Journal of Agricultural, Food and Environmental Sciences Vol 79 No 1 (2025) 1-9
DOI:

CHANGES IN THE GENETIC STRUCTURE OF BROWN TROUT (*Salmo trutta* Linnaeus, 1758) CAUSED BY INTENSIVE STOCKING IN THE UPPER COURSE OF THE NERETVA RIVER

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ABSTRACT

Brown trout (*Salmo trutta* Linnaeus, 1758) populations in Mediterranean river systems are characterized by high genetic structuring and local adaptation, making them particularly vulnerable to anthropogenic disturbance. This study assessed changes in the genetic structure of brown trout populations in the upper course of the Neretva River (Adriatic basin, Bosnia and Herzegovina) in relation to long-term stocking practices. Wild riverine populations were sampled at four natural sites and analyzed using mitochondrial DNA control-region markers and a nuclear LDH-C1 locus, complemented by morphometric and meristic analyses. Molecular results revealed a high proportion of autochthonous Adriatic-lineage individuals (≈90%) at all sites, indicating that native genetic integrity is still largely preserved. However, the consistent presence of Adriatic–Atlantic hybrid genotypes (≈10%) across all localities provides clear evidence of introgression from non-native lineages, most likely resulting from historical, non-selective stocking. Morphometric traits showed extensive overlap between genetic groups and proved unreliable for discriminating native and non-native individuals in wild populations, reflecting strong phenotypic plasticity. In contrast, selected meristic traits, particularly the ratio of red to black lateral spots, demonstrated meaningful diagnostic potential when combined with genetic data. Overall, the findings highlight both the conservation value and the genetic vulnerability of brown trout populations in the upper Neretva River and emphasize the need for genetically informed management, including the cessation of stocking with non-native lineages and the implementation of long-term genetic monitoring.

Keywords: brown trout; genetic introgression; stocking; Adriatic lineage

INTRODUCTION

Genetics plays a fundamental role in understanding the biology, evolution, and conservation of fish populations. Genetic diversity within and among populations determines their evolutionary potential, adaptive capacity, and long-term persistence under changing environmental conditions (Frankham et al., 2010; Allendorf et al., 2013). In freshwater fishes, genetic processes are particularly important because river systems are naturally fragmented, and populations are often structured along longitudinal gradients, shaped by hydrology, geomorphology, and historical connectivity (Ward et al., 2002; Hughes et al., 2009). Freshwater fish populations often exhibit lower genetic diversity than marine species due to smaller effective population sizes, limited dispersal, and frequent population bottlenecks (DeWoody & Avise, 2000; Waples et al., 2008). These effects are especially pronounced in endemic and range-restricted species, such as many salmonids and cyprinids inhabiting Mediterranean and Dinaric karst rivers (Crivelli, 1995; Freyhof and Brooks, 2011). Brown trout (*Salmo trutta* Linnaeus, 1758) is among the most genetically diverse freshwater fish species, exhibiting pronounced population structuring, strong local adaptation, and deep phylogeographic subdivision across its range (Bernatchez 2001, Laikre et al. 2005, Allendorf et al. 2013). This diversity is particularly evident in Mediterranean river systems, where long-term isolation, complex karst hydrology, and limited natural connectivity have promoted the persistence of genetically distinct lineages and locally adapted populations (Bianco 1998, Crivelli 1995, Freyhof and Brooks 2011). Previous studies have shown that brown trout populations in the Adriatic drainage are characterized by high genetic differentiation and limited effective population sizes, making them particularly vulnerable to genetic disturbance (Bernatchez 2001, Laikre et al. 2005).

Among anthropogenic pressures, stocking and restocking practices are widely recognized as one of the most significant threats to the genetic integrity of wild brown trout populations (Aprahamian et al. 2003, Araki and Schmid 2010, Laikre et al. 2010). Although stocking has historically been used to enhance fisheries and compensate for population declines, numerous studies have demonstrated that the introduction of hatchery-reared fish – often derived from non-native or genetically divergent lineages, leads to introgressive hybridization, loss of locally adapted alleles, reduced fitness, and long-term erosion of population genetic structure (Hansen et al. 2009, Laikre et al. 2010, Allendorf et al. 2013). In Mediterranean river systems, stocking has frequently involved the release of Atlantic brown trout strains into native Mediterranean lineages, resulting in widespread genetic admixture and homogenization of formerly distinct populations (Guyomard 1989, Laikre et al. 2005, Caudron et al. 2006). Such genetic homogenization undermines evolutionary distinctiveness and reduces the adaptive potential of native populations, particularly in environmentally heterogeneous and hydrologically dynamic systems (Fraser 2008, Frankham et al. 2010). In the Neretva River, intensive stocking of brown trout has been conducted for decades, primarily to support recreational fisheries and mitigate population declines caused by habitat alteration, river regulation, and hydroelectric development (Škrijelj 2002, Muhamedagić, 2019). However, despite the ecological and conservation importance of the basin, the genetic consequences of these long-term stocking practices remain insufficiently documented. Given the high level of endemism and the evolutionary significance of native Adriatic brown trout lineages, evaluating changes in genetic structure caused by stocking is essential for defining effective conservation and management strategies.

The aim of the present study is therefore to assess changes in the genetic structure of brown trout populations in the upper course of the Neretva River in relation to stocking activities, with particular emphasis on genetic introgression, loss of native genetic integrity, and implications for the conservation of indigenous Mediterranean lineages.

MATERIALS AND METHODS

The study was conducted in the upper course of the Neretva River (Adriatic Sea basin, Bosnia and Herzegovina), covering natural river sections and tributaries inhabited by wild populations of brown trout (*Salmo trutta* Linnaeus, 1758). The investigated river section extends from the source of the Neretva below the Gredelj massif to the upstream limit of the Jablaničko lake reservoir, including selected tributaries characterized by cold, fast, oligotrophic conditions typical of Dinaric karst systems.

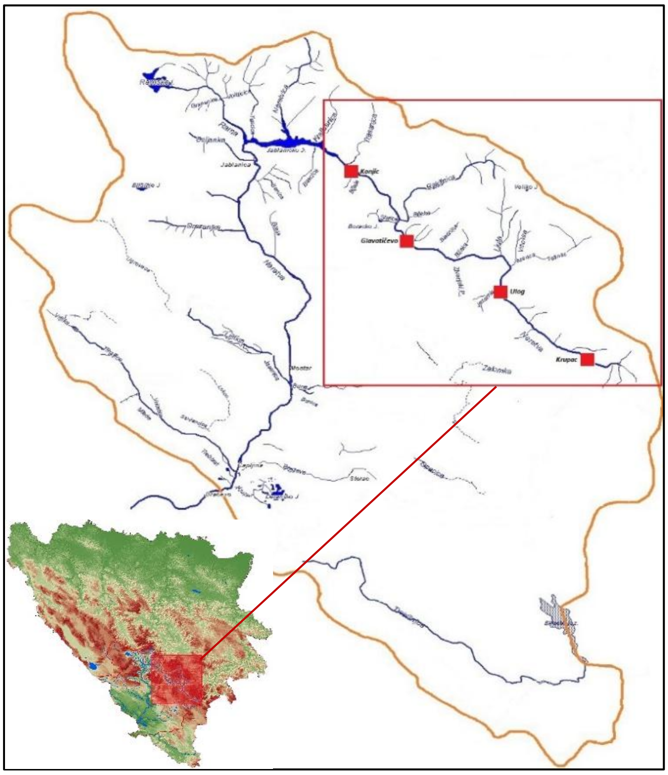

Figure 1. Study area - upper course of the Neretva River

The upper course of the Neretva river is geomor-phologically heteroge-neous and includes steep headwaters, canyon sec-tions and the alluvial valley of the parish, providing a mosaic of salmonid habitats with high ecological integri-ty. Sampling sites were selected to represent different hydromorpho-logical units, avoiding areas influenced by reservoirs or natural lakes. For analytical clarity, the study area was subdivided into three riverine sections following established geomorphological crite-ria (Huet 1959, Illies and Botosaneanu 1963, Crivelli et al. 1997): 1) source region – steep-gradient, high-altitude mountain river section with strong erosional dynamics; 2) parish region – submontane reach with reduced slope, increased habitat heterogeneity, and partial floodplain development; and 3) Konjic valley region – widened valley section immediately upstream of the reservoir influence zone. A natural longitudinal barrier, the Treskavac waterfall, separates the source region from the parish region and represents an important constraint on upstream gene flow. Fish samples were collected at four river locations, each assigned a unique location code (L1-L4) and an individual number for genetic analyses. All locations represent natural river habitats (Table 1).

Table 1. Basic geographical characteristics of the site and physical-chemical parameters of the water

Site				Physical and chemical parameters			
Name	Code	Coordinates	Altitude (m)	T (°C)	O_2 (mg/l)	pH	Conduct. (µS/cm)
Krupac	L1	43°19'21.1" N 18°25'45.1" E	810	14,2	10,4	7,6	245
Ulog	L2	43°24'59.3" N 18°18'48.2" E	659	13,8	10,7	7,5	270
Glavatičevo	L3	43°30'11.9" N 18°06'24.1" E	354	11,8	10,5	8,2	298
Konjic	L4	43°38'47.8" N 17°57'53.0" E	320	12,4	10,2	9,8	322

Brown trout were collected by backpack electrofishing using pulsed DC current (Honda OHV 5.5; 3.0 kW), following standardized multi-pass procedures to minimize sampling bias (Bohlin et al. 1989). Sampling was conducted during low-flow periods to reduce variability in capture probability. After capture, fish were anesthetized using MS-222 (tricaine methanesulfonate) solution. Anesthetized fish samples were processed in the field and then returned to their native habitat. Morphometric measurements were obtained with an accuracy of 1 mm for body length and 1 g for body weight. Identification and determination of fish was performed according to Vuković (1977) and Kottelat and Freyhof (2007). Fin clips were taken from live individuals and preserved in 96% ethanol for subsequent genetic analyses. Fish were released immediately after sampling. Only a limited number of specimens were euthanized using an overdose of MS-222 when required for reference analyses, in accordance with ethical guidelines.

Morphological characterization included a set of standard morphometric measurements (total length, standard length, body depth, head length, head depth, caudal peduncle length, eye diameter, and body mass) as well as selected qualitative markers traditionally associated with lineage differentiation in brown trout (e.g. parr marks, preopercular spot). Measurements were taken following established salmonid protocols to minimize observer bias.

Genetic structure was assessed using mitochondrial DNA (mtDNA) control region markers and a nuclear lactate dehydrogenase (LDH-C1) locus, widely applied in brown trout phylogeographic studies. These markers allowed discrimination between Adriatic (native), Atlantic, and Danubian lineages, as well as detection of hybrid individuals. PCR amplification and restriction fragment length polymorphism (RFLP) analyses followed standardized laboratory procedures.

Differences between genetic groups were evaluated using univariate and multivariate statistical approaches. Morphometric data were analyzed using analysis of variance (ANOVA) and post-hoc tests, while multivariate structure was explored using ordination techniques. The relationship between morphological traits and genetic lineage assignment was further assessed using ROC curve analyses.

3. Results and discussion

The application of molecular genetic markers targeting the mitochondrial DNA (mtDNA) control region (restriction enzymes *AluI* and *SatI*) and the nuclear genome (*LDH* locus) revealed a high proportion of autochthonous Adriatic-lineage (*Ad*) brown trout (*Salmo trutta*) in all investigated wild riverine populations of the upper Neretva River. At each sampled locality, 90% of individuals were classified as autochthonous, while 10% represented hybrid genotypes (Table 1).

Tabela 1. Frequency of mtDNA haplotypes and LDH genotypes

Site code	N	mtDNK		nuclear DNA				Ratio of autochthonous to allochthonous individuals		
		Ad	*Ne-Ad*	*Da*	*At*	*Ad/At*	*Da/At*	autoch.	alloch.	% auto.
L1	20	20	0	0	0	2	0	18	2	90%
L2	20	20	0	0	0	2	0	18	2	90%
L3	20	20	0	0	0	2	0	18	2	90%
L4	20	20	0	0	0	2	0	18	2	90%

The consistent detection of Adriatic × Atlantic (*Ad/At*) hybrids across all localities is of particular conservation concern. Although the majority of the gene pool remains autochthonous, the presence of hybrids, even at relatively low frequencies, indicates ongoing introgression of non-native genetic material, which may progressively erode the genetic integrity of native populations over time (Berrebi 2000, Cagigas et al. 1999, Laikre and Ryman 1996). The exclusive occurrence of *Ad/At* hybrids strongly suggests historical or ongoing stocking with Atlantic-lineage brown trout, most likely through non-selective restocking practices. This interpretation is consistent with earlier findings by Razpet et al. (2007), who documented Atlantic mtDNA haplotypes in several populations of the upper Neretva River, and detected interspecific hybrids between brown trout and softmouth trout (*Salmo obtusirostris*). Razpet (2004) further estimated that the proportion of introduced non-native nuclear genetic material in native Neretva brown trout populations likely exceeds 19.8%, based on the presence of Atlantic (*At*) and Danubian (*Da*) haplotypes. In addition to stocking, river fragmentation caused by hydropower dams must be considered a key driver shaping genetic structure. Studies on softmouth trout in the Neretva River demonstrated that physical barriers significantly reduce gene flow and genetic diversity between upper and middle river sections (Pojskić 2005, Durmić-Pašić 2008). Similar mechanisms are expected to operate in brown trout populations, where restricted migration and isolation may lead to divergent genetic trajectories and reduced long-term evolutionary potential (Aprahamian et al. 2003, Freyhof and Brooks 2011).

Brown trout is well known for its pronounced phenotypic plasticity, often developing locally adapted morphological forms in response to environmental heterogeneity, even at micro-spatial scales (Ferguson 1989, Elliott 1994). In this study, eight morphometric traits were analyzed to assess their potential for distinguishing autochthonous from allochthonous individuals in wild populations.

Table 2. Summary of morphometric statistics

Morphometric trait	Mean	Max.	Min.	SD	SE
Total length (TL)	22.7	37.9	14.8	5.0	0.56
Standard length (SL)	20.3	34.1	13.2	4.8	0.51
Body depth (BD)	5.0	11.5	3.1	1.5	0.15
Head length (HL)	4.4	8.3	3.0	1.1	0.12
Head depth (HD)	3.4	5.5	2.2	0.8	0.08
Caudal peduncle length (CPL)	3.5	5.7	2.2	0.8	0.08
Eye diameter (ED)	0.9	1.4	0.6	0.1	0.01
Body mass (BM)	162.8	781.0	35.7	151.2	15.30

Univariate statistical analyses (*t-tests*) indicated no consistent and reliable differentiation between autochthonous and allochthonous individuals across the examined morphometric parameters (total length, standard length, body depth, head length, head depth, caudal peduncle length, eye diameter, and body mass; Table 3).

Table 3. Comparisons of selected morphometric parameters between autochthonous and allochthonous groups

Multivariate analyses further supported these findings. MANOVA and NPMANOVA tests revealed no statistically significant overall separation between autochthonous and allochthonous groups when all morphometric traits were considered jointly (Wilks' $\lambda = 0.8235$, $P = 0.07$; NPMANOVA $P = 0.384$). Non-metric multidimensional scaling (nMDS) likewise showed extensive overlap between groups.

Trait	Group	Mean	SD	SE	t	P-value
TL	autochth.	35.4100	7.8253	1.0102	9.865	0.000
	allochth.	23.7778	6.3199	0.6081		
SL	autochth.	32.3833	7.7113	0.9955	9.583	0.000
	allochth.	21.3824	5.9396	0.5715		
BD	autochth.	9.7233	10.7560	1.3886	3.199	0.002
	allochth.	5.2546	1.5928	0.1533		
HL	autochth.	6.8750	1.5858	0.2047	9.244	0.000
	allochth.	4.6361	1.3451	0.1294		
HD	autochth.	6.2783	4.8135	0.6214	4.285	0.000
	allochth.	3.5843	0.9971	0.09595		
CPL	autochth.	5.2917	0.9713	0.1254	10.295	0.000
	allochth.	3.6778	0.9776	0.09407		
ED	autochth.	1.0750	0.1612	0.02081	6.709	0.000
	allochth.	0.9000	0.1635	0.01573		
BM	autochth.	544.8067	325.4682	42.0178	7.422	0.000
	allochth.	202.0176	199.2219	19.1701		

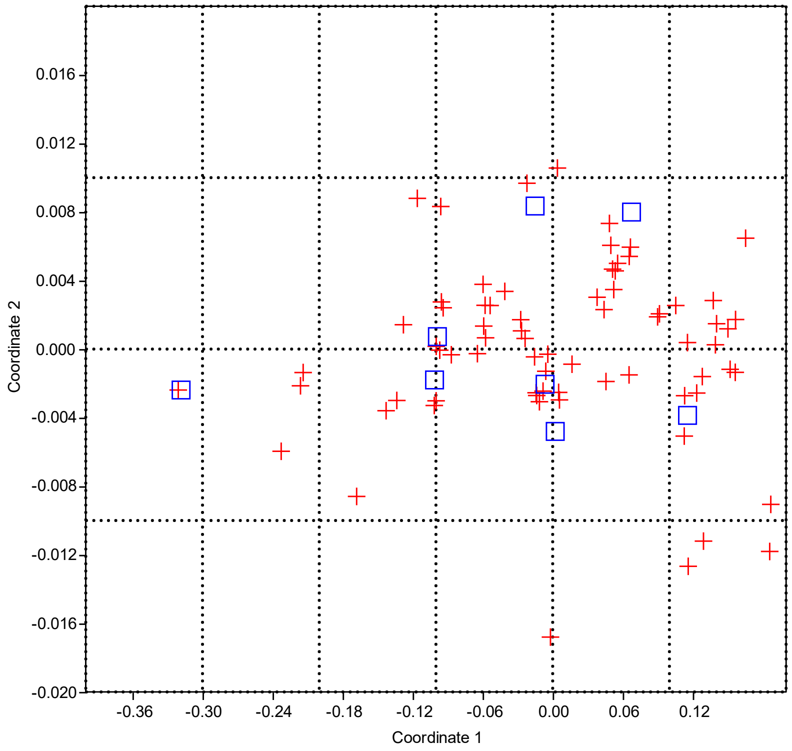

Figure 1. *Non-metric multidimensional scaling* (*nMDS*) ordination of morphometric traits: autochthonous (red) and allochthonous individals (blue)

These results indicate that, under natural riverine conditions, environmental effects override genetic background in shaping external morphology. Unlike hatchery populations – where environmental variation is minimized and genetic differences may be more readily expressed, wild trout experience heterogeneous ecological pressures, leading to convergence in phenotypic traits (Elliott 1994, Berrebi 2000). Consequently, classical morphometric markers alone are insufficient for reliable discrimination between native and non-native trout in wild populations. The presence of a dark preopercular spot behind the eye has previously been proposed as a phenotypic indicator of autochthonous Adriatic-lineage brown trout (Skaala et al. 1996; Aparicio et al. 2005). In the present study, agreement between the occurrence of this spot and molecularly determined autochthony was assessed using Cohen's Kappa statistics. Kappa tests indicated good to very good agreement between the presence of the preopercular spot and Adriatic mtDNA haplotypes ($K = 0.699–0.822$, $P < 0.001$), particularly when hybrid individuals were excluded. Fisher's exact test further confirmed a highly significant association between molecular autochthony and the presence of the spot ($P < 10^{-9}$). Despite this strong association, the marker is not fully diagnostic, as the spot was also observed in a subset of hybrid and non-Adriatic individuals (~16%). This limitation underscores the risk of relying solely on single phenotypic traits for conservation decisions, especially in systems affected by introgression.

The ratio of red to black lateral spots emerged as a more powerful meristic discriminator. While no significant differences were detected in the total number of spots, or in the number of red or black spots separately, the red-to-black spot ratio differed significantly between autochthonous and allochthonous groups ($t = 5.252$, $P < 0.001$).

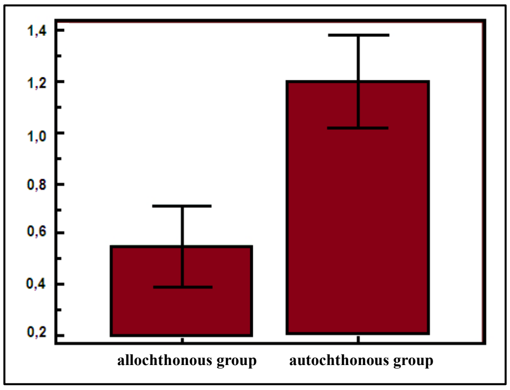

Figure 2. Comparative distribution of red-to-black spot ratios

Autochthonous individuals exhibited a higher mean ratio (≈ 1.2) compared to allochthonous individuals (≈ 0.55), indicating a relative dominance of red spots in native trout. ROC analysis confirmed the discriminatory potential of this parameter, with AUC values between 0.76 and 0.84, depending on dataset composition. A cut-off value of > 0.3586 provided high sensitivity (≈ 90%) and moderate specificity (≈ 52–66%), supporting its practical utility for rapid field-based screening, especially when combined with genetic analyses.

Overall, the results demonstrate that native Adriatic-lineage brown trout populations in the upper Neretva River remain largely intact, but are already affected by measurable introgression from non-native lineages. Morphometric traits alone are insufficient for reliable discrimination in wild populations, whereas selected meristic traits – particularly the red-to-black spot ratio, show promising diagnostic potential.

From a conservation perspective, these findings emphasize the urgent need for genetically informed management, including the cessation of non-selective stocking, the use of locally sourced broodstock, and the preservation of longitudinal connectivity where possible. Without such measures, continued introgression and fragmentation may irreversibly compromise one of the most valuable endemic salmonid gene pools in the Adriatic basin (Freyhof et al. 2014, Aprahamian et al. 2003).

CONCLUSION

The results of this study indicate that brown trout (*Salmo trutta* Linnaeus, 1758) populations in the upper Neretva River still largely retain the genetic characteristics of the native Adriatic lineage, with approximately 90% autochthonous individuals across all investigated sites. However, the consistent presence of Adriatic-Atlantic hybrids demonstrates that these populations are already affected by genetic introgression, most likely as a consequence of long-term, non-selective stocking practices. Morphometric traits proved unreliable for distinguishing genetic origin in wild populations, reflecting the pronounced phenotypic plasticity of brown trout and the strong influence of environmental conditions. In contrast, selected meristic traits—particularly the ratio of red to black spots—showed diagnostic potential and may support rapid field assessments when combined with molecular analyses. Overall, the findings highlight the urgent need for genetically informed management, including the cessation of stocking with non-native lineages, the use of local broodstock, and the implementation of long-term genetic monitoring to preserve the evolutionary integrity of native brown trout populations in the upper Neretva River.

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