ISSN 1995-0829, Inland Water Biology, 2008, Vol. 1, No. 1, pp. 76–83. © Pleiades Publishing, Ltd., 2008.
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ZOOPLANKTON, ZOOBENTHOS AND ZOOPERIPHYTON

Distribution and Special Traits of Naturalization of New and Rare Zooplankton Species in Waterbodies of the Upper Volga Basin

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Received October 18, 2006

Abstract—More than ten new zooplankton species were registered in reservoirs of the Upper Volga during 2002–2005. Since 2003, the cladoceran *Diaphanosoma orghidani* Negrea, had intensively settled in different biotopes of Ivankovo, Uglich, Rybinsk, and Sheksna reservoirs and is the most abundant (16 000 ind./m^3) in the latter one. The rotifer *Asplanchna henrietta* Langh. was found for the first time in Rybinsk Reservoir in 1985, and by 2004, this species had also occurred in Ivankovo, Uglich reservoirs, Lake Nero, and some small waterbodies of the basin. In Lake Nero its density reaches especially high values (>1 million ind./m^3). Causes, mechanisms, and ecological consequences of the expansion of new zooplankton species are discussed.

DOI: 10.1134/S1995082908010124

INTRODUCTION

The intensity of water fauna species expansion within the Holarctic has increased dramatically in the second half of the 20th century. Damming, navigation, as well as intentional introduction of alien species, promoted this process in the Volga River basin [16, 23]. New wave of southern species' expansion into the Upper Volga which is being linked to long-term climatic trends was noted at the turn of the century [23]. Abundance of a number of zooplankton species is increasing rapidly in the Upper Volga basin waterbodies [10]. The aim of the present study is to reveal the causes, origins, dynamics, and particular features of naturalization as well as some potential consequences of penetration of new species and expansion of rare ones in the region's waterbodies.

MATERIALS AND METHODS

Samples of summer (June–August) zooplankton collected in 2001–2005 in the Rybinsk, Uglich, and Ivankovo water reservoirs of the Volga and in 2000–2004 in Lake Nero (Gorky water reservoir basin) were studied. During the investigation of Sheksna (the Sheksna and Kovzha rivers and Lake Beloe) and Novinkinskoe (Vytegra River) water reservoirs, the samples were collected in the summer of 2001 and 2005. Central parts of the waterbodies, littoral zone, bays, and mouths of the tributaries were studied: >50 stations in the Rybinsk Reservoir, 15 in the Uglich, 11 in Ivankovo, 15 in Sheksna and Novinkinskoe, and 14 in Lake Nero. Plankton was collected totally from the bottom to the surface using two Juday nets with mesh numbers 47 and 70 and from each layer using DK planktobathometer (10 l). Methods of data collection and analysis are described in [10]. Description of surveyed waterbodies is presented in [1, 4, 22].

RESULTS

The following species that have not been noted previously in the Rybinsk Reservoir according to the published lists [8, 22] were found during the 2001–2004 surveys: pelagic crustaceans *Diaphanosoma orghidani* Negrea and *Arctodiaptomus laticeps* Sars*, phytophilous rotifers *Trichocerca mucosa* (Stokes)*, *T. (Diurella) weberi* (Jennings), pelagic rotifer *Synchaeta kitina* Rouss., benthic species *Biapertura intermedia* (Sars), *Diacyclops crassicaudis* (Sars)*, and a small commensal *Brachionus variabilis* Hempel* associated with crustaceans [10].

Large crustaceans *Diaphanosoma orghidani* and *Arctodiaptomus laticeps* are the most important in terms of monitoring.

The main part of the *Diaphanosoma orghidani* natural range is situated to the south of the taiga zone. This species was described in 1982 from Romanian lakes, and previously it was identified as *D. brachyurum* (Lievin) [6]. In Russia it was found by N.M. Korovchinski [6] in the vicinity of Kazan City, in the waterbodies of

* Species found in Volga reservoirs for the first time.

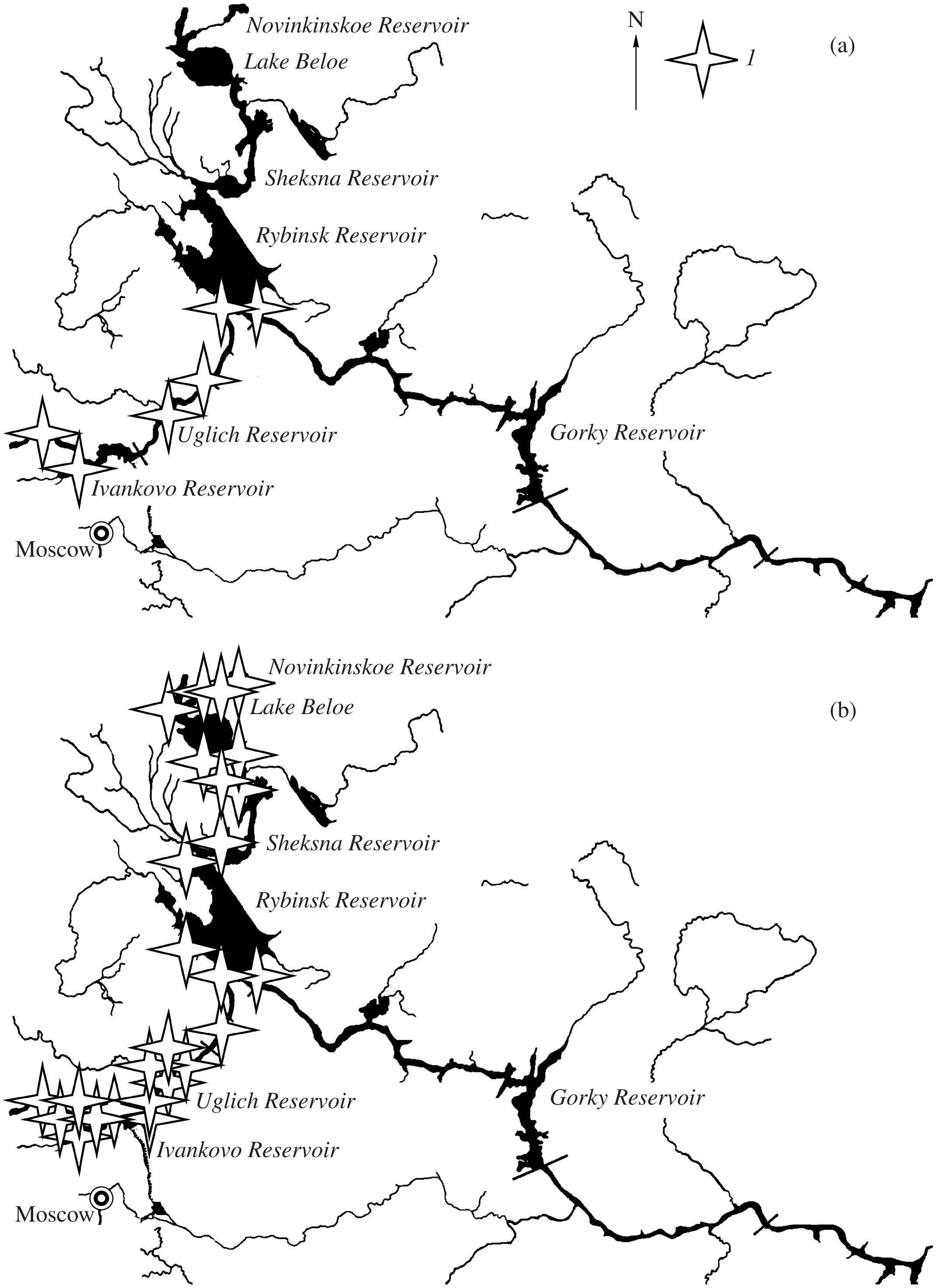

Fig. 1. Findings of *Diaphanosoma orghidani* in the Upper Volga basin in 2003 (a) and in 2005 (b). *1*, species location.

the Volga's delta, Krasnodarskii Krai, and Middle Asia, as well as in the Ivankovo Reservoir (verbal communication of N.M. Korovchinski).

In June of 2003, *D. orghidani* was found at two sampling sites of the southern part of Rybinsk Reservoir, two sampling sites of Ivankovo Reservoir, and two sampling sites of Uglich Reservoir (Fig. 1), its abundance reached <300 ind./m^3 (Table). In August of 2005, the species was found at six sampling sites in the Rybinsk Reservoir with highest abundance (1120 ind./m^3) noted in the Sheksna stretch downstream of City of Cherepovets. In the Ivankovo Reservoir, *D. orghidani* was

Abundance (ind./m^3) and distribution of *Diaphanosoma orghidani* and *Asplanchna henrietta* in June–August of 2001–2005 in the Upper Volga water reservoirs

Waterbody, biotope (depth)	*Diaphanosoma orghidani*		*Asplanchna henrietta*	
	2001–2003	2004–2005	2001–2003	2004–2005
	Rybinsk Reservoir			
Volga reach:				
littoral (3 m)	0	0	20–15000	0
riverbed (8–12 m)	130*	10–61	20–12600	790*
Other riverine reaches, riverbed (8–12 m)	0	12–1120	0	2200*
Main reach:				
river mouth (2–5 m)	0	54*	20–120	4440*
center (5–12 m)	22*	0	3100*	30–2400**
	Uglich and Ivankovo reservoirs			
Riverine parts, riverbed (2–11 m)	13–270	10–5840	110*	54–8980
Lacustrine parts (6–10 m)	4*	25–2860	100*	1587–2290
	Sheksna and Novinkinskoe reservoirs			
Northward of Lake Beloe (5–7 m)	0	230–3630	–	0
Southward of Lake Beloe (3–6 m)	0	400–16000	–	0
Novinkinskoe reservoir (10 m)	–	690*	–	0

Note: "–" lack of data.
* Species abundance in single samples.
** According to E.A. Sokolova.

registered at six sampling sites with maximum abundance (2860–3150 ind./m^3) in Shoshinski Bay and the flooded Volga riverbed from the mouth of the Shosha River to Sverdlovo Settlement. In the Uglich Reservoir the species was also found at six sampling sites with highest abundance (5560–5840 ind./m^3) in parts close to tributaries' (the Nerl' and Medveditsa) mouths.

In July of 2005, *D. orghidani* was found at seven sampling sites in the Sheksna water reservoir (Fig. 1); its maximum abundance was registered to the south from Lake Beloe in the Upper Sheksna part from Topornya Village to the Chaika Settlement (Table). This species was not found in Lake Beloe, Sizmen reach, and in the near-dam part of the reservoir. Apparently, *D. orghidani* penetrated into the Sheksna Reservoir not earlier than in 2002. It was not found in samples taken in this waterbody in June of 2001. Novinkino Reservoir (60°55′ N) is the northernmost site of all known ones where *D. orghidani* was found. It was thought previously [6] that it does not penetrate further north than 56° N.

D. orghidani frequently dwells together with *D. brachyurum*, and the maximum abundance of both species is observed in July–August. Unlike *D. brachyurum* that inhabits the littoral, shallow bays, and near-dam sites of the reservoir, predominantly, *D. orghidani* is most abundant in lotic parts—flooded riverbeds and the mouths of large tributaries. At joint habitation of species, *D. orghidani* abundance makes up from <1 to 16% of their total abundance in the Rybinsk Reservoir, 1–10% in the Uglich Reservoir, 12–80% in the Ivankovo Reservoir, and 70–86% in the Sheksna Reservoir. *D. orghidani* counts among the dominant species of summer zooplankton in the Sheksna Reservoir, forming up to 12% of all crustaceans' abundance and up to 19% of the community's biomass.

In June of 2004, reproducing females of copepod *Arctodiaptomus laticeps* (4–7 ind./m^3) were found in the northern part of the Rybinsk Reservoir near Myaksa Settlement. Most likely this species penetrated from Lake Beloe. Single specimens of *Arctodiaptomus laticeps* were noted in Lake Beloe in 1962 and 1977 [1], however they were not found in the following years [5]. Other reliable findings of this species in Russia are lacking; it is spread in the cold, including mountain, lakes of Northern Europe [2]. *A. laticeps* is larger (body length 1.7–1.8 mm) than *Eudiaptomus gracilis* Sars, common in Upper Volga water reservoirs; *A. laticeps* females carry ~13 eggs/spec.

Rapid expansion of *Asplanchna henrietta* Langh., a rotifer that invaded ~20 years ago, was noted in 2003–2005 in the Upper Volga basin. Comparatively high abundance (2000–8000 ind./m^3) of this relatively large (400–600 μm) spcecies was observed in the Rybinsk Reservoir in 1985 for the first time [8]. *A. henrietta* was found for the second time during summer of 2001 in the littoral of Volga's stretch of the Rybinsk Reservoir, its abundance was up to 15000 ind./m^3 [9]. In 2002–2003,

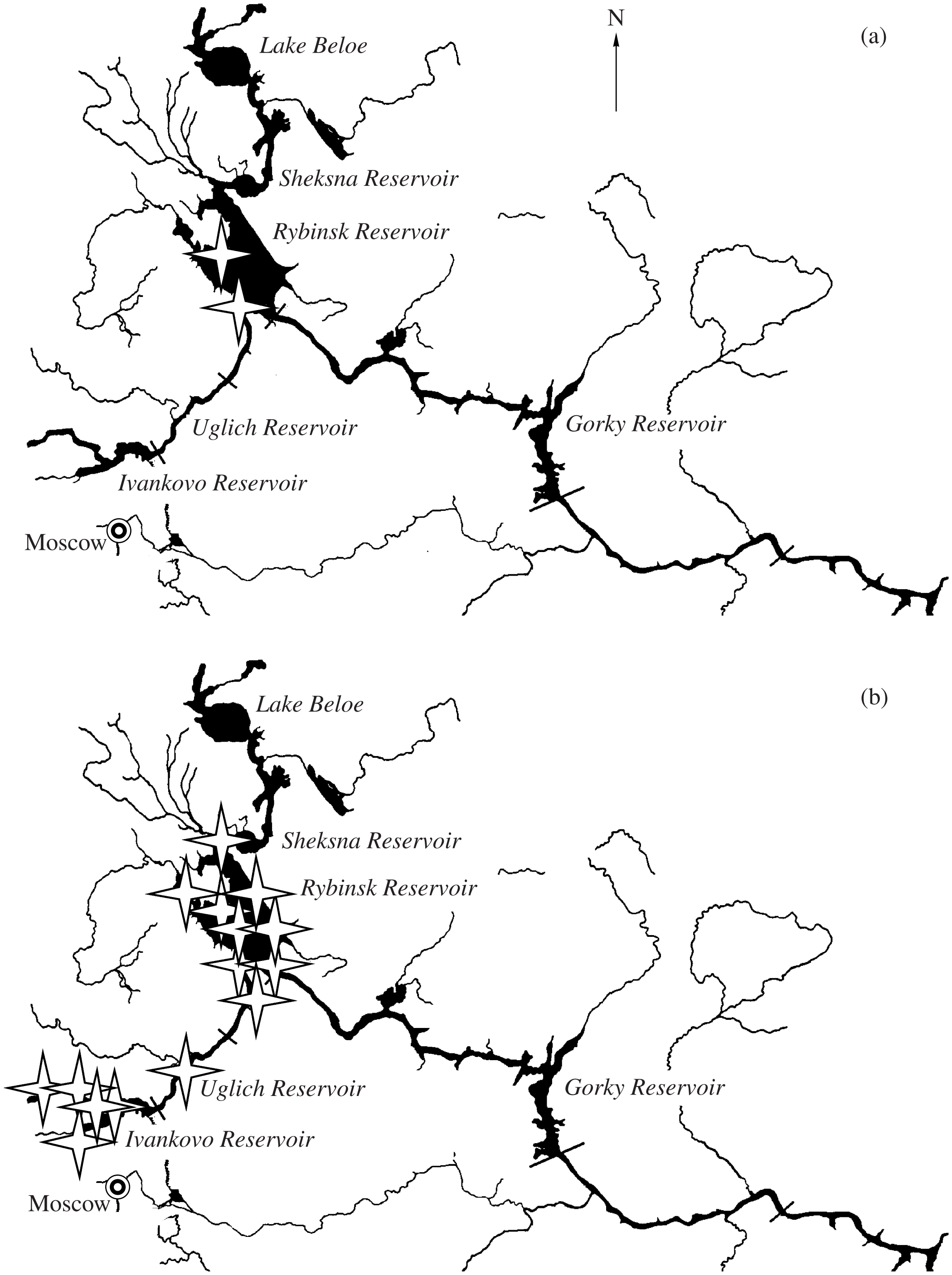

Fig. 2. First findings of *Asplanchna henrietta* (a) and its distribution in the Upper Volga reservoirs by 2005 (b). Legend: see Fig. 1.

A. henrietta was abundant (>10000 ind./m^3) in the center of the Volga stretch of the Rybinsk Reservoir; it was also found in the mouths of west tributaries of the reservoir's Main Reach and in the near-dam part (Table) where it was less abundant (up to 3000 ind./m^3). During the summer of 2004 and 2005, the abundance of *A. henrietta* was up to 2400–4400 ind./m^3; in some locations it formed 14–17% of overall rotifer abundance [10]. By 2005, *A. henrietta* has settled almost in the whole waterbody (Fig. 2). Its maximum abundance was observed in the eastern part of the Main stretch in June–July, and at the same time, the species was noted in 50% of samples from the central part of the reservoir (E.A. Sokolova, *personal communication*).

In 2003, the species was found in the Ivankovo and Uglich reservoirs in small numbers (Table). In 2005, *A. henrietta* was found on five sites in the Ivankovo Reservoir with maximum abundance (2300–3000 ind./m^3) observed on the part from the mouth of the Shosha to Sverdlovo Settlement, however this species was not found in the Uglich Reservoir. It was also not found in the Sheksna Reservoir. *A. henrietta* inhabits the same biotopes as congeneric *A. priodonta*. When dwelling together *A. henrietta* makes up 2–95% of the overall abundance of these species in the Rybinsk Reservoir, 4–80% in the Ivankovo, and ~1% in the Uglich.

In July of 2002, *A. henrietta* was abundant (64000 ind./m^3 or 36% of overall rotifer abundance) in small Lake Hotavets (Rybinsk Reservoir basin). In 2003, *A. henrietta* appeared and settled widely in Lake Nero (Gorky Reservoir basin), in July its abundance exceeded 1 million ind./m^3 with biomass of 4–6 g/m^3 at some sites [12]. In 2003–2005, this species was among the dominating zooplankton species of the lake and formed >60% of rotifer abundance in July and averaged 5–20% over the season (May–October). In 2006, single specimens of *A. henrietta* were observed in Lake Chistoe (Gorky Reservoir basin) and waterbodies of the Rybinsk Reservoir shores (S.M. Smirnova, *personal communication*).

From 2000 to 2004, eight species of rotifers new for Lake Nero were found: *Trichocerca pusilla* (Laut.), *T. mucosa*, *Asplanchna girodi* Guerne, *A. henrietta*, *Polyarthra luminosa* Kut., *Ascomorpha ecaudis* Perty, *Cephalodella forficula* (Ehrenb.), and *C. gibboides* Wulf. [12]. *Asplanchna girodi* and *A. henrietta* were in the majority of studied parts of the lake and were the most abundant rotifer species. Maximum density of *Asplanchna girodi* was up to 60000 ind./m^3, and this species was included in the lake's zooplankton dominant complex almost every year. It formed >10% of rotifer abundance in August–September and 7–18% over the season on average [12]. In July–August of 2001–2005 a small number of *A. girodi* was also found in the littoral of the Rybinsk Reservoir and in the riverine part of the Ivankovo Reservoir. In 2002, *Trichocerca pusilla* was abundant in Lake Nero (25000 ind./m^3), it formed 13% of overall rotifer abundance on average over the season. The remaining new species were found locally and in small numbers.

In the same period new species of crustaceans were found in lake Nero: *Daphnia pulex* Leydig, *Lynceus brachyurus* (O.F. Müll.), *Metacyclops gracilis* (Lill.), *Paracyclops fimbriatus* (Fish.), *Microcyclops varicans* (Sars), and *Diacyclops languidoides* (s. lat). The majority of them were scanty and found in single samples. Only benthic *Paracyclops fimbriatus* was found in the water column almost everywhere; in 2003–2004, its abundance reached up to 35000 ind./m^3 (6–9% of crustacean abundance on average over the season). The majority of species new for the lake are known from Upper Volga reservoirs from the 70's to the 80's of the last century, and some—from the 50's [22]. They penetrated into Lake Nero after colonizing the reservoirs.

DISCUSSION

In the Volga cascade of reservoirs, northern lacustrine species are spreading to the south, while Ponto-Caspian species are spreading to the north [15, 23]. Interchange of fauna between reservoirs and other waterbodies of the basin also facilitates the expansion of species' natural range. The direction in which a species spreads and the source waterbody from which it comes are sometimes hard to determine even for crustaceans. For example, *Diaphanosoma orghidani* may penetrate to the north along the Volga both from its delta and from the Ivankovo Reservoir. In 2005, abundance of *D. orghidani* in the Sheksna Reservoir exceeded that in the Ivankovo Reservoir. This may assume the Sheksna Reservoir as the new source of species' expansion to the south into the Upper Volga as well as to the north to the rivers Vytegra and Northern Dvina, linked with this reservoir by a system of channels.

The majority of rotifers inhabiting the Upper Volga basin are represented by species widely distributed in the Palearctic. They live in a big number of watercourses and waterbodies in the Volga's basin which makes the arguments on sources and vectors of contemporary migrations debatable. Thus, a rotifer *Asplanchna henrietta* may have penetrated into the Upper Volga reservoirs both from the Middle Volga, where it was noted at the end of the 1970s [4], and from the north: from the Northern Dvina delta [7]. The most probable waterbody source of this species' expansion is Kuybyshev Reservoir, where small numbers of it were found regularly from the 1960s [21]. Intensive expansion of *A. henrietta* not only into new biotopes in Volga's reservoirs but also beyond them, into neighboring waterbodies, is observed.

Southern rotifer *K. tropica* (Apstein) is spreading to the north, while until the end of 1970s, it was found only in the Lower Volga [4]. In 1989, it was found in the Rybinsk Reservoir, and its abundance reached 26000 ind./m^3, close to the City of Cherepovets [19]. This species was not found in the samples later (2005).

Caspian species are of major interest among species spreading up the Volga. Until damming only benthic crustaceans from the Caspian Sea penetrated through Upper Volga, and planktic species *Heterocope caspia* Sars did not go further north (upstream) of Saratov [15]. To 1965, this species penetrated into the Middle Volga and settled in the Kuybyshev Reservoir [15, 21]. In the beginning of 1970s, *Calanipeda aquaedulcis* Kritsch. and *Cornigerius maeoticus* (Pengo) [15] invaded the Volgograd Reservoir. *Calanipeda aquaedulcis* has been registered in the Saratov Reservoir since 1982. In 1994–1996 *Cornigerius maeoticus* has invaded the Saratov Reservoir and moved up to the north to the Kuybyshev Reservoir [3, 20, 21]. In 2002–2005, a new Caspian invader, *Cercopagis pengoi* (Ostroumov), was abundant in the lower part of the Volgograd Reservoir [13]; single specimens were found further to the north, in the Saratov Reservoir and the near-dam part of the Kuybyshev Reservoir [18].

Apart from the expansion of the natural ranges, the increase of abundance of some Caspian species in Volga's reservoirs is also noted. Thus, the abundance of *Heterocope caspia* in the Saratov Reservoir has exhibited 10-fold growth (up to 200–300 ind./m^3 on average over the season) to 2002 compared to that of the 1970s [20]. In 2001, this species was the most abundant one (890 ind./m^3) among crustaceans in the more southern Volgograd Reservoir [14]. Maximum abundance of *Cornigerius maeoticus* in the Kuybyshev Reservoir reaches up to 1000–2000 ind./m^3 [3]. These species were not found in the Upper Volga waterbodies to date. However the increase of their abundance in the Middle Volga supposes high probability of such findings in the near future.

The flow of northern crustacean species southward, downstream the Volga, formed immediately after the Rybinsk reservoir was impounded at the end of the 1940s. Towards the beginning of the 1970s, six northern lake species *Daphnia cristata* Sars, *Bosmina longispina* Leydig, *B. coregoni* Baird, *Bythotrephes longimanus* Leydig, *Cyclops kolensis* Lill., and *Eudiaptomus gracilis* from Lake Beloe naturalized in the Saratov and Volgograd reservoirs [15]. Some of them (*Bosmina longispina* and *Cyclops kolensis*) are still among the most abundant zooplankton species of the Lower Volga [13, 14, 18, 20].

In the mid-1970s F.D. Mordukhai-Boltovskoi and N.A. Dzyuban [15] made predictions that Saratov reservoir will be the southernmost boundary for distribution of northern lacustrine crustaceans (*Heterocope appendiculata* Sars, *Limnosida frontosa* Sars, *Bosmina coregoni kessleri* (Uljanin), and *B. crassicornis* P.E. Müller). In 1996–2005, *Heterocope appendiculata* was the most abundant species out of this group [18]; single specimens of *Limnosida frontosa* were found every year, *Bosmina coregoni kessleri* and *B. crassicornis*, locally and in certain years [20]. These species are found in Volgograd Reservoir only occasionally and in small numbers.

Creation of a cascade of lacustrine type reservoirs served as the main reason for spreading of northern stenolimnophilic species into the Lower Volga and of the Ponto-Caspian species northwards [15]. In the Middle and Lower Volga reservoirs, invasive species usually occur in the pelagial zone beyond vegetation and river estuaries [18, 20]. However, new species of zooplankton in the Upper Volga waterbodies, especially those of southern origin, initially find shelter in the littoral zone, bays, and tributaries' mouths predominantly. From here they spread into the open part of the waterbodies if conditions are favorable. Thus, in the first three years after invasion (2003–2005) into the Rybinsk Reservoir, *Diaphanosoma orghidani* was found only in the river reaches (Volga and Sheksna) and in the mouths of tributaries (the Sit, Sebla, and Yukhot). A similar situation was observed in other reservoirs of the Upper Volga basin.

A rotifer *Asplanchna henrietta* was observed occasionally in the littoral zone of the Rybinsk Reservoir for almost 20 years (1985–2003) and probably from here it has penetrated into the neighboring small shallow waterbodies. In 2004–2005, this species has rapidly occupied whole reservoir's area and now it is among the dominant species of summer zooplankton on some sites (>10% of overall rotifer abundance). This species must have got into the Gorky Reservoir with water flow, but it has not been found there until now. However, the fact that *A. henrietta* was abundant in Lake Nero from 2003 [12], and that it was found in Lake Chistoe in 2006 gives an indirect proof that it is widely distributed in the Gorky Reservoir to which basin both of these waterbodies belong.

Rapid distribution on the waterbodies' area and high abundance immediately after invasion is characteristic of some species (*Diaphanosoma orghidani*). Other species (*A. henrietta*) are characterized by a long period of naturalization with subsequent rapid expansion within the reservoir and close waterbodies. A particular feature of these species' spreading into reservoirs and lakes of the Upper Volga basin noted during the course of studies was their higher abundance compared with that of waterbodies from which they have probably originated.

It is thought [15] that southern plankton crustaceans spread upstream Volga passively with ships' ballast waters and in fish intestines. Such accidental introduction is probably the main way of new species' expansion. Local relatively abundant populations residing mainly in the littoral zone, bays, and mouths of tributaries are formed later at favorable climatic conditions. From there, new species distribute within the whole reservoir and penetrate into other waterbodies of the cascade.

As a rule, invaders displace congeneric taxa from the zooplankton dominant complex. Thus, in the 1990s *Polyarthra major* Bruck. has almost completely displaced *P. vulgaris* Carlin [10, 11] in the Rybinsk Reservoir and *Eurytemora affinis* Poppe replaced *E. velox* (Lill.) [21] in the Kuybyshev Reservoir.

Biology of *Diaphanosoma orghidani* is not studied yet [6]. Observations on spatial distribution and life cycle of this species in the Upper Volga reservoirs indicate some biotopic dissociation with congener *D. brachyurum*, though seasonal abundance peaks of these species concur. This gives hope that competitive relations of these species would be local. The probability of prolonged coexistence of these species in the same waterbody with high abundances in both of them is high.

The rotifer *Asplanchna henrietta* is close to *A. priodonta* Gosse, mass species in the Upper Volga waterbodies, in terms of size and feeding spectrum; both of them inhabit the same biotopes and are frequently found together [9]. The beginning of mass reproduction of *A. henrietta* (June) falls on maximum abundance of *A. priodonta*. Fecundity of asplanchnas is maximal in the beginning of reproduction, and pedogenesis is characteristic of all species to some extent [7, 9]. Therefore, different scenarios of competitive interactions between them are possible. Three results of interspecific competition are most likely: the decrease of June maximum of *A. priodonta* abundance, and decrease of its "peak" abundance, especially in autumn and complete displacement of one of the species in certain biotopes.

Relations of three asplanchna species were observed in Lake Nero over three years (2003–2005). From May to October they have replaced each other in the dominant complex in the following order: *A. priodonta* ⟶ *A. henrietta* ⟷ *A. girodi* ⟶ *A. priodonta*. After *A. henrietta* and *A. girodi* have penetrated into the lake, relative abundance of *A. priodonta* averaged over the season decreased from 24–36% in 1987–1989 to 9–15% in 2003–2005; its "peak" abundance decreased several times, although full displacement of *A. priodonta* by congeneric species was not observed [12].

With reference to the Rybinsk Reservoir, it was shown that most evident transformations of zooplankton structure happen during the shift of hydrologic phases, especially in the end of the low water period [11]. In the contemporary low water period which started in 1996, an increase of abundance of a few species (>10), many of which were observed in the 1970s–1980s for the first time [10], was noted. Some of them, *Synchaeta tremula* (O.F. Müll.), *Asplanchna girodi*, and *A. henrietta*, for example, became abundant in the reservoirs and lakes of the Upper Volga in 2–3 years, i.e., simultaneously on a succession scale. This confirms the leading role of regional edaphic, particularly climatic factors for new and rare plankton forms' dynamics.

In the 1980s–90s, expansion of *Dreissena polymorpha* (Pallas) and *D. bugensis* (Andrusov) mollusks into the Rybinsk Reservoir was noted [17, 22], and planktophagous fish—kilka *Clupeonella cultriventris* (Nordmann)—invaded the Rybinsk Reservoir in late the 1990s [22]. A 1.5–2-fold decrease of rotifers-microdetritophages registered from a 1991 to 1995 occurrence of their dense aggregations in the reservoir has exhibited a 4-fold decrease [11]. In 2003–2004, this tendency remained, and patches of high (>150000 ind./m^3) abundance were encountered twice rarely compared with the 1980s [10], which may probably be the result of competition between rotifers and dreissena over seston resources. Changes in the structure of a reservoir's pelagial trophic web provoked by these invaders are among the factors promoting the naturalization of new zooplankton species. In this situation new zooplankton species are successfully competing with forms that settled in the waterbodies immediately after their creation. Expansion of new species leads to an increase of species richness of the waterbody and changes in the zooplankton community structure. In the case of large zooplankton species, expansion and/or such of key species, pelagial trophic web structure, and nutritive base of plankton-eating fish are likely to change. The most profound transformations of trophic structure of the community may be caused by the cascade effects appearing due to expansion of species not belonging to zooplankton, but directly interfering with the community "from above" (kilka) and "from below" (dreissena). However, in order to solve these problems, further studies must be performed.

CONCLUSIONS

In the period from 2000 to 2005, over 10 new species of zooplankton have penetrated into the Upper Volga basin waterbodies, and an increase of occurrence and abundance of a number of species that invaded earlier is noted. Intensively spreading *Diaphanosoma orghidani* and *Asplanchna henrietta*, as well as *Arctodiaptomus laticeps*, which is likely to spread in the region's reservoirs, are of major interest as the objects of monitoring. The main reasons of expansion of southern lake species northwards and northern southwards in the Upper Volga basin are still hydroengineering and navigation. Migrations of species within the reservoirs' cascade and into other waterbodies of the basin become more intensive at favorable climatic conditions. The latter are more frequent in the low water period of the hydrologic cycle. The source of expansion of most of rotifer and crustacean species is hard to determine. It is possible that new species invade simultaneously from several sources. Naturalization of new species involves a few phases: (1) single findings of the species in single biotopes as a consequence of accidental introduction; (2) formation of local, sometimes abundant, aggregations in the littoral zone, bays, mouths of the tributaries, and river stretches; (3) further increase of species' abundance, expansion into the open part of the reservoir; and (4) competitive interactions of the new species with congeneric aboriginal species that result in the local, rarely—complete over all of the reservoir—displacement of the latter from zooplankton dominant complex.

ACKNOWLEDGMENTS

The author is grateful to S.M. Smirnova for help with processing the zooplankton samples from Ivankovo and Uglich reservoirs.

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