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RESEARCH PAPER

From Native to Invasive. Shifts in Strategy of Western Tubenose Goby in Slovakia

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Abstract

The western tubenose goby belongs to the family Gobiidae, which contains the most invasive species responsible for the invasion of waters in Europe as well as in North America. In our study, we analysed life-history traits, morphology, and tested the hypothesis of alternative ontogenies and invasive potential of nine *Proterorhinus semilunaris* populations coming from melioration channels of Žitný Island (Slovakia). Populations caught in April 2015 were female-dominated and characterized by rapid reproduction, since all samples were already mature. The gonadosomatic index (4.12 to 46.67%), absolute (118–2622), relative number of oocytes (94–4352), and the size of oocytes (0.06 to 1.46 mm) were significantly different compared to all native and non-native areas of occurrence. Samples were characterized with three size groups of oocytes. There was no significant difference in the condition between females and males within each population, thus, they were both in good and/or bad condition. The majority of morphological traits were statistically significant, while more than half can be suggested to have biological importance. Significant differences were related to characters located on the head, fins, and associated with the length or height of the body.

Introduction

Invasive species belong to one of the biggest threats to native biota (Glowka et al., 1994). They are characterized by specific traits, which predict them to be successful in new areas of occurrence (e.g. Hôrková & Kováč, 2014; Záhorská et al., 2013). The development of constructed channels (such as ship canals) and greater international trade over the past century have both expanded the possibilities for aquatic animals to spread their ranges throughout Europe (Panov et al., 2009; Roche et al., 2015). Despite this, our knowledge of locations at considerable risk of invasion remains incomplete. Whether the invasion will be successful, or it will fail depends not only on the biological attributes of the invader, but also on basic characteristics of the non-native habitat, including all factors, biotic and abiotic (Grabowska & Przybylski, 2015), with a predisposition of invasive fish species being more successful and resilient to human made changes – e.g. devastation of habitats by channelization of rivers.

Native to the Black Sea area, the Western tubenose goby (*Proterorhinus semilunaris*, Heckel 1837) is a Ponto-Caspian species of the Gobiidae family (Pinchuk et al., 2004). Among the invasive gobies found in the waterbodies of Europe, it is one of the smallest species (Slovák Švolíková et al., 2021). This species can be characterised by plasticity in life-history traits (Grabowska et al., 2019), feeding strategies (e.g. Ondráčková et al., 2019), use of habitats (e.g. Top et al., 2019), and broad temperature tolerance all of which predicts it to a success in new areas (Gebauer et al., 2018). In several European countries, the tubenose goby is regarded as invasive or non-native. Following its

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introduction through ballast water discharge, it was subsequently found for the first time in the Laurentian Great Lakes in 1990 (Grant et al., 2012). By 2000, the tubenose goby was common along the Huron-Erie Corridor (Leslie et al., 2002), and it was found amid aquatic macrophytes, on rocky and sandy substrates (Jude & DeBoe, 1996). The majority of previous Great Lakes tubenose gobie samples were taken from shallow depths, usually less than 3 meters. A small number of individuals were taken as deep as 5 meters, but none were taken farther (e.g. Dopazo et al., 2008). Tubenose gobies from river systems in the northern Black Sea (their natural habitat) also exhibited this pattern, where they were typically located in shallow, slowly moving areas with macrophytes. Due to similar environmental conditions in both native and non-native areas of occurrence, it is predicted that Ponto-Caspian species have colonised the Great Lakes with exceptional success (Ricciardi & MacIsaac, 2000). The species mentioned seems to have a relatively slow spread compared to another invasive species from the same family (e.g. round goby, *Neogobius melanostomus*, Pallas 1814), but this does not mean it has no direct effect on native biota (Grant et al., 2012). Besides that, it is considered as an invasive species in European rivers such as the Danube, Dnieper, Dniester, Rhine, Meuse, and Vistula River systems (Grabowska et al., 2021). Even though tubenose goby belongs to an invasive species affecting native fish species in Europe as well as in North America, there is little knowledge about its basic life-history traits and morphology. At the same time, there is a question of its possible invasiveness in some parts of Europe. For example, its first occurrence in western Slovakia was in the late 19th century. However, it was not recorded earlier than 2014 in eastern Slovakia (Slovák Švolíková et al., 2021). Therefore, the aims of this study were to 1) analyse the reproductive parameters, 2) analyse the morphological variability, and 3) test the hypothesis of alternative ontogenies and invasive potential of nine populations coming from an area of the Danube basin region in western Slovakia.

Material and Methods

Study Area

Fish were sampled at nine sites along a 10–160 m stretch of artificial melioration channels of Žitný Island, Slovakia (Table 1, Figure 1) using electrofishing gear during April 2015. All fishes caught were identified (Table 2), and either released or taken for further analyses (i.e. reproductive and morphometric). Collected specimens of tubenose goby (n=367; $n_{females}$=236, n_{males}=124) were anesthetised with a clove oil followed by immediate preservation in 4% formaldehyde. Every sample was kept at room temperature (about 20°C) in airtight plastic containers in a dark location. Within 5 to 9 months of preservation, the samples were tested and analysed; throughout this time, the somatic parameters shouldn't change by more than 2-3% (Paradis et al., 2007).

Fish Data Collection and Analysis

Using the KERN ABJ 120-4M balance, the weight, eviscerated weight, and gonad weight were all measured to the closest 1 mg. Females: Males (F:M) was the sex ratio, which was determined by dividing the total number of males by the total number of females. Specimens from the spawning period were analysed for oocyte diameter, size groups of oocytes, and absolute and relative number of oocytes. Gravimetric analysis was used to determine the absolute (ANO) and relative (RNO) number of oocytes (Holčík & Hensel, 1972). Using the eviscerated female body weight and the standard formula (e.g., Holčík & Hensel, 1972), the gonadosomatic index (GSI) was calculated. A subsample of 50 oocytes was randomly selected from the gonad to determine the size range of the oocytes. The diameter of each oocyte was measured to the nearest 0.0025 mm using an ocular micrometer. Oocyte size distribution, including size-groups determination, was then examined and evaluated. To examine the condition of the three populations, Fulton’s condition factor (Le Cren, 1951) was determined using the following formula:

$$K=100000.W/TL^3$$

Where W is the total body weight (g), and TL is the total length (mm).

The IMPOR 2.31E software was then used to measure 27 mensural characteristics, including standard length (SL) and total length (TL; Figure 2), using digital photos captured by a Pentax camera.

Table 1. Geographical location and code of nine examined sites of Žitný Island (Slovakia)

Site	Code	Latitude	Longitude
Dunajský Klátov	KK1	48.0314	17.6804
Potôňske lúky	KK2	48.0724	17.5404
Amadeho Kračany	KVK1	47.9599	17.5812
Štrkovec	KVK2	47.9782	17.5812
Mad	KB	47.9488	17.6392
Boheľov	KKB	47.9067	17.6813
Trstená – Jurová	KSJ	47.9276	17.4904
Vrbina	VH	47.8140	17.7264
Veľký Meder	VMH	47.8670	17.7849

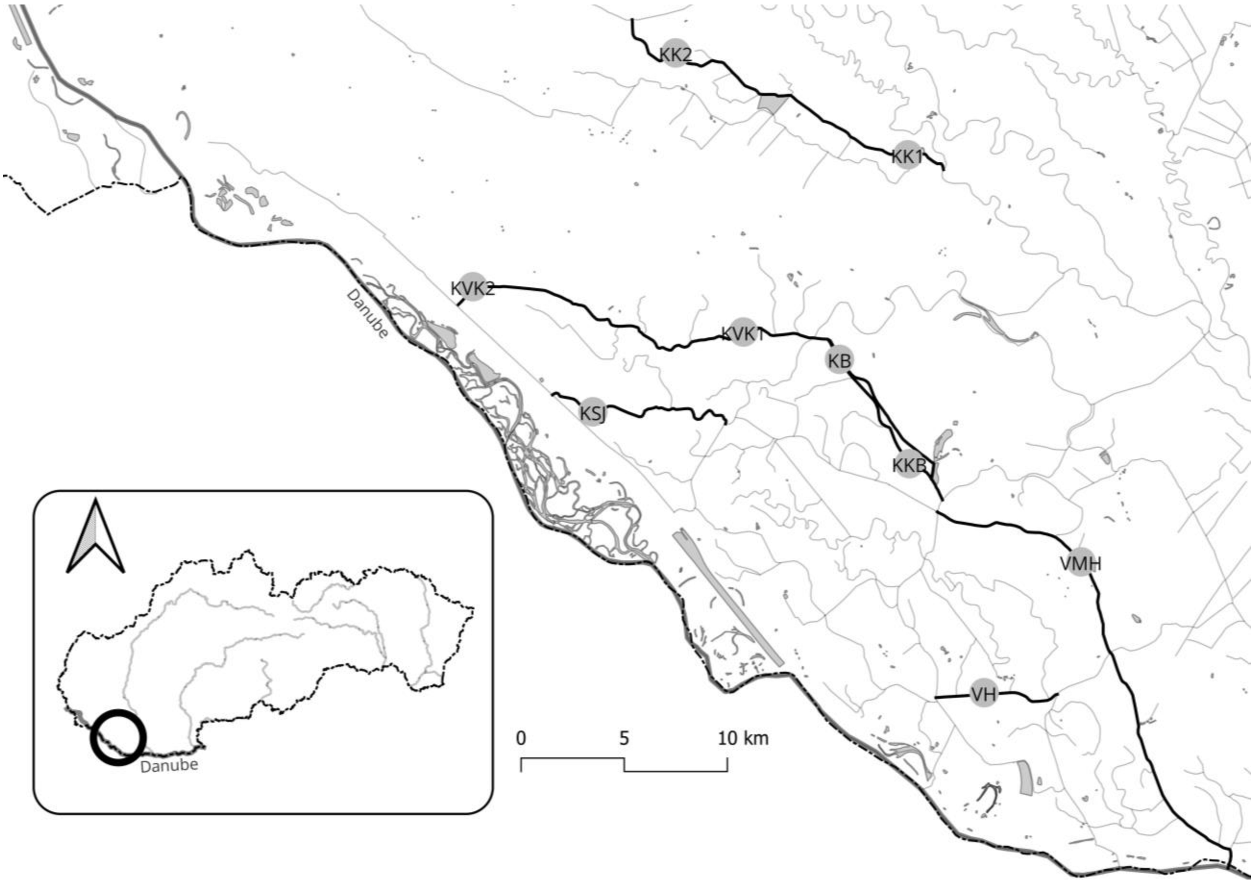

Figure 1. Location of sampling sites of tubenose goby (*Proterorhinus semilunaris*) at Žitný Island (Slovakia).

Table 2. List of fish species presented at examined sites from Žitný Island (Slovakia)

		Site								
Scientific name	Common Name	KK1	KK2	KVK1	KVK2	KB	KKB	KSJ	VH	VMH
Abramis brama	Common bream	x	x	-	-	-	-	-	x	-
Alburnus alburnus	Bleak	x	x	x	x	x	-	x	x	x
Blicca bjoerkna	White bream	x	x	-	-	x	x	x	x	x
Carrasius gibelio	Gibel carp	-	x	-	x	x	x	-	x	x
Cobitis elongatoides		-	-	x	x	-	-	-	-	-
Gasterosteus aculeatus	Three-spined stickleback	x	-	x	-	-	x	-	-	-
Gobio gobio	Gudgeon	x	-	x	-	-	-	x	-	-
Gymnocephalus cernus	Ruffe	-	x	-	-	-	-	-	-	-
Lepomis gibbosus	Pumpkinseed	-	x	-	-	-	-	x	x	x
Misgurnus fossilis	Weatherfish	-	-	x	x	-	-	x	-	-
Neogobius fluviatilis	Monkey goby	x	-	x	-	-	-	-	-	-
Neogobius kessleri	Ponticola kessleri	-	-	-	-	x	-	-	-	-
Neogobius melanostomus	Round goby	x	x	x	-	x	-	x	-	-
Proterorhinus semilunaris	Western tubenose goby	x	x	x	x	x	x	x	x	x
Pseudorasbora parva	Topmouth gudgeon	-	-	x	x	-	-	x	-	x
Rhodeus amarus	European bitterling	-	-	x	x	x	x	x	x	x
Rutilus rutilus	Roach	x	x	x	x	x	x	x	x	x
Sander lucioperca	Pikeperch	-	x	-	-	-	-	-	-	-
Scardinius erythrophthalmus	Rudd	-	x	-	x	-	x	x	x	x
Tinca tinca	Tench	-	-	-	x	-	x	x	x	x
Ameiurus melas	Black bullhead	-	x	x	-	-	x	-	x	x
Aspius aspius	Asp	-	x	-	-	-	-	-	-	-
Esox lucius	Northern pike	-	x	x	x	-	-	x	-	x
Leuciscus cephalus	Chub	x	x	x	x	x	x	x	x	x
Leuciscus idus	Ide	-	-	-	-	-	x	-	-	-
Perca fluviatilis	Eurasian perch	x	x	x	x	x	x	x	-	x
Silurus glanis	Europen catfish	x	x	-	-	-	-	-	-	-

Statistical Analyses

Fulton´s factor of condition was evaluated using a t-test for single means in females and males separately, while the differences between the males and females within the population were tested using a t-value test for dependent samples (STATISTICA 13, Dell Inc. 2016).

The differences in reproductive parameters (ANO, RNO) between all examined populations were evaluated by one-way ANOVA, LSD Post-Hoc test (STATISTICA 13, Dell Inc. 2016).

Allometric growth, or variations in body size between samples, can lead to variations in shape in morphometric analyses without revealing variations in body proportions between populations (Reist, 1985). In the current investigation, morphometric and meristic features showed strong associations with body length. As a result, before analysis, absolute measurements were converted to size-independent shape variables. Size-dependent variation for morphometric and meristic characters was removed using the formula by Elliott et al. (1995):

$$M_{adj}=M(L_s/L_o)^b$$

Where Madj is the size-adjusted measurement, M is the original morphometric measurement, Ls is the overall mean of standard length for all fish from all samples for each variable, and Lo is the standard length of fish.

With all specimens, the slope of the regression of log M on log Lo was used to estimate the parameter b for each character from the observed data. To determine if the data transformation was successful in eliminating the impact of size in the data, correlation coefficients between transformed variables and standard length were computed (Turan, 2004). On the same set of variables, discriminant functional analysis (DFA) was carried out. Wilk's λ, F, and P statistics were used to differentiate specimens based on their localisation in multidimensional space (STATISTICA 13, Dell Inc. 2016). We applied the rule established by McGarigal et al. (2000), which is grounded in empirical observations rather than mathematical concepts, to identify the characteristics influencing the species' overall biology. Accordingly, DFA-analyzed features with an absolute value of 0.3 are biologically important, and traits with an absolute value of 0.4 or above are thought to have biologically significant associations.

Results

A figtotal number of fish species caught on site ranged from 12 to 27 (Table 2).

Quantitative and Reproductive Parameters

The weight before dissection within all 9 populations was in interval from 0.22 g to 7.39 g, and after dissection from 0.18 g to 6.73 g. Weight of ovaries ranged from 0.002 g to 1.226 g (for more details see Table 3). Sex ratio (F:M) ranged from 1:0.21 (KB) to 1:0.93 (VH; Table 4). GSI ranged from 4.12 to 46.67%. Absolute number of oocytes (ANO) was in interval 118–2622, while relative number of oocytes (RNO) was 94–4352. Oocyte diameter ranged from 0.06 to 1.46 mm (Table 4). Oocytes were distributed in three size groups with different percentage portion at each site (the most dominant were females with 2 size groups of oocytes), and in variable size in each size group (Table 5). Analysis

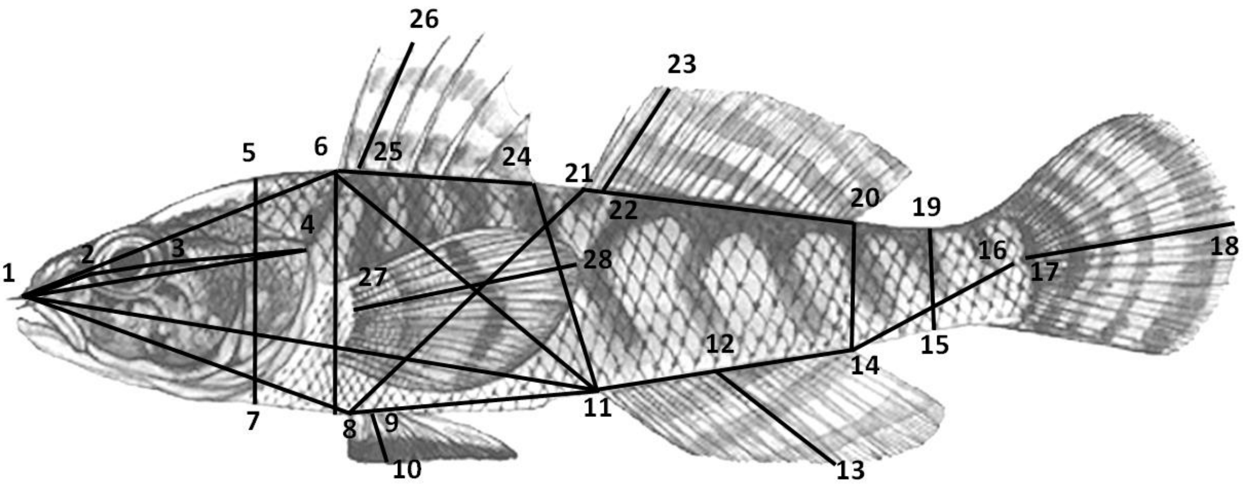

Figure 2. Schematic illustration of the distance-based morphometric characteristics taken from the lateral view of *Proterorhinus semilunaris*: (1–4) head length; (1–2) preorbital distance; (3–4) postorbital distance; (2–3) eye diameter; (5–7) head depth; (1–6) predorsal fin distance; (1–8) preventral fin distance; (1–11) preanal fin distance; (8–10) ventral to anal fin distance; (6–11) first dorsal to anal fin distance; (24–11) second dorsal to anal fin distance; (21-8) second dorsal to ventral fin distance; (14–16) caudal peduncle length; (20–14) caudal peduncle depth; (6 perpendicular) body depth; (19–15) minimum body depth; (25–26) first dorsal fin height; (22–23) second dorsal fin height; (12–13) anal fin height; (6–24) first dorsal fin base length; (21–20) second dorsal fin base length; (11–14) anal fin base length; (17–18) caudal fin length; (27-28) pectoral fin height; (9-10) ventral fin height.

of variance showed statistically significant differences between all localities in ANO ($F_{8,\ 233}$=10.086, P<0.01; Figure 3A) as well as RNO ($F_{8,\ 233}$=18.486, P<0.01; Figure 3B). Subsequently, LSD Post-Hoc test showed differences in comparison between individual populations (Table 6).

Differences in Fulton´s factor of condition was statistically significant (P<0.01) between females as well as males from all populations. It was the lowest in females at KSJ (0.28–1.35), and in males at KKB (0.94–1.12), and the highest at KB (females 1.42–2.60; males 1.13–1.51; Table 7). On the other side, the differences in condition between males and females within the population were not statistically significant.

Morphometric Analyses

The mean values of SL within all 9 populations ranged from 32.75 mm to 49.62 mm (Table 8). Majority of characters (14) were significantly different, and at the same time, there were 16 traits with biological importance (Table 9), from which 8 traits had biologically significant relationships (Figure 4).

Discussion

Sex Ratio

Females were found to be dominant in the sex ratio across all sampling sites. This could be explained by the reproductive behaviour of females and/or males. Since all females were already in the spawning period, males were protecting the nests under the stones, and thus their sampling was less efficient (Brandner et al., 2013). Comparable results were also found in other invasive populations of the same species originating from different areas of occurrence (e.g., Grabowska et al., 2019; Valová et al., 2015).

Table 3. Quantitative parameters in females within observed populations from Žitný Island (Slovakia). (n–number of females, SL–standard length, W-body weight, EW-eviscerated body weight, m–weight)

Pop	n	SL (mm)	W (g)	EW (g)	m gonads (g)
KK1	27	32.43–49.23 (38.81)	0.29–2.59 (1.23)	0.23–1.81 (0.87)	0.015–0.437 (0.177)
KK2	20	34.65–49.48 (42.06)	0.84–2.91 (1.65)	0.54–2.20 (1.17)	0.066–0.509 (0.223)
KVK1	45	30.23–49.99 (36.51)	0.58–3.12 (1.13)	0.40–2.17 (0.76)	0.028–0.360 (0.154)
KVK2	34	31.44–44.42 (38.41)	0.57–1.92 (1.33)	0.41–1.50 (0.88)	0.058–0.407 (0.210)
KB	34	29.54–48.86 (42.12)	0.37–2.61 (1.64)	0.29–1.70 (1.13)	0.012–0.514 (0.222)
KKB	16	36.70–55.08 (47.44)	0.96–3.49 (2.30)	0.67–2.45 (1.60)	0.106–0.667 (0.357)
KSJ	10	26.27–47.46 (31.83)	0.34–1.08 (0.62)	0.25–0.63 (0.43)	0.017–0.186 (0.083)
VH	14	36.72–49.48 (42.30)	0.92–2.85 (1.62)	0.67–1.90 (1.08)	0.090–0.487 (0.257)
VMH	36	37.97–59.69 (48.67)	1.23–4.81 (2.50)	0.72–2.96 (1.73)	0.063–1.226 (0.376)

Table 4. Reproductive parameters of females within observed populations from Žitný Island (Slovakia). (n–number of females, SR–sex ratio (F:M), GSI–gonadosomatic index, ANO–absolute number of oocytes, RNO–relative number of oocytes, OD–oocyte diameter; mean values are in brackets)

Pop	n	SR	GSI (%)	ANO	RNO	OD (mm)
KK1	27	1:0.35	5.83–46.21 (21.86)	429–1442 (794)	583–2247 (873)	0.11–1.35 (0.53)
KK2	20	1:0.55	5.09–31.74 (18.84)	593–1359 (1014)	613–1241 (903)	0.11–1.24 (0.51)
KVK1	45	1:0.40	4.17–39.63 (19.67)	124–2622 (1077)	152–2828 (1477)	0.10–1.35 (0.48)
KVK2	34	1:0.44	6.27–46.67 (24.42)	179–1435 (894)	119–1578 (1054)	0.07–1.46 (0.53)
KB	34	1:0.21	4.12–45.16 (19.33)	555–1611 (1093)	559–3111 (1030)	0.10–1.34 (0.45)
KKB	16	1:0.31	9.11–37.15 (22.11)	557–1722 (1192)	536–1145 (779)	0.10–1.35 (0.53)
KSJ	10	1:0.36	6.54–31.80 (17.85)	440–1397 (951)	1158–4352 (2354)	0.06–1.30 (0.46)
VH	14	1:0.93	10.80–43.89 (24.00)	174–1731 (1225)	158–2231 (1190)	0.11–1.31 (0.51)
VMH	36	1:0.40	6.14–41.48 (21.80)	118–2409 (1440)	94–1462 (875)	0.11–1.41 (0.55)

Table 5. Oocytes parameters in tubenose goby females from all examined sites from Žitný Island (Slovakia)

		Percentage of oocyte size groups			Size of oocytes in each size group		
Pop	n	1	2	3	I	II	III
KK1	27	11.1	70.4	18.5	0.11-0.75	0.55-1.35	0.86-1.31
KK2	20	20.0	55.0	25.0	0.11-0.85	0.67-1.24	0.84-1.20
KVK1	45	15.6	73.3	11.1	0.10-0.78	0.55-1.35	0.88-1.27
KVK2	34	3.0	73.5	23.5	0.07-0.73	0.56-1.46	0.91-1.33
KB	34	8.8	88.3	2.9	0.10-0.76	0.53-1.34	1.24
KKB	16	0.0	75.0	25.0	0.10-0.82	0.51-1.35	0.96-1.34
KSJ	11	20.0	70.0	10.0	0.06-0.67	0.73-1.30	0.97
VH	14	0.0	85.7	14.3	0.11-0.62	0.63-1.31	0.95-1.18
VMH	35	11.1	86.1	2.8	0.11-0.75	0.57-1.40	1.19

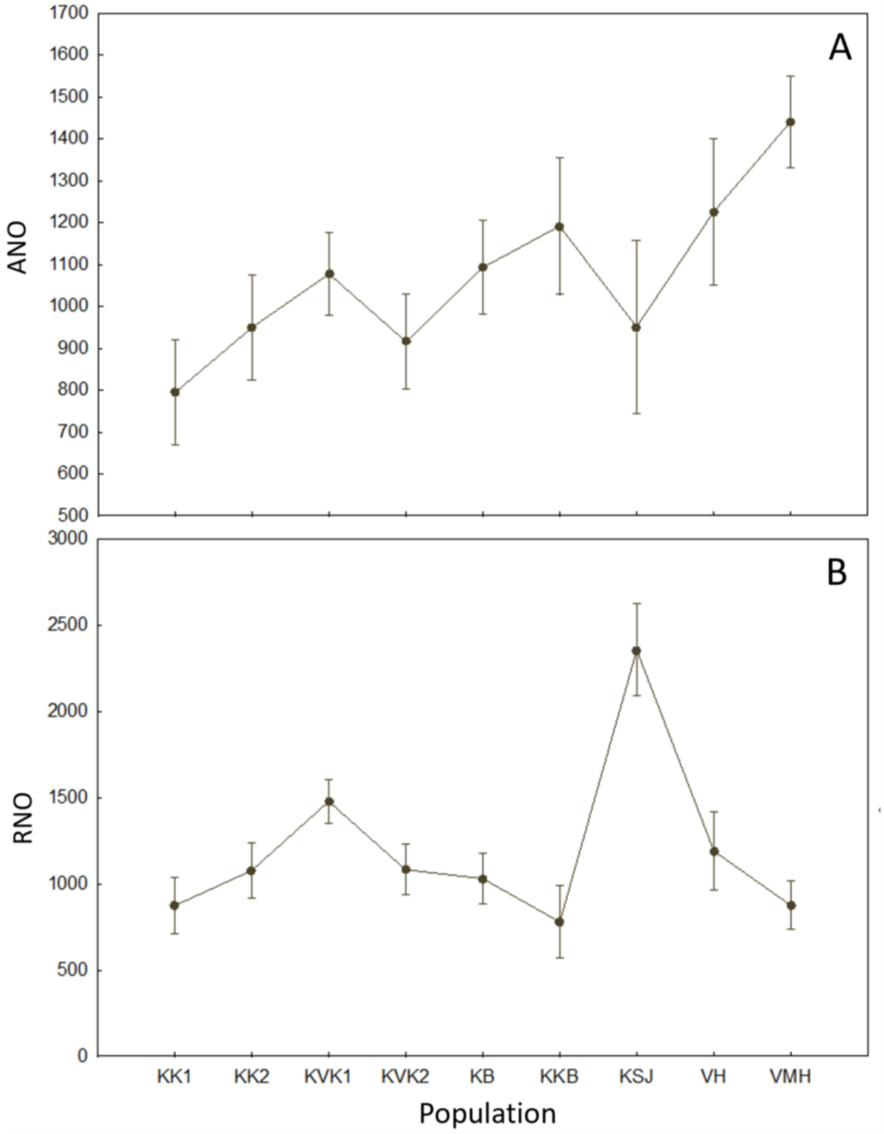

Figure 3. Differences between means of absolute (A) and relative (B) number of oocytes in 9 populations from Žitný Island (Slovakia). (KK1 – Dunajský Klátov, KK2 – Potôňske lúky, KVK1 – Amadeho Kračany, KVK2 – Štrkovec, KB – Mad, KKB – Boheľov, KSJ – Trstená – Jurová, VH – Vrbina, VMH – Veľký Meder).

Table 6. LCD Post-Hoc test between nine populations of western tubenose goby from Žitný Island (Slovakia). Significantly different traits are in bold face. (Pop – population, ANO – absolute number of oocytes, RNO – relative number of oocytes)

Pop/ANO	KK1	KK2	KVK1	KVK2	KB	KKB	KSJ	VH	VMH
KK1									
KK2	0.0870								
KVK1	**0.0006**	0.1155							
KVK2	0.1605	0.6937	**0.0347**						
KB	**0.0006**	0.0959	0.8387	**0.0301**					
KKB	**0.0002**	**0.0218**	0.2381	**0.0068**	0.3267				
KSJ	0.2045	0.9929	0.2766	0.7700	0.2358	0.0732			
VH	**0.0001**	**0.0124**	0.1473	**0.0038**	0.2106	0.7834	**0.0471**		
VMH	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0133**	**0.0001**	**0.0405**	
Pop/RNO									
KK1									
KK2	0.0817								
KVK1	**0.0000**	**0.0002**							
KVK2	0.0614	0.9633	**0.0001**						
KB	0.1569	0.6708	**0.0000**	0.6190					
KKB	0.4834	**0.0281**	**0.0000**	**0.0208**	0.0538				
KSJ	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**			
VH	**0.0254**	0.4214	**0.0293**	0.4279	0.2389	**0.0091**	**0.0000**		
VMH	0.9881	0.0650	**0.0000**	**0.0458**	0.1311	0.4542	**0.0000**	**0.0201**	

Table 7. Fulton's factor of condition for tubenose goby from all examined sites from Žitný Island (Slovakia). (n – number of females/males)

Population	n	Females	n	Males
KK1	27	1.00 – 1.32 (1.16)	10	0.89 – 1.23 (1.09)
KK2	20	0.95 - 1.34 (1.14)	12	0.99 – 1.28 (1.15)
KVK1	45	0.74 – 1.50 (1.18)	20	1.01 – 1.70 (1.27)
KVK2	34	0.86 – 1.53 (1.20)	13	0.91 – 1.32 (1.10)
KB	34	1.42 – 2.60 (2.13)	7	1.13 – 1.51 (1.28)
KKB	16	0.99 – 1.41 (1.15)	5	0.94 – 1.12 (1.03)
KSJ	10	0.28 – 1.35 (1.00)	4	1.02 – 1.17 (1.08)
VH	14	0.88 – 1.29 (1.08)	13	0.92 – 1.33 (1.13)
VMH	36	0.85 – 1.70 (1.15)	12	0.97 – 1.44 (1.25)

Table 8. Mean values of morphometric characters (*Proterorhinus semilunaris*) from nine sites in Žitný Island (Slovakia). (V – ventral fin, A – anal fin, D1 – first dorsal fin, D2 – second dorsal fin, C – caudal fin, P – pectoral fin)

Character	KK1	KK2	KVK1	KVK2	KB	KKB	KSJ	VH	VMH
SL	40.04	41.05	39.36	39.37	42.28	45.25	32.75	45.80	49.62
TL	50.15	50.76	48.77	49.12	52.30	55.50	41.48	57.09	61.07
Head length	11.22	11.55	11.35	10.76	11.22	12.50	9.46	12.02	13.05
Preorbital distance	2.98	3.06	3.09	2.96	2.97	3.49	2.50	3.12	3.44
Eye diameter	2.65	2.82	2.68	2.60	2.65	2.84	2.45	2.82	3.07
Postorbital distance	6.09	6.12	5.94	5.66	5.90	6.58	4.77	6.52	7.05
Head depth	9.15	9.27	9.03	8.68	9.40	9.96	7.49	10.32	11.27
Predorsal fin distance	14.74	14.90	14.62	14.22	14.98	16.34	12.13	16.34	17.68
Preventral fin distance	12.54	13.38	12.37	12.64	12.77	13.88	10.45	14.16	15.29
Preanal fin distance	24.33	24.91	23.76	23.10	25.87	27.56	19.80	27.64	30.35
V-A distance	12.71	12.67	12.20	12.48	14.04	14.56	9.84	14.58	16.02
D1-A distance	13.43	13.51	13.22	13.53	14.77	15.30	10.89	15.67	17.24
D2-A distance	9.22	9.19	9.20	9.29	10.04	10.70	7.42	10.67	11.87
D2-V distance	12.98	13.08	12.89	12.73	14.28	14.55	10.56	14.98	16.34
Body depth	10.18	9.99	10.18	10.12	11.14	11.46	8.33	11.54	12.62
C peduncle length	5.64	5.80	5.52	5.52	5.79	6.35	4.68	6.50	6.66
Min body depth	4.00	4.11	4.03	3.92	4.19	4.50	3.29	4.71	4.94
C peduncle depth	4.44	4.58	4.38	4.40	4.73	4.96	3.71	5.21	5.39
D1 fin base length	5.24	5.29	5.17	5.26	5.51	5.45	4.30	6.09	6.43
D2 fin base length	14.73	15.07	14.32	14.81	15.93	16.77	11.92	17.21	18.74
A fin height	11.26	11.01	10.65	10.66	11.40	12.23	8.81	12.71	13.48
P fin height	9.38	8.91	8.71	8.62	9.21	10.11	7.13	11.11	11.81
V fin height	7.62	7.15	6.73	6.70	7.86	8.70	5.55	9.54	9.34
C fin height	9.97	9.70	9.43	9.83	9.99	10.13	8.54	11.43	11.58
D1 fin height	3.80	3.82	3.97	4.28	3.67	4.38	3.66	4.80	4.94
D2 fin height	4.10	4.15	4.35	4.46	4.15	4.21	3.98	5.23	5.51
A fin height	3.04	3.27	3.31	3.32	3.39	3.61	2.66	3.72	3.93

Spawning

All females sampled in April were sexually mature (based on the values of GSI). Because sampling was carried out only once in April, it is impossible to say when the reproductive season started and finished. Usually, the spawning season lasts from April to July (Grabowska et al., 2019; Saç, 2019), or August (Harka & Farkas, 2006; Baruš & Oliva, 1995). The maximum GSI values in the native area of occurrence ranged from 11.6 to 12.4 (Saç, 2019). These values are comparable with other non-native areas (Thaye River, Czech Republic; GSI values 12; Valová et al., 2015). However, our results showed higher mean values of GSI (see Table 4 for more details). The smallest female with ripe oocytes had a standard length of 26.27 mm (at KSJ site) while the mean SL was 41.08 mm between all examined populations. In another non-native area of occurrence (Vistula River, Poland), SL in mature females varied between 46-47 mm (Grabowska et al., 2019), while in Istranca River (northwest of Istanbul, Turkey) SL of ripe females ranged from 24.0–54.0 mm (Saç, 2019). Tubenose goby usually matures at the second year of life, but there are evidence of sooner maturation, usually somewhere between the first and the second year (Cammaerts et al., 2012; Valová et al., 2015; Pinchuk et al., 2004) in

Table 9: Discriminant function analysis of western tubenose goby (*Proterorhinus semilunaris*) from nine sites in Žitný Island (Slovakia). Factor structure matrix (FSM) predicates biological importance of the trait. Significantly different traits are in bold face. (V – ventral fin, A – anal fin, D1 – first dorsal fin, D2 – second dorsal fin, C – caudal fin, P – pectoral fin)

Characters	Wilks λ	*F* test	*P*	FSM	
Head length	0.1243	0.9545	0.4648	0.2005	-0.2289
Preorbital distance	0.1303	3.0339	**0.0043**	0.1003	-0.1570
Eye diameter	0.1375	5.5233	**0.0000**	0.1164	-0.1766
Postorbital distance	0.1272	1.9588	0.0605	0.2593	-0.2613
Head depth	0.1301	2.9676	**0.0051**	**0.3098**	-0.1625
Predorsal fin distance	0.1289	2.5597	**0.0142**	**0.3768**	-0.1764
Preventral fin distance	0.1261	1.5834	0.1398	0.2915	-0.0412
Preanal fin distance	0.1353	4.7594	**0.0000**	**0.4749**	-0.1830
V-A distance	0.1244	0.9913	0.4376	**0.4573**	-0.0087
D1-A distance	0.1280	2.2458	**0.0307**	**0.4813**	0.0243
D2-A distance	0.1280	2.2311	**0.0318**	**0.4193**	0.0111
D2-V distance	0.1294	2.7166	**0.0096**	**0.4212**	-0.0364
Body depth	0.1259	1.5000	0.1668	**0.3121**	-0.0029
C peduncle length	0.1271	1.9183	0.0664	**0.3764**	-0.0921
Min body depth	0.1274	2.0184	0.0527	**0.3294**	-0.0808
C peduncle depth	0.1287	2.4742	**0.0176**	**0.3431**	-0.0370
D1 fin base length	0.1237	0.7369	0.6408	0.2276	0.0202
D2 fin base length	0.1285	2.3905	**0.0216**	**0.4371**	0.0278
A fin height	0.1231	0.5391	0.8046	**0.3316**	-0.0450
P fin height	0.1336	4.1689	**0.0002**	**0.4717**	-0.0680
V fin height	0.1318	3.5470	**0.0011**	**0.5611**	-0.0448
C fin height	0.1334	4.1045	**0.0003**	**0.3730**	0.0834
D1 fin height	0.1304	3.0503	**0.0041**	0.1556	0.1743
D2 fin height	0.1274	2.0267	0.0517	0.1658	0.1036
A fin height	0.1253	1.2967	0.2516	0.1802	0.0944

populations coming from non-native areas. It is a short-lived species reaching up to 12 cm, therefore, there is not so much space to search for statistically significant differences among populations. However, populations analysed in our research mature at a smaller size than is typical for invasive species at the beginning stages of their invasive process or in the populations with permanent disturbances in the inhabited areas (e.g. Grabowska et al., 2021; Záhorská et al., 2013).

Eggs

Tubenose goby belongs to a group of fish characterized by asynchronous oocyte development, which is associated with batch spawning protracted over the reproductive season (Grabowska, 2005; Hôrková-Žitňanová et al., 2021). This allows reserve oocytes in the ovary to ripen during the spawning period if the environmental conditions are favourable. Thus, it is usually characterised by 1 to 3 groups of oocytes ready for spawning events over time. However, a significant environmental disturbance, such as a flood or drought, can also trigger the appearance of several groups of oocytes. Females might then produce other batches to make up for the losses caused by the disturbance during that spawning period (Hôrková & Kováč, 2015). All examined populations were characterized with 3 size groups of oocytes with variable percentages, as well as sizes reached in different size groups (Table 5). The biggest oocyte reached 1.46 mm in size, and it was smaller compared to different authors (e.g. Grabowska et al., 2019; Valová et al., 2015). This could possibly be explained by the beginning stage of the invasive process as well as disturbances in the habitat. Another explanation would relate to the start of the reproductive season when the oocytes are still developing. As it was mentioned above, the analysed populations had higher values of GSI compared to populations coming from different regions, thus this claim is not likely, although possible.

Fecundity

The absolute as well as relative number of oocytes was higher compared to other studies from both native (e.g. Saç, 2019; Top et al., 2018) and non-native (e.g. Cammaerts et al., 2012; Valová et al., 2015; Grabowska et al., 2019) areas of occurrence. In connection with fecundity, it is always difficult to find the real reason for an increased number of oocytes. In invasive species, this phenomenon can be caused by at least three reasons. First, there is a difference in life-history traits manifested by the newcomers and established populations. Usually, the invasive species at the initial phase mature sooner and at smaller sizes, while they invest most of their energy into reproduction. This leads to bigger amounts of smaller oocytes (e.g. Záhorská et al., 2013; Záhorská et al., 2014), and thus to higher fecundity. The second, there are different patterns in the allocation of energy during the spread of population.

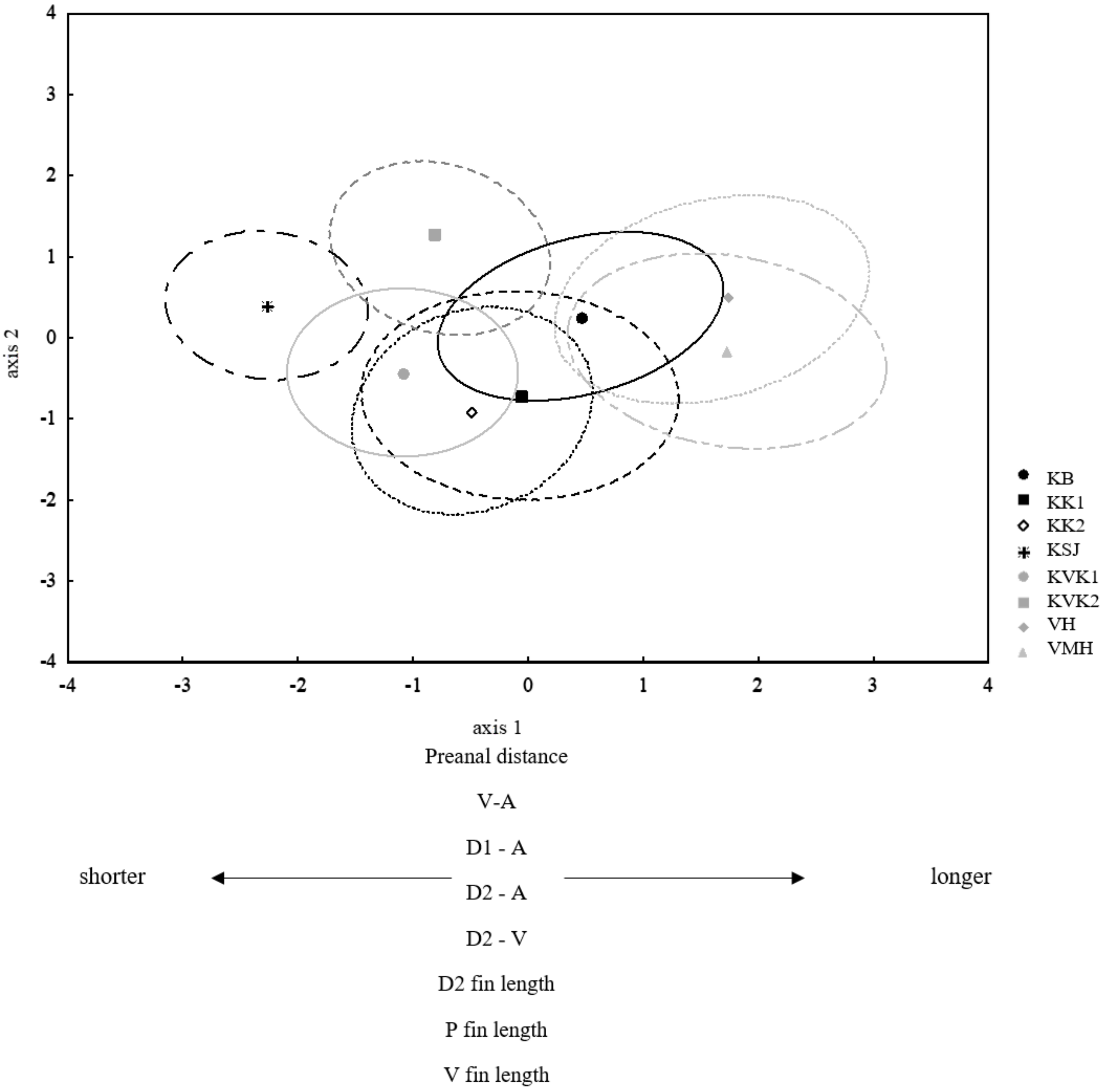

Figure 4. Discriminant functional analysis scatter plot (DFA) with means of canonical variables and 50% ellipsoids about the centroid of each population of western tubenose goby from nine different sites in Žitný Island (Slovakia), with discrimination based on morphological variability of characters. (KK1 – Dunajský Klátov, KK2 – Potôňske lúky, KVK1 – Amadeho Kračany, KVK2 – Štrkovec, KB – Mad, KKB – Boheľov, KSJ – Trstená – Jurová, VH – Vrbina, VMH – Veľký Meder).

Increased absolute fecundity indicates a change in life-history attributes from the long-established population to the freshly established population, which may be the cause of the effect of producing rapid population expansion in recently invaded areas. This kind of behaviour was not observed only in tubenose goby, but also in other invasive species with expanding ranges, including the highly invasive round goby (Masson et al., 2016; 2018), and topmouth gudgeon (Gozlan et al., 2010). The third, different levels of disturbance can lead to changes in life-history traits. If the habitat is under strong pressure (e.g. permanent changes in water level, presence of predators, few shelters, limited food supplies), invasive organisms act as if they are at the „beginning" of the invasive process. In other words, the ability to produce alternative ontogenies and life histories, or developmental flexibility, is advantageous to the successful invaders. In native areas where environmental conditions are stable (from an evolutionary perspective), their ontogenies produce more specialised forms; however, if conditions are uncertain, as they are in an unknown environment in the invaded areas, ontogenies shift towards more generalised alternatives (Geist, 1978). In this case, they display a high investment in reproduction, resulting in higher fecundity and smaller sizes of oocytes (e.g. Záhorská et al., 2013; Grabowska et al., 2021).

Condition

There was no significant difference in the condition between females and males within each population, thus, they were both in good and/or bad condition. Females are usually in worse condition due to the development of gonads, which is more energy demanding compared to males. On the other hand, males use more energy when protecting the nests. Unfortunately, the analysed samples were from the beginning of the reproductive season, thus we could not observe changes in condition throughout the entire reproductive cycle. Nevertheless, there were differences in condition between females as well as males between the examined populations. The habitats from which the samples came differed in many environmental factors, e.g., the bottom of the channel, percentage of the banks cover, the composition of the ichthyofauna, etc., and thus also the food sources, shelters and other parameters are expected to be variable and could affect the condition within each population.

Morphology

One useful method for comprehending the relationship between body shape and ecology is ecomorphology, which is the study of the relationship between functional morphology and species ecology (Norton et al., 1995). Our study shows variable differences in morphological traits in populations from different sampling sites. The majority of traits were statistically significant, while more than half had biological importance. Significant differences were related to characters located on the head, fins, and associated with the length or height of the body. These variations, which are crucial for species dispersion, are the outcome of evolutionary history and adaptation to a wide range of ecological niches (Motta et al., 1995).

The fish may be able to move amid plants and other physical structures that are employed for food and predator protection because of the longer parts of their heads, bodies, and fins. Additionally, their bigger proportion may help with competition and defence mechanisms

(e.g. Pflieger, 2004). Tubenose goby typically inhabits densely vegetated areas where it faces competition from a range of cyprinid yearlings (such as bream, roach, and tench) that seek refuge and food in weedy shallows, as well as the possibility of being preyed upon by pike and perch (Simonović et al., 2001). The head is more or less robust depending on the proportion of postorbital distance and head depth. Different habitat types and water flow can produce this effect; flattened or sloping heads save energy consumption and enable the fish to stay close to the substrate when swimming or staying motionless in flowing water (e.g. Webb et al., 1996). Eye diameter was also a trait that was significantly different between the populations. Larger eyes are traditionally explained as an adaptation towards a darker environment (e.g. Witte et al., 2008). Since the tubenose goby is a benthic species, this could bring a possible explanation. Animals with larger eyes have better visual acuity because their retinal images are larger. Eye size has been linked to predation danger in a number of studies, and eyes are often highly noticeable. Risk of predation is sometimes considered as one of the driving factors behind variation in eye size within species (Svanbäck & Johansson, 2019). Thus, larger eyes should aid both in detecting predators as well as finding food. And really, the biggest eye size (proportionally to SL) was found in samples from sites with at least 5 predators (KSJ, KK2; Table 2).

However, fin shape and body shape are also significant factors in swim mode, and varied fin configurations may be the cause of distinct movement specialisations (Feilich, 2016). From swimming to stability to manoeuvring, fin shape and configuration exhibit a broad spectrum of changes that are realised in numerous roles (Lauder & Drucker, 2004). One of the factors that can be responsible for changes in the external morphology of fins is the presence of predators (Naspleda et al., 2012). Usually, the fish that are under pressure from predators are characterized by deeper bodies and larger fins. On the other hand, longer ventral and pectoral fins are responsible for increased manoeuvrability and stability in flowing waters (Webb, 1984). In our study, we found statistically significant differences as well as differences with biological importance in the length of the majority of the fins (Table 9). Based on the biological importance of the traits we could distinguish between two patterns, where in the first group predominated lower values in biologically important traits, and second group was characterized by higher values (Figure 4). The reason for the differences was probably not caused by the presence of predators because their number was comparable at all sites. However, sites were separated from each other (Figure 1), which could lead to different environmental conditions and thus to changes in body shape. Due to their limited swimming capabilities, goby species are exclusively benthic and unable to make the quick environmental transitions that many other polymorphic fish species can, such as moving between pelagic and benthic habitats (Polačik et al., 2012).

Significant differences were also found in the abdominal area of the body. The possible reason is the increase due to activity during the reproductive season. Populations from VH and VMH were characterized by the highest number of oocytes (Figure 4). At the same time, the VH had the highest values of body proportions with significant differentiation. The proportion of energy devoted to reproduction varies greatly among fish populations (Fox & Crivelli, 1998). The majority of this energy is used by females to produce ovarian tissue and eggs. According to research on several small-bodied, multiple-spawning fish species, females produce more eggs over a year than they do in terms of body mass (e.g. Wootton, 1973; Burt et al., 1988) or volume (Gale & Bunyak, 1982).

Invasive Potential

Based on the theory of alternative ontogenies and invasive potential, we can say that a species' capacity for invasion increases with the range of phenotypes it can produce, from the most generalised to the most specialised (Kováč, 2010). The hypothesis tested predicts that individuals from invasive populations of tubenose goby will have higher fecundity, smaller oocytes, and earlier maturation than individuals from native populations. The same assumption can be used in comparison between populations coming from habitats with stable (comparable with native populations) and disturbed conditions (comparable with invasive populations; Záhorská et al., 2013). The problematic position of tubenose goby in Slovakian waters relates to its classification as a native species by some authors (Oliva & Hrabě, 1968; Hensel, 1995; Koščo et al., 2010), and according to the Slovak Republic's Fisheries Act No. 216/2018 and Executing Decree No. 381/2018 Coll, the tubenose goby is still listed among the country's native fish and lamprey species. But under the recent findings, it is considered a discreet invader with increased invasive potential which helps further spread to a variety of different habitats throughout Slovakia (Slovák Švolíková et al., 2021). Our findings support these statements, since populations achieved increased absolute number of oocytes, decreased oocyte diameter as well as smaller size at maturity in comparison with native and non-native areas of occurrence (e.g. Grabowska et al., 2019; Valová et al., 2015; Saç, 2019). Similar trend of changes in life-history traits during invasion process have been found also in other invasive species (e.g. vendace *Coregonus albula*, Bøhn et al., 2004; white perch *Morone americana*, Feiner et al., 2015; pumpkinseed *Lepomis gibbosus*, Cucherousset et al., 2009; topmouth gudgeon *Pseudorasbora parva*, Záhorská et al., 2013) and can be caused by phenotypic plasticity. The ability to alter morphology and all features associated with life strategies is likely due to phenotypic plasticity. It symbolises an organism's capacity to exhibit many phenotypes in response to its biotic or abiotic surroundings (Agrawal, 2001). The genotypes of interacting individuals and the environmental conditions in which they occur determine the phenotype that manifests in a particular habitat. Whether phenotypic plasticity develops as an organism's general strategy or in reaction to a specific environmental variation determines its ecological and evolutionary implications. Since most plastic features may respond to at least a few distinct environmental stimuli, the response is most likely intermediate (West-Eberhard, 2003). As it is obvious, tubenose goby populations in Slovak waters act as invasive, and thus its position on the list of native species should be reconsidered.

Conclusion

The variation in reproductive traits, condition, and morphology among all populations of the tubenose goby was significantly different. Even though the tubenose goby has a specific position in the waters of Slovakia (native vs. invasive), it differs in comparison with native as well as non-native populations. Populations from western Slovakia were different not just in higher values of GSI, but also in shorter size at maturation, smaller size of oocytes, higher values of fecundity, as well as morphological traits. Finally, we suggest that genetic analyses would be appropriate to find out whether the differences in traits are based only on different factors of the environment or also on the genetic variability of the species.

Ethical Statement

All fish used in this study were euthanized. No live animals were used in the study thus there is no need for Ethical Approval.

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Author Contribution

E. Záhorská: conceptualisation, methodology, formal analysis, investigation, writing original draft, writing review and editing, supervision. M. Kubala: formal analysis, writing review and editing. M. Balážová: methodology, visualisation, formal analysis.

Conflict of Interest

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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