DOI: 10.30906/1026-2296-2022-29-5-298-316

DISTRIBUTION AND POPULATION SYSTEMS OF WATER FROGS (THE *Pelophylax esculentus* COMPLEX) IN NORTHWESTERN RUSSIA

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Submitted May 4, 2022.

Peculiarities of distribution and population systems of water frogs of the *Pelophylax esculentus* complex in the northwest of Russia were studied using cytogenetic (genome size) and external morphological characters (439 specimens from 101 localities). We registered three species: *P. lessonae*, *P. ridibundus*, and *P. esculentus* of a hybrid origin. All frogs, including hybrids, were diploid. The first species was prevailing (82% localities); the second species was revealed in 18% localities and hybrid frogs in 13% localities. All species reach the northernmost limits of their distribution. *Pelophylax lessonae* is widely spread through Pskovskaya and Novgorodskaya oblast's, as well as in southern Leningradskaya oblast', preferring forest habitats. *Pelophylax esculentus* is found in Pskovskaya oblast' (forest and agricultural biotopes) in co-existence with *P. lessonae* only. *Pelophylax ridibundus*, which was introduced since the 18th century, is distributed in St. Petersburg City and Leningradskaya oblast' along southern coast of the Gulf of Finland and Narva River on the Estonian border. All populations of the species were usually observed in open water bodies and rivers that flow down on cultivated, urban or barren lands and were allopatric in relation to *P. lessonae* and *P. esculentus*. Water frogs of northwestern Russia form three types of population systems only: so called pure single-species (L or R) systems and a mixed (L – E) system; no type with unisexual hybrids was revealed. Thus, their diversity is lower than in other regions of central and eastern Europe.

Keywords: Ranidae; *Pelophylax lessonae*; *Pelophylax esculentus*; *Pelophylax ridibundus*; genome size; nuclear DNA content; DNA flow cytometry; mating calls; hybridization; Baltic region.

INTRODUCTION

The *Pelophylax esculentus* complex (Ranidae) is distributed in Europe and includes two parental species, the pool frog, *P. lessonae* (Camerano, 1882), and the marsh frog, *P. ridibundus* (Pallas, 1771), as well as their hybrid, the edible frog, *P. esculentus* (Linnaeus, 1758), which demonstrates unusual genetic phenomena associated with hybridization, clonality and polyploidy (Plötner, 2005). The edible frog is widely known across temperate Europe from France in the west to Volga River in the east and is characterized by a special mechanism of hemiclonal reproduction, known as hybridogenesis. Such a reproductive strategy resulted in a variety of population systems, where hybrids are able to reproduce with one or both of the parental species. Populations of *P. esculentus* can be represented by both sexes and only one sex and include not only diploid but also polyploid individuals. Diploid hybrids occur in almost all parts of the species' range. Triploid and, rarely, tetraploid hybrids have been recorded in some populations distributed in the western and central parts of Europe, Kaliningradskaya oblast' (= Kaliningrad Province, the Baltic part of Russia), as well as in the Seversky Donets River drainage in eastern Ukraine and adjacent Russia (Borkin et al., 2004, 2006; Plötner, 2005; Jakob, 2007; Litvinchuk et al., 2015).

In northwestern Russia, water frogs ("*Rana esculenta*") were reported for the first time by Cederhielm (1798). Later, "*R. esculenta*" were repeatedly indicated for the territory of St. Petersburg and adjacent regions (Porchinsky, 1872; Fischer, 1873; Esaulov, 1878; Redikorzew, 1901; Bianchi, 1909; Mertens, 1916; Nikolsky, 1918; Vasilkovsky, 1928; Pestinsky, 1929; Raykov and Rimsky-Korsakov, 1938; Gumilevsky, 1941; Banina, 1952; Meshkov, 1958). The marsh and pool frogs have been mentioned for the region since early 20th century

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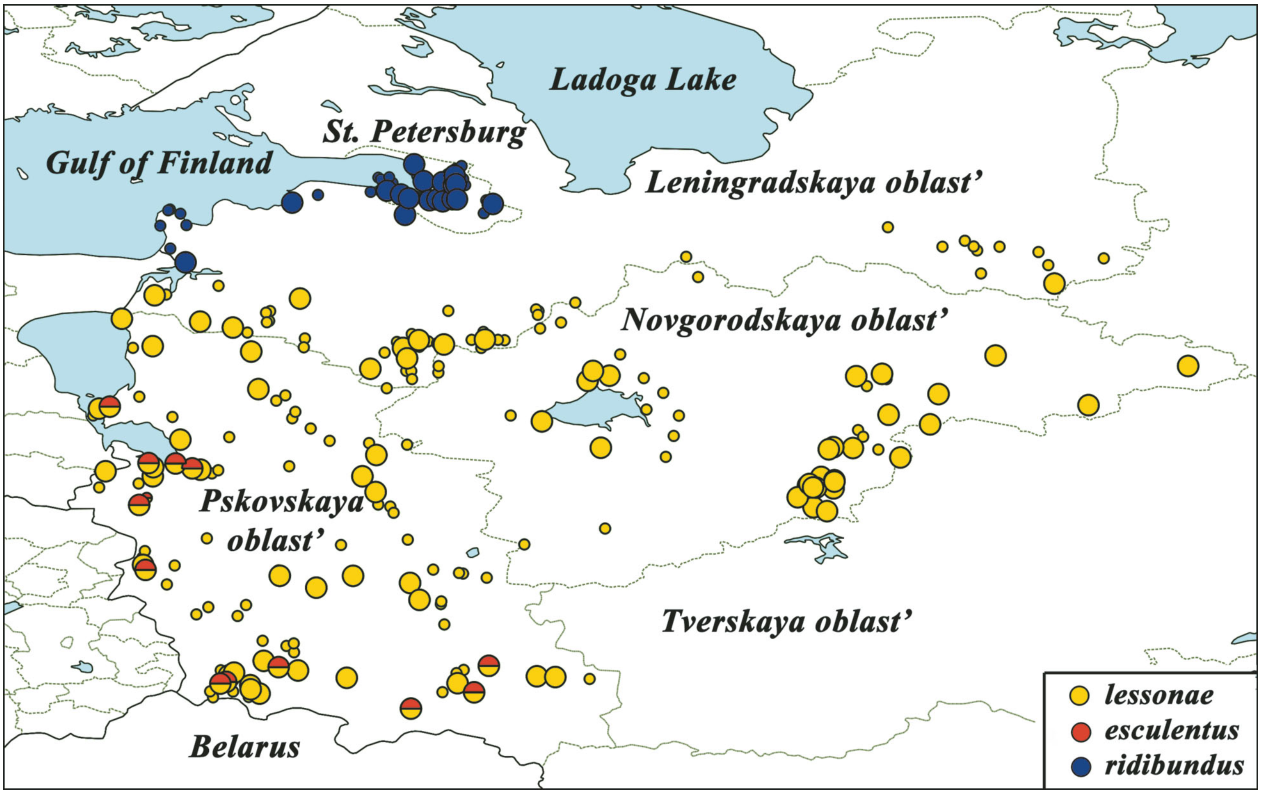

Fig. 1. The distribution of three species of water frogs in northwestern Russia based on genome size and morphometrical data (large cycles) as well as obtained during our field trips, from museum collections and literature data listed in the Appendix (small cycles).

(Mertens, 1916; Nikolsky, 1918; Terentjev, 1927). The first reliable record of the edible frog, which was confirmed by flow DNA cytometry, was published relatively recently (Borkin, 1998; Milto, 1999).

In the most part of Europe, species of the *P. esculentus* hybridogenous complex are sympatric, but they can distribute separately in marginal parts of their ranges. The northern limits of these species in the East European (or Russian) Plain were still obscure since, sometimes, these species are morphologically similar (Borissovsky et al., 2000; Nekrasova and Morozov-Leonov, 2001; Pisanets, 2007), and the majority of previous studies were based on external morphology. Reliable cytological or molecular markers should be used for their correct identification (Borkin et al., 2004). In this paper we used a complex of cytogenetic and external morphological characters as well as mating calls to study the peculiarities of distribution and population systems of water frogs in the northwest of Russia.

MATERIAL AND METODS

In 1994 – 2021, we accumulated numerous data covering the nuclear DNA content (genome size) and morphological variability of three species in 101 localities throughout the territory of Leningradskaya (= Leningrad Province), Pskovskaya (= Pskov Province), and Novgorodskaya (= Novgorod Province) oblast's, as well as St. Petersburg City in the northwestern part of European Russia (Fig. 1; Table 1). The DNA flow cytometry proved to be the most reliable method giving precise identification of species affinity and ploidy for each frog (Borkin et al., 1987, 2004). In total, we examined blood samples of 320 individuals from 79 localities (Table 1). Erythrocytes of *Rana temporaria* Linnaeus, 1758 collected in the northwest of Russia were used as a reference standard. The details of the method were previously published (Vinogradov et al., 1990, 1991).

Additionally, we analyzed various morphological characters to determine whether they can be used to reliably identify species. In total, 188 adults from 59 localities (76 males and 76 females of *P. lessonae* from 45 localities, 10 males and 13 females of *P. esculentus* from 9 localities, and 6 males and 7 females of *P. ridibundus* from 10 localities) were used for detailed morphometric treatment (Table 1). Some of them (52 adults of *P. lessonae*, ten *P. esculentus* and seven *P. ridibundus*) were stud-

TABLE 1. Localities, Genome Size Variation, and Specimens Used for Study of Morphology and Coloration Patterns of Three Species of Water Frogs from Northwestern Russia

N	Locality	Region	Type	Coordinates	Genome Size		Mor-phology
					sample size	mean ± SD (range)	
				P. lessonae			
1	Shulgino	Leningradskaya	L	59.227° N 34.778° E	2	13.85 ± 0.10 (13.78 – 13.92)	10m, 10f
2	Beloe Lake	Leningradskaya	L	58.804° N 30.477° E	—	—	1f
3	Zaplotye	Leningradskaya	L	58.767° N 30.168° E	—	—	2f
4	“125 km”	Leningradskaya	L	58.800° N 29.979° E	—	—	3m
5	Luga	Leningradskaya	L	58.741° N 29.859° E	—	—	7m, 3f
6	Rapti	Leningradskaya	L	58.663° N 29.890° E	—	—	2m, 3f
7	Serebryanka	Leningradskaya	L	58.584° N 29.612° E	—	—	1f
8	Bol’shoy Sabsk	Leningradskaya	L	59.114° N 29.081° E	—	—	1f
9	Luzhitsy – Neguba	Leningradskaya	L	58.895° N 28.574° E	—	—	3f
10	Zavastye	Leningradskaya	L	58.940° N 28.327° E	—	—	1m, 1f
11	Pechurki	Leningradskaya	L	59.138° N 27.984° E	8	13.59 ± 0.05 (13.51 – 13.68)	—
12	Pestovo	Novgorodskaya	L	58.605° N 35.787° E	2	13.92 ± 0.05 (13.89 – 13.95)	—
13	Orekhovno	Novgorodskaya	L	58.309° N 35.035° E	1	13.80	1f
14	Kocherovo	Novgorodskaya	L	58.684° N 34.333° E	—	—	1m, 1f
15	Borovichi	Novgorodskaya	L	58.393° N 33.902° E	1	13.77	1m
16	Piros Lake	Novgorodskaya	L	58.164° N 33.839° E	12	13.88 ± 0.06 (13.80 – 13.96)	—
17	Edrovo	Novgorodskaya	L	57.917° N 33.626° E	4	13.77 ± 0.02 (13.76 – 13.80)	4f
18	Uglovka	Novgorodskaya	L	58.237° N 33.525° E	12	13.88 ± 0.02 (13.83 – 13.92)	—
19	Toporok	Novgorodskaya	L	58.545° N 33.476° E	3	13.64 ± 0.02 (13.62 – 13.65)	1f
20	Gorushka	Novgorodskaya	L	58.528° N 33.281° E	3	13.70 ± 0.08 (13.64 – 13.79)	1m, 2f
21	Valday	Novgorodskaya	L	57.986° N 33.256° E	5	13.82 ± 0.05 (13.78 – 13.88)	2m, 3f
22	Bortsovo	Novgorodskaya	L	57.992° N 33.108° E	8	13.64 ± 0.07 (13.53 – 13.77)	—
23	Eryomina Gora	Novgorodskaya	L	57.976° N 33.074° E	—	—	2m, 4f
24	Ivanteevo	Novgorodskaya	L	57.742° N 33.116° E	8	13.76 ± 0.09 (13.66 – 13.93)	—
25	Sominets Lake	Novgorodskaya	L	57.732° N 33.116° E	3	13.70 ± 0.13 (13.58 – 13.83)	—
26	Sukhaya Vetosh	Novgorodskaya	L	57.681° N 33.110° E	2	13.82 ± 0.09 (13.76 – 13.88)	—
27	Novyi Skrebel	Novgorodskaya	L	57.509° N 33.060° E	5	13.79 ± 0.15 (13.65 – 13.95)	—
28	Myslovo	Novgorodskaya	L	57.768° N 33.016° E	5	13.78 ± 0.04 (13.74 – 13.84)	—
29	Dunaevshchina	Novgorodskaya	L	57.687° N 32.978° E	1	13.95	—
30	Lavrovo	Novgorodskaya	L	57.538° N 32.959° E	1	13.76	—
31	Dunaevskie ponds	Novgorodskaya	L	57.688° N 32.955° E	10	13.92 ± 0.05 (13.88 – 14.00)	—
32	Zaluzhskoe Lake	Novgorodskaya	L	57.714° N 32.928° E	3	13.84 ± 0.04 (13.80 – 13.87)	—
33	Zaluzye	Novgorodskaya	L	57.703° N 32.917° E	11	13.86 ± 0.08 (13.69 – 13.96)	—
34	Klin	Novgorodskaya	L	57.614° N 32.839° E	3	13.82 ± 0.01 (13.80 – 13.83)	—
35	Novoe Kunino	Novgorodskaya	L	58.532° N 31.418° E	1	13.60	—
36	Kolmovo	Novgorodskaya	L	58.568° N 31.293° E	1	13.80	—
37	Arkazhi	Novgorodskaya	L	58.493° N 31.253° E	1	13.58	—
38	Staraya Russa	Novgorodskaya	L	57.988° N 31.352° E	1	13.88	1m, 1f
39	Bolshaya Viton	Novgorodskaya	L	58.187° N 30.908° E	1	13.53	—
40	Zubrovo	Pskovskaya	L	56.257° N 31.009° E	—	—	1f
41	Krasnaya Veshnya	Pskovskaya	L	56.263° N 30.870° E	3	13.90 ± 0.07 (13.82 – 13.96)	2m, 1f
42	Velikie Luki	Pskovskaya	L	56.305° N 30.518° E	7	13.81 ± 0.04 (13.73 – 13.84)	3m, 1f
43	Polibino	Pskovskaya	L – E	56.142° N 30.396° E	2	13.94 ± 0.11 (13.87 – 14.02)	1m, 1f
44	Pekhovo	Pskovskaya	L	56.211° N 30.271° E	10	13.89 ± 0.04 (13.83 – 13.97)	—
46	Beloe Lake	Pskovskaya	L	56.251° N 29.434° E	—	—	1f
47	Yakoltsevskoe Lake	Pskovskaya	L	56.840° N 29.983° E	4	13.89 ± 0.03 (13.85 – 13.92)	—
48	Bezhanitsy	Pskovskaya	L	56.968° N 29.912° E	5	13.91 ± 0.06 (13.82 – 13.98)	—
49	Klimovo	Pskovskaya	L	57.021° N 29.482° E	—	—	1f
50	Agafonovo	Pskovskaya	L	56.932° N 29.204° E	1	13.85	1m
51	Pushkinskie Gory	Pskovskaya	L	57.021° N 28.929° E	—	—	1m
52	Logovino	Pskovskaya	L	57.653° N 29.652° E	2	13.62 ± 0.03 (13.60 – 13.64)	—
53	Porkhov	Pskovskaya	L	57.772° N 29.552° E	—	—	1m, 2f
54	Kamenka	Pskovskaya	L	57.933° N 29.658° E	2	13.72 ± 0.01 (13.72 – 13.72)	2m
55	Veretye	Pskovskaya	L – E	57.556° N 27.867° E	1	13.78	—
56	Bolbuki	Pskovskaya	L	56.307° N 29.066° E	—	—	1m, 2f
57	Idritsa	Pskovskaya	L – E	56.332° N 28.920° E	3	13.84 ± 0.04 (13.80 – 13.87)	5m, 1f

TABLE 1 (continued)

N	Locality	Region	Type	Coordinates	Genome Size: sample size	Genome Size: mean ± SD (range)	Mor-phology
58	Maksyutino	Pskovskaya	L	56.379° N 28.807° E	1	13.79	1m, 1f
59	Nishcha	Pskovskaya	L	56.132° N 28.776° E	2	13.81 ± 0.04 (13.78 – 13.84)	2m
60	Novikovo – Kovalyovka	Pskovskaya	L	56.165° N 28.709° E	—	—	1m, 2f
61	Anninskoe Lake	Pskovskaya	L	56.196° N 28.706° E	9	13.80 ± 0.04 (13.75 – 13.85)	—
62	Osyno Lake	Pskovskaya	L – E	56.221° N 28.522° E	1	13.78	—
63	Malkovo	Pskovskaya	L	56.291° N 28.583° E	1	13.94	1f
64	Prasni	Pskovskaya	L	56.269° N 28.544° E	2	13.78 ± 0.02 (13.77 – 13.80)	4f
66	Zabelye	Pskovskaya	L – E	56.208° N 28.480° E	5	13.86 ± 0.03 (13.82 – 13.89)	4m, 4f
67	Pytalovo	Pskovskaya	L – E	57.066° N 27.915° E	1	13.81	1m, 1f
68	Balastnitsa	Pskovskaya	L	57.104° N 27.896° E	7	13.75 ± 0.05 (13.66 – 13.81)	1m
69	Pskov	Pskovskaya	L	57.822° N 28.330° E	4	13.65 ± 0.09 (13.59 – 13.78)	—
72	Zamelnichye	Pskovskaya	L	58.049° N 28.178° E	4	13.76 ± 0.05 (13.71 – 13.81)	3m, 1f
73	Novy Izborsk	Pskovskaya	L	57.772° N 27.970° E	10	13.87 ± 0.04 (13.81 – 13.93)	2f
74	Malye Kalki	Pskovskaya	L	57.841° N 27.973° E	—	—	1f
76	Pechyory	Pskovskaya	L	57.810° N 27.613° E	—	—	1m, 3f
77	Kobylye Gorodishche	Pskovskaya	L – E	58.298° N 27.645° E	2	13.73 ± 0.03 (13.70 – 13.75)	—
78	Ostrov	Pskovskaya	L	58.283° N 27.564° E	1	13.69	—
79	Uzmino	Pskovskaya	L	58.430° N 28.767° E	1	13.81	1m
80	Kharlamova Gora	Pskovskaya	L	58.714° N 28.713° E	—	—	3m
81	Gdov	Pskovskaya	L	58.742° N 27.820° E	—	—	1m
82	Lugi	Pskovskaya	L	58.754° N 27.969° E	—	—	4m, 1f
83	Khitovo	Pskovskaya	L	58.961° N 27.736° E	1	13.53	—
				P. esculentus			
42	Velikolukskaya fortress	Pskovskaya	L – E*	56.342° N 30.507° E	2	15.01 ± 0.16 (14.90 – 15.12)	—
43	Polibino	Pskovskaya	L – E	56.142° N 30.396° E	1	15.10	1m
45	Nevel	Pskovskaya	L – E*	56.019° N 29.919° E	1	15.32	1f
55	Veretye	Pskovskaya	L – E	57.556° N 27.867° E	1	14.90	1m
57	Idritsa	Pskovskaya	L – E	56.332° N 28.920° E	1	15.03	1f
62	Osyno Lake	Pskovskaya	L – E	56.221° N 28.522° E	5	14.98 ± 0.07 (14.89 – 15.08)	—
65	Chernovo Reservoir	Pskovskaya	L – E*	56.221° N 28.524° E	4	15.06 ± 0.10 (14.92 – 15.13)	—
66	Zabelye	Pskovskaya	L – E	56.208° N 28.480° E	—	—	1m, 1f
67	Pytalovo	Pskovskaya	L – E	57.066° N 27.915° E	3	14.99 ± 0.04 (14.96 – 15.03)	4m, 10f
70	Borisovichi	Pskovskaya	L – E*	57.832° N 28.268° E	1	14.85	1m
71	Murovitsy	Pskovskaya	L – E*	57.869° N 28.142° E	1	15.15	1m
75	Krivsk	Pskovskaya	L – E*	57.872° N 27.938° E	1	14.84	—
77	Kobylye Gorodishche	Pskovskaya	L – E	58.298° N 27.645° E	2	14.99 ± 0.03 (14.97 – 15.01)	1m
				P. ridibundus			
84	Ivangorod	Leningradskaya	R	59.387° N 28.217° E	3	16.35 ± 0.09 (16.26 – 16.44)	—
85	Sosnovy Bor	Leningradskaya	R	59.838° N 29.022° E	16	16.59 ± 0.23 (16.26 – 16.91)	—
86	Ropsha	Leningradskaya	R	59.746° N 29.874° E	14	16.49 ± 0.12 (16.35 – 16.65)	—
87	Kronshtadtskaya Koloniya	St. Petersburg	R	59.928° N 29.738° E	2	16.38 ± 0.05 (16.34 – 16.42)	1m, 1f
88	Kritatellka River	St. Petersburg	R	59.900° N 29.843° E	—	—	1f
89	Novy Petergof	St. Petersburg	R	59.871° N 29.902° E	5	16.35 ± 0.10 (16.20 – 16.47)	—
90	Kurort	St. Petersburg	R	60.127° N 29.943° E	3	16.31 ± 0.05 (16.28 – 16.37)	1f
91	Lisiy Nos	St. Petersburg	R	60.000° N 30.014° E	13	16.28 ± 0.07 (16.17 – 16.43)	—
92	Strelna	St. Petersburg	R	59.856° N 30.059° E	16	16.41 ± 0.05 (16.34 – 16.49)	1m, 2f
93	LEMZ factory	St. Petersburg	R	59.862° N 30.117° E	—	—	1f
94	Lakhta	St. Petersburg	R	59.992° N 30.158° E	—	—	1m
95	Yuzhno-Primorsky park	St. Petersburg	R	59.848° N 30.159° E	—	—	1m
96	Ugolynaya Gavan	St. Petersburg	R	59.864° N 30.232° E	3	16.58 ± 0.10 (16.47 – 16.67)	—
97	Krestovky Island	St. Petersburg	R	59.970° N 30.241° E	—	—	1f
98	Shuvalovo	St. Petersburg	R	60.042° N 30.249° E	—	—	1m
99	Elagin Island	St. Petersburg	R	59.978° N 30.259° E	6	16.44 ± 0.09 (16.31 – 16.56)	—
100	Avtovo	St. Petersburg	R	59.863° N 30.266° E	1	16.36	1m
101	Rybatskoe	St. Petersburg	R	59.828° N 30.537° E	5	16.18 ± 0.11 (16.01 – 16.27)	—

* The presence of *P. lessonae* in the locality was detected in the field by external morphological characters only.

ied by DNA flow cytometry as well. All studied specimens (preserved in 70% ethanol) are kept in collections of the Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

We analysed 13 morphometrical characteristics: *SVL* is body length (from tip of snout to centre of cloacal opening); *Lc*, head length (distance from anterior tip of head to posterior edge of jaw articulations); *Ltc*, head width (distance between posterior edge of jaw articulations); *Dro*, snout length (distance from anterior edges of head to anterior edge of eye); *Lo*, eye length (greatest length of eye); *Spp*, distance between eyelids (smallest distance between eyelids); *Spn*, distance between nostril and eye (smallest distance between posterior edge of nostril and anterior edge of eye); *Ltym*, greatest length of the tympanic membrane; *F*, femur length (from centre of cloacal opening to distal end of the femur bone); *T*, tibia length (from knee to heel); *Dp*, length of the first toe; *Cint*, length of internal metatarsal tubercle; *Cinth*, height of internal metatarsal tubercle. Measurements were made with a digital caliper to the nearest 0.1 mm for each specimen by the first author.

Since almost all morphometrical characters (with exception of *Cinth*) were highly correlated with each other ($n = 66$; $r = 0.36 – 0.96$; $p < 0.05$). Therefore, we divided them into each other and obtained 78 ratios (indices). Additionally, we analyzed the Hemmer's (1979) index, which was previously considered to be useful for identification of various water frog species. It was estimated according to the formula $Hem = Dp/Cint + T/Cint$. For all these indices the natural logarithm conversion was made. The principal components and discriminant analyses were applied in order to find most valuable indices for differentiation of three studied species. To perform univariate analyses of variance, we applied the two-way ANOVA for comparison of means and the Sheffe test for post-hoc comparisons. The Kolmogorov – Smirnov test was used to compare samples. All these tests were performed using Past ver. 4.03 and Statistica ver. 8.0.

In addition to studying morphometric characters, we took into account the rugosity of skin on the dorsal surface, the presence or absence of a dorsal stripe in frogs, as well as dorsal and belly coloration patterns. We assigned specimens to *maculata* type (M) if them have large spots over the entire dorsal surface; *punctata* (P) — small specks over the entire dorsal surface; *maculata-punctata* (MP) — nearly half of the surface with large spots and half with small specks; *hemimaculata* (HM) — large spots occupying no more than half of the surface; *hemipunctata* (HP) — small specks occupying no more than half of the surface; *hemimaculata-hemipunctata* (HMH) — large spots and small specks occupying no more than half of the surface; *hemimaculata-punctata* (HMP) — large spots occupying no more than half of the surface and small specks over the entire surface.

Since mating (advertisement) calls are often used for preliminary identification of water frog species (Plötner, 2005), we also studied them. We recorded advertisement calls of water frogs (water temperature of 20 – 22°C) in 2014 and 2016 at eight localities in Pskovskaya and Leningradskaya oblast's, as well as St. Petersburg City (Table 2). We recorded calls using a camera SONY DSC-HX350 and analyzed them using Adobe Audition 2022 v. 22.1.1.23 and Raven Lite 2.0.1.

To reveal preferable environments of three water frog species, we estimated the percentage of forest and herba-

TABLE 2. Characteristics (mean ± SD, range) of Advertisement Calls of Water Frog Species

Species	Locality*	*N* (*n*)	Call duration, msec	Pulse group/call	Duration of pulse group, msec	Pulses/pulse groups
lessonae	I	1 (2)	513	2	96 ± 17 (84 – 108)	27.0 ± 4.2 (24 – 30)
lessonae	II	3 (8)	2607 ± 467 (2102 – 3024)	7.7 ± 0.6 (7 – 8)	127 ± 14 (108 – 148)	26.6 ± 1.8 (25 – 29)
lessonae	III	10 (7)	2582 ± 1238 (955 – 5242)	11.2 ± 7.6 (4 – 30)	74 ± 18 (40 – 93)	18.9 ± 4.4 (11 – 25)
lessonae	Total	14 (17)	2440 ± 1184 (513 – 5242)	9.8 ± 6.9 (2 – 30)	102 ± 30 (40 – 148)	23.5 ± 5.1 (11 – 30)
esculentus	IV	3 (13)	1653 ± 342 (1400 – 2042)	7.7 ± 2.1 (6 – 10)	101 ± 17 (72 – 124)	30.1 ± 3.3 (25 – 34)
esculentus	V	2 (9)	1136 ± 515 (772 – 1500)	6.0 ± 1.4 (5 – 7)	106 ± 9 (89 – 123)	29.7 ± 2.8 (25 – 34)
esculentus	VI	3 (9)	1490 ± 890 (819 – 2500)	5.7 ± 2.1 (4 – 8)	124 ± 20 (92 – 155)	32.8 ± 4.1 (25 – 37)
esculentus	Total	8 (31)	1463 ± 587 (772 – 2500)	6.5 ± 1.9 (4 – 10)	109 ± 19 (72 – 155)	30.7 ± 3.5 (25 – 37)
ridibundus	VII	8 (27)	2006 ± 886 (1092 – 3807)	15.0 ± 7.6 (8 – 27)	62 ± 10 (42 – 91)	7.2 ± 0.9 (5 – 9)
ridibundus	VIII	1 (5)	3107	10	96 ± 12 (83 – 114)	8.4 ± 1.1 (7 – 10)
ridibundus	Total	9 (32)	2128 ± 906 (1092 – 3807)	14.4 ± 7.3 (8 – 27)	67 ± 16 (42 – 114)	7.4 ± 1.0 (5 – 10)

Note. *N* is number of analyzed calls; *n* is number of analyzed pulse groups.
* I, Izborsk (Gorodishchenskoe Lake), Pskovskaya oblast'; II, Nochlegovo, Pskovskaya oblast'; III, "Shalovo-Perechitsky" sanctuary, Leningradskaya oblast'; IV, Vasil'evo, Pskovskaya oblast'; V, Borisovichi, Pskovskaya oblast'; VI, Kobylye Gorodishche, Pskovskaya oblast'; VII, Dudergofsky canal, St. Petersburg; VIII, Yuzhno-Primorsky park, St. Petersburg.

ceous vegetation, as well as agricultural, barren and urban lands on a square land area of 1 km^2 in all localities studied by us with genome size and morphometry (Table 1) using the QGIS Point Sampling Tool Plugin (https://plugins.qgis.org/plugins/pointsamplingtool), which extracted data from the global 1 km consensus land-cover maps (Tuanmu and Jetz, 2014).

Museum abbreviations used are: MCZ is Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; ZISP is Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; ZMB is Zoologisches Museum, Museum für Naturkunde Berlin, Germany; and ZMMSU is Zoological Museum, M. V. Lomonosov Moscow State University, Moscow, Russia.

RESULTS

Genome size variation. According to the nuclear DNA content, three water frog species were identified in the region (Table 1). Among 320 specimens studied by us all were diploids; no triploids were found. 210 individuals were allocated to *P. lessonae*, 23 to *P. esculentus*, and 87 to *P. ridibundus*. Their genome size varied from 13.51 to 14.02 pg in *P. lessonae* (mean is 13.80 pg, SD is 0.11 pg) and from 16.01 to 16.91 pg in *P. ridibundus* (16.42 ± 0.17 pg). The nuclear DNA content in hybridogenous *P. esculentus* was in intermediate position (Table 1) and ranged from 14.84 to 15.32 pg (the average was 15.01 ± 0.11 pg). The values of genome size displayed no correlation with sex or locality. The value ranges of species did not overlap, and this allowed us to identify each specimen with the 100% confidence (Table 1; Fig. 2).

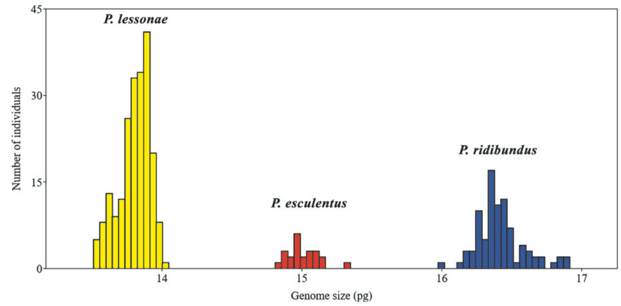

Fig. 2. The nuclear DNA content variation in three species of water frogs in northwestern Russia.

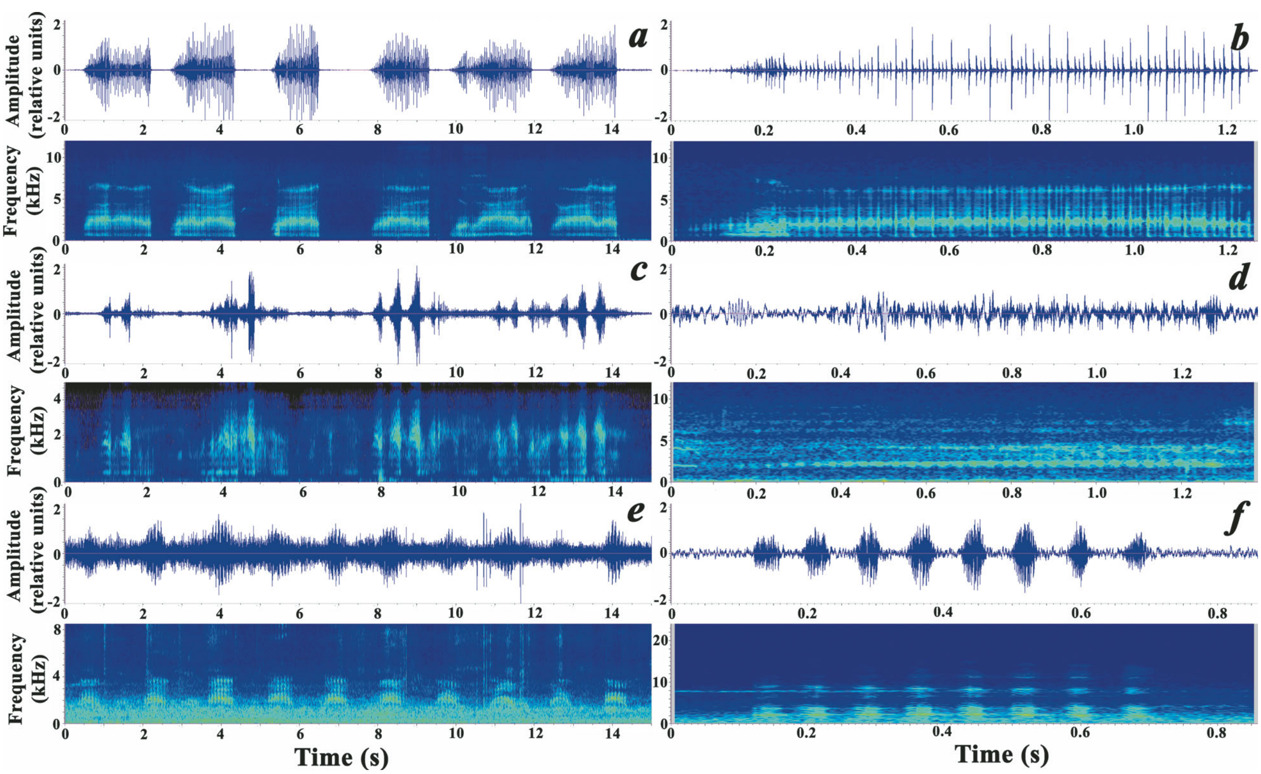

Fig. 3. Oscillograms and associated frequency sonograms of mating call groups (*a*, *c*, *e*) and separate calls (*b*, *d*, *f*) of *Pelophylax lessonae* (*a*, *b*) inhabiting "Shalovo-Perechitsky" sanctuary (Leningradskaya oblast'), *P. esculentus* (*c*, *d*) from Kobylye Gorodishche (Pskovskaya oblast'), and *P. ridibundus* (*e*, *f*) from Dudergofsky canal (St. Petersburg). Calls were recorded at 20 – 22°C water temperature.

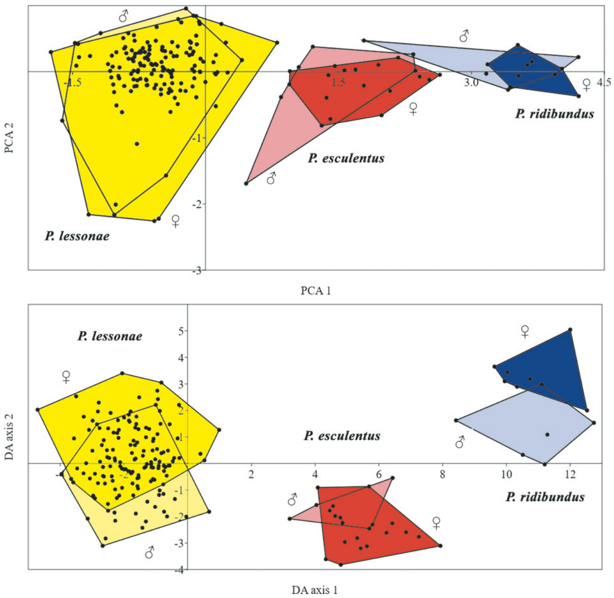

Fig. 4. Principal components (above) and discriminant (below) analyses biplot (species and sex as grouping variables) of morphometric indices for three species of water frogs in northwestern Russia.

Variation of morphological characters and coloration pattern. Results of the principal components analysis (PCA) performed on 79 morphometrical indices demonstrated good separation of all three species by the first principal component (PC1), which explains 64% of the total variance (Fig. 4). The first axis (PC1) had high loadings for ratios which are connected with height of the inner metatarsal tubercle. The second component (PC2) explained 10% of the total variance.

In the discriminant analysis, the first axis included 79% of variation and the second 9%. All three species formed distinct clusters without overlap (Fig. 4). The overall correct classification rate was 100% if species were selected as a grouping variable and 87.2% if both species and sexes were used as grouping variables. Based on the analysis results, the most valuable species-distinguishing indices were ratios connecting to height of the inner metatarsal tubercle (most high impacted ratios were *Dp/Cinth* and *T/Cinth*). The index *Ltym/Dp* was most related to the sex, but differences in this ratio for all three species were insignificant ($p \leq 0.05$).

Two-way ANOVA showed significant sex-related ($F = 3$, $df = 13$, $p < 0.001$) and species-specific ($F = 34$, $df = 26$, $p < 0.001$) differences. The post hoc comparison of all indices showed that both sex- ($p < 0.05$) and species-specific ($p < 0.001$) differences were significant. Individuals of both sexes of *P. lessonae* were the smallest, but *P. ridibundus* were the largest (Table 3; Fig. 5). The means of *SVL* for *P. esculentus* were intermediate between parental species. In females, limits for two ratios (*Dp/Cinth* and *T/Cinth*) were not overlapped between all three species.

Additionally, the noticeable differences between species were observed in the skin rugosity on the dorsal surface and some coloration pattern characters. In *P. ridibundus* all specimens of both sexes were characterized by rugose skin, while in *P. lessonae* and *P. esculentus* only 41 – 54% females and 54 – 60% males had the same state of the character (Table 4). Most specimens of both sexes (83 – 86%) in *P. ridibundus* had large dark spots on dorsal surface (Fig. 6), while *P. lessonae* and *P. esculentus* were predominantly characterised by other types of coloration (60 – 77%). In *P. lessonae*, males with completely light throat were predominated (78%), while such coloration were completely absent in *P. ridibundus* (Table 4). Males of *P. esculentus* were in intermediate position (30% with light throat).

Advertisement calls variation. The mating call of water frogs is a trill consisting series with several calls. Single calls consisted of series of pulse groups with several pulses (Fig. 3). On average, the call duration of

TABLE 3. The Variability (mean ± standard deviation and range) of Body Length (*SVL*) and Morphological Indices in Three Species of Water Frogs from Northwestern Russia

Species	Sex	*n*	*SVL*	*Dp/Cinth*	*T/Cinth*	*Hem*	*Ltym/Dp*
lessonae	Male	76	53.9 ± 4.6 (42.4 – 65.0)	3.1 ± 0.5 (2.1 – 4.8)	11.9 ± 1.6 (8.5 – 18.2)	7.3 ± 0.5 (5.7 – 8.4)	0.69 ± 0.08 (0.51 – 1.05)
esculentus	Male	10	63.3 ± 7.1 (52.8 – 75.6)	5.8 ± 1.1 (4.7 – 7.8)	21.4 ± 4.0 (15.2 – 28.9)	10.1 ± 1.0 (8.8 – 12.3)	0.62 ± 0.06 (0.52 – 0.69)
ridibundus	Male	6	78.8 ± 11.8 (61.2 – 94.8)	10.9 ± 2.4 (6.5 – 13.4)	39.0 ± 8.7 (23.1 – 48.6)	11.9 ± 1.4 (10.3 – 13.6)	0.49 ± 0.04 (0.44 – 0.56)
lessonae	Female	76	58.3 ± 7.0 (45.6 – 74.3)	3.1 ± 0.4 (2.1 – 4.3)	11.9 ± 1.4 (8.4 – 15.1)	7.3 ± 0.7 (5.9 – 9.2)	0.67 ± 0.07 (0.52 – 0.84)
esculentus	Female	13	63.7 ± 11.3 (50.1 – 87.4)	6.3 ± 1.1 (4.8 – 8.1)	24.5 ± 4.2 (18.7 – 33.0)	9.6 ± 0.9 (7.6 – 11.0)	0.64 ± 0.06 (0.58 – 0.75)
ridibundus	Female	7	90.9 ± 13.3 (75.8 – 109.7)	11.2 ± 1.4 (9.6 – 13.3)	40.9 ± 5.0 (34.2 – 50.0)	13.1 ± 1.4 (11.6 – 15.4)	0.53 ± 0.03 (0.49 – 0.60)

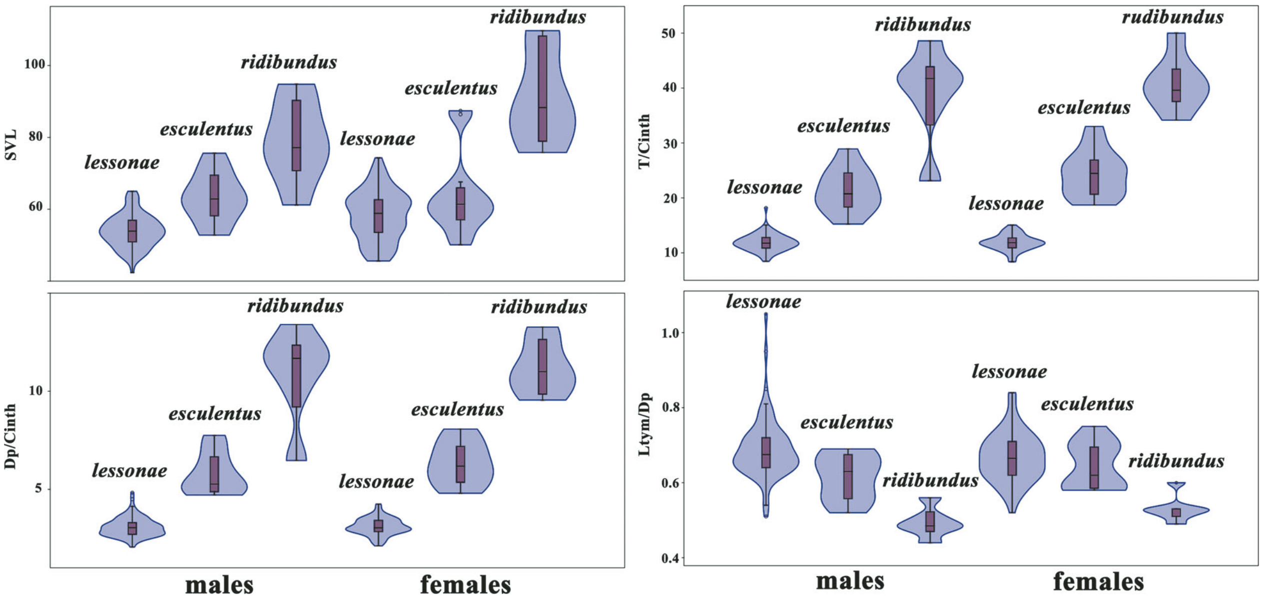

Fig. 5. The variability (violin plots) of body length (*SVL*) and three indices in three species of water frogs in northwestern Russia.

P. lessonae from northwest of Russia varies from 513 to 2607 msec (Table 2). The call consists of 2 – 30 pulse groups with average duration of 74 – 127 msec (on average 102 msec). Pulse groups include 11 – 30 pulses (mean 23.5). The advertisement call duration of *P. ridibundus* is usually some longer and on average varies from 2006 to 3107 msec (Table 2). The call consists of 8 – 27 pulse groups (mean is 14.4) with mean duration of 62 – 96 msec (on average 67 msec). Pulse groups include 5 – 10 pulses (on average 7.5). The significant differences ($p \leq 0.01$) between the species were revealed by the duration of pulse group and the number of pulses per pulse group.

The advertisement call duration of *P. esculentus* varies on average from 1136 to 1653 msec (Table 2). The call consists of 4 – 10 pulse groups (mean is 6.5) with av-

TABLE 4. Percentage of Specimens Which Have Dorsal Stripe (DL), without Dark Spots Throat (AT) and Belly (AB), with Rugose Skin on Dorsal Surface (RS), Various Types of Dorsal Coloration

Species	Sex	*n*	DL	AT	AB	RS	M	P	MP	HM	HP	HMH	HMP	U
lessonae	Male	76	96	78	45	54	32	18	7	18	20	3	3	1
esculentus	Male	10	100	30	20	60	40	0	10	10	30	0	0	10
ridibundus	Male	6	67	0	33	100	83	0	17	0	0	0	0	0
lessonae	Female	76	97	38	32	41	40	5	16	11	25	3	0	1
esculentus	Female	13	100	23	54	54	23	23	0	23	31	0	0	0
ridibundus	Female	7	71	0	43	100	86	0	0	0	0	0	0	14

Note. M, *maculata*; P, *punctata*; MP, *maculata-punctata*; HM, *hemimaculata*; HP, *hemipunctata*; HMH, *hemimaculata-hemipunctata*; HMP, *hemimaculata-punctata*; U, unicolor.

TABLE 5. Percentage (mean ± standard deviation and range) of Forest and Herbaceous Vegetation, Agricultural, Barren, and Urban Land in areas (1 km^2) Associated to Water Frog Population Systems

Population system	*n*	Forest	Agricultural	Urban	Barren	Herbaceous
L	70	46.2 ± 34.8 (0 – 100)	35.5 ± 31.7 (0 – 100)	4.0 ± 13.8 (0 – 74)	6.5 ± 12.2 (0 – 46)	2.0 ± 6.3 (0 – 30)
L – E	13	36.0 ± 33.7 (0 – 95)	42.8 ± 37.0 (0 – 95)	4.0 ± 8.5 (0 – 27)	1.0 ± 3.6 (0 – 13)	2.2 ± 8.0 (0 – 29)
L and L – E	83	44.6 ± 34.6 (0 – 100)	36.7 ± 32.4 (0 – 100)	4.0 ± 13.1 (0 – 74)	5.8 ± 11.7 (0 – 46)	1.8 ± 5.9 (0 – 30)
R	18	22.4 ± 27.3 (0 – 100)	12.9 ± 17.4 (0 – 54)	25.9 ± 32.7 (0 – 100)	14.9 ± 15.6 (0 – 45)	2.4 ± 7.4 (0 – 29)

Fig. 6. Water frogs in northwestern Russia: *a*, male of *Pelophylax lessonae*, Luzhitsy – Neguba, Leningradskaya oblast'; *b*, female of *P. lessonae*, Zavastye, Leningradskaya oblast'; *c*, male of *P. lessonae*, "Shalovo-Perechitsky" sanctuary, Leningradskaya oblast'; *d*, male of *P. esculentus*, Polibino, Pskovskaya oblast'; *e*, male of *P. esculentus*, Kobylye Gorodishche, Pskovskaya oblast'; *f*, female of *P. esculentus*, Kobylye Gorodishche, Pskovskaya oblast'; *g*, male of *P. ridibundus*, Baltysky boulevard, St. Petersburg; *h*, female of *P. ridibundus*, Kronshtadtskaya Koloniya, St. Petersburg.

erage duration 101 – 124 msec (on average 109 msec). Pulse groups include 25 – 37 pulses (mean 30.7). Between *P. esculentus* and *P. ridibundus*, significant differences ($p \leq 0.05$) were found by the pulse group per call, duration of pulse group and the number of pulses per pulse group; between *P. esculentus* and *P. lessonae* by the number of pulses per pulse group only.

Distribution of species and population systems. Among 445 individuals of water frogs studied by genome size and/or morphometrical traits, 93 (21%) were suggested to be *P. ridibundus*, 315 (71%) *P. lessonae*, and 37 (8%) *P. esculentus*. We registered the pool frog in 83 localities (82%), the marsh frog in 18 localities (18%), and the edible frog in 13 (13%) localities (Table 1). The individuals of *P. lessonae* were widely distributed through Pskovskaya and Novgorodskaya oblast's, as well as in the southern part of Leningradskaya oblast'. The edible frog was registered in Pskovskaya oblast' only and was in all cases sympatric to *P. lessonae*. The *P. ridibundus* populations were revealed in St. Petersburg City and Leningradskaya oblast' along southern coast of the Gulf of Finland and Narva River on the Estonian border (Fig. 1). The range of *P. ridibundus* in the studied region did not overlap to *P. lessonae* and *P. esculentus* ranges.

Pelophylax lessonae inhabits forest biotopes more often than other species (46% vs. 22 – 36%; Table 5, Fig. 7). The marsh frog is usually observed in open water bodies and rivers that flow down on cultivated, urban or barren lands (54%; Fig. 7). Edible frogs were predominantly registered in forest and agricultural biotopes (Table 5, Fig. 7).

Population systems with only one parental species (L or R; 87%) were most frequent (Table 1). We detected hybridogenous frogs co-occurring to *P. lessonae* (L – E systems) and did not find other hybrid or mixed (E, R – L, R – E and R – E – L) population systems.

In local L – E systems, hybrids were represented by both sexes, which were usually presented in approximately equal proportion (44% males; $n = 25$).

DISCUSSION

For a long time, zoologists were searching for diagnostic morphological traits in order to reliable identification of water frog species. Significant differences between parental species by means of various indices were revealed in numerous studies (e.g., Svinin et al., 2021). The characteristics and indices for the hybridogenetic *P. esculentus* were intermediate between parental species. However, the limits of these values in hybrids usually overlapped with those of parental species. An additional problem is associated with morphological identification of polyploid individuals of *P. esculentus* (Korshunov, 2010).

According to our data, as minimum two indices ($Dp/Cinth$ and $T/Cinth$) were diagnostic for all three species of water frogs from the northwest of Russia and their values did not overlap in females and very slightly overlap in males (Table 3; Fig. 5). The combination of these indices together with some other external morphological features (e.g., the coloration pattern of dorsal and ventral surfaces, as well as the shape of inner metatarsal tubercle) enables the reliable identification of water frog species. In the northwest of Russia, species identification using morphological characters showed correct diagnostics in 100% cases.

The distribution of water frogs and types of population systems in the studied region has notable differences with other parts of the East European Plain. First, local *P. esculentus* are not as numerous as in western and central European populations. That may be associated to a decrease in numbers at the northern border of its range. In the studied localities, hybrids (8% individuals) were found in 13% populations only (Table 1). Second, no polyploid hybrids were revealed. The nearest triploids were found more than 500 km to south in Poland, Kaliningradskaya oblast' of Russia, and eastern Ukraine (Rybatsky and Berger, 2001; Borkin et al., 2004; Litvinchuk et al., 2015; Biriuk et al., 2016; Dedukh et al., 2013, 2017). Third, we detected only three types of population systems in north-western European Russia. In particular, we observed population systems, with obvious majority of parental species only (R or L systems), and some localities where *P. esculentus* individuals co-existed with *P. lessonae*. In local L – E systems hybrids were represented by both sexes. Thus, water frogs of northwestern Russia demonstrated markedly lower diversity of population systems in comparison with central and eastern Europe including other parts of European Russia and Ukraine.

High correctness of species identification of water frogs using morphological characters only allowed us to attribute a captured frog to one of the three taxa directly in the field conditions or examining museum collections (without additional laboratory treatments). As a result, we added numerous localities ($n = 215$) during our field trips, from museum collections and literature data (see Appendix). That made possible to outline more precisely the distribution of each species (Fig. 1). The pool frog was found everywhere through Pskovskaya and Novgorodskaya oblast's. The northern border of its range passes in the south of Leningradskaya oblast' (Fig. 1). Here, the species lives in the west (Volosovsky and Slantsevsky districts), south (Luzhsky, Gatchinsky, Tosnensky and Kirishsky) and east (Tikhvinsky and Boksitogorsky) of

Fig. 7. Typical habitats of water frog species: *a*, *Pelophylax lessonae* in Zavastye, Leningradskaya oblast'; *b*, *P. esculentus* and *P. lessonae* in Kobylye Gorodishche, Pskovskaya oblast'; *c*, *P. ridibundus* in Kronshtadtskaya Koloniya, St. Petersburg.

the oblast'. The northern limit of distribution of *P. lessonae* is recorded in Tikhvin monastery (59.652° N 33.5201° E). This is the northernmost record of this species in Russia and one of the northernmost localities in Europe. More northern localities are known only in eastern Sweden (Sjögren, 1991).

We did not confirm the presence of *P. lessonae* in the Kingiseppsky District, in the south of Gatchinsky District, and the Ladoga Lake region, where the species was previously mentioned (Bianchi, 1909; Nikolsky, 1918; Borkin and Tikhenko, 1979; Borkin and Krever, 1987; Orlov and Ananjeva, 1995; Bublichenko and Bublichenko, 1998; Noskov and Boch, 1999). In addition, it should be noted that Paolucci et al. (1987: Table II) mentioned "Leningrad" (= St. Petersburg) as a locality of twelve specimens of "*Rana lessonae*" which were kindly provided by L. J. Borkin; however, the exact capture locality of these frogs was not published. Actually, *P. lessonae* were collected in the south of Leningradskaya oblast' (the environs of Luga Town).

We suggest that the 60-day period with an average daily temperature above 15°C and the sum of temperatures of 1600°C for a period with a stable temperature above 10°C may limit the distribution of *P. lessonae* in the region. The species inhabits floodplain reservoirs, ponds, shores of lakes and rivers, as well as drainage canals, various reservoirs and ditches. The frogs can be found in a forest far from suitable water bodies. In the south of Pskovskaya oblast', the abundance of *P. lessonae* was very high and comparable to that of brown frogs (*Rana temporaria* and *R. arvalis* Nilsson, 1842).

In the northwest of Russia, *P. esculentus* was found in Pskovskaya oblast' only. The northern border is located in Kobyl'e Gorodishche (58.298° N 27.645° E). This is the northernmost record in Russia and one of the northernmost records in Europe. More northern localities are known only in Estonia (Tabivere; 58.55° N 26.60° E; ZISP. 5299). The species prefers both artificial reservoirs near settlements and reed beds of lakes (e.g., Pskov and Peipus). Sometimes, the species was represented by giant neotenic tadpoles (up to 168 mm of total length), which were previously described in Chernovo village of Pskovskaya oblast' (ZISP. 7627). Three giant tadpoles of the species were found in a small reservoir, where they apparently overwintered successfully and reached sexual maturity (Milto, 2009, 2011a). In 1952 – 1954, giant neotenic larvae have been also observed in neighboring Latvia (Lusis and Zaune, 1984).

Pelophylax ridibundus is an invasive species in the northwest of Russia. It was first released here in the 18th century in park ponds of Yelagin Island (the northernmost island in the Neva River delta in St. Petersburg), when frogs were imported from southern Russia by order of Empress Elizabeth, who liked their breeding call concerts (Gerd, 1925). The marsh frogs were bred in ponds of the island at the beginning of the 19th century at the request of the wife of Emperor Alexander I (Vasilkovsky, 1928). This species was observed in the neighboring Krestovsky Island at the second part of the 19th century as well (Porchinsky, 1872).

Later, *P. ridibundus* spread across the north-western part of St. Petersburg City (Pestinsky, 1929; Raykov and Rimsky-Korsakov, 1938). In the 1960s, marsh frogs were released in Yuzno-Primorsky Park in the southwestern part of city, where they widely expanded along the southern coast of the Neva Bay and the Gulf of Finland up to Kronstadtskaya Koloniya and Bronka settlements. In the 1970s, an isolated population arose in Ropsha fish farm (Leningradskaya oblast') after import of fish fry from Angelinsky Settlement (45.543° N 38.417° E; Krasnodarsky Kray, northwestern Ciscaucasia, Russia). Additionally, number of populations of the marsh frog exists in Sosnovy Bor town, Kalishche and Kovashi settlements, and along the Baltic Sea coast on the Kurghalsky Peninsula and Rosson' River to Ivangorod town (Fig. 1). The northern border of the species is located in Kanavnoye bog, north of St. Petersburg (60.128° N 29.958° E). This is the northernmost record of *P. ridibundus* in Russia and Europe today.

It should also be mentioned that *P. ridibundus* was previously mentioned for vicinity of Novgorod, Izborsk and Pskov towns (Kauri, 1946; Tseytlina et al., 1977; Mazin and Borkin, 1979). In addition, several individuals are stored in collections of Senckenberg Naturhistorische Sammlungen Dresden, Germany (MTKD.3432, 7450 – 7455), which were collected in Shchepets (Schepzowsk) village (about 58.763° N 28.206° E) in Pskovskaya oblast' and were attributed by collectors to *P. ridibundus* (Kuzmin, 2012). However, our field research has shown that the presence of this species here is unlikely.

Importantly, the northern border of native range of *P. ridibundus* runs much further south through southwestern Latvia, Lithuania, Belarus and Tverskaya oblast' in Russia (Kuzmin, 2013). The species can penetrate to the southernmost part of Novgorodskaya oblast' in the Lake Seliger region. At this lake near the border of Tverskaya and Novgorodskaya oblast's, two males of the species were collected in October 1975 (ZMMSU. 1352). However, invasive populations of *P. ridibundus* are known from various regions of northern Europe. In southern Finland introduced populations were extinct in the early 1960s (Terhivuo, 1981; Hoogesteger et al., 2013). Introduced marsh frog populations were previously considered extinct in Estonia (Kauri, 1946; Talvi, 1992). However, the species was recently revealed again in the eastern part of the country near Narva and Tartu cities, as well as in Vyarsk Settlement (Laanetu, 2012; our data). Additionally, numerous invasive populations of *P. ridibundus* are recently known in Latvia and Kaliningradskaya oblast' of Russia (Borkin et al., 1979, 1986; Litvinchuk et al., 2020).

Some populations of *P. ridibundus* in St. Petersburg City are recently extinct. For example, in the 1930s the frogs were observed in Kristatelka River (ZISP. 3730), where they have now absent, possibly due to unfavorable hydrological conditions. In 1981 – 1982, the species was recorded in ponds of the St. Petersburg State University campus in Peterhof, where they are recently extinct. To date, frogs have also lacking in Aptekarsky Island, where they lived in the 1970 – 1980s. In the 1980th, *P. ridibundus* disappeared from the ponds of St. Petersburg Botanical Garden, due to a reconstruction of this pond system. In 1980, marsh frogs were recorded in Yukki Settlement, where they are now absent. From 1996 to 2000, a small population of marsh frogs lived in a reservoir on Kamenka River near Shuvalovo railway station. Perhaps, due to a heavy pollution of the reservoir, by 2001 the population had extinct. In 2001, the frogs disappeared in Kamenny Island after draining ponds. The marsh frogs are now completely absent in Yelagin Island, probably, because of a chemical treatment of water bodies. In 2003, a population that existed in ponds of the Bolshevik plant sport complex was gone after their reconstruction.

The marsh frog survival in the northwest of Russia is facilitated by thermal pollution in the city of St. Petersburg and Sosnovy Bor Town, as well as the presence of deep fresh and brackish water bodies suitable for their wintering. Marsh frogs inhabit mainly artificial heavily polluted reservoirs, dumps and construction sites in St. Petersburg City, as well as the coastal zone and floodplains of the Neva Bay and the Gulf of Finland (Fig. 7). Here *P. ridibundus* have limited distribution in reed beds along coasts and within cultivated landscape. Both habitats are unsuitable for most local native amphibians, and, therefore, marsh frogs have no negative impacts on their populations.

Sometimes, new populations of the marsh frog can arise as a result of *P. esculentus* × *P. esculentus* crosses (hybridolysis). For example, such populations of *P. ridibundus* were previously observed in southern Switzerland and Kaliningradskaya oblast' of Russia (Dubey et al., 2019; Litvinchuk et al., 2020). However, we did not found such type of *P. ridibundus* populations in the studied region.

It is also important that marsh frogs from southern Russia and the Caucasus were the source for introduction in the northwest of Russia. According to genetic data, the Caucasus and southern Russia are inhabited by two cryptic marsh frog species (*P. ridibundus* and *P.* cf. *bedriagae*) and their hybrids (Ohst, 2008; Akin et al., 2010; Ermakov et al., 2014, 2016a, 2016b). Moreover, based on mitochondrial DNA three specimens from Peterhof (Akin Peksen, 2015; NCBI numbers: GU812188 and GU812200) showed that they are close to *P.* cf. *bedriagae*. These data show that further research of genetic variability of marsh frogs inhabiting northwestern Russia can reveal here this marsh frog species. Additionally, it has also been previously shown that southern populations of the marsh frog (*P.* cf. *bedriagae* and hybrids between *P. ridibundus* and *P.* cf. *bedriagae*) from Turkey, Armenia and Kazakhstan differ from more northern ones in mating calls (Joermann et al., 1988; Schneider and Egiasarjan, 1991; Schneider and Sinsch, 1992, 1999). However, we did not find significant differences between the calls of *P. ridibundus* from northwestern Russia and other European populations (Lenné and Schneider, 1995; Zaks, 2008; Zaks and Ermakov, 2012).

Acknowledgments. We are thankful to S. A. Fetisov, S. Yu. Enden, G. Yu. Konechnaya, P. G. Efimov, I. V. Ilynsky, E. M. Litvinova, I. I. Komova, L. F. Litvinchuk, D. V. Skorinov, and V. G. Pchelintsev for help in field works. This work was supported by grant of the Russian Science Foundation No. 20-04-00918. The work was fulfilled under the Laboratory Project of Zoological Institute of Russian Academy of Sciences No. AAAA-A19-119020590095-9 and state contract 122031100282-2.

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APPENDIX.
The list of localities of water frogs in St. Petersburg City, as well as in Leningradskaya, Pskovskaya, and Novgorodskaya oblast’s

Pelophylax lessonae

Leningradskaya oblast’ (62 localities): “Mshinskoe Boloto” sanctuary, ~59.021° N 30.201° E (Noskov and Boch, 1999; Milto, 2007); Bolshoy Sabsk, 4 km from, ~59.114° N 29.081° E (ZISP.6748); Pechurki, 59.138° N 27.984° E (Milto, 2007); Bolshie Polya, 59.144° N 28.071° E (Milto, 2007); Zavastye road, 58.940° N 28.327° E (ZISP.5425; Milto, 2007); between Luzhitsy and Neguba, 58.895° N 28.574° E (ZISP.8643 – 8646; Milto, 2007); Dolgoe Lake, 58.857° N 28.684° E (Milto, 2007); Vervino, 59.210° N 28.466° E (our data); Samro, 58.935° N 28.831° E (our data); between Samro and Slavyanka, 58.945° N 28.848° E (our data); Poganoe Lake, 59.007° N 28.825° E (our data); between Koshelevichi and Rozhnovye, 59.019° N 28.856° N (our data); Luga, 58.741° N 29.859° E (ZISP.472, 3759, 3858 – 3861, 3869, 3882 – 3883, 3890 – 3893, 5430; ZMB.46849 – 46859; ZMMSU.1312 – 1313; Terentjev, 1927; Aleksandrovskaya and Milishnikov, 1977; Benevolenskaya, 1977; Borkin et al., 1979; Borkin and Tikhenko, 1979; Günther and Lübcke, 1979; Borkin et al., 1986; Sokolova and Borkin, 1991; Milto, 2007); Naplotka River, 58.753° N 29.857° E (ZISP.1698; Nikolsky, 1905; Terentjev, 1927); Luga River, 58.749° N 29.875° E (ZISP.6565, 6723); Shalovo, ~58.770° N 29.921° E (ZISP.5735; Milto, 2007); “Shalovo-Perechitsky” sanctuary, 58.768° N 29.915° E (Milto, 2007); “Shalovo-Perechitsky” sanctuary, 58.807° N 29.933° E (our data); Gorodok, 58.698° N 29.842° E (Milto, 2007); Luga River, 58.771° N 29.971° E (our data); Tolkova, 58.786° N 29.813° E (Mazaraky, 1902; Milto, 2007); Mayak summer camp, 58.791° N 30.049° E (our data); Zhemchuzhina, 58.706° N 29.720° E (our data); Klokino, 58.750° N 29.983° E (our data); Pochap, 58.802° N 30.377° E (our data); Tyosovo-4, 58.802° N 30.576° E (our data); Khrelyovka, 58.799° N 30.626° E (our data); Nadbelye, 58.862° N 30.466° E (our data); Ogorelye, 59.019° N 30.882° E (our data); Brod (=Brodsk), 58.568° N 29.884° E (ZISP.1340; Terentjev, 1927; Nikolsky, 1905; Milto, 2007); Zhiloe Gorneshno, 58.746° N 29.110° E (Milto, 2007); Zaplotye, 58.767° N 30.168° E (ZISP.5424, 5786, 5845; Milto, 2007); Rapti (= Dzerzhinskogo), “Cheremenetsky” sanctuary, ~58.663° N 29.890° E (ZISP.6570; Shnitnikov, 1924; Noskov and Boch, 1999; Milto, 2007); Ploskoe, 58.818° N 29.979° E (our data); Kolentsevo, 58.790° N 30.180° E (Milto, 2007); Zapolye, 58.776° N 30.116° E (Milto, 2007); “125 km,” 8 km E, 58.800° N 29.979° E (ZISP.5849; Milto, 2007); Oredezh, 8 km SE, 58.775° N 30.456° E (ZISP.5872; Milto, 2007); Butkovichi, 58.567° N 29.921° E (Milto, 2007); Konezerye, 58.506° N 29.927° E (Milto, 2007); Bolshie Toloni Lake, 58.685° N 29.860° E (our data); Serebryanka, 58.584° N 29.612° E (ZISP.5423; Milto, 2007); Zheltsy, 58.846° N 29.925° E (ZISP.6193; our data); “Syabersky” sanctuary, Gogolyonok Lake, 58.813° N 29.118° E (Milto, 2007); “Bely Kamen’” sanctuary, 58.741° N 30.450° E (Noskov and Boch, 1999); Beloe Lake, ~58.804° N 30.477° E (ZISP.5483; Noskov and Boch, 1999; Milto, 2007); Tesovo bogs, ~58.991° N 30.877° E (Milto, 2007); Selo-1, 58.555° N 30.126° E (our data); Poddubye, 59.032° N 30.864° E (Milto, 2007); Ravan River, 59.083° N 31.160° E (our data); Kirishi, 59.429° N 31.997° E (our data); Tikhvin monastery, 59.652° N 33.520° E (our data); Shulgino, 59.227° N 34.778° E (ZISP.4500, 5639, 5648, 5669, 5732; Borkin and Tikhenko, 1979; Milto, 2007); Pikalyovo, 59.550° N 34.101° E (Milto, 2007); Metallurg-1, 59.477° N 34.194° E (our data); Pokrovsky Creek, 59.366° N 34.731° E (our data); Yolzovo, 59.303° N 34.223° E (our data); Syogla, 59.505° N 33.932° E (our data); Chudtsy, ~59.505° N 34.363° E (our data); Efimovsky, 59.465° N 34.657° E (our data); Pikalyovo, 59.507° N 34.168° E (our data); interfluve of Belaya and Lid Rivers, ~59.417° N 35.150° E (our data).

Pskovskaya oblast’ (109 localities): Gdov, 58.742° N 27.820° E (ZISP.1339; Nikolsky, 1905; Dorowatowsky, 1913; Terentjev, 1927); Khitovo, 58.961° N 27.736° E (Milto, 2007); Kharlamova Gora (= Charlamova Gora), 58.714° N 28.713° E (ZISP.1683, 2044; Nikolsky, 1905; Dorowatowsky, 1913; Terentjev, 1927); Lugi, 58.754° N 27.969° E (ZISP.7125; Milto, 2007); Pnevo, 58.231° N 27.520° E (Milto, 2007); Nizovitsy, 58.373° N 27.868° E (our data); Samolva, 58.294° N 27.634° E (our data); Ostrov, 58.283° N 27.564° E (our data); Kobylye Gorodishche, 58.298° N 27.645° E (our data); “Remdovsky” sanctuary, 58.220° N 28.118° E (our data); Strugi Krasnye, 4 km W, 58.259° N 29.046° E (Milto, 2007); Mayakovo, 58.133° N 29.162° E (Milto, 2007); Zaplyusye, 58.437° N 29.736° E (Milto, 2007); Belsko, 58.451° N 28.781° E (ZISP.6008; Milto, 2007); Uzmino, 58.430° N 28.767° E (ZISP.6511; Milto, 2007); Sitenskoe and Radilovskoe Lakes, ~58.040° N 29.305° E (Bublichenko et al., 2005); Skovorodka, 58.383° N 28.971° E (our data); Novaya Zhizn, 58.343° N 28.902° E (our data); Perekhozha, 58.210° N 29.023° E (our data); Porkhov, 57.772° N 29.552° E (ZISP.6568; Milto, 2007); Kamenka, 57.933° N 29.658° E (ZISP.6926; Milto, 2007); Krasnodubye, 58.023° N 29.603° E (Milto, 2007); Logovino, 57.653° N 29.652° E (Milto, 2007); Krekshiny, 58.011° N 29.890° E (our data); Kresty, 57.794° N 28.416° E (Milto, 2007); Pskov, 57.822° N 28.330° E (Milto, 2007); Pskov, 6 – 7 km from, ~57.818° N 28.464° E (ZISP.4113; Milto, 2007); Borisovichi, 57.832° N 28.268° E (ZISP.12116 – 12117); Chudinkovo – Evakhnovo, 57.848° N 29.000° E (ZISP.6823; Milto, 2007); Zamelnichye, 58.049° N 28.178° E (ZISP.6927; Milto, 2007); Zabolotye, 58.068° N 28.547° E (our data); Pechyory monastery, 57.810° N 27.613° E (ZISP.7146; Milto, 2007); Malye Kalki, 57.841° N 27.973° E (ZISP.6919; Milto, 2007); Kozye Gorodishche, 57.808° N 27.620° E (our data); Novy Izborsk, 57.772° N 27.970° E (ZISP.6920, 7131; Milto, 2007); Izborsk, 57.718° N 27.863° E (our data); Viski, 57.754° N 27.933° E (our data); Panikovichi, 57.688° N 27.565° E (our data); Pytalovo, 57.066° N 27.915° E (ZISP.5432; Milto, 2007); Balastnitsa, 57.104° N 27.896° E (ZISP.5433, 5994; Milto, 2007); Antsiferovo, 57.159° N 27.892° E (our data); Drykushki – Besenyata, 56.956° N 28.076° E (our data); Kostretsy, 57.040° N 27.918° E (our data); Vanchonki, 57.208° N 27.910° E (our data); Vasilyevo, 57.609° N 27.924° E (our data); Veretye, 57.556° N 27.867° E (ZISP.12118; Milto, 2007); Usovo, 56.785° N 28.389° E (our data); Pushmachi, 56.730° N 28.299° E (our data); Dubrovka, 57.544° N 29.763° E (Milto, 2007); Yamok, 57.497° N 29.788° E (Milto, 2007); Obluchye, 57.559° N 29.672° E (our data); Bezhanitsy, 56.968° N 29.912° E (Milto, 2007); Konratovo road, 56.975° N 29.887° E (our data); Tsevlo, 57.043° N 30.282° E (Milto, 2007); Polistovsky Nature Reserve, 57.038° N 30.312° E (Milto, 2007); Krasny Luch, 57.068° N 30.087° E (Milto, 2007); Chikhachyovo, 57.294° N 29.895° E (our data); Yakoltsevskoye Lake, 56.840° N 29.983° E (ZISP.13220 – 13224); Loknya, 56.828° N 30.148° E (our data); Fyodorovskoe, 56.808° N 30.145° E (our data); Sosnovo, 57.007° N 30.491° E (Milto, 2007); Rdeysky Nature Reserve, 57.258° N 30.775° E (Bashinsky, 2013); Bashovo, 56.654° N 30.171° E (our data); Agafonovo, 56.932° N 29.204° E (ZISP.6015; Milto, 2007); Klimovo, 57.021° N 29.482° E (ZISP.6820; Milto, 2007); Vyoska, 57.254° N 29.391° E (our data); Puskinskie Gory, 57.021° N 28.929° E (ZISP.6821; Milto, 2007); Mikhaylovskoe, 57.061° N 28.916° E (our data); Trigorskoye, 57.026° N 28.893° E (our data); Beloe Lake, 56.251° N 29.434° E (ZISP.6007; Milto, 2007); Beloe Lake, 56.444° N 29.036° E; Nochlegovo, 56.511° N 29.034° E (our data); Mochalkovo, 56.531° N 28.799° E (our data); Goloshchapy, 56.718° N 28.610° E (our data); Kamenets Lake, 56.801° N 28.674° E (our data); Zankovo, 57.304° N 28.378° E (our data); Kholmatka, 57.099° N 28.135° E (our data); Novaya Derevnya, 56.308° N 28.483° E (Milto, 2007); Prasni, 56.269° N 28.544° E (ZISP.6011, 6013; Milto, 2007); Bolbuki, Mogilinskoe Lake, 56.307° N 29.066° E (ZISP.6140; Milto, 2007); Idritsa, 56.333° N 28.922° E (ZISP.6195, 6141, 6329; Milto, 2007); Maksyutino, 56.379° N 28.807° E (ZISP.6331; Milto, 2007); Malkovo, 56.291° N 28.583° E (ZISP.6014; Milto, 1999, 2007); Rudnya – Malkovo, 56.264° N 28.594° E (Milto, 2007); Zelenets Lake, 56.148° N 28.576° E (ZISP.6021; Milto, 2007); Dubishche tract, 56.165° N 28.709° E (ZISP.6142; Milto, 2007); Dolgoe Lake, 56.149° N 28.403° E (Milto, 2007); Rybolovka – Rudnya, 56.235° N 28.579° E (Milto, 2007); Krasikovo, 56.107° N 28.694° E (ZISP.6020; Milto, 2007); Nishcha, 56.132° N 28.776° E (ZISP.6328); Necheritsa – Lisna Lakes, 56.104° N 28.425° E (Milto, 2007); Zabelye, between Beloe and Ozeryavki Lakes, 56.208° N 28.480° E (ZISP.6009, 6012; Milto, 2007); Anninskoe Lake, 56.196° N 28.706° E (ZISP.6327; Milto, 2007); Argeykovo Lake, 56.492° N 28.979° E (our data); Pekhovo, 56.212° N 30.254° E (ZISP 13205 – 13214); Malakhovo, 56.287° N 30.263° E (our data); Demya, 56.311° N 30.317° E (our data); Darkino, 56.143° N 30.157° E (our data); Velikie Luki, 56.305° N 30.518° E (ZISP.12120 – 12124); Polibino, 56.142° N 30.396° E (ZISP.13215 – 13216); Zhizhitskoe Lake, 56.243° N 31.268° E (Milto, 2007); Krasnaya Veshnya, 56.267° N 30.871° E (ZISP.13217 – 13219); Nevel (= Nevelsk), 56.019° N 29.919° E (ZISP.1682; Terentjev, 1927; Milto, 2007); Zubrovo, 56.257° N 31.009° E (ZISP.14288); Chernovo reservoir, 56.221° N 28.524° E (our data); Osyno Lake, 56.221° N 28.522° E (ZISP.6194; Milto, 2007); Velikolukskaya fortress, 56.342° N 30.507° E (our data); Murovitsy, 57.869° N 28.142° E (our data); Krivsk, 57.872° N 27.938° E (our data).

Novgorodskaya oblast' (51 localities): Ivnya, 58.604° N 30.128° E (our data); Tesovo-Netylsky, 58.933° N 31.052° E (Milto, 2007); Oskuy, 59.276° N 32.087° E (Milto, 2007); Shimsk, 58.231° N 30.672° E (Milto, 2007); Bolshaya Viton, 58.187° N 30.908° E (Milto, 2007); Zharukha, 58.230° N 31.942° E (our data); Dubrovno, 58.077° N 31.903° E (our data); Pola, 57.919° N 31.843° E (our data); Kolmovo, 58.568° N 31.293° E (our data); Arkazhi, 58.493° N 31.253° E (Milto, 2007); Novoe Kunino, 58.532° N 31.418° E (Milto, 2007); Krasnye Stanki, 58.402° N 31.824° E (our data); between Novoseltsy and Bozhonka, 58.513° N 31.677° E (Milto, 2007); Tesovo Bogs, 58.888° N 30.894° E (Milto, 2007); between Kirillovka and Dubrovka, 58.692° N 31.499° E (Milto, 2007); Zamlenye, 58.276° N 31.697° E (Milto, 2007); Kulotino, 58.453° N 33.361° E (Milto, 2007); Gorushka, 58.528° N 33.281° E (ZISP.5426; Milto, 2007); Toporok, 58.545° N 33.476° E (ZISP.5427; Milto, 2007); Blizhnee Lake, 58.506° N 33.509° E (our data); Staraya Russa, 57.988° N 31.352° E (ZISP.733; Nikolsky, 1905; Terentjev, 1927; Borkin et al., 1986; Milto, 2007); Kholm District, Lovat River basin, ~57.378° N 31.385° E (Esaulov, 1878); Valday, 57.986° N 33.256° E (ZISP.6662; Chebakova, 1996; Milto, 2007; Milto and Leontyeva, 2012); Valday, 57.987° N 33.215° E (our data); Valday, 57.988° N 33.213° E (our data); Valday, 57.991° N 33.229° E (our data); Terekhovo, 58.071° N 33.333° E (ZISP.3613, 12255 – 12272; Gumilevsky, 1941; Milto, 2007; Milto and Leontyeva, 2012); Edrovo, 57.917° N 33.626° E (ZISP.6663; Milto, 2007; Milto and Leontyeva, 2012; Svinin et al., 2019); Eryomina Gora, 57.976° N 33.074° E (ZISP.7341; Milto, 2007; Milto and Leontyeva, 2012); Bortsovo, 57.992° N 33.108° E (ZISP.12125 – 12131; Milto, 2007; Milto and Leontyeva, 2012); Borovichi, 58.393° N 33.902° E (ZISP.6670; Milto, 2007; Milto and Leontyeva, 2012); Ivanteevo – Novoivanovka, 57.742° N 33.116° E (our data); Sukhaya Vetosh, 57.681° N 33.110° E (Milto and Leontyeva, 2012); Baluevo, 57.691° N 33.057° E (Milto and Leontyeva, 2012); Nikolskoe, 57.731° N 33.004° E (Redikorzew, 1901); Dunaevshchina, 57.687° N 32.978° E (Milto and Leontyeva, 2012); Dunaevshchina, 57.688° N 32.955° E (Milto and Leontyeva, 2012); Sominets Lake, 57.732° N 33.116° E (Milto and Leontyeva, 2012); Myslovo, 57.768° N 33.016° E (Milto and Leontyeva, 2012); Novotroitsy, 58.121° N 33.295° E (Milto and Leontyeva, 2012); Chernushka River, 57.974° N 33.448° E (our data); Uglovka, 58.237° N 33.525° E (Milto and Leontyeva, 2012); Zaluzhskoe Lake, 57.714° N 32.928° E (our data); Zaluzhye, 57.703° N 32.917° E (Milto and Leontyeva, 2012); Piros Lake, 58.164° N 33.839° E (Milto and Leontyeva, 2012); Novy Skrebel, 57.509° N 33.060° E (Milto and Leontyeva, 2012); Lavrovo, 57.538° N 32.959° E (Milto and Leontyeva, 2012); Klin, 57.614° N 32.839° E (Milto and Leontyeva, 2012); Kocherovo, 58.684° N 34.333° E (ZISP.3596 – 3599; Milto, 2007); Orekhovno, 58.309° N 35.035° E (ZISP.6023, 6661; Milto, 2007); Pestovo, 58.605° N 35.787° E (our data).

Pelophylax esculentus

Pskovskaya oblast' (14 localities): Kobylye Gorodishche, 58.298° N 27.645° E (ZISP.12114 – 12115); Borisovichi, 57.832° N 28.268° E (ZISP.12113); Murovitsy, 57.869° N 28.142° E (ZISP.10419); Veretye, 57.556° N 27.867° E (ZISP.12119); Pytalovo, 57.066° N 27.915° E (ZISP.5431, 6450, 6016, 6022; Milto, 2007); Krivsk, 57.872° N 27.938° E (ZISP.6822; Milto, 2007); Idritsa, 56.332° N 28.920° E (ZISP.6330; Milto, 1999, 2001, 2007); Chernovo reservoir, 56.221° N 28.524° E (ZISP.6196, 7627; Milto, 1999, 2001, 2007, 2009, 2011a); Osyno Lake, 56.221° N 28.522° E (ZISP.6194, 6197; Milto, 1999, 2001, 2007); Zabelye, between Beloe and Ozeryavki Lakes, 56.208° N 28.480° E (ZISP.6010; Milto, 1999, 2001, 2007); Nevel, 56.019° N 29.919° E

(ZISP.10420); Velikolukskaya fortress, 56.342° N 30.507° E (our data); Polibino, 56.142° N 30.396° E (ZISP.13225); Vasilyevo, 57.609° N 27.924° E (our data).

Pelophylax ridibundus

St. Petersburg City (68 localities): Yelagin Island, 59.978° N 30.259° E (Sorokhtin, 1920; Vasilkovsky, 1928; Borkin and Orlov, 1982; Milto, 2007); Krestovky Island, 59.970° N 30.241° E (ZISP.3817; Porchinsky, 1872; Milto, 2007); Aptekarsky Island, Botanical Garden, 59.970° N 30.328° E (Borkin and Orlov, 1982); Kamenny Island, 59.979° N 30.287° E (Milto, 2007); Obukhovskoy Oborony prosp., sports complex of “Bolshevik” factory, 59.855° N 30.488° E (our data); Rybatskoe, 59.837° N 30.519° E (our data); Sovetsky prosp., 59.828° N 30.537° E (ZISP.11827 – 11831); Slavyanka River, 59.827° N 30.529° E (our data); Slavyanka River, 59.819° N 30.530° E (our data); Udelnaya, 60.016° N 30.313° E (Pestinsky, 1929; Raykov and Rimsky-Korsakov, 1938); Pargolovo, 60.093° N 30.257° E (Orlov and Ananjeva, 1995); Lakhta (= Lachta), 59.992° N 30.158° E (ZISP.2397; Mertens, 1916; Nikolsky, 1918; Sorokhtin, 1920; Terentjev, 1927; Pestinsky, 1929; Raykov and Rimsky-Korsakov, 1938; Milto, 2007); Yakhtennaya ul., 60.009° N 30.226° E (Milto, 2007); Kamenka River, Shuvalovo, 60.042° N 30.249° E (ZISP.5429; Milto, 2007); Rzhavy Ruchey, 60.052° N 30.197° E (our data); Yukki, 60.114° N 30.301° E (Milto, 2007); Lisiy Nos, 60.000° N 30.014° E (ZISP.7514; Milto, 2007, 2008); “Northern Coast of Neva Bay” protected area, 59.992° N 30.094° E (Milto, 2020b); Olgino, 59.995° N 30.091° E (our data); Olgino, 59.998° N 30.067° E (our data); “Blizhnie Dubki” park, 59.999° N 30.054° E (our data); Verperluda Island, 59.997° N 30.016° E (our data); Gagarka park, 60.078° N 29.946° E (our data); Gagarka park, 60.084° N 29.933° E (our data); Sestroretsk, 60.095° N 29.942° E (MCZ. A-69180 – 69181; Milto, 2008, 2011b); Razliv, 60.079° N 29.948° E (our data); Gorskaya, 60.040° N 29.965° E (our data); Kurort, Malaya Sestra River, 60.127° N 29.943° E (ZISP.9578 – 9580; Milto, 2011b); Kanavnoye Bog, 60.128° N 29.958° E (our data); Lensovetovsky, 59.758° N 30.469° E (our data); Avtovo, Krasnenkoe cemetry, 59.863° N 30.266° E (ZISP.7513; Milto, 2007); Polezhaevsky park, 59.845° N 30.193° E (our data); Dudergofsky canal, 59.845° N 30.180° E (our data); Novoznametka park, 59.846° N 30.156° E (our data); Krasnenkaya River, 59.868° N 30.192° E (our data); Krasnenkaya River, 59.869° N 30.174° E (our data); Ugolnaya Gavan, 59.864° N 30.232° E (Milto, 2007, 2008); Yunona, 59.860° N 30.196° E (our data); Yuzhno-Primorsky park, 59.848° N 30.159° E (ZISP.7515, 10413 – 10418; Milto, 2007); Yuzhno-Primorsky park, 59.857° N 30.163° E (our data); Marshala Kazakova prosp., 59.870° N 30.164° E (our data); Vosmyorka Pond, 59.851° N 30.166° E (our data); Baltysky boulevard, 59.866° N 30.150° E (our data); LEMZ factory, 59.862° N 30.117° E (ZISP.6186); Konstantinovsky park, 59.856° N 30.059° E (ZISP.5428; Milto, 2007); Strelka River, 59.853° N 30.042° E (Milto, 2007); Strelna, 59.862° N 30.022° E (Milto, 2008); Strelna, 59.862° N 30.007° E (our data); “Znamenka” protected area, 59.871° N 29.989° E (our data); Znamenka, 59.875° N 29.981° E (Milto, 2007); “Alexandria” park, 59.883° N 29.954° E (Milto, 2007); “Alexandria” park, 59.885° N 29.942° E (our data); Mikhaylovka, 59.867° N 30.002° E (Milto, 2007); Novy Petergof, 59.871° N 29.902° E (ZISP.7026; Milto, 2007, 2008); Universitet, 59.880° N 29.834° E (Milto, 2007); Kritatellka River, 59.900° N 29.843° E (ZISP.3730; Milto, 2007); “Sobstvennaya Dacha” protected area, 59.900° N 29.853° E (our data); Martyshkino, 59.906° N 29.823° E (Orlov and Ananjeva, 1995; Milto, 2007, 2008); Kronshtadtskaya Koloniya, 59.928° N 29.738° E (ZISP.11832 – 11833; Rychkova et al., 2004); Oranienbaum-2, Karasta River, 59.923° N 29.754° E (Goncharenko, 2015); “Yuzhnoe Poberezhye” protected area, 59.924° N 29.759° E (our data); “Yuzhnoe Poberezhye” protected area, 59.928° N 29.753° E (our data); Bronka, 59.930° N 29.683° E (Milto, 2007); “Zapadny Kotlin” protected area, 60.027° N 29.672° E (Milto, 2021); Fort Konstantin, 59.997° N 29.703° E (our data); Patriot park, 60.014° N 29.691° E (our data); Kronshtadt, Petrovskaya ul., 59.987° N 29.780° E (Milto, 2007); Pervy Severny Fort, 60.030° N 29.755° E (our data).

Leningradskaya oblast’ (12 localities): Nizhnyaya Bronna, 59.919° N 29.615° E (our data); Ropshinsky park, 59.725° N 29.866° E (our data); between Ropsha and Novaya Ropsha 59.746° N 29.874° E (ZISP.7293, 9719, 9720; Milto, 2007); between Novoe Kalishche and Kovashi, 59.896° N 29.217° E (ZISP.7292; Milto, 2007); Sosnovy Bor, 59.838° N 29.022° E (our data); Ivangorod, 59.387° N 28.217° E (Lasakova, 2003; Milto, 2007); Lipovo, 59.755° N 28.179° E (Bublichenko and Bublichenko, 1998; Noskov and Boch, 1999; Milto, 2020a); Vybye, 59.668° N 28.224° E (our data); Kurghalsky Peninsula, 59.787° N 28.100° E (our data); Kurghalsky Nature Reserve, 59.780° N 28.086° E (our data); Gakkovo, 59.663° N 28.026° E (our data); Rosson River, 59.491° N 28.102° E (Milto, 2020).