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Ecology, threats, and conservation of the spirlin *Alburnoides bipunctatus* (Bloch, 1782)

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Abstract – Leuciscid fishes play a crucial role in riverine ecosystems due to their high abundance, diverse life-history strategies, and specific habitat requirements. The spirlin (*Alburnoides bipunctatus*) is a rheophilic, lithophilic, and oxyphilic species, highly sensitive to pollution. Because of its strict ecological requirements, it is particularly vulnerable to anthropogenic disturbances, making it a valuable bioindicator of habitat quality in the middle to upper river zones within its distribution range. This paper aims to synthesize existing scientific knowledge on various aspects of spirlin ecology, based on an extensive review of the literature. It addresses key topics such as European distribution, morphology and identification, reproduction and life cycle, diet, movement patterns of both adults and juveniles, and habitat preferences across life stages. Furthermore, it provides an overview of human impacts on the species' natural ecology and conservation status. A set of key research questions is proposed to stimulate further research and support the development of effective conservation strategies. This review is intended to support researchers in aquatic and fisheries sciences, river managers, and conservation practitioners.

Keywords: specialized species / small riverine species / conservation / ecology / threats

1 Introduction

The spirlin, *Alburnoides bipunctatus* (Bloch, 1782), a small-bodied riverine leuciscid, is a gregarious freshwater fish species of limited commercial importance, yet of increasing conservation interest (Copp *et al.*, 2010). It typically inhabits submontane regions, particularly the transitional zone between the "grayling zone" (*Thymallus thymallus*, Linnaeus, 1758) and the "barbel zone" (*Barbus barbus*, Linnaeus, 1758) (Huet, 1949; Copp *et al.*, 2010). *A. bipunctatus* is classified as a highly specialized rheophilic species whose entire life cycle occurs in flowing river habitats with structured substrates (Schiemer and Waidbacher, 1992). It is most commonly found in association with brown trout *Salmo trutta*, European minnow *Phoxinus phoxinus*, barbel *Barbus barbus*, gudgeon *Gobio* spp., and chub *Squalius cephalus* (Copp *et al.*, 2010), but may also co-occur in smaller numbers with more eurytopic species such as *Perca fluviatilis* Linnaeus, 1758 (Jakovljević *et al.*, 2023).

Jakovljević *et al.* (2024) highlighted that A. bipunctatus may function as an early-warning indicator of environmental degradation in freshwater systems, as incipient habitat changes are reflected in early and measurable shifts in population-level characteristics. Accordingly, monitoring A. bipunctatus provides integrative insight into the ecological condition of rivers by capturing population-level responses to cumulative environmental pressures across its distribution range.

This view is corroborated by large-scale studies that identified anthropogenic alterations of natural flow regimes, primarily the construction of dams and weirs, as the main factors limiting the occurrence of *A. bipunctatus* (Marszał and Smith, 2024). These studies also found that the likelihood of spirlin occurrence increases with local fish species richness, likely reflecting higher habitat heterogeneity and greater ecological integrity. These findings are consistent with earlier research by Kainz and Gollmann (1990), who noted that the species' frequency of occurrence is influenced by channel complexity and the structure of the accompanying fish assemblages. Additionally, they emphasized the importance of thermal conditions, reporting that the most abundant populations in Austria occurred in warmer streams where water temperatures during the spawning season (May–June) reached at least 18 °C.

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However, more recent studies (Jakovljević *et al.*, 2023, 2024) documented a greater degree of ecological plasticity in the species, particularly in parts of its range in the Central Balkans (Serbia), where *A. bipunctatus* demonstrated a dual ecological strategy. While it remains sensitive to environmental disturbances, it also shows the ability to persist in physically and chemically degraded aquatic habitats. This combination of rheophilic preference and tolerance of modified conditions highlights the species' flexible survival strategy and close dependence on local habitat conditions.

Despite this ecological significance, the spirlin remains poorly studied. Between 1993 and 2025, a bibliographic search using Scopus revealed only around 100 peer-reviewed publications mentioning the keywords "*alburnoides*" and "*bipunctatus*". Older references (<1993) were also found using Google Scholar and the consultation of grey literature or the bibliography of former articles. Of these, n=92 were directly relevant to spirlin ecology. The remaining studies were related to unrelated fields such as medicine, chemistry, computer science, or mathematics. Within the domains of agriculture and environmental sciences, the annual number of publications ranged from one to six, with a peak in 2012.

Taxonomic uncertainties, including the description of cryptic species and reclassification within the genus (*e.g.*, Stierandová *et al.*, 2016; Turan *et al.*, 2017), further complicate ecological assessments, limiting clear definitions of the species' distribution and hindering consistent ecological monitoring. This review addresses those challenges by synthesizing the current state of knowledge on *A. bipunctatus*, identifying key knowledge gaps, and proposing a set of research priorities to guide future studies. Particular attention is paid to ecological threats posed by human activity and climate change. The paper aims to support both the development of targeted conservation measures and the broader understanding of riverine fish ecology.

2 Morphology and identification

The spirlin has a relatively deep, laterally compressed body and a terminal, nearly horizontal mouth (Fig. 1). Pharyngeal teeth are arranged in two rows. The anal fin is noticeably longer than the dorsal fin. The body coloration is predominantly silvery, with a dark band along the upper lateral side and a curved lateral line consisting of 44–52 scales. This lateral line is flanked by black pigment spots arranged in two parallel rows, which gives the species its Latin name (*bipunctatus*) (Siryová, 2004). The eyes are relatively large in proportion to the head. The anal fin is long and well-developed. Orange pigmentation is present at the base of the pectoral, pelvic, and anal fins (Fig. 1). Juveniles can be identified at a very early age by the presence of a thin black line along the spine (Persat, 2020).

Ontogenetic changes in external morphometric traits are believed to reflect increasing specialization for complex, lotic microhabitats, as well as morphological developments associated with sexual maturation (Kováč *et al.*, 2006). Spirlin populations in the Nišava River display considerable morphological plasticity, which appears to be closely related to both spatial distribution and mesohabitat characteristics (Živković and Jovanović, 2011). According to Siryová (2024), none of the 43 morphometric traits examined were found to be useful for sex differentiation. Thus, sexual dimorphism in *A. bipunctatus* appears to be either absent or very limited (Siryová, 2024).

Fig. 1. Photo of a spirlin captured in the river Lienne, Belgium. Schematic representation of the spirlin with the position of the fins and lateral stripe (image generated by AI with the help of a photo).

3 Repartition and abundance of populations

The spirlin, was historically considered to have a broad distribution across Europe and parts of Central Asia, including regions of Turkey and Iran (Lelek, 1987; Bogutskaya, 1997; Živković and Jovanović, 2011). However, based on comprehensive morphological and genetic investigations describing new species within the genus Alburnoides (*e.g.*, Bogutskaya and Coad, 2009), the most recent IUCN Red List assessment (Ford, 2024) has resulted in a substantial revision and contraction of its recognized native range. Currently, *A. bipunctatus* is considered native to freshwater systems in Central and Western Europe, within the drainage basins of the North Sea, Baltic Sea, Mediterranean Sea, and Black Sea. Concurrently, recent biogeographical assessments indicate anthropogenic translocations of *Alburnoides* beyond its native range. For example, a population was documented in the Neretva basin (Bosnia and Herzegovina) and identified by molecular methods as an non indigenous *Alburnoides* lineage, likely originating from the Danube basin (Vukić *et al.*, 2019). In France, *A. bipunctatus* was introduced into the Ariège basin in 2012 and has since expanded its distribution within the Garonne basin, reportedly covering more than 350 km over

Table 1. von Bertalanffy growth parameters for spirlin (*Alburnoides bipunctatus*) populations from different regions. L∞ = asymptotic length, K = growth coefficient ($year^{-1}$), φ′ = growth performance index. For the Estonian population from the Emajõgi River and the Hungarian population, length values are reported as SL (standard length); for all other populations, length values are reported as TL (total length).

Country / River	L∞ (cm)	K ($year^{-1}$)	ϕ′	Source
Estonia, Emajõgi River	10.3	0.36	1.58	Froese and Pauly, 2024
Estonia, unknown	13.1	0.50	1.93	Froese and Pauly, 2024
Serbia, Danube tributaries	17.11	0.28	1.81	Jakovljević *et al.*, 2023
Romania, Radimna River	14.4	0.30	1.79	Papadopol and Cristofor, 1980
Poland, Dunajec River (Vistula basin)	20.1	0.15	1.78	Skóra, 1972
Hungary, Sajó River	14.3	0.31	1.81	Froese and Pauly, 2024
Slovakia, Turiec River	15.6	0.28	1.83	Bastl *et al.*, 1975
Croatia, Sava River	12.0	0.59	1.93	Treer *et al.*, 2006
Croatia, Dobra River	20.5	0.16	1.83	Treer *et al.*, 2000
Croatia, Bednja River	15.5	0.33	1.90	Treer *et al.*, 2000
Croatia, Korana River (middle)	15.1	0.28	1.81	Treer *et al.*, 2000
Croatia, Korana River (lower)	17.7	0.19	1.77	Treer *et al.*, 2000

9 years (Quoquillaud, 2022). At the global scale, the species was assessed as Least Concern (LC) in 2011 but was subsequently listed as Not Evaluated (NE) between 2022 and early 2023. In the most recent IUCN assessment (2024), it was reclassified once again as Least Concern, although this was accompanied by caveats regarding local threats and insufficient data to determine overall population trends (Ford, 2024). Moreover, across Europe, *A. bipunctatus* shows a wide gradient of national conservation statuses—from Near Threatened to Critically Endangered —primarily driven by hydromorphological alterations, pollution, habitat fragmentation, and species introductions, while protection measures generally include national legal protection, habitat restoration, water-quality improvement, and reinforced population monitoring (Jakovljević, 2025).

These shifts in distributional recognition and conservation status emphasize the importance of synthesizing and updating available data, as discrepancies between earlier literature and recent assessments can significantly influence ecological interpretation and conservation priorities.

Historically, *A. bipunctatus* was reported as widespread and abundant across large parts of Europe (Lelek, 1987; Bogutskaya and Coad, 2009). During the 1960s and 1970s, populations were particularly robust—for instance, in the Vistula River basin, the species accounted for up to 37% of total fish assemblages in the San River (Skóra, 1972) and up to 25% in the Drwęca River (Backiel, 1964). In the Rokytná River (Czech Republic), its average relative abundance was recorded at 22.4% (Lelek and Lusk, 1965). However, a substantial decline in population density was observed in many European countries in the latter half of the 20th century, largely associated with a deterioration in water quality and increasing anthropogenic pressures (Marszał and Przybylski, 1996; Treer *et al.*, 2006). By the 1980s and 1990s, the species was considered severely threatened or near extinction in several European regions (Lelek, 1987; Herzig-Straschil, 1991).

In recognition of these threats, the spirlin was listed in Annex III of the Bern Convention on the Conservation of European Wildlife and Natural Habitats (1979), as a protected species (Breitenstein and Kirchhofer, 2000a; Jakovljević *et al.*, 2023). The decline in abundance has been primarily attributed to a suite of anthropogenic stressors, including nutrient enrichment and eutrophication, sedimentation and degradation of spawning habitats, and hydromorphological alterations caused by river regulation and damming (Kruk, 2007; Marszał and Przybylski, 2024). Additional pressures include stocking or introduction of salmonids, which may affect recruitment success through predation, competition, and alterations of the food web (Penczak, 1999; Jakovljević *et al.*, 2023).

However, some regional studies have reported signs of recovery and local increases in spirlin abundance (Breitenstein and Kirchhofer, 2000a; Treer *et al.*, 2006; Kruk *et al.*, 2016; Benitez *et al.*, 2022; Irz *et al.*, 2024). In the River Aare (Switzerland), high densities of juveniles indicate strong reproductive output, while seasonal migrations contribute to the recolonization of newly accessible habitats (Breitenstein and Kirchhofer, 2000a). *A. bipunctatus* is subject to pronounced interannual variability in abundance, driven by fluctuations in physicochemical conditions, food availability, and predation pressure—particularly from piscivorous species such as brown trout (*Salmo trutta*) (Kainz and Gollmann, 1990). Furthermore, it should be borne in mind that for a small species like the spirlin, there can be schooling effects that sporadically increase abundance during fish pass monitoring and electrofishing surveys.

As with many small-bodied species, spirlin populations experience high natural mortality, which is compensated by traits such as early maturation and high fecundity, enabling rapid recovery after disturbances (Breitenstein and Kirchhofer, 2000a; Pelletier *et al.*, 2020). For example, in the River Meuse (Belgium), the species was nearly extirpated from the Lixhe fish pass until 2009. Since then, the number of individuals captured has increased substantially — in some years by over 1100% compared to the lowest records (Benitez *et al.*, 2022). This recovery is related to population structure and reproductive strategy, which enable the species to recolonize previously abandoned habitats following restoration measures and the implementation of fish migration facilities, as well as to exploit stretches of river with improved water quality.

Table 2. Mean back-calculated length-at-age (total length, TL, mm) of *Alburnoides bipunctatus* in different European water bodies.

Study site / Source	L1	L2	L3	L4	L5	L6	L7	L8	L9
Bulgaria, Iskar (Raikova-Petrova *et al.*, 2011)	32	49	61	77	92	104	–	–	–
Croatia, Sava (Treer *et al.*, 2006)	59	87	100	110	–	–	–	–	–
Switzerland, Aare(Breitenstein and Kirchhofer, 2000b)	29	72	107	120	132	–	–	–	–
Serbia, Morava (Sorić and Ilić, 1985)	32	46	56	66	73	78	86	–	–
Czechoslovakia, Rokytna* (Johal, 1979)	41	57	72	83	94	109	120	–	–
Romania, Radimna* (Papadopol and Cristofor, 1980)	35	63	83	98	–	–	–	–	–
Romania, Eliseva* (Papadopol and Cristofor, 1980)	44	61	84	95	–	–	–	–	–
Bulgaria, Ogosta* (Johal, 1979)	52	63	74	–	–	–	–	–	–
Poland, San (Skóra, 1972)	–	80	96	105	116	130	–	–	–
Poland, Dunajec (Skóra, 1972)	58	82	99	107	119	129	134	146	157

Data compiled from published sources (Breitenstein and Kirchhofer, 2000b; Treer *et al.*, 2006) and supplemented with additional published data. L1–L9 = mean end-of-year total length in years 1–9 (mm). Δ = value based on a single individual. * = standard length (SL) originally reported; converted to total length (TL) following the relationships provided by Papadopol and Cristofor (1980) and Johal (1979).

The recovery capacity of *A. bipunctatus* is supported by a combination of factors: short lifespan, rapid growth, small body size, early maturation (typically in the second year of life), multiple spawning events, high natural mortality, low habitat specialization, and migratory behaviour. These characteristics allow the species to recolonize formerly degraded or inaccessible habitats (Pelletier *et al.*, 2020; Jakovljević *et al.*, 2023; Hayes *et al.*, 2024).

In conclusion, while *A. bipunctatus* is not globally rare or threatened with extinction, many local populations are experiencing decline, mainly due to anthropogenic habitat degradation. Consequently, the spirlin is a particularly valuable bioindicator species for assessing ecological quality in lotic ecosystems across its native range.

4 Diet

The diet of *A. bipunctatus* exhibits spatial and ontogenetic variability, as reported across different studies and geographic regions. According to Allan and Castillo (2007), the species is considered a macroinvertebrate diet specialist. Based on gut length and content analyses, Vuković (1968) concluded that spirlin from the Zujevina and Ljubina Rivers (tributaries of the upper Bosna River, Bosnia and Herzegovina) exhibit a predominantly zoophagous feeding strategy. Similar findings were reported by Skóra (1972) in populations from the San and Dunajec Rivers, within the Vistula River system, where aquatic invertebrates consistently represented more than 60% of the dietary composition, regardless of the sampling season (May or September). The dominant prey taxa included Diptera (mainly Chironomidae), Ephemeroptera, Trichoptera, and Coleoptera.

In contrast, Vuković and Ivanović (1971) described *A. bipunctatus* as feeding primarily on planktonic and nektobenthic organisms. Filipović and Janković (1978) also reported that in the Mirovštica River (eastern Serbia), the diet was dominated by aquatic insect larvae, particularly Trichoptera and Chironomidae (see also Piria, 2003; Piria *et al.*, 2005). In the Jihlava River (Czech Republic), the spirlin's diet consisted mainly of zoobenthic taxa, but in spring, the diet also included filamentous algae, diatoms, and detritus (Losos *et al.*, 1980).

In populations from the Sava River (Croatia), Bacillariophyceae and Chlorophyceae were frequently recorded in the gut contents, suggesting algivory, while aquatic invertebrates appeared as secondary or incidental dietary items (Treer *et al.*, 2006). In the Skrwa Prawa River (tributary of the River Vistula), Marszał *et al.* (2018) observed that larger individuals preferentially consumed Coleoptera, Ephemeroptera, and unidentified insect taxa. They also noted a significant ontogenetic difference in prey origin: small individuals primarily consumed benthic organisms, while medium and large individuals increasingly foraged in the water column. These ontogenetic dietary shifts were accompanied by parallel changes in microhabitat use and were associated with the onset of sexual maturity (Marszał *et al.*, 2018) (Fig. 2).

5 Age and growth

The species is generally known to reach a maximum age of six years (Raikova-Petrova *et al.*, 2006), although Skóra (1972) reported older individuals in the Dunajec River population (Vistula basin, Poland), including age classes 7+ (n = 10), 8+ (n = 3), and 9+ (n = 5). Jakovljević *et al.* (2023) reported that the maximum recorded total length of spirlin was 13.7 cm, while the maximum body weight reached 29.2 g. According to Breitenstein and Kirchhofer (2000a), spirlin from the Aare River (Switzerland) exhibited allometric growth, attaining approximately 13 cm in length and 20 g in weight. Kováč *et al.* (2006) observed a two-phase isometric growth pattern, interrupted by a short period of allometric growth. Similar growth pattern was also reported by Treer *et al.* (2006).

Growth parameters are highly indicative of the environmental conditions within a given habitat and provide a valuable basis for inter-population comparisons (Treer *et al.*, 2006). Comparative analyses of the von Bertalanffy growth parameters ($L\infty$ and K) among various spirlin populations suggest an inverse relationship between growth rate and asymptotic length—faster-growing populations tend to attain smaller maximum sizes, and vice versa (Raikova-Petrova *et al.*, 2011,

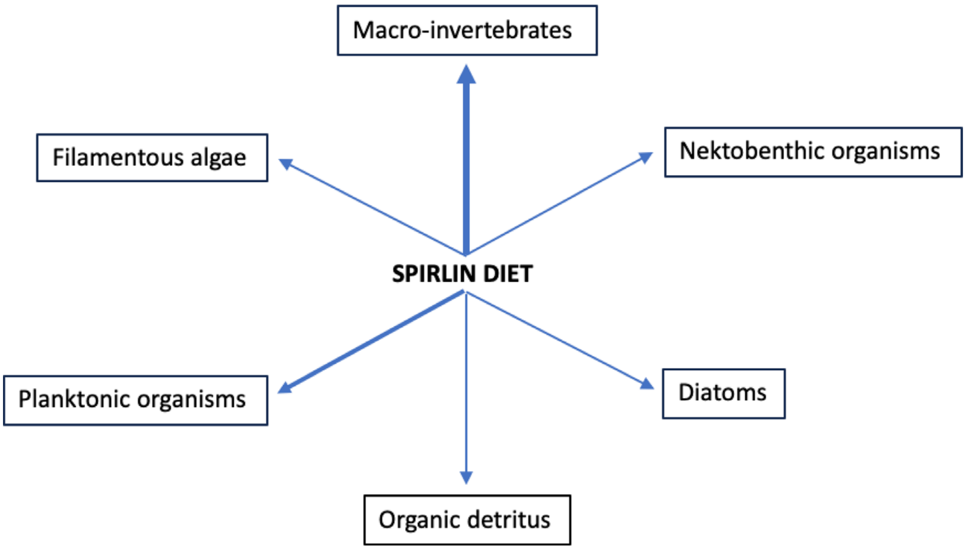

Fig. 2. The thickness of the line indicates the frequency with which a given type of food has been recorded in the literature on the diet of spirlin.

Jakovljević *et al.*, 2023). Spirlin generally demonstrates rapid growth during the first year of life, although relatively low K values are frequently reported (Raikova-Petrova *et al.*, 2011, Jakovljević *et al.*, 2023), highlighting species-specific growth dynamics.

Considerable variation in von Bertalanffy growth parameters has been documented across different geographic regions as well as growth performance index (Tab. 1).

These differences are further supported by the growth performance index (φ′), which shows a general regional consistency. Long-term data from Serbia yielded a mean φ′ of approximately 1.81 (N = 3,041; Jakovljević *et al.*, 2023), which aligns closely with values from the Balkans (1.77–1.90 in Croatia; Treer *et al.*, 2000) and Central Europe (approximately 1.80; Skóra, 1972; Bastl *et al.*, 1975). A notably lower value (1.58) was recorded in Estonia, likely reflecting reduced growth rates at the northern edge of the species' distribution. Overall, reported φ′ values for spirlin range from 1.58 to 1.9, suggesting a relatively consistent growth potential across its geographic range.

The rapid growth of spirlin, especially during the first year of life, indicates a high capacity for adjusting its growth rate (Marszał *et al.*, 2018; Breitenstein and Kirchhofer, 2000a; Jakovljević *et al.*, 2023). In some populations, such as that of the Iskar River in Bulgaria, a male-biased sex ratio (2:1) was observed in younger age classes, though this ratio declined with age, with the oldest individuals being exclusively female (Raikova-Petrova *et al.*, 2006).

Differences in the body length of individuals of the same age from various European water bodies are evident (Tab. 2). These patterns are driven by multiple factors, including the general decline in growth rate from south to north (Skóra, 1972) and the influence of local environmental conditions such as temperature, food availability, and competition (Breitenstein and Kirchhofer, 2000b). Within a single location, such variation is likely related to the occurrence of multiple spawning events within one reproductive season (multiple spawning), as well as individual differences in growth rate (Breitenstein and Kirchhofer, 2000b).

6 Reproduction

Both males and females of *A. bipunctatus* typically reach sexual maturity at 2 yr of age (Breitenstein and Kirchhofer, 2000b; Froese and Pauly, 2024).

Spawning occurs between May and June, when water temperatures range from 14 °C to 18 °C (Parkinson *et al.*, 1999). According to Polačik and Kováč (2006), the spawning season may extend from mid-April to early July. Other evidence suggests that in the Aare River, on the northern slopes of the Alps, the reproductive period may extend from June to August, as unscaled juveniles were found there at the end of January (Breitenstein and Kirchhofer, 2000b). Moreover, Jakovljević (2025) reported evidence of spawning activity in *A. bipunctatus* extending into late autumn, potentially associated with altered thermal and hydrological conditions documented across temperate rivers. Laboratory experiments simulating natural photoperiod and thermal regimes demonstrated that spawning commenced in the last week of April at a water temperature of 12 °C and continued for approximately 10 weeks, ending in early July (Bless, 1996). During this period, several females were observed to spawn repeatedly, confirming that spirlin is a multiple-spawning species. Gonads of sexually mature females contain gametes at multiple developmental stages, typically forming 2–3 successively laid batches (Polačik and Kováč, 2006; Marszał and Błońska, 2015), resulting in mean total seasonal fecundity of up to 3,000 eggs, depending on female body weight (Polačik and Kováč, 2006). A higher reproductive potential has been reported for Romanian populations, where individuals may spawn four to five times per season (Papadopol and Cristofor, 1980)., The adhesive eggs are deposited in the interstitial spaces between gravel and stones on the riverbed (Persat, 2020). Their surface is covered with evenly distributed adhesive filaments that ensure strong attachment to the substrate, thereby preventing freshly spawned eggs from being displaced by the current (Glechner *et al.*, 1993). Males release milt containing sperm in the

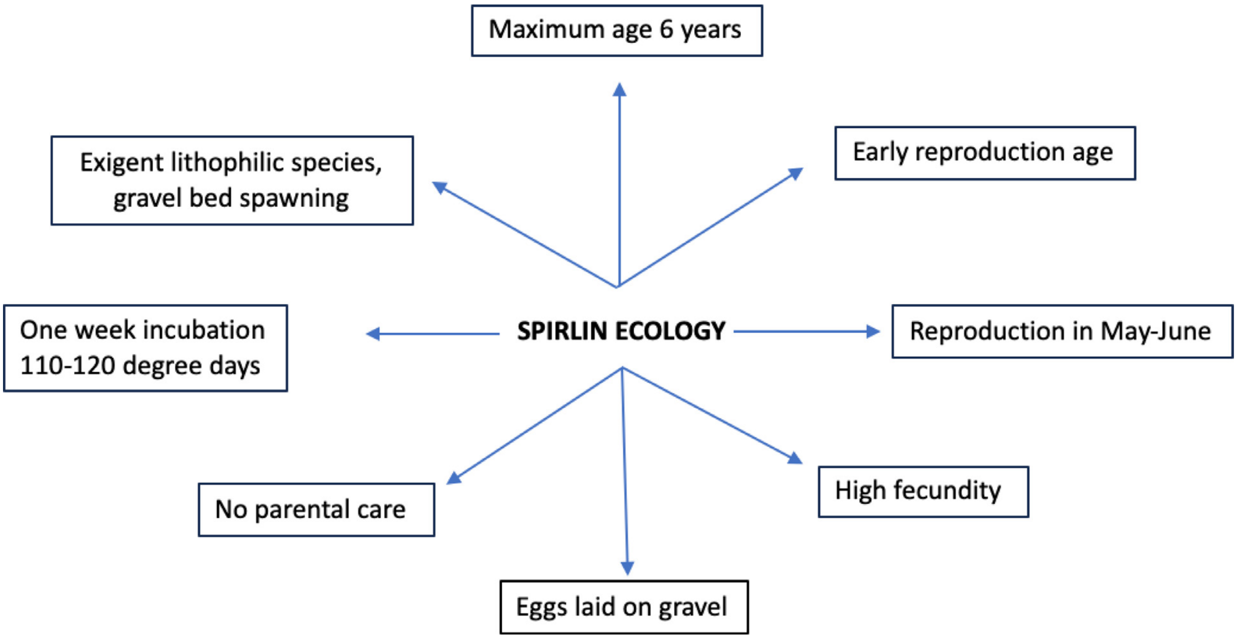

Fig. 3. Main reproductive characteristics of the spirlin (*Alburnoides bipunctatus*).

vicinity of the eggs, resulting in external fertilization as in other cyprinid fishes (Wootton, 1990).

Under controlled conditions, spawning occurred on a wide range of substrate particle sizes (2–15 cm), but a clear preference for water velocities around 0.4 m·s^{-1} was observed (Bless, 1996). Skóra (1972) and Bless (1996) reported that spirlin can reproduce on various substrate types—including sand, gravel, and cobbles—provided that suitable hydrodynamic conditions, particularly water flow, are maintained. Therefore, the availability of stable benthic structures combined with optimal flow conditions appears to be critical for the reproductive success of the species.

During the spawning period, adults display a distinct dark longitudinal band extending along the entire body length and covering the lateral line. The gonadosomatic index (GSI) peaks in April and May for females (Polačik and Kováč, 2006). Egg diameter depends on the developmental stage of the oocyte and female size (Marszał and Błońska, 2015), which is why the reported ranges tend to be broad. For example, the diameter of the measured oocytes in the population from the Rudava Stream (Slovakia) ranged from 0.20 to 1.96 mm (Polačik *et al.*, 2006), whereas in the population from the Skrwa Prawa River it ranged from 0.09 to 1.82 mm (Marszał and Błońska, 2015). Reported fecundity varies widely among populations and geographic regions: 740–3,000 eggs (Holčík and Hensel, 1972), 1,581–6,110 (Papadopol and Cristofor, 1980), 752–3,085 (Sorić and Ilić, 1985), 975–5,206 (Polačik and Kováč, 2006), and 308–3,081 (Marszał and Błońska, 2015). Marszał and Błońska (2015) also observed a positive correlation between female total length and fecundity. According to Wootton (1990), variation in fecundity and egg size is largely driven by phenotypic plasticity, which is typically induced by substantial changes in environmental conditions. Hatching occurs approximately one week after fertilization, corresponding to a cumulative thermal sum of 110–220 degree-days (Breitenstein and Kirchhofer, 2000b). Similar values were reported by Souchon and Tissot (2012), who observed hatching at around 100 degree-days, while Bless (1996) documented hatching after 5.2 days at 19.3 °C.

Larvae begin exogenous feeding 4–5 days after hatching at 18–20 °C, reaching a total length of approximately 8.5 mm (Penáz, 1976). A summary of the main reproductive characteristics of the spirlin is presented in Figure 3.

7 Habitats

Spirlin is a rheophilic, gravel-spawning species that inhabits the upper (“salmonid”) and middle sections of river courses (Fig. 4), characterized by fast-flowing, well oxygenated water and substrates composed of gravel and sand (Jakovljević *et al.*, 2023). It shows a strong preference for shallow, clear, well-oxygenated, and rapidly flowing waters during the reproductive period (Lusk *et al.*, 1995; Copp *et al.*, 2010; Treer *et al.*, 2006; Jakovljević *et al.*, 2023). Notably, high population densities are consistently restricted to small, localized stretches of stream habitats (Kainz and Gollmann, 1990).

Spirlin is also found in large lowland rivers, such as the Rhône (Daufresne *et al.*, 2004; Olivier *et al.*, 2009), Danube (Kováč, 2015), the Rhine (Wegscheider *et al.*, 2024) and Meuse (Benitez *et al.*, 2022). In the Warta River, a major tributary of the Oder (with a total length of 808 km), the species inhabited the middle reaches approximately 80 km long and up to 60 meters wide (Fig. 4), located upstream of a reservoir dam lacking a fish pass. In this stretch, spirlin co-occurred not only with other rheophilic species but also with a variety of eurytopic fish, including roach (*Rutilus*

Fig. 4. Typical habitats of spirlin within riverine ecosystems: left – Kosanica River (a right tributary of the Toplica River), right – Beli Timok (a headwater of the Timok River), Serbia (photos by M. Jakovljević), middle left – Skrwa Prawa River (a right tributary of the Vistula River) near the village of Parzeń, middle right – Skrwa Prawa River near the village of Lasotki, Poland (photos by L. Marszał). Lower left and right: Warta River near the village of Załęcze Wielkie, Poland (photos by G. Zięba).

rutilus), bleak (*Alburnus alburnus*), perch (*Perca fluviatilis*), pike (*Esox lucius*), white bream (*Blicca bjoerkna*), sunbleak (*Leucaspius delineatus*), and zander (*Sander lucioperca*) (Ciepłucha *et al.*, 2014). Similarly, in the lower reaches of the Meuse River (925 km in length), spirlin was primarily associated with eurytopic species as well (Benitez *et al.*, 2022). In Austria, it occurs in streams up to approximately 500 m a.s.l. (Kainz and Gollmann, 1990).

The species requires highly specific spawning conditions, reflecting a narrow ecological tolerance (Mann, 1996), and exhibits habitat preferences that shift across developmental stages and seasonal changes. Juvenile spirlin generally prefer calmer waters, whereas older age classes tend to occupy faster-flowing sections with greater depth, clearly avoiding very shallow areas (Kainz and Gollmann, 1990; Saladin, 1998; Breitenstein and Kirchhofer, 2000b; Kottelat and Freyhof, 2007; Plichard *et al.*, 2020). Young-of-the-year (YOY) are typically associated with littoral zones characterized by slow-flowing or stagnant waters and the presence of submerged structures, such as fallen branches or accumulations of leaf litter. In contrast, adult individuals inhabit open-water habitats during summer and migrate to more sheltered areas with reduced water levels in winter (Breitenstein and Kirchhofer, 2000b).

Spirlin's affinity for structurally complex environments was further confirmed by Pander *et al.* (2025), who demonstrated that beaver-created structures provide effective shelter for this species, resulting in increased population densities in streams where such features are present.

In the Danube catchment, spirlin predominantly utilizes microhabitats with water depths less than 40 cm, flow velocities between 0.1 and 5 $cm \cdot s^{-1}$, a river slope between 0.8 and 5‰, and located 1–2 meters from the riverbank (Kováč *et al.*, 2006). In the River Meuse basin, preferred physico-chemical parameters include, dissolved oxygen concentrations ranging from 9.2 to 10.8 $mg \cdot L^{-1}$, ammonium levels below 350 $\mu g \cdot L^{-1}$, calcium concentrations between 90 and 120 $mg \cdot L^{-1}$, and phosphate levels under 400 $\mu g \cdot L^{-1}$ (Philippart, 1989). The optimal temperature range for the larval stage is 19–24 °C, with 12 °C representing the lower developmental threshold and approximately 27 °C considered lethal (Souchon and Tissot, 2012).

8 Movement dynamics

Individual movements of spirlin have not been studied using tagging or telemetry methods, and current knowledge on their mobility mainly derives from fish pass monitoring studies. In the Amblève River (Belgium), captures occurred from April to September, with a peak in late June and early July, mostly between 21 and 23°C (Benitez *et al.*, 2015). In the River Meuse (Belgium), captures extended from late March to October, peaking from late May to late July, with P50 and P90 values at 22.9 and 24.7°C, respectively (Benitez *et al.*, 2022).

These observations indicate that spirlin preferentially moves under conditions of high temperature and low water flow, with migrations occurring during the spawning season (May–June) and continuing into the post-spawning period. Upstream movements have also been reported in early summer and autumn (Breitenstein and Kirchhofer, 2000b), consistent with Jakovljević *et al.* (2023), who suggested that such altitudinal shifts are associated with decreasing flow rates and increasing temperatures. Considering that upstream reaches are the most sensitive to temperature rise (Johnson *et al.*, 2024), climate change—through its impacts on flow regimes, water levels, and thermal conditions—is expected to further influence spirlin migration dynamics.

Using stable isotope analysis, Durbec *et al.* (2010) documented movements of spirlin between a main river channel and its tributary. Juvenile spirlin have also been reported to move repeatedly between areas of fast and slow flow (Breitenstein and Kirchhofer, 2000b).

Experimental studies (Meister *et al.*, 2022) have shown that spirlin exhibit moderate ability to ascend fishways, with passage efficiency strongly influenced by hydraulic conditions, particularly flow velocity and local acceleration. Migratory performance declines significantly at higher flow velocities. In laboratory experiments, spirlin demonstrated pronounced schooling behavior—rarely swimming alone—and strong positive rheotaxis, actively orienting against the current. Individuals predominantly swam near the bottom, favoring areas adjacent to channel walls, and avoiding zones with abrupt velocity changes. A typical movement pattern observed under experimental conditions involved zigzagging across the full channel width.

These behavioral characteristics suggest substantial physiological and sensory constraints in navigating hydraulic obstacles. Therefore, fishway designs intended for spirlin and other small-bodied riverine species should accommodate their limited tolerance for turbulent flow and account for their specific spatial preferences (Meister *et al.*, 2022).

9 Impact of anthropogenic pressures

Spirlin may serve as a valuable bioindicator of stress and a potential ecological indicator of key anthropogenic pressures (Virbickas and Kesminas, 2007; Jakovljević *et al.*, 2023, 2024; Marszał and Przybylski, 2024; Marszał and Smith, 2024; Wegscheider *et al.*, 2024). Although the species demonstrates considerable resilience and adaptability, its populations remain at risk if environmental conditions continue to deteriorate (Zhai and Lee, 2024). The persistence of spirlin populations strongly depends on the availability of high-quality habitats at the local scale—specifically, the presence of riffles, runs, pools, backwaters, floodplain connectivity, heterogeneous flow regimes, access to coarse substrates, and longitudinal river continuity (Breitenstein and Kirchhofer, 2000a; Valová *et al.*, 2006; Marszał and Smith, 2024).

Flow disruption, including river engineering, fragmentation by barriers such as dams, and flow alteration due to water abstraction, has been shown to negatively affect fish community structure and is associated with spirlin absence (Marszał and Smith, 2024). Complementing these findings, Simić *et al.* (2022) highlighted that the ecological niche of spirlin is strongly affected by anthropogenic pressures. Similarly, Musil *et al.* (2012) reported declines in rheophilic species, including spirlin, following damming, particularly within young-of-the-year (YOY) assemblages. Virbickas *et al.* (2020) further demonstrated that the operation of low-head hydropower plants (HPPs) significantly reduces habitat availability for *A. bipunctatus*, especially during periods of low discharge. As a consequence, downstream of such structures, habitat conditions become suboptimal, resulting in reduced population densities. Legally mandated environmental flows were found insufficient to maintain suitable conditions, and the authors proposed that flows based on mean low summer discharge would more effectively support sensitive species, such as spirlin.

Recent analyses by Waldock *et al.* (2024) corroborated these patterns, demonstrating that the natural distribution of *A. bipunctatus* is significantly constrained by anthropogenic pressures. The study estimated that approximately 89% of sub-catchments that would be environmentally suitable for the species under undisturbed conditions are currently affected by at least one human-induced stressor, including habitat degradation (*e.g.*, channel modification, floodplain disconnection), urban expansion, and especially the fragmentation of longitudinal connectivity due to migration barriers. The concept of “shadow distribution” introduced by the authors underscores that large areas of suitable habitat remain unoccupied due to these constraints, indicating that the species’ realized distribution is substantially narrower than its potential ecological range.

At the local scale, Marszał and Przybylski (2024) showed that dredging of a reservoir adversely affected spirlin populations by disrupting flow patterns and transporting fine sediments downstream. Moreover, this case study revealed a long-term trend of declining water levels over a 20 yr period, potentially linked to ongoing climate change. Spirlin is also considered sensitive to changes in water quality and in-stream habitat structure (Breitenstein and Kirchhofer, 2000a; Valová *et al.*, 2006). Water pollution and migration barriers, particularly those caused by hydrotechnical infrastructure, likely contributed to the disappearance of spirlin from the upper and middle sections of the Oder River, as evidenced by its absence in fish passes at the river’s lowermost weir (Kotusz *et al.*, 2006).

With regard to the potential threat posed to spirlin by non-native and invasive fish species, no studies specifically examining such interactions are currently available. Nevertheless, several works identify the presence or introduction of alien fishes as a potential risk factor for this taxon (Jakovljević *et al.*, 2023; Marszał and Przybylski, 2024). This concern is supported by well-documented mechanisms through which introduced salmonids negatively affect native fish communities (*e.g.*, Healy *et al.*, 2020), including predation, competition, and trophic-web alterations. Collectively, these processes strongly suggest that local co-occurrence of non-native salmonids and spirlin, whether resulting from deliberate stocking or the natural spread of invasive fishes, is likely to have adverse consequences for spirlin populations.

Complementing previous findings of Jakovljević *et al.* (2024), using an ecological modeling framework combined with advanced machine learning algorithms, identified water pollution and rising water temperatures as primary drivers influencing spirlin population dynamics. Moreover, their study highlighted that overexploitation of valued fish species such as trout, along with the expansion of invasive fishes, constitutes a major pressure constraining the Danube barbel zone, representing the core ecological niche of spirlin. Their long-term analysis (2003–2021) also revealed a previously underappreciated ecological duality in spirlin: traits typical of rheophilic fish coexist with a marked capacity to persist in moderately degraded and thermally elevated environments. This combination of environmental sensitivity and opportunistic tolerance generates population-level responses that possess strong indicator value under changing environmental conditions. Specifically, Jakovljević *et al.* (2024) documented: (1) measurable shifts in size structure and condition factor associated with elevated water temperatures; (2) changes in local abundance and spatial redistribution under organic and mixed pollution loads; (3) reduced average body condition in thermally stressed habitats; and (4) localized increases in population density where predation pressure decreased (*e.g.*, due to declines in trout). Collectively, these patterns reinforce the conclusion that although spirlin responds to a suite of anthropogenic and ecological pressures, temperature increase and pollution exert the strongest and most consistent effects. Consequently, its indicator value resides not in simple presence–absence patterns but in quantifiable and repeatable shifts in biological traits and population metrics that precede broader changes in fish community structure. At this stage, these results should be regarded as preliminary but foundational, opening a new field of inquiry into the use of *A. bipunctatus* as a fine-scale ecological indicator of habitat alteration. In this context, climate-driven increases in water temperature further amplify these responses, underscoring that spirlin’s sensitivity to thermal regimes may become an increasingly important component of its indicator value under ongoing climate change.

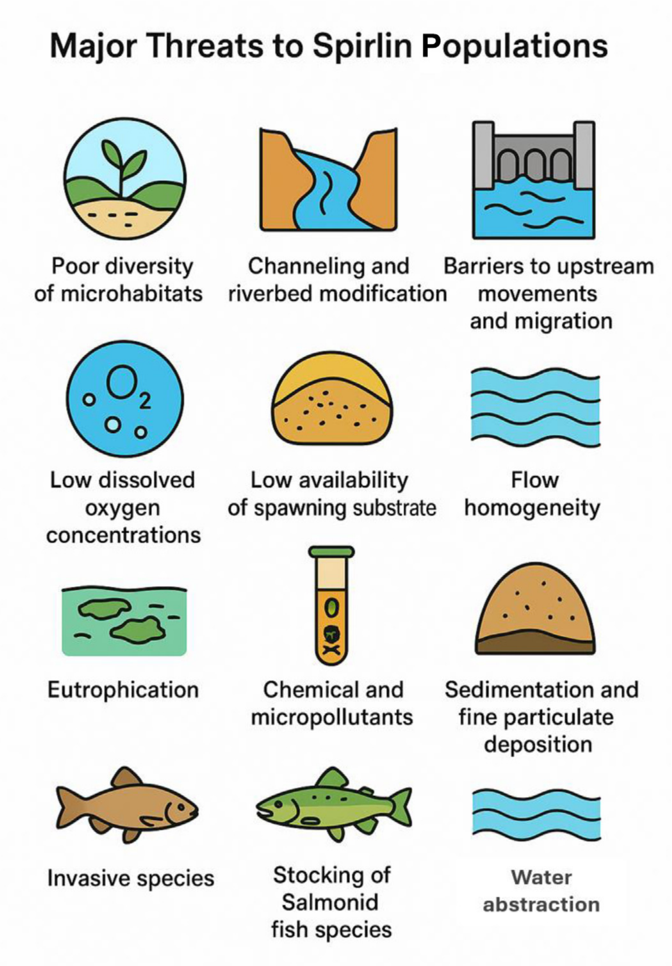

Fig. 5. Major anthropogenic pressures affecting spirlin (*A. bipunctatus*) populations. Figure created by the authors using the Canva platform.

Together, these findings highlight the vulnerability of spirlin populations to multiple interacting stressors at local scales, underscoring both its value as an indicator of habitat degradation and the need for integrated management approaches to conserve viable habitats (Fig. 5).

Although spirlin is representative of the rheophilic group, which is the most sensitive group among fish assemblages due to climate change and anthropogenic impacts (Isaak and Young, 2023; Hayes *et al.*, 2024), the lower level of ecological specialization allows spirlin to achieve high adaptability

Table 3. Proposed conservation measures for spirlin populations. The green circles represent a suggestion of prioritization (🟢🟢🟢 high, 🟢🟢 moderate, 🟢 low).

Guidelines for spirlin conservation
🟢🟢🟢 Restore high-quality aquatic environments by eliminating all sources of inorganic and organic chemical pollution.
🟢🟢🟢 Ensure the availability and quality of key habitats for reproduction, nursery, and year-round residency.
🟢🟢🟢 Maintain the availability and stability of suitable spawning substrates (*e.g.*, gravel, cobble) at least throughout the incubation period.
🟢🟢🟢 Prohibit hydraulic engineering activities that result in abrupt fluctuations in flow, water level, temperature, or turbidity, and that degrade critical habitats (*e.g.*, spawning grounds, nurseries, and residences).
🟢🟢🟢 Avoid the reduction in large areas of potential habitat caused by the canalization of watercourses(incompatible with the microhabitats of juveniles), dredging and cleaning (destruction of gravellyand stony beds essential for reproduction), abstraction of water leading to a permanent reduction inwater height, water intakes from hydroelectric power stations, causing a sudden variation in flow (hydropeaking), and direct discharge for cooling water.
🟢🟢🟢 Ensure longitudinal connectivity throughout the entire life cycle (*e.g.*, between mainstem rivers, tributaries, and floodplains) by equipping migration barriers with functional fish passes, bypass channels, or other appropriate devices, enabling the upstream migration of spirlin and the continued recolonization of upstream sectors.
🟢🟢🟢 Limit development work (cleaning, reprofiling, channelling, and backfilling of banks) as muchas possible to ensure the availability and stability of gravelly and stony substrates, at least throughout the breeding season.
🟢🟢🟢 Schedule necessary in-river works outside of the reproductive period to minimize disturbance.
🟢🟢🟢 Restore and protect all potential spawning grounds and nursery habitats.
🟢🟢🟢 Maintain habitat heterogeneity (riffles, pools, meanders, riparian vegetation) and diverse flow conditions to support different life stages.
🟢🟢 Prevent the introduction and spread of invasive species; prioritize stocking with native salmonids when restocking is required.
🟢🟢 Explore the individual sensitivity to artificial and natural temperature changes.
🟢 Raising awareness through local communities education on spirlin's ecological role and sustainable freshwater use (*e.g.*, informative boards, training for rural tourism stakeholders, and outreach materials).
🟢 Involve local communities in monitoring and conservation activities via citizen science and participatory management approaches.
🟢 Conduct regular environmental assessments using spirlin as an "early warning" indicator of ecosystem degradation, to inform climate-adaptive river management strategies.
🟢 Integrate socio-economic benefits into conservation planning by aligning river habitat protection with sustainable tourism, eco-labelling, and incentives for environmentally responsible practices.
🟢 Encourage research on non-commercial species like spirlin to enhance ecological knowledge and data availability, especially by supporting early-career scientists and promoting the ecological importance of such taxa.

(van Treeck *et al.*, 2020) and increase its chances of establishing sustainable populations in novel fish assemblage structures (Jakovljević *et al.*, 2024). On the other hand, spirlin's limited long-distance dispersal ability makes natural recolonization of restored river sections unlikely, due not only to geographic isolation but also to the lack of longitudinal connectivity with source populations.

Given the severity of these anthropogenic pressures and the resulting habitat fragmentation, reintroduction programs have been proposed and implemented in several rivers to restore spirlin populations. For instance, a program launched in central Germany, where spirlin was historically abundant until the second half of the last century, successfully re-established the species in most of the targeted rivers (Bobbe, 2024). Post-restocking monitoring confirmed that spirlin persisted, reproduced naturally, and expanded its range (Riaz *et al.*, 2020). Where reintroduction failed, key limiting factors included high predation pressure (particularly from brown trout), water pollution, and fine sediment accumulation—all of which negatively affect spawning success and early developmental stages.

Overall, these studies illustrate that anthropogenic pressures operate synergistically to constrain spirlin populations, but targeted restoration and management interventions can mitigate these impacts, maintaining both the species sustainability and its ecological role as a bioindicator.

10 Guidelines for spirlin conservation

Given its specific requirements, the protection of the spirlin requires sustained conservation management measures. The measures we propose are not species-specific and can be extended to most rheophilic species. However, it is possible to prioritize these measures to best meet the spirlin's needs (Tab. 3)

These recommendations should first be integrated into river management practices. In addition to the specific

Table 4. Priority research questions organized by key thematic areas.

Subject area	Research questions
Distribution and abundance of populations	Update the maps of natural distribution
	Monitor changes in distribution, abundance, population recovery, or decline
Diet	Understand diet adaptation in response to habitat and climate disruption conditions
Morphology and identification	Determine the potential for interspecific hybridization and improve identification tools
Habitats	Identify the microhabitat preferences for reproduction, activity, feeding, and resting
	Use individual tagging to reveal changes in habitat use over the diel cycle
Growth	Identify the repercussions of environmental disturbance on growth conditions
Reproduction	Estimate reproductive migration distances using individual tagging techniques
Movement dynamics	Evaluate the extent of home ranges at a seasonal or annual temporal scale
	Identify fine-scale movements associated with diel (day–night) shifts.
	Investigate potential shifts in distribution and assess the species' capacity to track changing favourable habitats under ongoing environmental and climatic change
Impacts of anthropogenic pressures	Assess population recovery following habitat restoration
	Determine relationships between population trends and environmental change, and identify whether increases in population size are linked to improvements in habitat condition
Climate change	Assess the effects of increasing water temperature on spatial and temporal habitat use, particularly during heatwave events
	Determine changes in the species' distribution range in relation to water temperature variationIncorporate climate-related parameters (water temperature trends, thermal anomalies, and hydrological variability) into freshwater biomonitoring programmes
	Determine whether observed differences reflect phenotypic plasticity in response to contrasting environmental conditions or instead result from deeper genetic divergence associated with evolutionary processes

conservation measures we emphasize the need for a holistic approach that includes socio-economic instruments, education, and adaptive management strategies to enhance long-term population viability and ecosystem resilience.

Special emphasis should be placed on public education concerning the ecological role of spirlin and the promotion of sustainable freshwater use, especially in rural tourism and local development contexts, where awareness of the species is limited due to its low commercial value. Furthermore, regular population monitoring and environmental assessments are essential to support adaptive management and facilitate timely responses to ongoing environmental change.

11 Key research questions for future studies

A. bipunctatus is not a commercially important fish species, therefore not exploited, and has historically attracted limited research attention. Consequently, securing funding and data for its conservation is often challenging. Nevertheless, a basic understanding of its ecology exists, although several aspects remain poorly understood. Further research, especially at the individual level (species-level studies), is crucial to address gaps in knowledge (*e.g.*, movement patterns, habitat use). The miniaturization of electronic tags may soon allow more precise tracking of small-bodied species like spirlin. We encourage researchers and practitioners to share relevant data or study proposals, which would contribute to a more comprehensive and quantitative synthesis of the ecological requirements and sensitivity thresholds of the spirlin.

The following Table 4 summarizes key areas and priority research questions for the future identified through this review.

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