Biological and Fishery Characteristics of the European Eel in Freshwater and Brackish-water Habitats of the Neretva Estuary and Adjacent Eastern Adriatic Coast

Biološke i ribolovne karakteristike europske jegulje (Anguilla anguilla) u slatkovodnim i bočatim staništima delte Neretve te istočnog Jadrana

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Abstract

The European eel, *Anguilla anguilla* (Linnaeus, 1758), is listed as Critically Endangered on the IUCN Red List, whereas habitat-specific biological and fishery data remain limited for the eastern Adriatic. Seasonal sampling was conducted from September 2023 to July 2024 in freshwater habitats of the Neretva River Basin and in adjacent brackish coastal habitats. A total of 132 eels were examined, including 54 from freshwater and 78 from brackish habitats. Freshwater eels were larger, heavier and older than brackish eels, but these differences mainly reflected differences in age structure and body-size composition. Length-weight relationships showed statistically significant positive allometric scaling in both habitat groups (b = 3.280–3.430; 95% confidence intervals excluded 3). The highest freshwater abundance index occurred in the Mala Neretva River (143.75 individuals/ha), whereas the highest freshwater biomass index occurred in the main Neretva River (28.13 kg/ha). Parila Lagoon had the highest brackish-water indices (1.375 individuals/trap-day and 0.183 kg/trap-day). Fulton's condition factor and length-adjusted weight did not differ significantly between habitat groups. Site-level temperature and salinity described the freshwater–brackish habitat contrast but did not independently explain eel size, age or condition in the exploratory site-level analysis. The study area therefore supports complementary habitat functions for eels: riverine freshwater habitats retain older and larger females, whereas shallow brackish lagoons support high seasonal catches of generally younger eels and serve as feeding, transitional and migration habitats.

KEY WORDS

Anguilla anguilla
Neretva River estuary
length-weight relationship
eel traps
electrofishing
Croatia

Sažetak

Europska jegulja, Anguilla anguilla (Linnaeus, 1758), uvrštena je na IUCN-ov Crveni popis (listu) kao kritično ugrožena vrsta, dok su podaci o biološkim i ribolovnim značajkama za istočni Jadran i dalje ograničeni. Sezonsko uzorkovanje provedeno je od rujna 2023. do srpnja 2024. u slatkovodnim staništima slijeva rijeke Neretve i u pripadajućim bočatim obalnim staništima. Ukupno su pregledane 132 jedinke jegulje, od čega 54 iz slatkovodnih i 78 iz bočatih staništa. Jegulje iz slatkovodnih staništa bile su veće, teže i starije od onih iz bočatih staništa, no te su razlike uglavnom odražavale razlike u dobnoj strukturi i veličinskom sastavu. Odnosi duljine i mase pokazali su statistički značajno pozitivno alometrijsko povećanje u objema skupinama staništa (b = 3,280 – 3,430; 95%-tni intervali pouzdanosti isključivali su vrijednost 3). Najveći indeks brojnosti u slatkovodnim staništima zabilježen je u Maloj Neretvi (143,75 jedinki/ha), dok je najveći indeks biomase u slatkovodnim staništima zabilježen u glavnom toku Neretve (28,13 kg/ha). Laguna Parila imala je najveće indekse u bočatim staništima (1,375 jedinki/vrša-dan i 0,183 kg/vrša-dan). Fultonov koeficijent kondicije i duljini prilagođena masa nisu se značajno razlikovali između stanišnih skupina. Temperatura i salinitet na razini postaja opisali su kontrast između slatkovodnih i bočatih staništa, ali nisu samostalno objašnjavali veličinu, dob ili kondiciju jegulja u eksploratornoj analizi na razini postaja. Istraživano područje stoga podupire komplementarne stanišne funkcije za jegulje: riječna slatkovodna staništa zadržavaju starije i veće ženke, dok plitke bočate lagune podupiru visoki sezonski ulov općenito mlađih jedinki te služe kao hranilišta te prijelazna i migracijska staništa.

KLJUČNE RIJEČI

Anguilla anguilla
delta Neretve
odnos duljine i mase
vrše za jegulje
elektroribolov
Hrvatska

* Corresponding author

1. INTRODUCTION / *Uvod*

The European eel, *Anguilla anguilla* (Linnaeus, 1758), is a catadromous species with a complex life cycle that includes oceanic leptocephalus larvae, recruiting glass eels and elvers, a continental yellow-eel growth phase spanning freshwater, transitional and coastal habitats, and a silver-eel spawning migration to the Sargasso Sea. This life history means that local stock structure reflects both broad-scale oceanic recruitment processes and local habitat quality, connectivity, salinity regime, fishing pressure and anthropogenic mortality [1].

The European eel is listed as Critically Endangered on the IUCN Red List [2]. Management is governed by a combination of European Union (EU) regulations, regional multiannual measures and national eel management plans. European eel management in the EU is primarily based on Council Regulation (EC) No. 1100/2007, which established measures for stock recovery and required Member States to prepare and implement Eel Management Plans aimed at achieving the target level of silver-eel escapement to the sea [3]. In the Mediterranean region, the General Fisheries Commission for the Mediterranean (GFCM) established a long-term regional framework aimed at reducing fishing mortality, extending closure periods, improving monitoring and traceability, and coordinating conservation across habitats and life stages (Recommendations GFCM/46/2023/16 and GFCM/47/2024/1) [4,5]. ICES advice has repeatedly emphasised the need to minimise all anthropogenic mortality while restoring habitat quantity, quality and connectivity [6,7]. These broad European objectives are difficult to implement without local data on eel size and age structure, habitat use, fishery indices and environmental context.

The Mediterranean component of the European eel range is particularly relevant because many productive eel habitats are shallow coastal lagoons, estuaries and river deltas. Long-term analyses of Mediterranean lagoon fisheries have shown strong declines in eel yields over several decades, with the decline beginning around the mid-1970s [8]. The GFCM European eel research programme further underlined that Mediterranean eel management requires harmonised data collection, standardised catch and effort information, and better integration of lagoon, estuarine and riverine habitats [9]. Recent studies from Mediterranean lagoons also show that silver-eel escapement and glass-eel entry are strongly shaped by hydrology, water exchange, timing and local environmental conditions [10-12].

Recent regional studies from the eastern and central Mediterranean further show that eel population status and habitat function are strongly area-specific. In Türkiye, analysis of official catch data for 2019–2023 showed divergent trends among Eel Management Areas, including a marked decline in one area and more stable catches in others [13]. In Italy, studies from Sardinian rivers and coastal lagoons and from the Comacchio Lagoon have shown that growth, otolith characteristics and length-weight relationships vary between riverine and lagoon habitats and between yellow- and silver-eel life stages [14,15]. These systems provide relevant comparisons because they combine Mediterranean riverine and lagoon habitats, salinity gradients and gear-dependent sampling structures similar to those occurring along the eastern Adriatic coast.

Historically, the Neretva estuary has been the most important eel fishery area on the eastern Adriatic coast. Historical analyses report much higher silver-eel catches before major habitat transformation, followed by a strong decline associated with wetland and lagoon reclamation and, more recently, pressures from recreational fishing, market demand and invasive species [16-18]. Earlier work analysed catches at Parila Lagoon and the Baćina Lakes outlet using traditional fishing gear (small and large fyke nets) and showed both the low efficiency of the gear used and contrasting length-weight patterns between freshwater and brackish habitats [19]. Studies from other Croatian karstic rivers provide additional reference values for length-weight relationships and CPUE in the eastern Adriatic [20,21].

A recent study by Glamuzina et al. [22] provides the closest broader reference for the present study. That study analysed 678 eels from 23 Croatian coastal locations and distinguished between freshwater and brackish components, reporting age ranges of 1–13 years in freshwater and 1–8 years in brackish habitats, a higher freshwater length-weight exponent, and different growth patterns along the freshwater–brackish gradient.

The objective of this study was to provide a biological and fishery analysis of eels in different habitats under specific local conditions. The six sampling sites belong to the Neretva Eel River Basin (ERB: N), which forms part of the Eastern Adriatic Eel Management Unit (EMU: EA), an administrative eel management area that includes the geographical Neretva River Basin in Croatia and adjacent eastern Adriatic coastal habitats. Specifically, the study compared freshwater and brackish eel samples, standardised fishery indices, length-weight relationships, condition, sex and age structure, and site-level temperature and salinity. We hypothesised that freshwater samples would contain larger, older and more female-biased eels because of longer residence in riverine growth habitats, whereas brackish trap samples would contain a greater proportion of younger and intermediate-sized eels. We further expected that raw weight differences would weaken after adjustment for total length and that condition factor would show no strong independent habitat effect.

2. MATERIALS AND METHODS / *Materijali i metode*

2.1. Study area / *Područje istraživanja*

Sampling was conducted seasonally in September and December 2023 and in March and June 2024, with field and laboratory processing completed by July 2024. Sites were selected within the national eel monitoring design to represent major freshwater and brackish-water habitats. Freshwater habitats comprised Baćinska Lakes (BAĆ), the main Neretva River channel (NER) and the Mala Neretva River (MNE). Brackish habitats comprised Parila Lagoon (PAR), Ston Lagoon (STN) and Ombla Estuary (OMB) (Fig. 1). Geographic coordinates and detailed habitat descriptors are provided in Supplementary Table S1. Temperature, salinity and depth were measured during each of the four seasonal field surveys using a YSI 850 multiparameter probe (YSI Inc., Yellow Springs, Ohio, USA), and the arithmetic mean of these four measurements was calculated for each site.

2.2. Sampling design / *Plan uzorkovanja*

Electrofishing was conducted using a Susan 1030SMP Ultrasonic Inverter Electro Fisher (Canglan Technology, Guangdong,

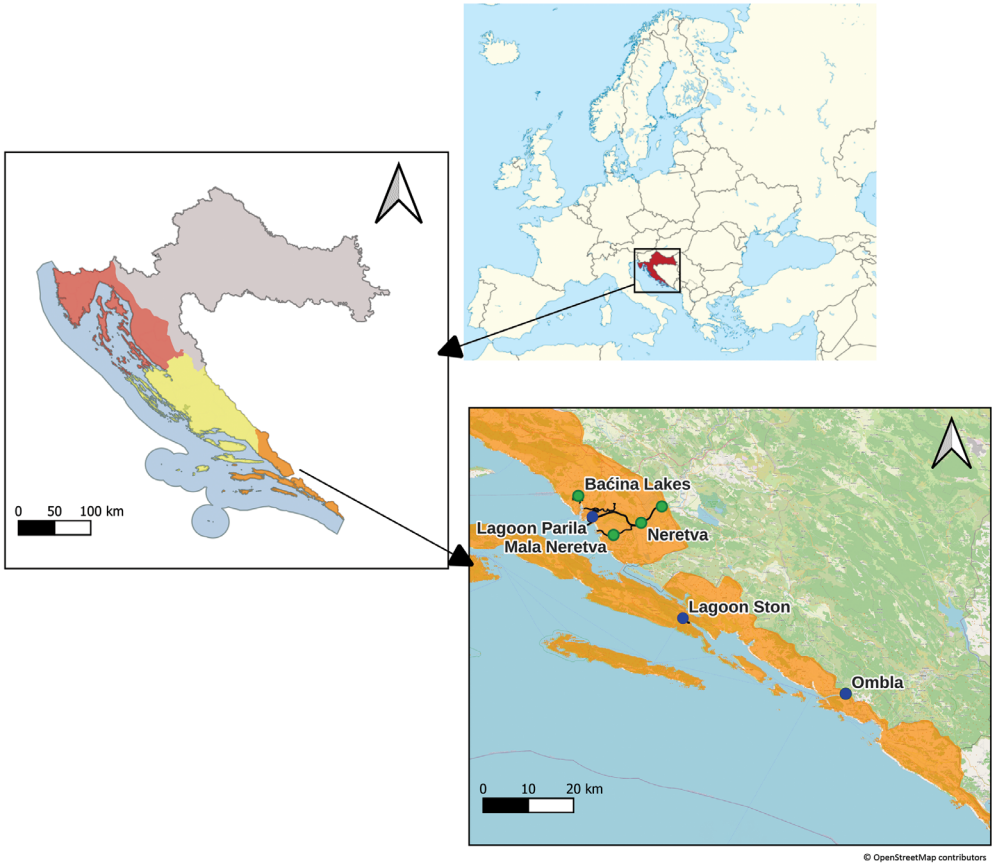


Figure 1 Map of the Neretva River Estuary and adjacent eastern Adriatic coastal sampling sites

Slika 1. Karta delte rijeke Neretve i pripadajućih postaja za uzorkovanje na istočnoj obali Jadranskog mora

Source: Authors' own work based on OpenStreetMap (Standard map layer), https://www.openstreetmap.org, map data © OpenStreetMap contributors, licensed under the ODbL (https://www.openstreetmap.org/copyright), accessed 20 July 2026. Sampling sites, site labels, highlighted areas, the overview map of Croatia, scale bars and north arrows were added by the authors. [42]

China), rated at 4000 W, with an effective operating power of approximately 2000–2500 W and a pulsed DC output of 400 V at 200 Hz with a 10% duty cycle. Transects were 100 m long and had an effective fishing width of 4 m. A single pass lasting 30 min was completed per transect. Baćinska Lakes and the Mala Neretva River each received one transect per season (four transects and 0.16 ha annually per site), whereas the main Neretva River received two spatially separated transects per season (eight transects and 0.32 ha annually). Brackish-water sampling used a local wingless eel trap: a cylindrical trap 30 cm in diameter and 1 m long, comprising a 0.7 m first chamber with 6 mm mesh and a terminal chamber with 4 mm mesh. Five unbaited traps were deployed at each site for 48 h, spaced 200 m apart, during each season. Before freezing, total length and body weight were measured in the field to the nearest 0.1 cm and 0.1 g, respectively. After field measurements, specimens were frozen for subsequent laboratory analyses. Following dissection, sex was assigned by macroscopic examination of the gonads as female, male or undetermined when the gonads could not be classified reliably. Freshwater indices were expressed as annual catch divided by the total electrofished area, whereas brackish-water CPUE was expressed as annual catch divided by the total number of trap-days.

2.3. Age determination / *Utvrđivanje starosti*

Age was determined from sagittal otoliths. Otoliths were extracted, ground and polished following the ICES Workshop on Age Reading of European and American Eel protocol [23]. Three readers (authors L.G., S.G. and B.G.) independently examined the prepared otoliths using microscopy and digital images. Initial readings were compared, and disagreements were resolved by joint re-examination and consensus. False or accessory rings were interpreted according to ICES guidance.

2.4. Biological variables and statistical analysis / *Biološki parametri i statistička obrada podataka*

The analysed biological variables were total length (TL), pectoral fin length (the linear distance measured from the anterior base to the distal tip of the longest fin ray), eye diameter, weight, age and sex. Sex was coded as 0 = undetermined, 1 = male and 2 = female. Descriptive statistics are presented as the mean ± standard deviation, with the minimum–maximum range. Differences between freshwater and brackish habitats were tested using two-sided Mann–Whitney U tests because sample sizes and distributions differed between habitats.

Length-weight relationships were estimated separately for freshwater and brackish samples using $W = aTL^b$, where W is weight in grams, TL is total length in centimetres, a is the intercept and b is the allometric exponent. Departure from isometry was tested using $t = (b - 3)/SE(b)$, and 95% confidence intervals for *b* were calculated. Positive allometry was concluded only when *b* was significantly greater than 3.

To strengthen the habitat comparison, four additional analyses were applied. First, Fulton's condition factor was calculated as $K = 100W/TL^3$, where W is weight in grams and TL is total length in centimetres. Because Fulton's K is

length-dependent when *b* differs from 3, it was treated as a complementary descriptive index rather than a length-independent measure of habitat quality [24]. Second, Mann–Whitney U tests were accompanied by Cliff's delta; positive values indicate higher ranks in freshwater samples. Third, habitat effects on the length-weight relationship were tested by ANCOVA using $\log_{10}$-transformed data: $\log_{10} W = \log_{10} a + b \log_{10} TL + habitat + \log_{10} TL \times habitat$. An additive model without the interaction term tested whether habitat affected weight after adjustment for TL. Linearity and residual plots were inspected; residual normality was evaluated with the Shapiro–Wilk test, homogeneity of variance with Levene's test, and homogeneity of slopes with the interaction term. Fourth, sex structure was evaluated using a chi-square test with all categories and Fisher's exact test after excluding undetermined individuals. Differences among sites in K were examined using Dunn's pairwise tests with Holm correction. Statistical analyses were performed in Microsoft Excel and Python (version 3.13.5), using the SciPy library (version 1.17.0) for numerical computations and the statsmodels package (version 0.14.6) for regression modelling and hypothesis testing.

2.5. Site-level environmental variables / *Okolišne varijable na razini postaja*

Site-level temperature and salinity were treated as arithmetic means of four seasonal in situ measurements at each location during the single annual monitoring cycle. Representative site-level depth values were recorded during habitat characterisation and are reported in Table 8 and Supplementary Table S1. Environmental variables were merged with biological data by capture site. Because freshwater and brackish habitats were sampled using different gear and effort units, electrofishing and trap indices were analysed and interpreted separately.

3. RESULTS / *Rezultati*

3.1. Habitat-level biological summary / *Sažetak bioloških podataka na razini staništa*

The sample included 132 eels, with 54 specimens from freshwater habitats and 78 from brackish habitats. The total sampled catch weight was 13.27 kg in freshwater and 11.14 kg in brackish habitats. Freshwater eels were larger, heavier and older than brackish eels (Table 1). Differences between habitats were statistically significant for total length (U = 2596.0, P = 0.023), weight (U = 2587.0, P = 0.026) and age (U = 2626.5, P = 0.013). Eye diameter and pectoral fin length did not differ significantly between habitats (P > 0.05).

3.2. Site-level biological structure / *Biološka struktura na razini postaja*

Freshwater-site catch structure was heterogeneous. The main Neretva channel had the highest annual freshwater catch weight (9.00 kg), including the largest individual in the dataset, whereas the Mala Neretva River contributed 4.12 kg. Baćinska Lakes yielded few individuals and was represented mainly by young, undetermined eels. In brackish habitats, Parila Lagoon dominated both abundance and catch weight (7.33 kg), followed by Ston Lagoon. Ombla Estuary was represented by a single eel (Table 2).

3.3. Length-weight relationships / *Odnosi duljine i mase*

Length-weight relationships were highly significant in both habitat groups. Freshwater eels showed $W = 0.000347\ TL^{3.430}$ ($R^2 = 0.982$), with $b = 3.430$ (95% CI: 3.302–3.557; t = 6.77, P < 0.001 for the test against $b = 3$). Brackish eels showed $W = 0.000599\ TL^{3.280}$ ($R^2 = 0.977$), with $b = 3.280$ (95% CI: 3.164–3.395; t = 4.82, P < 0.001 for the test against $b = 3$). The pooled sample also showed significant positive allometry ($b = 3.365$, 95% CI: 3.282–3.448; Table 3; Fig. 2). Site-specific fitted relationships are shown in Fig. 3.

Table 1 Biological descriptors of European eel by habitat type in the study area. Sex: 0 = undetermined, 1 = male, 2 = female
Tablica 1. Biološki pokazatelji europske jegulje prema tipu staništa u istraživanom području. Spol: 0 = neodređen, 1 = mužjak, 2 = ženka

Habitat	N	TL (cm)	Weight (g)	Age (years)	Eye diameter (mm)	Sex counts
Freshwater	54	45.4 ± 13.6 (20.3–86.2)	245.8 ± 310.2 (10.9–1750.4)	4.7 ± 2.0 (2.0–13.0)	5.65 ± 2.49 (2.52–12.10)	0=16, 1=8, 2=30
Brackish	78	40.7 ± 10.0 (28.4–66.3)	142.8 ± 128.6 (33.7–553.5)	4.0 ± 1.4 (2.0–8.0)	5.35 ± 2.06 (2.46–11.50)	0=29, 1=23, 2=26
Total	132	42.7 ± 11.8 (20.3–86.2)	185.0 ± 226.4 (10.9–1750.4)	4.3 ± 1.7 (2.0–13.0)	5.48 ± 2.24 (2.46–12.10)	0=45, 1=31, 2=56

Table 2 Biological descriptors of European eel by habitat and capture site
Tablica 2. Biološki pokazatelji europske jegulje po staništu i lokaciji ulova

Habitat	Code	Capture site	n	Catch weight (kg)	TL (cm)	Age (years)	Sex counts
Freshwater	BAĆ	Baćinska Lakes	4	0.15	26.8 ± 8.2 (20.3–38.4)	2.5 ± 1.0 (2.0–4.0)	0=4, 1=0, 2=0
Freshwater	NER	Neretva River	27	9	48.4 ± 16.0 (28.6–86.2)	5.1 ± 2.4 (2.0–13.0)	0=8, 1=1, 2=18
Freshwater	MNE	Mala Neretva River	23	4.12	45.1 ± 7.7 (34.9–74.2)	4.6 ± 1.0 (3.0–8.0)	0=4, 1=7, 2=12
Brackish	PAR	Parila Lagoon	55	7.33	39.8 ± 9.8 (28.4–65.4)	3.8 ± 1.3 (2.0–7.0)	0=25, 1=12, 2=18
Brackish	STN	Ston Lagoon	22	3.73	43.4 ± 10.2 (32.7–66.3)	4.4 ± 1.5 (3.0–8.0)	0=4, 1=10, 2=8
Brackish	OMB	Ombla Estuary	1	0.068	35.7 (35.7–35.7)	4.0 (4.0–4.0)	0=0, 1=1, 2=0

Table 3 Length-weight relationship parameters for European eel in the study area
Tablica 3. Parametri odnosa duljine i mase za europsku jegulju u istraživanom području

Group	n	a	b	SE(b)	R^2	P (LWR)	95% CI (b)	P (b = 3)
Freshwater	54	0.000347	3.430	0.064	0.982	<0.001	3.302–3.557	<0.001
Brackish	78	0.000599	3.280	0.058	0.977	<0.001	3.164–3.395	<0.001
Total	132	0.000440	3.365	0.042	0.980	<0.001	3.282–3.448	<0.001

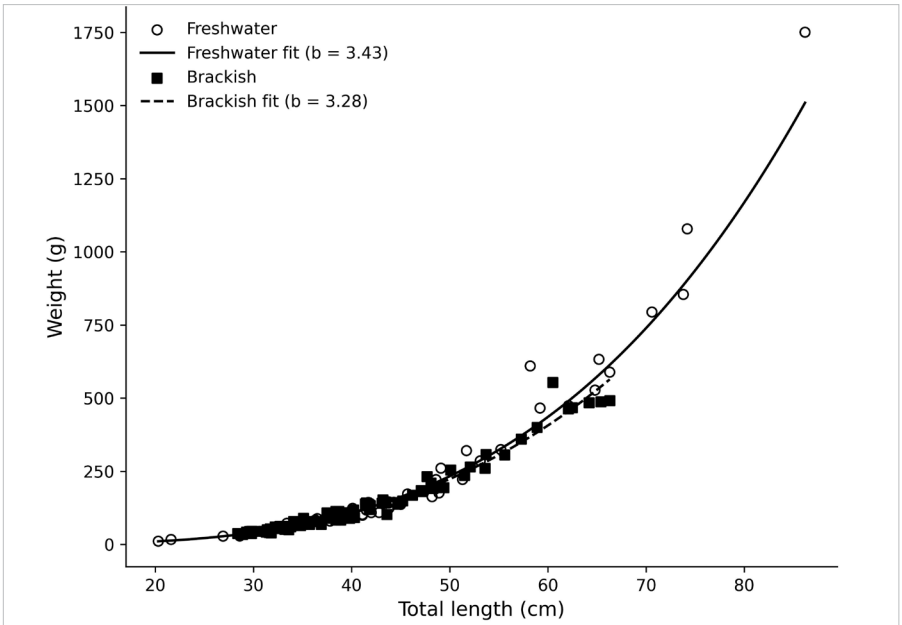


Figure 2 Length-weight relationships of the European eel, *Anguilla anguilla*, in freshwater and brackish water habitats of the study area, eastern Adriatic Sea, Croatia

Slika 2. Odnosi duljine i mase europske jegulje, Anguilla anguilla, u slatkovodnim i bočatim staništima istraživanog područja, istočno Jadransko more, Hrvatska

Source: Authors

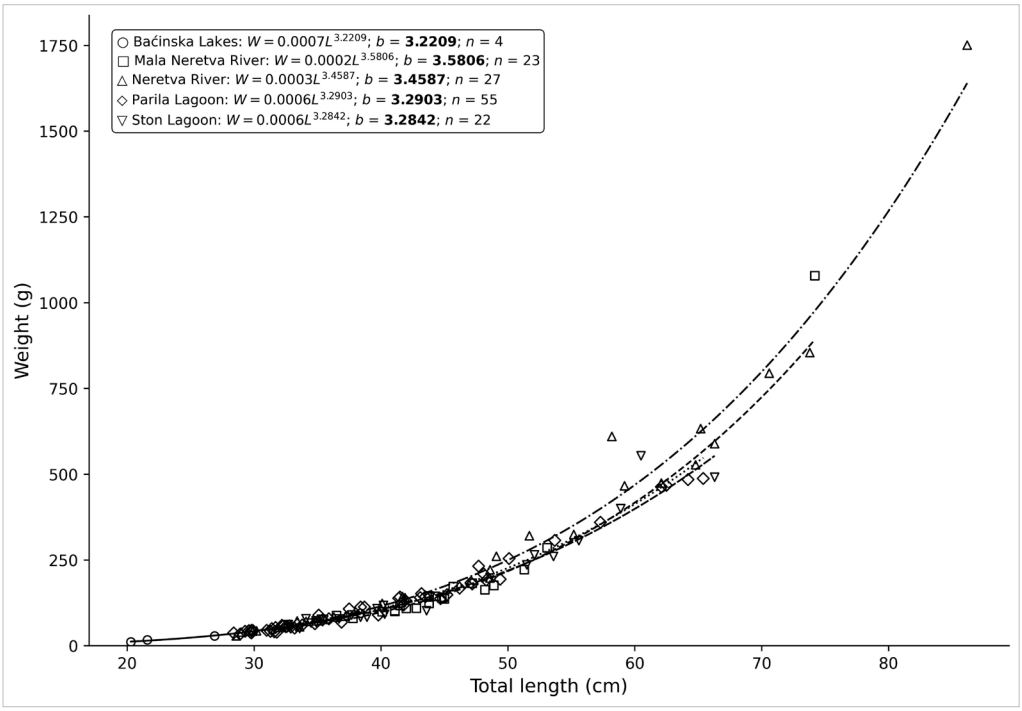


Figure 3 Site-specific length-weight relationships of the European eel, *Anguilla anguilla*, from all sampled sites except Ombla Estuary. Points represent individual eels, and black curves indicate site-specific fitted power functions.

Slika 3. Odnosi duljine i mase europske jegulje, Anguilla anguilla, specifični za pojedinu postaju, sa svih uzorkovanih postaja osim ušća Omble. Točke predstavljaju pojedinačne jegulje, a crne krivulje označavaju funkcije potencije prilagođene za pojedinu postaju.

Source: Authors

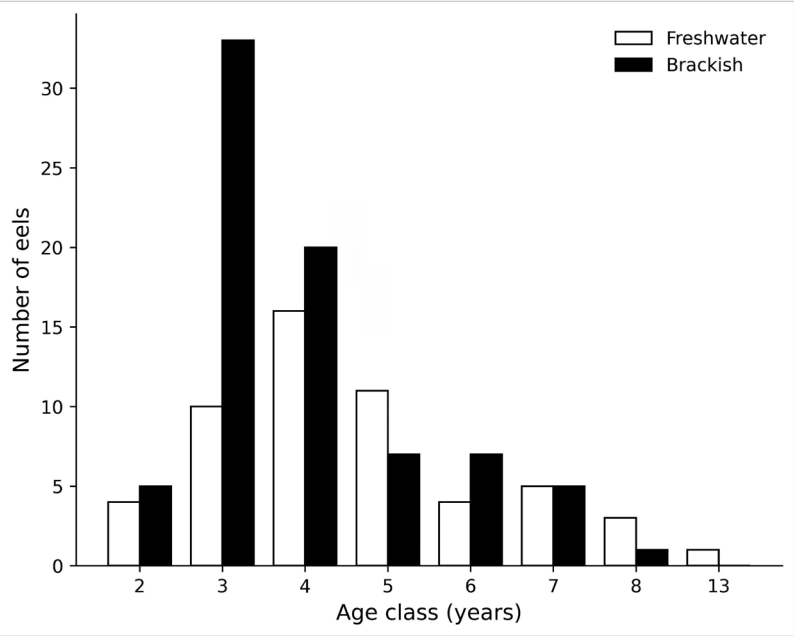


Figure 4 Age composition of the European eel, *Anguilla anguilla*, in freshwater and brackish water habitats of the study area, eastern Adriatic Sea, Croatia

Slika 4. Dobna struktura europske jegulje, Anguilla anguilla, u slatkovodnim i bočatim staništima istraživanog područja, istočno Jadransko more, Hrvatska

Source: Authors

3.4. Age and sex structure / *Dobna i spolna struktura*

The freshwater sample had a broader age range (2–13 years) than the brackish sample (2–8 years). Freshwater age classes were dominated by 4+ eels, followed by 5+ and 3+ eels, whereas brackish samples were dominated by 3+ and 4+ eels (Fig. 4). No age-1 eel was detected. This may reflect the absence of targeted glass eel/elver sampling at recruitment entry points and the selectivity of the gear and habitats for larger yellow eels. Females were more frequent in freshwater samples (30 females, 8 males and 16 undetermined), whereas brackish samples were more balanced (26 females, 23 males and 29 undetermined).

3.5. Fishery indices / *Ribolovni pokazatelji*

Fishery indices are presented in Tables 4A and 4B. Annual indices were calculated by dividing total annual catch by total annual effort: total electrofished area for freshwater sites and total trap-days for brackish sites. Baćinska Lakes and the Mala Neretva River each had four seasonal transects of 0.04 ha (0.16 ha annually), whereas the main Neretva River had eight transects (0.32 ha annually). Each brackish site had four seasonal sets of five traps soaked for two days, equivalent to 40 trap-days annually. The highest freshwater abundance index was recorded in the Mala Neretva River (143.75 individuals/ha), whereas the highest biomass index was recorded in the main Neretva River (28.13 kg/ha). Parila Lagoon had the highest brackish indices (1.375 individuals/trap-day and 0.183 kg/trap-day). Seasonal catches were combined to provide an annual standardised baseline; the limited number of events per site did not support robust site-by-season inference.

Table 4A Freshwater electrofishing indices

Tablica 4A. Indeksi elektroribolova u slatkovodnim staništima

Code	Capture site	Annual catch (N)	Annual catch weight (kg)	Effort (ha)	Mean catch (kg/seasonal transect)	N/ha	kg/ha
BAĆ	Baćinska Lakes	4	0.15	0.16	0.038	25	0.94
MNE	Mala Neretva River	23	4.12	0.16	1.031	143.75	25.77
NER	Neretva River	27	9	0.32	1.175	84.37	28.13

Table 4B Brackish trap indices

Tablica 4B. Indeksi lova vršama u bočatim staništima

Code	Capture site	Annual catch (N)	Annual catch weight (kg)	Trap-days	n/seasonal set	kg/seasonal set	N/trap-day	kg/trap-day
OMB	Ombla Estuary	1	0.068	40	0.25	0.017	0.025	0.002
PAR	Parila Lagoon	55	7.33	40	13.75	1.83	1.375	0.183
STN	Ston Lagoon	22	3.739	40	5.50	0.935	0.550	0.093

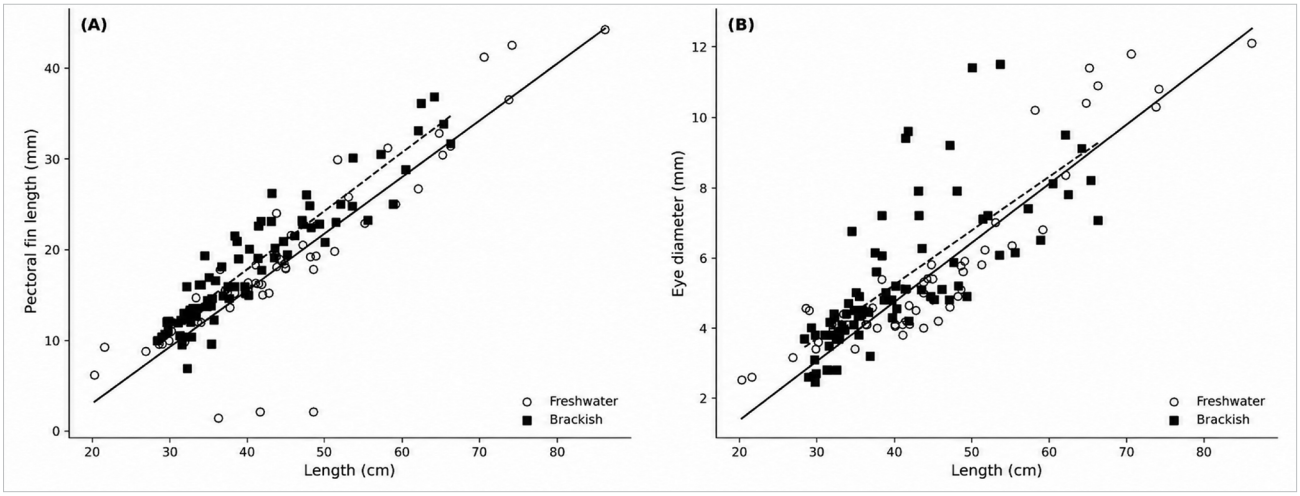


Figure 5 Morphometric relationships of the European eel, *Anguilla anguilla*, in freshwater and brackish water habitats: (A) total length versus pectoral fin length; (B) total length versus eye diameter

Slika 5. Morfometrijski odnosi europske jegulje, Anguilla anguilla, u slatkovodnim i bočatim staništima: (A) ukupna duljina u odnosu na duljinu prsne peraje; (B) ukupna duljina u odnosu na promjer oka

Source: Authors

3.6. Morphometric relationships: total length, pectoral fin length and eye diameter / *Morfometrijski odnosi: ukupna duljina, duljina prsne peraje i promjer oka*

Total length was positively related to pectoral fin length in both habitats (freshwater: n = 54, R^2 = 0.786, P < 0.001; brackish: n = 78, R^2 = 0.874, P < 0.001; Fig. 5A). Eye diameter also increased with total length, but the relationship was weaker in brackish than in freshwater samples (freshwater: R^2 = 0.846, P < 0.001; brackish: R^2 = 0.554, P < 0.001; Fig. 5B). Habitat-level median differences were not significant for pectoral fin length (Mann–Whitney U = 2145.0, P = 0.859) or eye diameter (U = 2205.5, P = 0.647), indicating that these variables primarily scaled with body size.

3.7. Effects of eel size and condition factor / *Učinci veličine jegulje i kondicijskog faktora*

The additional non-parametric effect-size analysis supported the earlier habitat comparison but indicated that the magnitude of freshwater–brackish differences was modest. Freshwater eels had higher ranks for total length, weight and age, with Cliff's delta values indicating small-to-moderate habitat differences. Pectoral fin length, eye diameter and Fulton's condition factor showed no meaningful habitat-level difference (Table 5A).

Fulton's condition factor did not differ significantly between freshwater and brackish habitats (P = 0.391). Condition factor differed among sites represented by more than one individual (Kruskal–Wallis H = 18.95, P = 0.0008). Dunn's tests with Holm correction indicated that the Neretva River had higher K than the Mala Neretva River (adjusted P = 0.0013), Parila Lagoon (adjusted P = 0.0263) and Baćinska Lakes (adjusted P = 0.0428). The Neretva–Ston comparison was not significant after correction (adjusted P = 0.0630), and other pairwise comparisons were non-significant. These site-level results remain exploratory because sample sizes differed markedly, with only four eels collected from Baćinska Lakes (Table 6).

The ANCOVA confirmed that $\log_{10}$-transformed total length explained nearly all variation in $\log_{10}$-transformed weight (Table 5B). In the full model, the $\log_{10}$ TL × habitat interaction was not significant ($F_{1,128}$ = 3.09, P = 0.081, partial η^2 = 0.024), indicating no statistically supported difference between slopes. Habitat was not significant ($F_{1,128}$ = 0.35, P = 0.553, partial η^2 = 0.003), whereas $\log_{10}$ TL was strongly significant ($F_{1,128}$ = 6251.74, P < 0.001, partial η^2 = 0.980). In the additive model, habitat remained non-significant after adjustment for TL ($F_{1,129}$ = 0.35, P = 0.556). The full model had an R^2 of 0.981. The residuals met the tested assumptions (Shapiro–Wilk W = 0.991, P = 0.571; Levene F = 1.93, P = 0.168). Thus, the higher raw weight of freshwater eels is best interpreted as a size- and age-structure effect.

Table 5A Habitat-level comparisons with effect sizes. Cliff's delta is positive when freshwater values have higher ranks than brackish values.

Tablica 5A. Usporedbe po staništima s prikazom veličina učinka. Cliffova delta pozitivna je kad su rangovi slatkovodnih vrijednosti viši od bočatih.

Variable	Freshwater median	Brackish median	Mann-Whitney U	P	Cliff's delta
Total length (cm)	43.8	38.05	2596.0	0.023	0.233
Weight (g)	139.45	89.2	2587.0	0.026	0.228
Age (years)	4	4	2626.5	0.013	0.247
Pectoral fin length (mm)	17.865	16.33	2145.0	0.859	0.019
Eye diameter (mm)	4.72	4.8	2205.5	0.647	0.047
Fulton's condition factor K	0.169	0.169	2292.0	0.391	0.088

Table 5B ANCOVA results for log_{10}-transformed eel weight in relation to log_{10}-transformed total length and habitat. The full model included the length × habitat interaction, whereas the additive model included only the main effects. Partial η^2 represents the effect size

Tablica 5B. Rezultati ANCOVA-e za log_{10}-transformiranu masu jegulja u odnosu na log_{10}-transformiranu ukupnu duljinu i stanište. Puni model uključivao je interakciju duljine i staništa, dok je aditivni model uključivao samo glavne učinke. Parcijalni η^2 predstavlja veličinu učinka

Model	Term	df	F	P	Partial η^2
Full	log_{10} TL	1	6251.74	<0.001	0.980
Full	Habitat	1	0.35	0.553	0.003
Full	log_{10} TL × habitat	1	3.09	0.081	0.024
Additive	log_{10} TL	1	6151.93	<0.001	0.979
Additive	Habitat	1	0.35	0.556	0.003

Table 6 Fulton's condition factor K for European eel by capture site

Tablica 6. Fultonov koeficijent kondicije K za europsku jegulju prema mjestu ulova

Code	Site	Habitat type	N	Mean K ± SD	Median K
BAĆ	Baćinska Lakes	Freshwater	4	0.152 ± 0.018	0.156
NER	Neretva River	Freshwater	27	0.195 ± 0.039	0.193
MNE	Mala Neretva River	Freshwater	23	0.164 ± 0.026	0.155
PAR	Parila Lagoon	Brackish	55	0.169 ± 0.021	0.169
STN	Ston Lagoon	Brackish	22	0.169 ± 0.026	0.169
OMB	Ombla Estuary	Brackish	1	0.149 ± –	0.149

3.8. Sex-structure comparison / *Usporedba spolne strukture*

Sex composition differed between habitat groups when undetermined individuals were retained as a category (chi-square = 7.17, df = 2, P = 0.028). Among sexed eels, females represented 78.9% of freshwater and 53.1% of brackish individuals; Fisher's exact test indicated a significant habitat difference in the male-to-female ratio (P = 0.014; Table 7). Undetermined eels were predominantly small: their median TL was 32.3 cm (range 20.3–52.1 cm), and 77.8% were <35 cm. This concentration among smaller eels is consistent with the difficulty of macroscopic sex assignment before clear gonadal differentiation, although several larger individuals also remained undetermined.

Table 7 Sex structure of freshwater and brackish samples

Tablica 7. Struktura spolova u slatkovodnim i bočatim uzorcima

Sex category	Freshwater	Brackish
Undetermined	16	29
Male	8	23
Female	30	26
Female proportion among sexed eels	78.9%	53.1%

3.9. Temperature and salinity framework of site-level eel patterns / *Kontekst temperature i saliniteta za pojavnost jegulje na razini postaja*

Environmental values showed a clear separation between freshwater and brackish habitats. Freshwater sites had mean annual salinities of 0.6–0.9 psu, whereas brackish sites ranged from 18.7 to 25.6 psu. Mean annual temperatures ranged from 15.6 °C in the Neretva River to 19.7 °C in the Mala Neretva River. Depth varied from less than 1 m at Parila and Ston lagoons to 10 m in Baćinska Lakes (Table 8).

When biological descriptors were considered together with temperature and salinity, freshwater sites contained fewer but generally larger, heavier and older eels, whereas brackish sites, especially Parila Lagoon, yielded higher catches of smaller and younger individuals. The main Neretva River had the greatest freshwater biomass index and the largest mean individual mass despite being one of the cooler sites. This pattern suggests that local growth habitat, depth, residence time and connectivity are likely to be more important than temperature alone (Table 9).

Table 8 Site-level environmental variables and biological descriptors of European eel in the study area
Tablica 8. Varijable okoliša na razini postaja i biološki pokazatelji europske jegulje u istraživanom području

Site	Type	Temperature (°C)	Salinity (psu)	Depth (m)	No. of eels	TL (cm)	Weight (g)	Age (years)
Baćinska Lakes	Freshwater	17.8	0.7	10	4	26.8 ± 8.2 (20.3–38.4)	37.5 ± 38.5 (10.9–94.3)	2.5 ± 1.0 (2.0–4.0)
Neretva River	Freshwater	15.6	0.6	8	27	48.4 ± 16.0 (28.6–86.2)	333.3 ± 378.1 (28.6–1750.4)	5.1 ± 2.4 (2.0–13.0)
Mala Neretva River	Freshwater	19.7	0.9	2	23	45.1 ± 7.7 (34.9–74.2)	179.3 ± 201.8 (72.3–1078.4)	4.6 ± 1.0 (3.0–8.0)
Parila Lagoon	Brackish	18.4	24.3	0.9	55	39.8 ± 9.8 (28.4–65.4)	133.3 ± 120.4 (33.7–487.3)	3.8 ± 1.3 (2.0–7.0)
Ston Lagoon	Brackish	17.6	25.6	0.8	22	43.4 ± 10.2 (32.7–66.3)	170.0 ± 148.6 (50.0–553.5)	4.4 ± 1.5 (3.0–8.0)
Ombla Estuary	Brackish	15.8	18.7	1.3	1	35.7	68.0	4

Table 9 Fishery indices and site-specific length-weight relationship coefficients of European eel in the environmental context
Tablica 9. Ribolovni pokazatelji i parametri odnosa duljine i mase za europsku jegulju u odnosu na okolišne uvjete po postajama

Site	Annual effort	Abundance index	Biomass index	LWR b	Biological interpretation
Baćinska Lakes	4 seasonal 100 m × 4 m transects (0.16 ha)	25.0 ind./ha	0.94 kg/ha	3.221	Low annual sample; young eels only
Neretva River	4 × 2 seasonal 100 m × 4 m transects (0.32 ha)	84.37 ind./ha	28.13 kg/ha	3.459	Highest freshwater biomass; older/larger eels
Mala Neretva River	4 seasonal 100 m × 4 m transects (0.16 ha)	143.75 ind./ha	25.77 kg/ha	3.581	Warmest freshwater site; high growth index
Parila Lagoon	4 seasonal sets × 5 traps × 2 days (40 trap-days)	1.375 ind./trap-day	0.183 kg/trap-day	3.290	Highest brackish catch and biomass CPUE
Ston Lagoon	4 seasonal sets × 5 traps × 2 days (40 trap-days)	0.550 ind./trap-day	0.093 kg/trap-day	3.284	High salinity; moderate trap CPUE
Ombla Estuary	4 seasonal sets × 5 traps × 2 days (40 trap-days)	0.025 ind./trap-day	0.002 kg/trap-day	-	Single individual; not interpretable statistically

*ind. = individuals.

Table 10 Exploratory Spearman rank associations between site-level environmental variables and biological means after exclusion of Ombla Estuary (five sites)
Tablica 10. Eksploratorne Spearmanove korelacije ranga između okolišnih varijabli i bioloških prosjeka po postajama, nakon isključenja ušća Omble (pet postaja)

Association	Spearman's rho	P	Interpretation
Temperature vs mean total length	-0.300	0.624	Exploratory; five sites only
Temperature vs mean weight	-0.300	0.624	Exploratory; five sites only
Temperature vs mean age	-0.300	0.624	Exploratory; five sites only
Temperature vs mean condition factor	-0.500	0.391	Exploratory; five sites only
Salinity vs mean total length	-0.300	0.624	Confounded with habitat and gear
Salinity vs mean weight	-0.300	0.624	Confounded with habitat and gear
Salinity vs mean age	-0.300	0.624	Confounded with habitat and gear
Salinity vs mean condition factor	-0.100	0.873	Confounded with habitat and gear

Ombla Estuary was excluded from the site-level Spearman analysis because only one eel was captured. Across the remaining five sites, no statistically significant association was detected between temperature or salinity and mean total length, mean weight, mean age or mean condition factor (Table 10). These correlations are strictly exploratory because they are based on only five site means; Baćinska Lakes had only four eels; environmental variables were represented by annual averages; and salinity was strongly confounded with habitat type and sampling gear. Temperature and salinity are therefore interpreted as descriptors of habitat context rather than independent causal predictors.

4. DISCUSSION / *Rasprava*

4.1. Freshwater and brackish habitats as different functional components / *Slatkovodna i boćata staništa kao različite funkcionalne komponente*

Separating freshwater and brackish samples revealed two complementary functional components of the study-area eel population. Freshwater habitats contained larger, heavier and older eels, including most females and the largest individual recorded. This pattern is consistent with deeper channels, tributaries and connected lakes acting as longer-term growth habitats for large yellow eels and potential future spawning

females. Brackish habitats contained more 3+ and 4+ eels and a more balanced sex composition, suggesting that lagoons and estuaries function as productive transitional habitats used by younger yellow eels and migrating individuals.

This local pattern partly agrees with, but also refines, the coast-wide Croatian analysis [22]. Both studies show that freshwater habitats can contain the oldest individuals and that brackish sites are important for smaller and intermediate size classes. The broader study pooled 23 coastal sites and therefore included several brackish systems with different eel-size structures, whereas the present analysis focused on six sites in the Neretva Eel River Basin management area and was strongly influenced by older, larger females in the main Neretva channel and younger eels in Parila Lagoon. Parila Lagoon was the dominant brackish habitat in terms of eel catches. This agrees with earlier studies in the Neretva Delta, where Parila Lagoon was identified as a key eel-fishing habitat used by traditional fishing gear [16,19]. However, the scientific monitoring traps used here (five traps soaked for two days) are not directly comparable with the larger traditional fyke-net systems used in commercial or artisanal fisheries [19]. The values for Parila Lagoon should therefore be interpreted as standardised monitoring indices of relative abundance and biomass, not as direct estimates of commercial yield.

A recent habitat-based study in Croatian karstic lotic systems further supports this functional interpretation. Piria and Tomljanović [25] showed that different eel length classes are associated with different habitat descriptors, including proximity to the sea, depth, channel width, conductivity, instream cover and substrate heterogeneity, whereas all length classes were sensitive to riverbank and riverbed modification. In the study area, these findings indicate that freshwater and brackish sites should not be interpreted solely in terms of salinity. Rather, they represent different structural and functional habitat units: shallow vegetated lagoons may support feeding, movement and seasonal capture of younger or intermediate eels, whereas deeper riverine habitats with greater residence potential may retain larger female eels for longer periods.

4.2. Growth and condition / *Rast i kondicijski status*

The positive allometric growth observed in both habitat categories differs from the generally negative allometry reported for six Croatian Adriatic karst rivers by Piria et al. [21], where *b* ranged from 2.596 to 2.816. It is more consistent with earlier Neretva and Baćina reports of higher *b* values in freshwater eel samples [19]. The difference probably reflects a combination of habitat productivity, sample composition, age structure and the presence of larger females in the Neretva freshwater dataset. The brackish *b* value in the present Parila-dominated monitoring sample was also higher than the *b* value previously reported for Parila Lagoon using traditional fyke-net gear [19], indicating that gear type, season and silver-eel contribution can strongly affect length-weight parameters.

The interpretation of the length-weight exponent should remain biologically cautious. Positive allometry probably reflects the combined effects of size structure and sex/life-stage composition, including the disproportionate influence of larger and older females, seasonal variation in yellow- and silver-eel condition and feeding state, and freshwater-resident yellow eels with habitat-specific age and growth trajectories [22,26-29]. The *b* coefficient is not a direct measure of growth rate alone; it also integrates body shape, condition, maturity stage, sex composition and the sampled length range [24].

The values recorded in the study area contrast with the negative allometry reported for six Croatian Adriatic karst rivers [21], but are more consistent with positive or near-positive allometric patterns reported in some productive Mediterranean systems. For example, İlhan et al. [30] reported positive allometry for European eels from Turkish inland waters, whereas Demirci et al. [31] showed lower and life-stage-specific *b* values for yellow and silver eels from the Asi River. Similarly, Partal et al. [32] reported positive allometry in pooled Lake Bafa eels, together with ages of 2–9 years and a strongly female-biased sex ratio. These comparisons indicate that positive allometry in the Neretva is not exceptional within the Mediterranean context, but its interpretation must consider habitat type, life stage, sex ratio, gear selectivity, season and length range.

At the same time, the ANCOVA and Fulton's K results show that the habitat contrast should be interpreted carefully. Freshwater eels were heavier in the raw comparison because they were generally larger and older, but habitat did not significantly affect weight after adjustment for total length. Mediterranean eel habitats differ strongly in catchability, age structure and sex composition. Lagoon systems can support high growth yet produce samples dominated by younger, smaller or fishery-selected eels, whereas riverine and freshwater habitats may retain larger females for longer periods [33-37].

Fulton's condition factor provided an important correction to the raw weight comparison. Although freshwater eels were heavier and older, median K was identical in freshwater and brackish habitats, and the habitat-level difference was not significant. This indicates that the contrast was mainly demographic and structural rather than indicating that one habitat group was consistently in better body condition [38,39].

The highest site-level K in the main Neretva River suggests locally favourable feeding or residence conditions. However, this result should be interpreted cautiously because Fulton's K is sensitive to body length when growth is allometric. Since *b* significantly exceeded 3 in both habitat groups, K should be treated as a complementary condition index rather than a stand-alone indicator of habitat quality [24]. This interpretation is consistent with Barić et al. [28], who found positive allometry in the overall Neretva-mouth sample and in silver eels, but no significant seasonal difference in condition between yellow and silver eels.

The lack of age-1 eels and the high proportion of undetermined sex categories also define the limits of interpretation. Sampling targeted yellow-eel habitats rather than glass-eel entry points, and both electrofishing and traps may underrepresent the smallest recruits. Most undetermined eels were <35 cm, supporting a biological explanation based on incomplete gonadal differentiation, but macroscopic sexing remains less reliable than histological examination. Eye diameter increased with body length in both habitats, whereas the weaker relationship in brackish samples may indicate greater heterogeneity in maturation or silvering stage. Eye enlargement is a component of established silvering classifications [40], but a complete silvering index was not calculated here; eye diameter alone cannot be used to assign migratory stage directly.

The broader Mediterranean literature supports the importance of lagoons and estuaries for eel production and

escapement. Large-scale analyses of Mediterranean lagoon fisheries reported substantial long-term declines in eel catches [8], whereas work by the GFCM has emphasised the need for harmonised data collection and management across Mediterranean eel habitats [4].

4.3. Monitoring and management implications / *Implikacije za praćenje stanja i upravljanje*

The results support several management priorities. Freshwater and brackish habitats should not be managed as isolated systems because eel production depends on connectivity among the main channel, the Mala Neretva River, lakes, lagoons and the sea. Parila Lagoon should remain a focal site for standardised trap monitoring and control of illegal fishing, while the main Neretva and Mala Neretva rivers should be treated as high-value freshwater growth habitats. Management recommendations should explicitly refer to the broader Croatian and Mediterranean evidence. For Croatian waters, a precautionary increase in the minimum landing size to at least 45 cm (currently 35 cm) was recommended to improve yield and population resilience [19]. For the study area, these findings support stricter protection of larger female eels, control of illegal fishing, protection of Parila Lagoon and other productive transitional habitats, and long-term gear-specific CPUE monitoring.

The Turkish examples further emphasise that eel management should remain spatially differentiated, as catch-based assessment across Turkish eel management areas showed divergent regional trends [13]. Biological studies from the Asi River and Lake Bafa also demonstrated that size structure, sex ratio and silvering stage can differ strongly among systems [31,32]. Historical analyses have indicated that the Neretva eel fishery has declined from much higher historical catches to a recent low level, with habitat loss, invasive predators, parasites, fishing pressure and market demand identified as major drivers [16,41]. The indices reported in the present article provide a baseline for conservation-oriented monitoring, habitat restoration and enforcement.

5. CONCLUSIONS / *Zaključak*

European eels in the study area showed clear habitat-associated differences in age and body-size composition. Freshwater samples contained larger, heavier, older and more female-biased eels; the main Neretva River had the highest freshwater biomass index, while the Mala Neretva River had the highest abundance index. Brackish samples were dominated by younger eels, and Parila Lagoon was the strongest brackish monitoring site. However, identical median Fulton's K and the absence of a habitat effect on weight after adjustment for total length show that the freshwater–brackish contrast was primarily demographic rather than a consistent difference in condition. Future work should target glass-eel and elver recruitment and repeat environmental measurements with greater temporal resolution.

The main limitations of the study are the absence of age-1 individuals, which prevents direct assessment of recent recruitment; the use of macroscopic sex determination, which is less reliable in small and undifferentiated yellow eels; incomplete event-specific metadata on electrofishing settings, which limits retrospective evaluation of gear performance and comparability among individual sampling events; and the reliance on single-year seasonal averages for temperature, salinity and depth. Future monitoring should therefore include multi-year seasonal CPUE series, targeted recruitment sampling, histological verification of sex for small or uncertain individuals, application of a full silvering index, and higher-frequency environmental measurements linked to each sampling event.

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