

Plasticity of life-history traits in the Draa barbel *Luciobarbus lepineyi* (Pellegrin, 1939) (Actinopterygii: Cyprinidae) in the sub-Saharan Draa basin, Morocco: effect of change in flow regime and salinity

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ABSTRACT

The Draa barbel *Luciobarbus lepineyi* (Pellegrin, 1939), an endemic and unique cyprinid of the arid Draa river basin, southern Morocco, faces a range of multiple environmental stressors, especially in intermittent rivers and ephemeral streams (IRES). We assessed the effects of flow intermittence and salinisation on the somatic condition, and life-history traits in Draa barbels. We used the scaled-mass index (SMi) to evaluate the mean individual somatic body condition in nine populations. For three contrasted localities: Iriri (IR), Mghimima (MG), and Sid El Mokhtar (SM), we aged fish from scales and calculated von Bertalanffy growth parameters using the Beverton-Holt procedure. We used these parameters to estimate growth indices and performance, size and age at maturity, longevity, and mortality rates. Mean SMi decreased markedly with increasing salinity, revealing a normal condition at 0.4 PSU in IR, a poor condition in MG at 4 PSU, and a very poor condition at 10 PSU in SM. Growth rates (k) increased with salinity. Conversely, asymptotic lengths L_{∞} and growth performances (ϕ -prime, ϕ') decreased with salinity and flow intermittency. The potential longevity $t_{\max}$ decreased with

the increase in salinity. On the other hand, the mortality rate increased with flow intermittence and salinity. The Draa barbels in the saline IRES of the arid Draa basin compensate for the high mortality by growing faster but less efficiently. They mature at an earlier age and have shorter longevity. With this high life-history plasticity, the Draa barbel would constitute a good ecological indicator and a sentinel for salinisation in variable aquatic environments in the arid Draa river basin.

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Key words: flow regime; salinisation; cyprinid; body condition; growth; survival.

Conflict of interest: the authors declare that they have no competing interests, and all authors confirm accuracy.

Funding: funding was provided by Bundesministerium für Bildung und Forschung (Grant Number 01UU1906).

Citation: Hanfouri S, Ait Boumallassa A, Naimi M, Znari M. Plasticity of life-history traits in the Draa barbel *Luciobarbus lepineyi* (Pellegrin, 1939) (Actinopterygii: Cyprinidae) in the sub-Saharan Draa basin, Morocco: effect of change in flow regime and salinity. *J Limnol* 2024;83:2196.

Edited by: Michela Rogora, National Research Council, Water Research Institute (CNR-IRSA), Verbania Pallanza, Italy.

Received: 27 May 2024.

Accepted: 2 August 2024.

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J. Limnol., 2024; 83:2196

DOI: 10.4081/jlimnol.2024.2196

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INTRODUCTION

The evolution of fish life histories in natural ecosystems is the result of a combination of several, often interdependent, environmental and biotic selective drivers, including density regulation, resource availability, predation, competition, and environmental variability (Winemiller and Rose, 1992; Mims and Olden, 2013; Glarou *et al.*, 2019).

Highly variable environments include intermittent rivers and ephemeral streams (hereafter IRES), which refer to running waters that stop flowing and/or dry up completely at some point in their course (Datry *et al.*, 2017). IRES comprise about half of the Earth's river basins (Schneider *et al.*, 2017) and span various climates and biomes, predominantly in arid regions. Their abundance is growing in response to climate change and water abstraction for human needs (De Graaf *et al.*, 2019). These phenomena have an impact on inland water biota and the ecosystem services that rivers supply to societies (*e.g.*, flood regulation, aquifer recharge, and wood and food supply) (Addy *et al.*, 2019; Kaletová *et al.*, 2019). The scarcity of data on the status of biodiversity in IRES is particularly relevant in North Africa, as the rivers in the region have recently undergone major changes (García *et al.*, 2010), including an expanding number of dams and the intensification of agricultural practices (García *et al.*, 2010), as well as the increasing global impact of climate change. Consequently, these IRES are increasingly exposed to multiple environ-

mental stressors. These comprise several anthropogenic stress factors and their interactions and, therefore, are less protected than permanent rivers.

Water salinity is a major abiotic driver of the activity and distribution patterns of fish and other aquatic animals and is a particularly important attribute of hydrosystems in arid environments (Williams, 1999). In fact, freshwater, brackish, and marine fauna have been the conventional classifications for aquatic biota based on their preferred salinity (Cañedo-Argüelles *et al.*, 2013). Salinity changes can induce stress due to interference with physiological homeostasis and general biological processes. In addition, salinity can also interact with other environmental factors (*e.g.*, flooding, intermittent flow, hypoxia, and hyperthermia) to have complex influences on aquatic populations and communities (Cañedo-Argüelles *et al.*, 2013).

Although fish in Mediterranean rivers do not have any specific adaptations to survive in dried-out habitats, they do show a high tolerance to environmental variability (Datry *et al.*, 2017). Most fish species in the IRES survive through a combination of adaptive strategies of colonization and recruitment (Datry *et al.*, 2017). One of these fishes, the Draa barbel *Luciobarbus lepineyi* (Pellegrin, 1939), a cyprinid that is unique and endemic to the arid catchments of the Ziz, Draa, and Noun rivers in southeast to southwest Morocco, exhibits ecological plasticity associated with a marked morphological polymorphism (Clavero *et al.*, 2015). This may be related to environmental variability (intermittent flow and salinity, among others) or to the process of isolation in Moroccan desert streams (Brahimi *et al.*, 2016). Apart from some naturally occurring (geological) brackish or saline reaches, the increase in salinity is mostly of a secondary type (*i.e.*, human-mediated) due to intensive groundwater pumping for crop irrigation.

Fish species living in environments with high levels of variability require phenotypic plasticity as distinctive and adaptable life-history traits (*e.g.*, short longevity, fast growth, high fertility, early sexual maturity and reproduction, and low food selectivity) (Magalhães *et al.*, 2007; Mims and Olden, 2012; Glarou *et al.*, 2019; Ainou *et al.*, 2023).

The Draa barbel, *L. lepineyi*, is a member of the primary freshwater fish group, comprising families of species that have exclusively evolved in freshwater (typically ostariophysi), which can tolerate salinities of up to 15–17 PSU, *i.e.*, around 50% of the salinity of normal seawater (29–34 PSU). Dispersal happens through freshwater, and low-salinity ‘seas’ or lakes (Bianco and Nordlie, 2008). The Draa barbel is a poorly studied species (Clavero *et al.*, 2015) and is categorized as LC on the IUCN Red List (IUCN, 2023). Growth in body size is a coevolved key feature of the life cycle, and it is linked with sexual maturation, lifespan, mortality, generation time, and the intrinsic growth rate of the population. Growth parameters are therefore required data in most assessment models used for conservation or fisheries management (Froese, 2022). Such data are quite important to assess the resiliency of the species in highly variable environments.

We hypothesized that the body condition and life-history traits of *L. lepineyi* would show high plasticity in response to the changing conditions experienced in the IRES of the sub-Saharan Draa basin, southeast Morocco. To test our hypothesis, we attempted to investigate the mean individual body condition, growth parameters, size and age at maturity, longevity, and mortality rate of Draa barbels under the impact of flow intermittence and salinity changes in the IRES of the arid Draa river basin.

We used body weight and length, as well as aging based on scalimetry and back-dated lengths, to evaluate the aforementioned variables.

METHODS

Study area

The sub-Saharan Draa basin is one of the world’s top 10 arid catchments (Revenga *et al.*, 1998). It is located mostly in the southeast and southwest of Morocco. It extends from 4,071 m in the High Atlas range to the Atlantic coast (de Jong *et al.*, 2005). The Draa is the longest river in Morocco (ca 1,100 km), intermittent, and supplied by two major perennial rivers that arise from the High Atlas: i) the Dades-M’Goun system to the east and ii) the Imini to the west, which join to form the Draa downstream of the Mansour Eddahbi reservoir near Ouarzazate. The other tributaries are mostly IRES, but very few are naturally brackish to saline perennial streams. In the upper-middle Draa, south of the dam, extends the world’s largest date palm oasean system (Fig. 1). The lower Draa basin is much drier, mostly IRES. The climate is predominantly hyper- to semi-arid, with marked circadian and seasonal thermal deviations, dry summers, and erratic rainfall (60 to 800 mm per year). The spring snowmelt from the High Atlas has a considerable impact on the basin’s hydrology. The vegetation comprises *Vachellia raddiana* (Acacia) desert forests at low altitudes, *Artemisia herba-alba* and *Stipa parviflora* steppes at medium elevations, thorny cushion shrubs, and relict Spanish junipers (*Juniperus thurifera*) at 2,400 m asl. Large parts of the uplands are barren, particularly the rugged slopes, due to intensive historic afforestation (de Jong *et al.*, 2008). The oases are irrigated by the artificial release from the reservoir, and by water pumping from shallow aquifers. The area is among the most affected by climate change, which has resulted in increased drought and flood frequency. Human-mediated salinisation increased southward from the dam because of water scarcity and excessive use of groundwater, driving salts to the soil surface (Busche, 2008).

Sampling sites

In preliminary field surveys, Draa barbels were collected (under permit) in nine sites (a total of 280 individuals) throughout the study area, from the southern slope of the High Atlas Mountains to the Sahara desert; 1250 to 560 m asl, based on their flow regime and salinity level. Thereafter, we selected three contrasted study sites for further investigations on life-history traits (Fig. 2): i) a perennial freshwater reach in Iriri (IR), an upstream tributary of the Draa River, ii) a segment of the brackish (primary or geological-originated salinisation) intermittent Mghimima (MG) stream (a tributary of Draa river), and iii) a highly intermittent and salinised (secondary or human-mediated salinisation) segment on the middle Draa river at Sid El Mokhtar (SM). These sites are described in Tab. 1.

Hydrological and physicochemical parameters

We measured physical and chemical parameters and streambed characteristics to describe the study sites and to detect differences in habitat characteristics. A multi-parameter meter (WTW MultiLine® Multi 3510 IDS) was used to measure water

temperature, pH, DO, and EC. River width and depth were measured using a tape measure. Salinity (*i.e.*, all the dissolved salts that contribute to the salinity of water) was not determined directly, but derived as practical salinity (expressed in practical salinity units, PSU) from the *in-situ* conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$) and temperature ($^{\circ}\text{C}$) measurements. All the conversions of conductivities into PSU were performed online using the salinity unit calculator at <https://reefapp.net/en/salinity-calculator>. Flow velocity was measured using a hydrological impeller (SEBA Hydrometrie) and subsequently combined with the area of the cross profile to calculate flow rate (Tab. 2).

Fish sampling

Fish were captured (under permit) in April, May, and July 2021, using a cast net (diameter: 2.5 m, mesh size: 15 mm) or a

gill net (15 x 2.5 m, 10 mm mesh size). When water conductivities were lower than $6000 \mu\text{S}\cdot\text{cm}^{-1}$, we used a portable electrofisher (model ELT60 II HI, Hans Grassl GmbH, Schöna am Königssee, Germany). Upon their capture, fish were anesthetized using clove essential oil (Eugenol). They were then weighed ($\pm 0.1\text{g}$) and measured for their total and standard body lengths ($\pm 0.1\text{mm}$). Individuals were released at six of nine sampling sites after recovering from anesthesia. 142 specimens from the three selected localities, IR, MG, and SM, were cryopreserved (at -20°C) for further laboratory investigations.

Somatic body condition

We used the Scaled Mass Index (SMi) (Maceda-Veiga *et al.*, 2014) for estimating the individual somatic body condition of 280 barbels from nine different reaches, as follows:

Tab. 1. Description of fish sampling sites in the arid Draa basin, SE Morocco.

Sub-basin	Stream	Coordinates (DDS)	Altitude (m)	Localisation	Flow regime	Substratum	Vegetation aquatic/riparian	Number of fish used
Upper Draa	Iriri river midstream (IR)	30,945731-7,199225	1265	35 Km west to Ouarzazate	Permanent	Stones, pebbles, and muddy sediments	Aquatic macrophytes, filamentous algae / Juncus Ruches	45
Middle Draa	Reach on Draa river midstream, at Sid El Mokhtar (SM)	30,1608010-5,520777	632	50 km SE to Zagora at Sid El Mokhtar	Intermittent	Pebbles, sandy-muddy sediments	Aquatic macrophytes, filamentous algae / Tamarix and Reeds	45
Lower Draa	Mghimima river midstream (MG)	29,8303980-7,20203350	519	56 km west to Fom-Zguid – Tissint	Intermittent	Stones, pebbles, and muddy sediments	Aquatic macrophytes, filamentous algae / Tamarix, Date palms	52

DDS, decimal degrees system.

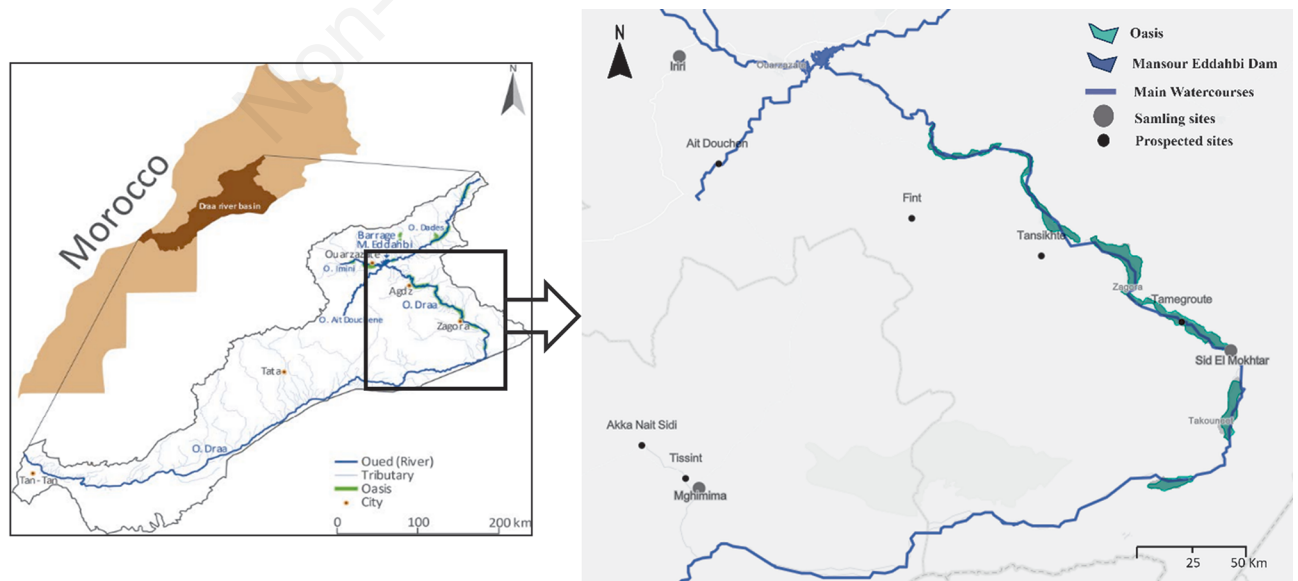


Fig. 1. Geographic location of the prospected and sampling sites (including Iriri, Mghimima, and Sid El Mokhtar) in the arid Draa River basin, SE Morocco (ArcGIS Online, Terrain Basemap, 2023).

$$SMi = Wi [L_0 / Li]^{b/SMA} \quad (\text{eq. 1})$$

Where W_i and L_i are the fresh body weight and standard length, respectively, of individual i , L_0 is a constant length used to standardize body condition values estimated by the arithmetic

mean of total lengths of all individuals captured, and b/SMA is the scaling component, which was obtained by dividing the slope of the least squares regression of weight on length (both of them log-transformed) divided by the Pearson's correlation coefficient of that relationship.



Fig. 2. The sampling localities. A) Iridi; B) Sid El Mokhtar (drying phase); C) Mghimima, in January 2021 (flowing phase); D) Mghimima, in July 2021 (drying phase).

Tab. 2. Physical and hydrological characteristics, dissolved oxygen and salinity at the time of barbel sampling in the three selected reaches in the Draa River basin, SE Morocco, in spring-summer 2021.

Parameter	Iridi	Mghimima	Sid El Mokhtar
pH (moles of H^+ . L^{-1} solution)	7.9	8.8	8.1
Temperature ($^{\circ}C$) (midday)	18.0	29.6	26.5
Conductivity ($\mu S.cm^{-1}$)	670	8300	17700
Salinity (PSU)	0.4	4.2	10.1
Dissolved oxygen ($mg.L^{-1}$)	3.1	2.8	3.3
Flow velocity ($m.s^{-1}$)	0.563	0.146	0.071
Flow rate ($m^3.s^{-1}$)	0.342	0.269	0.022

To establish the reference categories for the body condition in individuals from the nine barbel populations, mean SMi data were collated and separated by percentiles following Pedicillo *et al.* (2010). Thus, five categories were established: i) very poor, when the value of the variable is below the 10th percentile; ii) poor, when the value of the variable is between the 10th and the 30th percentile; iii) normal, when the value of the variable is between the 30th and the 70th percentiles; iv) high, when the value of the variable is between the 70th and the 90th percentiles; and v) very high, when the value of the variable is over the 90th percentile.

Back calculated body length

Five to eight intact scales were withdrawn from the left flank of 142 specimens (IR: n=45, MG: n=45, and SM: n=52) between the lateral line and dorsal fin, where it was assumed to have low scale regeneration. They were cleaned with an 8% sodium hypochlorite (NaOCl) solution, dried, and conserved in glycerin. Scales were then washed off with glycerin and mounted dry between two microscope glass slides for reading under an optical stereomicroscope (magnification: x40). Two different operators applied the scalimetric method for age determination separately.

Length at age was back-calculated using the formula below:

$$Ln = a + Sn / S (L - a) \quad (\text{eq. 2})$$

where Ln is the fish body length at age 'n', a is the constant, Sn is the radius of the annulus 'n', S is the scale radius, and L is the standard length of fish at capture.

Growth parameters

We estimated the theoretical growth for each studied population using the growth curve von Bertalanffy 3-parameters function (VBGF) considering the mean total lengths for age class:

$$L_t = L_{\infty} (1 - \exp(-k (t - t_0))) \quad (\text{eq. 3})$$

where L_t is the total length of the fish at age t (years), L_{∞} (mm) is the asymptotic length that fish could achieve, and k (year^{-1}) is the growth constant rate, which determines how fast the fish approach L_{∞} and t_0 are the hypothetical times at which the length of the fish is zero. The three parameters (L_{∞} , k , and t_0) of the equation were determined using Beverton-Holt's method (Rafail, 1973).

An index of growth (G) per age class (or Annual Specific Growth Rate) between years was calculated based on the mean length as follows (Karametsidis *et al.*, 2023):

$$G(a \rightarrow a+1), t = \ln ML_{(a+1), t} - \ln ML_{a, (t-1)} \quad (\text{eq. 4})$$

where $ML_{(a+1), t}$ and $ML_{a, (t-1)}$ mean lengths of age $a+1$ at time t and age a at time $t-1$, respectively.

The overall growth performance index (ϕ -prime, ϕ') was calculated based on the calculated VBGF parameters (Gallucci and Quinn, 1979):

$$\phi' = \log k + 2 \log L_{\infty} \quad (\text{eq. 5})$$

The mortality rates ($M_{\text{est}} \text{ yr}^{-1}$) were calculated using the updated Pauly_{nlst} estimator (when t_{max} is not available), as recommended by Then *et al.* (2015):

$$M_{\text{est}} = 4.118 K^{0.73} L_{\infty}^{-0.33} \quad (\text{eq. 6})$$

Size and age at maturity

Length at maturity (L_m) was estimated using the following relation established by Froese and Binohlan (2000):

$$\log L_m = 0.8979 * \log L_{\infty} - 0.0782 \quad (\text{eq. 7})$$

Age at first maturity (t_m), the average age at which fish of a given population mature for the first time, is calculated from the length at first maturity L_m following Froese and Binohlan (2000):

$$t_m = t_0 - \ln(1 - L_m / L_{\infty}) / K \quad (\text{eq. 8})$$

Potential life span or longevity (t_{max} , years) or the approximate maximum age that fish of a given population would reach was estimated using the following relation (Froese and Binohlan, 2000):

$$\log t_{\text{max}} = 0.5496 + 0.957 * \log(t_m) \quad (\text{eq. 9})$$

Statistical analysis

All datasets were processed using RStudio: Integrated Development Environment for R (RStudio Team, 2023). Data were normality-distributed after assessment using the Shapiro-Wilks test (Zar, 1999), with homoscedasticity being assumed through Levene's test (Sokal and Rohlf, 1995).

The total length-weight relationship (LWR) for each population was estimated by the least-squares method (Ricker, 1975), based on the logarithmic equation: $\log_{10} W = a + b \log_{10} L$ (cm). We calculated the standard error S_b for the slope (b), and isometric growth was tested by comparing the slope (b) of the log-transformed length-weight regression to the theoretical isometric value of 3. This comparison was performed by one-sample t -test using the equation: $t_s = b - 3 / S_b$ (Zar, 1999). The null hypothesis H_0 : $b = 3$ was tested against the alternative hypothesis H_1 : $b \neq 3$. A significant difference ($p < 0.05$) indicates allometric growth (negative or positive allometry, with $b < 3$ and $b > 3$, respectively), while a non-significant difference suggests isometric growth.

A Generalized Linear Model (GLM) was employed to examine the relationship between the Scaled Mass Index (SMi) and salinity. The analysis utilizes the Gaussian family with a log link function to appropriately modelling the anticipated non-linear relationship (McCullagh and Nelder, 1989). The log link function was selected to account for the positive skewness and heteroscedasticity in the SMi data, thereby providing a more accurate fit (Zuur *et al.*, 2009). In this model, salinity was treated as a continuous predictor variable, while SMi served as the dependent variable. We tested the differences in SMi values among the three populations using a one-way ANOVA followed by the Tukey HSD test for post-hoc comparisons. For comparing back-calculated length, MANOVA was used with length and age as dependent variables and reaches as the independent variable.

For comparing growth curves, we used the Allen's method (Allen, 1976). This method consists of describing growth for the i^{th} group by the linear equation:

$$L_i(t) = a_i + b_i \cdot r^t \quad (\text{eq. 10})$$

where $a = L_{\infty}$, $b = L_{\infty} \cdot e^{k \cdot t_0}$, $r = e^{-k}$, with r as a constant chosen to give

a suitable shape to the growth curves. The advantages of this linear growth equation over the von Bertalanffy equation, are easier analysis and a much simpler interpretation of the differences in the parameters in terms of growth rate and maximum size.

Standard regression techniques can be used to estimate the parameters a_i and b_i and to test for differences between them. Subsequent ANCOVA is used to compare growth curves.

Statistical differences were considered to be significant at $p < 0.05$ (Zar, 1999).

RESULTS

Body length and weight

The mean standard body lengths (SL, mm) of captured *L. lepineyi* were 93.88 ± 26.70 (range: 50.30 to 153.34), 80.27 ± 11.86 (range: 66.70 to 126.80), and 79.87 ± 2.41 mm (range: 72.70 to 83.3), respectively in IR, MG, and SM. The corresponding mean body weights (BW, g) were 20.74 ± 18.87 (range: 3.00–71.70), 10.83 ± 6.04 (range: 6.70–39.80), and 9.23 ± 1.36 (range: 7.30–12.20), respectively. There were no significant differences in both body length and weight among the three populations, due to high individual variability, particularly in IR ($p > 0.05$ in all cases).

Highly significant determination coefficients (r^2 range: 0.942 to 0.992) indicate that log-scaled Length-to-Weight Relationships, LWR (Log W = Log a + b * log SL) are linear in all cases. The assessment of the LWR with locality as a covariate indicated that standard length was a highly significant predictor of body weight (ANCOVA: $F_{1, 142} = 1511.63$, $p < 0.001$). Additionally, the effect of locality on body weight was also significant (ANCOVA: $F_{2, 142} = 21.62$, $p < 0.001$). *Post-hoc* comparisons using Tukey's HSD test indicated that the mean difference in body weight between the localities was significant for the following pairs: SM and IR (Difference in the estimated means of log-transformed body weight (Log BW) between the compared localities, $M_{diff} = -0.093$, $p < 0.001$), and SM and MG ($M_{diff} = -0.072$, $p < 0.001$). However, the difference between MG and IR was not significant ($M_{diff} = -0.021$, $p = 0.386$). This suggests that the LWR in SM is distinct from those observed in IR and MG.

The analysis of slopes 'b' of the log-transformed LWR revealed an isometric relationship between body weight and standard length in the IR locality, where the coefficient for the logarithm of standard length was not statistically different from 3 (t-value = -0.681, $p = 0.501$). However, in MG and SM, the LWRs were negatively allometric with coefficients significantly lower than 3 (MG: t-value = -2.83, $p < 0.001$; SM: t-value = -4.09, $p < 0.0001$). These results indicate a proportional increase in body weight relative to standard length in IR, but a disproportionate growth pattern in MG and SM.

Somatic body condition

A Generalized Linear Model (GLM), applied to the relationship between the scaled-mass index (SMi) and salinity, using a log link function, was highly significant ($F_{1, 7} = 34.95$, $p < 0.001$) (Fig. 3). This indicates that salinity is a good predictor of the body condition through the SMi. The regression equation was: Log (SMi) = $2.86 - 0.074 \times \text{salinity}$. The coefficient for salinity was very significant $\beta = -0.074$ ($t_{7} = -5.91$; $p < 0.001$) suggesting that for each unit increase in salinity, the log-SMi decreases by 0.074 units. This indicates a negative relationship between salinity and the

SMi. The model explained a significant proportion of the variance in the SMi ($r^2 = 0.83$) indicating that 83% of the variability in the SMi can be explained by salinity.

The mean individual SMi, sexes combined, declined from 17.4 in freshwater (salinity 0.5 PSU) to about 10 at salinities higher than a threshold of 4 PSU. The mean values for IR, MG, and SM were respectively 18.8 (SD=1.76, $n=45$), 14.3 (SD=1.31, $n=45$), and 13.2 (SD=1.96, $n=52$). There are highly significant differences among these values (One-way ANOVA: $F_{2, 142} = 150.00$, $p < 0.001$). *Post-hoc* comparisons using the Tukey HSD test indicated that the mean SMi in IR was significantly higher compared to both MG and SM (M_{diff} MG-IR = -4.57, M_{diff} SM-IR = -5.47, $p < 0.001$ in both cases), while there was no significant difference between these latter (M_{diff} MG-SM = 1.09, $p > 0.05$). Nevertheless, we propose different body condition (SMi) percentile categories for the three studied Draa barbel populations: a normal category for IR (13.2 to 38.2), a poor category for MG (9.7 to 13.2), and a very poor category for SM (<9.7) (Tab. 1).

Back-calculated length

The relationship between the standard body length (SL, mm) and the scale radius (R, mm) of *L. lepineyi* fitted to a linear model for the three localities are shown in Tabs. 3, 4, and 5, respectively for IR, MG, and SM. There was a statistically significant difference in back-calculated length and age across localities (MANOVA, $F = 4.341$, $p = 0.0022$). There was a statistically significant effect of locality on back-calculated length (one-way ANOVA: $F = 3.703$, $p = 0.0281$), but a marginally non-significant difference for age among localities (one-way ANOVA: $F = 3.007$, $p = 0.054$). The back-calculated length at annulus formation showed that growth increment (%) in *L. lepineyi* from IR and MG decreased slightly with age (0+ to 3+) from 28.9 to 22.5 and 30.8 to 21.9 (differences of 6.4 and 8.9, respectively). This decrease was much more marked in SM, from a higher value at 0+ (43.5) to a lower value at 3+ (15.7) (a difference of 27.8). The mean length (mm) reached at age 3+ decreased from 132.4 in permanent freshwater (IR) to 120.1 and

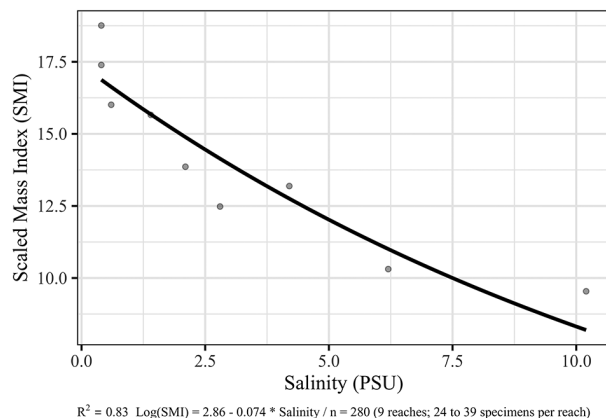


Fig. 3. Generalized Linear Model with Log Link Function of average individual scaled-mass index and water salinity in *Lucio-barbus lepineyi* across an increasing salinity gradient (9 reaches; 280 specimens; 24 to 39 specimens per reach) in the upper-middle Draa river basin, SE Morocco.

82 in intermediate- and high-salinity intermittent waters (MG and SM, respectively).

Growth parameters

The interaction between r^t and locality was highly significant (ANCOVA: $F_{2, 89}=76.124$, $p<0.001$), indicating that the slopes of the regression lines differ significantly among the localities (Fig. 4). Additionally, there were very significant main effects of r^t (ANCOVA: $F_{1, 89}=550.536$, $p<0.001$, and locality (ANCOVA: $F_{2, 89}=74.647$, $p<0.001$). Tukey Honest Significant Difference (HSD) *post-hoc* test indicated that the slope for the locality MG was significantly different from IR (estimate=-16.784, SE=1.665, $t=-10.079$, $p<0.001$). The slope for the locality SM was also significantly different from IR (estimate=-18.362, SE=1.450, $t=-12.662$, $p<0.001$). However, there was no significant difference between the slopes for localities SM and MG (estimate=-1.578, SE=1.590, $t=-0.993$, $p=0.583$). These results suggest that while the relationship (as represented by the slopes of the regression lines) in IR differs significantly from those in MG and SM, the relationships in MG and SM are similar.

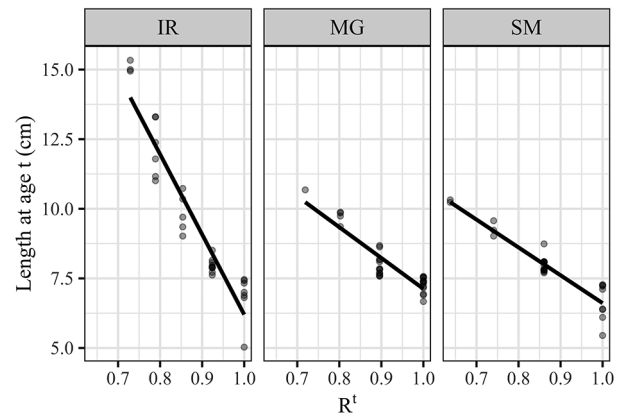


Fig. 4. Observed average lengths and the fitted regression lines (L_t vs r^t with $r=e^{-k}$) for Draa barbel *Luciobarbus lepineyi* from three reaches [Iriri (IR), Mghimima (MG), Sid El Mokhtar (SM)] with different flow regimes and salinities in the arid Draa River basin, SE Morocco.

Tab. 3. Mean back-calculated total lengths at age of *Luciobarbus lepineyi* in Iriri, Draa river basin, SE Morocco, in spring-summer 2021.

Reach: Iriri River (SL=2.49+53.86*R)		Length at age (mm)				N. of fish
Age (years)	0+	1+	2+	3+		
0-1	69.30					10
1-2	40.57	79.52				15
2-3	28.03	68.71	87.56			19
3-4	22.31	68.72	128.78	132.42		1
Mean length (mm)	40.05	72.31	103.17	132.42		N=45
Annual increment (mm)	37.56	32.26	30.85	29.25		
Growth increment (%)	28.9	24.8	23.7	22.5		

Tab. 4. Mean back-calculated total lengths at age of *Luciobarbus lepineyi* in Mghimima, Draa river basin, SE Morocco, in spring-summer 2021.

Reach: Mghimima River (SL=2.61+51.36*R)		Length at age (mm)				N. of fish
Age (years)	0+	1+	2+	3+		
0-1	63.47					9
1-2	36.22	65.84				16
2-3	24.01	45.01	75.08			18
3-4	31.14	69.23	108.61	120.1		2
Mean length (mm)	38.71	67.69	94.34	120.10		N=45
Annual increment (mm)	36.22	28.98	26.65	25.75		
Growth increment (%)	30.8	24.6	22.7	21.9		

Tab. 5. Mean back-calculated total lengths at age of *Luciobarbus lepineyi* in Sid El Mokhtar, Draa river basin, SE Morocco, in spring-summer 2021.

Reach: Sid El Mokhtar River (SL=2.73+49.98*R)		Length at age (mm)				N. of fish
Age (years)	0+	1+	2+	3+		
0-1	57.42					7
1-2	42.62	52.50				16
2-3	25.04	49.84	62.39			25
3-4	21.66	40.94	56.71	82.00		4
Mean length (mm)	35.68	47.76	59.55	82.00		N=52
Annual increment (mm)	34.18	21.09	11.76	12.45		
Growth increment (%)	43.0	26.5	14.8	15.7		

Estimated L_{∞} (mm) of Draa barbels from IR was higher than MG and SM, decreasing with salinity. Reversely, the growth constant rate k (year^{-1}) increased markedly with flow intermittence and salinity being higher in SM, intermediate in MG and lower in IR (Tab. 6 and Fig. 4). In contrast, the corresponding calculated growth performance (ϕ') was relatively lower in SM than in MG and IR (Tab. 6).

The growth index G varied differently among the three populations. It was low in the 1st year and then increased and remained constant in IR; lower in the 1st year and increased regularly with age in MG, and in SM; it was faster in the 1st and 2nd years and increased between 2nd and 3rd years of age (Tab. 6).

Estimated mortality rate and potential longevity

The estimated mortality rate (M , year^{-1}), increased with salinity from 0.18 in IR, to 0.28 in MG and 0.47 in SM. Reversely, estimated potential longevity ($t_{\max}$, years) decreased and was 20.7, 16.03 and 11.53 years, respectively for IR, MG and SM (Tab. 6).

DISCUSSION

The present study is the first one on the life-history traits of the Draa barbel, endemic to the sub-Saharan Draa basin of southern Morocco, under the effect of multiple environmental stressors, more specifically flow intermittency and salinity. As stated above, the main anthropogenic factors causing water intermittency in the studied area were the construction of the Mansour Eddahbi reservoir and water abstraction and derivation for agricultural uses along with the impacts of climate change. As for increased salinity, this was due to intensive groundwater pumping for irrigation combined with water scarcity related to

recurrent drought periods due to climate change impacts (Berger *et al.*, 2021).

As we expected, *L. lepineyi* exhibited a high plasticity in body condition, growth patterns, sexual maturity, mortality rate, and longevity, as an adaptive response to environmental changes (flow intermittency and salinity) in the IRES of the sub-Saharan Draa basin. Salinity and drought stress, combined with other environmental stressors (*e.g.*, hypoxia, hyperthermia, alkalinity, *etc.*) can induce biochemical and histopathological changes in fish (Banan *et al.*, 2020, 2022). This would cause an oxidative stress (*i.e.*, an imbalance of body free radicals and antioxidants that leads to cell damage affecting growth, reproduction and survival of fish) (Menon *et al.*, 2023).

Because LWR and body condition are biometric units that help in understanding the general health and growth trends of the fish population, these investigations are pertinent to the assessment and management of fisheries. Due to their impacts on survival, reproduction, and growth, these quantitative factors influence the success of a population (Richter, 2007). Therefore, they are crucial to fish management and conservation (Sarkar *et al.*, 2008; Muchlisin *et al.*, 2010).

As stated by Beverton and Holt (1957), fish rarely exhibit significant variations from isometric growth. Several authors have reported isometric or allometric (positive or negative) growths for various *Luciobarbus* species from different water bodies cited in Tab. 7. Nevertheless, most authors did not check for isometric statistical differences. Regardless of the sex, each of the studied *L. lepineyi* population had a different LWR. Isometric growth in IR means that there is no change in body shape as fish grow and that weight increases as the third power of length (Riedel *et al.*, 2007). In contrast, the negative allometric type of growth ($b < 3$) in both MG and SM, at respectively intermediate and high salinities, im-

Tab. 6. Growth parameters in terms of von Bertalanffy model (L_{∞} , k , and t_0), annual specific growth index (G), and growth performance (ϕ'), for the Draa barbel, *Luciobarbus lepineyi* in the three localities in Draa river basin, SE Morocco.

Locality	L_{∞} (mm)	K (year^{-1})	t_0 (years)	G 0-1	G 2-3	G 3-4	ϕ'
Iridi	477.2	0.079	-1.13	0.16	0.21	0.22	2.25
Mghimima	260.5	0.110	-1.00	0.09	0.27	-	1.87
Sid El Mokhtar	126.4	0.150	-1.32	0.18	0.27	-	1.38

Tab. 7. Inter- and intra-specific comparisons of the growth constant rate (k , year^{-1}), asymptotic body length (L_{∞} , mm) and relative growth performance (ϕ' , unit^{-1} of body length) among studied barbels of the genus *Luciobarbus*.

Species	Locality	L_{∞} (mm)	K (year^{-1})	ϕ'	Reference
<i>L. callensis</i>	Beni- Haroun Dam, Algeria	473.7	0.200	4.65	Berrouk <i>et al.</i> , 2020
	Oued El-Harrach, Algeria	265.2	0.230	4.21	Morsi, 2015
<i>L. labiosa</i>	Allal El Fassi dam, Morocco	332.5	0.100	4.04	Bouhouch, 2002
<i>L. esocinus</i>	Gamasiah River, Kermanshah, Iran	336.6	0.760	4.94	Hajiahmadian <i>et al.</i> , 2018
	Keban Reservoir, Turkey	229.7	0.035	3.27	Çoban <i>et al.</i> , 2012
<i>L. capito</i>	Shahid Rajaei Reservoir (Sari, Iran)	138.6	0.100	3.28	Naderi Jolodar <i>et al.</i> , 2017
<i>L. xanthopterus</i>	Al-Diwaniya River, Iraq	730.0	0.228	5.08	Mohamed and Al-Jubouri, 2019; 2020
<i>L. vorax</i>	Al-Diwaniya River, Iraq	610.0	0.220	4.91	Mohamed and Al-Jubouri, 2020
<i>L. graellssii</i>	Spain	683.0	0.190	2.95	Froese, 2022
<i>L. lepineyi</i>	Iridi, Draa basin, Morocco	477.2	0.079	2.25	This study
	Mghimima, Draa basin, Morocco	260.5	0.110	1.87	This study
	Sid El Mokhtar, Draa basin, Morocco	126.4	0.150	1.38	This study

plies that the fish becomes slenderer as it increases in body length (Riedel *et al.*, 2007). Inter-population variations in LWR may depend on multiple factors such as sample size, size and shape of fish examined, sex variation, stomach fullness, stage of maturity, parasite loads, disease, environment and season, food abundance and fishing pressure (Riedel *et al.*, 2007). The 'b' value may also depend on the different stages of genetic development and differences in age (Türkmen *et al.*, 2002; Alp *et al.*, 2005).

Wootton (1992) notes that the b value may be used as an indicator of food intake and growth regime, and that many different values are affected by factors like water temperature, food availability, and habitat type. Under salt and flow intermittency and other stressors in MG and SM, Draa barbels might eat less and then grow slower than in IR, where the conditions are more suitable.

The aquatic system (rivers or lakes), seasonal variations, nutritional quality, and other factors can all have an impact on the SMi, which is used to evaluate fish body condition and health under various physiological, climatic, and environmental conditions (Mouludi-Saleh and Eagderi, 2019). According to the current research, the mean SMi of the Draa barbel declined noticeably as the gradient in salinity increased. This makes it a simple and useful biological indicator of the quality of the environment. This is consistent with data obtained on the Butlamai barbel *L. capito* (Güldenstädt, 1773) from the Aral Sea in Uzbekistan, where variations in water salinity caused a salt stress that can impair ongoing biological processes as well as physiological homeostasis if it is not compensated for (Kültz, 2015). A decrease in the condition factor with increasing salinity among reservoirs in Southeast Spain, was also reported for the Andalusian barbel *L. sclateri* (Günther, 1868) Oliva-Paterna *et al.* (2003). The energy cost of osmotic-ionic control, which lowers energy allocated to growth, has been linked to the effect on growth in fish that encounter varying salinities among environments (Brett 1979).

An auximetric (*i.e.*, a double logarithmic) plot of k vs L_{∞} VBGF parameters (Fig. 5) indicated a non-significant linear re-

gression ($r^2=0.096$, $F_{(1, 10)}=1.067$, $p=0.326$) in the different studied of *Luciobarbus* species and populations including *L. lepineyi* (Tab. 7). Growth rate can therefore be considered as independent of body size, allowing for direct intra- and interspecific comparisons. A mere 9.6% of the variation in k among the examined species of *Luciobarbus* barbels is correlated with that in L_{∞} . Thus, more than 90% of the variation would result from a variety of factors, including habitat variations, fish size range variations, the number of individuals tested, fish activities, sex, maturation stage, food availability, and seasonal growth rates (Ricker, 1975; Lowe-McConnell, 1987).

Overall, the growth constant rate (k) for the Draa barbel is relatively low, but it increased from 0.079 to 0.150 from the permanent freshwater (IR) to saline intermittent reaches (MG and SM). This may be explained by the barbels' apparently accelerated growth rate to achieve a minimal size at sexual maturity for reproduction as fast as possible under the restricted conditions in the IRES in order to avoid the hazardous drying-up phase, as evidenced by their respective correspondingly shorter lifespans and higher mortality rates. Water salinity and flow intermittency are known to reduce age at sexual maturity and boost reproductive effort. In this regard, Ferreira *et al.* (2007) have reported that fish in Mediterranean rivers generally mature early and have high fecundity, and that some of them have multiple spawning events. Magalhães *et al.* (2007) suggested that early spawning could potentially mitigate recruitment failures caused by drought. Studying the reproductive life cycle across salinity and flow intermittency gradients is necessary to confirm each of these assertions.

Growth rates (k) of Draa barbel are within the range of those reported for other congeneric species (0.035 - 0.760) (Tab. 7). Such values are comparable to those recorded for *L. labiosa* (Pellegrin, 1920), from the Allal EL Fassi dam, Morocco and *L. capito* from the Shahid Rajaei reservoir, Iran (Naderi Jolodar *et al.*, 2017) ($k=0.100$ for both species). In contrast, and except the lowest value ($k=0.035$) in Mangar or pike barbel *L. esocinus* Hekel, 1843, from the Keban reservoir, Turkey, the growth rate in *L. lepineyi* is lower than those reported for the Algerian barbel *L. callensis* Valenciennes, 1842, from Algeria ($k=0.200$) (Morsi, 2016; Berrouk *et al.*, 2020), Yellowfin barbel *L. xanthopterus* Hekel, 1843, from Iraq (0.228) (Mohamed and Al-Jubouri, 2020), and the exceptionally high value ($k=0.760$) of *L. esocinus* from the Gamasiab River, Kermanshah, Iran (Hajiahmadian *et al.*, 2018) (Tab. 7). Moreover, the three studied populations of *L. lepineyi* showed growth performances ϕ' lower than those reported for other congeneric species (1.37 to 2.13 vs 3.27 to 5.08) (Tab. 7). These differences would be imputed to the higher environmental stress in the desert IRES in the sub-Saharan Draa basin. Nevertheless, and in addition to changes in environmental conditions, those differences could be also imputed to sample size, age determination, genetic features, fishing intensity, food availability and computations (Bajaj, 2017).

The marked decline in growth rate k (year^{-1}), and decrease in growth performance (ϕ') and longevity (t_{max}) in *L. lepineyi* with increasing salinity and flow intermittency, may be explained by the higher energy invested in ion-regulation and osmoregulation as the salinity stress increases. Ahirwal *et al.* (2021) showed that increased salinity had a significant effect on the growth and physiology of the cyprinid Catla *Labeo catla* (Hamilton, 1822), one of the major carps in South Asia. In this regard, Sarma *et al.* (2020) demonstrated, in a 90-day exposure experiment, that Rohu

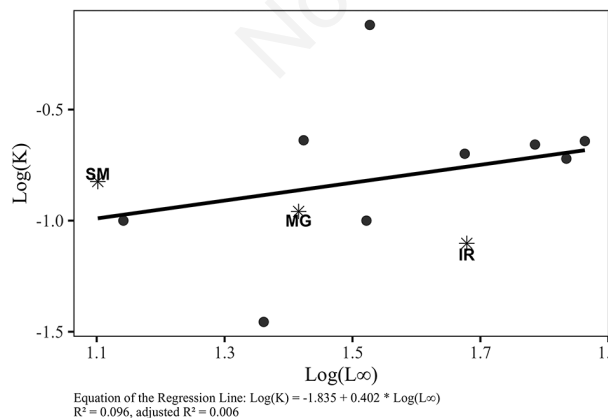


Fig. 5. Log-transformed regression for the relationship between k (year^{-1}) and L_{∞} (cm) in *Luciobarbus lepineyi* in the sub-Saharan Draa basin. The stars indicate the values corresponding to barbel populations from Iriri (IR), Mghimima (MG), and Sid El Mokhtar (SM). The other unspecified points represent published values for other *Luciobarbus* species.

barb *Labeo rohita* (Hamilton, 1822), a large Indian carp, exhibited decreased survival rate, growth rate and level of ascorbic acid in tissues with increased salinity. Reduced ascorbic acid concentration could be due to a high rate of vitamin C utilization at higher salinity levels. Vitamin C could have been used for the detoxification process or to prevent cellular peroxidation, which could have led to a functional decrease in vitamin C content in different tissues, causing possible damage (Sarma *et al.*, 2020, and references therein).

Other factors than salinity alone, could affect these parameters, namely the intermittence that may impact the life cycle of barbels forcing them to grow faster to reach the minimal size at sexual maturity (hence a lower asymptotic size) as quickly as possible before succumbing to drought or migrating to temporary aquatic refugia during the dry season. This was pictured by the increase in mortality rate and reduced longevity with increasing salinity level and flow intermittence.

Clavero (*unpublished data*) reported the occurrence of *L. lepineyi* from over 30 streams (freshwater with salinity <0.06 PSU to saline water at up 16 PSU), but not over 16 PSU in the desert area at the Coude (elbow) of the Draa river. The closely related species Zousfana barbel *L. pallaryi* (Pellegrin, 1919), was exceptionally captured in the arid Ziz river basin, Eastern Morocco, at a salinity of 24 PSU (Clavero, *unpublished data*). In Lake Ichkeul, Tunisia, local conditions were found to be lethal for the closely related Algerian barbels *L. callensis*, in summer; this would explain their seasonal dispersal into Oued Sejnane and the other tributaries. Tolerance in this species increased within a year (between 1984 and 1985) from LC_{50} =15.6 to 17.2 PSU in a population from Oued Mejdah (Kraiem and Pattee, 1988). This has been related to an increased salinity by dissolution of rock salt in the Sidi Salem reservoir. Algerian barbels were indeed present in the lake Ichkeul from November to July when salinity is low (14–43 PSU). They leave the lake when its salinity exceeds (43 PSU) and they never occur there from August to October when salinity reaches 57 PSU (Kraiem, 1986). This author showed that the fish from Oued Mejdah, Tunisia, started dying at a salinity of 15 PSU, but that those from the Ichkeul complex survived a salinity level of 15 PSU, mortality only appearing at 16 PSU. Consequently, barbels seem to remain in the lake as long as their acute tolerance to salinity allows them to survive. Salinity tolerance in *L. lepineyi* has not been investigated yet, but according to our extensive sampling and those of Clavero *et al.* (2015), this species could be comparable to its conspecific *L. callensis*. However, experimental exposures to increasing salinity are required to confirm this presumed similar physiological tolerance. Histological and physiological investigations are required to understand the processes behind this high tolerance to salinity.

When fish are forced to deal with different salinities, depending on marine or freshwater fish, they spend more energy to hold their osmotic homeostasis (by holding sodium and chloride ions in their bodies or take them off) and then grow less. In this regard, Geng *et al.* (2016) showed in the *L. capito* from Aral sea, that the plasma osmolality ranged from 280 to 457 mOsm. Thus, *L. capito* was considered as a euryhaline fish because its plasma osmolality varied between freshwater and those of marine teleost fishes; this could also explain the decrease in body condition and growth in the Draa barbell across the salinity gradient. When a bony fish enters a high-salinity water, osmotic adjustment typically occurs in two stages. First, passive water loss increases osmolality due to a

relative increase in plasma ion concentrations. Next, the activity of the Na^+/K^+ -ATPase enzyme in the gill threads increases, ion release mechanisms are activated, and the osmotic pressure gradually decreases and eventually levels off. In *L. capito*, the osmolality in the plasma initially increased normally with increasing salinity in the water, but gradually decreased and never stabilized. Therefore, changes in plasma osmolality in *L. capito* are a response to the external hypertonic environment. Whether this is a unique response of this species to saline and alkaline water requires further investigations, including in *L. lepineyi*. Geng *et al.* (2016) showed also that urea complemented other osmolality-regulating ions and improved the osmoregulation ability of *L. capito* in alkaline brine waters, thereby increasing its compatibility with saline-alkaline water. This could also be the case of *L. lepineyi* in brackish-alkaline waters of the middle-lower Draa basin, but *in situ* investigations along with experimental exposures are needed.

CONCLUSIONS

Luciobarbus lepineyi revealed a very plastic species with a broad salinity niche (euryhalinity). Individuals in highly intermittent and salinised reaches in the arid Draa river basin, are smaller and lighter and show a poor body condition, compared to those in freshwater/brackish streams with permanent flow and lower salinity. They compensate for high mortality by faster growth rate, but lower growth performance, earlier sexual maturity and reduced longevity. Because life-history traits are influenced by extreme conditions including flow intermittency and high anthropogenic salinisation and are critical in determining the population growth rate, they may be used as indices of population viability. Given its high life-history plasticity, Draa barbel would represent a good ecological indicator, based on simple measurements of body size and weight and life-history traits. It could be a suitable sentinel species of the quality (in terms of salinisation) of aquatic environments of the arid Draa basin.

Our findings might also constitute a prerequisite for supporting conservation strategies aimed at: i) preserving freshwater ecosystems, for instance, by maintaining minimum vital flows and natural local variability flows (*i.e.*, ecological flows), taking into account the intermittent flow regime of the studied streams, as well as by improving the water quality of the salinised streams; ii) conserving the biodiversity of native fish through the restoration of IRES and the prohibition of any restocking programs in the dry season “refugia”; and iii) controlling invasive species such as the syntopic competitor Pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758), through eradication programs.

ACKNOWLEDGEMENTS

This study was carried out under the scientific permit number 546/DEF/DLCPN, Morocco. It was funded in the framework of the collaborative project SaliDraa Juj ‘Salt in the System’ (BMBF-2019-2025 Germany-Morocco). We are indebted to M. Clavero for revising a first draft of the manuscript. We are also very grateful to H. Benaissa, E. Benlasri, K. Lazrak, and S. Mamouli, for their excellent assistance during the fieldwork. We also thanks C. Fouilloux for English revision. Our thanks go to M. and B. Lahni for the transportation and organization of the field trips.

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