, 2.58 Ma) (Gu et al., 2024). The origins of these polyploid lineages are hypothesized to be linked to refugial areas such as the hot springs of the southeastern Tibetan Plateau, which may have facilitated survival and diversification during periods of global cooling (Gu et al., 2024).

3.2. Biogeography

The genus *Schizothorax* is predominantly distributed across the high-altitude aquatic systems of Asia, encompassing the extensive mountain ranges of the Himalayas, Karakoram, Hindu Kush, Pamir, and Tien Shan, as well as the vast Tibetan Plateau. Its range extends into associated upland regions of Central, South, East, and Southeast Asia, with some species also occurring in parts of the Middle East (Fig. 2).

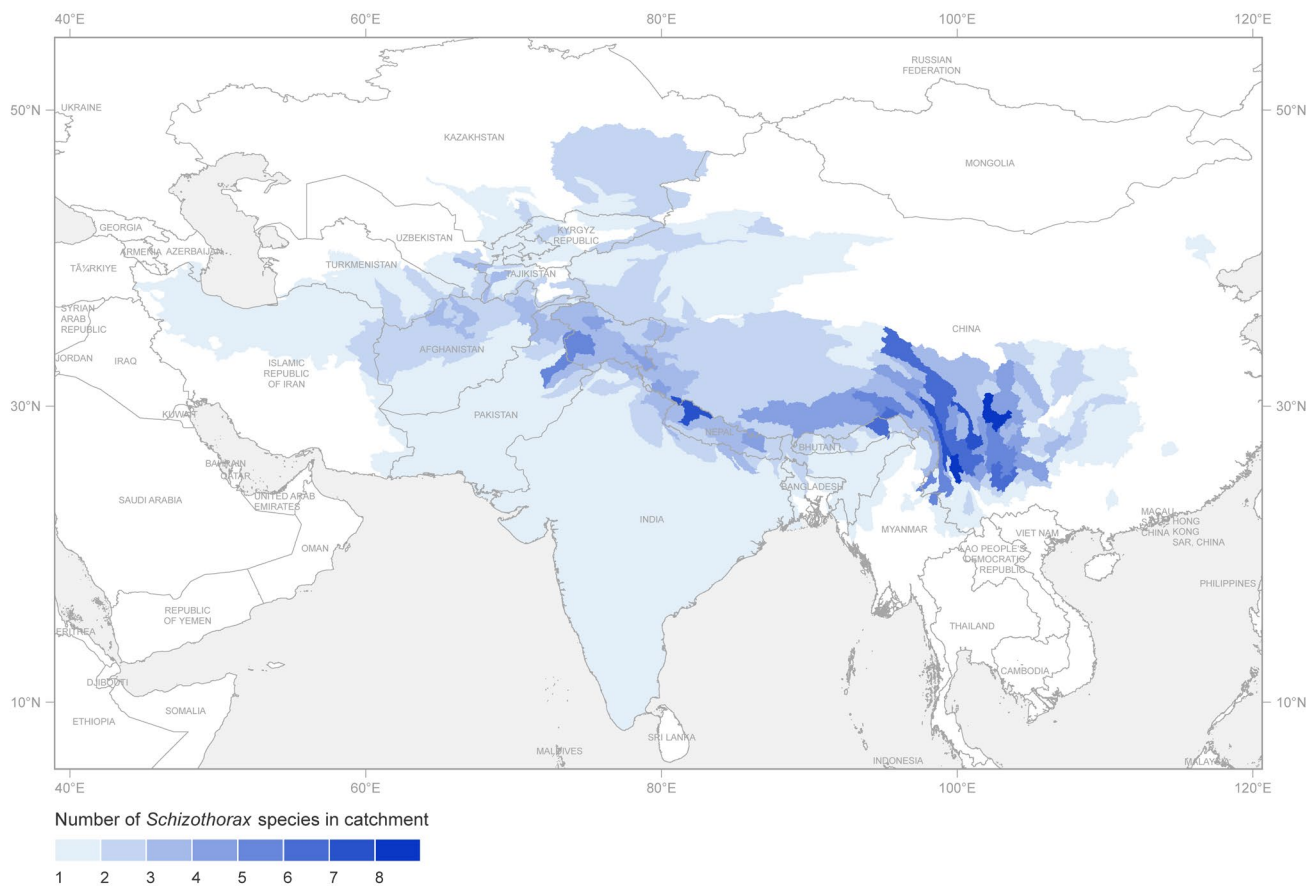


Fig. 2. Biogeographical distribution of snow trout (*Schizothorax* spp.). Data sources: IUCN Red List, HydroBASINS, and World Bank administrative boundaries (Lehner and Grill, 2013; IUCN, 2025; World Bank, 2025).

The genus occupies diverse river systems, including major drainages such as the Yangtze, Mekong (Lancang), Salween (Nujiang), Irrawaddy, Brahmaputra (Yarlung Zangbo), Indus, Ganges, and various Central Asian endorheic basins such as the Tarim and Ili-Balkhash systems (Regmi et al., 2023; Fricke et al., 2025). New records continue to refine this range, exemplified by the first record of *S. richardsonii* from the Kirong Tsangpo River in the Central Himalayas of China (Li et al., 2024a). A comprehensive list of specific localities is provided in Supplementary Table S2.

3.2.1. Species-specific distribution and endemism

Within this broad geographical range, individual *Schizothorax* species often exhibit more restricted distributions, with many endemic to specific river basins, lakes, or even particular stretches of rivers. For example, *S. taliensis* is narrowly distributed in Erhai Lake and the Lancang River, Yunnan Province, China (Wang et al., 2009; Chen et al., 2016; Rui et al., 2018); *S. biddulphi* is historically confined to the Tarim River system in Xinjiang, China (Liu and Hu, 2009; Gong et al., 2012; Fricke et al., 2025). The Nujiang River system in China hosts several endemic or near-endemic species, including *S. gongshanensis*, *S. nukiangensis*, and *S. yunnanensis* (Li et al., 2016b; Chen et al., 2017). Similarly, *S. raraensis*, *S. macrophthalmus*, and *S. nepalensis* are endemic to Lake Rara, Nepal (Terashima, 1984; Dimmick and Edds, 2002).

The Indian Himalayan region harbors numerous species, including *S. richardsonii*, which is widely distributed across Himalayan waters from Afghanistan to Bhutan (Petr, 1999; Bhatt et al., 2012; Sohail et al., 2014; Bhatt and Manish, 2023), *S. plagiostomus*, *S. esocinus*, and *S. progastus* (Chandra and Ganie, 2023). Central Asian river basins are home to species such as *S. eurycephalus*, *S. fedtschenkoi*, *S. argentatus*, and *S. pseudoaksaiensis* (Fig. 3) (Amirbekova et al., 2022; Rozimov et al., 2025). Specifically, ongoing taxonomic work in the Aral Sea catchment proposes recognizing three drainage-specific species previously lumped under or synonymized with *S. eurystomus*, i.e., *S. eurycephalus* in the Syr Darya, *S. fedtschenkoi* in the Zeravshan River, and *S. gobioides* in the Amu Darya (Rozimov et al., in prep.; see Section 4.1). In Tibet, the Yarlung Zangbo River system is inhabited by *S. oconnori*, *S. waltoni*, and *S. macropogon* (Zhu et al., 2013; Zhou et al., 2015; Guo et al., 2016). The upper reaches of the Yangtze River and its tributaries in Southwest China are inhabited by several endemic species, including *S. prenanti*, *S. chongi*, *S. davidi*, and *S. kozlovi* (Que et al., 2016; Wang et al., 2016; Li et al., 2021; Qin et al., 2024).

Some species are documented from specific drainages, such as *S. dulongensis* in the Dulong River (Irrawaddy River basin) (Ding et al., 2016) and *S. pelzami* in river basins flowing from Iran and Afghanistan into the Kara Kum desert (Coad and De Ville, 2004; Fricke et al., 2025).

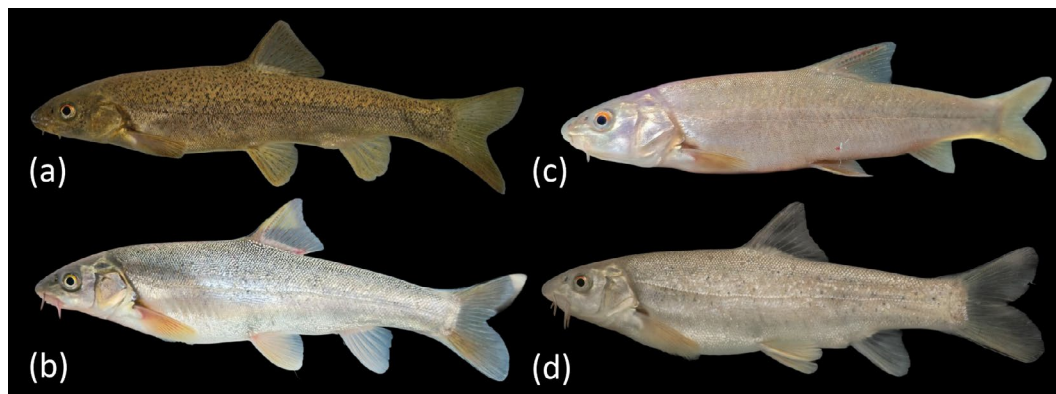


Fig. 3. Specimens of the genus *Schizothorax* from Central Asian river basins. (a) *Schizothorax gobioides* collected from the Topalang River, Amu Darya River basin (38.65049° N, 67.81337° E) on March 25, 2023; (b) *Schizothorax pseudoaksaiensis* collected from the Chu River, Chu River basin (42.38805° N, 76.09375° E) on August 21, 2023; (c) *Schizothorax fedtschenkoi* collected from the Kshtut River, Zeravshan River basin (39.39212° N, 68.04500° E) on September 4, 2024; (d) *Schizothorax eurycephalus* collected from the Margilonsoy River, Syr Darya River basin (40.30501° N, 71.80052° E) on March 29, 2023.

3.2.2. Historical biogeography, origins, and diversification drivers

The current distribution patterns of *Schizothorax* are the result of complex interactions between historical geological events, climatic fluctuations, and the evolutionary processes of vicariance and dispersal. The uplift of the Tibetan Plateau and associated orogenic events are considered pivotal in shaping the group's evolution and diversification (He and Chen, 2006; Rozimov et al., 2025). Several hypotheses attempt to explain the genus' origin and dispersal. One suggests an initial dispersal into the Qinghai-Tibetan Plateau from southeastern Asia, followed by isolation due to orogeny and climate change (Das and Subla, 1964; Regmi et al., 2023). Another hypothesis proposes that a primitive barbine clade was isolated by tectonism on the Qinghai-Tibetan Plateau, serving as the progenitor for *Schizothorax* (Cao et al., 1981; Regmi et al., 2023). More recent syntheses suggest the 'Tarim-Central Asia' clade as the most primitive, with the western Tien Shan and Pamir Mountains potentially being an origin area (He and Chen, 2006; Regmi et al., 2023; Gu et al., 2024; Rozimov et al., 2025).

Palaeoriver connections and subsequent river capture events have played a significant role in the genus dispersal and diversification (He and Chen, 2006). For example, the capture of the Yarlung Zangbo River by the Brahmaputra is thought to have facilitated an east-to-west dispersal south of the Himalaya and led to colonization of Himalayan drainages (Regmi et al., 2023). Molecular dating estimates place key vicariant events and drainage separations in the late Miocene, coinciding with periods of intense tectonic uplift in southeastern Tibet (He and Chen, 2006).

Six major biogeographic groups of *Schizothorax* have been proposed based on molecular data. This includes a Central Asiatic clade followed by five drainage-specific sister-clades: Yarlung Zangbo/Brahmaputra, Indus, Irrawaddy, Mekong/Salween, and Yangtze (He and Chen, 2006; Regmi et al., 2023). These patterns highlight the major influence of tectonic activity and climatic fluctuations in shaping the diversity and distribution of the genus (Chen et al., 2016; Gu et al., 2024; Li et al., 2024b).

3.2.3. Altitudinal distribution and ecological zonation

Schizothorax species are characteristically found in mountainous and sub-mountainous environments (Chandra and Ganie, 2023). However, altitudinal preferences vary among species. For example, in the Yarlung Zangbo River, *S. curvilabiatus* and *S. molesworthi* tend to prefer lower altitudes, while *S. macropogon* and *S. waltoni* are found at higher altitudes, and *S. oconnori* occurs across a broader altitudinal range (Liu et al., 2021). *S. waltoni* is noted to inhabit areas >3,600 m on the Qinghai-Tibet Plateau (Chen and Cao, 2000). *S. nukiangensis* in the Nujiang River predominates at altitudes between 1,800 and 2,700 m (Liu et al., 2024). Recent sampling campaigns in Central Asian rivers caught *Schizothorax* species at altitudes of 300–3,500 m (E. Karimov, pers. obs). In the Tibetan Plateau and adjacent regions, *Schizothorax* species richness is highest at mid-elevations, with a peak at 2000 m (Li et al., 2009).

3.3. Habitat

Schizothorax fishes are adapted to cold water conditions (Nikolsky, 1938; Chandra and Ganie, 2023). Nonetheless, they exhibit a wide temperature tolerance range and show a preference for temperatures 8–22°C (Petr, 1999); specifically, studies report suitable water temperatures in natural habitats from 7°C to 24°C for *S. kozlovi* (He et al., 2016), and 8–20°C for *S. richardsonii* (Singh and Sharma, 1995; Petr and Swar, 2002). Optimal temperatures for growth differ among species, with reported ranges of 14–18°C for *S. grahami* (Xu et al., 2024b), 16–17°C for *S. wangchiachii* (Xie et al., 2024a), and a mean preference of 12°C for *S. richardsonii* (Subedi et al., 2024). Some species exhibit seasonal habitat shifts in response to temperature changes, such as *S. richardsonii* moving downstream during winter when upstream temperatures drop to 6–11°C (Prakash et al., 1994). Overwintering in thermally stable habitats has also been observed for *S. eurycephalus* (Omonov et al., 2026).

In rivers, snow trout demonstrate adaptability to different conditions. Species such as *S. kozlovi*, *S. lantsangensis*, and *S. macropogon* are frequently reported

to inhabit main river channels, plateau rivers, or larger river systems (Raina and Petr, 1999; He et al., 2014, 2022). Conversely, species including *S. chongi*, *S. longibarbus*, *S. curvilabius*, *S. richardsonii*, *S. lissolabius*, and *S. prenanti* are found in faster-flowing streams and rivers (Li et al., 2011; Yan and Cao, 2013; Bhat et al., 2019; Subedi et al., 2024). In lacustrine environments, *S. taliensis* and *S. biddulphi* are known to inhabit open water (Liu and Hu, 2009; Wang et al., 2009).

Substrate preferences in riverine habitats vary among species and life stages. Many adult *Schizothorax* show an affinity for coarse substrates such as pebbles and cobbles, as in *S. lantsangensis* (Bai et al., 2022), *S. plagiostomus* (Khan et al., 2018), and *S. davidi* (Li et al., 2022c; Chandra and Ganie, 2023) (Fig. 4). However, they also occur over finer substrates. Indeed, some species, including *S. plagiostomus* (Khan et al., 2018), *S. macropogon* (Zhu et al., 2013), *S. esocinus* (Mir et al., 2014b), *S. leukus* (Sarma et al., 2024), *S. meridionalis* (Sarma et al., 2024), *S. microcephalus* (Sarma et al., 2024), *S. oconnori* (Wu, 1987), and *S. waltoni* (Wu, 1987), are reported to prefer sandy substrates.

Adult fish often utilize specific microhabitats for refuge, particularly during daytime, seeking cover in deep water pools near riverbanks and beneath large boulders, as observed for *S. griseus* (Yang et al., 2009) and similarly noted for others (Nikolsky, 1938; Wu, 1987).

Regarding hydraulic conditions, studies suggest that the optimal depth for the genus typically lies between 0.5 and 1.5 m in mountainous rivers, with suitable flow velocities of 0.5–2.0 m/s (Xie et al., 2024b; Yang et al., 2024a). Species-specific depth requirements are evident: *S. chongi*, for example, utilizes deeper waters (>3 m) in winter but shallower areas (<0.5 m) when foraging (Li et al., 2011), while *S. longibarbus* is found at depths of several meters (Yan and Cao, 2013). In contrast, *S. wangchiachii* has shallower depth preferences of 0.3–0.6 m (Xie et al., 2024a). Many species inhabit areas with significant current: *S. prenanti* is associated with a broad suitable velocity range of 0.5–2.5 m/s, with an optimal range of 0.5–0.8 m/s (Sun et al., 2023b; Yang et al., 2024a), though one study reports lower velocities (0.25–0.50 m/s) and avoidance of high turbulence (>0.05 m²/s²) (Li et al., 2022b). *S. chongi* prefers 0.7–1.0 m/s (Li et al., 2011), while *S. oconnori* avoids flows >0.9 m/s (Liang et al., 2021).

The literature indicates that juveniles favor smaller tributaries and shallow, low-velocity areas (Liang et al., 2021; Bhatt and Manish, 2023) (Fig. 4). Water temperature is a critical factor influencing juvenile growth and survival. Laboratory experiments on reared *S. kozlovi* larvae and juveniles identified optimal temperatures for maximum growth of 21–25°C; individuals reared at 10°C failed to reach the juvenile stage within a 180-day experimental period, whereas the 22°C group demonstrated the highest final mean total length and weight (He et al., 2014). Similarly, juvenile *S. biddulphi* exhibited maximum growth at 20°C (Zhao et al., 2021). Regarding substrate, studies on *S. wangchiachii* revealed a clear preference for large gravel substrates (10–15 cm) over finer materials such as sand (<1 mm) or small (2–3 cm) to medium-sized gravel (4–7 cm). Interestingly, juvenile *S. wangchiachii* also showed a preference for black substrates over white ones, a choice that was maintained irrespective of perceived predator presence (Zhang et al., 2022a).

3.4. Diet and growth

The dietary habits of *Schizothorax* species are characterized by opportunistic feeding, exhibiting a spectrum from predominantly herbivory and detritivory to omnivory, strongly influenced by geographic location, season, food availability, and developmental stage. Many species, including *S. richardsonii* (Shekhar et al., 1993; Rayal et al., 2020), *S. curvifrons* (Langer, 1985), *S. zarudnyi* (Gharaei, 2012), *S. wangchiachii* (Gu et al., 2022), *S. plagiostomus* (Khan et al., 2018; Ullah and Khan, 2024), and *S. niger* (Wanjari et al., 2026), primarily consume periphytic algae (often dominated by Bacillariophyceae), detritus, and associated sand and mud, indicative of an iliophagic or bottom-scraping feeding mode. In Central Asian water bodies, plant material and detritus constitute 50–80% of the food mass (Berg, 1948), and algae alone may represent over half the gut content volume in various species (Berg, 1948; Bhatt and Manish, 2023; Karimov et al., 2025).

Other species, or populations under different ecological conditions, display more omnivorous tendencies. *S. davidi* (Gu et al., 2022), *S. grahmi* (Jiao et al., 2023a), *S. biddulphi* (Liu and Hu, 2009; Wang et al., 2024b), *S. intermedius* (Wei et al., 2021), *S. oconnori*

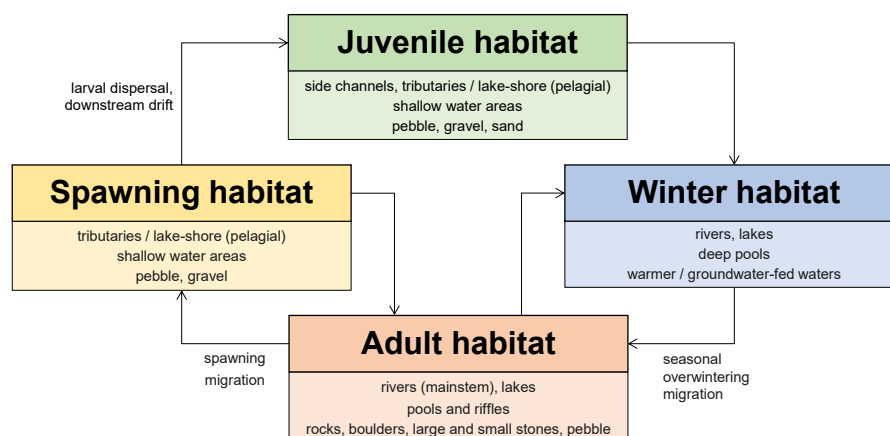


Fig. 4. Life cycle and habitats of *Schizothorax* spp.

(Ma et al., 2014), *S. esocinus*, and some populations of *S. curvifrons* (Kausar et al., 2010) incorporate a mix of plant matter and animal items such as protozoa, rotifers, crustaceans, and aquatic insect larvae. In specific habitats, such as the Tarim River basin, China, primary producers such as *Tamarix*, *Glycine*, and *Nitraria* can be key dietary components for *S. eurystomus*, and *S. irregularis* (Zhao et al., 2022), while lacustrine *S. taliensis* mainly feeds on zooplankton (Wang et al., 2009). Fish are generally a minor or accidental dietary component (Berg, 1948; Shekhar et al., 1993), though they can occasionally be more significant for larger individuals in certain Central Asian populations (Nikolsky, 1938). This dietary diversity is reflected in the gut microbiota, with significant differences observed between herbivorous (e.g., *S. wangchiachii*) and omnivorous species (e.g., *S. kozlovi*), indicating that gut microbiome composition is a key factor in digesting different food sources (Xu et al., 2022b).

The genus widely exhibits a distinct ontogenetic dietary shift from plankton and invertebrates towards herbivory and detritivory (Wanjari et al., 2026). For example, young *S. curvifrons* (<10 cm) and ~1 cm small *Schizothorax* in the Kafirnigan River, Tajikistan, first consume phytoplankton and fine detritus; later their diet changes to coarser detritus, more plant matter, and benthic invertebrates (Nikolsky, 1938; Sunder, 1984). Artificially bred juvenile *S. wangchiachii* began to ingest periphytic algae from the natural habitat by day 5, stabilizing at day 15 (Xu et al., 2023b).

Seasonal variations in feeding intensity are also evident. *S. plagiostomus* shows peak feeding in warmer months and minimal consumption in winter (Khan et al., 2018; Ullah and Khan, 2024). Conversely, *S. curvifrons* and *S. niger* (Langer, 1985) reduce feeding during their spawning periods and feed more actively in winter. For *S. oconnori*, however, feeding intensity appears more closely linked to food availability than spawning activity (Ma et al., 2014). In *S. labiatus*, slow winter growth has been linked to lower food availability and reduced winter metabolism (Jan et al., 2023b, 2024b), further highlighting seasonal feeding patterns.

3.4.1. Morphological adaptations for feeding

Morphological features of the mouth and jaw (see Section 3.1.1) are closely linked to feeding strategies. The predominantly inferior or sub-inferior mouth position observed in most *Schizothorax* is well-suited for benthic feeding, including scraping algae or detritus from substrates (Berg, 1948). The horny sheath or keratinized edge on the lower jaw, characteristic of species like *S. grahami*, *S. prenanti*, and *S. wangchiachii* (Gu et al., 2022; Jiao et al., 2023a; Sun et al., 2023b), facilitates the scraping of periphyton and detritus from hard surfaces. Similarly, the hard, papillated adhesive organ on the chin of *S. richardsonii*, while primarily noted for adhesion, also complements its bottom-feeding behavior (Bharti et al., 2023).

Variations in intestinal length and lip structure and thickness (see Section 3.1.1) have been identified as

key morphological variables related to feeding specialization (Zhao et al., 2022). Consistent with diets often rich in plant matter and detritus, the digestive tract is typically elongated; its allometric increase with body size may facilitate ontogenetic dietary shifts towards herbivory or detritivory. While most cyprinids lack a true stomach, the proximal intestine is often enlarged and acts as a temporary storage organ for ingested food (Bhat et al., 2019). *S. grahami* possesses an enlarged sac between the esophagus and intestinal tract that functions analogously to a stomach (Jiao et al., 2023a). Furthermore, the specialized, high number of long, thin gill rakers in *S. biddulphi* (Wang et al., 2024b) suggests an adaptation for efficient filtration of phytoplankton and small zooplankton from the water.

3.4.2. Maturity, growth, and longevity

The attainment of sexual maturity in *Schizothorax* species generally occurs within a few years of life, though the specific age and size vary among species. Several species, including *S. taliensis* (Wang et al., 2009), *S. argentatus* (Amirbekova et al., 2022), and *S. grahami* (Zhou et al., 2023a), reach maturity between 3 and 4 years of age. A common pattern is that males tend to mature earlier, typically at 3 years, while females mature later, often at 4 years (Amirbekova et al., 2022; Zhou et al., 2023a). In contrast, other *Schizothorax* species mature even later. For instance, *S. davidi* reportedly reaches sexual maturity at 6 years of age (Wang et al., 2016). Other examples of late-maturing species include *S. macropogon* (Guo et al., 2014), *S. pseudoak-saiensis* (Wang et al., 2023a), *S. biddulphi* (Wang et al., 2024b), and *S. oconnori* (Ma et al., 2012).

The size at first maturity varies considerably across the genus. For *S. eurycephalus*, a recent survey found mature males from 8 cm total length (TL) (Karimov et al., 2025). For *S. richardsonii*, reported sizes at first maturity range from 13 and 16 cm TL for males and females, respectively, to 40 cm TL (Mohan, 2005). For *S. plagiostomus*, maturity has been observed at 18–24 cm TL (Jan et al., 2017) and at a larger size of 33 cm TL (Ahmad et al., 2019). Other documented sizes at first maturity include 25 cm TL for *S. curvifrons* (Ahmad et al., 2019), and, for *S. labiatus*, 24 cm TL for males and 28 cm TL for females (Arafat and Bakhtiyar, 2022). For *S. oconnori*, the standard length at which 50% of individuals are mature (L_{50}) was determined to be 30 cm for males and 39 cm for females (Ma et al., 2012).

Schizothorax species are often characterized by slow growth (Li et al., 2011; Yan et al., 2017; Gul et al., 2019). *S. richardsonii* exhibits an average annual growth increment of 8–10 cm during early life, which decreases with age (Bhatt and Manish, 2023). Similarly, *S. niger* in Manasbal Lake reached an average length of 15 cm in the first year, growing to 39 cm by the sixth year (Yousuf et al., 2024). Several species, such as *S. oconnori*, are notably long-lived (Ma et al., 2011, 2014). In *S. wangchiachii*, maximum reported ages reach 11–12 years (He et al., 2023).

3.5. Spawning

Spawning in *Schizothorax* is seasonal and cued by environmental factors, primarily water temperature and photoperiod. The spawning season varies geographically and among species. Many species spawn in spring and early summer; for example, *S. niger* and *S. oconnori* spawn from February to April (Ma et al., 2012; Ahmad et al., 2019; Lai et al., 2024), *S. waltoni* and *S. pelzami* from March to April (Safari et al., 2014; Zhou et al., 2015), *S. grahami* from March to May (Xu et al., 2024b), *S. lissolabius* from March to May (Ding et al., 2023b), *S. lantsangensis* from April to August (Wu and Wu, 1992; Li et al., 2016a), *S. argentatus* from April to May (Amirbekova et al., 2022), and *S. chongi* and *S. pseudoaksaiensis* from April to July (Li et al., 2011; Wang et al., 2023a). Others, such as *S. curvifrons*, spawn later, from June to August (Langer, 1985). *S. wangchiachii* is reported to spawn from December to March (He et al., 2023; Jiao et al., 2023b). Some species, such as *S. richardsonii*, exhibit bi-annual spawning (Bharti et al., 2023; Chandra and Ganie, 2023). *S. plagiostomus* also typically spawns twice, though reported timings vary regionally, for instance, March–April and October–November in some areas (Kullander et al., 1999; Chen and Cao, 2000; Jan et al., 2017; Khan et al., 2018) versus September–October (principal) and February–March (residual, often associated with fresh rain) in the Garhwal Himalaya (Sharma et al., 2023). In Himachal Pradesh, *Schizothorax* spp. have even been reported to spawn three times a year (Chandra and Ganie, 2023).

3.5.1. Spawning migration and behavior

Many *Schizothorax* species undertake potamodromous migrations to reach suitable spawning habitats (Fig. 4). While some species, such as *S. zarudnyi* (Ghanbari et al., 2017), *S. davidi* (Li et al., 2022c), *S. prenanti* (Li et al., 2021; Yang et al., 2024a), and *S. lissolabius* (Sun et al., 2023a), are generally considered locally resident or short-distance migrants, others exhibit more extensive movements. For example, *S. richardsonii* within the Beas and Sutlej Rivers, India, undertake long-distance upstream migrations, covering tens of kilometers (Petr and Swar, 2002; Rai et al., 2002), although the exact migratory distances are not always specified. A telemetry study on *S. eurycephalus* in the Shakhimardan River basin, Central Asia, revealed migration distances of at least 15–18 km (Omonov et al., 2026).

Upstream spawning migrations to headwaters and tributaries are often initiated by seasonal environmental cues such as rising water temperatures and snowmelt in late winter and spring, prompting fish like *S. kozlovi* (He et al., 2022), *S. richardsonii* (Mohan, 2005), *S. wangchiachii* (Jiao et al., 2023b), and *S. taliensis* (Wang et al., 1998) to seek out warmer tributaries or assemble around geothermally influenced spring-fed benthic cavities and areas of upwelling groundwater for spawning. Rising mainstream temperatures and decreasing dissolved oxygen in summer can drive further upstream migration in *S. richardsonii*, leading to its absence from lower, warmer reaches (Bharti et al.,

2023). Downstream movements are also significant, particularly during winter when *S. richardsonii* migrates to lower river reaches (where temperatures may be 5–10°C) for feeding, overwintering, and notably, for a secondary spawning period often occurring between October and December (Prakash et al., 1994; Petr and Swar, 2002; Mohan, 2005) (Fig. 4). These downstream movements are crucial for survival, providing access to feeding grounds and refuge from harsh headwater conditions (Marmulla, 2001).

The timing of spawning is closely regulated by environmental conditions, particularly water temperature and photoperiod, with a compelling example seen in *S. plagiostomus*, which, despite possessing mature eggs during winter months, reportedly delays spawning until April–May when conditions of water temperature and photoperiod become favorable (Jan et al., 2017). Physiologically, the seasonal development of reproductive organs culminates when gonads reach their maximum size and weight during the spawning season, as reported for *S. niger*, *S. plagiostomus*, and *S. labiatus* (Jan et al., 2017; Ahmad et al., 2019; Arafat and Bakhtiyar, 2022). In addition to physical cues, chemical signals can play a role: in *S. richardsonii*, ovarian odors from conspecific and heterospecific females can prime males, stimulate gonad development, and increase milt production (Bhatt et al., 2004).

Spawning typically occurs in shallow waters with pebble, gravel, or sandy substrates (Wang et al., 2009; Zhu et al., 2013; Jan et al., 2017; Chandra and Ganie, 2023); ideal microhabitats for *S. prenanti* include deep grooves and submerged gravel bars (Zhong et al., 2024). Aggregation spawning has been noted for *S. oconnori* (Ma et al., 2012), and the sex ratio at spawning grounds can vary. A male to female ratio of 7:3 has been observed in *S. richardsonii* (Chandra and Ganie, 2023), though a 1:1 ratio is also reported (Nikolsky, 1938; Berg, 1948).

Reproductive activities also exhibit distinct diel patterns. Nocturnal upstream migrations have been documented for *S. wangchiachii* (Jiao et al., 2023b). The timing of the spawning act itself also varies by species. For example, *S. plagiostomus* spawns around midnight, *S. sinuatus* spawns in the early morning, and *S. richardsonii* mostly spawns before midnight (Bhatt et al., 2004).

3.5.2. Fecundity, egg characteristics, and early development

Fecundity in *Schizothorax* species is generally low to moderate but varies significantly with species, e.g., ranging from around 2,000 to 68,000 eggs (Table 1). Relative fecundity similarly shows variation, with reported values of 13–92 eggs/g (Table 1). While some species, such as *S. zarudnyi*, show high fecundity (Shahriari Moghadam et al., 2014), many others, including *S. oconnori* (Ma et al., 2012), *S. richardsonii* (Bhatt and Manish, 2023), *S. biddulphi* (Wang et al., 2024b), and *S. grahami* (Zhou et al., 2023a), are generally described as having low to moderate reproductive rates (Zhou et al., 2015). Fecundity increases with body size and age, particularly for females (Mohan, 2005).

Table 1. Reported fecundity and embryonic development characteristics of *Schizothorax* species.

Species	Absolute fecundity (eggs)	Relative fecundity (eggs/g)	Hatching time (hours)	Incubation temperature (°C)	Reference
<i>S. argentatus</i>	16,100–67,900	-	120	18	Amirbekova et al., 2022
<i>S. labiatus</i>	2,754–13,465	14–45	-	-	Arafat and Bakhtiyar, 2022
<i>S. kozlovi</i>	-	-	-	14–18	He et al., 2016
<i>S. niger</i>	3,224	69	-	-	Ahmad et al., 2019
<i>S. oconnori</i>	8,228–39,343	14	190	12–13	Ma et al., 2012
<i>S. plagiostomus</i>	14,670	35	-	-	Jan et al., 2019
<i>S. pseudoaksaiensis</i>	55,652	26	-	-	Wang et al., 2023a
<i>S. richardsonii</i>	-	15–58	116–122	16–21	Bhatt and Manish, 2023
<i>S. richardsonii</i>	2,248–8,726	39–92	-	17–21	Mohan, 2005
<i>S. waltoni</i>	21,693	13	264	10–12	Zhou et al., 2015

At temperatures of 16–21°C, hatching is recorded around 116 HAF (hours after fertilization), at colder temperatures it can require up to 264 HAF (Table 1). Newly hatched larvae emerge with a prominent yolk sac, relying on endogenous yolk absorption for several days, before developing functional mouthparts and transitioning to active exogenous feeding.

3.5.3. Aquaculture and artificial reproduction

Aquaculture and cultivation practices have been reported for several species, including *S. prenanti*, *S. davidi*, *S. wangchiachii*, *S. richardsonii*, and *S. zarudnyi* (Basade and Mohan, 2012; Ning et al., 2012; Zhao et al., 2020; Afshari et al., 2021; Wang et al., 2022; Gu et al., 2023). Significant progress in artificial breeding has been documented for *S. richardsonii*. Captive broodstock have been successfully stripped at experimental fish farms, achieving fertilization rates of 35–45% and hatching rates of 60–75% (Chandra and Ganie, 2023). Similarly, for *S. argentatus*, previously on the verge of extinction, artificial reproduction has been successfully achieved in hatcheries (Amirbekova et al., 2022). This species is also being evaluated for pond aquaculture (Mamilov et al., 2024).

Hybridization of female *S. wangchiachii* with male *Percocypris pingi* has been shown to improve offspring growth, thermal tolerance and disease resistance, alongside the expression of genetically and phenotypically sterile hybrid characteristics (Gu et al., 2023).

3.6. Physiological adaptations and environmental tolerances

Schizothorax species exhibit a suite of physiological adaptations and tolerances to various abiotic stressors. *S. waltoni* survives temperatures from 0°C to 30°C (He et al., 2020), *S. kozlovi* tolerates up to 32°C (He et al., 2014), and *S. richardsonii* has a thermal range of 0–27°C (Sharma and Mehta, 2010; Bharti et al., 2023). Optimal thermal ranges for growth and other physiological processes differ among species, however. Prolonged cold acclimation, for instance, at 6°C in *S. prenanti*, elicits significant changes in serum metabolites and energy metabolism pathways (Wang et al., 2024a). While generally adapted to well-oxygenated waters and

considered intolerant to chronic hypoxia or increased salinity (Li et al., 2023a), some species demonstrate resilience. *S. richardsonii* can survive periods of winter hypoxia (Bharti et al., 2023) and *S. prenanti* has a reported hypoxia tolerance threshold of 0.4–0.6 mg O₂/L (Fu et al., 2014). The body mass-corrected oxygen consumption rate for *S. richardsonii* ranges from 150 mg O₂/kg/h at 12°C to 315 mg O₂/kg/h at 26°C (Kamalam et al., 2019). Adaptations to ion-poor waters may include enhanced ion transport capacity via chloride cells on gill epithelia, as reported for *S. curvifrons* (Mir et al., 2011).

Tolerance to total dissolved gas (TDG) supersaturation, a potential stressor downstream of hydropower dams, has been investigated in several species. For *S. davidi*, the 96-hour LC₅₀ for TDG was 126% (Liang et al., 2013), and exposure to 116% TDG induced notable biochemical and transcriptomic changes in gill tissues, affecting pathways related to cell cycle, apoptosis, and immune signaling (Chen et al., 2023). Studies on *S. prenanti* revealed that median survival times decrease with increasing TDG levels (e.g., from ~24 hours at 120% to ~3 hours at 150% TDG) (Wang et al., 2015; Yuan et al., 2018). TDG exposure also impairs fishway passage success in *S. prenanti*, with higher mortality at TDG levels ≥120% (Yang et al., 2024b). In TDG-supersaturated waters, adult *S. prenanti* survival increased with water depth, though survivors experienced reduced growth. Interestingly, individuals re-exposed to TDG after a recovery period exhibited lower mortality than previously unexposed fish (Yuan et al., 2022). Furthermore, the interplay between TDG levels and flow velocity significantly impacts survival and swimming ability in juvenile *S. prenanti* (Yuan et al., 2023).

Swimming performance is crucial for navigating dynamic riverine habitats and undertaking migrations. In *Schizothorax*, swimming performance is influenced by multiple physical and environmental factors. While absolute critical swimming speed U_{crit} and burst speed U_{burst} increase with body length, relative U_{crit} and U_{burst} decrease in larger fish; in addition, U_{crit} increases with temperature up to approximately 15°C before declining (Hou et al., 2018). Significant variation exists between populations from different river systems. *Schizothorax* species in the Yarlung Zangbo River exhibit weaker

critical and burst swimming speeds compared to those in the Yangtze River basin (Wang et al., 2024c). Swimming ability generally decreases with increasing altitude (Cai et al., 2023) and is negatively correlated with body length, while temperature effects vary (Ke et al., 2022). Exercise training can improve swimming performance in juvenile *S. wangchiachii*, linked to genes like MYLPF (Zeng et al., 2024).

Sensory responses to light and flow are evident. *S. waltoni* demonstrated increased attraction to green and blue light and repulsion to red and yellow light under specific flow (0.3 m/s) and temperature (18°C) conditions (Xu et al., 2022a). Similarly, green and yellow light were identified as approach and repellent stimuli, respectively, for *S. prenanti* (Shi et al., 2022). *S. davidi* exhibits differential light preferences based on social context, with singletons preferring white light and groups favoring blue light, with altered mobility patterns observed under blue light (Li et al., 2022c).

Social behavior, such as schooling, has been documented. Under specific hydraulic conditions (flow velocity 0.27–0.70 m/s, turbulent kinetic energy 0.004–0.018 m²/s²), *S. prenanti* forms organized schools with polarized arrangements and synchronized swimming (Zhu et al., 2022). Furthermore, temperature differences can influence aggregation behavior, with *S. prenanti* observed to gather in warmer water zones near fishway inlets, affecting entry attempts (Zheng et al., 2023).

3.7. Threats

Schizothorax populations face numerous threats, leading to documented declines and increasing conservation concern for many species. IUCN threat data indicate that ‘biological resource use’, ‘natural system modifications’, and ‘pollution’ are the most frequently

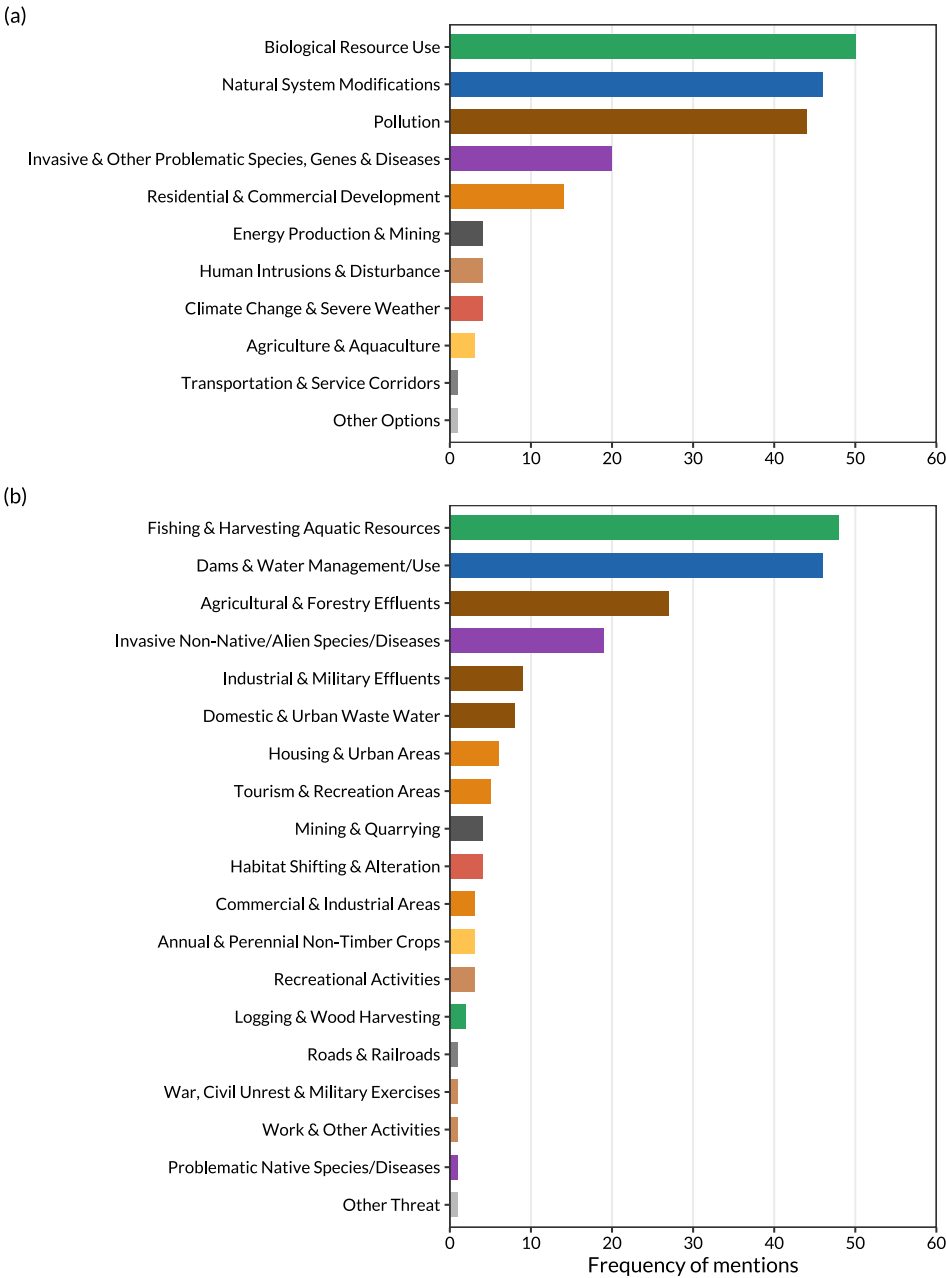


Fig. 5. Distribution of threat mentions for *Schizothorax* spp. across IUCN threat categories (a) and sub-categories (b), in descending order of citation frequency across species assessments (IUCN, 2025). Bar colors in (b) indicate the corresponding parent threat category shown in (a).

cited threat categories impacting snow trout (Fig. 5a). At the sub-category level, 'fishing & harvesting aquatic resources' and 'dams & water management/use' are the most prevalent threats. Other sub-categories are cited considerably less frequently, with 'agricultural & forestry effluents' and 'invasive non-native/alien species/diseases' being the third and fourth most frequently cited sub-categories (Fig. 5b).

3.7.1. Resource overexploitation

Overfishing poses a major threat to many *Schizothorax* populations (Fig. 5), which are frequently targeted for food due to their favorable size and palatability (Yan et al., 2017; Xu et al., 2024a). The consequences of this pressure are evident across the genus' range. Stock assessments demonstrate, for example, that *S. niger* in Manasbal Lake, India, and *S. wangchichii* in the Jinsha and Yalong Rivers, China, are either on the brink of or currently experiencing severe overexploitation (He et al., 2023; Yousuf et al., 2024). Furthermore, sustained overfishing is reflected in the declining average size of captured individuals, documented for *S. macropogon* and *S. waltoni* (IUCN, 2025).

Compounding these unsustainable extraction rates is the widespread use of destructive and unselective fishing methods for subsistence fisheries; these include illegal electrofishing, poisoning with plant-based toxins or chemicals, and dynamiting, which can rapidly decimate local stocks, particularly when spawning aggregations are targeted (IUCN, 2025). Ultimately, the persistence of illegal poaching, even in regions where fishing prohibitions or closed seasons are in place, highlights a critical enforcement gap.

3.7.2. Natural systems modification

The construction of dams and associated water infrastructures (e.g., sluices, diversions) represents a pervasive threat to *Schizothorax* populations (Fig. 5), with severe ecological consequences across their range (Qureshi et al., 2007; Yan et al., 2017; IUCN, 2025). Foremost among these impacts is the severance of longitudinal river connectivity. Even low-head dams and small hydropower plants can create insurmountable barriers that block up- and downstream migratory pathways essential for feeding and spawning (Schletterer et al., 2016; Tan et al., 2024). The demographic toll of this fragmentation is starkly illustrated in the Mekong basin, where barriers are significantly associated with the localized extirpation of *S. lissolabiatu*s, reducing the species' distribution range by around 20% (Sun et al., 2023a).

Beyond functioning as physical barriers, these structures fundamentally degrade ecosystems by inundating habitats, fragmenting populations, and altering downstream water quality and quantity and sediment transport (Hayes et al., 2018; Ding et al., 2023a). The operational management of reservoirs exacerbates these issues by generating artificial thermal regimes that disrupt the natural phenology of fish migration and spawning (Li et al., 2022a). An example of such an

operational impact is the Dahuaqiao dam on the upper Mekong River, where flow regime disruptions caused recruitment failure and the subsequent disappearance of young-of-the-year *S. lissolabiatu*s from downstream reaches (Ding et al., 2023a).

Concurrently, river systems are heavily modified by water abstraction for agricultural irrigation and urban supply, which diminishes river flows, disconnects adjacent water bodies, and, in severe instances, completely desiccates river sections. This anthropogenic dewatering has severely compromised essential spawning habitats, driving population declines in species such as *S. taliensis* (Wang et al., 2009). Finally, broader landscape modifications compound these instream pressures. Riparian deforestation and road construction drive riverbed siltation, while sand and gravel mining inflict direct physical damage (IUCN, 2025). Additionally, agricultural encroachment into riparian zones further degrades these ecosystems by promoting channelization (IUCN, 2025).

3.7.3. Pollution

Water pollution from anthropogenic sources severely degrades *Schizothorax* habitats (Fig. 5). Domestic sewage and agricultural run-off frequently drive eutrophication (Zargar et al., 2024). Concurrently, these ecosystems are compromised by chemical contaminants like pesticides and industrial mining waste (IUCN, 2025). Such chemical influxes provoke direct lethal or sub-lethal physiological consequences. For example, experimental evidence demonstrates that elevated salinity and alkalinity induce acute lethal toxicity in juvenile *S. biddulphi* following short-term exposure (Zhao et al., 2021). Furthermore, industrial pollutants drive the bioaccumulation of heavy metals (e.g., Zn, Fe, Mn, Cr, Ni, Cd, Pb) within fish tissues (Banday et al., 2023; Khan et al., 2023), triggering severe genotoxic, physiological, and biochemical damage (Banday et al., 2023).

Beyond traditional contaminants, emerging persistent organic pollutants represent a rapidly escalating conservation concern. Compounds including organochlorine pesticides, polycyclic aromatic hydrocarbons, and perfluoroalkyl substances are actively accumulating in species such as *S. macropogon* and exhibit alarmingly high risk ratios (Zhou et al., 2023b). Microplastic contamination, predominantly fibers, is widely documented across Himalayan rivers and is directly ingested by *S. richardsonii* (Badola et al., 2023) and *S. plagiostomus* (Bilal et al., 2023; Hayat et al., 2024; Khan et al., 2024).

3.7.4. Invasive species

The introduction of invasive species into *Schizothorax* habitats (Fig. 5) represents another ecological threat (Xiong et al., 2023). Invasive taxa can negatively impact native fish through direct resource competition for food and space alongside predation of eggs and juveniles and the potential introduction of novel diseases.

Introduced salmonids such as *Salmo trutta* and *Oncorhynchus mykiss* constitute a widespread threat across Himalayan streams (IUCN, 2025). Ecological assessments demonstrate a substantial habitat and climatic niche overlap of up to 96% between these introduced species and native populations, indicating a high potential for severe resource competition (Jan et al., 2023a). *Salmo trutta* specifically exhibits a strong competitive advantage over *Schizothorax* spp., actively out-competing and displacing native populations into isolated headwater refugia (Sharma et al., 2021b, 2021c; Subedi et al., 2024). Furthermore, direct predation on juvenile *Schizothorax* individuals by *Salmo trutta* exacerbates population decline (IUCN, 2025).

Beyond salmonids, the introduction of exotic fishes for aquaculture has negatively impacted native species such as *S. biddulphi* (IUCN, 2025). The increasing dominance of introduced *Cyprinus carpio* is directly linked to the decline of *S. esocinus* and *S. niger* in Kashmir (IUCN, 2025). The proliferation of *C. carpio* also coincides geographically and temporally with decreasing *S. richardsonii* populations throughout Himalayan river systems (Choudhary et al., 2023). Predation remains a critical stressor in these altered communities, as evidenced by *S. taliensis* populations suffering heavy losses due to exotic fish consuming their eggs (Yang, 1996). Finally, poorly managed conservation and aquaculture practices can drive intra-generic competition. Specifically, the introduction of captive-bred *Schizothorax* into aquatic systems outside their native range establishes direct resource competition with native species. For example, *S. prenanti*, as an ecologically similar species, is frequently released and competes with native *S. sinensis* (IUCN, 2025).

3.7.5. Climate change vulnerability

Climate change poses severe and widespread consequences for cold-water organisms, including *Schizothorax* (He et al., 2022; Bhatt and Manish, 2023). Shifts in precipitation patterns and altered snow cover and glacier melt dynamics are fundamentally disrupting local hydrological regimes (Regmi et al., 2023), resulting in increased frequency and intensity of droughts and floods which degrade overall habitat availability and quality (IUCN, 2025). Concurrently, rising water temperatures threaten to exceed thermal tolerance lim-

its of fishes while simultaneously reducing dissolved oxygen levels and altering critical phenological events such as spawning times.

In response to warming waters, *Schizothorax* populations shift toward higher-elevation streams to seek thermal refugia. However, these altitudinal shifts result in range contractions and population fragmentation (Sharma et al., 2021a; Regmi et al., 2023). Quantitative projections forecast a habitat reduction of up to 26% by 2070 for *S. richardsonii* (Sharma et al., 2021a). Similar reductions are anticipated for *S. plagiostomus*, which is increasingly restricted to higher elevations (Sharma et al., 2021a; IUCN, 2025). Ultimately, this climate-induced range shift increases the likelihood of novel interactions with invasive predators, further threatening these already vulnerable populations (Sharma et al., 2021a; Regmi et al., 2023).

3.7.6. Parasites

The highly specialized habitat requirements of *Schizothorax* may reduce resilience to environmental change, exacerbating vulnerability to parasitic infections. Population-level assessments demonstrate such acute susceptibility through high infection rates, for example, of >60% parasite prevalence in Pakistani rivers (Ahmad et al., 2021; Khalid et al., 2021). Endoparasitic helminth infections are particularly common (Ahmad et al., 2018; Nabi et al., 2020), with *Schizothorax* species functioning as documented hosts for cestodes such as *Ligula intestinalis* (Rahnama et al., 2024). Beyond helminths, *S. richardsonii* is susceptible to diverse parasitic taxa (Bharti et al., 2023). The diversity of parasites is further illustrated by ectoparasitic infestations of ciliophorans such as *Chilodonella*, crustaceans such as *Argulus* (Tak et al., 2014; Tandel et al., 2021), and the leech *Hemiclepsis marginata* (Solijonov et al., 2024).

S. wangchiachii and *S. macropogon* exhibit vulnerability to the parasitic ciliate *Ichthyophthirius multifiliis* and water molds *Saprolegnia* (Huang et al., 2024); for example, a mass mortality event caused by *I. multifiliis* was reported in high-altitude Tibetan regions (Li et al., 2022d). *Saprolegniasis* has been reported to elicit significant transcriptomic changes in the spleen (Kong et al., 2023).

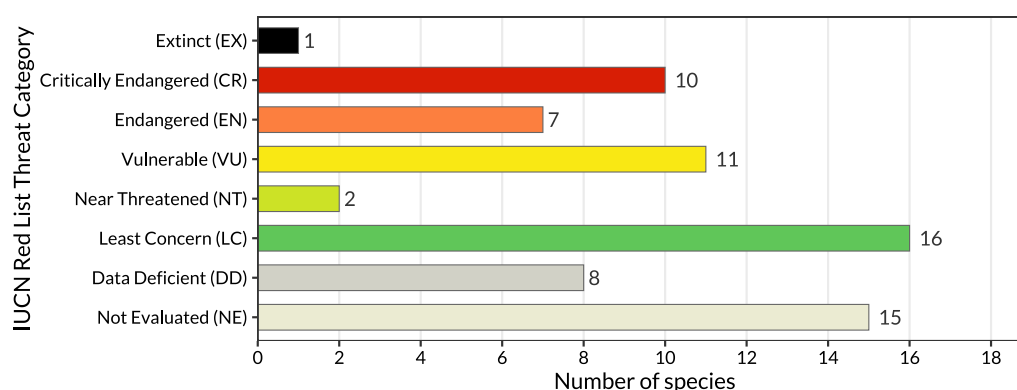


Fig. 6. Conservation status of *Schizothorax* spp. according to IUCN Red List categories ($n=70$ species compiled from the IUCN Red List [55 evaluated species] and Eschmeyer's Catalog of Fishes [15 Not Evaluated valid species]; Fricke et al., 2025; IUCN, 2025).

Gill infections are emerging as a localized threat, exemplified by the recent description of the parasitic flatworm *Paradiplozoon yarkandense* (Arken et al., 2022), while non-eukaryotic threats include vulnerability to the bacterial pathogen *Streptococcus agalactiae* (Wang et al., 2023c).

3.8. Current conservation status and observed trends

The anthropogenic threats facing *Schizothorax* populations have driven widespread demographic declines and resulted in varying conservation statuses across the genus (Fig. 6). The most severe case is *S. saltans*, which is now considered Extinct (EX) according to the International Union for Conservation of Nature (IUCN) Red List; extinction is attributed primarily to habitat deterioration from water abstraction, pollution, and overfishing (IUCN, 2025). Other taxa face imminent extirpation. *S. biddulphi* is formally assessed as Endangered (EN) following range contraction driven by water engineering projects and alien species introductions (Liu and Hu, 2009; Gong et al., 2012). Similarly, *S. taliensis* is listed as Endangered after experiencing drastic population declines from spawning habitat loss, exotic fish predation, and overfishing, and is now rare in Erhai Lake, China, where it historically constituted 30% of the local fisheries harvest (Wang et al., 2009).

Overall, 11 *Schizothorax* species are categorized as Vulnerable (VU) due to the stressors described in Section 3.7. Prominent Vulnerable taxa include *S. richardsonii*, *S. argentatus*, and *S. pseudoaksaiensis*. Their persistence is precarious. For instance, *S. argentatus* faced near-extinction prior to concerted conservation efforts (Amirbekova et al., 2022). In contrast, severe overfishing of *S. pseudoaksaiensis* threatens to drive it toward Critically Endangered (CR) or Extinct status in the near term (IUCN, 2025).

Beyond formal IUCN evaluations, empirical observations frequently report severe population distress in the 15 unassessed species and the eight listed as Data Deficient. A general decline across *Schizothorax* populations due to multiple human pressures is documented (Yan et al., 2017; Xu et al., 2024a). Specific regional assessments confirm the severe overexploitation of *S. niger* (Yousuf et al., 2024) and *S. wangchiachii* (He et al., 2023). Furthermore, habitat alterations from hydroelectric projects have rendered *S. plagiostomus*, *S. curvifrons*, *S. esocinus*, and *S. labiatus* scarce in local catches (Qureshi et al., 2007). Continuous exploitation pressure has also induced profound demographic shifts characterized by miniaturization and younger age structures (Yan et al., 2022; Han et al., 2025). This trend is reflected in the declining average catch sizes of *S. macropogon* and *S. waltoni* (IUCN, 2025).

Conversely, 16 species are currently assessed as Least Concern (LC). These taxa typically inhabit remote or less impacted areas and possess broader distributions that buffer them against endangerment. Nevertheless, localized declines and emerging threats may still jeopardize these populations as anthropogenic pressures continue to expand (e.g., De Keyser et al., 2026). While the IUCN Red List provides a standardized assessment

framework, existing data gaps obscure the full extent of this biodiversity crisis. For example, *S. lantsangensis*, *S. malacanthus*, *S. nukiangensis*, and *S. yunnanensis* are listed in the China Red List as Endangered or Vulnerable (Jiang et al., 2016) but have yet to receive a formal IUCN assessment. Similarly, *S. eurystomus*, *S. gri-seus*, and *S. waltoni* are designated as Endangered or Vulnerable in the China Red List (Jiang et al., 2016), despite being classified as Least Concern by the IUCN (IUCN, 2025).

4. Discussion

4.1. Evolutionary history, adaptation, and taxonomic complexity

The evolutionary trajectory of *Schizothorax* is inextricably linked to the dynamic tectonic and climatic histories of the Qinghai-Tibetan Plateau, the Tien Shan Mountains, and surrounding orogenic belts. Current hypotheses point to a Central Asian origin, where major geological events and palaeodrainage shifts drove subsequent dispersal and vicariant speciation (He and Chen, 2006; Regmi et al., 2023; Rozimov et al., 2025). To survive these dramatic geological transitions and episodes of global cooling, the genus relied on significant genomic adaptations, most notably the widespread occurrence of ancient polyploidy (Gu et al., 2024). This genome duplication likely originated in thermally stable refugia, such as hot springs, conferring genetic diversity and physiological tolerances that facilitated colonization of extreme, high-velocity, low-temperature riverine habitats (Gu et al., 2024; Rozimov et al., 2025).

However, the evolutionary mechanisms that facilitated this rapid adaptive radiation have generated profound systematic complexities. Species delimitation remains heavily contested because reliance on traditional morphological characteristics is confounded by high phenotypic plasticity driven by localized environmental conditions (He and Chen, 2006; Rajput et al., 2013), natural hybridization (Cheng et al., 2022), and unrecognized cryptic speciation (Regmi et al., 2023). Consequently, debates persist over species boundaries, the validity of numerous subspecies, and the differentiation between true species, localized ecomorphs, and hybrid forms (Liu et al., 2023; Purohit et al., 2023; Rozimov et al., 2025).

These taxonomic ambiguities are not merely academic; they present significant operational hurdles for conservation. The inability to accurately define management units or evaluate distinct evolutionary lineages impedes targeted conservation interventions (Guo et al., 2016; He et al., 2022). The conservation landscape is further obscured by historical misidentifications and unresolved synonymies, exemplified by the invalidation of *S. prophyllax* (Coad and De Ville, 2004). This is also evident in the Aral Sea basin, where ongoing revisions seek to clarify species status across major sub-drainages by recognizing *S. eurycephalus* in the Syr Darya (currently *S. eurystomus*), *S. fedtschenkoi* in the Zeravshan (a synonym of *S. eurystomus*), and *S. gobioides* in the Amu Darya River. Overcoming these

systematic barriers requires a shift towards an integrative taxonomic approach. Combining detailed morphological phenotyping with robust molecular sequencing (e.g., Cytb and 16S rRNA) is the most effective pathway to resolving evolutionary relationships, securing accurate biodiversity assessments, and implementing actionable conservation strategies for this genus (Awasi et al., 2023).

4.2. Ecological traits and conservation implications

Several intrinsic biological characteristics contribute to the vulnerability of *Schizothorax* species to external threats. These include slow growth rates (Mir et al., 2013b; Bhatt and Manish, 2023), late sexual maturation in some species (Liu et al., 2016; Wang et al., 2023a, 2024b), and generally low to moderate fecundity (Ma et al., 2012; Farooq et al., 2019; Bhatt and Manish, 2023; Wang et al., 2024b). While such traits may be evolutionarily advantageous in historically stable, resource-limited cold-water environments, they limit the capacity of *Schizothorax* populations for rapid demographic recovery following significant disturbances such as overexploitation or habitat degradation (Wagle et al., 2015; Bhatt and Manish, 2023).

Reliance on scraping periphyton and detritus from firm substrates (Nikolsky, 1938; Petr and Swar, 2002) renders *Schizothorax* highly susceptible to habitat alterations that affect substrate conditions. Widespread habitat degradation through riverbed siltation from mining, agriculture, and infrastructure development directly smothers these feeding grounds, reduces food abundance, and has been identified as a major threat (Bhatt and Manish, 2023; IUCN, 2025).

Habitat fragmentation from dams and weirs is another significant driver of decline, as these barriers block essential migrations to spawning habitats, directly impacting recruitment (Qureshi et al., 2007; Sun et al., 2023a; IUCN, 2025). Climate change may amplify this further: warming waters are projected to force populations towards higher altitudes, yet dams may block these adaptive movements, trapping populations in thermally unsuitable habitats (Sharma et al., 2021a; Regmi et al., 2023). Finally, the introduction of invasive alien species adds another layer of pressure. Native *Schizothorax* are frequently outcompeted and displaced into headwater refugia by invasive species, further fragmenting populations and exacerbating decline (Wagle et al., 2015; Sharma et al., 2021c; Jan et al., 2024a; Subedi et al., 2024). The combination of slow life history, ecological specialization, and the cumulative impact of habitat fragmentation, climate change, and invasive species creates a high-risk environment for the persistence of many *Schizothorax* species.

4.3. Critical knowledge gaps and future research directions

Despite the increasing number of publications (Fig. 1), significant knowledge gaps continue to hinder

comprehensive conservation planning. Foundational research must first address the persistent taxonomic uncertainty outlined in Section 3.1. Taxonomic clarity remains elusive for Data Deficient species and taxa with large disjunct distributions. Resolving these uncertainties requires an integrated approach that combines robust molecular markers with comprehensive morphological and ecological data to accurately identify distinct conservation units (Regmi et al., 2023; Rozimov et al., 2025). Clarifying the extent and evolutionary implications of natural hybridization within the genus is equally critical.

Concurrent with systematic refinement is a pressing demand for fundamental life history data. Information regarding population dynamics, (seasonal) habitat requirements, reproductive biology, dietary ecology, and environmental tolerances is lacking for non-commercial species and those restricted to remote watersheds. Furthermore, demographic models are heavily restricted by insufficient data on juvenile habitat preferences relative to those of adults.

While broad anthropogenic threats are well documented (Section 3.7), quantitative data on the specific impacts of these stressors remain scarce. Generating precise physiological thresholds is necessary for establishing rigorous environmental quality standards and effective mitigation targets. Behavioral responses to hydraulic structures also warrant further assessment to secure passage in regulated rivers (Li et al., 2022b; Bao et al., 2025). A similarly urgent requirement is quantifying the physiological and behavioral adaptive capacity of these fishes to warming waters and shifting hydrological regimes to model future persistence and identify climate refugia (Bhatt and Manish, 2023; Regmi et al., 2023).

Finally, successful long-term conservation requires a stronger understanding of the socio-economic dimensions impacting *Schizothorax* populations. Future research must evaluate regional dependence on *Schizothorax* fisheries and document traditional ecological knowledge to integrate within formal management frameworks (Reid et al., 2021). Understanding socio-economic drivers of unsustainable fishing can foster co-management and build local support. In parallel, future studies must critically evaluate the effectiveness of existing conservation interventions to guide funding and policy decisions.

4.4. Conservation imperatives

Addressing the declining status of many *Schizothorax* species requires a multi-pronged conservation approach informed by the synthesis of their ecological characteristics and the distinct threats they face. A cornerstone of this approach is the protection and restoration of critical habitats. This necessitates prioritizing the safeguarding of known spawning grounds and migratory corridors. It also requires implementing stringent regulations for new dam construction with mandatory provisions for effective fish passage and adequate environmental flows (Schmutz et al., 2025). The success of such passage facilities is contingent on design specifications matching the swimming

capabilities of target species (Katopodis and Williams, 2012; Schletterer et al., 2016). For instance, *S. wangchiachii* faces passage limitations if flow exceeds critical thresholds (Song and Xie, 2024). Active restoration of degraded freshwater ecosystems is also required, which can include the strategic placement of gravel and boulders (Li et al., 2023b).

Concurrently, existing *Schizothorax* fisheries must be managed sustainably through measures based on scientific stock assessments, including catch limits and seasonal closures to protect spawning stocks, and the elimination of destructive fishing practices. While aquaculture of *Schizothorax* species is practiced (Basade and Mohan, 2012; Ning et al., 2012; Zhao et al., 2020; Afshari et al., 2021), these facilities demand careful management. Even though hybridization can improve cultivation characteristics (Gu et al., 2023), the risk of farmed or hybrid individuals escaping and undermining the genetic integrity of wild populations must be managed, even where hybrids exhibit low fertility and fitness in the wild (Gu et al., 2023). Furthermore, concerted efforts are required to prevent new introductions of invasive alien species and control existing populations that negatively impact *Schizothorax* species.

Finally, conservation planning must proactively integrate climate change considerations and international policy. Key actions include: identifying potential thermal or hydrological refugia, enhancing habitat connectivity to facilitate adaptive range shifts, and developing strategies to bolster population resilience to climate-induced stressors. Given that many *Schizothorax* species inhabit transboundary river basins, effective conservation depends on enhanced international cooperation and coordinated management among riparian nations (Regmi et al., 2023). Central to this is engaging local communities, integrating traditional ecological knowledge, promoting local stewardship, and exploring sustainable livelihood diversification to build local support for conservation initiatives. These efforts must be supported by a long-term commitment to sustained research and monitoring programs.

5. Conclusions and perspectives

The snow trout (*Schizothorax* spp.) are integral inhabitants of the mountainous and sub-mountainous aquatic ecosystems of Asia. This review synthesizes current knowledge on their complex taxonomy, biogeographical history, ecology, and conservation status. The cumulative impacts of habitat degradation, over-exploitation, invasive species, and climate change pose substantial threats to numerous *Schizothorax* populations. Effective conservation demands an integrated, catchment-scale approach that restores longitudinal connectivity, secures environmental flows, and engages local communities, while carefully managing emerging aquaculture practices.

Future research should prioritize an integrated taxonomic approach, combining genomic and morphological data, to resolve species boundaries and define clear conservation units. Furthermore, quantitative assessments of stressors' cumulative impacts and the adaptive capacity of species to environmental

change will support predictive modeling and proactive management.

Author contributions

Conceptualization, E.K., M.S. and D.S.H.; methodology, E.K., M.S. and D.S.H.; validation, E.K., M.S. and D.S.H.; formal analysis, E.K.; investigation, E.K.; resources, E.K. and D.S.H.; data curation, E.K.; writing—original draft preparation, E.K., M.S. and D.S.H.; writing—review and editing, E.K., M.S. and D.S.H.; visualization, E.K. and D.S.H.; supervision, M.S. and D.S.H.; project administration, D.S.H.; funding acquisition, E.K., M.S., and D.S.H. All authors have read and agreed to the published version of the manuscript.

Compliance with ethical standards

No approval of research ethics committees was required to accomplish the goals of this study because this is a literature review.

Acknowledgments

The authors thank Bakhtiyor K. Karimov, Johan Coeck, Pieterjan Verhelst, and Bernhard Zeiringer for fruitful discussions on snow trout ecology. They also thank Justine Carey for preparing Fig. 2, and Jörg Freyhof and Akbarjon Rozimov for inputs on species taxonomy.

This project received funding from the European Union's Horizon 2020 Research and Innovation Program under grant agreement No. 101022905. E.K. received support (Ernst Mach Grant) from the Austrian Federal Ministry of Education, Science and Research, via the OeAD-GmbH (Agency for International Mobility and Cooperation in Education, Science and Research).

Conflicts of interest

The authors declare no conflicts of interest. The funders had no role in the design of the study, in the collection, analyses, or interpretation of data, in the writing of the manuscript, or in the decision to publish the results.

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