

DOI: 10.2478/s13545-013-0088-5
Original research paper

Received: November 05, 2012
Accepted: May 23, 2013

Food spectrum of the omnivorous rotifer *Asplanchna priodonta* in two large northeastern European lakes of different trophic

Katarina Oganjan^{1,*}, Taavi Virro², Velda Lauringson²

¹*Estonian Marine Institute, University of Tartu, Mäealuse 14, EE-12618 Tallinn, Estonia*

²*University of Tartu, Institute of Ecology and Earth Sciences, Department of Zoology, Tartu, Estonia*

Key words: diet, feeding, lake trophic state, omnivory, rotifer, stomach contents

Abstract

In this paper we examine the stomach contents of the omnivorous rotifer, *Asplanchna priodonta*, to evaluate possible trophic interactions between this rotifer and its potential prey in two large northeastern European lakes: moderately eutrophic Lake Peipsi and strongly eutrophic Lake Võrtsjärv. Our results show that the *A. priodonta* diet consisted of Bacillariophyta, Chlorophyta, Cyanobacteria, and Dinoflagellata. Ciliata were detected on rare occasion. Bacillariophyta were the most frequent food items in stomachs. There were no between-lake differences in the consumption of Chlorophyta and Cyanobacteria, whereas Bacillariophyta were consumed more in Lake Peipsi. However, neither Dinoflagellata nor Ciliata were found in stomach samples in Lake Võrtsjärv. We conclude that *A. priodonta* is an opportunistic feeder that is capable of influencing the phytoplankton community structure in large lakes.

* Corresponding author e-mail: katarina.oganjan@ut.ee

INTRODUCTION

Feeding selectivity of omnivorous species is an important factor that potentially affects food web dynamics (Kneitel 2007, Polis & Strong 1996, Tardiff & Stanford 1998). An omnivore may hardly fit into a simple trophic model, as it can have a range of various impacts on ecosystem processes, for example, either by grazing on primary producers or, on the other hand, decreasing the grazing pressure on primary producers by feeding on herbivorous prey species (e.g. Dorn & Wojdak 2004). Thus, an omnivorous species can easily remain a „black box“ in any particular ecosystem model, unless its diet is studied closely. Indeed, collecting data about the diet of an omnivorous species in multiple ecosystems might eventually help to gain understanding about the environmental interactions behind any particular feeding pattern of the studied omnivore. However, in most cases, such meta-analyses are missing.

Intensive investigation of zooplankton has been conducted for many decades now, and yet data on the diet of raptorial omnivorous zooplankton species has remained scattered and incomplete. Zooplankton studies have been mostly restricted to crustacean plankton, and insufficient attention has been given to rotifers, which often dominate metazooplankton communities in shallow eutrophic lakes (Mayer et al. 1997, Haberman 1998). Rotifers are, however, recognized as important components of freshwater zooplankton communities - be they herbivores, predators, or omnivores (Dumont 1997, Pourriot 1977, Starkweather 1980, Nogrady et al. 1993). They also serve as a major food source for many invertebrates (Williamson 1983, Hampton & Gilbert 2001, Brandl 2005). Amongst several genera of predatory rotifers, the various species of *Asplanchna* are considered some of the most widespread and abundant (Williamson 1983). The cosmopolitan and

eurythermic species *Asplanchna priodonta* (Gosse 1850) is among the largest of the rotifers in the Northern Hemisphere (Kutikova 1970, José De Paggi 2002). Because *Asplanchna* is believed to exhibit both functional and numerical responses to prey density, it may have an important regulatory effect in freshwater ecosystems (Gilbert 1980). There have been several studies on the feeding of *Asplanchna priodonta* in Europe and Japan, indicating that this species has a broad plasticity in diet, and that it is able to survive on an exclusively zoophagous diet, an omniphagous diet or an exclusively phytophagous diet. It can thus affect plankton biomass, aquatic food web structure and production in many different ways (Kappes et al. 2000, Chang et al. 2010).

According to several authors (Dumont 1977, Guiset 1977, Milovskaya & Bonk 2004, Chang et al. 2010), the diet of *A. priodonta* consists of algae, including diatoms, dinoflagellates, Cyanobacteria, Volvocales, Chlorococcales, and Desmidiaceae. *Asplanchna priodonta* is known for raptorial feeding, such that it is capable of swallowing whole rotifers and crustaceans, as well as colonial algae. Thus, the rotifer *Keratella cochlearis* and protozoans like *Codonella*, *Diffugia*, and tintinnids are frequently consumed as prey (Pourriot 1977, Gilbert & Williamson 1978, Gilbert 1980, Hofmann 1983).

Unfortunately, the diet of *A. priodonta* is not well known. In the lakes of the study area, *A. priodonta* is supposed to feed on algae and small rotifers and in doing so may effectively control these populations (Virro et al. 2009). Previously, when calculating zooplankton production and food ratio *A. priodonta* was considered semi-predaceous (i.e., consuming algal and animal food in equal amounts) in the studied lakes (Haberman et al. 2000, Haberman 2001, Agasild et al. 2007, Virro et al. 2009). This assumption may have led to inaccurate assessments of the trophic dynamics at the basal consumer level, as differences between the diets of populations of the same *Asplanchna* species often occur (Chang et al. 2010). The possible existence of such differences suggests using caution in generalizing from one population of omnivores to another. Accurate knowledge of the *A. priodonta* diet will assist in calculating energy carried to the next trophic level, which in turn will help to determine the efficiency of the aquatic food web.

In this paper, we determine the diet and food selectivity of the rotifer *A. priodonta* and evaluate trophic interactions between it and its potential prey

in two large northeastern European lakes, Lake Peipsi and Lake Võrtsjärv.

MATERIALS AND METHODS

Study site

Two large shallow lakes were studied during this investigation, Lake Peipsi and Lake Võrtsjärv (Fig. 1). Together they make up about 88.8% of the total area covered by lakes in Estonia. L. Peipsi (named also L. Peipus in earlier literature) is considered a lake of moderate eutrophy, while L. Võrtsjärv is a strongly eutrophic water body (Haberman & Laugaste 2003).

L. Peipsi, the fourth largest lake in Europe, is located on the border between Estonia and Russia. The total area of the lake is 3555 km² with mean and maximum depths of 7.1 and 15.3 m, respectively. The water residence time is about two years. The zooplankton biomass is dominated by cladocerans and copepods. Small rotifers dominate zooplankton in abundance. Pelagic phytoplankton consists of about 500 algal species. Cyanobacteria, Bacillariophyta, and Chlorophyta dominate phytoplankton biomass. Cyanobacteria constitute up to 90% of phytoplankton biomass (Kangur et al. 2002, Zingel & Haberman 2008).

L. Võrtsjärv is a large shallow lake located in the watershed of L. Peipsi. The total area of the lake is 270 km² and its mean and maximum depths are 2.8 m and 6 m, respectively. The water residence time is about one year. Despite considerable biomass of phytoplankton in the lake, Võrtsjärv is poor in species. Cyanobacteria and Bacillariophyta dominate the phytoplankton community. Other groups, such as Chlorophyta, Chrysophyta, and Pyrrophyta, are minor components of the phytoplankton assemblage. Rotifers, crustaceans, and ciliates dominate the zooplankton community. Usually the most abundant members of the zooplankton community are rotifers; these are perennial in the lake, but planktonic ciliates also have an important role in L. Võrtsjärv, as they account for almost two-thirds of the total zooplankton biomass (Nõges et al. 2007, Zingel & Haberman 2008, Virro et al. 2009).

Samples

The present study is based on plankton samples collected from the study lakes by the staff of the Võrtsjärv Centre for Limnology within different monitoring and research programs. Zooplankton

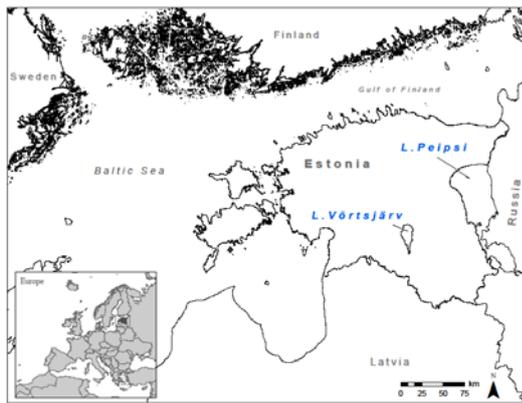


Fig. 1. Location of lakes Peipsi and Võrtsjärv

samples were obtained with a 2 l Ruttner sampler from the entire water column at 1 m intervals from the surface to the bottom, pooled (20 l) and then filtered through a 48- μ m mesh plankton net. The samples were preserved in 4% formaldehyde solution. The methods of collecting and analyzing samples, including biomass calculations, are described in detail in Laugaste et al. (2001), Haberman (2001) and Virro et al. (2009).

Stomach content analysis

The stomach contents of *Asplanchna priodonta* were analyzed to determine its prey preference. For the analysis, samples from both lakes from 2005–2009 were used. For the identification of stomach contents, the individuals were lifted from the fixed samples with a pipette and transferred onto the slides. They were then squashed with a cover slip on a microscope slide and viewed under an OLYMPUS BX 50 microscope at the maximum magnification of 10 \times 40.

Although some individuals were transparent enough that stomach contents could be easily recognized in intact animals, the majority needed to be treated prior to examination. Stomach contents were studied first on intact animals and then by progressive dissolving of the soft parts of the body with the household disinfectant Domestos[®], which contains sodium hypochlorite NaClO (<5%). Several drops of this NaClO solution were added to slides under the cover slip with a pipette. It was assumed that most of the food items had the same percent digestibility. However, stomach content analysis is not a fully reliable tool for quantitative estimates of the consumption of ciliates by *Asplanchna*, because ciliates lack hard body structures and may be digested

faster than other prey. Nevertheless, several studies have used the same technique and still found ciliates in *Asplanchna* stomachs (Kappes et al. 2000, Chang et al. 2010).

Rotifers may have ejected some food items during sample fixation. However, the occurrence of this behaviour has probably been uniform across all food types and thus not significantly influential for the interpretation of results. Rotifers were fixed immediately after sampling, and individuals that had their stomach turned inside out were not further analyzed.

Composition of phytoplankton in the stomachs of *A. priodonta* was determined to major taxonomic group: i.e., Bacillariophyta, Chlorophyta, Chrysophyta, Cryptophyta, Cyanobacteria and Dinoflagellata. Small rotifers and Ciliata were classified to the lowest taxonomical level possible. The relative amount of each food item category present was calculated. The methods for phytoplankton and zooplankton wet weight calculation are described in Laugaste et al. (2001) and Haberman (2001).

The identification of a food item in the stomach does not necessarily signify that it constitutes an important food supply for the rotifer. Food and the exuvia of cladocerans can be ingested without being digested. Ingestion of indigestible particles can be casual and can be related to their abundance in the environment and not to their suitability as food. Ivlev's index of food selectivity was calculated using the formula:

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

where g is the percentage of a given food component in the stomach, and e is the percentage of a given food component in the environment (Pourriot 1977).

Ivlev's selectivity index assumes values between -1.0 and +1.0, negative values indicating avoidance of a certain prey item, and positive values indicating selective preference for a prey item. Values around zero relate to prey that are present in the lake water but are ingested non-selectively (Xie 2001).

Frequency of occurrence index was calculated to characterize occurrence frequencies of the food items in the stomachs. Frequency of occurrence was calculated using the formula:

$$Fi = 100 \frac{ni}{n}$$

where F_i is the frequency of occurrence of the food item i in the sample; n_i is the number of stomachs in which the i item is found; n is the total number of stomachs with food in the sample (Hyslop 1980, Lima-Junior & Goitein 2001).

The diets of *A. priodonta* from lakes Peipsi and Vörtsjärv were compared using Arcsine square root transforms of the data, but as the observed data were still not normally distributed, we employed the Wilcoxon Mann-Whitney rank sum test to quantify the differences between the gut contents.

Trophic interactions

Biomass and abundance data of *A. priodonta* and its potential prey were derived from the database of the Vörtsjärv Centre for Limnology. These data date from the years 2000–2009. Possible predator-prey interactions of *Asplanchna priodonta* with the other plankton organisms in the lakes were evaluated by correlation analysis. Potential interrelations were assessed between *A. priodonta* and small rotifers, which are all likely prey for the animal in both lakes, as well as Bacillariophyta, Chlorophyta, Chrysophyta, Cryptophyta, Cyanobacteria, Dinoflagellata and Ciliata. Biomasses of *A. priodonta* were compared to the biomasses of phytoplankton and zooplankton groups (for example, Ciliata and small rotifers like *Anuraeopsis*, *Brachionus*, *Kellicottia*, and *Keratella*). Correlation analysis was used to evaluate these relationships. Variables were first log-transformed, and the non-parametric Spearman's rank correlation test was used to examine the data.

All statistical analyses were performed using *Statistica 7.0* and *R 1.40*.

RESULTS

Diet

The number of samples analyzed was 26 from L. Vörtsjärv and 25 from L. Peipsi. The total number of *Asplanchna priodonta* specimens studied was 121 in L. Peipsi and 106 in L. Vörtsjärv. The total number of full stomachs in the samples from L. Vörtsjärv was 83, and the total number of full stomachs in the samples from L. Peipsi was 112.

In L. Vörtsjärv, *A. priodonta* was exclusively phytophagous with Bacillariophyta constituting an average of 50% (SD \pm 0.37), Chlorophyta 30% (SD \pm 0.32) and Cyanobacteria 20% (SD \pm 0.22) of the total food consumed. The frequency of occurrence

index showed that Bacillariophyta were the most frequent in the stomachs of *A. priodonta*, followed by Cyanobacteria and Chlorophyta (Table 1). Ivlev's indices of selectivity indicate that Cyanobacteria, Cryptophyta, Chrysophyta, and Dinoflagellata were avoided, whereas Chlorophyta and Bacillariophyta were selected, serving as the preferred prey (Table 1).

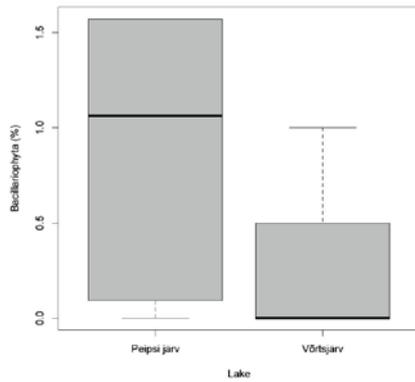
Table 1

Frequency of occurrence index (F) and Ivlev's index of selectivity (S) of the items ingested by *A. priodonta* in Lake Peipsi in 2005–2009 and in Lake Vörtsjärv in 2005–2009

| Order | S | | F (%) | |
|-----------------|--------------|-----------|--------------|-----------|
| | L. Vörtsjärv | L. Peipsi | L. Vörtsjärv | L. Peipsi |
| Bacillariophyta | 0.35 | 0.27 | 69.88 | 92.86 |
| Chlorophyta | 0.875 | 0.5 | 46.99 | 30.36 |
| Chrysophyta | -1 | -1 | 0 | 0 |
| Cryptophyta | -1 | -1 | 0 | 0 |
| Cyanobacteria | -0.55 | -0.61 | 49.39 | 16.96 |
| Dinoflagellata | -1 | -0.2 | 0 | 16.07 |

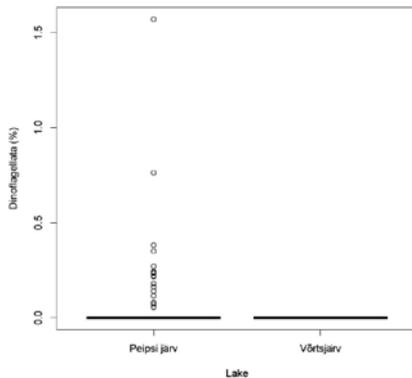
The diet of *Asplanchna* in L. Peipsi included predominantly algal components. The preferred food items were Bacillariophyta, which constituted 60% (SD \pm 0.42), Cyanobacteria, which made up 29% (SD \pm 0.23), Chlorophyta, which constituted 10% (SD \pm 0.21), and Dinoflagellata which was less than 1% (SD \pm 0.1) of the total food items consumed. Frequency of occurrence indices calculated for the food items in the stomach of *A. priodonta* in L. Peipsi showed that Bacillariophyta were the most frequent food items in the stomach of *A. priodonta*, followed by Chlorophyta, Cyanobacteria, Dinoflagellata, and occasionally Ciliata (Table 1). Resulting from the calculated Ivlev's indices of selectivity, Cyanobacteria, Cryptophyta, Chrysophyta and Dinoflagellata were avoided and were selected negatively, whereas Chlorophyta and Bacillariophyta were selected positively and served as the preferred prey items (Table 1).

There were noticeable differences in the diet composition of *A. priodonta* between the lakes. Bacillariophyta were consumed more in L. Peipsi, than in L. Vörtsjärv ($Z = 7.57$, $P < 0.001$) (Fig. 2). Dinoflagellata constituted less than 1% in L. Peipsi, while in L. Vörtsjärv they were not consumed at all ($Z = 3.94$, $P < 0.001$) (Fig. 3). Ciliata were consumed in L. Peipsi, but were not found in gut contents in L. Vörtsjärv ($Z = 2.29$, $P = 0.022$) (Fig. 4). No differences were found between the lakes in



Y axis denotes the Arcsine square root transformed percentage of the wet weight of Bacillariophyta relative to all the food items in the stomachs of *A. priodonta*.

Fig. 2. Differences between two lakes in the consumption of Bacillariophyta by *A. priodonta*



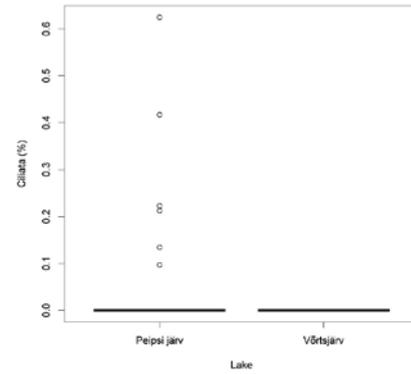
Y axis denotes the Arcsine square root transformed percentage of the wet weight of Dinoflagellata relative to all the food items in the stomachs of *A. priodonta*.

Fig. 3. Box-plot showing the differences between two lakes in the consumption of Dinoflagellata

the consumption of Cyanobacteria ($Z = -1.68$, $P = 0.093$), and in the consumption of Chlorophyta ($Z = -1.08$, $P = 0.28$) (Fig. 5, 6).

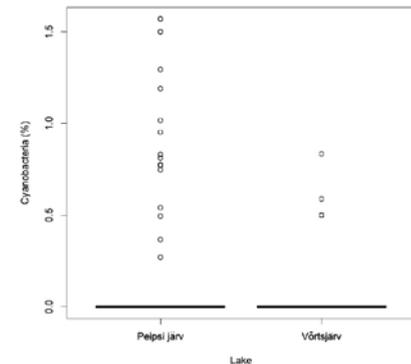
Population dynamics

In both lakes, *A. priodonta* was regularly present in the samples during the whole study period. Maximum abundance in L. Võrtsjärv was in 2003 (Fig. 7). In L. Võrtsjärv, the biomass of *A. priodonta* covaried with that of Bacillariophyta, Chlorophyta, Cyanobacteria, and Ciliata, but the correlations were weak. *A. priodonta* biomass fluctuated independently



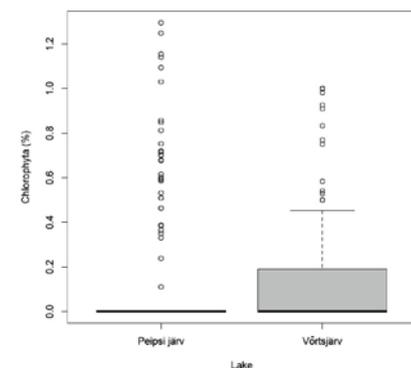
Y axis denotes the Arcsine square root transformed percentage of the wet weight of Ciliata relative to all the food items in the stomachs of *A. priodonta*.

Fig. 4. Box-plot showing the differences between two lakes in the consumption of Ciliata



Y axis denotes the Arcsine square root transformed percentage of the wet weight of Cyanobacteria relative to all the food items in the stomachs of *A. priodonta*.

Fig. 5. Box-plot showing the differences between two lakes in the consumption of Cyanobacteria



Y axis denotes the Arcsine square root transformed percentage of the wet weight of Chlorophyta relative to all the food items in the stomachs of *A. priodonta*.

Fig. 6. Box-plot showing the differences between two lakes in the consumption of Chlorophyta

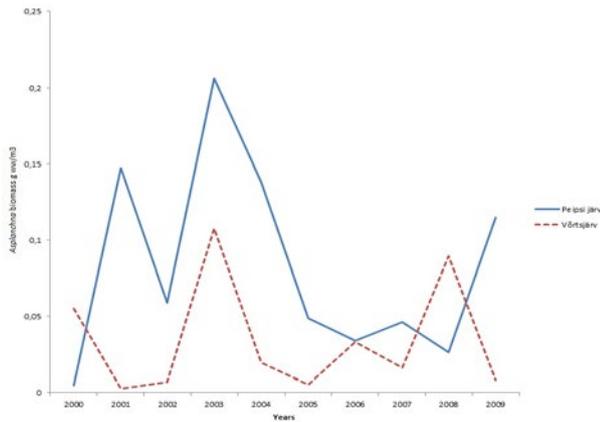


Fig. 7. Annual variation of *A. priodonta* biomass in Lake Võrtsjärv and Lake Peipsi in 2000–2009

from the biomass of small rotifers, Chrysophyta, Cryptophyta, and Dinoflagellata (Table 2).

In L. Peipsi, *A. priodonta* was most abundant in 2002. Since then its abundance has noticeably decreased (Fig. 7). In L. Peipsi, the biomass of *A. priodonta* had weak correlations with the biomass of Bacillariophyta, Ciliata, and that of small rotifers. *A. priodonta* abundance was also related to small rotifer abundance. The biomass of *A. priodonta* was not related to the biomass of Cyanobacteria, Chlorophyta, Chrysophyta, Cryptophyta, or Dinoflagellata (Table 3).

DISCUSSION

Although the phytoplankton and zooplankton communities occurring in L. Võrtsjärv and L. Peipsi are well studied, the importance of *A. priodonta* has not been thoroughly examined. This predator is generally considered to be omnivorous, preferring to feed on other smaller rotifers (Guiset 1977, Pourriot 1977, Salt 1977). It also has been considered a predominantly zoophagous species among metazooplankton in L. Võrtsjärv and L. Peipsi (Haberman 1997, Nöges et al. 1998, Laugaste & Haberman 2005, Agasild et al. 2007, Virro et al. 2009). Due to the specific algal composition, which comprises mainly large and filamentous forms, the zooplankton community is generally considered to have little grazing impact on the phytoplankton in these two lakes (Agasild et al. 2007). Large-sized phytoplankton is a suitable food resource only for some copepods and *Asplanchna*. However, the grazing impact on phytoplankton by *Asplanchna* may be low, if the animal feeds mainly on other rotifers.

Table 2

Correlation of the *A. priodonta* biomass with its potential prey biomass in L. Võrtsjärv (Spearman R, n=134 observations)

| | R | p |
|------------------------|-------------|-----------------|
| Bacillariophyta | 0.29 | <0.01 |
| Chlorophyta | 0.31 | <0.01 |
| Cyanobacteria | 0.29 | <0.01 |
| Ciliata | 0.34 | <0.01 |
| Chrysophyta | 0.17 | 0.05 |
| Cryptophyta | 0.04 | 0.62 |
| Dinoflagellata | -0.12 | 0.16 |
| Small rotifers | -0.02 | 0.84 |

Table 3

Correlation of the *A. priodonta* biomass with its potential prey biomass in L. Peipsi (Spearman R, n=543 observations)

| | R | p |
|------------------------|-------------|-----------------|
| Bacillariophyta | 0.14 | <0.01 |
| Chlorophyta | -0.02 | 0.68 |
| Cyanobacteria | 0.06 | 0.18 |
| Ciliata | 0.12 | 0.04 |
| Chrysophyta | 0.02 | 0.61 |
| Cryptophyta | 0.05 | 0.22 |
| Dinoflagellata | 0.05 | 0.29 |
| Small rotifers | 0.19 | <0.01 |

Zoophagous nutrition is considered advantageous owing to a high assimilation index (Pourriot 1977) but *A. priodonta* also may reach a considerable growth rate when feeding exclusively on algae (Stemberger & Gilbert 1985).

Our research indicates that the *A. priodonta* populations of lakes Peipsi and Võrtsjärv are phytophagous. The preferred food in both lakes was Bacillariophyta, followed by Chlorophyta; these were the most abundant phytoplankton groups in the lakes. Bacillariophyta were consumed more in L. Peipsi than in L. Võrtsjärv, but differences in consumption of Chlorophyta between the two lakes were not observed. The biomass of Bacillariophyta covaried with the biomass of *A. priodonta* in both lakes, which shows the dependence of *Asplanchna* on this prey. Yet, the values of Ivlev's index of selectivity for Bacillariophyta are close to zero, suggesting that this prey might be ingested less selectively. Diatoms are considered to be a "food refuge", when other food items are scarce or unavailable (Salt et al. 1978). The values of Ivlev's index of selectivity for Chlorophyta were high,

indicating a selective preference for this prey item. Chlorophyta biomass covaried with *A. priodonta* biomass in L. Vörtsjärv, suggesting thus the trophic interactions of *Asplanchna* with this prey. Remarkably, this relation was absent in L. Peipsi. In L. Peipsi, Chlorophyta rank third by biomass, after Bacillariophyta and Cyanobacteria, but they rarely become dominant in the lake (Haberman et al. 2000, Laugaste et al. 2008). Therefore, in this lake *A. priodonta* probably depends more on the most abundant phytoplankton, Bacillariophyta, and is independent from Chlorophyta.

In strongly eutrophic L. Vörtsjärv, 49% of the food was colonial Cyanobacteria. In L. Peipsi, the frequency of Cyanobacteria as a food item was lower (17%). In general, the overall consumption of this item was relatively high in both lakes. This is remarkable because Cyanobacteria are reported to be negatively selected and generally account for an insignificant proportion of the food consumed by rotifers (Guiset 1977). On the other hand, studies by Dumont (1977) and Kappes et al. (2000) showed that Cyanobacteria should be considered food for *A. priodonta*. Nevertheless, Ivlev's index of selectivity for Cyanobacteria was negative in both lakes, indicating avoidance of this prey. There was no correlation between *A. priodonta* and Cyanobacteria biomasses in L. Peipsi. The biomass of *A. priodonta* covaried with that of Cyanobacteria in L. Vörtsjärv, although the correlation was weak. However, one explanation for this correlation might be that one common factor affects both *Asplanchna* and Cyanobacteria, creating coherence between them.

Cyanobacteria may be avoided by herbivorous zooplankton for several reasons, including that they are nutritionally deficient food for zooplankton because they may be toxic through the production of microcystins (Ghadouani et al. 1998, Nandini & Rao 1998). Zooplankton feeding and growth rates have been shown to decrease when exposed to microcystins. Although toxicity has been reported to negatively affect herbivorous zooplankton, there are also studies showing that some large zooplankters feed successfully on potentially toxic genera of Cyanobacteria. Some species may develop stronger tolerance for toxic microcystins (Hansson et al. 2007, Nandini 2000). *A. priodonta* may be one of those species, able to cope with the cyanobacterial blooms and thus able to live in the lakes where Cyanobacteria are dominant. This is an area in need of additional research.

Asplanchna priodonta also may feed on Dinoflagellata (Guiset 1977, Pocięcha & Wilk-Wozniak 2008, Chang et al. 2010). In L. Peipsi, Dinoflagellata were occasionally found to be a source of food (1%), but they had almost the same frequency of occurrence index as Cyanobacteria. In L. Vörtsjärv, *A. priodonta* did not feed on dinoflagellates, and the biomass of *A. priodonta* and Dinoflagellata did not covary, suggesting a lack of relationship of *A. priodonta* with this prey. However, the effect of prey abundance on selectivity might be important. Dinoflagellata abundance in these two lakes is low; consequently they are encountered rarely and therefore are less accessible for predation.

A. priodonta is reported to be an effective predator of ciliates (Guiset 1977, Gilbert & Jack 1993, Pocięcha & Wilk-Wozniak 2008, Zurek 2007, Chang et al. 2010). Ciliates were occasionally found during the stomach analyses in L. Peipsi, where the biomass of ciliates constituted only 6% of the total zooplankton biomass (Zingel & Haberman 2008). In L. Vörtsjärv, ciliates were not found in the stomachs, however, the biomasses of *A. priodonta* and Ciliata covaried. According to Zingel & Haberman (2008), in L. Vörtsjärv, Ciliata biomass constituted almost 66% of the total zooplankton biomass and ciliates should presumably be a part of the rotifer diet.

The incidence of ciliates in the stomachs of *A. priodonta* probably underestimates the importance of ciliates to the rotifer. The absence of these protozoans in the animal's stomach does not indicate that they are not eaten. The stomach may contain few or no ciliate remains because ciliates may be broken up by mastax into unrecognizable pieces. Also, the time between ingestion and egestion may be rather short, and treatment of *Asplanchna* with NaClO also may affect the results. Other methods should likely be used or even combined to determine the ability of *A. priodonta* to prey on ciliates, e.g. studying unpreserved individuals (Kappes et al. 2000), incubating ciliates with or without predators (Gilbert & Jack 1993), culturing *A. priodonta* on different food sources (Robertson & Salt 1981), and feeding *A. priodonta* with labelled ciliates (Sorokin & Paveljeva 1972).

Asplanchna priodonta is considered an important predator of rotifers, and is believed to efficiently regulate the density and biomass of its prey, as well as affect the size structure of the rotifer assemblage (Dumont 1977, Hessen & Nilssen 1985, Virro et al. 2009). However, Salt et al. (1978) argue that *A. priodonta* relies heavily on different kinds of algae

rather than larger prey because it has weak trophi. The structure of the trophi of this species noticeably differs in morphology from the trophi of the other zoophagous *Asplanchnidae* species, which are capable of dealing with larger prey, such as copepods or other rotifers (Salt et al. 1978). In lakes Peipsi and Vörtsjärv, *A. priodonta* is one of the largest rotifers, thus all smaller rotifers are potential prey. In some earlier materials, in addition to algae, small rotifers *Keratella cochlearis* and *Trichocerca rousseleti* have been detected in the stomachs of *A. priodonta* in L. Peipsi, as well as *Anuraeopsis fissa* in L. Vörtsjärv (T. Virro, unpublished data). Detailed analyses of the diet of *A. priodonta* revealed that predation on metazooplankton occurred neither in L. Vörtsjärv nor in L. Peipsi. This was supported by correlation analyses, which showed that in L. Vörtsjärv, *Asplanchna* biomass and abundance were uncoupled from smaller rotifers. However, the correlation analysis between *A. priodonta* and smaller rotifers in L. Peipsi, showed that their population dynamics were correlated with one another. One explanation for this correlation might be that one common factor affects both *Asplanchna* and smaller rotifers creating coherence between them. Differences between the two lakes may be related to the different pelagic community and food web structures. L. Vörtsjärv, where no correlation between *A. priodonta* and other rotifers occurred, is characterized by less efficient energy processing pathways with a highly important microbial loop and a larger proportion of protozoan ciliates in plankton communities (Zingel & Haberman 2008). Chang et al. (2010) showed that the population dynamics of *A. priodonta* were not directly related to food abundance. They report that *Asplanchna* is far more likely to consume rotifers in a manipulated environment than in natural conditions. In the present study, the presence of large phytoplankton also may have been important. Feeding on abundant large algal colonies might eventually be more energy-efficient for *A. priodonta* than selective hunting for smaller rotifers in such an environment. Our data suggest that predation by *A. priodonta* in the studied lakes probably cannot exert any important controlling effect on other rotifers.

The between-years fluctuations in maximum abundance and biomass of *A. priodonta* in both lakes were wide (Fig. 7), but due to the complexity of lake ecosystem structures, the reason for this is still unknown. Kangur et al. (2002) suggested that this difference might be the change in climate accompanied by alteration of food webs, increased

predation by fish, or harmful effects of Cyanobacteria, whose abundance has increased during recent decades. These fluctuations are presumably independent of changes in the rotifer community, at least in L. Vörtsjärv. Also, competition for food resources between *Asplanchna* and smaller rotifers is doubtful in these study sites. Small rotifers are incapable of feeding on most of the algae found in the stomachs of *A. priodonta*. Indeed, large and colonial algae, which dominated the phytoplankton community, could only be consumed by *Asplanchna* and some copepods, while small rotifers mainly feed on smaller algae. Copepods are presumably sensitive to fish predation. By contrast, fish predation is unlikely to affect *A. priodonta* that much, owing to its smaller size and transparent body (Gilbert 1985, Kappes et al. 2000). However, no definite research has been conducted on the predation of fish on this species yet. Analyses of the influences of environmental parameters by Kappes et al. (2000) suggest that interannual fluctuations of abundance and biomass most likely reflect between-years variations of climate, implying that temperature is the most powerful predictor of *A. priodonta* abundance. Nevertheless, biomass and abundance of *A. priodonta* can still be affected to some extent by the structure of phytoplankton community, especially by the availability of Bacillariophyta and Chlorophyta, which are important food sources for the animal.

This study demonstrated that in lakes Peipsi and Vörtsjärv, the rotifer *A. priodonta* used algae as its primary food resource. Protozoa, which were highly abundant in one of the lakes, were most likely consumed by *A. priodonta* but could not be detected in the stomachs of the rotifer by the techniques employed in the study. Trophic interactions with other rotifers were likely absent. Yearly variations of *A. priodonta* abundance were noticeable and uncoupled from changes in the abundance and community structure of other rotifers in one of the studied lakes. Furthermore, the overall abundance of *A. priodonta* has decreased during the last decade. To explain such changes, complementary fieldwork and experimental research is needed. It is not yet fully understood, to what extent annual variations of *A. priodonta* abundance are induced by environmental factors or food web structure; little is known about the top-down control of this species. Such data are necessary for the development of correct management practices and will add to the understanding of lake ecosystems.

ACKNOWLEDGEMENTS

In this study, hydrobiological collections of the Võrtsjärv Centre for Limnology and the data of the Estonian State Monitoring Program were used. The authors are grateful to Dr. Reet Laugaste and Dr. Juta Haberman for providing data on phytoplankton and zooplankton, respectively. We are grateful to many others for their constructive criticism and suggestions, all of which contributed to this research.

REFERENCES

- Agasild H., Zingel P., Tõnno I., Haberman J. & Nõges T. (2007). Contribution of different zooplankton groups in grazing on phytoplankton in shallow eutrophic Lake Võrtsjärv (Estonia). *Hydrobiologia*, 584, 167-177.
- Brandl Z. (2005). Freshwater copepods and rotifers: predators and their prey. *Hydrobiologia*, 546(1), 475-489.
- Chang K.-H., Doi H., Nishibe Y. & Nakano S.-I. (2010). Feeding habits of omnivorous *Asplanchna*: comparison of diet composition among *Asplanchna berricki*, *A. priodonta* and *A. girodi* in pond ecosystems. *Journal of Limnology*, 69, 209-216.
- Dorn N.J. & Wojdak J.M. (2004). The role of omnivorous crayfish in littoral communities. *Oecologia*, 140, 150-159.
- Dumont H.J. (1977). Biotic factors in the population dynamics of rotifers. *Archiv für Hydrobiologie – Beiheft Ergebnisse der Limnologie*, 8, 98-122.
- Ghadouani A., Pinel-Alloul B., Zhang Y., Prepas E.E. (1998). Relationships between zooplankton community structure and phytoplankton in two lime-treated eutrophic hardwater lakes. *Freshwater Biology* 39, 775-790.
- Gilbert J.J. & Williamson C.E. (1978). Predator-prey behavior and its effect on rotifer survival in associations of *Mesocyclops edax*, *Asplanchna girodi*, *Polyarthra vulgaris*, and *Keratella cochlearis*. *Oecologia* 37, 13-22.
- Gilbert J.J. (1980). Observations on the susceptibility of some protists and rotifers to predation by *Asplanchna girodi*. *Hydrobiologia*, 73, 87-91.
- Gilbert J.J. (1985). Competition between Rotifers and *Daphnia*. *Ecology*, 66, 1943-1950.
- Gilbert J.J. & Jack J.D. (1993). Rotifers as predators on small ciliates. *Hydrobiologia*, 255/256, 247-253.
- Guiset A. (1977). Stomach contents in *Asplanchna* and *Ploesoma*. *Archiv für Hydrobiologie – Beiheft Ergebnisse der Limnologie*, 8, 126-129.
- Haberman J. (1997). A comparative study of zooplankton in two large lakes of Estonia. *Proceedings of the Estonian Academy of Sciences: Biology, Ecology*, 46, 225-245.
- Haberman J. (1998). Zooplankton of Lake Võrtsjärv. *Limnologica*, 28, 49-65.
- Haberman J., Jaani A., Kangur A., Kangur K., Laugaste R., Milius A., Mäemets H. & Pihu E. (2000). Lake Peipsi and its ecosystem. *Proceedings of the Estonian academy of Science: Biology, Ecology*, 49, 3-18.
- Haberman J. (2001). Zooplankton in Lake Peipsi: Fauna and Flora (Pihu E., Haberman J., eds).. *Sulemees Publishers, Tartu*, 50 - 62
- Haberman J. & Laugaste R. (2003). On characteristics reflecting the trophic state of large and shallow Estonian lakes (L. Peipsi, L. Võrtsjärv).. *Hydrobiologia*, 506, 737-744.
- Hampton S. E., & Gilbert, J. J. (2001). Observations of insect predation on rotifers. *Hydrobiologia*, 446(1), 115-121.
- Hansson L.A., Gustafsson S., Rengefors K., Bomark L. (2007). Cyanobacterial chemical warfare affects zooplankton community composition. *Freshwater Biology*, 52, 1290-1301.
- Hessen D. & Nilssen J. (1985). Factors controlling rotifer abundances in a norwegian eutrophic lake: an experimental study. *Annales de Limnologie – International Journal of Limnology*, 21, 97-105.
- Hofmann W. (1983). Interactions between *Asplanchna* and *Keratella cochlearis* in the Plußsee (north Germany).. *Hydrobiologia* 104, 363-365.
- Hyslop E. (1980). Stomach contents analysis - a review of methods and their application. *Journal of Fish Biology*, 17, 411-429.
- José de Paggi S. (2002). Family Asplanchnidae Eckstein, 1883. In: *Rotifera. Vol. 6: Asplanchnidae, Gastrotrichidae, Lindiidae, Microcoididae, Synchaetidae, Trochosphaeridae and Filinia* (Eds T. Nogrady & H. Segers), pp. 1-27. *Guides to the identification of the microinvertebrates of the continental waters of the world 18*. Backhuys Publishers, Leiden.
- Kangur K., Milius A., Mols T., Laugaste R. & Haberman J. (2002). Lake Peipsi: Changes in nutrient elements and plankton communities in the last decade. *Aquatic Ecosystem Health and Management*, 5, 363-377.
- Kappes H., Mechenich C. & Sinsch U. (2000). Long-term dynamics of *Asplanchna priodonta* in Lake Windsborn with comments on the diet. *Hydrobiologia*, 432, 91-100.
- Kneitel J.M. (2007). Intermediate-consumer identity and resources alter a food web with omnivory. *Journal of Animal Ecology*, 76, 651-659.
- Kutikova L.A. (1970). Rotifers of the fauna of the USSR. Nauka, Leningrad. (in Russian).
- Laugaste R., Nõges P., Nõges T., Yastremskij V.V., Milius A., Ott I. (2001). Algae in Lake Peipsi: Flora and Fauna (Pihu, E., Haberman, J., eds). *Sulemees Publishers, Tartu*, 31-49.
- Laugaste R. & Haberman J. (2005). Seasonality of zoo- and phytoplankton in Lake Peipsi (Estonia) as a function of water temperature. *Proceedings of the Estonian Academy of Sciences: Biology, Ecology*, 54, 18-39.
- Laugaste R., Nõges T., Tõnno I. (2008). Algae in Lake Peipsi (Haberman J., Timm, T., Raukas A., eds.). *Eesti Loodusfoto, Tartu*, 251 – 270.
- Lima-Junior S. & Goitein R. (2001). A new method for the analysis of fish stomach contents. *Acta Scientiarum Maring*, 23, 421-424.
- Mayer J., Dokulil M.T., Salbrechter M., Berger M., Posch T., Pfister G., Kirschner A.K.T., Velimirov B., Steitz A. & Ulbricht T. (1997). Seasonal successions and trophic relations between phytoplankton, zooplankton, ciliate and bacteria in a hypertrophic shallow lake in Vienna, Austria. *Hydrobiologia*, 342, 165-175.
- Milovskaya L.V. & Bonk T.V. (2004). State of pelagic zooplankton community in the lake Kurilskoye during fertilization and post fertilization periods (1980-2000). Research of water biological resources of Kamchatka and of the northwest part of Pacific Ocean. *Selected Papers, Petropavlovsk-Kamchatski: KamchatNIRO*, 7, 94-102.
- Nandini S., Rao T.R. (1998). Somatic and population growth in selected cladoceran and rotifer species offered the cyanobacterium *Microcystis aeruginosa* as food. *Aquatic Ecology*, 31, 283-298.

- Nandini S. (2000). Responses of rotifers and cladocerans to *Microcystis aeruginosa* (Cyanophyceae): A demographic study. *Aquatic Ecology*, 34, 227-242.
- Nogrady T., Wallace R.L. & Snell T.W. (1993). Rotifera. Vol. 1: Biology, ecology and systematics. Guides to the identification of the microinvertebrates of the continental waters of the world 4. SPB Academic Publishing bv, The Hague.
- Nõges T., Kisand V., Nõges P., Põllumäe A., Tuvikene L. & Zingel P. (1998). Plankton seasonal dynamics and its controlling factors in shallow polymictic eutrophic lake Võrtsjärv, Estonia. *International Review of Hydrobiology*, 83, 279-296.
- Nõges T., Järvet A., Kisand A., Laugaste R., Loigu E., Skakalski B. & Nõges P. (2007). Reaction of large and shallow lakes Peipsi and Võrtsjärv to the changes of nutrient loading. *Hydrobiologia*, 584, 253-264.
- Pociecha A. & Wilk-Wozniak E. (2008). Comments on the diet of *Asplanchna priodonta* (Gosse, 1850) in the Dobczycki dam reservoir on the basis of field sample observations. *Oceanological and Hydrobiological Studies*, 37, 63-69.
- Polis G.A. & Strong D.R. (1996). Food web complexity and community dynamics. *American Naturalist*, 147, 813-816.
- Pourriot R. (1977). Food and feeding habits of Rotifera. *Archiv für Hydrobiologie – Beiheft Ergebnisse der Limnologie*, 8, 243-260.
- Robertson J. R. & Salt G. W. (1981). Responses in growth mortality, and reproduction to variable food levels by the rotifer, *Asplanchna girodi*. *Ecology*, 62, 1585-1596.
- Salt G.W. (1977). An analysis of the diets of five sympatric species of *Asplanchna*. *Archiv für Hydrobiologie – Beiheft Ergebnisse der Limnologie*, 8, 123-125.
- Salt G. W., Sabbadini, G. F. & Commins, M. L. (1978). Trophic morphology relative to food habits in six species of rotifers (Asplanchnidae). *Transactions of the American Microscopical Society*, 469-485.
- Soroki Y. I., & Paveljeva E. B. (1972). On the quantitative characteristics of the pelagic ecosystem of Dalnee Lake (Kamchatka). *Hydrobiologia*, 40(4), 519-552.
- Stemberger R. S. & Gilbert J. J. (1985). Assessment of threshold food levels and population growth in planktonic rotifers. *Archiv für Hydrobiologie – Beiheft Ergebnisse der Limnologie*, 21, 269-275.
- Starkweather P.L. (1980). Aspects of the feeding behavior and trophic ecology of suspension-feeding rotifers. *Hydrobiologia*, 73(1), 63-72.
- Tardiff S.E. & Stanford J.A. (1998). Grizzly bear digging: Effects on subalpine meadow plants in relation to mineral nitrogen availability. *Ecology*, 79, 2219-2228.
- Virro T., Haberman J., Haldna M. & Blank K. (2009). Diversity and structure of the winter rotifer assemblage in a shallow eutrophic northern temperate Lake Võrtsjärv. *Aquatic Ecology*, 43, 755-764.
- Williamson C.E. (1983). Invertebrate predation on planktonic rotifers. *Hydrobiologia*, 104, 385-396.
- Xie P. (2001). Gut contents of bighead carp (*Aristichthys nobilis*) and the processing and digestion of algal cells in the alimentary canal. *Aquaculture*, 195, 149-161.
- Zingel P. & Haberman J. (2008). A comparison of zooplankton densities and biomass in Lakes Peipsi and Võrtsjärv (Estonia): Rotifers and crustaceans versus ciliates. *Hydrobiologia*, 599, 153-159.
- Zurek R. (2007). The basic paths of energy flow and matter transformations in a lowland dam reservoir ecosystem. *Oceanological and Hydrobiological Studies*, 36, 5-147.