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RESEARCH ARTICLE

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Growth variation in the endangered fish *Zingel asper*: Contribution of substrate quality, hydraulics, prey abundance, and water temperature

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Abstract

1. Intraspecific variation in life histories and its environmental correlates can indicate the degree of vulnerability to extinction of endangered taxa and guide conservation actions.
2. *Zingel asper* (Percidae) is an endangered fish endemic to the Rhône catchment (France and Switzerland), where five populations subsist in separate river systems (Loue, Beaume, Durance, Verdon, and Doubs). Two populations of *Z. asper* differ in growth and longevity, but the existence of broader intraspecific differentiation in life histories and the environmental origins of this variation (if any) remain unknown. The age structure and growth profile of four populations of *Z. asper* (Loue, Beaume, Durance, and Verdon) and nine additional sub-populations within the Durance system were determined by scale-reading analysis, before evaluating the contribution of measured variation in substrate quality, hydraulics, prey availability, and water temperature to growth differentiation among and within populations.
3. A trade-off between early growth and longevity largely differentiated the populations of *Z. asper* along a slow (i.e. slower growth, smaller adult size, longevity of >5 years) to fast (i.e. faster growth, larger adult size, longevity of <4 years) continuum of life histories. This continuum differentiated populations from different river catchments along a south (Durance, Verdon) to north (Beaume, Loue) latitudinal gradient, and mapped onto an upstream–downstream gradient of sub-populations within the Durance system. Differences in prey availability, hydraulics, and water temperature explained most of the growth variation among populations from different catchments, whereas local variation in prey availability, substrate quality, and water temperature mostly contributed to within-river growth differentiation.
4. These results indicate that short life cycles strongly expose all populations of *Z. asper* to extirpation and should motivate additional conservation actions. This study illustrates how quantifying intraspecific variation in life histories and its sensitivity to ecological context can reliably assess extinction risk and guide conservation actions by identifying endangered populations requiring priority management.

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KEYWORDS

conservation, life histories, percids, phenotypic plasticity, scalimetry, trade-off

1 | INTRODUCTION

Large-scale alterations of freshwater habitats through human activities (e.g. channel fragmentation; Dudgeon et al., 2006) have led to the decline of many fish populations and have facilitated their geographical isolation in ecologically contrasting river catchments (Brinker et al., 2018; Coleman et al., 2018). Isolation may precede extinction by limiting opportunities to escape unfavourable habitat conditions, unless fragmented populations rapidly adapt their phenotypes to local ecological constraints by accumulating environmentally induced plasticity or genetically fixed variation (Fox et al., 2019). Such episodes of intraspecific phenotypic differentiation may be particularly frequent in small benthic fish species (Reynolds, Webb & Hawkins, 2005), whose limited dispersive potential may favour isolation in sub-optimal habitats and impose rapid adaptations to prevent local extirpation.

Vulnerability to extinction differs among fragmented populations (McKinney, 1997; Webb, Brook & Shine, 2002) based on variation in life-history traits (Reynolds, Webb & Hawkins, 2005). For instance, growth rate and longevity constitute key life-history attributes that largely differentiate life-history strategies among individuals, populations, and species (Arendt, 1997; Dmitriew, 2011), through their associations with reproductive traits such as size at maturity. Such multivariate phenotypic differentiation often occurs along a slow-to-fast continuum, where fast life-history strategies (e.g. fast somatic growth, early maturity, and low longevity; Réale et al., 2010) may increase ecological resilience and maximize fitness in highly productive but frequently disturbed environments (i.e. demonstrating an opportunistic suite of traits; Winemiller, 2005). Alternatively, slow life-history strategies (e.g. slow somatic growth, late maturity, and high longevity) that provide higher fitness in unproductive and predictable habitats may reduce resilience to environmental stochasticity (i.e. demonstrating a periodic suite of traits; Winemiller, 2005). Because growth rate and longevity constitute strong life-history and ecological correlates of extinction risk in fishes (Angermeier, 1995; Reynolds, Webb & Hawkins, 2005; Liu, Comte & Olden, 2017), assessing the degree of variation in growth and longevity among fragmented populations can help evaluate their vulnerability to extinction and guide conservation actions (Akçakaya & Sjögren-Gulve, 2000; Glass, Corkum & Mandrak, 2017).

Evaluating the contribution of ecological context to growth differentiation is also fundamental for assessing vulnerability to continuing environmental change. Many macroecological factors select for faster growth in nature, including achieving minimum size thresholds that maximize overwinter survival (Quinn & Peterson, 1996; Post & Parkinson, 2001) in seasonal habitats with shorter growing seasons (Billerbeck, Schultz & Conover, 2000; Billerbeck, Lankford & Conover, 2001), which may select juvenile fishes for rapid growth but

induce trade-offs with other life-history traits, such as survival (Biro et al., 2004). Achieving fast juvenile growth may also require mosaics of optimal rearing conditions including high prey availability to maximize consumption (Monnet, Rosenfeld & Richards, 2020), elevated temperatures to accelerate development (Boltaña et al., 2017), or large substrates used as shelters to reduce swimming costs and increase energy allocation to growth (Fischer, 2000). However, few studies comparing growth trajectories among endangered fish populations (Hamidan & Britton, 2015) have also correlated observed growth patterns with environmental context, leaving uncertainties regarding the capacity of life-history variation to limit extinction risk by buffering ecological variability related to substrate quality, hydraulics, temperature, and prey availability.

Zingel asper is a benthic and rheophilic percid endemic to the Rhône catchment (France and Switzerland), where it preferentially selects run and riffle habitats of the grayling zone (Huet, 1959), characterized by heterogeneous substrates and intermediate depth and water velocity (Labonne, Allouche & Gaudin, 2003). Spawning occurs from March to April, before young-of-the-year larvae hatch in June or July and rapidly adopt a benthic lifestyle (Labonne & Gaudin, 2005). Primarily nocturnal, *Z. asper* has a largely insectivorous diet that changes seasonally from dipteran larvae (Simuliidae and Chironomidae) in autumn and winter to mayfly nymphs (Baetidae and Heptageniidae) and caddisfly larvae (Hydropsychidae) in spring and summer (Cavalli, Pech & Chappaz, 2003; Villsen et al., 2021). Sexual maturity is reached after 2–3 years of development (Chevalier, De Conto & Exbrayat, 2011), and the adult size typically varies from 12 to 20 cm (Labonne & Gaudin, 2005). *Zingel asper* is Critically Endangered throughout the Rhône catchment, where intensive channel fragmentation, flow regulation, and pollution (Mari, Labonne & Gaudin, 2002) have reduced its native range by up to 80% over the last century (Crivelli, 2006). The fragmentation of the Rhône channel has largely resulted from the construction of multiple hydroelectric and nuclear power plants on the main course of the river over the past 75 years (Olivier et al., 2009; Bravard & Gaydou, 2015), which has considerably reduced the naturally flowing portion of the Rhône River and created unfavourable habitat conditions (e.g. low flow velocity) for the development of *Z. asper* (Labonne, Allouche & Gaudin, 2003). Small and genetically differentiated populations of *Z. asper* now subsist in four river systems throughout the French part of the Rhône catchment: namely, from north to south, the Loue, Beaume, Durance, and Verdon river basins (Laroche & Durand, 2004; Georget, 2017; Georget, 2019). Although growth and longevity differ between the Durance (Cavalli, Pech & Chappaz, 2003) and Beaume populations (Danancher et al., 2007), the existence of broader differentiation in growth and longevity among and within populations of *Z. asper*, as well as the environmental correlates of this variation (if any), remain unexplored.

This study compared the age structure and growth patterns of four populations of *Z. asper* from different river catchments (Loue, Beaume, Durance, and Verdon) and nine additional sub-populations within the Durance system (i.e. nine sampling sites distributed along a 60-km gradient of upstream-to-downstream habitats in the Durance River) by performing scale-reading measurements on a unique dataset of 1,258 individuals (all populations combined), before evaluating the relative contribution of measured variation in the environmental context, i.e. prey availability, water temperature, hydraulics (depth and current velocity), and substrate quality (size and clogging), to growth differentiation among and within populations.

2 | METHODS

2.1 | Study sites and scale collection

The study area includes four of the last tributaries of the Rhône catchment (south of France) that contain viable populations of *Z. asper*: from north to south, the Loue, Beaume, Durance, and Verdon

ivers (Figure 1). The Loue River is a moderate-sized karstic river (with bankfull width of approx. 50 m and mean annual discharge of $60 \text{ m}^3 \cdot \text{s}^{-1}$; Banque Hydro, French Ministry of the Environment), characterized by limestone underground drainage systems and caves facilitating groundwater inputs. The Beaume River is a small river (with bankfull width of approx. 15 m and mean annual discharge of $10 \text{ m}^3 \cdot \text{s}^{-1}$) in the Cevennes Mountains, with a typical Cevennes hydraulic regime, characterized by low summer flows preceding stochastic floods in autumn and winter. In contrast, the Durance and Verdon rivers are two regulated Alpine-Mediterranean rivers (with bankfull widths of approx. 15 and 30 m, respectively, and mean annual discharges of 30 and $175 \text{ m}^3 \cdot \text{s}^{-1}$, respectively), presenting shallow habitats shaped by seasonal floods and droughts.

Zingel asper individuals were sampled for scales in the Loue (PLN station; Figure 1; Table 1), Beaume (PLT), and Durance (HEN) rivers in spring and autumn of 2014 and 2015, during annual estimates of population size conducted as part of national conservation programmes (for detailed sampling dates, see Table S1). High flows prevented the collection of fishes and scales in the Verdon River (VER) in 2014, and the Verdon population was instead sampled three

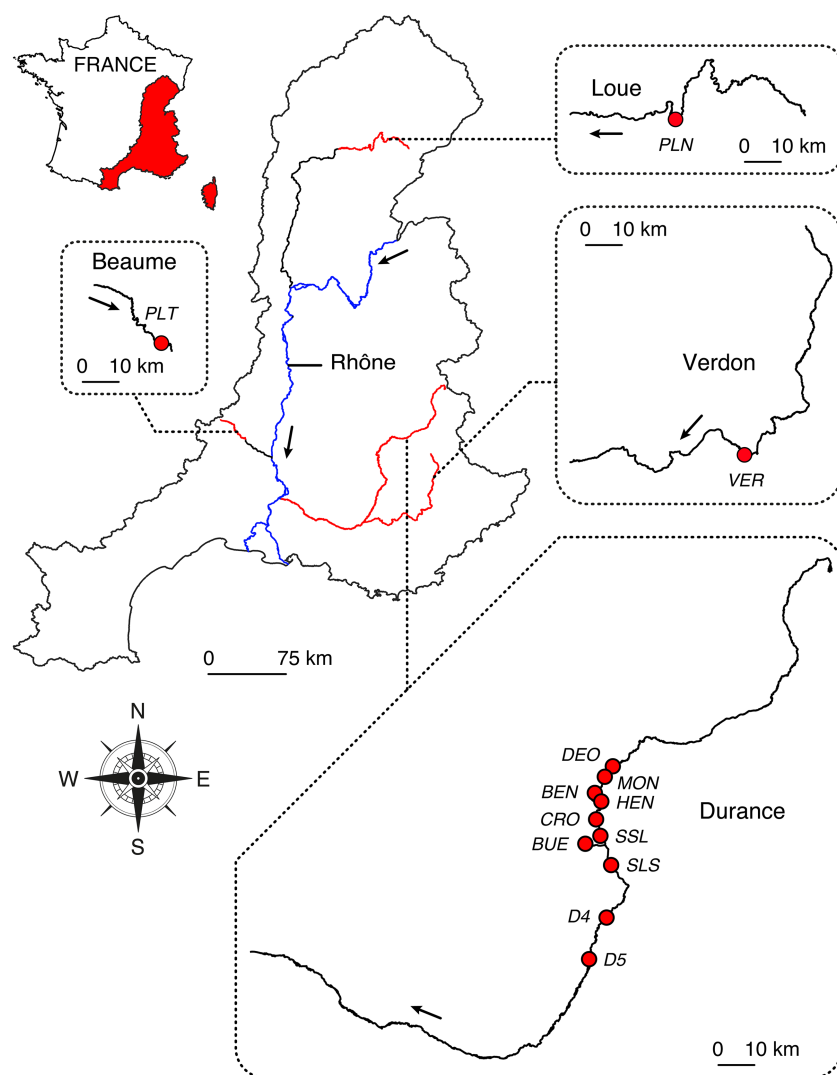


FIGURE 1 Locations of the four rivers and 13 sampling sites in the Rhône catchment (south of France): Loue (PLN), Beaume (PLT), Durance (from upstream to downstream: DEO, MON, BEN, HEN, CRO, SSL, BUE, SLS, D4, and D5), and Verdon (VER). The Rhône River is indicated in blue

TABLE 1 Number of *Zingel asper* collected and used for scalimetric analysis, and summary of thermal, substrate-related, hydraulic, and trophic data collected in four populations from different catchments (Loue, PLN; Beaume, PLT; Durance, HEN; and Verdon, VER) and in five additional sub-populations retained for the Durance catchment (SSL, BUE, SLS, D4, and D5)

Station	Loue		Beaume		Durance					Verdon			
	PLN	2014, 2015	PLT	2014, 2015	HEN	2014, 2015	SSL	BUE	SLS	D4	D5	VER	2015
Growth													
Year	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2015
N sampled	253	151	201	201	130	74	90	158	108	191	165	191	191
N used	210	124	196	196	108	73	84	131	91	165	165	165	165
0+	3	22	7	7	1	32	0	3	1	6	6	6	6
1+	105	55	43	43	31	4	39	112	67	93	93	93	93
2+	28	22	77	77	41	21	16	10	15	27	27	27	27
3+	45	22	45	45	20	9	24	6	6	8	8	8	8
4+	21	2	19	19	15	6	5	0	2	3	3	3	3
5+	8	0	4	4	0	1	0	0	0	24	24	24	24
6+	0	1	1	1	0	0	0	0	0	4	4	4	4
Water temperature													
Year	2015	2014	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015
N Degree days > 18 °C	306	320	21	21	200	666	121	319	205	46	46	46	46
Substrate quality													
Year	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015
Substrate size (mean ± SE)	7.6 ± 0.4	7.9 ± 0.3	7.7 ± 0.3	7.7 ± 0.3	7.8 ± 0.1	8.1 ± 0.2	7.8 ± 0.2	8.0 ± 0.2	8.0 ± 0.3	7.8 ± 0.1	7.8 ± 0.1	7.8 ± 0.1	7.8 ± 0.1
Substrate clogging (mean ± SE)	1.6 ± 0.1	1.3 ± 0.1	1.8 ± 0.1	1.8 ± 0.1	1.6 ± 0.1	1.4 ± 0.1	1.5 ± 0.1	1.4 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.3 ± 0.1
Hydraulics													
Year	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015	2015
Depth (cm) (mean ± SE)	33.1 ± 1.9	31.3 ± 1.9	30.5 ± 2.0	30.5 ± 2.0	26.2 ± 2.1	28.9 ± 1.5	26.2 ± 1.9	34.5 ± 1.8	29.4 ± 2.3	25.7 ± 0.8	25.7 ± 0.8	25.7 ± 0.8	25.7 ± 0.8
Current velocity ^a (cm.s ⁻¹) (mean ± SE)	21.1 ± 2.0	14.8 ± 2.0	33.0 ± 2.8	33.0 ± 2.8	34.4 ± 2.5	32.3 ± 3.3	26.8 ± 3.2	25.7 ± 2.2	31.6 ± 3.1	25.1 ± 1.3	25.1 ± 1.3	25.1 ± 1.3	25.1 ± 1.3
Density of benthic invertebrates^b													
Year	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014, 2015	2014	2014, 2015	2014	2015	2015	2015	2015	2015
Chironomidae ^c	58.7 ± 23.5	37.2 ± 0.2	9.4 ± 2.7	9.4 ± 2.7	2.9 ± 0.5	17.7 ± 16.7	19.8 ± 14.0	12.6 ± 23.7	8.1 ± 12.5	4.0 ± 0.9	4.0 ± 0.9	4.0 ± 0.9	4.0 ± 0.9
Orthocladinae	42.9 ± 11.3	68.1 ± 27.2	81.7 ± 35.7	81.7 ± 35.7	39.4 ± 22.3	39.5 ± 43.7	138.4 ± 67.6	19.1 ± 32.2	15.0 ± 18.5	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.1
Baetiidae	17.7 ± 4.3	27.8 ± 9.6	18.3 ± 1.2	18.3 ± 1.2	36.1 ± 15.1	184.0 ± 223.0	76.4 ± 41.5	104.5 ± 167.3	27.9 ± 54.3	4.7 ± 1.5	4.7 ± 1.5	4.7 ± 1.5	4.7 ± 1.5
Heptageniidae	1.9 ± 0.3	2.8 ± 0.6	3.0 ± 0.3	3.0 ± 0.3	7.4 ± 1.0	7.5 ± 6.7	5.7 ± 1.3	14.1 ± 13.2	14.4 ± 13.2	8.2 ± 1.8	8.2 ± 1.8	8.2 ± 1.8	8.2 ± 1.8

^aCurrent velocity at substrate (cm.s⁻¹).

^bDensity of benthic invertebrates (n per Surber net). Densities are indicated as mean ± SE across sampling years for stations PLT, HEN, SSL, SLS, PLN, and VER, and as mean ± SD for stations BUE, D4, and D5.

^cChironomidae (Orthocladinae excluded).

times in 2015 (sampling dates in Table S1). The PLN, PLT, HEN, and VER stations are considered as reference stations for the Loue, Beaume, Durance, and Verdon rivers, respectively, i.e. stations where ecological conditions and fish distributions are assumed to be representative of each catchment. Together with this interpopulation comparison, the collection of fishes was extended to eight locations (i.e. intrapopulation comparison, DEO, MON, BEN, CRO, SSL, SLS, D4 and D5 stations; Figure 1; Table 1) and one tributary of the Durance River (Buëch River, BUE station; Figure 1), in which the genetically undifferentiated populations of *Z. asper* contribute to the broad genetic cluster of the Durance system (Dubut, Gilles & Chappaz, 2011). These nine additional stations were sampled in 2014 and/or 2015 (Table S1). Fish collection occurred at night, from approx. 2:00 AM to 5:00 AM, when the nocturnal activity of *Z. asper* and optimal flow conditions (low turbidity and depth) facilitated the detection, with flashlights, of juvenile and adult individuals and their capture with large dip nets (40-cm wide, 5-mm mesh net), which ensured maximum capture efficiency as most of the fishes collected exceeded 10 cm in length. Although this collection method is effective on the Beaume (Danancher et al., 2007), Loue (Zaugg & Plomb, 2012) and Verdon (Chappaz & Dubut, 2018) rivers, the high flow speed and turbidity on the Durance and Buëch rivers required the collection of fishes by electrofishing (200–500 V; EFKO, Leutkirch im Allgäu, Germany) during the daytime. Once captured, the fork length of every individual was measured (FL, in mm) before between six and 12 dorsal scales were collected for later scale-reading analysis at Aix Marseille Université (Marseille, France). Fish were temporarily held in the flow using grid tanks placed in the river before biometric measurements and scale collection, preventing any fish recapture. All fishes were released within the sampling area at the end of each sampling session.

2.2 | Determination of age structure and growth patterns by scale-reading analysis

Differences in growth and longevity among and within populations of *Z. asper* were assessed by performing scale-reading measurements, a reliable method for estimating age and past growth rates in endangered fish species (Hamidan & Britton, 2015; for *Z. asper*, see Cavalli, Pech & Chappaz, 2003; Danancher et al., 2007). Scales calcify by the continuous accumulation of growth rings (circuli), the spacing of which decreases during winter lethargy to form an annulus, i.e. a visible area of closely spaced circuli. The strong positive relationship between scale radius and body size repeatedly observed in fishes (Francis, 1990; for *Z. asper*, see Danancher et al., 2007; Fontez & Cavalli, 2014) makes interannuli distance a reliable and sensitive indicator of past individual growth rates, whereas the total number of annuli on a scale indicates the age of the fish. Once processed, scales were gently cleaned with potassium hydroxide before being mounted between glass slides and analysed under a stereoscopic microscope equipped with an ocular micrometer. On each scale, interannuli distances were measured between the nucleus of the scale and the anterior edge of each annulus (as described for this species by

Danancher et al., 2007; see Figure S1 for details). Interannuli measurements and age determination were performed on three scales per individual by two independent observers, with no indication of fish body length. Scale measurements and age estimates were considered definitive when both observers agreed on age determination. In case of disagreement, scales were read by a third observer and considered definitive if two of the three estimates corresponded; otherwise, dubious scales were discarded from the dataset. This protocol prevented any age overestimation by counting 'false annuli', i.e. calcification artefacts induced by thermal stress or low food intake during early development (Coble, 1970).

The average longevity of each population was estimated by designing a quantitative maximum age index (MAI) based on age structure. The number of individuals in each age class from 3 to 6 years was multiplied by a coefficient of 1–4, respectively; the average score across the four age classes gives the population MAI. For example, a population with four individuals (one 3+, one 4+, one 5+ and one 6+ years) would be assigned a MAI of 2.5, i.e. $(1 + 2 + 3 + 4)/4$. A standard deviation was then attributed to each MAI by bootstrap resampling (1,000 iterations). Growth and longevity data were then averaged across all sampling sessions for each population.

2.3 | Variation in ecological context among rearing rivers

To determine the contribution of environmental context to early growth among and within populations, key substrate-related, hydraulic, thermal, and trophic attributes of the available habitats were measured in each river during the day preceding or following scale collection. Depending on the rivers, a total of between 60 (SSL, BUE, SLS, D4, and D5 stations) and 90 habitat data points (PLN, PLT, HEN, and VER stations) were sampled in 2014 or 2015. Depth (cm) and bottom current velocity (in $\text{cm}\cdot\text{s}^{-1}$) were measured for each habitat data point, with bottom current velocity measured using a flow meter (Flo-Mate 2000; Cometec, Chapareillan, France) placed above the substrate. Similar to previous studies that used categorical classifications of increasing substrate size and clogging level to assess habitat preferences in fishes (Lamouroux et al., 1999; for *Z. asper*, see Labonne, Allouche & Gaudin, 2003), the granulometry and clogging of dominant substrates were assessed by defining 10 categorical classes of increasing substrate granulometry (silt, fine sand, coarse sand, fine gravel, coarse gravel, small pebble, large pebble, small cobble, large cobble, and boulder) and five categorical classes of substrate clogging (<25%, <50%, <75%, <90%, and 100%), respectively. The dominant substrate of each habitat data point was then attributed a score of between 1 and 10 as a function of increasing substrate granulometry, and a score of between 1 and 5 as a function of increasing substrate clogging. For example, a first habitat data point with silt and a second with boulders as dominant substrates gives a population score of 5.5, i.e. $(1 + 10)/2$, for substrate granulometry; a first habitat data point with <25% substrate clogging and a second with 100% substrate clogging gives a

population score of 3, i.e. $(1 + 5)/2$, for substrate clogging. Prey availability was estimated in spring and/or summer of 2014 and/or 2015 by sampling benthic invertebrate larvae at each habitat data point using standard Surber nets (0.05-m² surface area, 500- μ m mesh size). Invertebrate larvae were preserved in 70% ethanol before identification to family level under a stereoscopic microscope. The densities of each of four key prey taxa (as the number of invertebrates per Surber net) that dominate the diet of *Z. asper* (Villsen et al., 2021) – Chironomidae (Orthocladiinae excluded, order Diptera), Orthocladiinae (order Diptera), Baetidae (order Ephemeroptera), and Heptageniidae (order Ephemeroptera) – were then calculated for each population. Temperature loggers installed in each river allowed the comparison of thermal conditions among sampling sites (one record per hour) by calculating the number of degree-days above 18 °C during the period of fish growth, set from 1 April to 1 October (Cavalli, Pech & Chappaz, 2003). All environmental variables (current velocity, depth, substrate granulometry score, substrate clogging score, densities of Chironomidae, Orthocladiinae, Baetidae, and Heptageniidae, and number of degree days above 18 °C) were then averaged across all data points and sampling years for each site.

2.4 | Data analysis

Growth rates were compared for each age class, both among (Loue, Beaume, Durance (HEN station), and Verdon rivers) and within river systems (Durance sub-populations), by performing individual analyses using R 1.1.456 (R Core Team, 2018). Distribution normality and variance homoscedasticity were tested using the Shapiro–Wilk test and the *F*-test, respectively; as assumptions of normality and homoscedasticity were never met, even after log transformation, all data on growth and longevity (i.e. MAI) were compared using nonparametric tests (Kruskal–Wallis test and post-hoc Mann–Whitney *U*-test). A similar protocol was used to compare growth rates between successive age classes within populations. Although the genetic basis of growth may be correlated with successive growth rates and therefore reduce data independence, Mann–Whitney *U*-tests (i.e. comparing independent, unbalanced data) were preferred over Wilcoxon *W*-tests (i.e. comparing dependent, paired data) to retain all individuals with available growth data (e.g. at 1 year, 2 years, or 1 and 2 years) and avoid any further reduction in sample size by only considering individuals with paired growth data for the two age classes compared (e.g. at 1 and 2 years only). As the first 3 years of life dominated most of the total sample size and growth variation among and within populations, the second part of the analysis (i.e. environmental effects on growth) exclusively included growth data at 1, 2, and 3 years for each population.

Scalimetric and biometric data were used to back-calculate individual FLs during winter annulus formation, which was assumed to occur on 1 January of each year (i.e. in the middle of winter). The most parsimonious relationship between FL measured on collection and total scale radius was determined by comparing separate linear,

polynomial (second order), and exponential models for each of the four populations from different river catchments (PLN, PLT, HEN, and VER). The intercept of each model, representing the FL at which scales appear, was fixed to 19 mm based on observations of individuals reared in captivity (Béjean, 2019). Linear, polynomial, and exponential models were ranked based on their coefficient of determination (R^2), and the model with the highest R^2 was retained as the most parsimonious for each population. Equations of retained models were then used to back-calculate FLs (in mm) based on the interannuli distances of every individual currently or previously in the age class of interest: for example, 2+, 3+, 4+, 5+, and 6+ year individuals were used to back-calculate FLs at 2 years. Back-calculated FLs from 1 to 4 years (i.e. age classes with sufficient sample size) were then averaged across all individuals for each age class and population, before being compared among populations using nonparametric Kruskal–Wallis tests.

The relative contribution of environmental context to early growth was assessed among and within populations of *Z. asper* by hierarchical variance partitioning (HIER.PART in R; Nally & Walsh, 2004). Separate variance partitioning analyses on scaled and centred data were performed for each age class (1, 2, and 3 years) and comparison level (inter- vs intra-population) to determine the relative percentage of growth variance explained by each of the nine environmental variables considered (number of degree days above 18 °C, substrate size, substrate clogging, depth, current velocity, and densities of Chironomidae, Orthocladiinae, Baetidae, and Heptageniidae). Percentages were then averaged per category of environmental factor (i.e. temperature, substrate quality, hydraulics, and prey availability) and scaled to 100% for each age class and comparison level. Note that hierarchical partitioning analyses were performed on populations for which all data on growth, water temperature, physical habitat, and prey availability were available, resulting in low replication both among catchments ($n = 4$) and within the Durance catchment ($n = 6$) (Table 1).

3 | RESULTS

3.1 | Scale-reading analysis

Of the 1,433 individuals collected in total (all populations and sampling sessions combined), 175 (12.2%) were excluded from the analysis as they had scales that were either illegible or a source of disagreement among observers. The effective sample size comprised 1,258 individuals, for a total of 3,412 valid scales. Overall, the ages varied from 0+ (i.e. young of the year) to 6+ years, with fishes aged 1+, 2+, and 3+ years constituting the dominant age classes.

Growth significantly differed among populations from different catchments in the first four years of life (Kruskal–Wallis tests, $P < 0.01$; Figure 2), and was maximal in the Beaume and Loue populations at 1 year, in the Beaume and Verdon populations at 2 years, and in the Verdon population at 3 years (Table 2). Growth rates gradually decreased over ontogeny in the Durance population

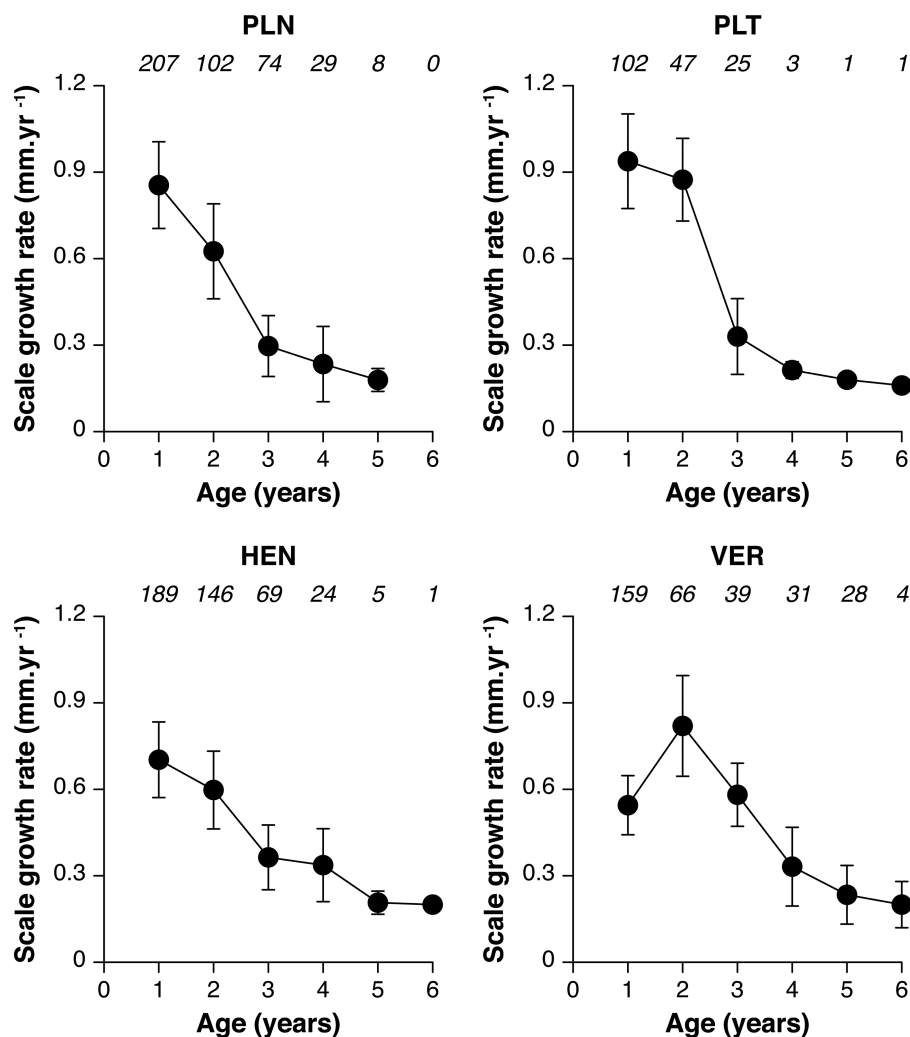


FIGURE 2 Growth profile and age structure of four populations of *Zingel asper* from different catchments (Loue, PLN; Beaume, PLT; Durance, HEN; and Verdon, VER). Vertical bars represent standard deviations and the number of individuals used for each age class is indicated above each graph

(HEN station), but plummeted significantly after 2 years in the Beaume and Loue populations (Mann–Whitney tests, $P < 0.001$); in contrast, the Verdon population showed significant compensatory growth at 2 years (Mann–Whitney, $U = 1080.0$, $P < 0.001$). Growth rates also differed within the Durance catchment during the first three years of life (Kruskal–Wallis tests, $P < 0.001$; Figure 3), with significant declines between 1, 2, and 3 years in stations SSL, BUE, and D5 (Mann–Whitney tests, $P < 0.001$). Longevity differed marginally among river systems (Kruskal–Wallis, $\chi^2 = 3.0$, $P = 0.39$; Figure 4) and was similar in the Beaume (1.20 ± 0.13 , mean \pm SD), Loue (1.50 ± 0.08), and Durance (HEN, 1.43 ± 0.08) populations, but was higher in the Verdon population (2.62 ± 0.15). Longevity also differed marginally within the Durance catchment (Kruskal–Wallis, $\chi^2 = 9.0$, $P = 0.44$). Overall, a moderate growth versus longevity trade-off emerged from the scale-reading measurements, as indicated by the negative and significant correlation between growth rate at 1 year and MAI (Pearson, $r = -0.60$, $P = 0.029$).

As reported elsewhere for *Z. asper* (Danancher et al., 2007), the relationship between FL and total scale radius was better fitted by polynomial models for all populations ($R^2 = 0.99$, on average), compared with linear ($R^2 = 0.98$) and exponential ($R^2 = 0.90$) models. The Beaume and Loue populations presented higher back-calculated

FLs for individuals aged 1–4 years, relative to the Durance and Verdon populations (Table 3). Differences in back-calculated FLs among populations were significant at 1 year (Kruskal–Wallis, $\chi^2 = 359.3$, $P < 0.001$), 3 years (Kruskal–Wallis, $\chi^2 = 75.2$, $P < 0.001$), and 4 years (Kruskal–Wallis, $\chi^2 = 48.4$, $P < 0.001$) (Table 3), but not at 2 years (Kruskal–Wallis, $\chi^2 = 5.05$, $P = 0.17$).

3.2 | Environmental bases of growth in *Z. asper*

The Loue, Beaume, Durance, and Verdon rivers differ in their hydraulic, thermal, trophic, and substrate-related characteristics (Table 1). The Loue River has deep, slow, and warm waters with small-sized substrates, where abundant dipteran larvae (Chironomidae and Orthoclaadiinae) were recorded. The Beaume River presented a similar ecological profile despite lower current velocity and higher densities of Baetidae. In contrast, the Durance (with tributaries included) and Verdon rivers have shallow habitats and high current velocities, with moderately clogged substrates where ephemeropteran larvae (Baetidae or Heptageniidae) were abundant.

Growth variation among populations from different catchments was mostly explained by local variation in water temperature,

TABLE 2 Scale growth rates during the first 4 years of life and maximum age index (MAI) of four populations of *Zingel asper* from different catchments (Loue, PLN; Beaume, PLT; Durance, HEN; and Verdon, VER)

Station	Loue PLN	Beaume PLT	Durance HEN	Verdon VER
Scale growth rate (mm.yr ⁻¹) (mean ± SD)				
1 year	0.86 ± 0.15	0.94 ± 0.16	0.70 ± 0.13	0.54 ± 0.10
2 years	0.63 ± 0.16	0.87 ± 0.14	0.60 ± 0.13	0.82 ± 0.17
3 years	0.30 ± 0.11	0.33 ± 0.13	0.36 ± 0.11	0.58 ± 0.11
4 years	0.23 ± 0.13	0.21 ± 0.03	0.34 ± 0.13	0.33 ± 0.14
MAI (mean ± SD)	1.50 ± 0.08	1.20 ± 0.13	1.43 ± 0.08	2.62 ± 0.15

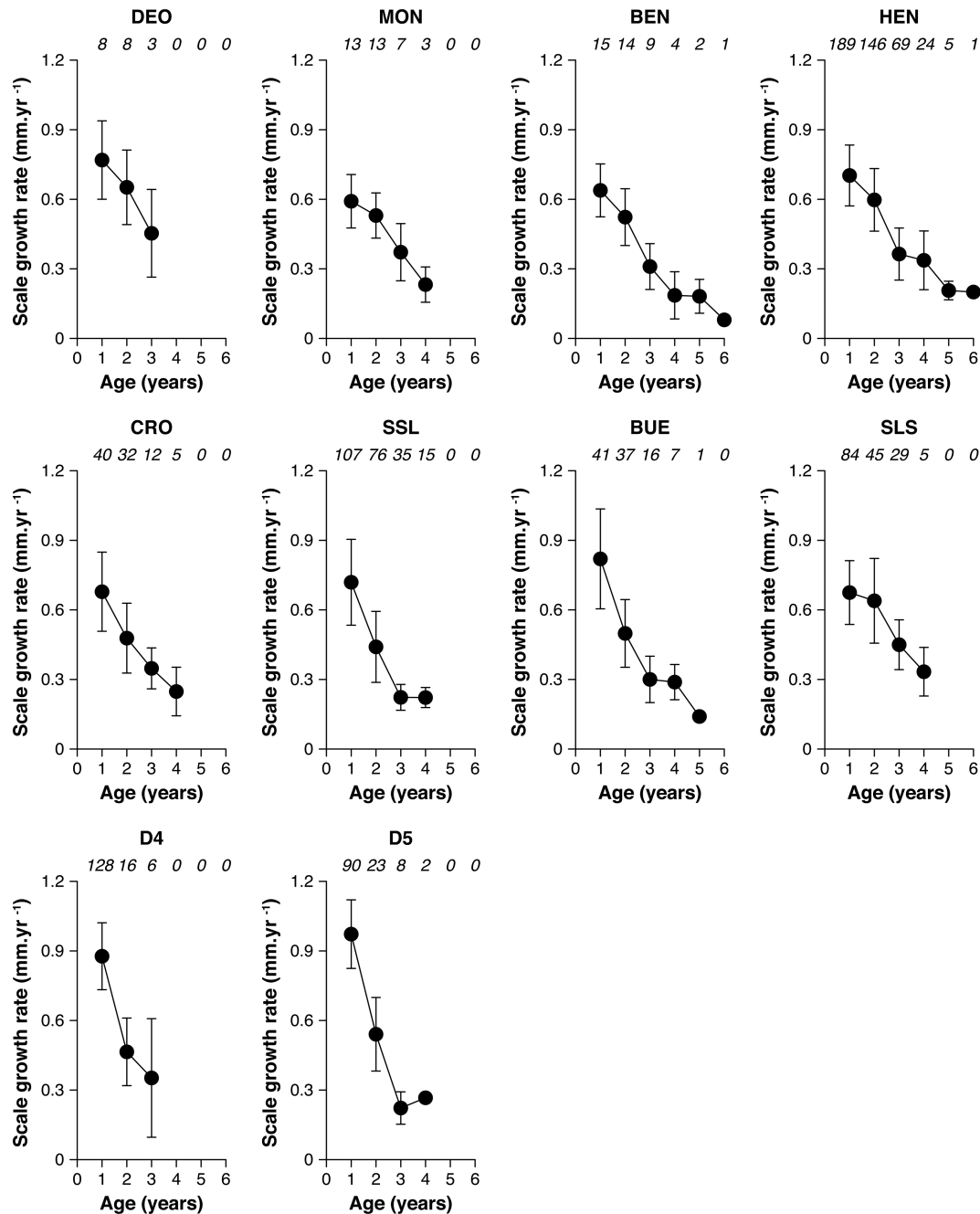


FIGURE 3 Growth profile and age structure of the nine sub-populations of *Zingel asper* within the Durance system (DEO, MON, BEN, CRO, SSL, BUE, SLS, D4, and D5). The reference station for the Durance River (HEN) is also included for comparison. Vertical bars represent standard deviations and the number of individuals used for each age class is indicated above each graph

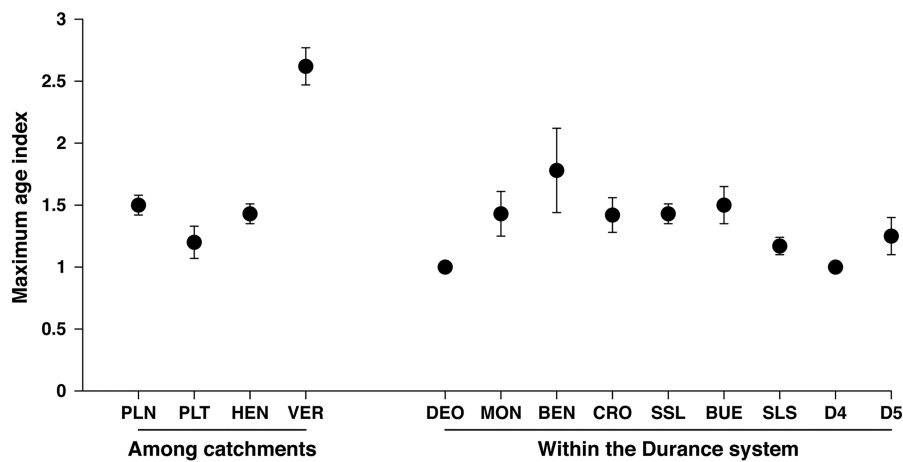


FIGURE 4 Maximum age index (MAI) for four populations of *Zingel asper* from different catchments (Loue, PLN; Beaume, PLT; Durance, HEN; and Verdon, VER) and the nine additional sub-populations within the Durance system (DEO, MON, BEN, CRO, SSL, BUE, SLS, D4, and D5). Vertical bars represent standard deviations

TABLE 3 Measured and back-calculated fork lengths (FLs) for the first 4 years of life in four populations of *Zingel asper* from different catchments (Loue, PLN; Beaume, PLT; Durance, HEN; and Verdon, VER). The polynomial model used to back-calculate fork lengths is also indicated for each population

Station	Loue PLN	Beaume PLT	Durance HEN	Verdon VER
FL (mm) (mean ± SD)				
1+ year	116 ± 7	106 ± 6	102 ± 5	86 ± 9
2+ years	141 ± 17	131 ± 7	115 ± 9	117 ± 7
3+ years	164 ± 6	150 ± 6	128 ± 6	141 ± 5
4+ years	180 ± 13	169 ± 5	140 ± 9	158 ± 9
Calculated FL (mm) (mean ± SE)	$FL = -5.56S^2 + 80.52S + 19$	$FL = -5.66S^2 + 69.01S + 19$	$FL = -11.22S^2 + 76.45S + 19$	$FL = -4.41S^2 + 65.12S + 19$
1 year	84 ± 0.1	79 ± 0.1	67 ± 0.1	53 ± 0.1
2 years	124 ± 0.1	123 ± 0.2	98 ± 0.1	100 ± 0.2
3 years	143 ± 0.2	135 ± 0.5	110 ± 0.1	129 ± 0.3
4 years	156 ± 0.5	159 ± 1.0	123 ± 0.3	144 ± 0.5

Note: Example of how to back-calculate a FL (mm) for an individual aged 1+ years from the Loue River with a distance from the nucleus to the first annulus of the scale of 1 mm: $FL = -5.56 \times (1)^2 + 80.52 \times 1 + 19$.

hydraulics, and prey availability at 1 year (combined explained variance, 88%; Figure 5; Table S2), by hydraulics and substrate quality at 2 years (66%), and by prey availability and hydraulics at 3 years (63%). Differences in growth among sub-populations of the Durance system were mostly explained by local variation in temperature, substrate quality, and prey availability at 1 year (combined explained variance, 85%), by temperature and prey availability at 2 years (64%), and by hydraulics and prey availability at 3 years (61%) (Figure 5).

4 | DISCUSSION

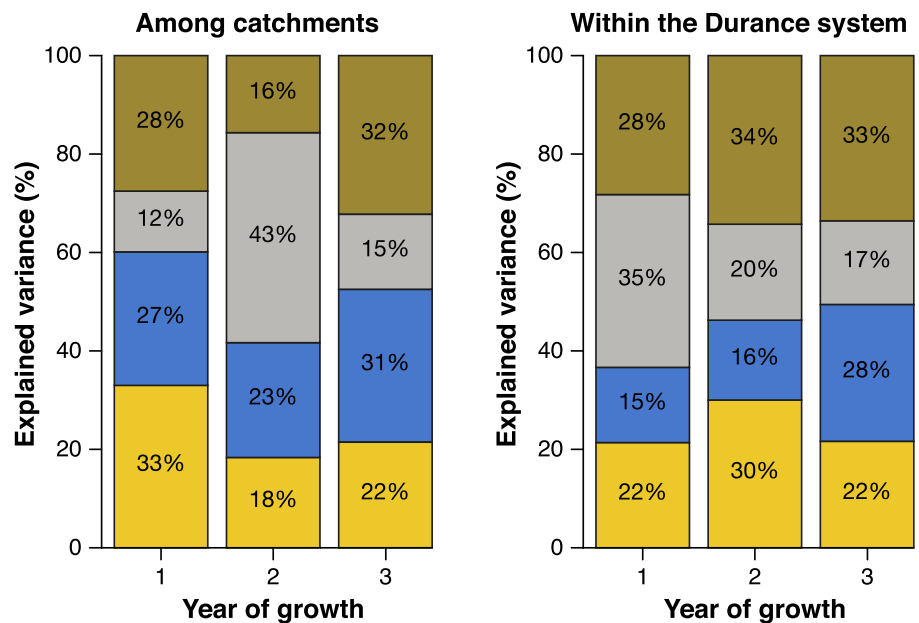
4.1 | Differentiation of *Z. asper* populations along a slow-to-fast continuum of life histories

The scalimetric comparison of growth and longevity among remnant populations of *Z. asper* provided evidence of their phenotypic

differentiation along a slow-to-fast continuum of life histories. Among river systems, the Beaume and Loue populations presented an overall pattern of fast life histories (i.e. faster growth at 1 or 1–2 years, larger adult body size (i.e. higher back-calculated lengths at 3 and 4 years after sexual maturity at 2–3 years; Chevalier, De Conto & Exbrayat, 2011), and longevity of 3–4 years), relative to the Durance (HEN station) and Verdon populations, with overall slow life histories (i.e. slower growth at 1 or 1–2 years, smaller adult body size, and longevity of 4–5 years). Within the Durance system, a similar continuum differentiated upstream populations (i.e. DEO, MON, BEN, HEN, and CRO) with an overall pattern of slow life histories (slower growth and higher longevity) from downstream populations (i.e. SSL, BUE, SLS, D4, and D5) with fast life histories (faster growth and lower longevity).

Variation in life-history strategies among populations of *Z. asper* appeared to be partly driven by a trade-off between growth rate during the first year and longevity, which has been suggested in

FIGURE 5 Percentages of growth variance explained by water temperature (yellow), hydraulics (blue), substrate quality (grey), and prey availability (brown) for the first, second, and third year of growth of *Zingel asper*. The left panel includes four populations from different catchments (Loue, PLN; Beaume, PLT; Durance, HEN; and Verdon, VER); the right panel shows the five additional sub-populations retained for the Durance system (SSL, BUE, SLS, D4, and D5) and the reference station for the Durance River (HEN)



vertebrates, including mammals (Bartke et al., 2001), reptiles (Olsson & Shine, 2002), and fishes (Craig, 1980). The mechanisms underlying this trade-off remain unclear (Lee, Monaghan & Metcalfe, 2013) and may include various physiological or behavioural constraints associated with faster growth (Metcalfe & Monaghan, 2003) as a requirement to increase adult body size (Sibly et al., 2015). For instance, maximizing metabolic activity to support faster growth may shorten longevity by increasing cellular and molecular oxidative damage (Cichoń, 1997; Rollo, 2002), or by reducing investment in repairing tissues damaged by oxidative stress (Morgan, McCarthy & Metcalfe, 2000; Geiger et al., 2012). Achieving faster growth to target larger adult body size also requires maximizing prey consumption by extending foraging activity, which may ultimately reduce survival through the pervasive fast growth versus low survival trade-off (Biro et al., 2004; Stamps, 2007); however, this scenario remains speculative as the ecological characteristics of *Z. asper* are largely unknown. Alternatively, an early growth versus longevity trade-off may result from selection for higher longevity to maximize breeding opportunities and associated fitness in predictable environments (Winemiller, 2005), such as the Durance and Verdon rivers, where longevity and environmental predictability are high (and vice versa for the Beaume and Loue rivers, where stochastic droughts or floods may reduce survival).

The four populations of *Z. asper* from different catchments differed significantly in their developmental trajectories. Growth rate gradually decreased over ontogeny in the Durance population but significantly plummeted after 2 years in the Beaume population, in line with previous studies (Cavalli, Pech & Chappaz, 2003; Danancher et al., 2007). Allometric growth is typical in fishes (Casselman, 1990), and partly results from ontogenetic shifts in energy allocation from growth to reproduction (Post & Parkinson, 2001). Contrasting growth trajectories between the

Durance and Beaume populations illustrate different energy balances between growth and reproduction constrained by longevity, where slower growth and higher longevity in the Durance population may delay sexual maturity and result in more progressive shifts in energy allocation to reproduction, relative to the Beaume population. In parallel with the Beaume and Durance populations, the age structure and growth profiles of the Loue and Verdon populations were determined here for the first time. The Loue population showed a similar life-history strategy to that of the Beaume population, suggesting the existence of similar developmental constraints among faster growth, larger adult size, and lower longevity in both river systems. Interestingly, the Verdon population showed an atypical pattern of compensatory growth at 2 years, which has already been reported in other fish species of this system (e.g. the common chub *Squalius cephalus*; Bouchard et al., 1998). Although compensatory growth allowed individuals of the Verdon River to compensate for slow development at 1 year by catching up on body size at 3 and 4 years, the ecological drivers of compensatory growth in this population remain unclear but are likely to be associated with variation in prey availability between 1 and 3 years. A recent study (Villsen et al., 2021) suggests that the diet of first-year *Z. asper* is dominated by chironomids (including Orthoclaadiinae). The low densities of chironomids observed in the Verdon River (4.8 individuals per Surber sample on average; Table 1) compared with the other catchments (ranging from 91.1 in the Durance River (HEN station) to 105.3 in the Beaume River; Table 1), associated with the high density-dependent competition for prey that typically follows fry emergence in fishes, constitute potential bottom-up mechanisms limiting growth during the first year in the Verdon population of *Z. asper*. Strong shifts in diet composition, from chironomids to mayfly larvae, and particularly Heptageniidae (Villsen et al., 2021), and habitat use from 1 to 3 years in *Z. asper* (Labonne, Allouche &

Gaudin, 2003; Danancher et al., 2004) may then reduce density-dependent competition for prey and promote faster growth at 2 and 3 years in the Verdon population. Although compensatory growth is beneficial for surviving temporary ecological constraints on early development, such as low prey availability (Ali, Nicieza & Wootton, 2003), it may come at the cost of deleterious effects on adult performance and associated fitness, such as smaller organ size and higher metabolic loading (Metcalf & Monaghan, 2003).

4.2 | Environmental drivers of growth in *Z. asper*

Many macroecological factors select for faster growth and larger body size in nature, including shorter growing seasons at higher latitudes (Billerbeck, Schultz & Conover, 2000). This is consistent with the latitudinal countergradient in growth rate and adult body size observed among populations of *Z. asper*, where capacity for growth during the first year or first and second years and ultimate adult size were maximal in the northernmost Beauce and Loue populations and were reduced in the southernmost Durance and Verdon populations. Latitudinal countergradients of growth constitute common patterns of growth-rate evolution (Conover & Schultz, 1995), and illustrate the need to maximize growth to achieve minimum size thresholds, thereby maximizing overwinter survival (Quinn & Peterson, 1996) in higher latitude habitats with shorter growing seasons (Billerbeck, Schultz & Conover, 2000). Rapid growth at 1 or 1–2 years in the northernmost populations of *Z. asper* may therefore constitute an adaptive response to greater seasonality at higher latitudes (Loue) and higher thermal variation imposed by the continental climate of central (Beauce) and north-eastern France (Loue). As the four river catchments also differ along a low (Beauce and Loue) to high (Durance and Verdon) altitudinal gradient (Table S1) that largely overlaps with their latitudinal distribution, it is likely that part of the differentiation in growth among these populations can be explained by variations in an ecological context associated with altitude (e.g. changes in temperature or prey abundance). However, the effects of altitude on growth are probably marginal, as populations at similar elevation (e.g. upper Durance vs Verdon or Beauce vs Loue) largely differ in growth, whereas populations at different altitudes (e.g. Loue vs Durance) still have similar developmental trajectories. In contrast, altitudinal effects may largely contribute to within-river growth differentiation in the Durance system, where growth rate during the first year substantially increases along an upstream-to-downstream river gradient.

Differences in juvenile growth among populations of *Z. asper* also emerged as plastic responses to local variation in the environmental context. High prey availability and rearing temperature often elevate energy intake and metabolic activity (Schulte, 2015; Monnet, Rosenfeld & Richards, 2020; Volkoff & Rønnestad, 2020), in support of faster growth. These expectations are somewhat consistent with the apparent mapping of ecological gradients of temperature and prey availability onto the slow-to-fast continuum of growth among populations of *Z. asper* from different catchments, whereby elevated

temperatures and/or high densities of dipteran and mayfly larvae that constitute the main diet of *Z. asper* (Cavalli, Pech & Chappaz, 2003; Villsen et al., 2021) are positively associated with faster growth at 1 year in the Loue and Beauce populations and at 3 years in the colder Durance and Verdon rivers. In contrast, local variation in prey availability (higher prey densities), substrate quality (larger and less clogged substrates), and temperature (warmer waters) explained most of the growth variation from 1 to 3 years within the Durance system. However, the nature of the relationship between substrate quality and growth remains somewhat speculative. Larger substrates used as shelters may decrease swimming costs and increase energy allocation to growth (Fischer, 2000; Egger et al., 2021), whereas less clogged substrates may indirectly support faster growth by increasing substrate complexity and associated prey availability (Bo et al., 2007). However, the small number of fish populations available for this study substantially limits inference, and caution is advised when interpreting the contribution of environmental factors to growth, as reported here. In addition, this study focuses exclusively on the environmental (plastic) origins of growth variation among and within populations of *Z. asper*. It is likely that part of the differentiation in growth observed among river catchments can be explained by genetic (i.e. fixed) differences that have accumulated in these populations (Laroche & Durand, 2004) following their geographical isolation over the past century, equivalent to a minimum of 30–50 generations, considering sexual maturity at 2–3 years in this species (Chevalier, De Conto & Exbrayat, 2011).

4.3 | Implications for conservation

From a conservation perspective, the Beauce population of *Z. asper* appears to be highly vulnerable to extinction as a result of particularly short individual life cycles. The rapid growth rates and low longevities observed in this population, associated with sexual maturity at 2–3 years in *Z. asper* (Chevalier, De Conto & Exbrayat, 2011), may considerably limit adult reproduction and juvenile recruitment, and reduce resilience to environmental stochasticity. The temperature dependence of growth combined with an emerging trade-off between early growth and longevity may further accelerate individual life cycles, weaken population dynamics and increase the risk of extirpation of the Beauce population in the continuing context of global warming (for an example in lizards, see Bestion et al., 2015).

As suggested by previous studies (Cavalli, Pech & Chappaz, 2003; Danancher et al., 2007), scale reading emerged as a valid method for assessing the degree of variation in life histories among remnant populations of *Z. asper*. Although scale reading has been repeatedly used as an indicator of key life histories in fishes (e.g. age at sea in salmonids; Bacon et al., 2011; population structure in esocids, Sauvanet et al., 2013), this method suffers from problems of repeatability that limit its universal application to all fish taxa. The feasibility and accuracy of scale reading are largely conditioned by intrinsic factors specific to individuals (e.g. age; Riffart et al., 2006) or species studied (e.g. scale morphology), and by environmental factors

that influence scale calcification (e.g. water chemistry; Campbell et al., 2015). The methodology (e.g. the level of expertise of each scale reader; Aulus-Giacosa et al., 2019) and statistical analysis used to infer life-history data from fish scales constitute additional sources of variability that are likely to alter the feasibility and conclusions of scalimetric analyses. For example, the use of a simple polynomial relationship between body length and scale size to back-calculate body length, as presented in this study and elsewhere (Danancher et al., 2007), may constitute an over-simplistic approach largely outweighed by recent Bayesian methods that can account for ecological (e.g. cohort variability; Fontez & Cavalli, 2014) and statistical (e.g. uncertainty during the process of age estimation; Dorte et al., 2013) sources of error in their back-calculated size estimates. Scalimetric analyses may therefore benefit from advanced statistical approaches to gain in accuracy and predictive power, but nevertheless constitutes a reliable alternative to conventional methods of population monitoring (such as mark-recapture) owing to their ethical nature (as a minimally invasive process) and easy applicability (i.e. low requirements for time, budget, and sampling conditions).

Intraspecific variation in life histories can indicate the degree of vulnerability to extinction of endangered taxa and guide conservation actions. Establishing a reference database detailing how suites of life-history attributes vary among wild populations of a given endangered species can facilitate the identification of populations requiring priority management or contribute to the long-term monitoring of individuals reintroduced into the wild. For example, the age structures and growth profiles established for the Beume and Durance (HEN) populations of *Z. asper* in this study may be used as a monitoring tool in a continuing conservation programme, the objective of which is to re-establish and maintain a viable population of *Z. asper* of Beume and Durance origins in the Drôme River (south-east France) after the recent collapse of the local population (Georget, 2017; Georget, 2019). More broadly, identifying intraspecific variation in life histories is fundamental to enabling a better prediction of the response of endangered species to multivariate environmental stressors and adapting the legislation accordingly. For instance, growth, reproductive age, and lifespan have been identified repeatedly by recent multivariate analyses (Tarkan et al., 2016) as key developmental bottlenecks increasing the sensitivity of endangered species to climate change (Glass, Corkum & Mandrak, 2017) or invasive species (Liu, Comte & Olden, 2017). As time and resources are limited, developing non-lethal methods (e.g. scale reading and multivariate trait-based models) that provide rapid and reliable estimates of extinction risk based on intraspecific variation in life histories constitutes a critical step towards improving conservation decisions for endangered species.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest associated with this work.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author, upon request.

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