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Microcrustacean (Cladocera, Copepoda) source-sink dynamics in a lowland river ecosystem with a dam reservoir

by

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Abstract

Dispersal of crustacean zooplankton from a reservoir in a lowland river was observed over a relatively long distance. Zooplankton samples were collected by a unique technique from "the same water". Large Cladocera (*Daphnia cucullata* and *Diaphanosoma brachyurum*) showed the greatest reduction in a river, but they were common over a distance of up to 130 km below a dam. These two planktonic species revealed a low potential for colonizing oxbow lakes. Eurytopic *Chydorus sphaericus* and *Mesocyclops leuckarti* transferred from the Siemianówka Reservoir had a great dispersal capacity in the Narew River and could effectively support local populations in oxbow lakes over a distance of 180 km.

Similarity between the crustacean communities in the river and the reservoir significantly decreased with the increasing distance from the dam. At the same time, crustacean communities in oxbow lakes were not affected by the distance from the source. Dispersal from the large source of zooplankton to local communities is a very important process but the local environmental factors such as habitat heterogeneity, aquatic vegetation and the hydrological connectivity can be strong enough to affect the structure of local crustacean communities in oxbow lakes.

Key words: zooplankton, metacommunity, dispersal, colonization, oxbow lakes

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Introduction

The study focuses on river-floodplain systems, which are particularly challenging in terms of a metacommunity. In addition to the spatial heterogeneity and the high (often stochastic) temporal variability of environmental conditions, they are characterized by the network configuration of their waterbodies and dispersal directionality (Funk et al. 2013). The source-sink dynamics enable species to exist at sites normally considered marginal or outside of their environmental range because high dispersal ensures a constant supply of new colonizers to these sites (Leibold et al. 2004). Therefore, these species have very different niche requirements, essentially a species-sorting framework, but dispersal maintains species in sites with negative growth rates (Winegardner et al. 2012). Colonization and extinction can determine local community structure in habitats which are colonized from a large "mainland" source (MacArthur, Wilson 1963). Then, the local factors such as habitat heterogeneity, water quality and community interactions can affect the survival and reproduction of individuals once they reach a new habitat (Cottenie et al. 2001; Michels et al. 2001; Shurin, Allen 2001; Beisner et al. 2006; Czerniawski et al. 2013). The importance of local environmental vs regional spatial processes in the metacommunity is currently hotly debated (Cottenie 2005; Borthagaray et al. 2015; Kuglerová et al. 2015).

Many rivers are regulated by reservoirs which are their main source of crustacean plankton. Spatial distribution of zooplankton communities in the river below the dam reservoirs were described by many authors and generally zooplankton suffers qualitative and quantitative reduction, which is most pronounced for large crustaceans (Akopian et al. 1999; Walks, Cyr 2004; Kentzer et al. 2010; Czerniawski, Domagała 2013). The previous study revealed that the Siemianówka Reservoir significantly affects the zooplankton community in the Narew River along the distance of 55 km below the dam, but the species from the reservoir were found along the distance of 130 km (Grabowska et al. 2013). Crustacean zooplankton has a great ability to disperse in river valleys. In addition to the dispersal of the active population which is very important over relatively short distances, crustaceans produce resting eggs which are most important for long-range dispersal (Michels et al. 2001). However, do reservoirs (being large sources of zooplankton) affect the crustacean communities in limnic ecosystems of the river valley? We hypothesized that a distance from the source could be an important factor affecting the crustacean communities in oxbow lakes.

The impact of a reservoir on river-valley habitats is very important because nowadays most rivers are regulated by reservoirs which are huge and continuous sources of crustacean zooplankton. The dispersal of crustacean species from the Siemianówka Reservoir has been studied in the Narew River along the distance of 130 km. The second objective was to determine the colonization of oxbow lakes by species from the reservoir along the distance of 180 km. Furthermore, the relative importance of local and regional factors affecting the crustacean communities in oxbow lakes was investigated.

Study sites

The study was conducted in the semi-natural Upper Narew Valley located in NE Poland (Fig. 1). The flow regime of the Narew is typical of large lowland floodplain rivers in Central Europe. The upper part of the Narew River is characterized by low flow velocity, ranging from 0.21 to 1.00 m s^{-1} (Grabowska et al. 2013), and the discharge – from 5 to 21 m^3 s^{-1} (Mioduszewski et al. 2004). The peak flows occur during spring snowmelt periods, while the low flows take place usually in late summer. The Narew basin is the core part of the region known as "the Green Lungs of Poland" (Piniewski et al. 2011). The Siemianówka Reservoir (SR) is located at the beginning of the study system. The reservoir is a large and shallow, lowland water-body (maximum area 32.5 km^2, maximum capacity 79.5 km^3, mean depth 2.5 m) with mean water residence time ranging from 4 to 6 months. Water quality in SR varied in different seasons but always indicate an eutrophic to hypertrophic level, with strong cyanobacteria blooms in the summer (Górniak, Karpowicz 2014; Grabowska et al. 2014; Grabowska, Mazur-Marzec 2014). Below the dam, the Narew is a meandering river with flooded marshes and meadows. The river is anastomosing from 90 to 130 km below the dam and consists of a network of interconnected channels and inter-channels. This section is protected within the Narew National Park (NNP). Below the NNP, the valley is strongly altered by drainage works and the river becomes regulated (Table 1) with a large number of oxbow lakes.

Zooplankton analyses

Zooplankton sampling was performed biweekly in the 2009-2010 growing season in different environments of the lowland river ecosystem, including the Siemianówka Dam Reservoir with the Narew River over a distance of 130 km below the dam and oxbow lakes in the Upper Narew Valley (Fig. 1). Crustacean

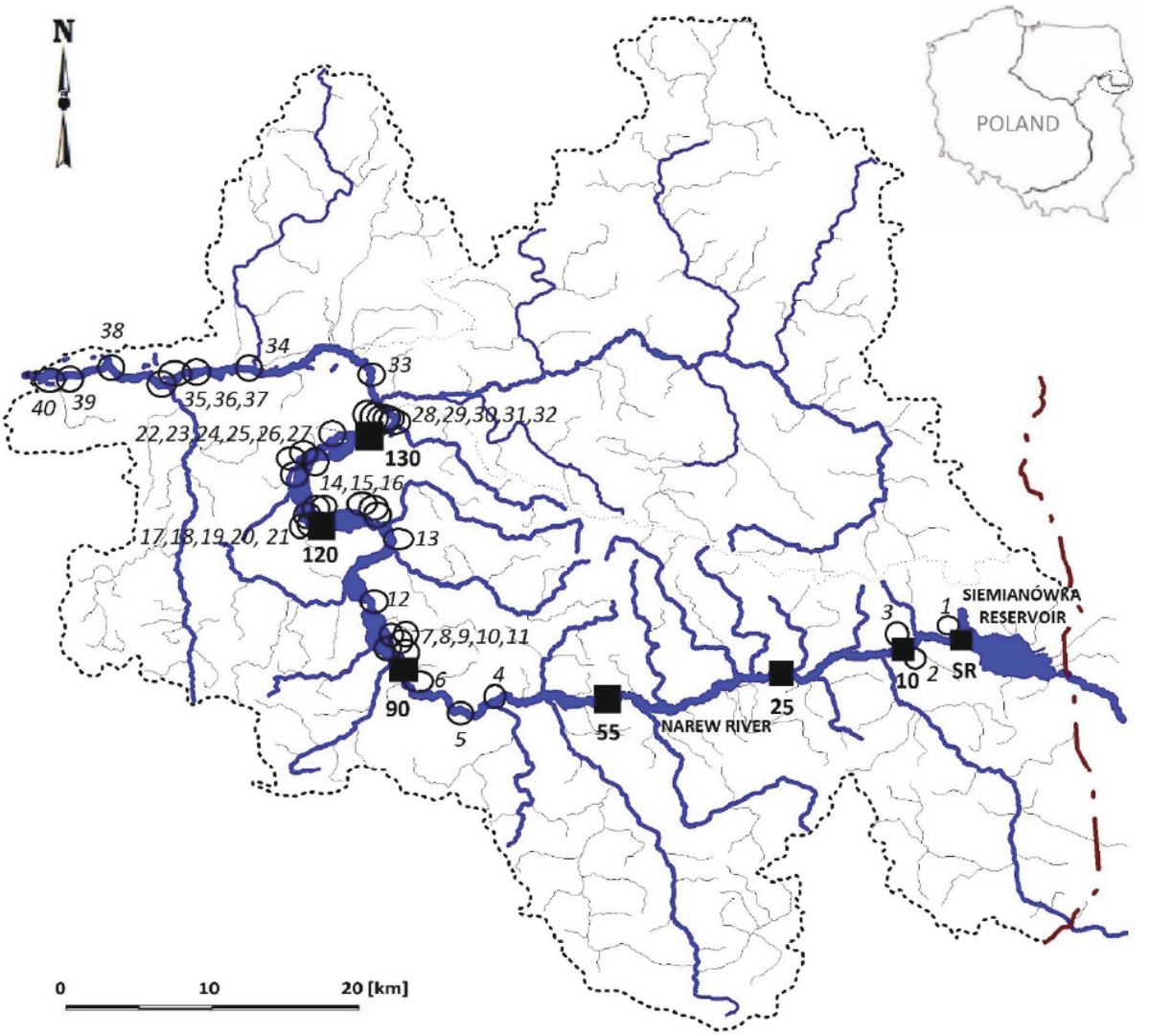

Figure 1

Map of the study sites with the location of the sampling stations; square: Siemianówka Reservoir (SR) and Narew River (km distance from the dam:10, 25, 55, 90, 120, 130); circle: oxbow lakes (*1 - 40*)

Table 1

Characteristics of the study stations in the Siemianówka Reservoir (SR) along the Narew River (distance from the dam: 10, 25, 55, 90, 120, 130 km) and in oxbow lakes (according to Grabowska et al. 2013)

Station name	Distance from the dam (km)	Character of the river	Velocity (m s^{-1})	Average discharge (m^3 s^{-1})	Number of samples
SR	0	Reservoir	-	4.1	19
10	9.1	Meandering	0.52-0.64	4.6	19
25	25.5	Meandering	0.44-0.51	8.2	19
55	56.0	Meandering	0.35-0.42	13.2	19
90	88.2	Meandering	0.65-0.80	15.1	19
120	118.0	Anastomosing	0.40-0.60	16.0	19
130	130.0	Anastomosing	0.62-0.75	18.2	9
OXBOW LAKES					
1-6	0.3-90	Meandering			17
7-32	91-130	Anastomosing			72
33-40	131-180	Regulated			12

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zooplankton (Cladocera and Copepoda) was sampled with a 10 l sampler and concentrated using a plankton net with a 50-µm mesh size. The material was preserved in 4% formaldehyde solution. Species were identified using specialized taxonomic literature (Flössner 1972; Flössner 2000; Smirnov 1996; Dussart, Defaye 2001; Rybak, Błędzki 2010).

The dispersal of crustacean species from the Siemianówka Reservoir in the Narew River was analyzed by the unique technique of taking samples from "the same water" (Grabowska et al. 2013; Napiórkowski, Napiórkowska 2013). Each time water samples were collected over three consecutive days, because water needs just as much time to travel 130 km between the dam and the last station. The ability to colonize new habitats by planktonic species coming from the reservoir was studied in 40 oxbow lakes located at distance of 180 km below the dam (Table 1).

Similarity between crustacean communities (%) in the Narew River and oxbow lakes and crustacean communities in the Siemianówka Reservoir was illustrated by Kulczyński's similarity index. Ivlev's index (Ivlev 1961) modified by Jacobs (1974) and applied by Ejsmont-Karabin (2008) was used as a measure of habitat preference (HPI) for planktonic species from the reservoir:

$$HPI = \frac{g - e}{g + e}$$

where g = percentage of species in Siemianówka Reservoir, e = percentage of species in an oxbow lake.

The effect of aquatic vegetation cover and hydrological connectivity on crustacean species in oxbow lakes was presented as internal preference mapping based on principal component analysis. The differences between samples were tested with the non-parametric Kruskal-Wallis test ($p<0.05$). Statistical analyses were performed with XLSTAT 2013 (Addinsoft).

Results

The Siemianówka Reservoir was a major source of crustacean zooplankton from June to November when the Narew River was enriched with 600 kg to 1500 kg (fresh weight) of crustacean zooplankton every day. The composition of zooplankton leaving the reservoir was relatively stable and more than 80% of the crustacean zooplankton biomass was represented by: *Chydorus sphaericus*, *Mesocyclops leuckarti*, *Daphnia cucullata* and *Diaphanosoma brachyurum*. The greatest reduction in the Narew River was observed in large Cladocera, especially in the *Diaphanosoma brachyurum* population (Table 2). However, large planktonic species (*Diaphanosoma brachyurum* and *Daphnia cucullata*) from the reservoir were found at a distance of 130 km below the dam (Table 2). These two species showed

Table 2

Average ± SD population density and frequency of planktonic species in the Siemianówka Reservoir (SR), along the Narew River as in Table 1 and in oxbow lakes. Potential for colonization of oxbow lakes by the planktonic species leaving the Siemianówka Reservoir was expressed by the habitat preference index (HPI).

		Diaphanosoma brachyurum	*Daphnia cucullata*	*Chydorus sphaericus*	*Mesocyclops leuckarti*
population density (ind. l^{-1})	SR	12 ± 24	17 ± 11	51 ± 77	41 ± 29
	10	1.4 ± 2	15 ± 14	51 ± 46	55 ± 106
	25	0.3 ± 0.7	3.1 ± 3.6	5.5 ± 6.4	12.4 ± 35
	55	0.1 ± 0.3	2.5 ± 5.4	7.4 ± 20	7 ± 16.7
	90	0.01 ± 0.04	0.4 ± 1.2	11.2 ± 42	1.3 ± 2.7
	110	0.03 ± 0.1	0.3 ± 0.5	4.3 ± 15	1.4 ± 4.8
	130	0.4 ± 1	0.2 ± 0.3	1.2 ± 2.1	0.1 ± 0.2
	oxbow lakes	0.7 ± 0.9	1.6 ± 4.6	8.3 ± 23.5	3.3 ± 7
frequency	SR	79%	100%	100%	100%
	10	44%	100%	94%	100%
	25	16%	58%	84%	84%
	55	11%	37%	79%	68%
	90	5%	11%	63%	58%
	110	5%	21%	47%	37%
	130	11%	33%	33%	22%
	oxbow lakes	4%	17%	67%	51%
HPI		-0.99	-0.90	-0.63	-0.77

a low potential for colonization of oxbow lakes, which was reflected in a low frequency, low density of populations in the oxbow lakes and a very low value of the habitat preference index – HPI (Table 2).

Species with a wide ecological tolerance (*Chydorus sphaericus* and *Mesocyclops leuckarti*) were commonly found in all habitats, but their most important source was the outflow from the Siemianówka Reservoir. A statistically significant growth of the *Chydorus sphaericus* population was also observed in the Narew River at a station located 90 km below the dam (Table 2). The highest density of *Ch. sphaericus* and *M. leuckarti* was noted in the Siemianówka Reservoir and in the Narew River 10 km below the dam (Table 2). No statistically significant differences were determined between the density of *Ch. sphaericus* and *M. leuckarti* populations in the Siemianówka Reservoir and in the Narew River 10 km below the dam. These two species showed high dispersal abilities and were commonly found in the Narew River at a distance of 130 km below the dam. *Chydorus sphaericus* and *Mesocyclops leuckarti* were found in more than half of the oxbow lakes but with lower densities than in the reservoir, thus HPI in their case had negative values (Table 2).

The similarity between the crustacean communities in the river and the reservoir significantly decreased ($R^2 = 0.3975$) with the increasing distance from the dam (Fig. 2). At the same time, crustacean communities in oxbow lakes were not affected by the distance from the source. Surprisingly, the crustacean zooplankton from the most distant oxbow lakes is more similar to the Siemianówka Reservoir (Fig. 2).

The preference mapping based on the principal component analysis revealed a significant effect of aquatic vegetation cover on the occurrence of most of the littoral and planktonic species. Even typically planktonic cladocerans such as *Diaphanosoma brachyurum*, *Daphnia cucullata* and *Bosmina* species reached greater density among the macrophytes. Habitats without vegetation were preferred by larval forms of copepods (nauplii, copepodites) and benthic cladocerans like: *Disparalona rostrata*, *Graptoleberis testudinaria* (Fig. 3).

Connectivity with the river is yet another factor which may affect the crustacean communities. The majority of planktonic and littoral organisms prefer oxbow lakes connected with the river, while isolated objects were preferred by larval forms of copepods and some cladocerans, like: *Daphnia pulex*, *Pleuroxus truncatus* and *Ceriodaphnia* species. The two *Daphnia* species differ in their preferences: *Daphnia cucullata* prefers oxbow lakes connected with the river, while *D. pulex* prefers isolated objects. Benthic copepods (Harpacticoida spp., *Paracyclops* spp. and *Ectocyclops phaleratus*) were not affected by the cover of macrophytes and the connectivity with the river (Fig. 3).

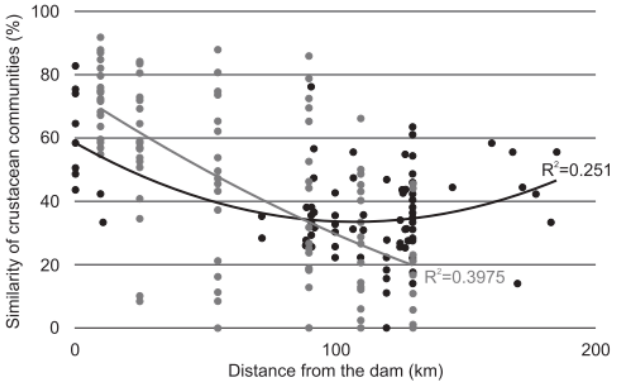

Figure 2

Similarity between crustacean communities (%) in the Narew River (grey) and oxbow lakes (black) to crustacean communities in the Siemianówka Reservoir

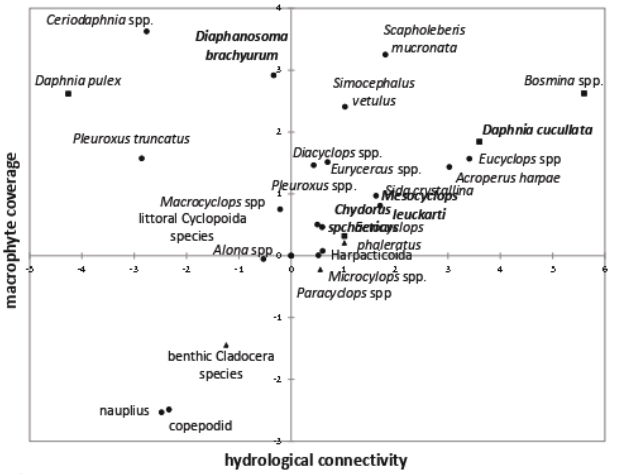

Figure 3

Internal preference mapping of the hydrological connectivity and the cover of macrophytes on the crustacean communities (dot – littoral species; square – planktonic species with eurytopic *Chydorus sphaericus* and *Mesocyclops leuckarti*; triangle – benthic species)

Discussion

The Siemianówka Reservoir is large and continuous source of crustacean zooplankton in the Upper Narew River. Many studies have shown that large zooplankton leaving the reservoir with the outflow

suffers qualitative and quantitative reduction (Akopian et al. 1999; Walkc, Cyr 2004; Czerniawski, Domagała 2013). Some experimental studies have shown that zooplankton disperse rapidly over very short distances, below 60 m (Cohen, Shurin 2003). The presented field study revealed the dispersal of crustacean zooplankton from the reservoir over a relatively long distance. Large Cladocera (*Daphnia cucullata* and *Diaphanosoma brachyurum*) showed the largest reduction in the river, but the active population dispersal was observed over a distance of up to 130 km below the dam. *Daphnia cucullata* and *Diaphanosoma brachyurum* were not found in the Upper Narew Valley before the creation of the Siemianówka Reservoir (Ejsmont-Karabin, Karabin 2004). *Diaphanosoma brachyurum* occurred in the Siemianówka Reserovir in 2003 (Górniak, Karpowicz 2014). Therefore, the reservoir was the main source of these species in the Upper Narew Valley.

The colonization of oxbow lakes by the species from the reservoir in the Upper Narew Valley was affected by local factors rather than by the distance from the source. Dispersal from the regional species pool supplies local communities with colonists, while local factors, such as water quality and community interactions, can affect the survival and reproduction of individuals once they reach a new habitat (Shurin, Allen 2001; Beisner et al. 2006; Louette et al. 2006; Pasztaleniec et al. 2013). However, dispersal can play another distinct role when its extent is so large that the abundance of local populations is significantly affected both by the emigration of individuals and by the immigration of individuals from other sites via ''source-sink'' (Mouquet, Loreau 2002; Leibold, Norberg 2004). As a large source of crustacean zooplankton, the dam reservoir could support populations at local sites that are not self-sustaining, by having such populations competitively suppress other populations that would be self-sustaining and potentially driving them extinct (Amarasekare, Nisbet 2001; Leibold, Norberg 2004). *Diaphanosoma brachyurum* from the Siemianówka Reservoir does not seem adapted to the environmental conditions in oxbow lakes. While the occurrence of *Daphnia cucullata* in oxbow lakes of the Narew Valley could be limited by local habitat conditions and representatives may still come from the source located at a fairly large distance. Common eurytopic *Chydorus sphaericus* and *Mesocyclops leuckarti* coming from the Siemianówka Reservoir were important components of zooplankton communities in the Narew River and could effectively support local populations in oxbow lakes over a distance of 180 km.

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