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SHORT COMMUNICATION

Genetic homogeneity of the European squid *Loligo vulgaris* across the eastern Adriatic Sea: New evidence from the Southern Adriatic

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Abstract: The European squid *Loligo vulgaris* supports an economically important fishery throughout the Adriatic Sea. Previous genetic analyses revealed a lack of population structure in the Northern and Central eastern Adriatic, but the absence of Southern Adriatic samples prevented a basin-wide assessment. Here, we analysed mitochondrial cytochrome c oxidase subunit I (COI) sequences from 39 *L. vulgaris* individuals collected in the Southern Adriatic and combined them with 121 previously published sequences, generating the first COI dataset covering all three eastern Adriatic sub-basins. The Southern Adriatic population showed high haplotype diversity (Hd = 0.742) and low nucleotide diversity (π = 0.00308), consistent with recent demographic expansion. Genetic differentiation among the Northern, Central, and Southern Adriatic sub-basins was low and non-significant (Φ_{ST} = 0.01396, p = 0.062), with negligible divergence even between the geographically most distant Northern and Southern populations. Most Southern Adriatic haplotypes were shared with Northern and/or Central Adriatic populations, and the star-shaped network was retained across the basin. No spatial genetic structure was detected with COI among the sampled eastern Adriatic sub-basins. If confirmed by studies with broader spatial and temporal sampling and nuclear markers, these results would support the management of *L. vulgaris* in the eastern Adriatic as a single stock unit.
***Keywords*:** cephalopods; *Loligo vulgaris*; COI; genetic connectivity; Adriatic Sea

Sažetak: GENETIČKA HOMOGENOST EUROPSKE LIGNJE *LOLIGO VULGARIS* U ISTOČNOM DIJELU JADRANSKOG MORA: NOVI DOKAZI IZ JUŽNOG JADRANA. Europska lignja *Loligo vulgaris* predstavlja jednu od ključnih i ekonomski najvažnijih ribolovnih vrsta u Jadranskom moru. Prethodna genetička istraživanja pokazala su izostanak populacijske strukture u sjevernom i srednjem dijelu istočnog Jadrana, no nedostatak uzoraka iz južnog Jadrana onemogućio je procjenu na razini cijelog bazena. U ovom radu analizirane su sekvence dijela mitohondrijskog gena podjedinice I citokrom c oksidaze (COI) 39 jedinki vrste *L. vulgaris* prikupljenih u južnom Jadranu te objedinjene sa 121 prethodno objavljenom sekvencom, čime je izrađen prvi cjeloviti skup podataka za istočni Jadran. Populacija južnog Jadrana pokazala je visoku raznolikost haplotipova (Hd = 0,742) i nisku nukleotidnu raznolikost (π = 0,00308), što upućuje na nedavnu demografsku ekspanziju. Genetička diferencijacija između sjevernog, srednjeg i južnog Jadrana bila je niska i statistički neznačajna (Φ_{ST} = 0,01396, p = 0,062), uz zanemarivu divergenciju čak i između geografski najudaljenijih sjevernih i južnih populacija. Većina haplotipova iz južnog Jadrana bila je zajednička populacijama iz sjevernog i/ili srednjeg Jadrana, a zvjezdasta struktura mreže haplotipova zadržana je na razini cijelog istraživanog područja. Analizom gena COI nije utvrđena prostorna genetička struktura u istraživanim područjima istočnog Jadrana. Potvrde li ove rezultate buduća istraživanja s obuhvatnijim prostornim i vremenskim uzorkovanjem te nuklearnim markerima, to će značiti da se vrstom *L. vulgaris* u istočnom Jadranu može upravljati kao jedinstvenim stokom.
Ključne riječi: glavonošci; *Loligo vulgaris;* COI; genetička povezanost; Jadransko more

INTRODUCTION

The European squid *Loligo vulgaris* Lamarck, 1798 (Loliginidae) is an economically important cephalopod species throughout the Adriatic Sea, where sustainable fisheries management depends on an understanding of population connectivity and stock structure (Petrić *et al.*, 2025). As a semi-enclosed sub-basin of the Mediterranean, the Adriatic Sea is characterized by marked bathymetric and hydrographic heterogeneity that influences dispersal and gene flow of many marine species. Determining whether *L. vulgaris* constitutes a geneti-

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cally homogeneous population across the Adriatic basin is therefore important for both evolutionary and fisheries management perspectives.

Our recent study provided the first multi-year assessment of the population genetics of *L. vulgaris* in the eastern Adriatic, analysing mitochondrial cytochrome c oxidase subunit I (COI) sequences from 121 individuals collected in the Northern and Central eastern Adriatic (Petrić *et al*., 2025). The study revealed high haplotype diversity, low nucleotide diversity, and no evidence of spatial or temporal genetic structure, indicating a single panmictic population that had undergone recent demographic expansion. These findings were consistent with an earlier study based on nuclear microsatellite markers, which also found no significant population differentiation within the Adriatic Sea (Garoia *et al.*, 2004a). However, because samples from the Southern Adriatic were unavailable, the previous study by Petrić *et al*. (2025) could not determine whether this pattern extended across the entire basin.

This unresolved question is particularly relevant because the South Adriatic Pit, the deepest part of the Adriatic Sea, is associated with persistent hydrographic features that could potentially limit dispersal and gene flow between the central and southern sub-basins. Although previous studies using nuclear microsatellites and mitochondrial COI have generally indicated high connectivity in *L. vulgaris* (Garoia *et al.*, 2004a; Petrić *et al*., 2025), recent studies suggest that population structure may vary across the species' distribution. García-Mayoral *et al*. (2024) detected subtle but significant latitudinal differentiation at adaptive single-nucleotide polymorphism (SNP) loci along the western Iberian Peninsula despite genetic homogeneity at neutral loci, while Pertesi *et al*. (2025) reported marked mitochondrial divergence between eastern and western Mediterranean populations. Although the latter study analysed a shorter COI fragment than that used here, limiting direct comparison, its results indicate that barriers to gene flow may occur at broader spatial scales within the Mediterranean basin.

In the present study, we address the remaining geographic gap in the Adriatic genetic dataset by analysing *L. vulgaris* specimens collected from the Southern Adriatic along the Montenegrin coast. By integrating these new data with the previously published Northern and Central Adriatic sequences, we complete the first COI dataset for the species covering all three eastern Adriatic sub-basins and test whether the genetic homogeneity previously documented in the northern and central sub-basins extends throughout the entire eastern Adriatic Sea or whether the South Adriatic Pit represents a barrier to gene flow.

MATERIAL AND METHODS

Sampling

A total of 39 *Loligo vulgaris* individuals were collected in October 2025 from Montenegrin coastal waters (south Adriatic Sea) using a commercial bottom trawl equipped with a square-mesh codend (45–50 mm mesh size). The trawl haul was conducted between 42°06′30.87″ N, 18°54′04.47″ E and 42°08′32.19″ N, 18°38′59.07″ E. After collection, a small arm-tip tissue sample was excised from each specimen and preserved in 96% ethanol for subsequent molecular analyses.

DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted following a salt precipitation protocol. Tissue samples were lysed overnight at 55 °C in 200 µL of SSTNE extraction buffer (0.3 M NaCl, 50 mM Tris Base, 0.2 mM EDTA, 0.2 mM EGTA, 0.5 mM spermidine, 0.2 mM spermine tetrahydrochloride), supplemented with 10 µL of 10% SDS and 4 µL of 20 mg/mL proteinase K solution. After lysis, proteinase K was inactivated by incubation at 70 °C for 15 min, after which RNA was removed by addition of 1.5 µL of RNase A (20 mg/mL), followed by incubation at 37 °C for 60 min. Proteins were precipitated by high-speed centrifugation at 16,000 × g for 10 min, after addition of 155 µL of 5 M NaCl and incubation on ice for 10 min. The supernatant was collected and DNA was precipitated by addition of room-temperature isopropanol. Samples were incubated on ice for 10 min before centrifugation at 16,000 × g for 10 min. Following the removal of the supernatant, the DNA pellet was washed in 75% ethanol overnight, to reduce salt impurities and improve the 260/230 absorbance ratio. The pellet was collected by centrifugation at 16,000 × g for 5 min, ethanol was completely removed by pipette, and the pellet was air-dried at 37 °C for 5 min. DNA was resuspended in 5 mM Tris-HCl and DNA quantity and purity were assessed spectrophotometrically.

A fragment of the mitochondrial COI gene was amplified using the universal primer pair LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al*., 1994). PCR amplification conditions and reaction composition were as described in Petrić *et al*. (2025), using GoTaq® G2 Hot Start Polymerase (Promega Corporation, Madison, WI, USA). Negative controls were included in each amplification batch to monitor for potential contamination. All PCR products were verified by 1% agarose gel electrophoresis prior to sequencing. Amplicons were sequenced by Microsynth AG (Balgach, Switzerland) using Sanger sequencing in the forward direction with the LCO1490 primer.

Population genetic analyses

Raw sequences were imported into MEGA 12 (Kumar *et al*., 2024) and aligned using the MUSCLE algorithm. Low-quality sequence ends were trimmed before the Southern Adriatic sequences were added to the Northern and Central Adriatic alignment of Petrić *et al*. (2025). To ensure compatibility with the existing

dataset, all sequences were trimmed to a common length of 548 bp, resulting in an eastern Adriatic dataset comprising 160 individuals. Species identity of all sequences was verified by BLASTn searches against the GenBank nucleotide database, and sequences were translated using the invertebrate mitochondrial genetic code to check for stop codons.

Genetic diversity indices, including the number of haplotypes (H), haplotype diversity (Hd), number of polymorphic sites (S), nucleotide diversity (π), and average number of nucleotide differences (k), were calculated using DnaSP v6.12.03 (Rozas *et al*., 2017). A median-joining haplotype network was constructed in PopART v1.7 (Leigh and Bryant, 2015) to visualise haplotype relationships across the Adriatic basin. Population genetic structure was evaluated through analysis of molecular variance (AMOVA) and pairwise genetic differentiation (Φ_{ST}), calculated in ARLEQUIN v3.5.2.2 (Excoffier and Lischer, 2010) based on the Tamura–Nei distance model. Tajima's *D* and Fu's *Fs* neutrality tests, also implemented in ARLEQUIN, were used to infer demographic history. Spatial genetic structure was examined by comparing the Southern Adriatic population with the previously analysed Northern and Central Adriatic populations from Petrić *et al*. (2025).

RESULTS AND DISCUSSION

The 39 Southern Adriatic *Loligo vulgaris* COI sequences yielded a 627 bp alignment containing 22 polymorphic sites (15 singletons, 7 parsimony informative) and 14 haplotypes (Hd = 0.795, π = 0.00302, k = 1.892). Two newly identified haplotypes were deposited in GenBank (accession numbers PZ713251 and PZ713252). To enable comparison with the previously published dataset, Southern Adriatic sequences were trimmed to 548 bp and combined with 121 sequences from the Northern and Central Adriatic (Petrić *et al*., 2025; GenBank accession numbers PV023191–PV023311), producing the first eastern Adriatic dataset for *L. vulgaris* (160 individuals). All comparative analyses were based on this 548 bp alignment common to all samples. Trimming removed three polymorphic sites located in the excluded end regions, reducing the number of Southern Adriatic haplotypes to 12 (Hd = 0.742, k = 1.690), whereas π increased slightly (0.00308) because the number of pairwise differences decreased proportionally less than sequence length.

The combined dataset contained 29 polymorphic sites and 32 haplotypes, with an overall haplotype diversity of 0.806 and nucleotide diversity of 0.00264 (Table 1). Haplotype diversity was highest in the Central Adriatic (Hd = 0.863, H = 21) and lowest in the Southern Adriatic (Hd = 0.742, H = 12), while nucleotide diversity was highest in the Southern Adriatic (π = 0.00308) and lowest in the Northern Adriatic (π = 0.00208) (Table 1). These genetic diversity indices fell within the range reported for other loliginid squids (García-Mayoral *et al*., 2020; Göpel *et al*., 2022).

The median-joining haplotype network retained the star-shaped topology previously described for the Northern and Central Adriatic populations (Fig. 1), with a single dominant haplotype (Hap_1) shared among all three sub-basins and most remaining haplotypes differing by only a single mutational step. Of the 12 haplotypes detected in the Southern Adriatic, 10 were shared with Northern and/or Central Adriatic populations, while only 2 were unique to the South. The inclusion of Southern Adriatic samples did not reveal any geographically distinct lineage or alter the previously observed network structure, indicating extensive haplotype sharing and connectivity across the eastern Adriatic. A single peripheral haplotype (Hap_31), separated by 10 mutational steps from the main network, was found in one individual from the Southern Adriatic. BLASTn confirmed its identity as *L. vulgaris* (99.53% identity to accession no. MN977133), and its translation contained no stop codons.

Analysis of molecular variance (AMOVA) attributed 98.60% of the total genetic variation to differences within sub-basins and 1.40% to differences among them (Φ_{ST} = 0.01396, p = 0.062). Pairwise Φ_{ST} values were low: 0.00126 between the Northern and Southern Adriatic (p = 0.858), 0.00870 between the Northern and Central Adriatic (p = 0.378) and 0.02861 between the Central and Southern Adriatic (p = 0.486).

Tajima's *D* was significantly negative in all three sub-basins, with the most negative value recorded in the Southern Adriatic (*D* = -2.061, p = 0.006), followed by the Northern (*D* = -1.776, p = 0.012) and Central Adriatic (*D* = -1.698, p = 0.025). Fu's *Fs* was significantly

Table 1. Genetic diversity estimates for COI sequences of *Loligo vulgaris* from the Adriatic Sea. N, number of individuals; S, number of polymorphic sites; H, number of haplotypes; Hd, haplotype diversity; SD, standard deviation; π, nucleotide diversity; k, average number of nucleotide differences.

Area	N	S	H	Hd ± SD	π	k
Southern Adriatic	39	19	12	0.742 ± 0.068	0.00308	1.690
Central Adriatic	67	17	21	0.863 ± 0.025	0.00280	1.535
Northern Adriatic	54	13	17	0.756 ± 0.054	0.00208	1.141
Overall	160	29	32	0.806 ± 0.003	0.00264	1.445

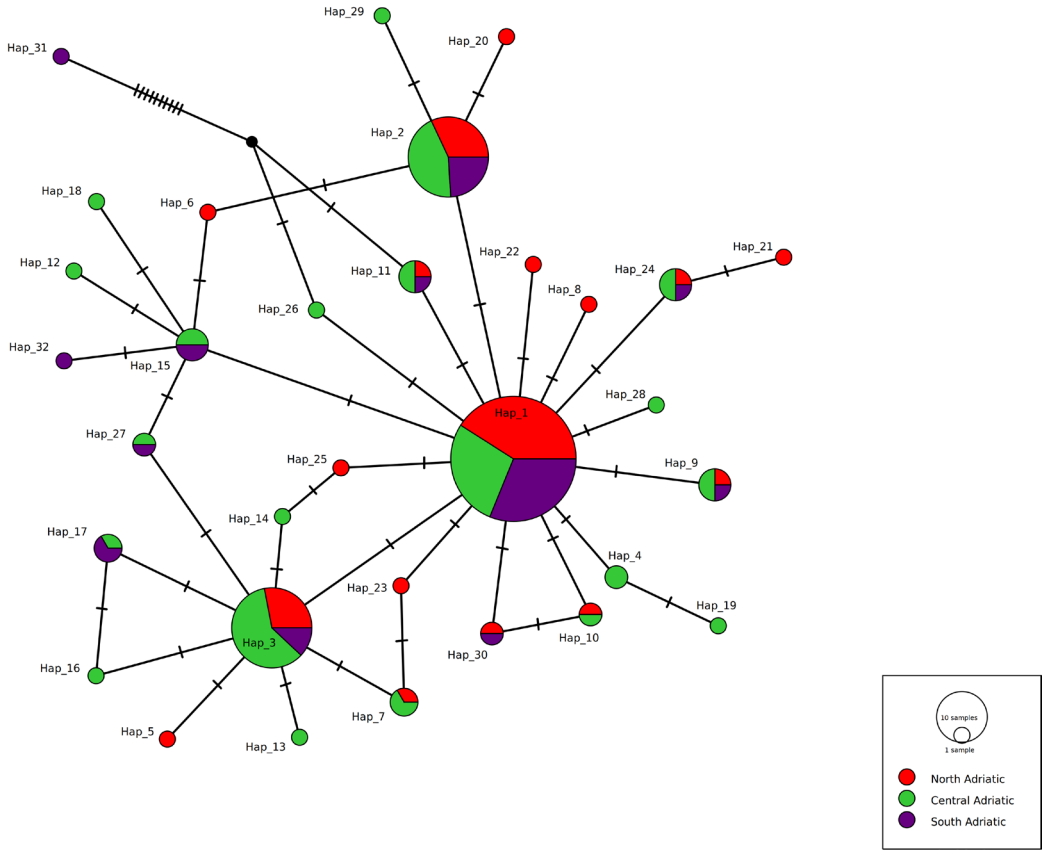


Fig. 1. Median-joining haplotype network of *Loligo vulgaris* COI sequences from the Adriatic Sea (N = 160). Circle sizes are proportional to haplotype frequency. Colours represent sub-basins in the eastern Adriatic: North Adriatic (red), Central Adriatic (green), and South Adriatic (purple). Bars on branches indicate the number of mutations between haplotypes. Black dots represent missing (unsampled) haplotypes.

negative across all sub-basins: Southern Adriatic (Fs = -5.529, p = 0.003), Central Adriatic (Fs = -18.047, p < 0.001), and Northern Adriatic (Fs = -15.751, p < 0.001). Both statistics reflect an excess of rare, low-frequency haplotypes in all regions, a pattern characteristic of recent population growth (Grant and Bowen, 1998).

Patterns of genetic connectivity in the Adriatic vary considerably among marine taxa and largely reflect differences in life-history traits and dispersal potential. While genetic discontinuities associated with Adriatic hydrographic features have been reported for several benthic or relatively low-dispersal species (López-Márquez *et al*., 2019; Sefc *et al*., 2020; Šegvić-Bubić *et al*., 2020), highly dispersive species often exhibit basin-wide genetic homogeneity (Garoia *et al*., 2004b; Pavičić *et al*., 2020; Hamilton *et al*., 2023). The present results position *L. vulgaris* within the latter group. Its extended planktonic paralarval stage, coupled with high adult mobility, likely facilitates sufficient dispersal to maintain gene flow throughout the Adriatic, preventing the South Adriatic Pit from producing detectable genetic differentiation at the mitochondrial level.

Because the Southern Adriatic represents the region where potential restriction of gene flow would be expected to be strongest, the genetic similarity observed between Montenegrin and Northern/Central Adriatic populations provides no evidence that the South Adriatic Pit acts as a barrier to gene flow for *L. vulgaris* along the eastern Adriatic. Rather than acting as a barrier, the South Adriatic Pit might contribute to maintaining connectivity between southern and northern Adriatic populations through its circulation dynamics. The South Adriatic Pit is characterized by a persistent cyclonic circulation system that forms part of the broader Adriatic circulation pattern, with northward transport along the eastern Adriatic coast and cross-basin exchange toward the western Adriatic margin (Orlić *et al*., 1992). Such circulation features may enhance the retention and redistribution of pelagic larvae throughout the basin. However, because the South Adriatic Pit represents the main gateway between the Adriatic and the wider Mediterranean, future studies incorporating genome-wide markers and comparative sampling from Ionian and eastern Mediterranean populations will be important for determining whether gene flow through this corridor contributes to broader Mediterranean connectivity.

The star-shaped haplotype network and significantly negative Tajima's D and Fu's Fs values across all three sub-basins indicate recent demographic expansion.

These signatures may also reflect a selective sweep or population expansion following a bottleneck (Tajima, 1989; Fu, 1997). Under such demographic conditions, relatively little time may have elapsed for genetic drift to generate detectable spatial structure at mitochondrial markers, even if gene flow is not entirely unrestricted.

Several limitations should be considered. COI is a single, maternally inherited marker and may not detect subtle structure revealed by genome-wide nuclear markers, as shown for *L. vulgaris* by García-Mayoral *et al*. (2024). In addition, the Southern Adriatic was represented by a single locality sampled in a single year, with a smaller sample size than the Northern and Central Adriatic. These factors reduce power to detect weak population subdivision. Therefore, absence of significant COI differentiation should be interpreted as consistent with high connectivity along the eastern Adriatic rather than as proof of a single panmictic stock.

CONCLUSION

By adding Southern Adriatic samples to the previously published Northern and Central Adriatic dataset, this study extends the COI-based assessment of *Loligo vulgaris* to all three eastern Adriatic sub-basins. No spatial genetic structure was detected, and there was no evidence that the South Adriatic Pit acts as a barrier to gene flow. Studies with broader spatial and temporal sampling, including the western Adriatic, and nuclear markers are needed before these results can be used to define stock units for fisheries management.

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