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# Reproductive traits of the invasive round goby (*Neogobius melanostomus*) along a latitudinal span in Europe

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**Abstract** The Ponto-Caspian region is a hotspot of the successful establishment of non-native species in freshwater ecosystems, with the round goby *Neogobius melanostomus* being a notorious example. However, comparing data on its reproductive biology is complicated due to differing data collection methods, traits examined, and sampling times. To address these inconsistencies, we conducted a study of five established round goby populations across a broad latitudinal range in Europe during a similar period adjusted to the species' spawning period. The sample included 83 female round gobies from Türkiye, Croatia, Slovakia, Poland, and Finland. We compared reproductive traits, including absolute, batch, and relative fecundity, oocyte size, and gonado-somatic index (GSI), as well as body condition factor. Relative fecundity and condition factor exhibited an interesting pattern, indicating high reproductive investment

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in the Turkish population through significantly higher values of relative fecundity and lower condition factor compared to other populations. Although no significant differences in GSI values were found among populations, a trend was observed, with the highest values in Türkiye and the lowest in Finland. Generalized Linear Modeling revealed that relative fecundity was positively associated with latitude but negatively influenced by condition. Our findings support the suggested high phenotypic plasticity, particularly in this life-history trait.

**Keywords** Fecundity · Phenotypic plasticity · GSI · GLM

## Introduction

Global biodiversity and ecosystem functioning are profoundly compromised by invasive species. While their life-history traits and interactions within recipient communities have been the subject of numerous studies, there are still some knowledge gaps such as limited knowledge on the impact of epigenetic and rapid evolutionary changes (Ricciardi et al. 2017). Among the various features that are considered, reproductive parameters are often the most studied, as they determine the potential for population growth, spread, persistence, and sustainability (Sakai et al. 2001). Data such as fecundity, age at maturity, occurrence of parental care, or reproductive investment can reveal effective reproductive tactics and provide valuable insights into the success and potential impact of invasive species (Grabowska and Przybylski 2015). Many studies have investigated the relationship between life-history traits and environmental factors to better understand invasion patterns and processes (e.g. Alcaraz and García-Berthou 2007; Masson et al. 2015; Santi et al. 2020; Kurtul et al. 2022). Research on one of the most invasive fish, eastern mosquitofish, *Gambusia holbrooki* Girard, 1859, has shown that salinity and thermal regime can influence body size and reproduction (Alcaraz and García-Berthou 2007; Santi et al. 2020; Kurtul et al. 2022). Temperature plays a crucial role in increasing reproductive investment and juvenile growth, and early maturity in another successful invader, pumpkinseed, *Lepomis gibbosus* (Linnaeus, 1758) (Fox et al. 2007; Masson et al. 2015). Also, several environmental factors significantly affect non-native goldfish, *Carassius auratus* (Linnaeus, 1758) in China, including elevation, population density, and isothermality (Jia et al. 2019). Similarly, its congener gibel carp *Carassius gibelio* (Bloch, 1782) is known for its ability to change its mode of reproduction (i.e., bisexual and unisexual reproduction) depending on environmental conditions and the stage of invasion (Tarkan et al. 2012; Przybył et al. 2020). Understanding the reproductive biology of invasive species in relation to the environmental effects is, therefore, crucial in predicting and managing their populations and ecosystem dynamics.

The Ponto-Caspian round goby, *Neogobius melanostomus* (Pallas, 1814), is one of the most successful freshwater invaders in Europe and North America (Kornis et al. 2012). The species displays several phenotypic traits that facilitate its rapid range expansion, such as an opportunistic feeding strategy and wide tolerance to various environmental factors (Charlebois et al. 1997; Kornis et al. 2012). Another crucial feature that promotes the establishment of new populations is observed variations in reproductive parameters, especially in non-native areas (Hôrková and Kováč 2014). Relatively high fecundity, parental care, existence of alternative male reproductive tactics, and early maturation of the species are considered beneficial and increase its invasive potential (Dashinov and Uzunova 2021). The round goby is a batch spawner with a relatively long spawning season lasting from March/April to September (Charlebois et al. 1997; Kornis et al. 2012; Cerwenka et al. 2023).

The reproduction of round goby has been evaluated in different locations (Kornis et al. 2012; Cerwenka et al. 2023), compared between native and non-native populations (Hôrková and Kováč 2014; Konečná et al. 2016), and established and expanding populations (Brandner et al. 2013; Kornis et al. 2017; Masson et al. 2018; Dashinov and Uzunova 2021). Most of the studies indicate similar spawning period beginning in March with highest GSI values in April or May (Hôrková and Kováč 2014; Gertzen et al. 2016; Aydin 2021; Dashinov and Uzunova 2021). Differences regarding the origin were shown

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by Hôrková and Kováč (2014), where non-native populations displayed higher values in the absolute number of oocytes, the real absolute fecundity and relative fecundity. However, the results were discussed by Konečná et al. (2016), who implied that round goby traits are influenced by local environmental conditions, not their "nativeness". On the other hand, studies of invasive round goby in different water bodies on two continents revealed similar patterns in life-history, including reproductive traits, despite differences in environmental parameters and genetic divergences (Masson et al. 2018). Variations between frontal (according to Brandner et al. 2013) and established populations were also observed, with body condition and reproductive investment variability dependent on time of the introduction (Brandner et al. 2013; Kornis et al. 2017; Masson et al. 2018; Dashinov and Uzunova 2021). Nonetheless, regardless of the differences between the compared populations, most studies indicate a significant plasticity of the species in reproductive traits (Hôrková and Kováč 2014; Kornis et al. 2017; Masson et al. 2018; Dashinov and Uzunova 2021).

Invasion of Ponto-Caspian round goby has lasted over four decades at some locations (Kornis et al. 2012), and the species is increasingly being used as a model species for invasion biology (Cerwenka et al. 2023). Despite the vast amount of literature on round goby biology (Charlebois et al. 1997; Kornis et al. 2012; Dashinov and Uzunova 2021), comparing reproductive traits is often biased due to disparities in methods used to process the data, the various traits examined, and different sampling times (Hôrková and Kováč 2014; Gertzen et al. 2016). To address these discrepancies, we sampled five established round goby populations along a wide latitudinal span in Europe during a similar period adjusted to the suggested onset of species spawning based on the available data and personal knowledge. We aimed to investigate the reproductive parameters along the latitudinal span and predicted that round goby shows variability in response to reproductive traits at a large spatial scale. We posit that southern populations exhibit higher reproductive investment than northern ones, as warmer waters provide longer access to available resources. Additionally, given the large latitudinal span, populations on both edges (Finland and Türkiye) are expected to display more pronounced differences.

## Materials and methods

### Study area and sampling

Round goby females were collected from one location in each of five countries (Fig. 1; Table 1), covering the species native (Türkiye) and non-native range (Croatia, Slovakia, Poland, and Finland). Except for Finland, all sampling sites were located on freshwater rivers (Sava, Danube, Radunia, and Bağırganlı Rivers; Table 1). In Finland, all fish were caught from the coastal area of Helsinki in the Baltic Sea, characterized by low salinity due to freshwaters and semi-enclosed locations (4 PSU measured at the sites; Table 1). However, increased salinity might translate into larger body size of collected specimens, which was shown in this species before (Kornis et al. 2012). The climate data set used in Fig. 1 was sourced from WorldClim version 2.1, which includes climate data for the period 1970 to 2000, specifically the mean max temperature for April (Fick and Hijmans 2017) to illustrate temperature trends along the latitudinal gradient. The sampling sites were homogeneous based on substrate type including a mix of sand and gravel with stones or rip-raps. Only established populations (at least 10 years since first observation) at each site were sampled (Kornis et al. 2012; Cerwenka et al. 2023). Fish were caught during the reproductive season (from April until mid-May; Table 1), and each time we attempted to catch the peak of spawning to maintain the uniformity of gonad development based on the published data, weather conditions, and own experience. Round gobies were obtained by backpack electrofishing (EFGI 650; BSE Specialelektronik Bretschneider, Germany) or fishing rod (Finland only) and euthanized by a spinal cord rupture. In the field, all specimens were measured for total length (TL) to the nearest 1 mm and weighed (W) to the nearest 10 mg before euthanasia and dissection. Dissection was done in the field immediately following euthanasia. Female gonads were removed, weighed (WG) (nearest 10 mg), and frozen on dry ice.

### Reproductive parameters analysis

In the laboratory from each ovary, three subsamples (anterior, central, and posterior part of one gonad) were collected and weighed (nearest 0.1 mg). Oocytes were photographed under a stereomicroscope (Nikon

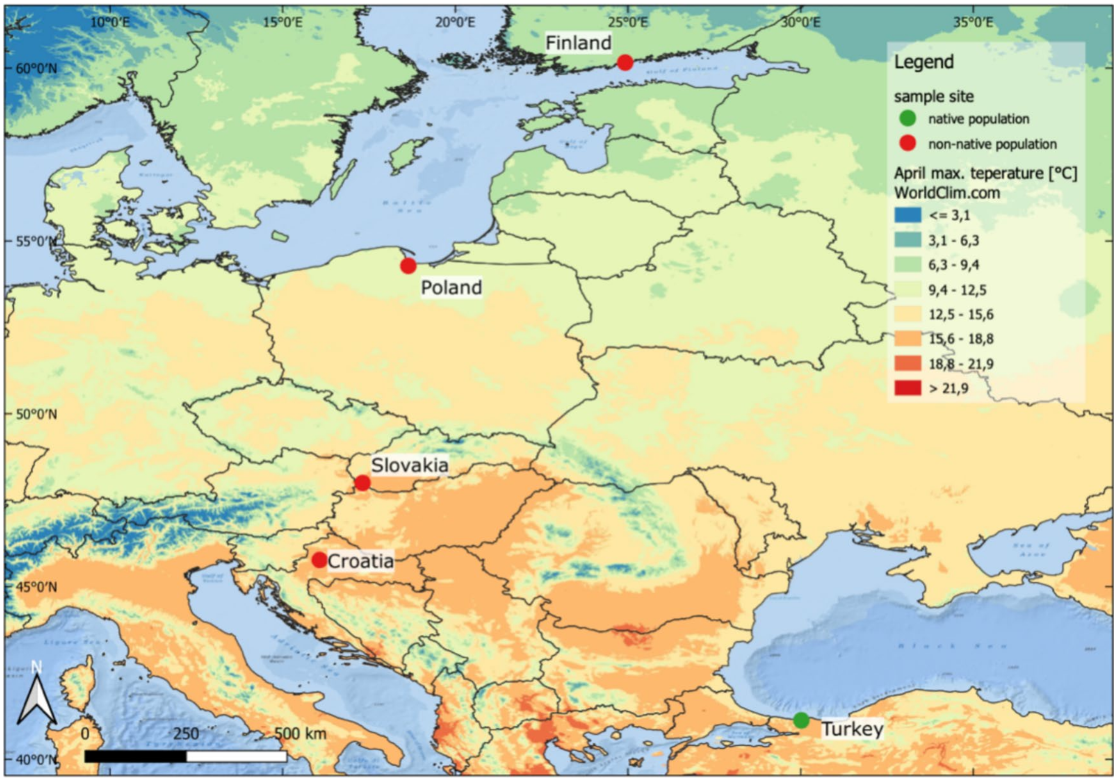

**Fig. 1** Map of the sampling sites. The locations where round goby (*Neogobius melanostomus*) populations were sampled in April and May 2022 (map created in QGIS 3.16.4-Hannover)

**Table 1** Water temperature, salinity, and characteristics of round goby *Neogobius melanostomus* in sampling sites collected in Türkiye, Croatia, Slovakia, Poland, and Finland. Mean values with standard deviation and range for total length (TL) and body weight (W)

| Country | Sampling site | Date | No. of mature females | TL (mm) min–max (mean) | Body weight (g) min–max (mean) | Water temperature (°C) | Salinity (PSU) |
|---|---|---|---|---|---|---|---|
| Türkiye | Bağırganlı River | 09/04/2022 | 15 | 65–94 (82) | 2.5–9.0 (5.5) | 13 | 0.21 |
| Croatia | Sava River | 22/04/2022 | 17 | 71–132 (104) | 4.5–28.5 (16.1) | 13 | 0.18 |
| Slovakia | Danube River | 27/04/2022 | 21 | 57–114 (75) | 2.8–19.9 (6.2) | 12 | 0.16 |
| Poland | Radunia River | 19/05/2022 | 16 | 71–120 (97) | 4.6–25.0 (13.2) | 16 | 0.18 |
| Finland | Coastal area of Helsinki, Baltic Sea | 10/05/2022 | 14 | 91–150 (116) | 8.6–58.2 (24.2) | 9 | 4.33 |

SMZ1000), counted, and their diameters measured to the nearest 0.001 mm using LUCIA 5 image analysis software. The following reproductive traits were analyzed: (i) absolute fecundity (FA)—number of mature eggs produced by a female during a breeding season; (ii) relative fecundity (FR)—number of eggs produced per unit of body weight; (iii) batch fecundity (Fb)—number of mature eggs per batch; and (iv) gonado-somatic index (GSI)—gonad development and reproductive investment (Miller and Kendall 2009; Wootton and Smith 2014). The gravimetric method was used to evaluate FA—total oocytes number per female and FR; i.e., number of oocytes per 1 g of female body weight was calculated (Bagenal

1978). For each sampling site, oocyte diameter data were pooled and used to obtain their size-frequency histograms. If the frequency of oocyte size distribution was polynomial, the Bhattacharya method followed by modal class progression analysis was used to decompose observed distributions into Gaussian components (Bhattacharya 1967). This procedure allows separation of discrete normal distributions in the data based on a separation index in the case that the difference between successive Gaussian means divided by the difference between their standard deviations exceeds 2 (Gayanilo et al. 2005). Since gobies exhibit batch spawning behavior (Grabowska et al. 2021), we additionally calculated Fb. This parameter was quantified as the count of mature oocytes following the classification outlined by Tomczak and Sapota (2006) and accessible in the gonad. We set a threshold of 0.76 (considering all eggs with diameter greater than 0.76), corresponding to stages 3–5 of gonad maturation (Tomczak and Sapota 2006). To determine reproductive allocation, GSI (Wootton and Smith 2014) was calculated as follows: $GSI = 100 \times WG \times W^{-1}$, where WG is the gonads weight (g) and $W$ is the body weight (g). For each fish, the Fulton condition factor (referred as $K$ or condition) was calculated using the following equation: $K = 100 \times W \times TL^{-3}$, where $W$ is the body weight (g) and $TL$ is the total length (cm) (Le Cren 1951).

To compare reproductive traits—FA, FR, and Fb (log-transformed) and GSI and $K$ (arcsine-transformed)—across round goby populations, an analysis of covariance (ANCOVA) was conducted with country of origin as a fixed factor and total body length (TL, mm) as a covariate. When significant differences were observed, multiple comparison tests (post-hoc HSD Tukey test) were used (Zar 2010). All values were reported as mean ± standard error. Before running ANCOVA, the data were examined for normality (the Shapiro–Wilk test) and homogeneity of variance (Levene's test). When assumptions of ANCOVA were not met, the Kruskal–Wallis non-parametric analysis of variance following the Dunn post-hoc test was used.

To identify the most important drivers of FR as a proxy of reproductive production, a model construction initially assessed the collinearity (using the variance inflation factor, VIF) among the numeric predictor variables (nativeness status, total length, weight, condition, temperature, salinity, and latitude) using the function *corvif* (Zuur et al. 2009), where 3 was used as the threshold for indicating high collinearity. Then, to account for potential biases in the data, we performed a model selection based on the Akaike Information Criterion (AIC) with the Information Theoretic approach (AIC-IT) building a "base-model" and using the dredge function from MuMIn R package (Bartoń 2024). The dredge function creates a subset of candidate models based on an algorithm called "dredging," with different combinations of fixed effects balancing the trade-off between model complexity and model fit. The model with the lowest AIC value was chosen as the best-fit model. While multiple models were considered, we ultimately selected the model with the minimum AIC value as the most parsimonious. Therefore, the final model contained the predictors nativeness status, latitude, and condition and was fitted using a Gaussian GLM. The significance level for all tests was set at $p = 0.05$. All analyses were performed in R (version 4.2.3, R Core Team 2023).

## Results

### Fecundity

Fecundity was estimated for 83 mature females from all sites (Tables 1 and 2). The ANCOVA revealed a significant effect of both country and body size on FA ($F_{4,77} = 5.79$, $p < 0.001$) with TL showing a strong positive association with FA ($F_{1,77} = 186.42$, $p < 0.001$). For FR, both country ($F_{4,77} = 11.54$, $p < 0.001$) and TL ($F_{1,77} = 13.97$, $p < 0.001$) also had significant effects. A post-hoc HSD Tukey test showed significant differences between Croatia and Finland ($p = 0.015$), Croatia and Poland ($p = 0.037$), Croatia and Türkiye ($p < 0.001$), Türkiye and Poland ($p = 0.042$), and Slovakia and Türkiye ($p < 0.001$; Table S1, Figure S1). Relative fecundity reached the highest values in Türkiye (63), followed by Poland, Slovakia, Finland, and Croatia (43, 41, 41, and 34, respectively). The highest values of FA were observed in females sampled in Finland (FA = 887), while the lowest in Slovak specimens (FA = 241) (Fig. S2). The multiple comparisons (the post-hoc Tukey's test) showed differences between Croatia and Finland ($p = 0.034$), Croatia and Poland ($p = 0.007$), and Poland and Slovakia ($p = 0.019$) (Table S2).

The maximum Fb was recorded in females sampled in Finland (Fb = 74), whereas the minimum was observed in specimens from Slovakia (Fb = 46). Batch

**Table 2** Absolute fecundity (FA), relative fecundity (FR), oocyte diameter (OD), Fulton condition, and gonado-somatic index (GSI) measured in round goby *Neogobius melanostomus* collected in Türkiye, Croatia, Slovakia, Poland, and Finland

| Country | FA min–max eggs (Mean ± SD) | FR min–max eggs/g of body weight (mean ± SD) | OD [mm] min–max (Mean ± SD) | Condition Mean ± SD | GSI Mean ± SD |
|---|---|---|---|---|---|
| Türkiye | 164–463<br>(336 ± 85.55) | 46–98<br>(63 ± 15.40) | 0.32–2.20<br>(1.10 ± 0.37) | 0.95 ± 0.07 | 9.76 ± 5.80 |
| Croatia | 158–1172<br>(500 ± 257.98) | 9–51<br>(33 ± 11.13) | 0.26–2.47<br>(1.11 ± 0.44) | 1.23 ± 0.12 | 7.31 ± 4.79 |
| Slovakia | 110–639<br>(241 ± 146.50) | 30–55<br>(41 ± 7.94) | 0.34–2.36<br>(1.16 ± 0.38) | 1.31 ± 0.16 | 7.62 ± 5.06 |
| Poland | 199–1107<br>(559 ± 261.68) | 33–57<br>(43 ± 7.76) | 0.44–2.30<br>(1.27 ± 0.34) | 1.36 ± 0.13 | 9.51 ± 4.92 |
| Finland | 333–2400<br>(887 ± 515.76) | 27–58<br>(40 ± 11.06) | 0.26–1.89<br>(1.01 ± 0.33) | 1.37 ± 0.21 | 4.52 ± 2.07 |

fecundity of round goby exhibited no significant variation for country ($F_{4,84} = 2.28$, $p = 0.068$) and TL ($F_{4,84} = 0.78$, $p = 0.381$; Fig. S3).

### Oocyte size

In all study sites, egg diameter histograms were polymodal and Bhattacharya's method revealed two distinctive size groups in each population. The size of the largest (ready for spawning) oocytes differed between sites ($H_{4,\ 5093} = 1986.58$, $p < 0.001$). A post-hoc Dunn test revealed differences between all sites.

Only in Türkiye the number of small oocytes was similar to the number of larger oocytes, and differences in their size were less distinct (Fig. S4). The diameter of small oocytes was on average 0.83 mm (±0.20) and of the larger class of oocytes 1.42 mm (±0.20). In Croatia, Slovakia, Poland, and Finland, groups of smaller oocytes were more numerous (Fig. S4). In Croatia, the diameter of small oocytes was on average 0.87 mm (±0.20) and the average size of the larger class of oocytes was 1.67 mm (±0.27); in Slovakia, it was 1.07 mm (±0.21) and 1.78 mm (±0.18); in Poland, it was 1.21 mm (±0.28) 1.94 mm (±0.10); in Finland, it was 0.83 mm (±0.22) 1.35 mm (±0.17).

### Gonado-somatic index and fish condition

No significant effects were observed for GSI ($F_{4,76} = 2.48$, $p = 0.051$; TL $F_{1,76} = 0.46$, $p = 0.498$); Table S3, Fig. S5). However, the highest average GSI value of round goby females was observed in Türkiye (GSI = 9.7), followed by Poland (9.5), Slovakia (7.6), Croatia (7.3), and Finland (4.5).

The highest average *K* value was observed in Finland. The *K* varied significantly among sites ($F_{4,\ 76} = 22.41$, $p < 0.001$), with TL showing a positive association with *K* ($F_{1,76} = 5.39$, $p < 0.023$), and post-hoc HDS Tukey test revealing significantly lower values for fish from Türkiye only ($p < 0.001$; Table S4, Fig. S6).

### Association of environmental factors with relative fecundity

The results indicate that the FR of the native population was significantly higher than that in non-native populations (Table 3). Latitude had a significant positive effect on FR, with higher latitudes associated with greater relative fecundity. However, temperature and condition had significant negative effects on FR.

## Discussion

Regarding the large latitudinal scale, phenotypic patterns can be driven by thermal regime (Riesch et al. 2018), which would likely be most intense in

**Table 3** Summary of Gaussian GLM to model relative fecundity of round goby *Neogobius melanostomus* as a function of nativeness status, latitude, and condition. All tests are significant at $p = 0.05$

| Model parameter | Estimate | SE | *p* |
|---|---|---|---|
| $\text{Intercept}_{(\text{native})}$ | 63.85 | 11.92 | 0.001 |
| $\text{Status}_{(\text{non-native})}$ | − 21.32 | 4.79 | 0.001 |
| Latitude | 0.49 | 0.24 | 0.045 |
| Condition | − 21.290 | 8.29 | 0.012 |

freshwater systems (Pankhurst and Munday 2011). Gaining insight into the impacts of latitude on a species' life-history traits is crucial in predicting its capacity for successful invasion, especially in the face of current climate change scenarios (Benejam et al. 2009). Life-history traits of invasive species are surveyed across limited (Cucherousset et al. 2009) as well as wide geographical gradients (Santi et al. 2020; Zhou et al. 2022). In general, reproductive investment tends to decrease as latitude increases in various fish species (Benejam et al. 2009; Riesch et al. 2018), including non-native ones. For example, invasive eastern mosquitofish display higher breeding allocation and lower condition in southern compared to northern populations (Benejam et al. 2009). This is similar to our results for round goby, where relative fecundity was highest for the most southern population (Türkiye) with the lowest condition factor at the same time. The same relationship was observed for invasive pumpkinseed in northwestern Europe (Copp et al. 2002); however, recent studies on this species (Cucherousset et al. 2009) did not support this, suggesting context-dependency. In the present study, we did not focus on temperature directly; rather, we considered thermal regime as derived from latitudinal span. Round goby exhibits a wide temperature tolerance, allowing it to establish across a broad range of temperatures, with preferences for warmer waters (Kornis et al. 2012). The species' endocrine system is active throughout the year (Charlebois et al. 1997), enabling it to extend the spawning period in response to favorable conditions (MacInnis and Corkum 2000). There was a trend for reproductive investment (based on GSI), which was highest in Türkiye and lowest in Finland; however, this difference was not significant. A lower energetic investment in reproduction reflected in GSI of round goby in Finland may stem from a reduced energy reserve available, which is in accordance with our predictions. At lower temperatures, the energetic cost of survival may limit the energy available for gonadal development. Fish in temperate and higher latitudes often rely on the photoperiod as a consistent and accurate cue for predicting changes in the environment, which, in combination with water temperature, is an even more dependable cue than either factor alone (Wootton and Smith 2014). In the case of round goby, Gertzen et al. (2016) suggested that photoperiod has no effect due to high variety on spawning onset (i.e., the onset of spawning differs across the years).

Population comparisons across different years and locations suggest a high degree of phenotypic plasticity in round goby (Hôrková and Kováč 2014; Masson et al. 2018). In the current study, we focused on reproductive parameters, which are critical for population establishment and growth. Oocyte size and number are considered to be primary reproductive effort, typically measured as GSI (Miller 1984). Our results indicate that GSI did not vary significantly across the sampled populations and fell within the range reported by other authors during spawning peaks in April and/or May (MacInnis and Corkum 2000; Hôrková and Kováč 2014; Gertzen et al. 2016; Dashinov and Uzunova 2021). The lack of variation in GSI among the investigated populations suggests similar reproductive investment along the tested latitude span; however, some trend with decreasing GSI values from Türkiye to Finland was noted. We observed a much higher ratio between the number of oocytes and body mass, defined as relative fecundity, in the native Turkish population compared to the non-native populations in Croatia, Slovakia, Poland, and Finland. The reverse pattern was observed in the condition factor, which may indicate a direct investment of available energy resources into spawning by the native population. The better condition of Ponto-Caspian gobies in the non-native range could result from various factors, including reduced competitive interactions and competitive advantage in resource acquisition over native species (Gutowsky and Fox 2012; Kornis et al. 2012; Valová et al. 2015). In contrast, in the site of origin, round goby may have reached ecological equilibrium through coevolution and may not necessarily be superior to populations of other species (Charlebois et al. 1997).

Regarding the differentiating factor shaping the reproductive performance of round goby "nativeness", environment, or invasion phase are usually taken into consideration (Gutowsky and Fox 2012; Hôrková and Kováč 2014; Konečná et al. 2016; Masson et al. 2018). There is no unambiguous premise as to which factor plays a crucial role. A comprehensive analysis of various species, both animals and plants, indicates that, in general, they perform better in invasive compared to native ranges (Parker et al. 2013). Hôrková and Kováč (2014) found that the theory of alternative ontogenies and invasive potential (AOIP) applies to round goby.

This theory predicts that phenotypic plasticity facilitates invasion success and that species can perform different life-history strategies in response to stable/unstable conditions. Their findings showed higher values of relative fecundity in non-native populations than in native ones, suggesting that influencing factors could be the origin. However, the results we obtained were contradictory to Hôrková and Kováč (2014) regarding relative fecundity, which was enhanced in the native population. In accordance with the AOIP hypothesis predictions, established non-native populations should exhibit a reversal in life-history strategies, characterized by a gradual decrease in relative fecundity compared to frontal populations (i.e., those at the beginning of invasion). Konečná et al. (2016) found that reproductive traits of the round goby are shaped by local environmental conditions rather than "nativeness" or invasion stage. One of the main evaluated parameters was absolute fecundity, which was lower in non-native populations than in the native one. It is worth highlighting that, in the mentioned studies, the non-native population was at an early stage of settlement. This parameter (absolute fecundity) in our samples showed no clear pattern concerning the location. Masson et al. (2018) demonstrated, through a comparison of round goby populations on two continents, that life-history traits, including reproductive investment, are driven by the time of introduction instead of environmental conditions. Still, only non-native populations were compared. In the current study, we tried to avoid discrepancies as variation in invasion stage, sampling time, sampled habitat, material processing, and even the persons performing research were the same. As in most field surveys, we were not able to control numerous factors such as weather conditions and water level. The results allowed us to compare populations regarding the potential thermal and geographic span; it is important to stress that nativeness was not our primary focus. The study provides an insight into round goby reproduction in a wide latitudinal span at the same moment, which is the first such comprehensive approach for this species.

In conclusion, the invasion success of round goby is strongly supported by its phenotypic plasticity, including the reproductive strategy. Various studies, including the present one, have shown that the species can display alternative tactics depending on different factors. Despite our results, we are not certain that origin ("nativeness") has the most decisive effect. One possible explanation for the differences between native and non-native populations is the stable relationship between organisms and their environment. Over an extended period of evolution, organisms in their native habitat may have developed specialized adaptations, whereas those in non-native habitats may exhibit more generalized traits (Hôrková and Kováč 2014). However, climate change scenarios cover both the native and invasive range of the species, and shifts in the apparently stable circumstances can lead to more extreme and demanding conditions at the origin site, which can currently be observed. Thus, external factors could cause native populations to adopt more generalized traits, while non-native populations may thrive under optimal conditions. The ongoing successful invasion of round goby seems to support this hypothesis.

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**Author contributions** D.B.* and B.J. conceived the idea. D.B.*, B.J., A.S.T, M.P, J.L., D.B., K.S.S., B.S., organized field surveys and collected materials. K.P. and A.S.T. analysed the samples and performed the data analysis. D.B.* and K.P. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication. (*Dagmara Błońska)

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**Data availability** All data constituting the basis of the present and previous study are available at https://doi.org/10.18150/LKZ9HM.

## Declarations

**Ethics approval** This article does not contain any studies with human participants performed or experiments conducted on animals by any of the authors. All care and use of animals were complied with animal welfare international/national laws, guidelines, and policies. The collection of round goby individuals did not require special approval from an Ethical Committee in all the countries sampled, including Türkiye, Croatia, Slovakia, Poland, and Finland. In each country, the capture of fish was conducted in accordance with national regulations, which, in the cases of Türkiye, Croatia, and Poland, necessitated additional tenancy agreements (E-67852565–140.03.03–5071302, UP/I-324–01/22–01/5, and PGR-W/Z/704/2022, respectively). The euthanasia procedure involved the use of spinal cord rupture, a method chosen to ensure the humane treatment of animals and to prevent unnecessary suffering in accordance with ARRIVE guidelines.

**Competing interests** The authors declare that they have no competing interests.

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