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# Distribution and Ways of Dispersion of American Rotifer *Kellicottia bostoniensis* (Rousselet, 1908) (Rotifera: Brachionidae) in Waterbodies of European Russia

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**Abstract**—In the first decade of the 21th century, the findings of a new invader, the American rotifer, *Kellicottia bostoniensis* (Rousselet, 1908), has become more frequent in Russia. By 2015 *K. bostoniensis* had been detected in more than 40 different waterbodies and watercourses of European part of Russia. American rotifer is a widely spread and common species in forest lakes and rivers of the Baltic Sea basin, Volga-Baltic watershed; in the Volga River basin it has spread southward to 55° N (lakes of the Oka and Pra rivers) and eastward to 45° E (the Kerzhenets River, Cheboksary Reservoir basin). The rotifers inhabit small ($<3$ km$^2$) and large ($>200$ km$^2$), shallow ($<1$ m) and deep ($>20$ m) waterbodies with a trophy range from oligo- to eutrophy. In Russia *K. bostoniensis* occurs in a wide range of color of water (30–680 degrees Pt–Co-scale) compared to waterbodies of Western Europe. The rotifer is tolerant to temperature regime and oxygen concentrations in water. In the hypolimnion of stratified lakes, *K. bostoniensis* reaches high abundance ($>100000$ ind./m$^3$) at a very low concentration of dissolved oxygen (2.5 mg/L or about 20% of saturation) and water temperature of 5–12°C. The invader and aboriginal species *K. longispina* coexisted in deep lakes and deep parts of reservoirs (the depth more than 5 m); in shallow lakes only *K. bostoniensis* was found. On the contrary, in most parts of large reservoirs of the Upper Volga only *K. longispina* was recorded. The possibility and the direction of transfer of the rotifer by swimming birds are discussed.

*Keywords: Kellicottia bostoniensis*, distribution, ways of dispersion, waterbodies of European Russia

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## INTRODUCTION

The genus *Kellicottia* Ahlstrom, 1938 (family Brachionidae) includes two species, *K. longispina* (Kellicott, 1879) and *K. bostoniensis* (Rousselet, 1908) (Kutikova, 1970; Koste, 1978). *K. longispina* is a widespread inhabitant of waterbodies in northern latitudes. It is a pelagic limnophilic euryhaline species (Kutikova, 1970). The anterior dorsal edge of the lorica has six unpaired unequal spines. The middle right spine is the longest and the left spine is much shorter. The lateral spines are rather long. The total body length ranges from 400 to 1000 μm (Koste, 1978). *K. bostoniensis* has four unequal spines on the anterior dorsal margin of the lorica. The longest spine is ≤140 μm, the body length is ≤380 μm (Koste, 1978). Photos of the both species are presented in the publications (Zhdanova and Dobrynin, 2011; Lazareva and Zhdanova, 2014; Bayanov, 2014).

The North American *K. bostoniensis* is known as the species which actively spreads over waterbodies of South America (De Paggi, 2002) and Europe (Segers, 2007). In United States and Canada the rotifer is common for humic acid waterbodies (Roff and Kwiatkowski, 1977; Blouin et al., 1984; Havens, 1991; Scruton et al., 1991), Great Lakes (Barbiero and Warren, 2011), bays and river mouths, and many bogs (Biêdzki and Ellison, 2003). *K. bostoniensis* has been reported as a dominant species in zooplankton in some reservoirs of Mexico (Nandini et al., 2006; Figueroa-Sanchez et al., 2014). *K. bostoniensis* has been recently recorded in lakes and reservoirs of different trophy in Brazil (Ferraz et al., 2002; Landa et al., 2002; Bezerra-Neto et al., 2004; Peixoto et al., 2010) and Argentina (De Paggi, 2002). Since the middle of the past century the rotifer has inhabited waterbodies of Western Europe (Pejler, 1998).

In Europe, *K. bostoniensis* was first recorded in one of the lakes in Sweden in the area of wastewater discharge from a pulp and paper mill in the first half of the 20th century (Carlin, 1943). By the beginning of the 21st century the species has become common for waterbodies in the south of Sweden (Arnemo et al., 1968; Brett, 1989; Josefsson and Andersson, 2001). *K. bostoniensis* is also a common species in humic acid and weakly polluted waterbodies in the Netherlands (Leentvaar, 1961), Finland (Eloranta, 1988; Jarvinen et al., 1995; Keskitalo et al., 1998; Lehtovaara et al., 2014), and France (Balvay, 1994). The rotifer has been found in the Elbe and Ems rivers (Germany) (Rühymann, 1962; Schulz, 1964; Streble and Krauter, 2006) and in the Ohře River (the Czech Republic) (Kosik et al., 2011). *K. bostoniensis* has been recently detected in an oxbow of the Sozh River (the Dnieper River basin) (Vezhnavets and Litvinova, 2015).

In lakes of the northern part of European Russia (the Karelian Isthmus) *K. bostoniensis* was first recorded in 2000 (Ivanova and Telesh, 2004). Later, its high abundance has been reported in some rivers and lakes in the basin of the Upper and Middle Volga (Zhdanova and Dobrynin, 2011; Lobunicheva et al., 2011; Bayanov, 2014), in Lake Onega and waterbodies of its basin, in Lake Ladoga and its tributaries (Lobunicheva et al., 2011; Makartseva and Rodionova, 2011; Aleshina et al., 2014; Fomina and Syarki, 2015). In Europe, habitats of the species are confined to rivers and lakes; in 2005–2012 *K. bostoniensis* was found in large reservoirs of the Upper Volga (Lazareva and Zhdanova, 2014).

The aim of this work is to describe locations of *K. bostoniensis* and to analyze the ways of its dispersal in waterbodies of European Russia.

## MATERIALS AND METHODS

The work is based on materials of hydrobiological studies which were conducted in three large reservoirs on the Sheksna (Sheksna Reservoir) and Volga rivers (Uglich and Ivankovo reservoirs) and in a small reservoir on the Okhta River (Okhta Reservoir), Lake Ladoga, more than 30 small (<3 km$^2$) lakes of the Valdai Hills (Novgorod oblast), the Central Forest Reserve (Tver oblast) and the Oka Nature Reserve (Ryazan oblast), Nizhny Novgorod, Vladimir, Leningrad and Vologda oblasts, a river in Nizhny Novgorod oblast and two brooks in Vologda oblast (Table 1). The studies were conducted in most waterbodies in summer and in some waterbodies in spring (April).

Rotifers were counted in the total samples of zooplankton fixed in 4% formalin. Samples were collected with a Juday net (a mesh size of 85 and 64 μm, respectively) and with samplers of different design of 2–4 L in volume with the subsequent filtration through a sieve (Zhdanova and Dobrynin, 2011; Lobunicheva et al., 2011; Makartseva and Rodionova, 2011; Aleshina et al., 2014; Lazareva and Zhdanova, 2014; Bayanov, 2014).

## RESULTS

**Locations of the species.** According to our and published data *K. bostoniensis* inhabits 44 waterbodies and watercourses in a vast territory of European Russia from 54° to 61° N and from 29° to 44° E (Fig. 1). All waterbodies in Leningrad oblast (Table 1) belong to the Baltic Sea basin (particular basins of the Neva River, Lake Ladoga and the Gulf of Finland in the Baltic Sea); it also includes Kupetskoe and Tonkoe lakes (a particular basin of the Andoma River, an eastern tributary of Lake Onega) in Vologda oblast and Bolshoe and Maloe Yaichko lakes (a particular basin of the Volkhov River) in Novgorod oblast. Other waterbodies belong to the basin of the Caspian Sea (particular basins of the Upper and Middle Volga). Out of them the most northern lakes Lainozero and Ekozero (Vologda oblast) belong to the Kema River basin (a tributary of the Sheksna River, Sheksna Reservoir), Lake Trestino (Tver oblast) belongs to the basin of the system of Upper Volga lakes, Peno, Volgo, Sterzh, and Vselug. Waterbodies in Ryazan, Vladimir, and Nizhny Novgorod oblasts belong to the basins of the Oka and Volga rivers (Cheboksary Reservoir). Most of surveyed lakes have closed basins (no visible outlets); they are located near upper riches of the rivers at watersheds of large river basins (the Karelian Isthmus, the southern part of Valdai Hills, and the Andoma Upland).

Water objects where the rotifer has been recorded differ in origin, trophic status, color of water and water pH (Table 1). Small (<1 km$^2$) and shallow (<5 m) lakes of glacial or karstic origin predominate; most of them are eutrophic with humic water color and

**Table 1.** Characteristics of waterbodies where *Kellicottia bostoniensis* was detected

| No. | Waterbody/Coordinates | Area, km$^2$ | Depth, m | Transparency, m | pH | Color, grad. according to Pt–Co scale | Trophy |
|---|---|---|---|---|---|---|---|
| | Vologda oblast | | | | | | |
| 1 | Brook from Lake Tonkoe 61°21′ N 37°25′ E | – | 1.5 | – | 7.0 | – | – |
| 2 | Brook from Lake Krivoe 61°27′ N 37°25′ E | – | 0.3 | – | 7.0 | – | – |
| 3 | Lake Kupetskoe 61°20′ N 37°19′ E | 1.05 | 5 | 0.5 | 7.0 | – | Eutrophic |
| 4 | Lake Ekozero 61°24′ N 37°24′ E | 0.13 | 2 | 0.5 | 6.7 | – | Dystrophic |
| 5 | Lake Tonkoe 61°24′ N 37°20′ E | 0.50 | 2 | 0.5 | 6.8 | – | Eutrophic |
| 6 | Lake Lainozero 61°26′ N 37°25′ E | 1.70 | 4 | 1.0 | 7.1 | – | Eutrophic |
| 7 | Sheksna Reservoir 60°17′ N 37°19′ E | 1665 | 2.0 | 1.8 | 8.0 | 63 | Mesotrophic |
| | Leningrad oblast | | | | | | |
| 8 | Lake Maloe Lugovoe 60°35′ N 30°09′ E | 0.02 | 5 | 0.12 | 5.8 | 440–680 | Mesotrophic |
| 9 | Lake Bolshoe Morozovskoe 60°36′ N 29°52′ E | 1.10 | 3.1 | 0.4–1.0 | 7.6–8.4 | 80–84 | Eutrophic |
| 10 | Lake Simagino 60°16′ N 29°48′ E | 2.70 | 19 | 0.8 | 7.6 | 76 | Eutrophic |
| 11 | Lake Chernyavskoe 60°23′ N 29°45′ E | 0.88 | 4.5 | 1.5 | 7.1 | 74 | Eutrophic |
| 12 | Lake Okhotnichie 60°36′ N 29°19′ E | 0.08 | 13 | 1.1–1.3 | 5.3–6.8 | 57–94 | Oligo-mesotrophic |
| 13 | Okhta Reservoir 60°53′ N 30°29′ E | 1.08 | 3.8 | 0.7 | 6.7 | 210 | – |
| 14 | Lake Pionerskoe* 60°18′ N 29°16′ E | 0.06 | 18 | – | 5.5–7.3 | 46–353 | Mesotrophic |
| 15 | Lake Pridorozhnoe* 60°18′ N 29°18′ E | 0.04 | 16 | – | 5.1–7.1 | 2–40 | Oligotrophic |

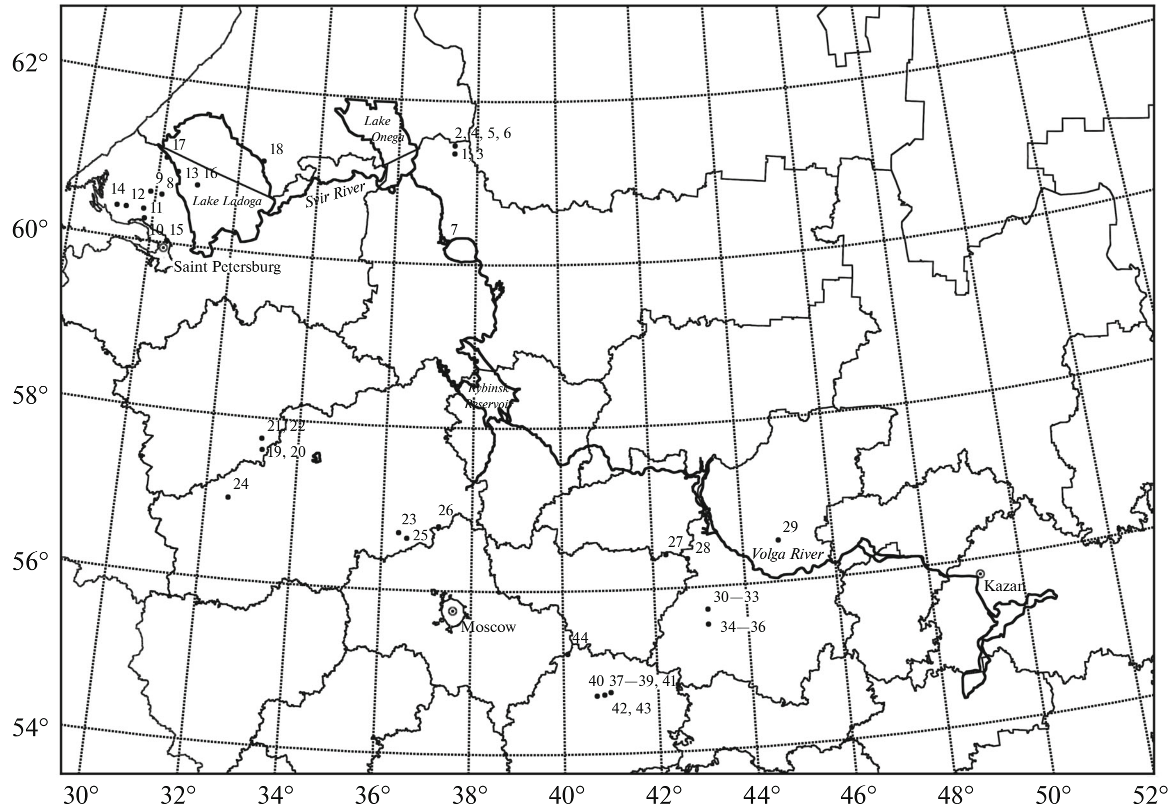
**Table 1.** (Contd.)

| No. | Waterbody/Coordinates | Area, km$^2$ | Depth, m | Transparency, m | pH | Color, grad. according to Pt–Co scale | Trophy |
|---|---|---|---|---|---|---|---|
| 16 | Lake Ladoga<br>60°45′ N<br>31°00′ E | 18135 | 46.9 | 1–3.4 | 6.8–9.5 | – | Mesotrophic |
| 17 | Vuoksa River<br>61°02′ N<br>30°09′ E | – | – | – | 7.1 | 74 | – |
| 18 | Tuloksa River<br>61°08′ N<br>32°36′ E | – | – | – | 6.4 | 181 | – |
| | Novgorod oblast | | | | | | |
| 19 | Lake Maloe Yaichko<br>57°37′ N<br>33°11′ E | 0.30 | 4.2 | 0.75 | 5.6 | 170 | Eutrophic |
| 20 | Lake Bolshoe Yaichko<br>57°36′ N<br>33°10′ E | – | 1.5 | 0.5 | 6.5 | 370 | Eutrophic |
| 21 | Lake Glukhoe<br>57°45′ N<br>33°09′ E | – | 3.5 | 0.7 | 7.0 | 220 | – |
| 22 | Lake Bragino<br>57°45′ N<br>33°11′ E | – | 1.4 | 2.40 | 6.9 | 170 | – |
| | Tver oblast | | | | | | |
| 23 | Lake Vidogoshch**<br>56°42′ N<br>36°22′ E | 0.17 | 21.9 | 0.5–1.1 | – | 50–55 | Eutrophic |
| 24 | Lake Trestino<br>57°00′ N<br>32°31′ E | 0.65 | 4 | 2 | 4.5 | 55 | Eutrophic |
| 25 | Ivankovo Reservoir<br>56°38′ N<br>36°33′ E | 327 | 9 | 0.7–0.9 | – | 30–55 | Eutrophic |
| 26 | Uglich Reservoir<br>56°47′ N<br>37°15′ E | 249 | 7 | 0.8 | – | 30–55 | Mesotrophic |
| | Vladimir oblast | | | | | | |
| 27 | Lake Kshchara<br>56°25′ N<br>42°17′ E | 1.14 | 12 | 2.4 | 7.6 | 35 | Mesotrophic |
| | Nizhny Novgorod oblast | | | | | | |
| 28 | Lake Elovoe<br>56°21′ N<br>42°46′ E | 0.02 | 17.3 | 3.7 | 5.7 | 30 | Mesotrophic |
| 29 | Kerzhenets River<br>56°30′ N<br>44°48′ E | – | 1.5 | 0.7 | 6.8 | 175 | – |

**Table 1.** (Contd.)

| No. | Waterbody/Coordinates | Area, $km^2$ | Depth, m | Transparency, m | pH | Color, grad. according to Pt–Co scale | Trophy |
|---|---|---|---|---|---|---|---|
| 30 | Lake Roy<br>55°43′ N<br>43°09′ E | 0.74 | 20 | 1.5 | 6.3–7.2 | – | Eutrophic |
| 31 | Lake Rodionovo<br>55°43′ N<br>43°09′ E | 0.11 | 17 | 3.5 | 5.6–7.0 | – | Mesotrophic |
| 32 | Lake Svyato<br>55°43′ N<br>43°09′ E | 0.22 | 14.6 | 1.3 | 7.0 | 54 | – |
| 33 | Lake Svyatoe Dedovskoe<br>55°43′ N<br>43°09′ E | 1.36 | 14 | 3.0 | 6.1 | – | – |
| 34 | Lake Komsomolskoe<br>55°32′ N<br>43°09′ E | 0.06 | 8 | 3 | 5.9–6.8 | – | – |
| 35 | Lake Bolshoe<br>55°32′ N<br>43°09′ E | 0.44 | 21.6 | 2.5 | 5.6 | – | Eutrophic |
| 36 | Lake Charskoe<br>55°31′ N<br>43°11′ E | 0.31 | 16 | 1.5 | 6.2 | 143 | – |
| | Ryazan oblast | | | | | | |
| 37 | Lake Lopata<br>54°45′ N<br>41°00′ E | 1.20 | 5 | 0.4 | 7.2 | 440 | Eutrophic |
| 38 | Lake Alekseevskoe<br>54°44′ N<br>41°00′ E | 0.03 | 1 | 0.4 | 6.7 | 440 | Eutrophic |
| 39 | Lake Nefedovo<br>54°44′ N<br>40°58′ E | 0.03 | 1 | 0.4 | 6.9 | 70 | Eutrophic |
| 40 | Lake Beloe<br>54°43′ N<br>40°42′ E | 0.01 | 1 | 0.3 | 6.9 | 380 | Eutrophic |
| 41 | Lake Glushitsy<br>54°44′ N<br>40°59′ E | – | 1 | 0.3 | 6.6 | – | Eutrophic |
| 42 | Lake Aleshina Luka<br>54°43′ N<br>40°52′ E | – | 1.2 | 0.5 | 7 | 540 | Eutrophic |
| 43 | Lake Sovkhozny vodopoi<br>54°43′ N<br>40°52′ E | – | 0.7 | 0.6 | 7.5 | – | Eutrophic |
| 44 | Lake Shagara<br>55°14′ N<br>40°06′ E | 4.24 | 0.5 | – | 6.9 | – | – |

* According to : (*Zakonomernosti gidrobiologicheskogo*..., 2004); ** in the flooded plain of the Volga River within the Ivankovo Reservoir; "–" means the data are absent.




The map of European Russia with locations of findings of *K. bostoniensis*. Digits on the map correspond to numbers of the reservoirs in Table 1.

pH 5.6–8.4. Only large Lake Ladoga (>18 thousand km$^2$) of glacial-tectonic origin enters the European system of Great Lakes and is the closing one in the system of large lakes (Onega, Saima, and Ilmen) with the total catchment area of 258 thousand km$^2$ (*Ladozhskoe ozero* ..., 2002). It is a deep mesotrophic waterbody with slow water exchange (the water exchange coefficient equals to 0.08 year$^{-1}$), weakly mineralized (63.7 mg/L) oligohumic water and pH ranging from neutral to weakly alkaline. The rotifer was recorded in the littoral zone of the lake and its tributaries, Vuoksa and Tuloksa rivers (Aleshina et al., 2014).

*K. bostoniensis* was documented in reservoirs not long ago, in 2005–2012 (Lazareva and Zhdanova, 2014). Large reservoirs belong to the Upper Volga basin and are characterized by humic water with pH close to neutral values (Mineeva, 2009; Lazareva et al., 2013). The most upstream Ivankovo and Uglich reservoirs are of valley type shallow (the depth along the river channel is 5–8 m; average length 3.4–5 m); they are characterized by high water exchange (the water exchange coefficient is 10.1–10.6 year$^{-1}$) (Mineeva, 2009). The Sheksna Reservoir is 5–6 times larger and is characterized by s slow water exchange (the water exchange coefficient is 0.96 year$^{-1}$) and complex configuration of the water area where comparatively deep parts along the channel (up to 17 m) neighbor with vast shallows (the average depth 3.9 m) (*Sovremennoe sostoyanie*..., 2002; Lazareva et al., 2013). The reservoir is a separate northern branch of the Volga River system and is a part of the Volga-Baltic waterway. The reservoir includes vast Lake Beloe (1284 km$^2$) and two reaches of the river: northern Kovzhinsky and southern Sheksna reaches. The Sheksna and Uglich reservoirs are mesotrophic, and the Ivankovo Reservoir is eutrophic one (Mineeva, 2009). In all three reservoirs, the rotifer was detected in the deep-water parts: flooded channels of the Volga and Sheksna rivers, flooded lowland Lake Vidogoshch.

The small (1.3 km$^2$) Okhta Reservoir is located on the Okhta River (a right tributary of the Neva River) within the precincts of St. Petersburg. It is a shallow polyhumic waterbody with neutral values of water pH; it is strongly polluted because is used for water supply of industrial enterprises and as a receiving water body.

In addition to lakes and reservoirs, *K. bostoniensis* was recorded in the Kerzhenets River (a left tributary of the Volga River within the Cheboksary Reservoir) with high water color and in brooks which outflow from lakes Tonkoe and Krivoe (the Andoma River basin).

**Species abundance.** The rotifer was usually found in the summer season (June–August). Thus, in Lake Shagara, zooplankton was collected monthly from May through September, but *K. bostoniensis* was recorded only in July and August (Table 2). The density of rotifers varied considerably in different waterbodies (Table 2). The maximum density (>100 thousand ind./$m^3$) was recorded, mainly, in the central part of meso- or eutrophic small shallow watershed and floodplain lakes and in deep karst lakes. In floodplain Lopata and Nefedovo lakes (the floodplain of the Oka and Pra rivers) the contribution of *K. bostoniensis* to the total density of zooplankton (Rotifera, Cladocera, Copepoda) constituted up to 50% and its contribution to the abundance of rotifers was up to 74%. The species formed the major portion of the abundance (60–80%) of rotifers in the hypolimnion of karst stratified Lake Elovoe. On the whole, *K. bostoniensis* was a component of the dominant species (>10% of the total density of zooplankton) in 15 different waterbodies (Table 2).

*K. bostoniensis* frequently (56%) co-occurred with *K. longispina* in the surveyed waterbodies (Table 2). In Lake Elovoe the density of *K. bostoniensis* was 50 times greater than that of *K. longispina* (Table 2). The maximum densities of the both species were recorded in the hypolimnion of the lake at water temperature 5–7°C (Bayanov, 2014). In four other lakes (Komsomolskoe, Kupetskoe, Trestino, and Vidogoshch) *K. bostoniensis* prevailed in abundance over *K. longispina*. Only *K. bostoniensis* was documented in all floodplain waterbodies of the Oka River, some watershed waterbodies in Leningrad (Maloe Lugovoe and Bolshoe Morozovskoe), Vologda (Ekozero and Tonkoe), Novgorod (Maloe Yaichko) oblasts and in Okhta Reservoir. *K. longispina* prevailed over *K. bostoniensis* or the abundance of the both species were similar in >40% of the surveyed waterbodies.

Thus, *K. bostoniensis* was abundant and prevailed over aboriginal *K. longispina* in small shallow waterbodies in floodplains of rivers and watersheds of river basins.

## DISCUSSION

In waterbodies of Western Europe (France, Finland, and Netherlands) the rotifer more often inhabits humic (>100 mg Pt/L) or weakly polluted lakes and rivers in a wide range (5.2–6.5) of water pH values (Leentvaar, 1961; Eloranta, 1988; Balvay, 1994; Jarvinen et al., 1995). In waterbodies of Sweden influenced by effluents of the pulp and paper industry, *K. bostoniensis* is distributed in a wide range of environmental conditions (pH 4.8–8.5, oxygen content, 2.4–12.0 mg/L, color of water, 20–150 mg Pt/L) (Arnemo et al., 1968). In the territory of European Russia the rotifer was also found in waterbodies which differed considerably in morphometry, abiotic and biotic environmental conditions (Table 1). On the whole, in Western Europe *K. bostoniensis* dwells in small (<3 $km^2$) and large (>200 $km^2$), shallow (<1 m) and deep (>20 m) waterbodies with the trophy range from oligo- to eutrophy (Leentvaar, 1961; Arnemo et al., 1968; Eloranta, 1988; Balvay, 1994; Jarvinen et al., 1995). In waterbodies of European Russia the species dwells in the same range of environmental conditions. Habitation in different waterbodies indicates high ecological plasticity of the species and the possibility of its further dispersal.

In the waterbodies surveyed, the rotifer was found along the entire water column. In deep stratified Kshchara (Zhdanova and Dobrynin, 2011), Elovoe (Bayanov, 2014), and Pridorozhnoe (Ivanova and Telesh, 2004) lakes the rotifer preferred meta- and hypolimnion where the density of the population was 2–100 times higher than in the epilimnion. This indicates low dissolved oxygen requirements of *K. bostoniensis*. The rotifer can exist at its very low concentrations. Thus, in Lake Kshchara the abundance of *K. bostoniensis* in the hypolimnion at the depth of 8–12 m was 170–750 thousand ind./$m^3$ at the oxygen concentration <2.5 mg/L or about 20% saturation (Zhdanova and Dobrynin, 2011). The maximum concentration of rotifers (>4 mln/$m^3$) was recorded at the depth of 7 m in the layer of the temperature jump ($O_2$ ~ 6 mg/L, >50% saturation). In October 2000, the abundance of *K. bostoniensis* was 490 thousand ind./$m^3$ in the epilimnion of Lake Pridorozhnoe and reached 2 million ind./$m^3$ in the hypolimnion (Ivanova and Telesh, 2004). But the rotifer was absent in the anaerobic ($O_2$ < 1 mg/L) hypolimnion of Lake Vidogoshch; it inhabited only its epilimnion (the layer 0–4 m) (Lazareva and Zhdanova, 2014). The published data (Campbell, 1941) indicate that in stratified waterbodies *K. bostoniensis* dwells in the hypolimnion at the beginning of summer but by the end of summer it moves up to the epilimnion as anoxic conditions develop.

The rotifer is tolerant to temperature regime. In the surveyed lakes it reaches high abundance at temperature 5–12°C in lower layers of the water column, and at 15–20°C in shallow waterbodies. In lakes of Scandinavia the high abundance of *K. bostoniensis* is also recorded in a wide range of water temperatures (9–15°C); it occurs from the end of April through November; the maximum portion of egg-bearing females was recorded in August (Arnemo et al., 1968). In the territory of Russian Federation (Shagara and Elovoe lakes), the highest densities of rotifers were recorded in July. The maximum abundance of *K. bostoniensis* in waterbodies of Russia reaches 150–1230 thousand ind./$m^3$ (Table 2) that is comparable with the maximum abundance documented in the native habitats of North America (1200 thousand ind./$m^3$) (Roff and Kwiatkowski, 1977; Blouin et al., 1984; Havens, 1991; Scruton et al., 1991; Biêdzki and Ellison, 2003; Barbiero and Warren, 2011), Brazil (190 thousand ind./$m^3$) (Landa et al., 2002; Bezerra-Neto et al., 2004; Ferraz

**Table 2.** Abundance (thous. ind./m$^3$) of *Kellicottia bostoniensis* and *K. longispina* in the surveyed waterbodies

| Waterbody | Date of sampling | *K. bostoniensis* | | *K. longispina* | |
|---|---|---|---|---|---|
| | | central part | littoral | central part | littoral |
| Brook from Lake Tonkoe | 08.2011 | 1.0 (3) | | 1 (3) | |
| Brook from Lake Krivoe | 08.2011 | 12.0 (36) | | 0.5 (2) | |
| Lake Kupetskoe | 08.2010 | 154.3 (48) | 188.2 | 3.7 (1) | |
| Lake Ekozero | 08.2011 | – | 123.4 (43) | 0.0 | 0.0 |
| Lake Tonkoe | 08.2012 | 5.3 (7) | 14.6 | 0.0 | 0.0 |
| Lake Lainozero | 08.2010 | 1.1 (1) | 4.0 | 0.8 (<1) | |
| Sheksna Reservoir opposite the Kema River mouth | 08.2005 | 0.3 (<1) | 0 | 0 | 1.6–3.4 (2–6) |
| Lake Maloe Lugovoe* | 07.2010 | 180.0 (43) | – | 0.0 | – |
| Lake Bolshoe Morozovskoe* | 04.2010 | 30.7 (7) | – | 0.0 | – |
| Lake Simagino* | 07.2012 | – | – | – | – |
| Lake Chernyavskoe* | 07.2012 | 6.5 | – | – | – |
| Lake Okhotnichie* | 07.2010 | 11.5 (16) | – | 2.3 (3) | – |
| Okhta Reservoir | 08.2013 | 59.0 (6) | – | 0.0 | – |
| Lake Ladoga | | | | | |
| Shchuchiy Bay | 07.2010 | – | 0.4 (<1) | – | 80.0 (<1) |
| Volkhov Bay | 07.2011 | – | 34 (<1) | – | 0.0 |
| Petrokrepost Bay | 07.2010 | – | 0.5 (<1) | – | 8 (10) |
| Transition zone | 07.2010 | 0.1 (<1) | – | 1 (1) | – |
| Lake Elovoe | 08.2011 | 365.3 (83) | – | 0.7 (<1) | – |
| Kerzhenets River | 07.2013 | 0.01 (<1) | | 0.0 | |
| Lake Svyatoe Dedovskoe | 08.2011 | 0.3 (<1) | – | 4.3 (13) | – |
| Lake Bolshoe | 06.2010 | 0.2 (<1) | – | 11.8 (15) | – |
| Lake Komsomolskoe | 06.2010 | 26.4 (56) | – | 0.3 (<1) | – |
| Lake Rodionovo | 07.2010 | 1.7 (3) | – | 37.8 (68) | – |
| Lake Roy | 07.2010 | 1.8 (1) | – | 27.9 (23) | – |
| Lake Svyato | 07.2011<br>07.2013 | 4.3 (5)<br>42.8 (46) | –<br>– | 2.7 (3)<br>4.4 (5) | –<br>– |
| Lake Charskoe | 07.2014 | 18.0 (19) | – | 34.1 (37) | – |
| Lake Maloe Yaichko | 07.2007 | 11.1 (14) | 0.1 (<1) | 0.0 | 0.0 |
| Lake Bolshoe Yaichko | 07.2007 | 0.5 (<1) | 0.4 (<1) | 16.8 (1) | 12.4 (4) |
| Lake Glukhoe | 07.2007 | 0.2 (1) | – | 4 (19) | – |
| Lake Bragino | 07.2007 | 1.6 (<1) | 0.1 (<1) | 37.5 (20) | 19 (4) |
| Lake Lopata | 07.2007 | 1236.8 (68) | 5.8 (2) | 0.0 | 0.0 |
| Lake Alekseevskoe | 07.2007 | 21.0 (4) | 56.4 (18) | 0.0 | 0.0 |
| Lake Glushitsy | 07.2007 | 0.1 (<1) | – | 0.0 | 0.0 |
| Lake Nefedovo | 07.2007 | 0.8 (<1) | 603.0 (16) | 0.0 | 0.0 |
| Lake Beloe | 07.2007 | 5.0 (1) | 144.0 (31) | 0.0 | 0.0 |
| Lake Aleshina Luka | 07.2007 | 0.7 (<1) | 8.0 (2) | 0.0 | 0.0 |
| Lake Sovkhozny vodopoi | 07.2007 | 0.1 (<1) | 0.0 | 0.0 | 0.0 |
| Lake Shagara | 07.2010<br>08.2010 | 11.6 (<4)<br>0.5 (<1) | – | – | – |
| Uglich Reservoir opposite the Dubna River mouth | 08.2012 | 0.1 (<1) | – | 1.3 | – |
| Ivankovo Reservoir opposite the Shosha River mouth | 08.2012 | 0.4 (<1) | – | 0.2 (<1) | – |
| Lake Vidogoshch | 08.2005<br>08.2012 | 0.5–3.3 (<2) | – | 0.5–21.9 (<1–8) | – |
| Lake Trestino | 08.2008 | 14.9 (34) | – | 1.1 (3) | – |

The portion (%) in the total abundance of zooplankton is given in brackets, "–" the data are absent, * the data obtained by E.S. Makartseva.

et al., 2009; Peixoto et al., 2010) and Scandinavia (560–3000 thousand ind./m$^3$) (Arnemo et al., 1968; Eloranta, 1988).

The rotifer inhabits waterbodies with different degree of humification and forms numerous populations in oligohumic and polyhumic waterbodies. In Russia, *K. bostoniensis* occurs in a wider range of color of water (30–680 grad according to Pt–Co scale ) then it has been reported for other European countries (20–180 mg Pt/L) (Arnemo et al., 1968; Eloranta, 1988; Balvay, 1994).

Earlier publications (Arnemo et al., 1968; Balvay, 1994) report the co-existence of *K. bostoniensis* and *K. longispina*. In the surveyed waterbodies of Russian Federation, *K. bostoniensis* occurred separately from the aboriginal species or coexisted with it. The coexistence of the two representatives of the genus was typical for deep-water lakes and parts of reservoirs (the depth more than 5 m), *K. bostonieinsis* was often recorded only in shallow lakes. In reservoirs of the Upper Volga only *K. longispina* was found (Lazareva and Zhdanova, 2014).

The expansion of *K. bostoniensis* is an example of bioinvasions into fresh waters as a result of human activity (Dumont, 1983; Pejler, 1998). The appearance of the species in Europe is caused by its transfer via ballast waters of ships (Arnemo et al., 1968; Gray et al., 2007). Further dispersal of the species occurs, probably, downstream the rivers and/or via migratory waterfowl. Many of the surveyed waterbodies do not have any visible outlet and it can be suggested that resting eggs of *K. bostoniensis* were translocated to these habitats namely by birds. Air transport of dry resting eggs of hydrobionts by dust-raising winds from the coast of waterbodies is common for arid regions (Aladin and Plotnikov, 2004). But the dispersal of rotifers by wind is hardly possible in the zone of excessive moistening because the coasts remains damp and rotifers and their eggs remain buried in wet soil among littoral vegetation even if the water level in waterbodies drops. In the course of experimental studies using traps installed on Antarctic islands and in the United States it has been established that only few species of rotifers (only *Keratella cochlearis* Gosse from Brachionidae) can be transported to long distances by wind and rain (Janiec, 1996; Jenkins and Underwood, 1998).

The dispersal of rotifers by other migratory animals (zoochory) has been studied poorly but there are many arguments against the possibility of the transport of rotifers at viable developmental stages in the digestive tract of birds (Segers and De Smet, 2008). Nevertheless, birds as well as amphibians and insects can transport resting eggs and live rotifers on the body surface (Maguire, 1959, 1963; Schlichting and Milliger, 1969). During spring and autumn migrations the flying speed of ducks and geese is >80 km/h and they cover 500–600 km for one passage (Yakobi, 1966). According to other data the flying speed of mallard during migration is 40–80 km/day (*Migratsii ptits*..., 1997) and the speed of northern pintail is 90–100 km/day (*Ptitsy Sovetskogo Soyuza*..., 1952). Many species of river and sea ducks perform molt migrations in summer (*Monitoring i sokhranenie*..., 2010), young mallards usually undertake autumn migrations in non-migratory direction at a distance of more than 100 km (*Migratsii ptits*..., 1997). Most river ducks perform short-distance feeding flights from a waterbody to a waterbody (*Ptitsy Sovetskogo Soyuza* ..., 1952). In such a way birds can transport, at least, resting eggs on the body surface at long distances during their migrations. During short-distance migrations from waterbody to waterbody birds can also transport live rotifers. This fact can explain frequent findings of *Kellicottia bostoniensis* in groups of closely located lakes (lakes of the Karelian Isthmus, Valdai Hills, Andoma Upland and floodplains of the Pra and Oka rivers).

In the central and northern parts of European Russia mallard (*Anas platyrhynchos* L.), northern pintail *A. acuta* (L.), common teal (*A. crecca* L.), and garganey (*A. querquedula* L.) are common in nesting places. Wintering grounds of these ducks cover all water areas in West Europe from the central Baltic Sea region to the Atlantic Ocean; birds which live in the north of Western Siberia also migrate to wintering grounds in Western Europe (*Monitoring i sokhranenie*..., 2010). The estimated total abundance of ducks flying along the White Sea-Baltic Canal was several millions of specimens (Delany and Scott, 2002). Bird ringing makes it possible to establish that water birds migrating long distances use large lakes and rivers as landmarks of their general direction and to make stops for rest (Steinbacher, 1951; Malchevsky and Pukinsky, 1983). Birds fly from wintering grounds in Western Europe through the Baltic Sea to the east, north-east and south-east to the upper reaches of rivers flowing westward. Thus, the migration routes of transient sea species (e.g. the long-tailed duck *Clangula hyemalis* (L. 1758)) pass from the Gulf of Finland through the Karelian Isthmus and Neva River to Lake Ladoga and farther north-east to the coast of the Barents Sea; many flocks of these ducks stop to rest and feed on lakes of the Karelian Isthmus (Mal'chevskii and Pukinskii, 1983). To the east of this migration route the group of lakes is located in the Andoma Upland watershed (Table 1) at the distance of <200 km from Lake Ladoga and about 50 km from Lake Onega, i.e., 1–2 days of flight of ducks. In the direction to southeast large groups of lakes are located at the distance of 700–1000 km (two large migration passages) in the Valdai Hills (Verkhnevolzhskie lakes), in upper reaches of the Pra River, a left tributary of the Oka River (the system of Klepikovskie lakes in the north of Meshchera Lowlands) and Orshinskie lakes in the upper reaches of the Soz River, a left tributary of the Volga River which can be used for orientation and rest of birds. Out of the abovementioned four groups of lakes we surveyed three groups, only Orshinskie lakes were not studied. The rotifer *Kellicottia bostoniensis* was detected in all three groups and/or in neighboring small waterbodies of their basins.

We suppose that the rotifer *K. bostoniensis* is transported from Western Europe to waterbodies on the eastern coast of the Baltic Sea and farther eastward to waterbodies of the Volga-Baltic watershed against the current of rivers that drain into the basin by birds during their migratory flights and post-nesting migrations. To the east along with this vector of invasion, live specimens of *K. bostoniensis* and resting eggs can be probably dispersed with water of rivers in the Volga River basin flowing south and east. The fact that the species has been already recorded in waterbodies of the Middle Volga basin (right-bank waterbodies to 43° E and left-bank waterbodies to 45° E, Table 1) indicates the high speed of its dispersion to the east. In the Volga River the rotifer was not found to the south of 56° N and to the east of 38° E (the upper part of the Uglich Reservoir) (Lazareva and Zhdanova, 2014). Its findings in small lakes and rivers along the both banks of the Volga River farther southeast indicate involvement of birds in the species dispersion. To date, the distribution of the rotifer in Russia is limited by the forest zone. But in Central and South America the rotifer inhabits arid and tropical regions (Landa et al., 2002; De Paggi, 2002; Bezerra-Neto et al., 2004; Figueroa-Sanchez et al., 2014). In the Volga basin, the boundary of the forest zone, will not, probably, impede the rotifer dispersal southward.

First findings of *K. bostoniensis* in Russia became more frequent in the first decade of the 21st century. Most waterbodies were surveyed for the first time and it is not known how long the rotifer has inhabited them. But the studies of some waterbodies have been conducted for many decades (Lake Ladoga, Lake Okhtinskoe, Ivankovo, Uglich, and Sheksna reservoirs) (*Ladozhskoe ozero*…, 2000; *Ekologicheskie problemy*…, 2001; *Sovremennoe sostoyanie*…, 2002; Lazareva et al., 2013) that makes it possible to determine the period of appearance of the invader in plankton. Thus, the rotifer has been recorded in zooplankton samples in the Ivankovo (Lake Vidogoshch) and Sheksna reservoirs since 2005, in the downstream Uglich Reservoir in the Volga cascade since 2012, in Lake Ladoga since 2012, and in the Okhta Reservoir since 2011.

The introduction of *K. bostoniensis* into Lake Ladoga could occur by two ways: from Finnish lakes along the system of the Vuksa River to Shchuchiy Bay and Lake Okhotnichie and to the southern part of Lake Ladoga via ship's ballast waters (Makartseva and Rodionova, 2011). The rotifer, probably, penetrated to the Sheksna Reservoir with water current from the upper reaches of the Kema River; *K. bostoniensis* is numerous in waterbodies of the Andoma Upland (Lainozero, Ekozero, and Kupetskoe lakes) connected with the Kema River (Lobunicheva et al., 2011). The rotifer was introduced into the Ivankovo Reservoir with water of the Volga River or was transported by water birds from the system of the Upper Volga lakes (Lazareva and Zhdanova, 2014). *K. bostoniensis* penetrated into waterbodies of Nizhny Novgorod oblast along the water current of the Oka River from the west and was transported by birds from waterbodies in Vladimir oblast (Bayanov, 2014) where to date the species is numerous and, probably, has appeared quite recently (Zhdanova and Dobrynin, 2011). The dispersal of rotifers in waterbodies of the left-bank Middle Volga is, apparently, caused by their transfer by birds. The basin of the river is not hydrographically connected with the waterbodies where the species was found and is located far from them. The river flows from north to south along the meridian; the nearest habitat of *K. bostoniensis* is in the vicinity of the city of Nizhny Novgorod on the right bank of the Volga River (Cheboksary Reservoir) 70 km to the northwest from the Kerzhenets River mouth.

## CONCLUSIONS

In Russia, the American rotifer *K. bostoniensis* was first recorded in lakes of the Karelian Isthmus in 2000. By 2013 it had been documented in more than 40 water objects of European Russia. The rotifer is widespread and common in forest lakes and rivers of the Baltic Sea basin, Volga-Baltic watershed; in the Volga River basin it has spread southward to 55° N (lakes of the basins of the Oka and Pra rivers) and eastward almost to 45° E (the Kerzhenets River, the Cheboksary Reservoir basin).

The rotifer *K. bostoniensis* was transported by water birds during migratory flights and post-nesting migrations from Western Europe to waterbodies on the eastern coast of the Baltic Sea and farther east to waterbodies of the Volga-Baltic watershed against the currents of rivers which drain into the basin. The role of birds in dispersal of the species is indirectly confirmed by the fact that the rotifer is more frequent in small waterbodies including those located in watersheds and having no visible outlet, in non-navigable rivers and brooks. To the east, along with this vector of invasion live specimens of *K. bostoniensis* and resting eggs are, probably, spread with water of rivers of the Volga basin which flow southward and eastward.

The rotifer inhabits small ($<3$ km$^2$) and large ($>200$ km$^2$), shallow ($<1$ m) and deep ($>20$ m) waterbodies with a trophy range from oligo- to eutrophy. In Russia *K. bostoniensis* occurs in a wide range of color of water (30–680 degrees Pt–Co-scale) compared to waterbodies of Western Europe. The rotifer is tolerant to temperature regime and oxygen concentrations in water. In the hypolimnion of stratified lakes, *K. bostoniensis* reaches high abundance ($>100000$ ind./m$^3$) at a very low concentration of dissolved oxygen (2.5 mg/L or about 20% of saturation) and water temperature of 5–12°C. The ability to live in different waterbodies indicates high ecological plasticity of the species and the possibility of its further dispersal.

In waterbodies of European Russia, *K. bostoniensis* was detected separately from the aboriginal species *K. longispina* as well as together with it. The invader and aboriginal species *K. longispina* coexisted in deep lakes and deep parts of reservoirs (the depth more than 5 m); in shallow lakes only *K. bostoniensis* was found. On the contrary, in most parts of large reservoirs of the Upper Volga only *K. longispina* was recorded.

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