

Plasticity in habitat use of two native Ponto-Caspian gobies, *Proterorhinus semilunaris* and *Neogobius fluviatilis*: implications for invasive populations

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Abstract – The Ponto-Caspian region is an important source area for some invasive gobiid fishes. These fishes have colonised several freshwater ecosystems in Europe, as well as in North America. As knowledge on their habitat utilisation in their native range remains limited, the seasonal habitat uses of Western tubenose goby, *Proterorhinus semilunaris* and monkey goby *Neogobius fluviatilis* were studied in four natural lakes in the Marmara Region (NW Turkey). Habitat use of both species was highly variable between the lakes and seasons, with *P. semilunaris* showing higher plasticity. In general, the main habitats used by *P. semilunaris* were shallow waters in littoral areas that had vegetation cover, whereas *N. fluviatilis* consistently used sandy substratum in deeper waters that lacked vegetation. These results suggested there was high plasticity in the habitat utilisation of these two gobiids, especially in *P. semilunaris*, which potentially facilitates their ability to establish and invade novel environments. The habitats that are especially vulnerable to *P. semilunaris* invasion are medium size substrates which provide individuals with sufficient interstitial space for refuge. Waters providing differing habitats, such as sandy substrata, might inhibit their colonisation, but are potentially more vulnerable to *N. fluviatilis* invasion.

Keywords: Gobiidae / microhabitat / natural lakes / native range / habitat plasticity

Résumé – Plasticité dans l'utilisation de l'habitat de deux gobies natifs de la région Ponto-Caspienne, *Proterorhinus semilunaris* et *Neogobius fluviatilis* : implications pour les populations envahissantes. La région de Ponto-Caspienne est une source importante de certains poissons gobiidés envahissants. Ces poissons ont colonisé plusieurs écosystèmes d'eau douce en Europe, ainsi qu'en Amérique du Nord. Comme les connaissances sur l'utilisation de leur habitat dans leur aire de répartition indigène restent limitées, les utilisations saisonnières de l'habitat du gobie demi-lune, *Proterorhinus semilunaris* et du gobie fluviatile *Neogobius fluviatilis* ont été étudiées dans quatre lacs naturels de la région de Marmara (Nord-Ouest de la Turquie). L'utilisation de l'habitat des deux espèces était très variable entre les lacs et les saisons, *P. semilunaris* présentant une plus grande plasticité. En général, les principaux habitats utilisés par *P. semilunaris* étaient des eaux peu profondes dans les zones littorales couvertes de végétation, alors que *N. fluviatilis* utilisait systématiquement un substrat sablonneux dans les eaux profondes dépourvues de végétation. Ces résultats suggèrent une grande plasticité dans l'utilisation de l'habitat de ces deux gobiidés, en particulier chez *P. semilunaris*, ce qui facilite potentiellement leur capacité à s'établir et à envahir de nouveaux environnements. Les habitats particulièrement vulnérables à l'invasion de *P. semilunaris* sont des substrats de taille moyenne qui fournissent aux individus un espace interstitiel suffisant pour se réfugier. Les eaux offrant des habitats différents, comme les substrats sableux, peuvent inhiber leur colonisation, mais sont potentiellement plus vulnérables à l'invasion de *N. fluviatilis*.

Mots-clés : Gobiidae / microhabitat / lacs naturels / aire de répartition indigène / plasticité de l'habitat

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1 Introduction

Non-native species continue to be introduced outside of their natural range, resulting in their range expansion and the development of invasive populations that impact native biodiversity (Lockwood *et al.*, 2007; Seebens *et al.*, 2017). Integral to determining the ability of an introduced species to establish and develop invasive populations is their adaptation to the available foraging and spawning habitat in the introduced environment (Van Kessel *et al.*, 2011; Top *et al.*, 2016). Generalist species that have high plasticity in their habitat selectivity are often more successful invaders, as there are lower costs involved in their adaptation to the new environment (Gozlan *et al.*, 2010; Davidson *et al.*, 2011). Consequently, developing understandings of the habitat use and plasticity of utilisation of invasive species in their native range can help inform invasion risk assessments (Copp *et al.*, 2009, 2016).

The Ponto-Caspian (P-C) region (Black Sea, Sea of Azov and Caspian Sea) remains an important donor region of many invasive species, including invasive gobiid fishes (Roche *et al.*, 2013). Invasions of P-C gobies are now apparent across much of Europe (Wiesner, 2005, Naseka, 2005, Rizevsky *et al.*, 2007, Antsulevich, 2007, Janáč *et al.*, 2012, Konečná and Jurajda, 2012) and in North America (Dillon and Stepien, 2001; Kornis and Vander, 2010; Kocovsky *et al.*, 2011). Invasive gobiids include the western tubenose goby *Proterorhinus semilunaris* and the monkey goby *Neogobius fluviatilis*. Their native range is the Black Sea region of Turkey, where they represent an important component of native fish communities and have value for food consumption (Özuluğ *et al.*, 2005; Çınar *et al.*, 2013; Tarkan *et al.*, 2018). The transport of *N. fluviatilis* into Europe was via ship ballast waters at major ports, followed by natural dispersal into inland freshwaters thereafter, which resulted in their invasion (Copp *et al.*, 2005; Grabowska *et al.*, 2009; Jakovlić *et al.*, 2015). In North America, *N. fluviatilis* has been listed as a potentially high-impact non-native species in the Great Lakes (Pagnucco *et al.*, 2015). The introduction of *P. semilunaris* into Europe occurred in the early 1990s, presumably by anglers using them as live bait (Lusk and Halačka, 1995), and to North America in 1990 (the Laurentian Great Lakes, St. Clair River) via ballast water release (Jude *et al.*, 1992). Although the invasion of *P. semilunaris* has been spatially constrained due to the dispersal restrictions of being within lake systems (*e.g.* Lake St. Clair and Erie; Vanderploeg *et al.*, 2002), studies of invading populations in Europe (*e.g.* the Danube Basin) have demonstrated negative impacts on macroinvertebrate communities through predation (Všetičková *et al.*, 2014).

For *P. semilunaris* and *N. fluviatilis*, ecological knowledge on their populations in their native range is limited, but has recently increased in relation to the expression of their life history traits and their trophic relationships with other species (Tarkan *et al.*, 2018; Karakuş *et al.*, 2018; Top *et al.*, 2018). There remain, however, considerable knowledge gaps in the habitat use of both native *P. semilunaris* and *N. fluviatilis*, as well as other common gobiids, such as round goby *Neogobius melanostomus* (Kornis *et al.*, 2012). Indeed, there is only a single study on microhabitat use of *P. semilunaris* completed in their native Turkish range (Gürsoy Gaygusuz *et al.*, 2010). For

N. fluviatilis, literature is limited to indirect reports arising during ichthyofaunal studies (Berg, 1949; Svetovidov, 1964, Sindilariu *et al.*, 2006). There is also very limited information on seasonal differences in habitat use for both species, with only a single study from the invasive range of *N. fluviatilis* (Erös *et al.*, 2005). Consequently, these knowledge gaps on the utilisation of habitats of these P-C gobies in their native range presents a considerable challenge for horizon scanning exercises and invasion risk assessment processes for these fishes in their non-native range. This is despite these exercises and processes being essential components of the invasion risk management toolkit (Britton *et al.*, 2011; Roy *et al.*, 2014). The aim of this study was, therefore, to overcome this knowledge gap through quantifying the seasonal habitat use of *P. semilunaris* and *N. fluviatilis* across an environmental gradient in their native range.

2 Materials and methods

2.1 Study sites

Four natural lakes in the Marmara Region (north-west Anatolia, Turkey) were used in the study; two were relatively shallow (Manyas and Uluabat) and two were relatively deep (İznik and Sapanca) (Tab. 1, Fig. 1). Both *P. semilunaris* and *N. fluviatilis* are considered as native to the lakes (*e.g.* Numann, 1958). These lakes provided a range of physical environments that enabled inter-lake differences to be assessed in relation to the species' seasonal habitat use. However, in the two deeper lakes (İznik and Sapanca), gobies were not captured from the deeper areas, only in littoral areas (<1.5 m deep). The fish assemblages of all lakes were dominated by fishes of the Cyprinidae family; other native gobiids were present, including round goby *Neogobius melanostomus* and Caucasian dwarf goby *Knipowitchia caucasica*. Other fishes present included northern pike *Esox lucius*, European catfish *Silurus glanis*, gibel carp *Carassius gibelio*, Eastern mosquitofish *Gambusia holbrooki*, pumpkinseed *Lepomis gibbosus* and topmouth gudgeon *Pseudorasbora parva*, most of which are alien species to the lakes (Geldiay and Balık, 2009).

Lake İznik is a deep (to 80 m) tectonic lake, but with shallower deltas around the lake shore, fringed with reeds where tributary streams enter. The lake's trophic status has shifted from oligotrophic to mesotrophic in recent decades due to high agricultural activity around the lake, coupled with waste-waters from nearby residential areas (Akçaalan *et al.*, 2009). The most abundant fish species present is *P. semilunaris*, enabling their capture from littoral habitats. However, samples collected in autumn were poor due to adverse weather conditions at the time of sampling. Lake Sapanca is also a deep (to 55 m) tectonic lake fed by numerous small streams. The lake suffers from substantial water level fluctuations and frequent algal blooms due to abstraction for potable water and high agricultural activity in the catchment. These water level fluctuations negatively impacted the littoral area during the sampling period, resulting in the absence of gobies in samples from these areas. Consequently, samples of *P. semilunaris* were instead mainly collected from the mouth of five steep mountain streams feeding into the lake.

Both Lake Manyas and Uluabat have a RAMSAR designation, and are also impacted by abstraction and nutrient

Table 1. Latitude (Lat), longitude (Lon), surface area (SA, km²), altitude (Alt, m), minimum (Min), maximum (Max) and mean temperature (°C), mean and maximum depth (m) of four lakes in the Marmara Region (Karakuş *et al.*, 2018; Top *et al.*, 2018).

Lake	Lat	Lon	SA	Alt	Temperature			Depth	
					Min	Max	Mean	Mean	Max
İznik	40°26'	29°32'	313	85	7.2	28.4	16.4	40.0	80.0
Sapanca	40°42'	30°15'	47	30	8.4	27.5	15.8	26.0	55.0
Uluabat	40°10'	28°35'	136	9	4.1	28.9	18.1	2.5	4.5
Manyas	40°12'	27°56'	178	18	7.1	27.1	18.6	1.5	3.6

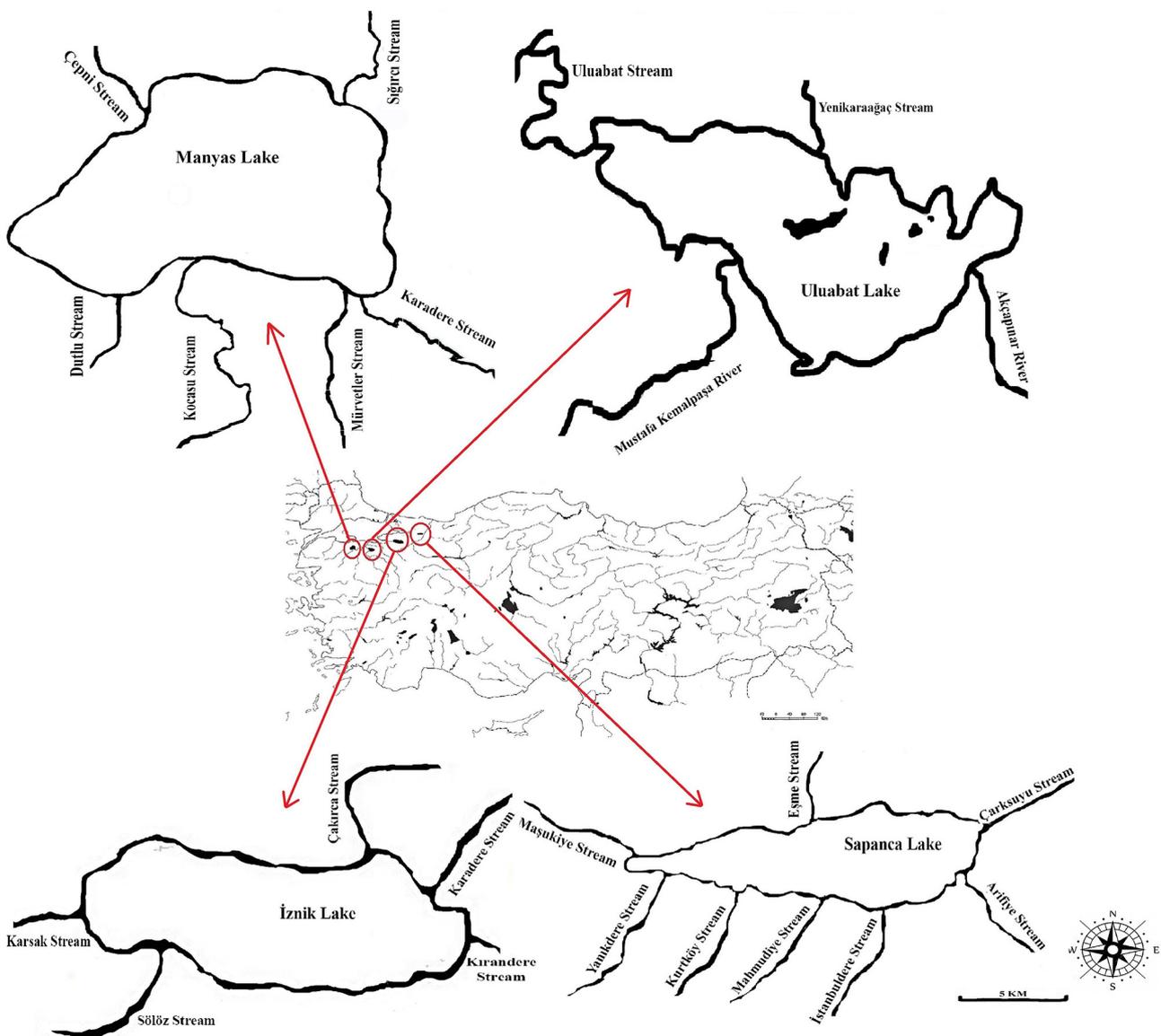


Fig. 1. Study sites (mouths of the streams) in the Marmara region (north-west Turkey) for Western tubenose goby *Proterorhinus semilunaris* and monkey goby *Neogobius fluviatilis*.

enrichment, resulting in water level fluctuations and algal blooms (Magnin and Yazar, 1997; Albay and Akçaalan, 2003; Arslan *et al.*, 2010). In Lake Manyas, sampling sites for *N. fluviatilis* were located in mouths of the small creeks generally

characterised by muddy to sandy substrata and some large rocks. In Lake Uluabat, *P. semilunaris* was abundant in the littoral areas, with *N. fluviatilis* collected both from littoral areas and deeper parts of the lake.

Table 2. Seasonal variations between total number of specimens caught and percentage of goby presence on sampled points and p -values of χ^2 test for differences between seasons ($p < 0.001$ means there are significant differences).

		Sampled points	Total number of specimens	% with goby presence	p -value between seasons
<i>P. semilunaris</i>					
İznik	Autumn	50	–	–	<0.001
	Winter	50	32	57	
	Spring	50	30	54	
	Summer	50	34	63	
Sapanca	Autumn	50	36	58	<0.001
	Winter	50	–	–	
	Spring	50	30	53	
	Summer	50	34	63	
Uluabat	Autumn	50	51	92	<0.001
	Winter	50	18	20	
	Spring	50	29	47	
	Summer	50	28	46	
<i>N. fluviatilis</i>					
Sapanca	Autumn	50	–	–	n/a
	Winter	50	–	–	
	Spring	50	18	32	
	Summer	50	–	–	
Manyas	Autumn	50	21	41	0.45
	Winter	50	31	60	
	Spring	50	34	66	
	Summer	50	34	65	
Uluabat	Autumn	50	21	41	0.003
	Winter	50	15	26	
	Spring	50	33	65	
	Summer	50	34	65	

2.2 Fish sampling and habitat data collection

Sampling of the gobies was completed seasonally (summer, autumn, winter, spring) between August 2014 and May 2015 using Point Abundance Sampling (PAS; [Nelva *et al.*, 1979](#)) by electric fishing (SAMUS-725MP; the radius of the electricity around the anode was approximately 2 m). This method provides reproducible and quantifiable samples of fish, and is efficient across the entire length range of the focal species ([Copp, 1989](#)). On each sampling occasion per lake, 50 selected points were sampled within a predefined area by wading. The sampling areas were approximately 3 m from the bank, especially around river mouths in Lake Sapanca. Within these areas, all accessible habitats under 1 m depth were sampled, except those that were inaccessible due to dense plant growth. The area in which the point samples were taken were kept consistent between seasonal samples where possible, although water level fluctuations in Lakes Sapanca and Uluabat prevented this, with more open water areas sampled during seasons of relatively low water levels.

Sampling was carried out in each point with the power of the electric fishing equipment turned on for 10 s and all fish in the vicinity of the anode ring being captured with a hand net. The fish were then held in water filled bucket, before being identified to species, counted and measured. Measurements of microhabitat variables were as per [Beyer *et al.* \(2007\)](#): (i) depth

(to nearest cm), (ii) substratum composition (visually estimated as: mud, <50 μm ; silty sand, >50 μm to 0.06 cm; sand, >0.06–0.2 cm; gravel, >0.2–2.0 cm; mud + stone, >2.0–20.0 cm; rock, >20 cm), (iii) distance from bank (cm), (iv) distance from vegetation (cm), (v) submersed aquatic vegetation, (vi) submersed woody structure (roots or other ligneous material), (vii) plant cover (all in % of point area), (viii) water velocity, (ix) turbidity (estimated visually as: low, medium and high), and (x) light intensity (at the water surface and categorised as: shady, sunny-shady, and sunny).

2.3 Data analysis

Chi-square test was used to test seasonal variations between percentage of goby presence on sampled points. The seasons with no presence data were not included in this analysis ([Tab. 2](#)). Fish-habitat relationships were analysed by Constrained Quadratic Ordination (CQO) ([Yee, 2004](#)). This method overcomes the unrealistic assumptions of equal tolerances, equal maxima and uniformly distributed optima and site scores over the range of the environmental gradient, unlike Canonical Correspondence Analysis (CCA) ([Yee, 2004](#)), and has been applied successfully to fish–habitat relationships studies ([Vilizzi *et al.*, 2012](#); [Top *et al.*, 2016](#)). CQO estimates an optimal linear combination of the microhabitat variables and regresses the species' data upon the latent variable axis using a quadratic curve

fitted across the species' scores. In the analyses, each response curve in the ordination diagram represents the distributional range of the species across the microhabitat gradient (*i.e.* the latent variable). Hence, the relative position of the curve along the gradient indicates the preference of the species for certain values of the microhabitat variables summarised into the microhabitat gradient, and as determined by the species' probability of occurrence (as the fish data are entered as presence/absence), which indicates the optimum value (Yee, 2004). CQO was fitted under a binomial model of rank 1, with three non-linear degrees of freedom and unequal tolerances and after choice of the 'best' 100 models (Yee, 2006). Models were run in R x64 v3.0.3 (R Development Core Team, 2015) using library VGAM v0.9-7. Negative scores correspond to a higher value of the descriptor (and optimum) on the left-hand axis of the CQO plot, positive scores to a higher value of the descriptor on the right-hand axis.

Individual CCA models were run for each seasonal sampling occasion per lake and gobiid species. The data entered in each model were the presence/absence (as 1/0) of the gobiid species, and then the 10 descriptors that identify the microhabitat latent variable (depth, substratum composition, distance from bank, distance from vegetation, submersed aquatic vegetation, submersed woody structure, plant cover, velocity, turbidity and light intensity).

3 Results

3.1 Fish samples

In total, 563 gobiids were sampled (322 *P. semilunaris* and 241 *N. fluviatilis*) across the entire study. A total of 800 point samples was used for the habitat use analysis, out of which gobies were present at 506 points (63.3%). In each lake, there were some seasonal differences in the proportion of point samples where the gobies were captured, with the highest proportions generally in spring and summer, and the lowest in winter and autumn (Tab. 2). Between the species and across the four lakes, *P. semilunaris* was recorded in a significantly higher proportion of points than *N. fluviatilis* ($\chi^2=0.0001$, $P < 0.001$). In general, points where both gobies were present among all sites tended to be relatively shallow with a coarser substratum, with relatively low turbidity and more vegetated than points where they were absent (Tab. 3).

In Lake Manyas, *P. semilunaris* were sampled in very low numbers so they were excluded from further analyses, whereas *N. fluviatilis* was not present in Lake İznik. There were not enough *P. semilunaris* specimens to plot CQO diagram in autumn for Lake İznik. Similarly, *N. fluviatilis* individuals could be captured only in spring and no species were captured in the winter survey from Lake Sapanca (Tab. 2, Fig. 2).

3.2 Habitat use of *P. semilunaris*

Abundance and percentage of *P. semilunaris* presence were significantly higher in Lake Uluabat than in Lakes Sapanca and İznik ($P < 0.001$; Tab. 2). In Lake İznik, *P. semilunaris* were present in points with coarser stones in more turbid waters with vegetation, especially close to the riparian zone, and were less likely to be captured from relatively deeper areas in winter and spring. However, in summer, finer substrate was used and the

species tended to be in deeper water with plant cover that was located further from the lake shore. Although there was consistency in avoiding areas of water velocity and woody structures in all seasons, there was generally high variability in habitat use (Fig. 2; Tab. 3).

In Lake Sapanca, *P. semilunaris* always avoided areas of deeper water over fine substrates and most specimens occurred around riparian trees in areas of no flow in spring and autumn. In summer, they tended to be closer to vegetated areas and stream mouths (Tab. 3, Fig. 2). In general, there was no specific habitat use of *P. semilunaris* in Sapanca, with fish sampled from all combinations of substrates and water levels, especially in spring. In Lake Uluabat, *P. semilunaris* also had few seasonal differences in their habitat use, except for spring when it was detected in most of habitat types. In summer, when there was a decrease in water level, they revealed a shift in habitat use to either being present further from the shore or to points with increased vegetation cover (Tab. 3, Fig. 2).

3.3 Habitat use of *N. fluviatilis*

The presence and abundance of *N. fluviatilis* was significantly lower in Lake Sapanca than in Lakes Uluabat and Manyas (Tab. 2). In Sapanca, *N. fluviatilis* was only present in spring, when they were captured from 32% of the points sampled (Tab. 2) and they used deeper habitats without vegetation, flow and woody structure (Tab. 3, Fig. 2). In Lake Manyas, habitat use of *N. fluviatilis* varied significantly between the seasons, with no specific habitat affinity in autumn (Tabs. 2 and 3). However, in summer and winter, they were generally found in deeper water with minimal vegetation and riparian tree cover (Tab. 3, Fig. 2). Conversely, in spring, their presence increased with distance from the bank and over finer substratum (Fig. 2). In Lake Uluabat, there were no significant differences in habitat use of *N. fluviatilis* between seasons ($P=0.45$; Tab. 2), with fish tending to avoid deeper waters and vegetated areas with riparian trees in all seasons (Tab. 2).

4 Discussion

The two gobiids have previously been reported to have variable microhabitat use in their native (*e.g.* Gürsoy Gaygusuz *et al.*, 2010) and non-native ranges (*e.g.* Erős *et al.*, 2005; Janáč *et al.*, 2012). This suggests some adaptive capacity of both species regarding habitat utilization (*e.g.* Karakuş *et al.*, 2018; Top *et al.*, 2018). The results here are congruent with this, with both native gobiids revealing high variability in their habitat use, with this apparent between seasons and lakes. This plasticity in habitat use enhances their ability to colonise and invade new environments, and is thus important for informing their invasion risk management (Copp *et al.*, 2009; Britton *et al.*, 2011).

Comparisons of *P. semilunaris* habitat utilisation data here with other studies revealed some consistencies and emphasised the high plasticity in their habitat utilisation. For example, the habitat uses of age 0+ *P. semilunaris* in two connected rivers in the non-native range of the Danube River Basin revealed a tendency for inhabiting areas comprising of relatively large stones (10–30 cm) and avoidance of areas of fine substrates, such as silt, sand and gravel (Grabowska *et al.*, 2008; Janáč

Table 3. Constrained Quadratic Ordination (CQO) results for occurrence of *Proterorhinus semilunaris* and *Neogobius fluviatilis* from four natural lakes over four seasons. For each component, scores of the descriptors on the latent microhabitat variable are given. For each species, the optimum and tolerance on the range of the latent variable are indicated. Negative scores correspond to a higher value of the descriptor (and optimum) on the left-hand axis of the CQO plot, positive scores to a higher value of the descriptor on the right-hand axis (*cf.* Fig. 2). (DFB: distance from bank, DFV: distance from vegetation, SAV: submersed aquatic vegetation, SWS: submersed woody structure, PC: plant cover).

Lake	CQO	Optimum	Tolerance	Depth	Substratum	DFB	DFV	SAV	SWS	PC	Velocity	Turbidity	Light
Íznik	Winter <i>P. semilunaris</i>	-0.943	1.000	3.146	-1.727	-1.701	0.237	-2.218	3.813	0.595	1.638	-0.174	2.031
	Spring <i>P. semilunaris</i>	-0.253	1.000	1.925	0.623	-2.553	0.872	0.905	1.345	-2.490	-1.137	1.420	-2.632
	Summer <i>P. semilunaris</i>	2.582	1.000	3.449	0.336	-2.400	0.205	-0.387	-0.161	1.950	-1.090	0.466	3.240
	Autumn <i>P. semilunaris</i>	1.572	1.000	-0.111	0.242	-0.370	0.491	0.174	-0.226	0.581	0.055	-1.042	1.386
Sapanca	Spring <i>P. semilunaris</i>	n/a	n/a	0.234	-0.122	-0.011	-0.089	-0.053	0.368	-0.676	0.333	0.137	0.455
	Summer <i>P. semilunaris</i>	0.850	1.000	0.866	-0.082	-0.473	0.058	-0.331	1.205	0.001	-0.721	-1.236	-0.179
	Autumn <i>N. fluviatilis</i>	n/a	n/a	-2.221	-0.379	-1.433	6.046	-0.527	-0.842	2.609	-3.698	-5.768	-4.302
	Winter <i>N. fluviatilis</i>	-3.373	1.000	-0.690	-0.316	-0.009	-0.241	0.816	0.512	-2.069	-0.329	2.247	-3.317
Manyas	Spring <i>N. fluviatilis</i>	-25.150	1.000	0.256	-0.012	-0.227	0.170	0.020	-0.018	0.111	-0.094	0.175	-0.087
	Summer <i>N. fluviatilis</i>	0.720	1.000	1.147	-0.250	-1.107	-0.569	-0.450	0.071	0.849	-0.790	-0.395	1.972
	Autumn <i>P. semilunaris</i>	2.074	2.795	-1.342	3.539	-0.315	-2.826	-1.218	-0.614	-0.528	0.683	-4.455	-3.276
	Winter <i>N. fluviatilis</i>	0.716	1.000	5.183	0.987	-4.503	-1.204	-2.624	1.342	-0.383	-1.069	2.334	-5.338
Uluabat	Summer <i>P. semilunaris</i>	-0.886	1.000	0.054	-0.381	-0.231	-1.378	-0.377	-0.969	-1.591	-1.334	0.251	-0.161
	Spring <i>N. fluviatilis</i>	-2.808	1.000	0.381	0.064	-0.017	0.638	0.125	0.266	0.933	1.023	-0.861	-1.597
	Autumn <i>P. semilunaris</i>	-2.007	1.000										
	Winter <i>N. fluviatilis</i>	-3.641	1.000										

et al., 2012). Other studies have suggested, however, that other populations either show no choice in substrate type (Erös *et al.*, 2005) or for fine substrates (Gürsoy Gaygusuz *et al.*, 2010). This difference might, however, just relate to a lack of larger material in the substrates measured in the latter study, since the streams were relatively small and had a low velocity (Gürsoy Gaygusuz *et al.*, 2010). In invasive *P. semilunaris* lake populations in North America, the species occurs in riprap habitats (Jude and DeBoe, 1996), but not in fine substrates (Kocovsky *et al.*, 2011). In our results, the use of stony substrates was only apparent in *P. semilunaris* in winter in Lake İznik. The only location where fine substratum was used was in Lake Sapanca, where the species was present around the mouth of the streams flowing into the lake. However, large rocks are only used when they are smaller than 40 cm diameter (Janáč *et al.*, 2012) because the larger stones are associated with silt or did not provide sufficient interstitial space (Polačik *et al.*, 2008, 2009). These results have important implications

for their invasion risk management, as they suggest that habitat structure and substrate are unlikely to be limiting factors in their colonisation and establishment processes, and thus a wide range of habitats will be vulnerable to their invasion.

There is relatively less information available on the habitat use of *N. fluviatilis*. The main habitat requirement of *N. fluviatilis* has consistently been demonstrated as shorelines with sandy and gravel substrates (Čáková *et al.*, 2008). This habitat use is thought to assist predator avoidance (Holčík *et al.*, 2003), although it is also considered that their strong presence on sandy substrata could inhibit the expansion of their invasive range (Čáková *et al.*, 2008; Piria *et al.*, 2016). Indeed, previous data on habitat uses of *N. fluviatilis* has also demonstrated their use of sandy substrata in the shoreline (Erös *et al.*, 2005; Adámek *et al.*, 2007; Borcharding *et al.*, 2013; Piria *et al.*, 2016), which was also detected here. Direct comparison of the present results on seasonal habitat uses of *N. fluviatilis* is only possible with Erös *et al.* (2005), who

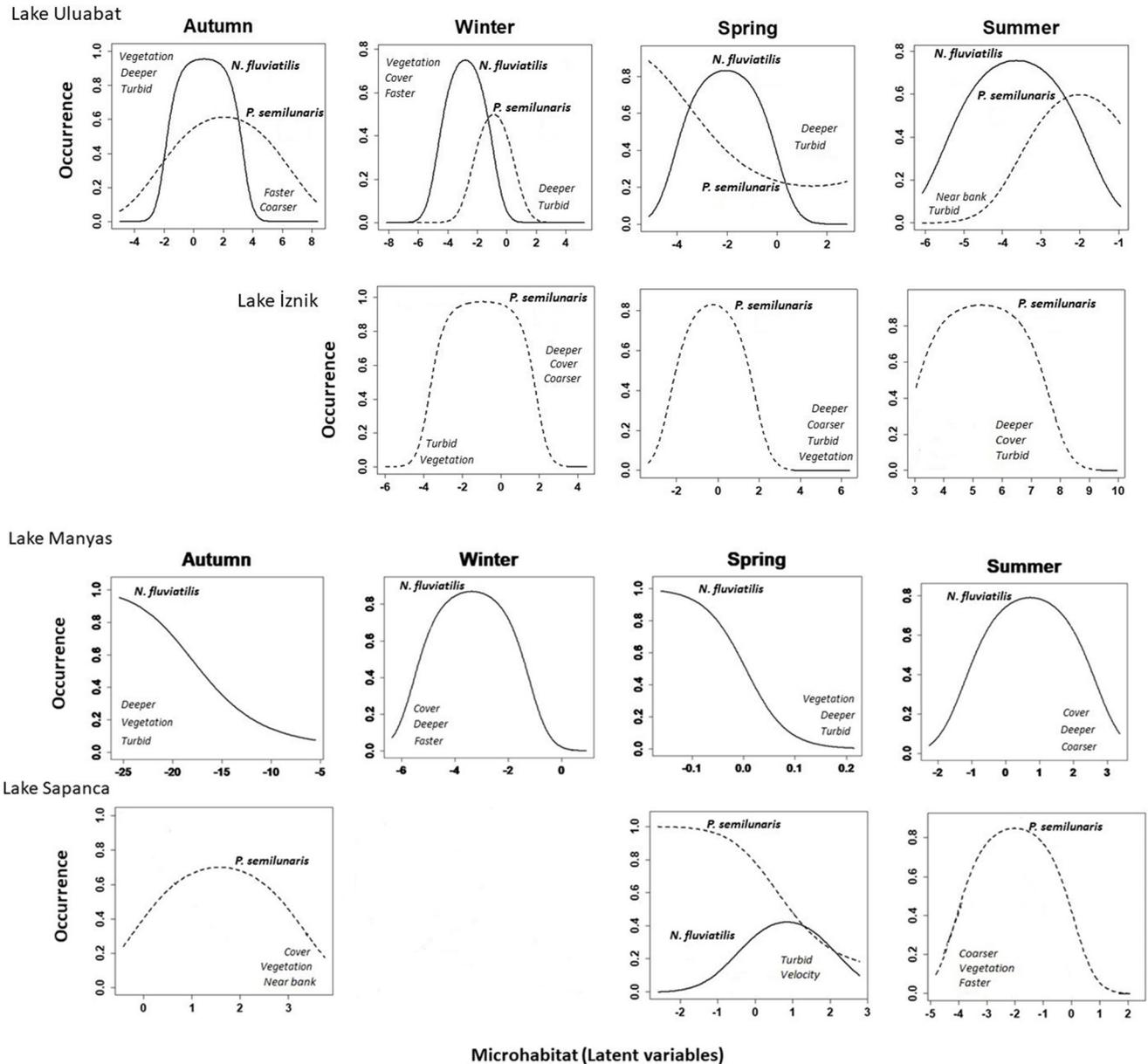


Fig. 2. Constrained Quadratic Ordination (CQO) plots for Western tubenose goby *Proterorhinus semilunaris* and monkey goby *Neogobius fluviatilis* sampled from four lakes in Marmara Region by season. A summary indication of the main microhabitat features is provided on the negative and positive boundaries of the microhabitat (latent) variable axis.

presented similar data from littoral zone of the Danube in Hungary. Notably, they detected seasonal differences in *N. fluviatilis* abundance in some specific habitats (e.g. Erös *et al.*, 2005), a contrast to our results that showed minimal differences between seasons. The only consistency in our results with Erös *et al.* (2005) was the presence of *N. fluviatilis* in habitats away from the shore in spring. However, the spring habitats used by *N. fluviatilis* in the Danube were of high velocity and of gravel substratum with decreasing water depth (Erös *et al.*, 2005), the opposite of our results.

Across both gobies, the four lakes and all seasons, their habitat uses were thus highly variable. This plasticity, in conjunction with other traits, including a generalist life history, plasticity in growth and capability of shifting reproductive

features, is likely to confer considerable advantages in their establishment and invasion (e.g. Tarkan *et al.*, 2018; Karakuş *et al.*, 2018; Top *et al.*, 2018). There was more evidence of some specialisation in the habitat uses of *N. fluviatilis* (e.g. for fine substratum), suggesting that *P. semilunaris* is more general and so more probable to successfully establish and invade new areas following introduction, despite their current spatial restriction to European water courses and North American lakes (Vanderploeg *et al.*, 2002). Moreover, our results for *P. semilunaris* suggest they will be able to continue to spread in environments that provide substrata of medium sized stones with interstitial spaces and shallow waters of low velocity. Although some contrasting habitats might slow the spread of *P. semilunaris* (e.g. absence of vegetation, water with high

velocity), the strong occurrence of *N. fluviatilis* on sandy habitats has not prevented their invasion (Copp *et al.*, 2005; Grabowska *et al.*, 2009; Jakovlić *et al.*, 2015). Invasions of these gobies are thus unlikely to be inhibited by habitat availability, with their high plasticity in habitat use ensuring to be able to adapt to most new environments. These findings are important in the context of horizon scanning exercises and invasion risk assessment processes, as they now can be completed using information on the habitat uses of both fishes that show high plasticity.

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