



## THE REVIEW OF ECOLOGICAL AND GENETIC RESEARCH OF PONTO-CASPIAN GOBIES (Pisces, Gobiidae) IN EUROPE

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### ABSTRACT

Invasive Ponto-Caspian gobies (monkey goby *Neogobius fluviatilis*, round goby *Neogobius melanostomus* and bighead goby *Ponticola kessleri*) have recently caused dramatic changes in fish assemblage structure throughout European river systems. This review provides summary of recent research on their dietary habits, age and growth, phylogenetic lineages and gene diversity. The principal food of all three species is invertebrates, and more rarely fish, which depends on the type of habitat, part of the year, as well as the morphological characteristics of species. According to the von Bertalanffy growth model, size at age is specific for the region, but due to its disadvantages it is necessary to test other growth models. Phylogenetic analysis of monkey goby and round goby indicates separation between the Black Sea and the Caspian Sea haplotypes. The greatest genetic diversity is found among populations of the Black Sea, and the lowest among European invaders. The lack of molecular research on bighead goby requires further studies.

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### INTRODUCTION

In the last few decades, Ponto-Caspian gobies (P-C gobies) – monkey goby *Neogobius fluviatilis* (Pallas, 1814), round goby *Neogobius melanostomus* (Pallas, 1814) and bighead goby *Ponticola kessleri* (Günther, 1861) – were transported from their natural habitat by ships to the main European ports and then migrated into the majority of European inland waters (Jazdzewski and Konopacka, 2002; Corkum et al., 2004; Copp et al., 2005; Polačik et al., 2008; Leuven et al., 2009; Manné et al., 2013; Povž, 2016). It has been suggested that increased annual water temperature

(Bonacci et al. 2008) or pressure of anthropogenic stressors contributed to their success in expanding distribution (Copp et al., 2005; Wiesner, 2005; Harka and Bíró, 2007). P-C gobies have shown a relatively high invasive potential in the Balkan countries (Simonović et al., 2013), as well as a medium high and high invasive potential in Croatia (Piria et al., 2016a). Each of these species has its own particularities regarding its habitat requirements and can survive in both, the gravel-sand and rocky bottom (Kessel van et al., 2011; Kottelat and Freyhof, 2007). They live up to five years (Kottelat and Freyhof, 2007), growing to a maximum standard length of 220 mm (Erős et al., 2005; Bogut et al.,

2006; Vassilev et al., 2012) and feed mostly on invertebrates (Adamek et al., 2007; Piria et al., 2016b). Molecular analyses of round goby have shown increase in the genetic diversity of round goby due to the passive transportation of larvae to new habitats caused by different currents. In this way, genes from distant populations are transmitted (Kocovsky et al., 2011). The genetic diversity is, therefore, increased by ship transportation during which juveniles are transported into ballast water (Brown and Stepien, 2008), making the populations more similar than when the transmission of genes is caused by natural or biological mechanisms (LaRue et al., 2011). Several review papers are related to biology, distribution and ecological implications on P-C gobies (Vanderploeg et al., 2002; Kornis et al., 2012; Roche et al., 2013), but there is not a single comprehensive review on their natural diet, growth or genetic characteristics in native and non-native distribution.

Thus, the aim of this study is to give a review of ecological and genetic research of monkey goby, round goby and bighead goby in European inland waters. The specific aims are: (1) to review diet, age and growth of the three species of Ponto-Caspian gobies in their native and non-native habitats; (2) to discuss phylogenetic lineages and genetic diversity of Ponto-Caspian gobies in the areas of native and non-native habitats; and (3) to discuss their potential impact on native fish species.

## STUDY AREA

The freshwater area of Eastern and South-Eastern Europe is divided into the Black, Caspian and Azov Sea, Lake Manyas, Sasyk Lagoon and Simferopol Reservoir, as well as the lower Danube, Dnieper, Dniester, Don, Volga and Moscow. The freshwater area of Central Europe covers the Baltic Sea, the Vistula, Hron, Ipel', middle and upper Danube, Sava and Rhine, and also Western Europe covers the Albert and Gent-Terneuzen Canals in the Rhine River Basin.

## ORIGIN

Monkey goby was first registered in the Danube in 1960 (Bănărescu, 1970). Its upstream expansion was recorded in the Romanian/Bulgarian section (Smirnov, 1986), Hungary (Ahnelt et al., 1998), Slovakia (Jurajda et al., 2005) and in the Sava in Croatia (Čaleta, 2007). Round goby was recorded in the Danube in Serbia (Simonović et al., 1998), Slovakia (Adamek et al., 2007), Croatia (Mustafić, 2005), Hungary (Erős et al., 2005), in the Sava in Croatia (Piria et al., 2011b), in the Rhine River Basin in Belgium (Verreycken et al., 2011) and Switzerland (Kalchhauser et al., 2013), and in the Baltic Sea (Sapota, 2004). In 1910, the first individuals of bighead goby were caught in the Danube in Serbia (Vutskits, 1911). Also, it was recorded in the Danube in Hungary (Erős et al., 2005), Croatia and Slovakia (Polačik et al., 2008), Germany

(Seifert and Hartmann, 2000) and in the Rhine in Germany (Borcherding et al., 2011) and Switzerland (Kalchhauser et al., 2013).

## DIET

### *Dietary items*

Research on monkey goby diet in the non-native area of Europe, in the Vistula in Poland (Kakareko et al., 2005; Grabowska et al., 2009), the Sava in Croatia (Piria et al., 2011a), the Danube and the Hron in Slovakia (Adámek et al., 2007), indicates that its preferred diet is Chironomidae, Trichoptera and Amphipoda. Additionally, important nutritional taxa were Bivalvia and Odonata (Piria et al., 2016b). Round goby in the Danube River in Serbia and in its tributary, the Sava River in Croatia, feeds mostly on Bivalvia (Simonović et al., 1998, 2001; Piria et al., 2016b), however, in the Danube River in Slovakia (Števove and Kováč, 2013), Germany (Brandner et al., 2013) and Hungary (Borza et al., 2009) on Diptera (Chironomidae) and alien Ponto Caspian Amphipoda (*Dikerogammarus* sp.). The principal food of bighead goby is Amphipods and small fishes (Adámek et al., 2007; Piria et al., 2016b). In an area invaded by *Dikerogammarus* sp., *C. curvispinum* and Asian molluscs *C. fluminea* (Ponto-Caspian invertebrates), most of the research reveals positive selection for these species (Adámek et al., 2007; Borza et al., 2009; Brander et al., 2013b). These preferences represent one of the possible solutions to the problem of invertebrate invaders which are still expanding their distribution (Žganec et al., 2009; Paunović et al., 2012). The preferred diet of monkey goby in the native area consists of Bivalvia (Sindilariu and Freyhof, 2003; Pinchuk et al., 2003) in the Danube Delta. Round goby in the Azov Sea feeds mostly on Polychaeta (Svietovidov, 1964), and in the Black Sea in Romania on Bivalvia and Gastropoda (Bănaru and Harmelin-Vivien, 2009). Bighead goby in the Dniester estuary (Vasil'Eva and Vasil'Ev, 2003) and the lower Danube (Polačik et al., 2009) feeds mostly on Amphipoda and Pisces.

List of dietary items found in non-native and native habitat for all three P-C gobies are presented in Table 1 with a note on preferred taxa.

### *Diet overlap between P-C gobies and other fish species*

Significant overlap in the diet between monkey goby and round goby from the Sava River in Croatia was recorded (Piria et al., 2016b). However, bighead goby and round goby diets did not overlap in the Sava (Piria et al., 2016b), contrary to the findings of Števove and Kováč (2013). Another research conducted in Hungary found that

**Table 1.** Taxa found in the diet of monkey goby, round goby and bighead goby in their non-native and native habitat [+ , presence of dietary item; p, preferred item; n.d., not determined; a=e=m, Danube Slovakia; b, Sava River Basin; c=g, Vistula Poland; d, Sava Croatia; f, Danube Hungary; h, Danube Serbia; i=k, Baltic Sea Gdansk; j, Baltic Sea Denmark; l, laboratory studies; n, Danube Germany; o, Rhine Germany; p, Danube Danube Delta; q, Lake Razelm Danube Delta; r, Dnieper estuary; s, Black and Azov Sea Basin; t=u, Azov Sea; v, Black Sea Romania; z, Dniester estuary; x, lower Danube; y, Bug, Grigoryevskiy, Dnieper and Azov Utlukskiy estuary; 1, Adámek et al. (2007); 2, Piria et al. (2016b); 3, Grabowska et al. (2007); 4, Piria et al. (2011a); 5, Števove and Kováč (2013); 6, Borza et al. (2009); 7, Kakareko et al. (2005); 8, Simonović et al. (2001); 9, Karlson et al. (2007); 10, Azour 2011; 11, Skóra and Rzeznik (2001); 12, Chotkowski and Marsden (1999); 13, Copp et al. (2008); 14, Brandner et al. (2013); 15, Borcherdin et al. (2013); 16, Sindilariu and Freyhof (2003); 17, Pinchuk et al. (2003); 18, Smirnov 1986; 19, Svetovidov 1964; 20, Kovtun et al. (1974); 21, Bănaru and Harmelin-Vivien (2009); 22, Vasil'Eva and Vasil'Ev (2003); 23, Polačik et al. (2009)]

Dietary item	Monkey goby	Round goby	Bighead goby	Sampling location	References
<b>Non-native habitat</b>					
<b>Trichoptera</b>					
Brachycentridae			+ <sup>5</sup>	e <sup>5</sup>	5
<i>Brachycentrus subnubilus</i>			+ <sup>1</sup>	a <sup>1</sup>	1
Goeridae		+ <sup>5</sup>		e <sup>5</sup>	5
Hydropsychidae		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
<i>Hydropsyche</i> sp.	+ <sup>1</sup>	+ <sup>6</sup>	+ <sup>1,6</sup>	a <sup>1</sup> , f <sup>6</sup>	1, 6
<i>H. angustipennis</i>	+ <sup>4</sup>			d <sup>4</sup>	4
Hydroptilidae		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
<i>Hydroptila sparsa</i>			+ <sup>1</sup>	a <sup>1</sup>	1
Limnephilidae		+ <sup>5</sup>		e <sup>5</sup>	5
Polycentropodidae		+ <sup>5</sup>		e <sup>5</sup>	5
<i>Sericostoma</i> sp.		+ <sup>5</sup>		e <sup>5</sup>	5
Leptoceridae			+ <sup>1</sup>	a <sup>1</sup>	1
Trichoptera n.d.	+ <sup>2,3,7</sup> p	+ <sup>2,14</sup>	+ <sup>2,5,14</sup>	b <sup>2</sup> , c <sup>3</sup> , e <sup>5</sup> , g <sup>7</sup> , n <sup>14</sup>	2, 3, 5, 7, 14
<b>Ephemeroptera</b>					
Baetidae		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
Caenidae		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
Heptageniidae			+ <sup>1</sup>	a <sup>1</sup>	1
<i>Caenis</i> sp.	+ <sup>1</sup>		+ <sup>1</sup>	a <sup>1</sup>	1
<i>Baetis</i> sp.			+ <sup>1</sup>	a <sup>1</sup>	1
<i>P. luteus</i>	+ <sup>1</sup>	+ <sup>5</sup>	+ <sup>1,5</sup>	a <sup>1</sup> , e <sup>5</sup>	1, 5
<i>Ephoron virgo</i>	+ <sup>1</sup>		+ <sup>1</sup>	a <sup>1</sup>	1
<i>Oecetis albicorne</i>	+ <sup>1</sup>			a <sup>1</sup>	1
Ephemeroptera n.d.	+ <sup>3</sup>	+ <sup>6,14</sup>	+ <sup>5,6,14</sup>	c <sup>3</sup> , e <sup>5</sup> , f <sup>6</sup> , n <sup>14</sup>	3, 5, 6, 14
<b>Plecoptera</b>					
Plecoptera n.d.		+ <sup>8,14</sup>	+ <sup>14</sup>	h <sup>8</sup> , n <sup>14</sup>	8, 14
<b>Odonata</b>					
Zygoptera	+ <sup>3</sup>			c <sup>3</sup>	3
Coenagrionidae			+ <sup>5</sup>	e <sup>5</sup>	5
Gomphidae			+ <sup>5</sup>	e <sup>5</sup>	5
Odonata n.d.	+ <sup>2</sup>			b <sup>2</sup>	2
<b>Heteroptera</b>					
<i>Aphelocheirus aestivalis</i>			+ <sup>1</sup>	a <sup>1</sup>	1
<i>Micronecta</i> sp.		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
Heteroptera n.d.		+ <sup>6</sup>	+ <sup>5</sup>	e <sup>5</sup> , f <sup>6</sup>	5, 6
<b>Coleoptera</b>					
Dytiscidae		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
<i>Dytiscus</i> sp.		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
Elmidae		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5

**Table 1.** Continued

Dietary item	Monkey goby	Round goby	Bighead goby	Sampling location	References
Hydraenidae		+ <sup>5</sup>		e <sup>5</sup>	5
Coleoptera n.d.	+ <sup>2, 3</sup>	+ <sup>2</sup>		b <sup>2</sup> , c <sup>3</sup>	2, 3
<b>Diptera</b>					
Chironomidae	+ <sup>1, 2, 3, 4, 7, 15</sup> p	+ <sup>1, 2, 5, 13, 14, 15</sup> p	+ <sup>1, 5, 13, 14, 15</sup> p	a <sup>1</sup> , b <sup>2</sup> , c <sup>3</sup> , d <sup>4</sup> , e <sup>5</sup> , g <sup>7</sup> , m <sup>13</sup> , n <sup>14</sup> , o <sup>15</sup>	1, 2, 3, 4, 5, 7, 13, 14, 15
<i>Chironomus</i> sp.	+ <sup>7</sup>			g <sup>7</sup>	7
<i>Cladotanytarsus</i> sp.	+ <sup>7</sup>			g <sup>7</sup>	7
<i>Cricotopus</i> sp.	+ <sup>7</sup>			g <sup>7</sup>	7
<i>Dicrotendipes</i> sp.	+ <sup>7</sup>			g <sup>7</sup>	7
<i>Glyptotendipes</i> sp.	+ <sup>7</sup>			g <sup>7</sup>	7
<i>Polypedilum</i> sp.	+ <sup>7</sup>			g <sup>7</sup>	7
<i>Tanytarsus</i> sp.	+ <sup>7</sup>			g <sup>7</sup>	7
<i>Cryptochironomus</i> sp.	+ <sup>7</sup>			g <sup>7</sup>	7
Simuliidae	+ <sup>3</sup>	+ <sup>5</sup>	+ <sup>5</sup>	c <sup>3</sup> , e <sup>5</sup>	3, 5
Tipulidae	+ <sup>2, 3</sup>		+ <sup>2</sup>	b <sup>2</sup> , c <sup>3</sup>	2, 3
Ceratopogonidae	+ <sup>3</sup>	+ <sup>5</sup>	+ <sup>1, 5</sup>	a <sup>1</sup> , c <sup>3</sup> , e <sup>5</sup>	1, 3, 5
Ephydriidae		+ <sup>5</sup>		e <sup>5</sup>	5
Limoniidae		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
<i>Psychoda</i> sp.		+ <sup>5</sup>		e <sup>5</sup>	5
Syrphidae		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
Diptera n.d.	+ <sup>3, 7</sup>	+ <sup>5, 8</sup>		c <sup>3</sup> , e <sup>5</sup> , g <sup>7</sup> , h <sup>8</sup>	3, 5, 7, 8
<b>Ostracoda</b>					
Ostracoda n.d.	+ <sup>1, 3, 7</sup>	+ <sup>5, 6</sup>	+ <sup>5, 6</sup>	a <sup>1</sup> , c <sup>3</sup> , e <sup>5</sup> , f <sup>6</sup> , g <sup>7</sup>	1, 3, 5, 6, 7
<b>Turbellaria</b>					
Turbellaria n.d.		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
<b>Bryozoa</b>					
Bryozoa n.d.		+ <sup>5, 6, 14</sup>	+ <sup>5</sup>	e <sup>5</sup> , f <sup>6</sup> , n <sup>14</sup>	5, 6, 14
<b>Copepoda</b>					
Copepoda n.d.	+ <sup>3, 7</sup>	+ <sup>1, 5</sup>	+ <sup>5</sup>	a <sup>1</sup> , c <sup>3</sup> , e <sup>5</sup> , g <sup>7</sup>	1, 3, 5, 7
<b>Rotatoria</b>					
Rotatoria n.d.	+ <sup>7</sup>			g <sup>7</sup>	7
<b>Gastropoda</b>					
<i>Potamopyrgus</i> sp.	+ <sup>7</sup>	+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup> , g <sup>7</sup>	5, 7
<i>Viviparus</i> sp.			+ <sup>5</sup>	e <sup>5</sup>	5
Gastropoda n.d.	+ <sup>2, 3, 7</sup> p	+ <sup>2, 5, 9, 10, 11</sup> p		b <sup>2</sup> , c <sup>3</sup> , e <sup>5</sup> , g <sup>7</sup> , i <sup>9</sup> , j <sup>10</sup> , k <sup>11</sup>	2, 3, 5, 7, 9, 10, 11
<i>L. peregra</i>		+ <sup>8</sup>		h <sup>8</sup>	8
<i>T. danubialis</i>		+ <sup>8</sup>		h <sup>8</sup>	8
<i>T. fluviatilis</i>		+ <sup>6</sup>		f <sup>6</sup>	6
<i>L. naticoides</i>		+ <sup>6</sup>		f <sup>6</sup>	6
Eggs			+ <sup>5</sup>	e <sup>5</sup>	5
<b>Bivalvia</b>					
Sphaeriidae	+ <sup>7</sup>	+ <sup>6, 8</sup> p		f <sup>6</sup> , g <sup>7</sup> , h <sup>8</sup>	6, 7, 8
<i>D. polymorpha</i>	+ <sup>7</sup>	+ <sup>6, 8</sup>		f <sup>6</sup> , g <sup>7</sup> , h <sup>8</sup>	6, 7, 8
Unionidae		+ <sup>6, 8</sup> p		f <sup>6</sup> , h <sup>8</sup>	6, 8
<i>C. fluminea</i>		+ <sup>6</sup> p		f <sup>6</sup>	6
<i>Anodonta</i> sp.		+ <sup>8</sup>		h <sup>8</sup>	8
Bithyniidae		+ <sup>5</sup>		e <sup>5</sup>	5
<i>Pisidium</i> sp.	+ <sup>1, 7</sup>	+ <sup>5, 8</sup>	+ <sup>5</sup>	a <sup>1</sup> , e <sup>5</sup> , g <sup>7</sup> , h <sup>8</sup>	1, 5, 7, 8
<i>Sphaerium</i> sp.	+ <sup>7</sup>	+ <sup>5</sup>		e <sup>5</sup> , g <sup>7</sup>	5, 7
Sphaeriidae n.d.	+ <sup>7</sup>			g <sup>7</sup>	7
<i>Valvata</i> sp.		+ <sup>5</sup>		e <sup>5</sup>	5
Bivalvia n.d.	+ <sup>2</sup>	+ <sup>2, 5, 9, 10, 11</sup>		b <sup>2</sup> , e <sup>5</sup> , i <sup>9</sup> , j <sup>10</sup> , k <sup>11</sup>	2, 5, 9, 10, 11
<b>Polychaeta</b>					
<i>Hypania invalida</i>		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5

**Table 1.** Continued

Dietary item	Monkey goby	Round goby	Bighead goby	Sampling location	References
Polychaeta n.d.		+ <sup>9,11</sup>		j <sup>9</sup> , k <sup>11</sup>	9, 11
<b>Oligochaeta</b>					
Lumbricidae	+ <sup>1</sup>			a <sup>1</sup>	1
Oligochaeta n.d.	+ <sup>2,3,7</sup>	+ <sup>2,5,6,8,14</sup>	+ <sup>5,14</sup>	b <sup>2</sup> , c <sup>3</sup> , e <sup>5</sup> , f <sup>6</sup> , g <sup>7</sup> , h <sup>8</sup> , n <sup>14</sup>	2, 3, 5, 6, 7, 8, 14
<b>Hirudinea</b>					
<i>Erpobdella</i> sp.			+ <sup>1</sup>	a <sup>1</sup>	1
Hirudinea n.d.	+ <sup>3,7</sup>	+ <sup>6</sup>	+ <sup>5,6</sup>	c <sup>3</sup> , e <sup>5</sup> , f <sup>6</sup> , g <sup>7</sup>	3, 5, 6, 7
<b>Nematomorpha</b>					
Nematomorpha n.d.		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
<b>Hydracarina</b>					
Hydracarina n.d.		+ <sup>1,5,6</sup>	+ <sup>5</sup>	a <sup>1</sup> , e <sup>5</sup> , f <sup>6</sup>	1, 5, 6
<b>Cladocera</b>					
<i>Daphnia</i> sp.			+ <sup>1</sup>	a <sup>1</sup>	1
Cladocera n.d.	+ <sup>3,7</sup>	+ <sup>5,6</sup>	+ <sup>5</sup>	c <sup>3</sup> , e <sup>5</sup> , f <sup>6</sup> , g <sup>7</sup>	3, 5, 6, 7
<b>Nematoda</b>					
Nematoda n.d.	+ <sup>1</sup>			a <sup>1</sup>	1
<b>Ostracoda</b>					
Ostracoda n.d.	+ <sup>1,3,7</sup>	+ <sup>5,6</sup>	+ <sup>5,6</sup>	a <sup>1</sup> , c <sup>3</sup> , e <sup>5</sup> , f <sup>6</sup> , g <sup>7</sup>	1, 3, 5, 6, 7
<b>Copepoda</b>					
Copepoda n.d.	+ <sup>3,7</sup>	+ <sup>1,5</sup>	+ <sup>5</sup>	a <sup>1</sup> , c <sup>3</sup> , e <sup>5</sup> , g <sup>7</sup>	1, 3, 5, 7
<b>Isopoda</b>					
<i>Jaera istri</i>		+ <sup>5,6</sup>	+ <sup>5,6</sup>	e <sup>5</sup> , f <sup>6</sup>	5, 6
<i>Jaera sarsi</i>		+ <sup>14</sup>	+ <sup>14</sup>	n <sup>14</sup>	14
Isopoda n.d.		+ <sup>10,11</sup>		j <sup>10</sup> , k <sup>11</sup>	10, 11
<b>Amphipoda</b>					
<i>P. robustoides</i>	+ <sup>3</sup>			c <sup>3</sup>	3
<i>D. haemobaphes</i>	+ <sup>3</sup>			c <sup>3</sup>	3
<i>Cheliochorophium</i> sp.		+ <sup>14</sup>	+ <sup>14</sup>	n <sup>14</sup>	14
<i>C. curvispinum</i>	+ <sup>3</sup>	+ <sup>6</sup>	+ <sup>1,6</sup>	a <sup>1</sup> , c <sup>3</sup> , f <sup>6</sup>	1, 3, 6
Amphipoda n.d.	+ <sup>3,7 p</sup>	+ <sup>5,9,10,11</sup>	+ <sup>5</sup>	c <sup>3</sup> , e <sup>5</sup> , g <sup>7</sup> , i <sup>9</sup> , j <sup>10</sup> , k <sup>11</sup>	3, 5, 7, 9, 10, 11
<i>Corophium</i> sp.		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
Gammaridae		+ <sup>13</sup>	+ <sup>13</sup>	m <sup>13</sup>	13
<i>Dikerogammarus</i> sp.		+ <sup>5,6,14 p</sup>	+ <sup>5,6,14 p</sup>	e <sup>5</sup> , f <sup>6</sup> , n <sup>14</sup>	5, 6, 14
<i>Echinogammarus</i> sp.		+ <sup>14</sup>	+ <sup>14</sup>	n <sup>14</sup>	14
<i>Pontogammarus</i> sp.		+ <sup>14</sup>	+ <sup>14</sup>	n <sup>14</sup>	14
<i>Obesogammarus</i> sp.		+ <sup>14</sup>	+ <sup>14</sup>	n <sup>14</sup>	14
<i>D. villosus</i>		+ <sup>1</sup>	+ <sup>1</sup>	a <sup>1</sup>	1
<i>Gammarus</i> sp.	+ <sup>2,4</sup>	+ <sup>2,5,8</sup>	+ <sup>2,5</sup>	b <sup>2</sup> , d <sup>4</sup> , e <sup>5</sup> , h <sup>8</sup>	2, 4, 5, 8
<i>Gammarus roeseli</i>		+ <sup>14</sup>	+ <sup>14</sup>	n <sup>14</sup>	14
<i>O. obesus</i>		+ <sup>6</sup>	+ <sup>6</sup>	f <sup>6</sup>	6
<i>E. ichnus</i>		+ <sup>6</sup>	+ <sup>6</sup>	f <sup>6</sup>	6
<i>Niphargus</i> sp.		+ <sup>6</sup>		f <sup>6</sup>	6
<b>Mysida</b>					
<i>Lymnopsis benedeni</i>		+ <sup>5</sup>	+ <sup>5,6</sup>	e <sup>5</sup> , f <sup>6</sup>	5, 6
Mysida n.d.			+ <sup>14</sup>	n <sup>14</sup>	14
<b>Pisces</b>					
Cyprinidae			+ <sup>2,5,14</sup>	b <sup>2</sup> , e <sup>5</sup> , n <sup>14</sup>	2, 5, 14
<i>L. cephalus</i>			+ <sup>2</sup>	b <sup>2</sup>	2
<i>P. fluviatilis</i>			+ <sup>14</sup>	n <sup>14</sup>	14
<i>S. lucioperca</i>			+ <sup>1</sup>	a <sup>1</sup>	1
<i>Z. zingel</i>			+ <sup>1</sup>	a <sup>1</sup>	1
<i>Gymnocephalus</i> sp.			+ <sup>5</sup>	e <sup>5</sup>	5
Gobiidae	+ <sup>2</sup>		+ <sup>2,5</sup>	b <sup>2</sup> , e <sup>5</sup>	2, 5
<i>Neogobius</i> sp.			+ <sup>5</sup>	e <sup>5</sup>	5

**Table 1.** Continued

Dietary item	Monkey goby	Round goby	Bighead goby	Sampling location	References
<i>Neogobius</i> sp.			+ <sup>5</sup>	e <sup>5</sup>	5
<i>P. kessleri</i>			+ <sup>5</sup>	e <sup>5</sup>	5
<i>N. melanostomus</i>		+ <sup>5</sup>	+ <sup>5, 14</sup>	e <sup>5</sup> , n <sup>14</sup>	5, 14
<i>P. semilunaris</i>			+ <sup>5</sup>	e <sup>5</sup>	5
Eggs		+ <sup>5, 6</sup>	+ <sup>5</sup>	e <sup>5</sup> , f <sup>6</sup>	5, 6
Macrophytes		+ <sup>5</sup>	+ <sup>5</sup>	e <sup>5</sup>	5
Pisces n.d.	+ <sup>3, 7</sup>	+ <sup>5, 9, 10</sup>	+ <sup>1, 2, 5, 6</sup> p	a <sup>1</sup> , b <sup>2</sup> , c <sup>3</sup> , e <sup>5</sup> , f <sup>6</sup> , g <sup>7</sup> , i <sup>9</sup> , j <sup>10</sup>	1, 2, 3, 5, 6, 7, 9, 10
<i>S. namaycush</i>		+ <sup>12</sup>		l <sup>12</sup>	12
<i>A. fluvescens</i>		+ <sup>12</sup>		l <sup>12</sup>	12
<b>Terrestrial Arthropoda</b>					
Linyphiidae		+ <sup>5</sup>		e <sup>5</sup>	5
Auchenorrhyncha		+ <sup>5</sup>		e <sup>5</sup>	5
Diplopoda		+ <sup>5</sup>		e <sup>5</sup>	5
Dipteran imagines		+ <sup>5</sup>		e <sup>5</sup>	5
Chilopoda			+ <sup>5</sup>	e <sup>5</sup>	5
Thysanoptera		+ <sup>5</sup>		e <sup>5</sup>	5
Terrestrial Arthropoda n.d.			+ <sup>5</sup>	e <sup>5</sup>	5
<b>Terrestrial Isopoda</b>					
Terrestrial Isopoda n.d.		+ <sup>6</sup>	+ <sup>6</sup>	f <sup>6</sup>	6
<b>Terrestrial Hymenoptera</b>					
Terrestrial Hymenoptera n.d.		+ <sup>6</sup>	+ <sup>6</sup>	f <sup>6</sup>	6
<b>Native habitat</b>					
<b>Bivalvia</b>					
Corbicula	+ <sup>16</sup>			p <sup>16</sup>	16
<i>D. polymorpha</i>	+ <sup>17</sup> p			q <sup>17</sup> , r <sup>17</sup>	17
Bivalvia n.d.		+ <sup>17, 21</sup> p		v <sup>21</sup> , y <sup>17</sup>	17, 21
<b>Gastropoda</b>					
Lithoglyphus	+ <sup>16</sup>			p <sup>16</sup>	16
<b>Isopoda</b>					
Isopoda n.d.		+ <sup>21</sup>		v <sup>21</sup>	21
<b>Amphipoda</b>					
<i>Cheliochorophium</i> sp.		+ <sup>17</sup>	+ <sup>22</sup>	z <sup>22</sup> , y <sup>17</sup>	17, 22
Gammaridae		+ <sup>17</sup>		y <sup>17</sup>	17
Amphipoda n.d.	+ <sup>18</sup>	+ <sup>21</sup>	+ <sup>22, 23</sup> p	s <sup>18</sup> , v <sup>21</sup> , z <sup>22</sup> , x <sup>23</sup>	18, 21, 22, 23
<b>Mysida</b>					
Mysida n.d.			+ <sup>22</sup>	z <sup>22</sup>	22
<b>Cirrhipoda</b>					
Cirrhipoda n.d.		+ <sup>21</sup>		v <sup>21</sup>	21
<b>Trichoptera</b>					
Trichoptera n.d.		+ <sup>21</sup>		v <sup>21</sup>	21
<b>Heteroptera</b>					
Corixidae	+ <sup>16</sup>			p <sup>16</sup>	16
<b>Diptera</b>					
Chironomidae	+ <sup>16, 18</sup>	+ <sup>17</sup>	+ <sup>22</sup>	p <sup>16</sup> , s <sup>18</sup> , z <sup>22</sup> , y <sup>17</sup>	16, 17, 18, 22
Diptera n.d.		+ <sup>21</sup>		v <sup>21</sup>	21
<b>Polychaeta</b>					
Polychaeta n.d.	+ <sup>18</sup>	+ <sup>17, 19, 20, 21</sup>	+ <sup>22</sup>	s <sup>18</sup> , t <sup>19</sup> , u <sup>20</sup> , v <sup>21</sup> , z <sup>22</sup> , y <sup>17</sup>	17, 18, 19, 20, 21, 22
<b>Oligocheta</b>					
Oligocheta n.d.	+ <sup>18</sup>			s <sup>18</sup>	18
<b>Pisces</b>					
Eggs	+ <sup>18</sup>			s <sup>18</sup>	18
Gobiidae			+ <sup>22</sup>	z <sup>22</sup>	22
Pisces n.d.	+ <sup>18</sup>	+ <sup>17, 20, 21</sup>	+ <sup>22, 23</sup> p	s <sup>18</sup> , u <sup>20</sup> , v <sup>21</sup> , z <sup>22</sup> , x <sup>23</sup> , y <sup>17</sup>	17, 18, 20, 21, 22, 23

bighead and round goby diets did not overlap in spring, but significantly overlapped in summer and autumn (Borza et al., 2009). Beside this, an overlap in individual dietary items varies by season (Števove and Kováč, 2013; Brandner et al., 2013), which could be the reason for different results. High values of dietary overlap were found between round goby and bighead goby in the middle Danube (Copp et al., 2008) and the lower Rhine (Borcherding et al., 2013), indicating high levels of interspecific competition on food resources. Also, in the same river in Slovakia, round goby and bighead goby showed a significant overlap with perch *Perca fluviatilis* and Balon's ruffe *Gymnocephalus baloni* in their diet (Copp et al., 2008). In the Baltic Sea, the diet of round goby and European flounder *Platichthys flesus* overlapped (Karlson et al., 2007).

In the Danube Delta in Romania, the diet of monkey goby and white bream *Blicca bjoerkna*, stellate tadpole-goby *Benthophilus stellatus*, as well as striped ruffe *Gymnocephalus schraetser* overlapped (Sindilariu and Freyhof, 2003).

## AGE AND GROWTH

Scale analysis of monkey goby in Lake Manyas (Sasi and Berber, 2010) and the River Ipel' (Plachá et al., 2010) and bighead goby in the rivers Sava (Simonović, 1996) and Danube (Copp et al., 2008) demonstrated five different age groups. Furthermore, the analysis of scales in round goby in the Danube showed four age groups (Gruľa et al., 2012). Moreover, by analysing the otoliths of round goby in the Baltic Sea (Sokołowska and Fey, 2011) and the Great Lakes (Huo et al., 2014), five and six age groups were found, respectively. Lower growth of P-C gobies in invaded freshwater areas of Europe may not surprisingly be due to their lower growth in their native freshwater habitat (Corkum et al., 2004). Thus, round goby in the southern Baltic Sea is

reported to have a longer life span (up to 6 years) and larger size at age than most round goby populations (Sokołowska & Fey, 2011), further suggesting larger sizes in saline water (Kornis et al., 2012). The introduced round goby exhibits its sexual maturity at a smaller length and age groups than the majority of native populations (MacInnis and Corkum, 2000a, 2000b; L'avrinčiková and Kováč, 2007), and the same is valid for bighead goby (Kováč et al., 2009).

The authors who studied the scales of monkey goby (Plachá et al., 2010) and round goby (Gruľa et al., 2012) showed the unreliability of the von Bertalanffy growth model (Table 2). In both cases, the reason for that was in the breaking of confidence limits by 95% of calculated growth parameters. However, it is possible that the annuli on the scales are imprecisely determined (Britton et al., 2004), that this model describes well the somatic growth only after sexual maturity (Lester et al., 2004) and that it does not contain a variable of water temperature which affects physiological processes while determining growth (Kielbassa et al., 2010). In contrast to previous considerations, Sasi and Berber (2010) found five age groups for monkey goby in Lake Manyas in Turkey and by using the von Bertalanffy model they managed to measure von Bertalanffy growth parameters. The same model was successfully applied by MacInnis (1997) and Huo et al. (2014) who studied the otoliths of round gobies from Lake Michigan.

Due to lack of research on bighead goby, von Bertalanffy growth parameters only for monkey and round goby in native and non-native part of Europe are presented in Table 2.

## GENOTYPING

The analysis of mitochondrial DNA cytochrome b haplotypes in monkey goby from the Black and the Caspian Sea Basin manifested the greatest genetic diversity among populations living in the Azov and the Caspian Sea, and the lowest among populations living in the European rivers, the Vistula

**Table 2.** Von Bertalanffy growth parameters, age and sex of monkey goby and round goby. The symbol \* indicates the standard length, otherwise the total length is shown, while the symbol \*\* denotes counting annuli on the otoliths, otherwise annulus count on the scales is shown (M =males; F=females; N=ative; A=non-native)

Species	Age	(cm)	(year <sup>-1</sup> )	(year)	Sex	Distribution	References
	-	14.70	0.42			N	Froese and Pauly, 2015
Monkey goby	I - V	22.89	0.489	-1.390	M + F	A	Sasi and Berber, 2010
	I - IV	8.037	0.30	-0.95	F	A	Plachá et al., 2010 *
	I - V	11.129	0.23	-0.77	M		
	I - IV	12.35±2.38 23.69±10.54	0.24±0.10 0.11±0.07	-1.06±0.38 -0.95±0.30	F M	A	Gruľa et al., 2012 *
Round goby	II - VII	13.285±0.943	0.263±0.037	-0.275±0.087	F	A	Huo et al., 2014 **
		18.447±2.375	0.162±0.032	-0.144±0.086	M		
	-	13.30	0.35	-0.21	M	N	Froese and Pauly, 2015
	-	21.90	0.11	-1.62	F		
	I - III	10.18±3.84	0.61±0.51	0.28±0.23	M + F	A	MacInnis, 1997 * **



and Hron (Neilson and Stepien, 2011). Study of the cytochrome b gene and microsatellites of round gobies by Stepien and Tumeo (2006) demonstrated the greatest genetic diversity among populations living in the Black Sea and the Great Lakes, and the lowest among European freshwater populations. However, Brown and Stepien (2008) reported that in many locations in the Black, Caspian, Azov and Baltic Sea, and the Danube, Dnieper, Moscow and Volga, genetic diversity was higher among the native than among the introduced populations. For the individuals from the upper Danube flow, the most common Black Sea haplotype 1 was determined and genetic diversity was low (Table 3; Cerwenka et al., 2014). However, in the introduced populations of the River Rhine Basin in Germany (Cerwenka et al., 2014) and Belgium (Table 3; Mombartes et al., 2014), a relatively high level of genetic diversity was demonstrated. It was assumed that it occurred due to the geopolitical changes in the 1990s; namely, at the time ship traffic was eight times higher in the River Rhine Basin than in the Danube due to the collapse of the Communist government and the Croatian War of Independence (Roche et al., 2013). By analysing the non-coding control region of round gobies, Stepien et al. (2005) reported that the North American populations have a greater genetic diversity than the native Eurasian populations. Also, by analysing the control region sequences of round goby, Dillon and Stepien (2001)

found a relatively high genetic diversity in the introduced populations of the Great Lakes of North America, the Gulf of Gdansk in Poland and the native populations of the Black Sea.

Genetic diversity was similar for native and introduced populations, which suggested numerous populations that were found and the absence of a bottleneck. The reason for these diverse results could be found in continuous intake of individuals which enables the transfer of genes between populations (LaRue et al., 2011). Besides, non-coding control region has a higher level of genetic diversity than cytochrome b gene (Stepien and Kocher, 1997). The research on microsatellites of round gobies and bighead goby from the Danube in Slovakia showed a low to moderate genetic diversity, i.e. limited polymorphism as a result of founder effect (Vyskočilová et al., 2007). Furthermore, the same level of genetic diversity was found between the native Black Sea and introduced Eurasian or North American round goby populations (Feldheim et al. 2009). As shown for microsatellites of round goby from Lake Michigan, a correlation between geographic distance and genetic diversity was not found, but it was found between the amount of ship traffic and genetic diversity (LaRue et al., 2011). Moreover, by analysing microsatellites of round goby in the Baltic Sea, Björklund and Almqvist (2010) found the greatest genetic diversity just between locations with the most different habitats.

**Table 3.** Cytochrome b haplotypes and sampling locations for monkey goby, round goby and bighead goby (N = native; I = invasive)

Species	Haplotype designation	Sampling location	Distribution	References
Monkey goby	haplotype 1	Vistula Poland, Hron Slovakia	I	
	haplotype 1	Ozero Manych, Tsimlyanska Reservoir, Russia	N	
	haplotype 2	Rioni River Georgia, Tyligul Estuary Ukraine	N	
	haplotype 3	Dniester, Dnieper, Khadzhibey Estuary Ukraine, Chagraiskoye Reservoir Russia	N	
	haplotype 4	Azov Sea, Ukraine	N	
	haplotype 5	Lake Sarpa, Chernozemel'skii Connector, Russia	N	Neilson and Stepien, 2011
	haplotype 6	Danube, Ukraine	N	
	haplotype 7	Dniester delta, Ukraine	N	
	haplotype 11	Dniester, Ukraine	N	
	haplotype 37- 99	Caspian Sea, Volga delta	N	
	haplotype 1-36, 100-107	Black Sea, Volga, Don	N	
	ALL13	Volga, Russia	N	
	ANT5	Ozero Manych, Russia	N	Neilson and Stepien, 2009b
	AGV7	Danube, Ukraine	I	
	AGV9	Azov Sea, Ukraine	N	
	ANG11	Chernozemelskii Chann., Russia	N	
	FJ526752	Don, Ukraine	N	
	Nf1, Nf3, GQ444338	Lake Sasyk, Ukraine	N	Medvedev et al., 2013
Nf2, GQ444372	Caspian Sea, Volga Delta	N		



**Table 3.** Continued

Species	Haplotype designation	Sampling location	Distribution	References
Round goby	ame1	Baltic Sea, Poland	I	
	ame1, 23	Danube, Slovakia	I	
	ame1, 7	Danube, Serbia	I	
	ame1, 10, 11, 62, 65, 67, 68, 77, 78, 79	Black Sea, Bulgaria	N	
	ame 1-10, 18, 48, 60-66, 69, 74-76, 80	Black Sea, Ukraine	N	
	ame 1, 18, 49, 50, 51, 58, 72, 73	Bug, Ukraine	N	
	ame 1, 7, 8, 57	Dnieper, Ukraine	N	Brown and Stepień, 2008
	ame 1, 58, 59	Dnieper, Ukraine	I	
	ame 18, 41-48	Kerch Strait, Ukraine	N	
	ame 11-19	Azov Sea	N	
	ame 24-28	Moskva River, Russia	I	
	ame 20	Volga-Don Canal	I	
	ame 20, 24, 25, 29, 30	Volga, Russia	I	
	ame 20-22	Caspian Sea, Russia	N	
	ame 31-33, 35, 70, 71, 81-85	Caspian Sea, Azerbaijan	N	
	ame 31-40, 86	Caspian Sea, Iran	N	
	AKB1, APT1, ALK6	Caspian Sea, Azerbaijan	N	
	AHF8	Black Sea, Ukraine	N	
	APC8	Kerch Strait, Ukraine	N	Neilson and Stepień, 2009b
	AMP2	Volga, Russia	I	
	AHC3	Dnieper, Ukraine	I	
	Nm1, EU331215	Chernaya River, Russia	N	
	Nm 2	Lake Sasyk, Ukraine	N	
	Nm3, EU331165	Black Sea, Ukraine	N	Medvedev et al., 2013
	ame10	Black Sea, Bulgaria, Ukraine	N	
	ame 1-10	Dniester	N	
	ame 41-48	Azov Sea	N	Brown and Stepień, 2009
	ame 20-22, 24-30	Volga	N	
	haplotype 1	Danube, Germany	I	Cerwenka et al., 2014
	NSB1, NSB2, NSB3	Rhine Basin, Belgium	I	
	APT7	Lake Simferopol, Ukraine	N	
	APT8	Danube, Serbia	I	Neilson and Stepień, 2009b
ALC2	Dniester, Ukraine	N		
Bighead goby	APT8	Rhine, Switzerland	I	Kalchhauser et al., 2014
	NkeAGV3	Black Sea Basin	N	Neilson and Stepień, 2009a
	Nk1, FJ526770	Lake Sasyk, Ukraine	N	Medvedev et al., 2013
	Nk 2	Danube, Ukraine	N	

The large number of haplotypes found outside their natural range (Table 3) suggests a relatively large number of introduced populations (Dillon and Stepień, 2001; Ađđamar et al., 2015), thus increasing the probability of

their establishment and persistence (Stepień and Tumeo, 2006; Facon et al. 2008; Fitzpatrick et al. 2012), which consequently has the strength of their invasive potential (Simonović et al., 2013; Piria et al., 2016a).

## IMPACT ON NATIVE FISH SPECIES

Most concern for the impact of P-C gobies in newly invaded areas is focused on native protected species. Such possible negative impact on the protected fish species zingel *Zingel zingel* by bighead and round goby in Croatia (Piria et al. 2016b) and by bighead goby in Slovakia was reported (Adámek et al., 2007). Also, a negative impact on abundance of zander *Stizostedion lucioperca* by bighead goby (Adámek et al., 2007), bullhead *Cottus gobio*, stone loach *Barbatula barbatula* and white-finned gudgeon *Gobio albipinnatus* by bighead goby (Jurajda et al., 2005), chub *Squalius cephalus* by round and bighead goby (Piria et al., 2016b) and a decline in the ratio of gudgeon *Gobio gobio* (Jakovlić et al., 2015) were noted. Also, the possibility of competition for food between P-C gobies and Eurasian perch *Perca fluviatilis*, as well as Balon's ruffe *Gymnocephalus baloni*, has been proposed (Copp et al., 2008). Contrary to these findings, several researches reveal positive impact of P-C gobies on cod *Gadus morhua*, perch (Almqvist et al., 2010), burbot *Lota lota* (Corkum et al., 2004), catfish *Silurus glanis* and zander populations (Lenhardt et al., 2011) as their prey. Moreover, an increasing trend in abundance of Balkan golden loach *Sabanejewia balcanica* in response to round goby, as well as of crucian carp *Carassius carassius*, Balkan loach *Cobitis elongata* and burbot in response to the presence of monkey goby, were noted (Piria et al., 2016b).

In laboratory studies, Chotkowski and Marsden (1999) reported that round goby fed on eggs and fry of lake trout *Salvelinus namaycush*, and eggs of lake sturgeon *Acipenser fluvescens*, reducing the hatching of these species. In the St Clair River, Janssen and Jude (2001) indicated that recruitment failure of mottled sculpins *Cottus bairdi* resulted from spawning interference by round goby, while Dubs and Corkum (1996) predicted that round goby would induce mottled sculpins to desert nearshore habitats and be forced into deeper habitats where sculpins would be more susceptible to large predators.

## CONCLUSION

Based on the gut content analyses, depending on the season, life stage, habitat and food availability, all three P-C gobies partake different kind of invertebrates in native and non-native territory. In an area invaded by Ponto-Caspian species, positive diet selection of P-C gobies on P-C invertebrates was found. Also, based on the fact that several top predators feed on them, it could be assumed that they have found a specific role in the ecological niche of new invaded area. Impact of P-C gobies on endemic, rare or protected species still can be only speculative, but possible consequences can not be excluded. Presented age and growth results suggest that growth rates are highly variable and site specific. This can lead to a statistically unreliable von Bertalanffy model for P-C gobies and the necessity of testing

other growth models. The combination of DNA variation and risk assessment procedures offers an important diagnostic and monitoring tool for evaluating the relative success of invasive species.

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## Sažetak

## PREGLED EKOLOŠKIH I GENETSKIH ISTRAŽIVANJA PONTO-KASPIJSKIH GLAVOČA (Pisces, Gobiidae) U EUROPI

Invazivni ponto-kaspijski glavoči riječni glavočić *Neogobius fluviatilis*, glavočić okrugljak *Neogobius melanostomus* i Keslerov glavočić *Ponticola kessleri* nedavno su uzrokovali dramatične promjene struktura ribljih zajednica diljem europskih riječnih sustava. Ovaj rad daje pregled novijih istraživanja o njihovim prehranbenim navikama, dobnoj strukturi i rastu, filogenetskim linijama i genetskoj raznolikosti. Osnovna hrana svih triju vrsta su beskralježnjaci, nešto rjeđe ribe, što ovisi o vrsti staništa, dobu godine, kao i morfološkim karakteristikama vrste. Prema von Bertalanffyjevom modelu rasta, veličina i starost je specifična za područje, ali zbog njegovih nedostataka potrebno je testirati i druge modele rasta. Filogenetske analize riječnog glavočića i glavočića okrugljaka ukazuje razdvajanje između haplotipova Crnog i Kaspijskog mora. Najveća genska raznolikost je pronađena među populacijama Crnog mora, a najniža među europskim invazivnim populacijama. Nedostatak molekularnih istraživanja Keslerova glavočića zahtijeva daljnja istraživanja.

**Ključne riječi:** europski riječni sistem, invazivni glavoči, ekologija, genetika

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