DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
55

LIFE CYCLES OF PLANKTONIC ROTIFERS IN LAKE PEIPSI

TAAVI VIRRO

TARTU 1999

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

55

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
55

LIFE CYCLES OF PLANKTONIC ROTIFERS IN LAKE PEIPSI

TAAVI VIRRO

TARTU UNIVERSITY
PRESS

Chair of Hydrobiology, Department of Zoology and Hydrobiology, University of Tartu, Estonia

The dissertation was accepted for commencement of the degree of Doctor of Philosophy in Hydrobiology on May 31, 1999, by the Council of the Faculty of Biology and Geography, University of Tartu

Opponent: Paula Kankaala, Ph. D., senior researcher,
Lammi Biological Station, University of Helsinki, Finland

Commencement: room 301, Vanemuise St. 46 at 10.15 on October 29, 1999

Publication of this dissertation is granted by the University of Tartu

© Taavi Virro, 1999

Tartu Ülikooli Kirjastuse trükikoda
Tiigi 78, 50410 Tartu
Tellimus nr. 603

CONTENTS

LIST OF ORIGINAL PUBLICATIONS 6

INTRODUCTION 7

THE LAKE 10

MATERIALS AND METHODS 11

RESULTS AND DISCUSSION 13
    Taxonomic composition 13
    Seasonal dynamics 14
    Life cycle patterns 17

CONCLUSIONS 22

REFERENCES 23

APPENDIX 27

PEIPSI JÄRVE PLANKTILISTE KERILOOMADE ELUTSÜKLID. Summary in Estonian 37

ACKNOWLEDGEMENTS 38

PUBLICATIONS 39

LIST OF ORIGINAL PUBLICATIONS

This dissertation is based on the following papers referred to by their Roman numerals.

I Virro, T., 1989. Sravnenie metodov sbora planktonnykh kolovratok (Rotatoria) na primere Chudskogo ozera. Proc. Acad. Sci. Estonian SSR. Biol. 38: 119–122. [The comparison of sampling methods of planktonic rotifers (Rotatoria) on the example of Lake Peipsi. In Russian].

II Virro, T., 1993. Rotifers from Lake Yaskhan, Turkmenistan. Limnologica 23: 233–236.

III Virro, T. & J. Haberman, 1993. The rotifers of Lake Peipus. Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 389–396.

IV Virro, T., 1995. The genus *Polyarthra* in Lake Peipsi. Hydrobiologia 313/314 (Dev. Hydrobiol. 109): 351–357.

V Virro, T., 1996. Taxonomic composition of rotifers in Lake Peipsi. Hydrobiologia 338: 125–132.

VI Virro, T. Taxonomic problems in the genus *Polyarthra* from Lake Peipsi. Proc. Estonian Acad. Sci. Biol. Ecol. (Submitted).

INTRODUCTION

Wide distribution and often numerous occurrence makes rotifers (Ph. Rotifera) an important component of fresh- and brackish water ecosystems. This group of aquatic micrometazoan invertebrates constitutes an essential and frequently dominating part of zooplankton, which is crucial link in the aquatic food web. Due to high population growth rates and short generation times, giving them a highly opportunistic character, rotifers can populate vacant niches in a very short time. Because of rapid reproduction, high ingestion rates and assimilation efficiencies, rotifers have remarkable production potential and play a considerable role in energy flow and nutrient cycling, competing successfully with microcrustaceans. Rotifers serve as food for many invertebrate predators (e.g. other rotifers, protozoans, cladocerans, copepods, malacostracans, insect larvae) and planktivorous fish, especially fish larvae. Feeding mainly on algae, bacteria, protozoa and detritus, rotifers can have a significant impact on these components of the aquatic food web. Rotifers are considered important (even most important in oligo- and mesotrophic lakes) carbon transporters between pico- and nanoplankton and macrozooplankton (Nogrady *et al.*, 1993). Rotifers are used as the indicators of water quality and trophic status of lakes.

The population sizes of rotifers in the field display extensive seasonal and random variations. Due to short generation times, annual development of rotifer communities is characterised by rapid temporal fluctuations of both their quantitative and qualitative parameters in response to environmental fluctuations. The dynamics of natural rotifer populations is governed by complex interrelationships between many biotic and abiotic factors. Among these, food, water temperature, oxygen content and predation are considered more significant (Dumont, 1977; Hofmann, 1977; Halbach, 1979; Walz, 1997).

The specific features of rotifer life cycles play also an important role in the determining of their population dynamics. The order Seisonidea (Cl. Digononta; 2 marine ectoparasitic species) reproduces exclusively bisexually, while the order Bdelloidea (Cl. Digononta; *ca* 360 non-planktonic species) reproduces entirely parthenogenetically. The present study deals with the rotifers of the class Monogononta (this class includes *ca* 1600 species). As a rule, the life cycle of monogonont rotifers is characterised by cyclical parthenogenesis (heterogony), where parthenogenetic (amictic) and bisexual (mictic) modes of reproduction alternate during population development (see, e.g. Kutikova, 1970; Birky & Gilbert, 1971; Gilbert, 1977; King & Snell, 1977a; Nogrady *et al.*, 1993). Parthenogenetic reproduction by amictic females is prevalent in this life cycle. In general, the development of the population begins with the hatching of amictic females from resting eggs deposited in previous periods. Owing to rapid reproduction of several parthenogenetic generations, the population can reach high densities in a short time taking maximum advantages of a favourable habitat. Switch from parthenogenetic to bisexual reproduction and resting egg production will reduce population growth, because amictic females are replaced by slowly reproducing mictic females and males. Depending on the proportion of mictic females in the population it may decrease to termination and continue in the diapausing phase in the form of resting eggs capable of surviving harsh environmental conditions.

The factors inducing transition to mictic female production are not yet thoroughly understood. It is evident that there are involved specific controlling stimuli, but not simply a change of the environment (Birky & Gilbert, 1971). A number of laboratory studies on some species of *Asplanchna*, *Notommata*, and *Brachionus* have revealed several external and internal factors initiating mictic female production (Birky & Gilbert, 1971; Hino & Hirano, 1976; Gilbert, 1977, 1980; Pourriot & Snell, 1983; Snell & Boyer, 1988). Dietary tocopherol (vitamin E), photoperiod, and population density have been stressed as external inducing stimuli. The effect of population density (crowding effect) is mediated by accumulation of a substance, probably a metabolite, released into the medium by rotifers (Gilbert, 1977; Carmona *et al.*, 1993). The rate of mictic female production has been found to be modulated by the age of parental female, food condition, water temperature, salinity, population density, and photoperiod (Birky & Gilbert, 1971; Gilbert, 1977; Pourriot & Clément, 1977; Pourriot & Snell, 1983; Carmona *et al.*, 1993; Lubzens *et al.*, 1993; Gómez *et al.*, 1997). Genetic factors play an important role in determining switch from amictic to mictic reproduction, sensitivity to mictic stimuli, and the extent of mictic response (Hino & Hirano, 1976; Buchner, 1977; Gilbert, 1977, 1980; Pourriot & Snell, 1983; Lubzens *et al.*, 1985; Carmona *et al.*, 1993; Walsh, 1993; Carmona *et al.*, 1995). Previous studies have shown that both inducing stimuli and their responses are species, population, and even clone specific.

Transition to bisexual reproduction may occur in different phases of the population cycle. The moment of timing is important for its consequences on the genetic structure of the population and on its dynamics (Birky & Gilbert, 1971; King, 1980). Concerning timing, different life cycle patterns are distinguished (King, 1980). They represent specific adaptations to environmental unpredictability. Differences in life cycle patterns can favour the ecological and genetic divergence, and eventual speciation of rotifers in varying environments (Gómez *et al.*, 1995; Gómez *et al.*, 1997). Successful resting egg production (i.e., long-term fitness of a genotype), which has to be completed before deterioration of the environment, is also critically dependent on the timing of mixis (Birky & Gilbert, 1971; Pourriot & Snell, 1983; Gómez & Serra, 1996).

Special life cycle studies are carried out overwhelmingly in laboratory conditions. Although many field investigations deal with the dynamics of rotifer populations, studies addressing bisexual periods in natural populations of rotifers are not numerous (e.g. Dieffenbach, 1912; Wesenberg-Lund, 1930; Carlin, 1943; Pejler, 1957; Nipkow, 1961; Bogoslovsky, 1963, 1967, 1969; Amrén, 1964; Bosselmann, 1981; Carmona *et al.*, 1995; Miracle & Armengol-Díaz, 1995; Gómez *et al.*, 1997), and data on life cycle patterns can be obtained for some twenty or thirty species. In Estonia, Kutikova & Haberman (1986) and Haberman (1995) have dwelt on the life cycles of rotifers from Lake Võrtsjärv. Rotifers form an important component of zooplankton in Lake Peipsi (Haberman, 1978, 1996; Paper III). However, comparatively few studies deal particularly with rotifers (see Paper V for a short historical survey). Most studies have focussed on the dynamics of rotifer numbers, biomass, and production. Taxonomic composition has not been thoroughly investigated, nor have there been conducted any life cycle studies yet.

The aim of the present work is to examine the life cycles of dominating planktonic rotifers in Lake Peipsi. The following aspects have been investigated:

1. The taxonomic composition of rotifers and its seasonal changes.
2. The seasonal dynamics of rotifers with a focus on dominating species and their seasonal succession.
3. Alternation of parthenogenetic and bisexual phases of reproduction in population development (i.e., life cycles *s. str.*).

The dominating genus *Polyarthra* has been dealt with in greater detail regarding taxonomic problems in particular. Concerning methodological problems of rotifer sampling, plankton net and sedimentation methods have been compared. In the present thesis, as a result of the more profound investigation of recent years, some new information has been added to complement the results and conclusions published in earlier papers.

THE LAKE

Lake Peipsi (58°22'N–59°00'N, 26°57'E–27°59'E, surface area 2,611 km^2, average depth 8.3 m, maximum depth 12.9 m) is the northern part of the compound Lake Peipsi–Pihkva (3,558 km^2; named also L. Peipus–Pskov in some earlier papers; L. Pskovsko–Chudskoe in Russian) situated on the eastern border of Estonia.

L. Peipsi is eutrophic, with mesotrophic features in the northern part. Mean transparency is 2.12 m, and pH 8.21. The mean concentrations of total nitrogen, total phosphorus, chlorophyll *a*, and oxygen are 724 mg m^{-3}, 33 mg m^{-3}, 14.7 mg m^{-3}, and 11 mg l^{-1}, respectively (Nõges *et al.*, 1996; Möls *et al.*, 1996). Data on several chemical characteristics are presented also in Table 1, Paper V. L. Peipsi is holomictic-dimictic, unstratified. The ice cover lasts from December to April. Maximum surface temperatures (21–22°C) are usually reached in July (Jaani, 1996).

In the phytoplankton of Lake Peipsi, dominating are diatoms (*Melosira, Stephanodiscus*, *Asterionella*), cyanobacteria (*Aphanizomenon*, *Microcystis*, *Anabaena*, *Gloeotrichia*) and green algae (Nõges *et al.*, 1996). In L. Peipsi phytoplankton has usually three seasonal maxima: the spring peak in April–May, the summer peak in July–August, and the autumn rise in October–November (Nõges *et al.*, 1996).

The lake is rich in zooplankton, with numbers fluctuating between 43,600–2,241,500 ind m^{-3} (average 974,000 ind m^{-3}), and biomass from 0.09–3.69 g m^{-3} (average 1.86 g m^{-3}) (Haberman, 1996). L. Peipsi is one of the richest in fish among North European lakes. Total fish catches have usually been 9,000–12,000 tons (25–34 kg ha^{-1}) a year (Pihu, 1996).

MATERIALS AND METHODS

The present study is based on 335 qualitative and quantitative zooplankton samples collected (4 to 6 times a month) from June 1986 till March 1988 from the littoral (depth 0.5–1 m, sandy bottom) and pelagial (depth 7 m, clayey bottom) stations in the north-western part of Lake Peipsi (Paper V, Fig. 1). Due to technical problems and unfavourable weather, sampling from the pelagial was not possible during some short periods in 1986, 1987, and 1988. Qualitative samples were taken with a cone net (80 µm mesh) by repeated horizontal or vertical hauls. Integrated quantitative samples were collected with a 1-litre Ruttner sampler. One-litre sub-samples were subsequently taken and concentrated by sedimentation method after fixation. The samples were fixed with formaldehyde (final concentration 3–4%). Simultaneously, water temperature and transparency (Secchi depth) were measured (Paper V, Table 2; Paper III, Fig. 2).

It is generally accepted that plankton nets (especially with mesh sizes larger than 50 µm) do not retain efficiently smaller (e.g. *Anuraeopsis*) or soft-bodied rotifers (e.g. *Synchaeta*, *Polyarthra*) (Bottrell *et al.*, 1976; Green, 1977; Ruttner-Kolisko, 1977). Though widespread and simple, net method yields erroneous numbers and, consequently, a distorted structure for a rotifer community. In Paper I, plankton net and water-sampler-based sedimentation methods are compared. It appears that net method is absolutely unreliable for the quantitative collecting of rotifers. The total number of rotifers in net samples was 1 to 27 times (8.8 times on the average) lower than in sedimentation samples (Paper I). To correct the values of rotifer numbers in net samples, correction coefficients are suggested in Paper I. Considering the shortcomings of plankton nets, sedimentation method was chosen for quantitative sampling in the present study.

Rotifers were identified according to Lauterborn (1900), Kutikova (1970, 1978), Koste (1978), Mäemets & Kutikova (1979), Stemberger (1979), Koste & Shiel (1987), Shiel & Koste (1993). Illoricate rotifers were identified by their trophi that were dissolved out using a solution of potassium or sodium hypochlorite (KClO and NaClO, respectively). Identification of rotifers may be difficult, particularly in case of illoricate taxa, as is illustrated by the genus *Polyarthra* (Paper VI). External morphological features are not always reliable for species discrimination. Therefore, analysis of trophi is indispensable. Rotifer trophi appear to be species-specific and are considered extremely valuable taxonomic discriminators (Markevich, 1985; Koste & Shiel, 1989; Shiel & Koste, 1993).

Periods of bisexual reproduction were detected on the basis of the occurrence of haploid eggs, males or resting eggs.

Details of methods in each particular case are described in appended original papers.

RESULTS AND DISCUSSION

Taxonomic composition

The taxonomic composition of rotifers is analysed in Papers V and IV. A total of 161 rotifer taxa have been identified (Paper V, Table 3). Of these, approximately 70 are new in the lake, including 46 new records for Estonia. The greatest number of taxa occurred in August (93), followed by September (79) and June (66). In all, 19 families (Monogononta) with 41 genera are represented in the material. The dominant families are Brachionidae (32 taxa) and Synchaetidae (16). The most remarkable change in the rotifer assemblage takes place in May–June when, during rapid increase in water temperature, the winter complex (e.g. *Keratella hiemalis*, *Notholca cinetura*, *N. squamula*, *Synchaeta verrucosa*) is replaced by the summer community which consists of relatively eurythermal (e.g. *Filinia longiseta*, *Keratella cochlearis*, *K. irregularis*, *Polyarthra major*, *P. remata*, *Synchaeta oblonga*) or warm stenothermal taxa (e.g. *Anuraeopsis fissa*, *Polyarthra longiremis*, *Trichocerca pusilla*). The composition of the dominating group as well of the whole rotifer assemblage is typical of eutrophic lakes in the northern temperate zone (Kutikova, 1970; Bērziņš, 1978). Presence of oligotrophic species reflects the transition stage of L. Peipsi from moderately eutrophic to eutrophic. Nearly all recorded taxa are rather common with either cosmopolitan or widespread distribution. Some species of zoogeographic interest, including the supposedly endemic *Ploesoma peipsiense*, are reported in Paper V.

Among the dominating genera, the genus *Polyarthra* has been examined more thoroughly (Papers IV, VI). The genus, represented with six species in this material, appears to be quite interesting taxonomically. Due to high phenotypic similarity and wide intraspecific variability in the *Polyarthra* species, their external morphological features are not always reliable for species discrimination. As a result of the extensive overlap of most morphometric criteria, the *Polyarthra* species are difficult to distinguish by morphometric data only (Papers IV, VI). Analysis of trophi proves to be the most valuable tool in the discrimination of these taxa. This is particularly obvious on the example of taxonomic problems discussed in Paper VI. Thorough analysis of external and trophy morphology revealed that the confusing *Polyarthra* morphotaxa (see also Paper IV), camouflaging each other morphologically and ecologically and coexisting with *P. remata*, are actually *P.* cf. *dolichoptera* and *P.* cf. *vulgaris*. The possibility that these atypical forms are actually sibling species cannot be excluded.

Seasonal dynamics

The seasonal dynamics of the rotifers is described and analysed in Papers III and IV. Further studies have revealed some new information (unpublished) complementing these publications.

The numbers, biomass and production of rotifers in Lake Peipsi are high. Their contribution to total zooplankton production varies from 13.6% to 89.8% (Paper III). Rotifers are very important in the energy flow of the lake, assimilating 43.5% of all the energy assimilated by zooplankton (Paper III).

Seasonal development of rotifers is highly fluctuating with rapid changes in numbers (Paper III, Fig. 2; Appendix, Fig. 1). Two main peaks (first in May, the second in August or September), and a slight rise in winter (January–March) can be distinguished. In 1986, maxima occurred in August (1,570 ind l^{-1}) and September (750 ind l^{-1}), in the littoral and pelagial, respectively. In 1987, maxima occurred in June, both in the littoral and pelagial (1,630 and 310 ind l^{-1}, respectively). The June maximum in the littoral is built up by *Synchaeta oblonga*, in the pelagial by *Conochilus unicornis, C. hippocrepis* and *Polyarthra dolichoptera*. The August maximum of the littoral is produced mainly by *Keratella cochlearis*, *Polyarthra remata* and *Anuraeopsis fissa*. *K. cochlearis* is prevailing also in the September maximum of the pelagial, while *K. hispida* and *S. kitina* occupy the second place. *Notholca squamula* and *Synchaeta verrucosa* are making winter rise both in the littoral and pelagial.

The following species are dominating: *Anuraeopsis fissa*, *Conochilus hippocrepis*, *C. unicornis*, *Kellicottia longispina*, *Keratella cochlearis*, *K. irregularis*, *Notholca squamula*, *Polyarthra dolichoptera*, *P. longiremis*, *P. luminosa*, *P. major*, *P. remata*, *Synchaeta kitina*, *S. oblonga*, *S. verrucosa* (Papers III, IV, V).

The population dynamics of the dominants is given in Papers III and IV, and in Appendix (Figs 2–8). Development of the dominant species displays distinct temperature related seasonality.

Notholca squamula, *Polyarthra dolichoptera* and *Synchaeta verrucosa* can be considered winter dominants. Together with the less numerous *Keratella hiemalis*, *Notholca cinetura* and *Polyarthra vulgaris* they form a typical thermophobic association. The most abundant was *N. squamula* (240 ind l^{-1} in February). The summer occurrence of *N. squamula*, although few in numbers, presents interest (Paper V; Appendix, Fig. 2). *N. squamula* is regarded as a cold stenothermic species, with optimal temperatures below 10°C, but able to tolerate higher temperatures for some time (Carlin, 1943; May, 1980; Bērziņŝ & Pejler, 1989a; Paper II). Intensive development of *S. verrucosa* starts in early spring (Paper III; Appendix, Fig. 3). Development of this cold stenotherm in Lake Võrtsjärv, where it also dominates, is similar (Haberman, 1995). Regarding *P. dolichoptera*, considered generally strictly cold stenothermal, it seems to be quite eurythermal in L. Peipsi, occurring from September till July (at 0–21.9°C) and having maxima in spring or early summer, while avoiding only the warmest period in July–August (Paper IV; Appendix, Fig. 2). Presence of *P. dolichoptera* at temperatures above 15°C, and its spring maxima have been reported from elsewhere as well (Carlin, 1943; May, 1983; Bērziņŝ & Pejler, 1989a; Shiel & Koste, 1993). Probably, *P. dolichoptera* prefers the water temperature range between 5–15°C (*op. cit.*).

In May–June, the winter complex is replaced by the summer assemblage which consists of relatively eurythermal or warm stenothermal species (Papers III, IV, V). The best expressed seasonal succession is revealed in the genera *Polyarthra* and *Synchaeta*. In June, *Polyarthra luminosa*, *P. major* and *P. remata* begin their development simultaneously (Papers III, IV; Appendix, Figs 3–4). Chujkov (1985) has reported that *P. luminosa* and *P. major* are food competitors, which excludes their simultaneous mass development. Preferring lower trophy (Ruttner-Kolisko, 1972), *P. major* is more abundant in the pelagial. *P. remata*, a eutrophic species (Bērziņŝ & Pejler, 1989b), has the highest densities among the summer *Polyarthra* species, particularly in the littoral (300 ind l^{-1} in August). *P. longiremis* joins them in July (Papers III, IV; Appendix, Fig. 5). This warm stenothermal and eutrophic species (Kutikova, 1970) was present only in the littoral.

In place of *Synchaeta verrucosa* there appear the summer dominants *S. kitina* and *S. oblonga*. *S. pectinata* and the warm-water stenotherm *S. stylata* occur synchronously but in low numbers (Paper III; Appendix, Figs 5–6). In spite of its wide distribution, there are relatively few data about *S. kitina* in the literature. Evidently, this is caused by difficulties in determination of the *Synchaeta* species. In the present material *S. kitina* occurred from June to October (at water temperatures 5.9–21.9°C), with maxima in August or June (Paper III; Appendix, Fig. 5). This is in good accordance with the existing literature data (Carlin, 1943; Bērziņŝ & Pejler, 1989a; May, 1993) and confirms that *S. kitina* is eurythermal, having higher population densities at higher temperatures. In Lake Võrtsjärv, *S. kitina* is present from April till September, but does not dominate there (Kutikova & Haberman, 1986). On the ground of the present material it can be said that *S. oblonga* is the most abundant among the rotifers of L. Peipsi (1,560 ind l^{-1} in the littoral, in June) (Appendix, Fig. 6). *S. oblonga* is a widespread species, preferring eurythermal eutrophic waters (Bērziņŝ & Pejler, 1989a, 1989b; Shiel & Koste, 1993).

Anuraeopsis fissa is a typical thermophilic dominant in the littoral zone. *A. fissa* peaks in August (260 ind l^{-1}) at a temperature maximum (21.8°C) and disappears practically at the end of the month (Paper III; Appendix, Fig. 5). It is considered a good indicator of eutrophic conditions (Bērziņŝ & Pejler, 1989b). The summer pelagic complex is dominated by *Conochilus hippocrepis* and *C. unicornis*. Their development is asynchronous (Paper III; Appendix, Figs 6–7). These close species are both feeding on detritus and bacteria (Pourriot,

1977) and have similar demands for pH, temperature (eurytherms), and oxygen content (Bērziņš & Pejler, 1987, 1989a, 1989c). Competition between *C. hippocrepis* and *C. unicornis* must be severe. Slight differences in their temperature optima (18°C and 16.5°C, respectively) (Bērziņš & Pejler, 1989a) cause a shift in their seasonality, an evident adaptation for avoiding competition.

Kellicottia longispina, *Keratella cochlearis* and *K. irregularis* are practically perennial, although they have population maxima in summer (Paper III; Appendix, Figs 7–8). *K. longispina* is an indicator of oligotrophy, but it is found in relatively eutrophic lakes as well, often quite abundantly (Haberman, 1976; Bērziņš & Pejler, 1989b). In L. Peipsi, the water temperature range for *K. longispina* was 0–21.9°C. In the pelagial, population maxima appeared in June (70 ind l^{-1} at 16.4°C, in 1986) or July (50 ind l^{-1} at 16.9°C, in 1987). In the littoral, *K. longispina* was not abundant. Frequently, this species has been regarded as a cold-water stenotherm. Evidently, *K. longispina* is actually eurythermal, as is shown on the basis of our data and those of Bērziņš & Pejler (1989a). Perennial occurrence and maxima in different months seem to be characteristic of this species (Carlin, 1943; Haberman, 1976; Larsson, 1978; Pontin, 1978). The polymorphic species *Keratella cochlearis* and *K. irregularis* inhabit plankton with several seasonally alternating morpho-ecological forms (Paper III; Appendix, Fig. 8).

In 1987, the population densities of rotifers were lower than in 1986, which was probably caused by the longer period of warming-up and lower summer temperatures in 1987.

Seasonal development of the majority of dominants (excl. stenotherms) (Appendix, Figs 2–8) reveals major increases in numbers both in the colder and warmer periods of the season (e.g. *K. longispina*, *K. cochlearis*, *K. irregularis*, *P. dolichoptera*, *P. luminosa*, *P. major*, *P. remata*, *S. kitina*, *S. oblonga*), or occurrence of maxima at different temperature ranges in different years (e.g. *P. major*, *P. remata*, *S. kitina*). The populations of these species may consist of distinct ecotypes with different demands for temperature. This possibility has been suggested by Pejler (1957), Bērziņš & Pejler (1989a) and Serra *et al.* (1997). It has been proved experimentally (King, 1972, 1977) that rotifer populations consist of temporarily restricted genotypically distinct and practically discrete demes adapted to different environmental conditions. Regarding the summer occurrence of *Notholca squamula*, mentioned above, the explanation could be the same (existence of winter and summer races). The data, given in Paper II, on the occurrence of *N. squamula* at water temperatures from 14–17°C, in a desert lake, also seem to support this opinion.

It should be considered that rotifer population dynamics is actually affected by an intricate complex of interacting abiotic and biotic factors, different in each particular water-body. Although it is generally accepted that water temperature and food are the most important factors (Dumont, 1977; Hofmann, 1977; May, 1983; Walz, 1997), it is very difficult to associate seasonal dynamics with concrete factors, and to extrapolate the pattern of seasonal dynamics from one lake to another.

Life cycle patterns

Occurrence of bisexual (mictic) reproduction has been detected in 26 species (Table 1). Concerning resting eggs, only those attached to females have been considered. For example, detached resting eggs of *Filinia terminalis* and *Synchaeta verrucosa*, often encountered outside their developmental cycles, could have originated from previous cycles. Owing to long periods of dormancy (from some weeks to several decades or even longer) the resting eggs of rotifers accumulate in aquatic sediments from which they emerge into plankton after passing the diapause or when stirred up by water movements (Pourriot & Snell, 1983; Nogrady *et al.*, 1993; Hairston, 1996). In case of *Polyarthra remata*, there were found amphoteric females carrying amictic and resting eggs (Paper IV). So far amphoteric females with the reproductive characteristics of both mictic and amictic females have been described for a few species of *Asplanchna*, *Conochiloides* and *Sinantherina* (Bogoslovsky, 1960; Kutikova, 1970; King & Snell, 1977b; Nogrady *et al.*, 1993). The amphoteric type of females can be regarded as a peculiar "bet-hedging" adaptation, which may be of use in unpredictable habitats.

Analysis of the life cycles of rotifers with inclusion of additional data (Table 1; Appendix, Figs 2–8), does not actually allow to distinguish definite periods of bisexual reproduction established in earlier Papers III and IV. Concentrating mostly on the vegetation period (in L. Peipsi from May to October), spread of mictic reproduction merely reflects the general seasonal distribution of rotifers. Data from Lake Yaskhan (Paper II) seem to display the same pattern. Bisexual reproduction can be initiated at any time of the year and can appear concurrently with parthenogenesis (Bogoslovsky, 1958; Nipkow, 1961; Nogrady *et al.*, 1993).

Life cycle patterns have been determined for 17 species (Table 2). Although mictic reproduction was registered for nine more species, their population maxima could not be detected because of the sporadic occurrence and low numbers, and their life cycle patterns were impossible to establish. All three basic life cycle patterns are represented in L. Peipsi (Table 2; Appendix, Figs 2–8; Papers III, IV). According to King (1980), one can distinguish: (1) early cycle species, initiating bisexual reproduction in the early phase of the population cycle; (2) midcycle species whose bisexual reproduction occurs near the population maximum; and (3) late cycle species whose bisexual reproduction occurs toward the end of the population cycle. In the two dominants, *Conochilus hippocrepis* and *C. unicornis* (Appendix, Figs 6–7), mictic periods have not been detected. As a rule, seasonally occurring monogononts must have

Table 1. Occurrence of bisexual reproduction in Lake Peipsi 1986–1988. o = haploid eggs; ♂ = males; ☼ = resting eggs

	J	F	M	A	M	J	J	A	S	O	N	D
Anuraeopsis fissa							☼	☼				
Asplanchna priodonta						♂						
Collotheca mutabilis									☼			
C. ornata										☼		
Euchlanis deflexa									♂	♂		
E. dilatata									♂	♂		
E. lyra											♂	
Filinia longiseta								o☼	o	o		
F. terminalis						☼						
Kellicottia longispina						o☼						
Keratella cochlearis						☼						
K. irregularis						☼		☼				
K. quadrata						o						
Lecane lunaris									☼			
Notholca squamula		☼	☼									
Polyarthra dolichoptera					☼	o☼					o☼	
P. longiremis								o				
P. luminosa								o	o	o		
P. major							o	o	o	☼		
P. remata						o	o☼	o☼	o			
Synchaeta kitina										☼		
S. lakowitziana										☼		
S. oblonga					☼			☼				
S. pectinata						☼	☼					
S. stylata							☼					
S. verrucosa				♂	♂☼							

bisexual reproduction to survive in a changing environment. When the mictic period was very short it might have remained unnoticed. In some years, owing to unfavourable conditions, mictic reproduction may not take place (Pozuelo & Lubian, 1993). Several, often perennial, species (e.g. *C. unicornis*, *K. longispina*, *K. cochlearis*) can be acyclic, with no periodicity in bisexual reproduction. In larger lakes they can reproduce throughout the year or even in many years only parthenogenetically, omitting mixis altogether (Carlin, 1943; Pejler, 1957; Bogoslovsky, 1963, 1967; Kutikova, 1970). Perennial occurrence of *C. unicornis* has been reported earlier from L. Peipsi by Haberman (1976). Most likely, majority of the species discussed here are monocyclic, having one mictic period per year. *Polyarthra dolichoptera* and *Synchaeta oblonga* may be dicyclic with two bisexual periods (Paper IV; Appendix, Figs 2 & 6). However, resting eggs, causing the second cycle, may originate from previous years, but not from the first cycle of the current year (Kutikova, 1970).

Both the given (Table 2) and literature data (Table 3) demonstrate that life cycle patterns are not fixed at the species level. All data reveal extensive intraspecific variability. The same species can have different patterns in different habitats, and further, spatially or temporally differentiated sub-populations behave differently within one and the same habitat. Available data from both natural (Carlin, 1943; Birky & Gilbert, 1971; Gilbert, 1977; King, 1980; Carmona *et al.*, 1995) and experimental rotifer populations (Carmona *et al.*, 1993, Pozuelo & Lubian, 1993) confirm that the high intraspecific and intrapopulational variability of life cycle patterns is a general law.

Table 2. Life cycle patterns of rotifers in Lake Peipsi 1986–1988. L = littoral; P = pelagial

Early cycle	Midcycle	Late cycle
K. cochlearis (L, P)	*A. fissa* (L)[1]	*N. squamula* (L, P)
P. remata (L)	*A. priodonta* (P)[4]	*P. dolichoptera* (L)
S. oblonga (L)[3]	*F. longiseta* (L)[5]	*P. luminosa* (P)
S. pectinata (P)[4]	*K. longispina* (P)[2]	*S. kitina* (P)[2]
S. stylata (L)[3]	*K. irregularis* (L, P)	
	P. dolichoptera (P)	
	P. longiremis (L)[1]	
	P. luminosa (L)	
	P. major (L, P)	
	P. remata (P)	
	S. verrucosa (L)[3]	

[1] Occurred only in littoral.
[2] Bisexual reproduction did not occur in the littoral.
[3] Bisexual reproduction did not occur in the pelagial.
[4] In the littoral population density was too low to determine the life cycle pattern.
[5] In the pelagial population density was too low to determine the life cycle pattern.

In the life cycle of monogonont rotifers, advantages of parthenogenetic (higher growth rates) and bisexual reproduction (greater variance among genotypes) are combined (King, 1977; Gómez *et al.*, 1995). Bisexual reproduction has two functions of adaptive significance: genetic recombination and production of resting eggs, i.e. resistant diapausing stages in rotifers (King, 1980). Resting eggs, able to disperse in space and time, as well as the egg banks created by them, are adaptations directed to survival in varying environments (Hairston, 1996).

Although bisexual reproduction can occur in any phase of the population cycle, it has most often been observed during population maxima (midcycle pattern), i.e. in the most favourable conditions (Tables 2 & 3). For two reasons, it would be adaptively advantageous for a rotifer population to have mixis at times of high population density (Birky & Gilbert, 1971; Gilbert, 1977; Serra & Carmona, 1993). First, mixis must lead to effective production of energy-rich resting eggs. This requires resources — abundant food supply. Second, resting egg production requires fertilisation, which may be more effective at higher population densities, when male-female encounter probability is higher. It can be hypothesized that early cycle rotifers have an advantage in highly unpredictable environments. On the contrary, late cycle species may have an advantage in stable environments. Midcycle rotifers, using optimal strategy, are best suited for "normal", moderately varying habitats. The effect of different life cycle patterns on the genetic structure of rotifer populations has been analysed by King (1980). Mixis in the early phase of the population cycle must preserve more genetic variability because it occurs before selection has eliminated most of the diverse genotypes hatched recently from resting eggs. Genotypic heterogeneity provides early cycle species with an evolutional advantage in unstable environments or when colonising new habitats. Bisexual reproduction in the middle or late cycle should fix homogeneity of the population, a suitable adaptation to occupying narrower niches.

Table 3. Life cycle patterns in other water-bodies. EC = early cycle; MC = midcycle; LC = late cycle; AC = acyclic

Species	Life cycle pattern (reference)
Anuraeopsis fissa	MC (4; 7), LC (7)
Asplanchna priodonta	EC (3; 5), MC (2)
Conochilus unicornis	MC (2; 6), LC (2), AC (2)
Filinia longiseta	MC (3), LC (3; 5)
Kellicottia longispina	AC (2; 6)
Keratella cochlearis	EC (5), MC (3; 4)
Notholca squamula	AC (2)
Polyarthra dolichoptera	EC (2; 5), MC (1; 2; 4)
P. luminosa	MC (4), LC (5)
P. major	EC (2), MC (2), LC (2), AC (2)
P. remata	MC (2), LC (2)
Synchaeta kitina	AC (2)
S. oblonga	AC (2)
S. pectinata	AC (2)
S. stylata	AC (2)
S. verrucosa	MC (4)

References (water-body):

1 = Amrén, 1964 (coastal ponds, Spitzbergen); 2 = Carlin, 1943 (Motalaström, Sweden); 3 = Dieffenbach, 1912 (ponds, Germany); 4 = Haberman, 1995 (L. Võrtsjärv, Estonia); 5 = Kutikova & Haberman, 1986 (L. Võrtsjärv, Estonia); 6 = Larsson, 1978 (L. Øvre Heimdalsvatn, Norway); 7 = Miracle & Armengol-Díaz, 1995 (L. Arcas-2, Spain).

Timing of bisexual reproduction has also general adaptive significance, related to environmental stability. In any case (early, mid-, late cycle), formation of resting eggs must be completed before a critical change of the environment (Pourriot & Snell, 1983).

CONCLUSIONS

1. Considering the shortcomings of plankton nets, water-sampler-based sedimentation method appears to be the only reliable method for quantitative sampling of rotifers.
2. The taxonomic composition of rotifers in Lake Peipsi is rich (161 taxa). The composition of the dominating group as well of the whole assemblage is highly typical of eutrophic lakes. Presence of species, characteristic of oligotrophic waters, reflects the current transition stage of the lake from moderately eutrophic to eutrophic.
3. The numbers, biomass and production of rotifers in Lake Peipsi are high. In their seasonal development, two main peaks (first in May, the second in August or September), and a rise in winter (January–March) can be distinguished.
4. The following species are dominating: *Anuraeopsis fissa*, *Conochilus hippocrepis*, *C. unicornis*, *Kellicottia longispina*, *Keratella cochlearis*, *K. irregularis*, *Notholca squamula*, *Polyarthra dolichoptera*, *P. longiremis*, *P. luminosa*, *P. major*, *P. remata*, *Synchaeta kitina*, *S. oblonga*, *S. verrucosa.*
5. Development of the dominant species reveals distinct seasonality. Among the dominating genera, the seasonal succession of congeneric clusters of *Polyarthra* and *Synchaeta* is best expressed. In several dominants, the increases in numbers at different temperature ranges suggest the possibility that the populations of these species may consist of distinct ecotypes with different demands for temperature.
6. The most remarkable change in the rotifer assemblage of Lake Peipsi takes place in May–June, when, during rapid increase in water temperature, the winter complex is replaced by the summer community.
7. Definite periods of bisexual reproduction can not be distinguished in Lake Peipsi. When concentrating mostly on the vegetation period, spread of mictic reproduction merely reflects the seasonal distribution of rotifers. Majority of the discussed species are monocyclic; *Polyarthra dolichoptera* and *Synchaeta oblonga* may be dicyclic.
8. All three basic life cycle patterns are represented in Lake Peipsi. The midcycle pattern is prevailing. The results of the study demonstrate intraspecific variability of life cycle patterns. Expressing adaptive trade-off between the advantages of parthenogenetic and bisexual reproduction, the patterns reflect conditions of the concrete habitat. It is apparent that mixis is an anticipating event, and not a response to environment deterioration, or an ending of rotifer population cycle.

REFERENCES

Amrén, H., 1964. Ecological and taxonomical studies on zooplankton from Spitsbergen. Zool. Bidr. Upps. 36: 209–276.

Bērziņš, B., 1978. Rotatoria. In J. Illies (ed.), Limnofauna Europaea. Gustav Fischer Verlag, Stuttgart, New York, Swets & Zeitlinger B. V., Amsterdam: 54–91.

Bērziņš, B. & B. Pejler, 1987. Rotifer occurrence in relation to pH. Hydrobiologia 147 (Dev. Hydrobiol. 42): 107–116.

Bērziņš, B. & B. Pejler, 1989a. Rotifer occurrence in relation to temperature. Hydrobiologia 175: 223–231.

Bērziņš, B. & B. Pejler, 1989b. Rotifer occurrence and trophic degree. Hydrobiologia 182: 171–180.

Bērziņš, B. & B. Pejler, 1989c. Rotifer occurrence in relation to oxygen content. Hydrobiologia 183: 165–172.

Birky, C. W. & J. J. Gilbert, 1971. Parthenogenesis in rotifers: The control of sexual and asexual reproduction. Am. Zool. 11: 245–266.

Bogoslovsky, A. S., 1958. Novye dannye po razmnozheniyu geterogonnykh kolovratok. Nablyudeniya za razmnozheniem *Sinantherina socialis* (Lin.). Zool. Zh. 37: 1616–1623. [New data on the reproduction of heterogonous rotifers. Observations on the reproduction of *Sinantherina socialis* (Lin.). In Russian].

Bogoslovsky, A. S., 1960. Nablyudeniya za razmnozheniem *Conochiloides coenobasis* Skorikov i ustanovlenie novoj dlya geterogonnykh kolovratok fiziologicheskoj kategorii samok. Zool. Zh. 39: 670–677. [Observations on the reproduction of *Conochiloides coenobasis* Skorikov and the statement of a physiological category of females new to heterogonous Rotifera. In Russian].

Bogoslovsky, A. S., 1963. Materialy k izucheniyu pokoyashchikhsya yaits kolovratok (soobshchenie 1). Byull. Mosk. Obshch. Isp. Prirody. Ot. Biol. 68 (6): 50–67. [Materials to the study of the resting eggs of rotifers (communication 1). In Russian].

Bogoslovsky, A. S., 1967. Materialy k izucheniyu pokoyashchikhsya yaits kolovratok. Soobshchenie 2. Byull. Mosk. Obshch. Isp. Prirody. Ot. Biol. 72 (6): 46–67. [Materials to the study of the resting eggs of rotifers. Communication 2. In Russian].

Bogoslovsky, A. S., 1969. Materialy k izucheniyu pokoyashchikhsya yaits kolovratok. Soobshchenie 3. Byull. Mosk. Obshch. Isp. Prirody. Ot. Biol. 74 (3): 60–79. [Materials to the study of the resting eggs of rotifers. Contribution 3. In Russian].

Bosselmann, S., 1981. Population dynamics and production of *Keratella hiemalis* and *K. quadrata* in Lake Esrom. Arch. Hydrobiol. 90: 427–447.

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24 (4): 419–456.

Buchner, H., 1977. Physiological basis of the reproduction of heterogonous Rotatoria. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 167–168.

Carlin, B., 1943. Die Planktonrotatorien des Motalaström. Zur Taxonomie und Ökologie der Planktonrotatorien. Medd. Lunds Univ. limnol. Inst. 5: 1–256.

Carmona, M. J., A. Gómez & M. Serra, 1995. Mictic patterns of the rotifer *Brachionus plicatilis* Müller in small ponds. Hydrobiologia 313/314 (Dev. Hydrobiol. 109): 365–371.

Carmona, M. J., M. Serra & M. R. Miracle, 1993. Relationships between mixis in *Brachionus plicatilis* and preconditioning of culture medium by crowding. Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 145–152.

Chujkov, Yu. S., 1985. Nekotorye dannye po ekologii kolovratok v evtrofirovannykh vodoemakh nizov'ev delty Volgi. In L. A. Kutikova (ed.), Kolovratki. Materialy vtorogo vsesoyuznogo simpoziuma po kolovratkam. Nauka, Leningrad: 167–171. [Some data about the ecology of rotifers in eutrophic water-bodies of the Volga delta. In Russian].

Dieffenbach, H., 1912. Biologische Studien an pelagischen Rädertieren. Int. Rev. ges. Hydrobiol. Hydrogr. Biol. Suppl. 3: 9–47.

Dumont, H. J., 1977. Biotic factors in the population dynamics of rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 98–122.

Gilbert, J. J., 1977. Mictic female production in monogonont rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 142–155.

Gilbert, J. J., 1980. Female polymorphism and sexual reproduction in the rotifer *Asplanchna*: Evolution of their relationship and control by dietary tocopherol. Am. Nat. 116: 409–431.

Gómez, A. & M. Serra, 1996. Mate choice in male *Brachionus plicatilis* rotifers. Functional Ecology 10: 681–687.

Gómez, A., M. J. Carmona & M. Serra, 1997. Ecological factors affecting gene flow in the *Brachionus plicatilis* complex (Rotifera). Oecologia 111: 350–356.

Gómez, A., M. Temprano & M. Serra, 1995. Ecological genetics of a cyclical parthenogen in temporary habitats. J. evol. Biol. 8: 601–622.

Green, J., 1977. Sampling rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 9–12.

Haberman, J., 1976. An ecological characterization of the rotifers dominating in the pelagic region of Lakes Peipsi–Pihkva and Võrtsjärv. In H. Haberman, J. Haberman & K. Elberg (eds), Productivity of Estonian fresh waters, Estonian Contributions to the International Biological Programme, 10. Acad. Sci. Estonian SSR, Tartu: 35–59.

Haberman, J., 1978. Seasonal dynamics of pelagic rotifers of Lakes Peipsi–Pihkva and Võrtsjärv. Proc. Acad. Sci. Estonian SSR, Biol. 27: 16–30.

Haberman, J., 1995. Dominant rotifers of Võrtsjärv (Estonia). Hydrobiologia 313/314 (Dev. Hydrobiol. 109): 313–317.

Haberman, J., 1996. Contemporary state of the zooplankton in Lake Peipsi. Hydrobiologia 338: 113–123.

Hairston, N. G. Jr., 1996. Zooplankton egg banks as biotic reservoirs in changing environments. Limnol. Oceanogr. 41 (5): 1087–1092.

Halbach, U., 1979. Introductory remarks: Strategies in population research exemplified by rotifer population dynamics. Fortschr. Zool. 25 (2/3): 1–27.

Hino, A. & R. Hirano, 1976. Ecological studies on the mechanism of bisexual reproduction in the rotifer *Brachionus plicatilis*. I. General aspects of bisexual reproduction inducing factors. Bull. jap. Soc. sci. Fish. 42: 1093–1094.

Hofmann, W., 1977. The influence of abiotic environmental factors on population dynamics in planktonic rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 77–83.

Jaani, A., 1996. Hydrology and water balance of Lake Peipsi. Hydrobiologia 338: 11–23.

King, C. E., 1972. Adaptation of rotifers to seasonal variation. Ecology 53: 408–418.

King, C. E., 1977. Genetics of reproduction, variation, and adaptation in rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 187–201.

King, C. E., 1980. The genetic structure of zooplankton populations. In W. C. Kerfoot (ed.), Evolution and Ecology of Zooplankton Communities. The University Press of New England, Hanover (N. H.): 315–328.

King, C. E. & T. W. Snell, 1977a. Sexual recombination in rotifers. Heredity 39: 357–360.

King, C. E. & T. W. Snell, 1977b. Genetic basis of amphoteric reproduction in rotifers. Heredity 39: 361–364.

Koste, W., 1978. Rotatoria. Die Rädertiere Mitteleuropas. (Überordnung Monogononta). Gebrüder Borntraeger, Berlin, Stuttgart, 673 pp., 234 pl.

Koste, W. & R. J. Shiel, 1987. Rotifera from Australian inland waters. II. Epiphanidae and Brachionidae (Rotifera: Monogononta). Invertebr. Taxon. 7: 949–1021.

Koste, W. & R. J. Shiel, 1989. Classical taxonomy and modern methodology. Hydrobiologia 186/187: 279–284.

Kutikova, L. A., 1970. Kolovratki fauny SSSR (Rotatoria). Podklass Eurotatoria (otryady Ploimida, Monimotrochida, Paedotrochida). Nauka, Leningrad, 744 pp. [Rotifers of the fauna of the USSR. In Russian].

Kutikova, L. A., 1978. Kolovratki. In O. S. Zvereva (ed.), Flora i fauna vodoemov Evropejskogo Severa (na primere ozer Bol'shezemel'skoj tundry). Nauka, Leningrad: 48–51, 168–170. [Rotifers. In Russian].

Kutikova, L. & J. Haberman, 1986. Rotifers (Rotatoria) of Lake Võrtsjärv. 1. Taxonomical and ecological survey. Proc. Acad. Sci. Estonian SSR, Biol. 35: 113–121.

Larsson, P., 1978. The life cycle dynamics and production of zooplankton in Øvre Heimdalsvatn. Holarct. Ecol. 1: 162–218.

Lauterborn, R., 1900. Der Formenkreis von *Anuraea cochlearis*. Ein Beitrag zur Kenntnis der Variabilität bei Rotatorien. I. Teil: Morphologische Gliederung des Formenkreises. Verhandl. d. heidelb. naturhist.-med. Vereins 6: 412–448.

Lubzens, E., G. Minkoff & S. Marom, 1985. Salinity dependence of sexual and asexual reproduction in the rotifer *Brachionus plicatilis*. Mar. Biol. 85: 123–126.

Lubzens, E., Y. Wax, G. Minkoff & F. Adler, 1993. A model evaluating the contribution of environmental factors to the production of resting eggs in the rotifer *Brachionus plicatilis*. Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 127–138.

Markevich, G. I., 1985. Osnovnye napravleniya idioadaptivnoi evolyutsii kolovratok. Chelyustnoj apparat. In L. A. Kutikova (ed.), Rotifera. Proceedings of the 2nd All-Union rotifer symposium. Nauka, Leningrad: 17–37. [The main trends of idioadaptive evolution of rotifers. Jaws. In Russian].

May, L., 1980. On the ecology of *Notholca squamula* Müller in Loch Leven, Kinross, Scotland. Hydrobiologia 73 (Dev. Hydrobiol. 1): 177–180.

May, L., 1983. Rotifer occurrence in relation to water temperature in Loch Leven, Scotland. Hydrobiologia 104 (Dev. Hydrobiol. 14): 311–315.

May, L., 1993. The ecology of *Synchaeta kitina* Rousselet in Loch Leven, Scotland. Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 305–315.

Mäemets, A. & L. Kutikova, 1979. A new rotifer *Ploesoma peipsiense* sp. nov. in Lake Peipsi. Proc. Acad. Sci. Estonian SSR, Biol. 28: 98–101.

Miracle, M. R. & X. Armengol-Díaz, 1995. Population dynamics of oxiclinal species in lake Arcas-2 (Spain). Hydrobiologia 313/314 (Dev. Hydrobiol. 109): 291–301.

Möls, T., H. Starast, A. Milius & A. Lindpere, 1996. The hydrochemical state of Lake Peipsi–Pihkva. Hydrobiologia 338: 37–47.

Nipkow, F., 1961. Die Rädertiere im Plankton des Zürichsees und ihre Entwicklungsphasen. Schweiz. Z. Hydrol. 23: 398–461.

Nogrady, T., R. L. Wallace & T. W. Snell, 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, 142 pp.

Nõges, T., J. Haberman, A. Jaani, R. Laugaste, S. Lokk, A. Mäemets, P. Nõges, E. Pihu, H. Starast, T. Timm & T. Virro, 1996. General description of Lake Peipsi–Pihkva. Hydrobiologia 338: 1–9.

Pejler, B., 1957. Taxonomical and ecological studies on planktonic Rotatoria from northern Swedish Lapland. K. svenska Vetensk. Akad. Handl. 6 (5): 1–68.

Pihu, E., 1996. Fishes, their biology and fisheries management in Lake Peipsi. Hydrobiologia 338: 163–172.

Pontin, R. M., 1978. A key to the freshwater planktonic and semi-planktonic Rotifera of the British Isles. Freshwater Biol. Assoc. sci. Publ. 38. Titus Wilson & Son Ltd., Kendal, 178 pp.

Pourriot, R., 1977. Food and feeding habits of Rotifera. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 243–260.

Pourriot, R.. & P. Clément, 1977. Comparison of the control of mixis in three clones of *Notommata copeus*. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 174–177.

Pourriot, R. & T. W. Snell, 1983. Resting eggs in rotifers. Hydrobiologia 104 (Dev. Hydrobiol. 14): 213–224.

Pozuelo, M. & L. M. Lubian, 1993. Asexual and sexual reproduction in the rotifer *Brachionus plicatilis* cultured at different salinities. Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 139–143.

Ruttner-Kolisko, A., 1972. Rotatoria. In H.-J. Elster & W. Ohle (eds), Die Binnengewässer, 26. Das Zooplankton der Binnengewässer, 1. E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart: 99–234.

Ruttner-Kolisko, A., 1977. Comparison of various sampling techniques, and results of repeated sampling of planktonic rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 13–18.

Serra, M., A. Galiana & A. Gómez, 1997. Speciation in monogonont rotifers. Hydrobiologia 358: 63–70.

Shiel, R. J. & W. Koste, 1993. Rotifera from Australian waters. IX. Gastropodidae, Synchaetidae, Asplanchnidae (Rotifera: Monogononta). Trans. r. Soc. S. Aust. 117: 111–139.

Snell, T. W. & E. M. Boyer, 1988. Threshold for mictic female production in the rotifer *Brachionus plicatilis* (Müller). J. exp. mar. Biol. Ecol. 124: 73–85.

Stemberger, R. S., 1979. A guide to the rotifers of the Laurentian Great Lakes. US EPA Publication EPA-600/4-79-021. Cincinnati, 185 pp.

Walsh, E. J., 1993. Rotifer genetics: integration of classic and modern techniques. Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 193–204.

Walz, N., 1997. Rotifer life history strategies and evolution in freshwater plankton communities. In B. Streit, T. Städler & C. M. Lively (eds), Evolutionary Ecology of Freshwater Animals. Birkhäuser Verlag, Basel: 119–149.

Wesenberg-Lund, C., 1930. Contributions to the biology of the Rotifera. Part II. The periodicity and sexual periods. Kgl. danske vidensk. Selsk. Skrifter, nat. math. Afd., 9, 2: 1–230.

APPENDIX

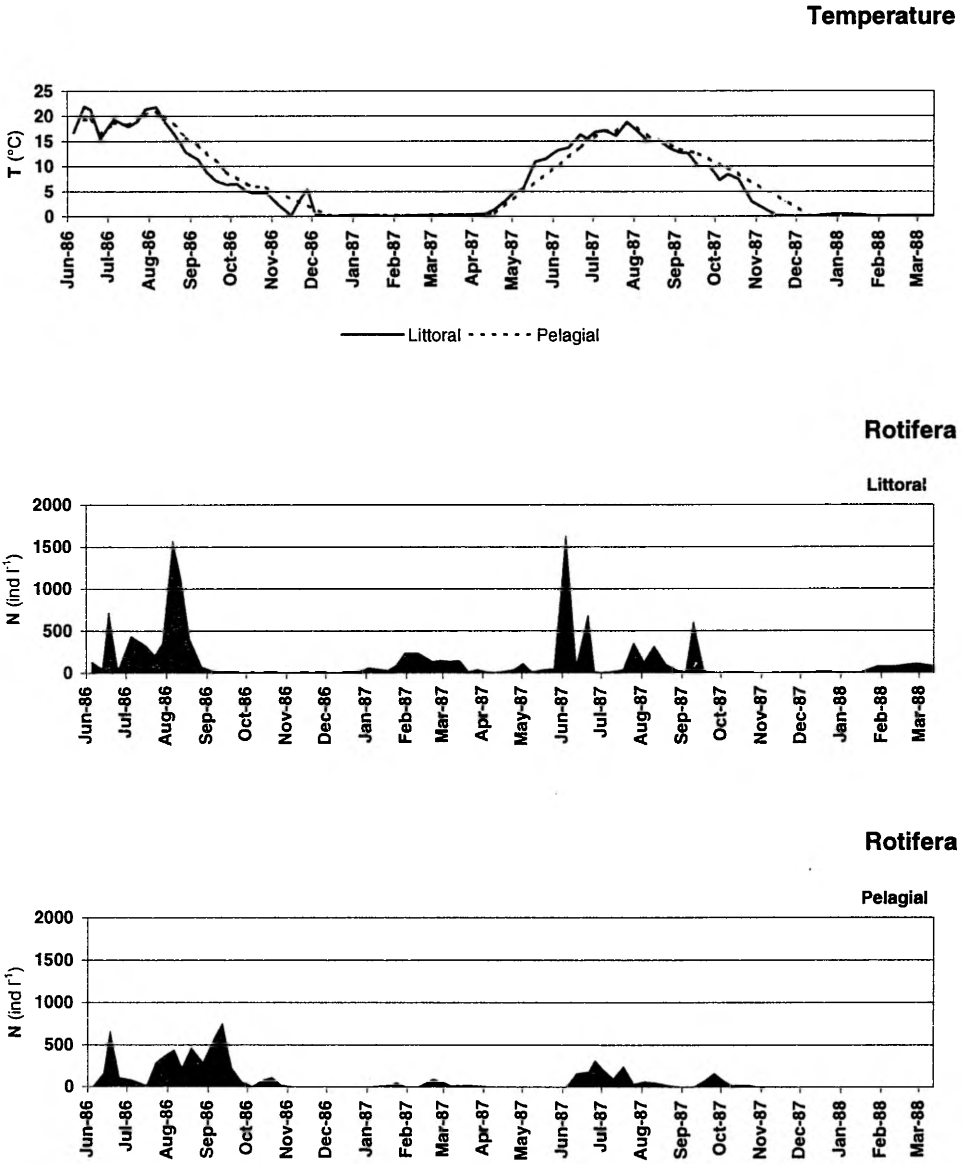
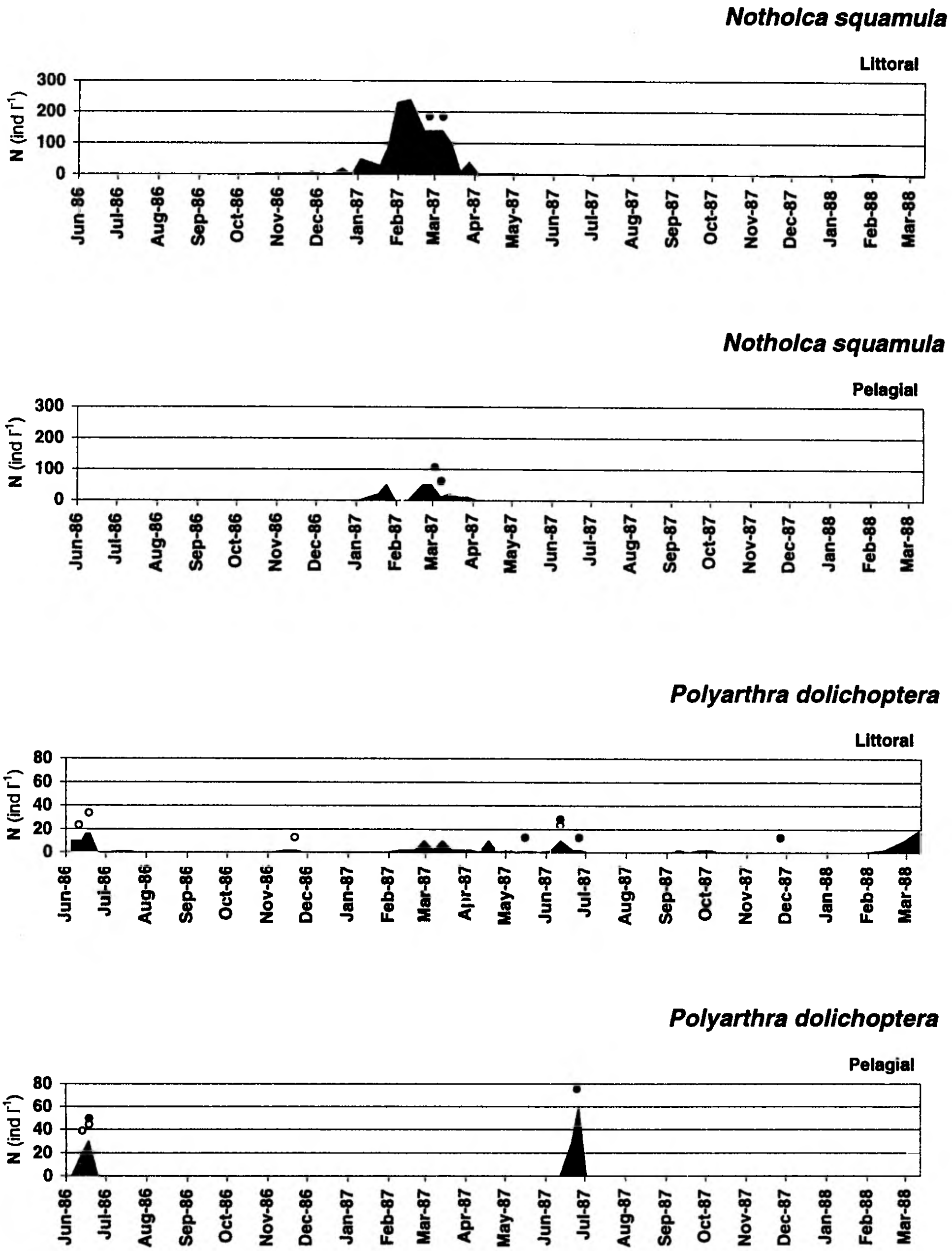


Fig. 1. The seasonal dynamics of rotifers and water temperature in Lake Peipsi in 1986–1988. T = temperature (°C); N = population density (ind l^{-1}).



Notholca squamula

Littoral

Notholca squamula

Pelagial

Polyarthra dolichoptera

Littoral

Polyarthra dolichoptera

Pelagial

Fig. 2. The seasonal dynamics of *Notholca squamula* and *Polyarthra dolichoptera* in Lake Peipsi in 1986–1988. N = population density (ind l^{-1}); o = haploid eggs, ● = resting eggs.

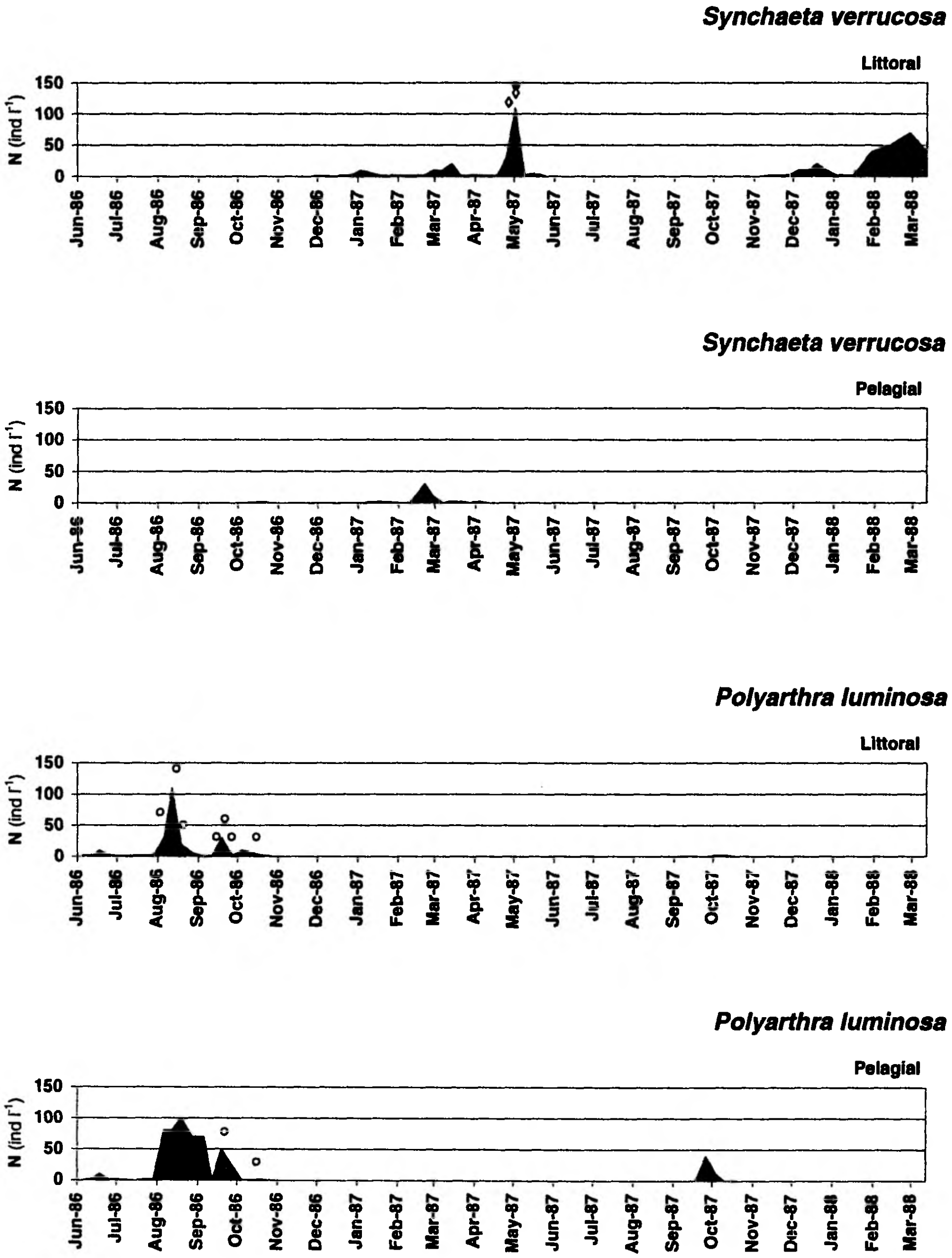


Fig. 3. The seasonal dynamics of *Synchaeta verrucosa* and *Polyarthra luminosa* in Lake Peipsi in 1986–1988. N = population density (ind l^{-1}); o = haploid eggs; ● = resting eggs; ◇ = males.

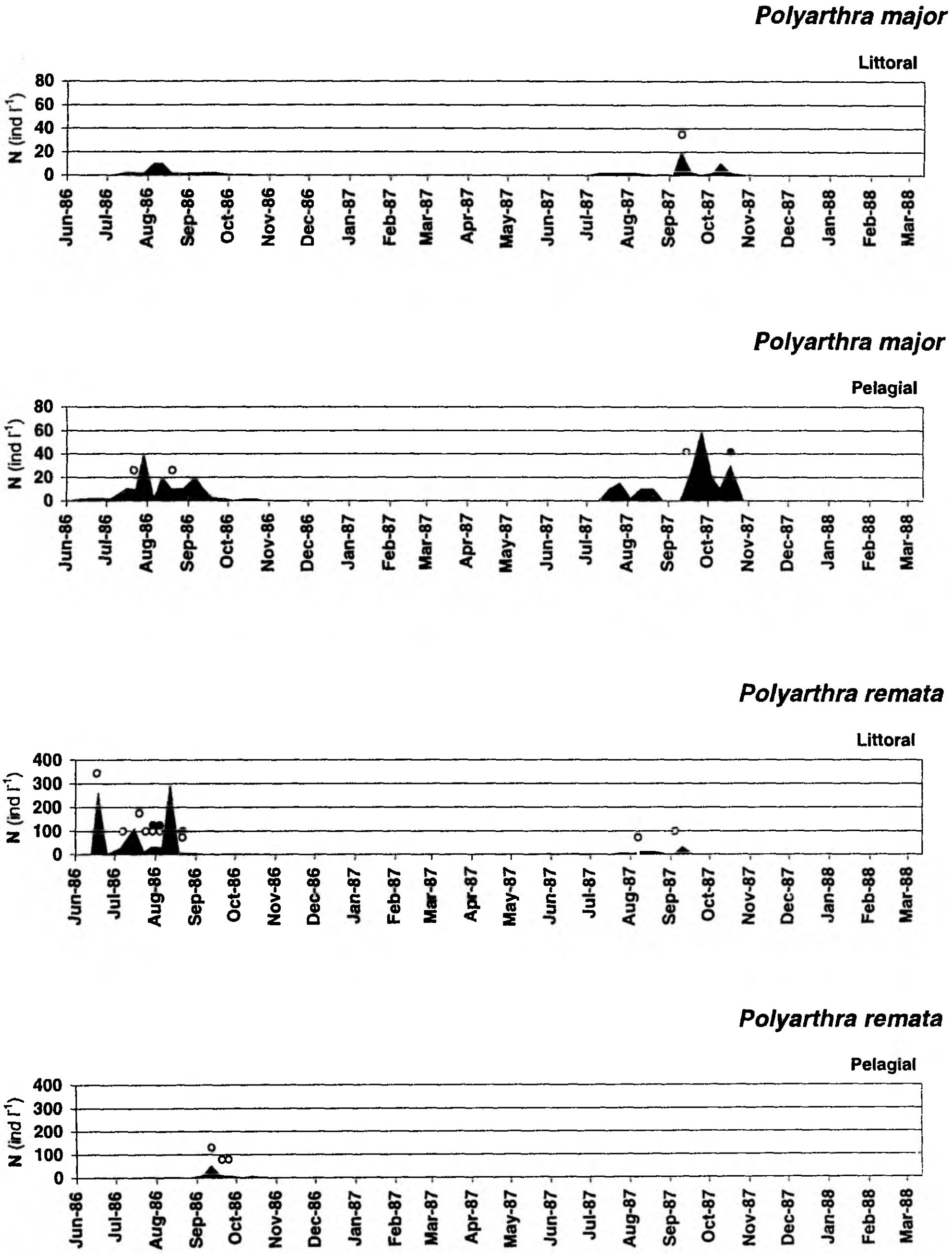


Fig. 4. The seasonal dynamics of *Polyarthra major* and *Polyarthra remata* in Lake Peipsi in 1986–1988. N = population density (ind l^{-1}); o = haploid eggs; ● = resting eggs.

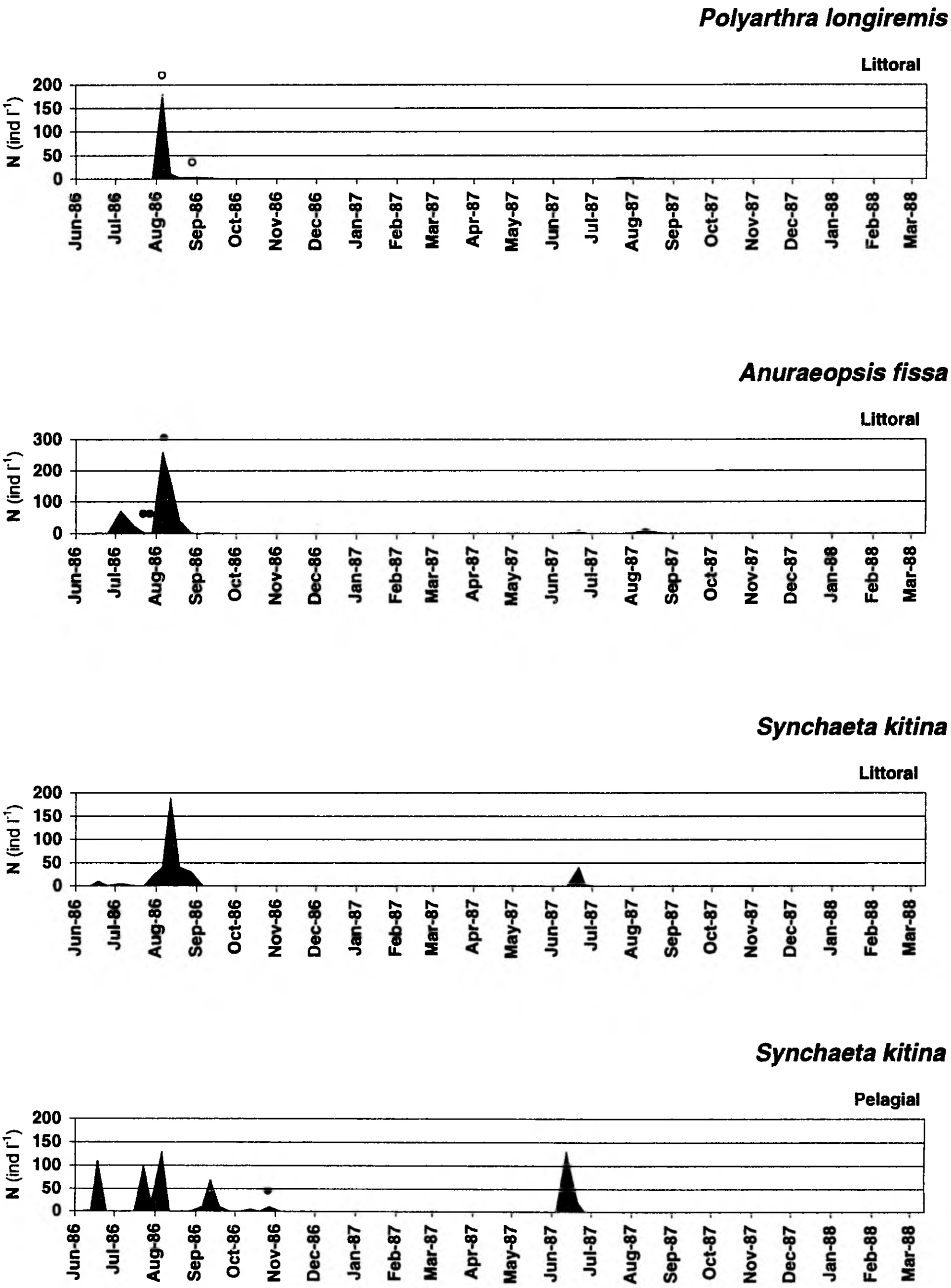


Fig. 5. The seasonal dynamics of *Polyarthra longiremis*, *Anuraeopsis fissa* and *Synchaeta kitina* in Lake Peipsi in 1986–1988. N = population density (ind l^{-1}); o = haploid eggs; ● = resting eggs.

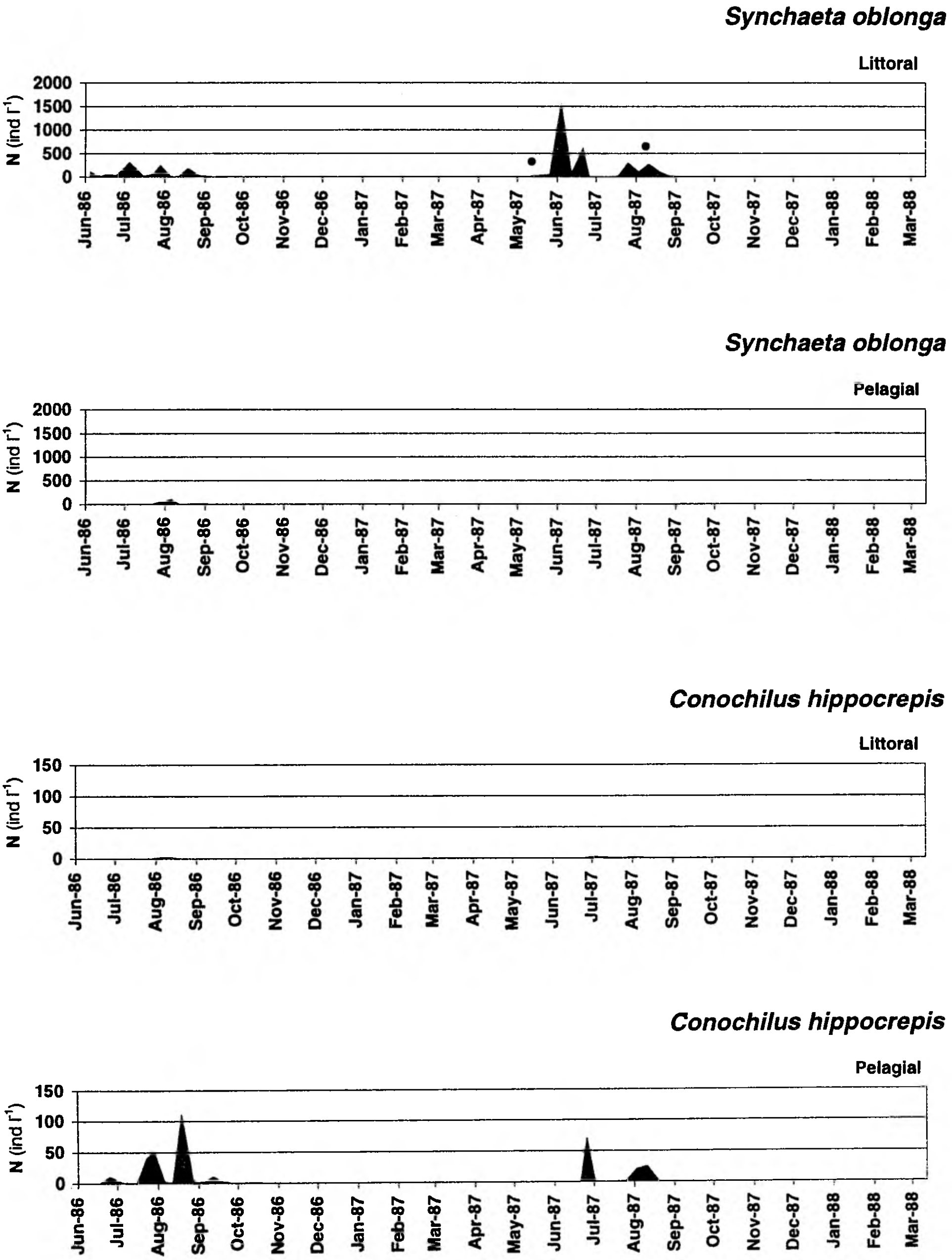


Fig. 6. The seasonal dynamics of *Synchaeta oblonga* and *Conochilus hippocrepis* in Lake Peipsi in 1986–1988. N = population density (ind l^{-1}); ● = resting eggs.

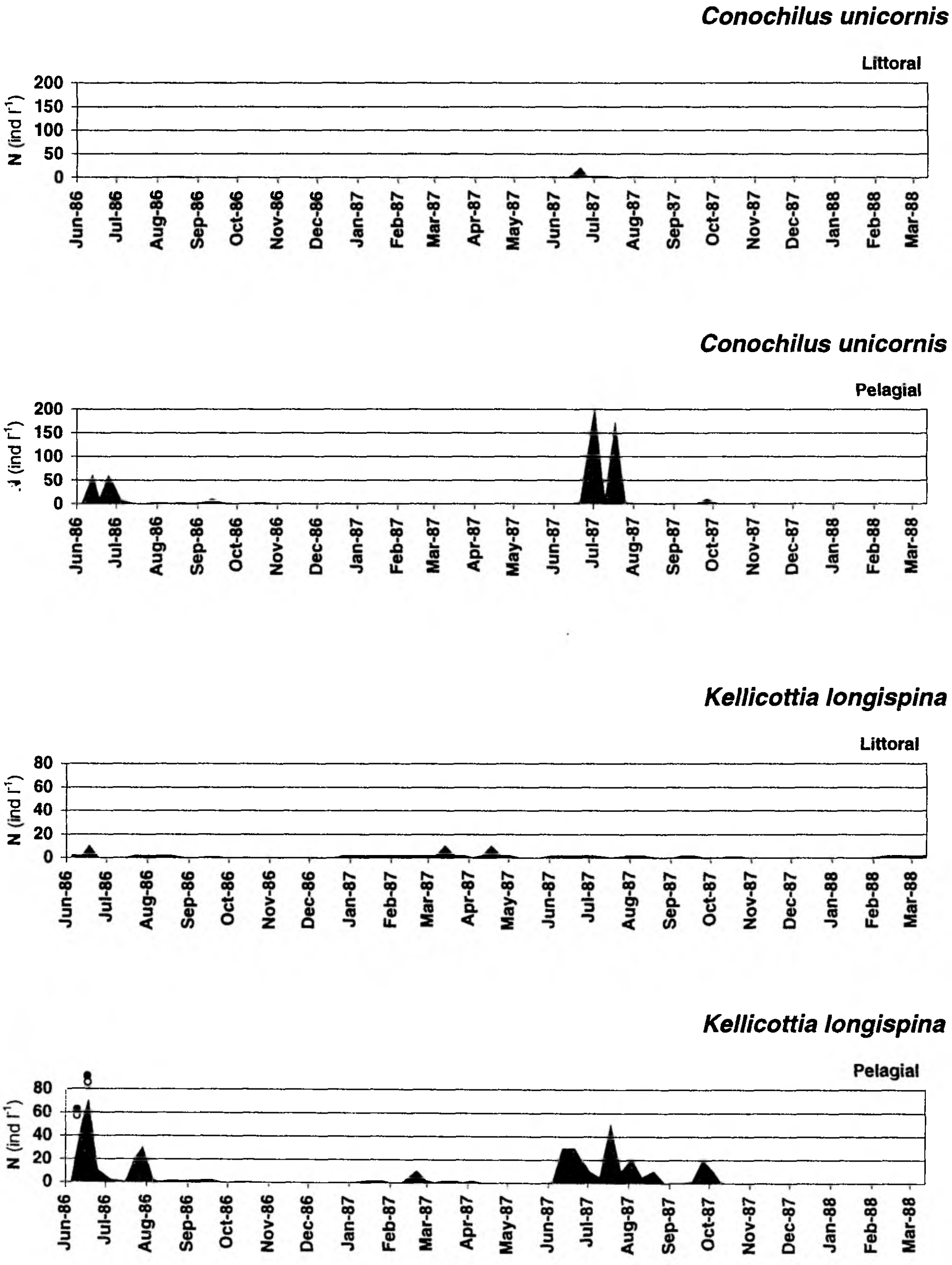


Fig. 7. The seasonal dynamics of *Conochilus unicornis* and *Kellicottia longispina* in Lake Peipsi in 1986–1988. N = population density (ind l^{-1}); o = haploid eggs; ● = resting eggs.

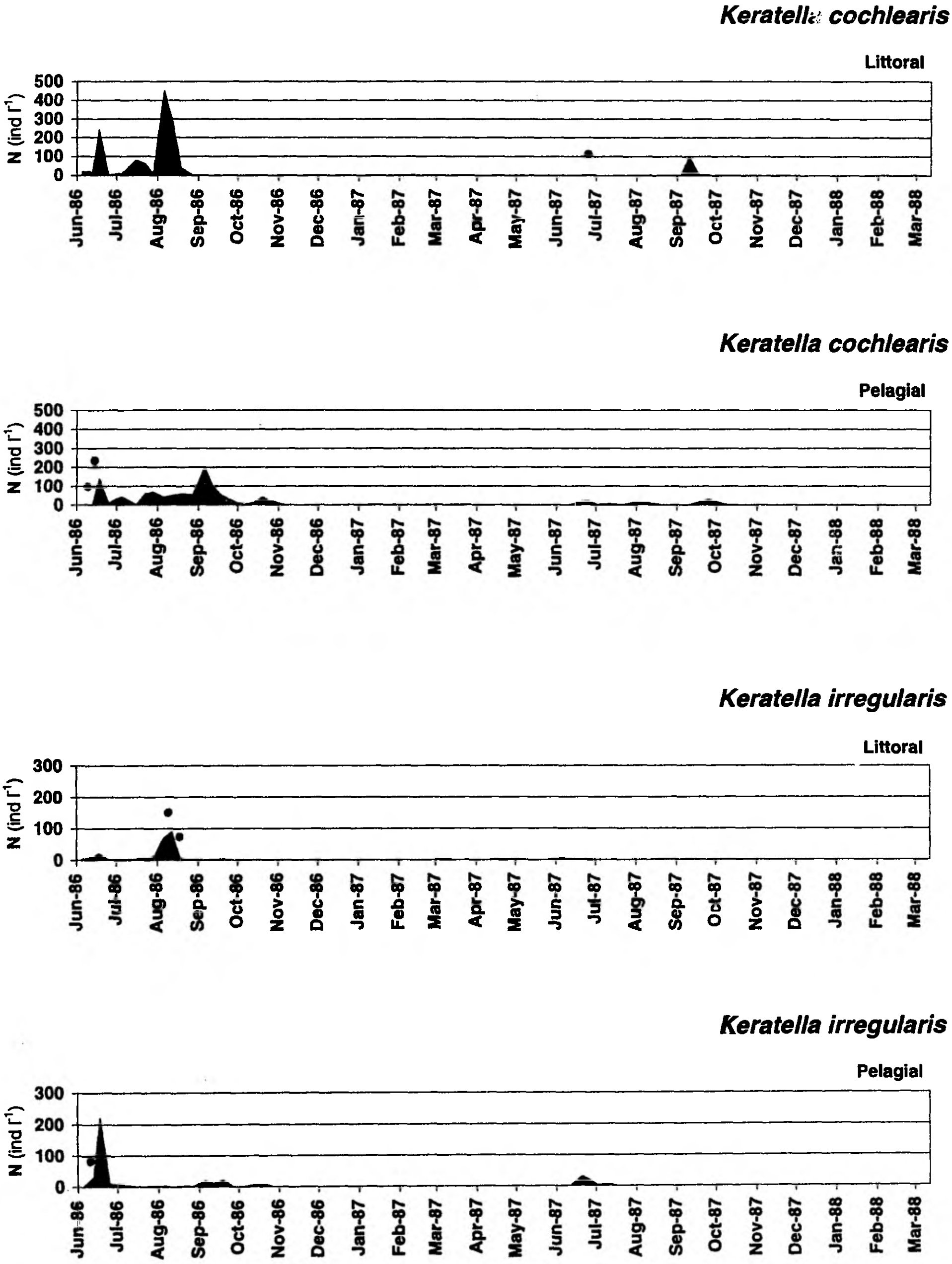


Fig. 8. The seasonal dynamics of *Keratella cochlearis* and *Keratella irregularis* in Lake Peipsi in 1986–1988. N = population density (ind l^{-1}); ● = resting eggs.

PEIPSI JÄRVE PLANKTILISTE KERILOOMADE ELUTSÜKLID

Kokkuvõte

Käesoleva töö eesmärgiks on saada ülevaade Peipsi järve domineerivate planktiliste keriloomade elutsüklitest. Selleks uuriti järgmisi aspekte: (1) keriloomakoosluse taksonoomilist koostist ning selle aastaringset muutumist; (2) keriloomade arvukuse sesoonset dünaamikat; (3) partenogeneetilise ja biseksuaalse sigimisfaasi vaheldumist keriloomapopulatsioonide arengus (e. elutsükleid *s. str.*). Süvendatult vaadeldi üht domineerivat perekonda *Polyarthra*. Sobiva püügimeetodi valimiseks võrreldi võrgu- ja sedimentatsioonimeetodit. Viimane tõestas ennast kui ainus usaldusväärne meetod keriloomade kvantitatiivsel kogumisel.

Leiti 161 taksonit keriloomi. Peipsi järve keriloomakoosluse taksonoomiline koostis on parasvöötme eutroofsetele järvedele tüüpiline. Domineerisid järgmised liigid: *Anuraeopsis fissa*, *Conochilus hippocrepis*, *C. unicornis*, *Kellicottia longispina*, *Keratella cochlearis*, *K. irregularis*, *Notholca squamula*, *Polyarthra dolichoptera*, *P. longiremis*, *P. luminosa*, *P. major*, *P. remata*, *Synchaeta kitina*, *S. oblonga*, *S. verrucosa*.

Kardinaalseim muutus Peipsi keriloomakoosluses toimub mais–juunis, kui talvised liigid asenduvad suvise kompleksiga. Kõige ilmekam on sesoonne suktsessioon perekondades *Polyarthra* ja *Synchaeta*. Mitme dominandi sesoonne levik, arvukuse tõusudega erinevates temperatuurivahemikes, vihjab võimalusele, et nende liikide populatsioonid koosnevad erisuguse temperatuurinõudlusega ökotüüpidest.

Kui vaadelda keriloomade kooslust tervikuna, siis ei eristu kindlaid sesoonselt piiritletud biseksuaalse sigimise perioode, vaid seda esineb aasta ringi, koondudes kõige enam vegetatsiooniperioodile. Suurem osa vaadeldud liikidest on tõenäoliselt monotsüklilised, kaks liiki, *Polyarthra dolichoptera* ja *Synchaeta oblonga* võivad olla ditsüklilised.

Miksist täheldati üldse 26 liigil, neist elutsüklite tüüpe oli võimalik määrata 17-l. Esindatud on kõik kolm põhilist tsüklitüüpi: vara-, kesk- ja hilistsüklilised. Valdab kesktsükliline strateegia. Tsüklitüüpidele on omane liigisisene varieeruvus. Väljendades adaptiivset kompromissi partenogeneetilise ja biseksuaalse sigimise eeliste vahel, peegeldavad tsüklitüübid pigem konkreetse elupaiga tingimusi. On ilmne, et miksis ei ole vastusreaktsioon keskkonnatingimuste halvenemisele ega keriloomade populatsioonitsükli lõppfaasiks, vaid ennetav sündmus.

ACKNOWLEDGEMENTS

In the first place, I would like to thank my family, my wife Viive and my sons Holger and Leiger, for creating an inspiring atmosphere at home. I am grateful to my parents for support, and to my brother Siimo for all kind of computer and technical assistance.

My sincere gratitude belongs to Dr. Juta Haberman and Dr. Lyudmila Kutikova for their valuable help and good scientific advice. Under the friendly guidance of these two ladies, I made my first steps in the field of rotiferology. I am obliged to Mrs. Ester Jaigma for revising the English text.

I would also like to thank my colleagues for their supportive and understanding attitude.

Finally, I thank the Estonian Science Foundation, Open Estonia Foundation, Stefan Batory Foundation and Polish Academy of Sciences for financial support during my studies.

PUBLICATIONS

I

Virro, T., 1989.
Sravnenie metodov sbora planktonnykh kolovratok (Rotatoria)
na primere Chudskogo ozera.
Proc. Acad. Sci. Estonian SSR. Biol. 38: 119–122.
[The comparison of sampling methods of planktonic rotifers (Rotatoria)
on the example of Lake Peipsi. In Russian].

EESTI NSV TEADUSTE AKADEEMIA TOIMETISED. BIOLOOGIA
ИЗВЕСТИЯ АКАДЕМИИ НАУК ЭСТОНСКОЙ ССР. БИОЛОГИЯ
PROCEEDINGS OF THE ACADEMY OF SCIENCES OF THE ESTONIAN SSR. BIOLOGY

1989, 38, 2

УДК 59.08 : 595.18

Таави ВИРРО

СРАВНЕНИЕ МЕТОДОВ СБОРА ПЛАНКТОННЫХ КОЛОВРАТОК (*ROTATORIA*) НА ПРИМЕРЕ ЧУДСКОГО ОЗЕРА

Основной задачей современных планктонологических исследований, особенно на продукционном уровне, является получение наиболее полных данных о численности всех компонентов планктона. Это крайне актуально и при исследовании коловраток. Разумеется, для получения таких данных необходимы достоверные методы сбора.

Известно, что самый простой и широкораспространенный метод сбора зоопланктона — сетной — не обеспечивает получения достоверных данных о численности особей, в том числе и коловраток. Большая часть коловраток из-за очень мелких размеров проходит полностью или частично сквозь сеть даже из самого плотного газа. В результате этого представление о зоопланктоне не соответствует истине:

1) показатели численности и биомассы коловраток значительно ниже реальных;

2) структура сообщества коловраток искажается в пользу более крупных, т. е. лучше улавливаемых форм;

3) структура зоопланктона в целом искажена: завышена роль ракообразных и занижена — коловраток.

Во избежание этого недостатка обычно предлагается ввести пересчетные коэффициенты.

Необходимость вычисления пересчетных коэффициентов возникла и для изучения численности коловраток Чудского озера. В настоящей статье рассмотрены предварительные данные пересчетных коэффициентов планктонных коловраток Чудского озера.

Материал и методика

Материал собирали с июня до октября 1986 г. и с января до апреля 1987 г. с одной пелагиальной станции озера на глубине 7 м в четырех километрах от г. Муствеэ. Тотальные вертикальные пробы собирали количественной сетью Джеди (газ № 75, размер ячеи 87 мкм). Параллельно отбирали интегральные осадочные пробы батометром Руттнера (объем 1 л). Обработку проб проводили по общепринятой методике (Киселев, 1956). Для предварительной оценки пересчетных коэффициентов сравнивали 13 пар проб из собранных 29 (по две пары в месяц в летне-осенний и по одной паре в месяц в зимне-весенний период).

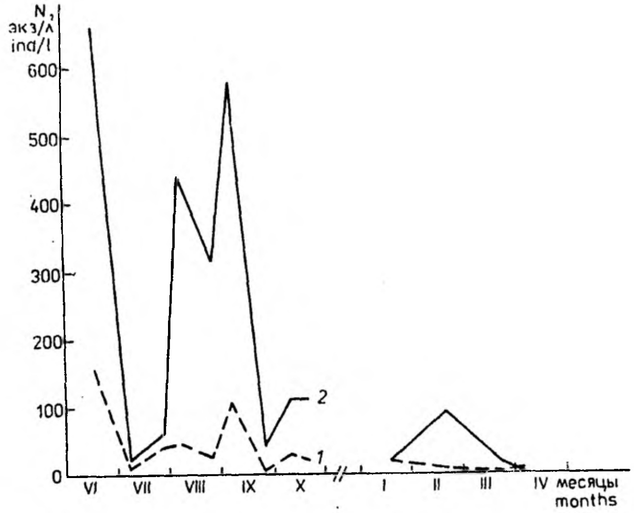
Пересчетные коэффициенты (K) определяли по формуле

$$K=\frac{N_o}{N_c},$$

где N_o — численность коловраток в осадочной пробе, N_c — численность в сетной пробе.

Результаты и обсуждение

Суммарная численность коловраток в наблюдаемый период по данным сетных проб не превышала 156 экз/л (рисунок). Однако данные



Численность (N) коловраток по сетной (*1*) и осадочной (*2*) пробам.
The number (N) of rotifers in net (*1*) and sedimentation samples (*2*).

осадочных проб показали, что численность их гораздо выше и достигает 660 экз/л, т. е. в среднем 8,8 раз выше, чем по сетным (таблица). Наибольшие различия наблюдались в июне и августе—сентябре в периоды массового развития коловраток, когда в планктоне появляется много мелких форм.

Несмотря на свои средние среди коловраток размеры, виды *Polyarthra luminosa* и *P. major* (130 и 160 мкм соответственно) имеют высокие пересчетные коэффициенты (таблица). Максимальная численность популяции *P. luminosa*, по данным осадочных проб, наблюдалась в начале августа и составляла 90 экз/л, в то время как сетной анализ показал 3 экз/л. Такое расхождение может быть связано с тем, что оба эти вида имеют низкую уловистость, так как из-за своих перистых плавников и мягких покровов или застревают, или проскальзывают через ячеи при фильтрации. Низкая уловистость рода *Polyarthra* указывается и другими авторами. По данным И. В. Телеша (1986), средний пересчетный коэф-

Средние пересчетные коэффициенты (K) для некоторых доминирующих видов коловраток Чудского озера

Mean correction factors (K) for several dominating rotifer species in Lake Peipsi

Виды Species	K_{min}—K_{max}	K	n
Kellicottia longispina (Kellicott)	1,9—2,0	2,0	2
Keratella cochlearis (Gosse)	1,2—21,3	9,0	8
Keratella irregularis (Lauterborn)	3,0—9,3	6,0	4
Polyarthra luminosa Kutikova	10,3—26,6	18,8	4
Polyarthra major Burckhardt	2,6—23,6	14,6	3
Synchaeta oblonga Ehrenberg	5,9—39,4	22,6	2
в целом для Rotatoria total Rotatoria	1,0—26,6	8,8	12

фициент для *P. dolichoptera*, *P. luminosa* и других подобных видов этого рода составляет 25,2 (газ № 72). Н. И. Силина (1987) отмечает, что сеткой из газа № 70—76 улавливается около 2% ($K=50$) особей *Polyarthra* размерами 100—150 мкм, и 10% ($K=10$) размерами 150—200 мкм.

Аналогично уменьшается уловистость вида *Synchaeta oblonga* (имеет мягкое сократимое коническое тело длиной около 160 мкм).

Пересчетный коэффициент для *Keratella cochlearis* (общая длина около 150 мкм) оказался тоже довольно высоким (таблица). Узкая ложкообразная форма тела позволяет особям легко проходить через ячеи. Максимум развития численности наблюдался в начале сентября и достигал по осадочной пробе 240 экз/л, но сетной — 25 экз/л.

Низкий пересчетный коэффициент установлен для *Kellicottia longispina* (таблица). Видимо, наличие длинных шипов препятствует прохождению особей через ячеи. По данным Н. И. Силиной (1987), этот вид улавливался (газ № 70—76) в среднем на 50% ($K=2$).

Несомненно, было бы идеально иметь пересчетные коэффициенты для всех видов коловраток в отдельности. Однако такие данные пока еще отсутствуют. Поэтому мы сочли целесообразным применять коэффициенты по размерным группам коловраток с учетом сходства телосложения.

При группировке коловраток учитывали характер их покрова, длину, ширину и форму тела, а также наличие длинных шипов или придатков. Принимали во внимание также размеры сита — не только ширину (87 мкм), но и диагональ (123 кмк). Так, через использованное нами сито № 75 проходили успешно особи от 90 до 120 мкм.

Исходя из вышеприведенного и полученных предварительных данных для 19 видов, мы выделили четыре фракции коловраток.

I. «Мелкие», $K=27$.

Коловратки длиной тела до 120 мкм. Полностью или почти полностью проходят через сито. Попадание их в сетные пробы крайне случайно. Поэтому пересчетный коэффициент для этой группы может быть гораздо выше приведенного.

Представители: *Anuraeopsis fissa, Cephalodella exigua, Polyarthra remata, Synchaeta kitina, Trichocerca rousseleti.*

II. «Средние», $K=14$.

Коловратки с удлиненным телом (длина 120—200 мкм, ширина 50—100 мкм), а также более полные мягкотелые коловратки. Довольно легко проскальзывают через ячеи.

Представители: *Conochilus unicornis, Keratella cochlearis, Polyarthra luminosa, Synchaeta oblonga, Trichocerca porcellus.*

III. «Умеренно крупные», $K=3$.

Коловратки с конусовидным мягким телом (длина 200 мкм и более), а также особи с очень длинными шипами или придатками (тело в этом случае может быть немного короче — около 150 мкм). Процент прохождения сквозь ячеи относительно низкий.

Представители: *Filinia longiseta, Kellicottia longispina, Keratella quadrata, Synchaeta pectinata, Trichocerca cylindrica.*

IV. «Очень крупные», $K=1$.

Панцирные и беспанцирные коловратки (230 мкм и более). Практически не проскальзывают сквозь ячеи.

Представители: *Asplanchna priodonta, Bipalpus hudsoni, Euchlanis dilatata, Notholca cinetura.*

Однако нельзя забывать, что использование пересчетных коэффициентов — действие вспомогательное. Теоретически получаемые усредненные величины численности коловраток приблизительны и могут значительно отличаться от действительности, так как мелкие особи, стопроцентно проходящие через сито, в общей сумме все-таки не учитываются.

Коэффициенты уместны для более общих случаев, таких, например, как для приблизительной оценки кормовой базы в рыбном хозяйстве или балансовых расчетов.

Осадочный метод более точен для определения количественных параметров коловраточного планктона. Единственный его недостаток: виды с очень низкой численностью могут не попадать в маленькие по объему батометры. Поэтому видовой состав в осадочных пробах может оказаться немного беднее, чем в сетных. По нашим данным, в осадочных пробах встречалось в среднем 1,4 раза меньше таксонов коловраток, чем в сетных. Для адекватного отражения видового состава следует употреблять батометры бóльших объемов, а также параллельно собирать пробы количественной сетью из плотного газа. Упомянутый минус существенно не снижает плюсы осадочного метода, оставаясь притом относительно простым и разумно трудоемким.

ЛИТЕРАТУРА

Киселев И. А. Методы исследования планктона // Жизнь пресных вод СССР. Т. 4. Ч. I. 1956, М.—Л., 183—265.

Силина Н. И. О методике количественного учета коловраток // Гидробиол. ж., 1987, **23**, № 5, 97—102.

Телеш И. В. Сравнительная эффективность методов количественного учета планктонных коловраток // Гидробиол. ж., 1986, **22**, № 4, 99—102.

Институт зоологии и ботаники
Академии наук Эстонской ССР

Поступила в редакцию
6/VI 1988

Taavi VIRRO

PLANKTILISTE KERILOOMADE (*ROTATORIA*) KOGUMISE MEETODITE VÕRDLUS PEIPSI JÄRVE NÄITEL

Võrgumeetodi ja sedimentatsioonimeetodi sobivuse hindamiseks ning paranduskoefitsientide esialgsete väärtuste leidmiseks kasutati Peipsi järve pelagiaali ühest proovipunktist kogutud materjali (juunist oktoobrini 1986, jaanuarist aprillini 1987).

Laialt levinud võrgumeetod ei anna keriloomade (*Rotatoria*) koosluse struktuuri ning parameetrite kohta usaldatavat teavet. Keriloomade rühma summaarne arvukus võrguproovide põhjal oli keskmiselt 8,8 korda madalam reaalsest. Ainus usaldusväärne ja töömahult mõistlik meetod on seetõttu sedimentatsioonimeetod.

On leitud paranduskoefitsientide (K) esialgsed väärtused mõnedele Peipsi järves domineerivatele keriloomadele: *Kellicottia longispina* $K=2{,}0$, *Keratella cochlearis* $K=9{,}0$, *K. irregularis* $K=6{,}0$, *Polyarthra luminosa* $K=18{,}8$, *P. major* $K=14{,}6$, *Synchaeta oblonga* $K=22{,}6$. Kuna praegu ei ole veel andmeid kõikide liikide kohta, siis pakutakse ajutise lahendusena välja paranduskoefitsientide kasutamine keriloomade suurusgruppide kaupa. Peetakse sobivaks eristada neli sellist gruppi.

Taavi VIRRO

THE COMPARISON OF SAMPLING METHODS OF PLANKTONIC ROTIFERS (*ROTATORIA*) ON THE EXAMPLE OF LAKE PEIPSI

For comparing the plankton net and sedimentation methods and for establishing the correction factors for rotifers parallel zooplankton samples were collected from a pelagic sampling station of L. Peipsi.

The widespread net method gives the distorted structure of a rotifer community and and its parameters and is therefore absolutely unreliable. The total number of rotifers in net samples was at an average 8.8 times lower than the real value.

The preliminary values of correction factors (K) for several dominating species are given: *Kellicottia longispina* $K=2.0$, *Keratella cochlearis* $K=9.0$, *K. irregularis* $K=6.0$, *Polyarthra luminosa* $K=18.8$, *P. major* $K=14.6$, *Synchaeta oblonga* $K=22.6$. As such data are still lacking for all the species, the system for using the correction factors by the size groups is suggested. Four size groups of rotifers were established: small, $K=27$; medium, $K=14$; moderately large, $K=3$; very large, $K=1$.

The sedimentation method appears to be the only reliable and, at the same time, reasonably labour-consuming for the adequate estimation of rotifer abundances and their community structure,

II

Virro, T., 1993.
Rotifers from Lake Yaskhan, Turkmenistan.
Limnologica 23: 233–236.

Limnologica 23 (3)
(1993) 233–236

LIMNOLOGICA

© by Gustav Fischer Verlag Jena

Department of Zoology, University of Tartu,
Tartu, Estonia

Rotifers from Lake Yaskhan, Turkmenistan

TAAVI VIRRO

With one Figure

Key words: Rotifers; Brackish and saline environments; Turkmenistan

Summary

29 rotifer taxa, 19 of which are new records, were identified in the pelagial of Lake Yaskhan, Turkmenistan. *Brachionus plicatilis* (represented by 3 forms), *Hexarthra fennica*, *Keratella quadrata* (4 forms) and *Synchaeta oblonga* were dominating. In addition to eurytherms, the presence of thermophilic *Hexarthra fennica* and *Brachionus* spp. is characteristic of the lake. The occurrence of *Notholca acuminata* and *N. squamula salina* is noteworthy. The rotifer community in Lake Yaskhan can be characterized as a complex of euryhaline and halophilic species. The typical halophilic assemblage, consisting of *Brachionus plicatilis* and *Hexarthra fennica*, is present.

Introduction

In 1981 and 1988 the Institute of Zoology and Botany (Tartu, Estonia) organized two expeditions to Lake Yaskhan, located in the river-bed of the Western Uzboi, in the Kara-Kum desert, in Turkmenistan. In the present paper the qualitative composition of the rotifer plankton of Lake Yaskhan is reported.

Lake Yaskhan consists actually of two different and isolated parts: Freshwater Yaskhan (length 1170 m, width 220 m, maximum depth 6.4 m, salinity 2.2–2.7 g · l^{-1}) and Salty Yaskhan (length 2300 m, width 200 m, maximum depth 3.4 m, salinity 25–50 g · l^{-1} depending on season) (KALLEJÄRV 1981). Lake Yaskhan feeds on fresh phreatic water, which causes relatively low mineralization in spite of desert climate. The salinity is fluctuating seasonally depending on the balance between evaporation and the underground water inflow.

Previous data about the rotifers of the lake are quite fragmentary. The first report on the zooplankton of Lake Yaskhan, based on samples collected in August 1936, was given by STAROSTIN (1948). 4 rotifer taxa were listed from Freshwater Yaskhan, none from Salty Yaskhan. More detailed data were published by HABERMAN (1981) as a result of the first expedition to Lake Yaskhan, organized by the Institute of Zoology and Botany in the spring of 1975. 14 rotifer taxa were recorded in Freshwater Yaskhan and 6 in Salty Yaskhan.

Material and Methods

Qualitative zooplankton samples were collected from the pelagic regions of Freshwater Yaskhan (henceforth FWY) and Salty Yaskhan (henceforth SY), from 3 and 2 sampling stations re-

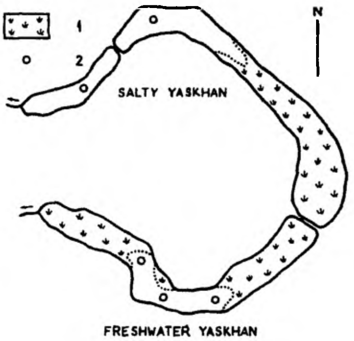


Fig. 1. Location of the sampling stations in Lake Yaskhan (1 = club-rush thickets; 2 = sampling station).

spectively (Fig. 1). Sampling was performed on the following dates:

13. 04. 1981 FWY
18. 07. 1981 FWY
27. 10. 1981 FWY, SY
14. 04. 1988 FWY, SY
19. 04. 1988 FWY
12. 07. 1988 FWY
04. 11. 1988 FWY

The samples were taken with a qualitative cone net of 87 µm mesh and fixed with formalin (final concentration 3–4%). It must be considered that the zooplankton net of 87 µm mesh used, not retaining species of smaller size, is actually too coarse for the adequate collection of rotifers (Bottrell et al. 1976; Hollowday 1985; Virro 1989). Owing to this, the possible smaller fraction of the rotifer community could not be detected here. In spring 1988 several samples from FWY were studied alive, focusing on iloricate rotifer species which are difficult to identify after fixation. The rotifer taxa were identified according to Kutikova (1970), except Bdelloida, which remained unidentified. Iloricate rotifers were identified on the basis of their trophi which were dissolved out using Eau de Javelle. The nomenclature of Kutikova (1970) is followed in the taxonomic list.

Results and Discussion

In total 29 rotifer taxa (19 species) were identified from Lake Yaskhan (Table 1). Of these, 19 are new to the lake. As shown in Table 1, 28 taxa (18 species) of rotifers were recorded from FWY. When compared to the earlier lists given by Starostin (1948) and Haberman (1981) 5 taxa were not encountered in the present material: *Brachionus calyciflorus calyciflorus* Pallas 1766, *B. quadridentatus cluniorbicularis* Skorikov 1894, *Keratella cochlearis* (Gosse 1851), *Lecane (Monostyla) bulla* (Gosse 1886) and *Trichocerca (Trichocerca) pusilla* (Lauterborn 1898). The taxonomic composition of rotifers in SY is poorer,

Table 1. List of rotifers from Lake Yaskhan, with comments on presence and relative abundance (– = not recorded, 1 = rare, 2 = common, 3 = abundant). FWY = Freshwater Yaskhan, SY = Salty Yaskhan.

Taxon	FWY						SY	
	1981			1988			1981	1988
	Apr.	July	Oct.	Apr.	July	Nov.	Oct.	Apr.
Asplanchna girodi Guerne 1888	–	–	–	1	–	–	–	–
Bdelloida *(indet.)*	–	1	–	1	–	1	–	1
Brachionus plicatilis plicatilis Müller 1786	–	1	1	–	–	–	1	–
B. plicatilis longicornis Fadeev 1925	1	1	1	1	3	1	1	1
B. plicatilis rotundiformis Tschugunoff 1921	–	1	2	–	–	–	–	–
B. quadridentatus ancylognathus Schmarda 1859	–	–	1	–	–	–	1	–
B. quadridentatus brevispinus Ehrenberg 1832	–	–	–	–	1	–	–	–
B. quadridentatus rhenanus Lauterborn 1893	–	–	1	–	–	–	1	–
Filinia longiseta limnetica (Zacharias 1893)	–	–	1	–	–	–	–	–
Hexarthra fennica (Levander 1892)	–	1	–	–	–	–	2	3
Keratella quadrata quadrata (Müller 1786)	–	–	–	–	–	1	3	–
K. quadrata dispersa Carlin 1943	2	1	–	1	–	–	–	–
K. quadrata frenzeli (Eckstein 1895)	–	–	–	–	–	1	–	–
K. quadrata reticulata Carlin 1943	3	2	1	3	1	3	1	1
Lecane (Lecane) luna luna Müller 1776	–	1	–	–	1	1	–	–
L. (L.) luna presumpta Ahlstrom 1938	–	1	–	–	–	–	–	–
L. (Monostyla) closterocerca (Schmarda 1859)	–	–	–	–	1	–	–	–
L. (M.) stenroosi (Meissner 1908)	–	1	–	–	–	–	–	–
Lepadella (Lepadella) ovalis (Müller 1786)	1	–	–	1	–	–	–	–
Lophocharis oxysternon (Gosse 1851)	1	–	–	1	–	1	–	–
Notholca acuminata acuminata (Ehrenberg 1832)	1	–	–	1	–	–	–	–
N. squamula salina Focke 1961	–	–	–	1	–	–	–	–
Notommata sp.	–	1	–	–	–	–	–	–
Polyarthra major Burckhardt 1900	–	–	–	–	–	1	–	–
Synchaeta oblonga Ehrenberg 1831	1	–	1	2	–	1	1	1
Testudinella mucronata (Gosse 1886)	–	–	–	–	–	–	1	–
T. patina patina (Hermann 1783)	1	–	–	1	1	–	1	1
T. patina intermedia (Anderson 1889)	–	1	–	–	–	–	–	–
Trichocerca (Diurella) porcellus major Hauer 1935	–	–	–	–	–	1	–	–

with only 11 taxa (7 species) recorded (Table 1). This is probably caused by the extremity of the biotope (much higher salinity than in FWY), and partially, of course, by the insufficient number of samples. *Brachionus calyciflorus calyciflorus* and *Notholca acuminata* (Ehrenberg 1832) which had previously been found in SY (Haberman 1981) did not reoccur.

The following species dominated in Lake Yaskhan: *Brachionus plicatilis* (represented with 3 forms), *Hexarthra fennica*, *Keratella quadrata* (4 forms) and *Synchaeta oblonga*.

Analysing the composition of the planktonic rotifer community of Lake Yaskhan, it should be mentioned that it consists of widespread taxa.

Of the 29 taxa found, 17 are euplanktonic, namely from the genera *Asplanchna*, *Brachionus*, *Filinia*, *Hexarthra*, *Keratella*, *Notholca*, *Polyarthra* and *Synchaeta*. The representatives of the other genera *(Lecane*, *Lepadella*, *Lophocharis*, *Notommata*, *Testudinella*, *Trichocerca)* and the order Bdelloida belong to non-planktonic (periphytic, plankto-benthic or benthic) forms, but their occurrence in the pelagic zone of lakes is not uncommon.

Nearly all the species recorded here are more or less eurythermal (Kutikova 1970; Ruttner-Kolisko 1972; Bērzinš & Pejler 1989). The presence of thermophilic *Hexarthra fennica* and *Brachionus* spp. is typical of the waterbodies of southern regions (Kutikova 1970; Ruttner-Kolisko 1972).

Of interest is the occurrence of *Notholca acuminata* and *N. squamula* in FWY in April, at water temperatures from 14–17 °C. These species are generally known as cold-stenothermal which prefer northern latitudes but are sometimes encountered also in southern areas, in the cold season. According to Kutikova (1970) both *N. squamula* and *N. acuminata* are cold-stenothermal in fresh waters but eurythermal in saline waters. The optimal temperatures being far below 10 °C, they can tolerate higher temperatures for some time (Carlin 1943; May 1980; Bērzinš & Pejler 1989). These points could probably explain their presence in this desert lake.

The taxonomic composition of rotifers in Lake Yaskhan reflects very well the peculiar conditions of this lake. FWY being under the influence of inflowing fresh phreatic water, is brackish, while SY has a distinctly euhaline character. As a result of such conditions, the rotifer community here consists of euryhaline and halophilic species. *Brachionus plicatilis* and *Hexarthra fennica* form a typical halophilic rotifer assemblage preferring high salinity (Kutikova 1970; Ruttner-Kolisko 1972; Ovander 1985; Shiel & Koste 1986). Therefore, the occurrence of *B. plicatilis*, even in great numbers in FWY, is quite interesting. Probably, this could be explained by higher salinity in summer and autumn, caused by intensive evaporation. *H. fennica*, being dominant in SY, seems to be clearly depressed in FWY. *Brachionus quadridentatus* (with 3 forms in this material) and *Notholca squamula salina* are characteristic of brackish conditions (Kutikova 1970, 1980; Ruttner-Kolisko 1972; Ovander 1985). The rest of the species found are, to a smaller or greater extent, euryhaline. The occurrence of *Keratella quadrata*, *Synchaeta oblonga*, *Testudinella mucronata* and *T. patina* in SY indicates that these species can tolerate quite a wide range of salinity.

The occurrence of haploid and resting eggs, indicating the periods of sexual reproduction in rotifers, is of interest too. Resting eggs were detected in the case of *Brachionus plicatilis longicornis* (in July in FWY and in April in SY), *Filinia longiseta limnetica* (in October), *Hexarthra fennica* (in April in SY only), *Keratella quadrata reticulata* (in April and July in FWY only) and *Synchaeta oblonga* (in April in FWY only); haploid eggs in the case of *H. fennica* (in April in SY only) and *K. quadrata reticulata* (in April in FWY only).

References

Bottrell, H. H., Duncan, A., Gliwicz, Z. M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. & Weglenska, T. (1976): A review of some problems in zooplankton production studies. Norw. J. Zool. **24** (4): 419–456.

Carlin, B. (1943): Die Planktonrotatorien des Motalaström. Zur Taxonomie und Ökologie der Planktonrotatorien. Medd. Lunds Univ. Limnol. Inst. **5**: 1–256.

Haberman, J. (1981): Vesennii zooplankton nekotorykh ozyor rusla Uzboya (The spring zooplankton of some lakes in the river-bed of Uzboi). In: L. Seppa (ed.), Produktsionno-biologicheskiye osobennosti i usloviya obitaniya ryb v ozere Yaskhan Turkmenskoi SSR. pp. 53–66. Tallinn (English summary).

Hollowday, E. D. (1985): Some hints and tips on the collecting and handling of monogonontid Rotifera. Microscopy **35**: 208–220.

Kallejärv, T. (1981): Kratkii fiziko-geograficheskii ocherk presnovodnykh ozyor Zapadnogo Uzboya (A brief physiographical description of freshwater lakes of Western Uzboi). In: L. Seppa (ed.), Produktsionno-biologicheskiye osobennosti i usloviya obitaniya ryb v ozere Yaskhan Turkmenskoi SSR, pp. 9–27. Tallinn (English summary).

Kutikova, L. A. (1970): Kolovratki fauny SSSR (Rotifers of the fauna of the USSR). Leningrad.

– (1980): On the evolutionary pathways of speciation in the genus *Notholca*. In: H. J. Dumont & J. Green (eds.), Developments in Hydrobiology I. Rotatoria. Proceedings of the 2nd International Rotifer Symposium, Gent, September 17–21, 1979, pp. 215–220. The Hague, Boston, London.

May, L. (1980): On the ecology of *Notholca squamula* Müller in Loch Leven, Kinross, Scotland. Hydrobiologia **73**: 177–180.

Ovander, E. N. (1985): Vidovoi sostav kolovratok v vodoyomakh raznoi solyonosti (The species composition of rotifers in waterbodies of various salinity). In: L. A. Kutikova (ed.), Kolovratki. Materialy Vtorogo vsesoyuznogo simpoziuma po kolovratkam, pp. 171–176. Leningrad.

Berzinš, B. & Pejler, B. (1989): Rotifer occurrence in relation to temperature. Hydrobiologia **175**: 223–231.

Ruttner-Kolisko, A. (1972): Rotatoria. In: H.-J. Elster & W. Ohle (eds.), Die Binnengewässer. 26. Das Zooplankton der Binnengewässer, 1, pp. 99–234. Stuttgart.

Shiel, R. J. & Koste, W. (1986): Australian Rotifera: Ecology and biogeography. In: P. de Deckker & W. D. Williams (eds.), Limnology in Australia, pp. 141–150. Melbourne, Dordrecht.

Starostin, I. V. (1948): Materialy po gidrobiologii reliktovykh ozyor Uzboya (Materials on the hydrobiology of the relict lakes of Uzboi). Izvestiya Turkmenskogo filiala AN SSSR **1**: 58–68.

Virro, T. (1989): Sravneniye metodov sbora planktonnykh kolovratok (Rotatoria) na primere Chudskogo ozera (The comparison of sampling methods of planktonic rotifers (Rotatoria) on the example of Lake Peipsi). Izvestiya AN EstSSR. Biologiya **38** (2): 119–122 (English summary).

Received: 17. 12. 1992

Address of the author: Taavi Virro, Institute of Zoology and Botany, 21 Vanemuise Street, EE2400 Tartu, Estonia.

III

Virro, T. & J. Haberman, 1993.
The rotifers of Lake Peipus.
Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 389–396.

Hydrobiologia **255/256**: 389–396, 1993.
J. J. Gilbert, E. Lubzens & M. R. Miracle (eds), Rotifer Symposium VI.
© 1993 *Kluwer Academic Publishers. Printed in Belgium.*

The rotifers of Lake Peipus

Taavi Virro & Juta Haberman
Institute of Zoology and Botany, 21 Vanemuine St., 202400 Tartu, Estonia

Key words: rotifers, seasonal dynamics, production, dominant species, sexual periods, life cycles

Abstract

In the northern part of Lake Peipus, 140 taxa of rotifers were identified, with species of *Anuraeopsis*, *Conochilus*, *Keratella*, *Polyarthra* and *Synchaeta* dominating. Two main periods of sexual reproduction occur, in the spring and autumn. Different life cycle patterns are represented. Rotifer number and biomass have two maxima between spring and early autumn. The contribution of rotifers to total zooplankton production varies from 13.6% (Oct.) to 89.8% (May). The average production of grazing rotifers is 485.1 kJ m^{-2}, while that of predatory rotifers (*Asplanchna*) is 10.0 kJ m^{-2}.

Introduction

Lake Peipus (L. Peipsi) is situated on the eastern border of Estonia. It is the fifth largest lake in Europe (surface area 3555 km^2). It consists of three parts: the large northern part, Lake Peipus s.str. (2611 km^2, average depth 8.3 m), southern Lake Pihkva (L. Pskov) (708 km^2, 3.8 m), and narrow Lake Lämmijärv (236 km^2, 2.5 m) connecting the two other parts. On the basis of primary production (Nõges *et al.*, 1989), zooplankton production (Haberman, 1990), water transparency, and nitrogen, phosphorus and chlorophyll-*a* concentrations (Lindpere *et al.*, 1989; Starast *et al.*, 1990), the lake is eutrophic. Lake Peipus is one of the richest in fish among European lakes. The total catch of fish has usually been 9000–12000 tons (25–35 kg ha^{-1}) a year. Planktivorous fishes, e.g. smelt and vendace, dominate the fish fauna, making the zooplankton a very important component of this ecosystem.

The present paper deals with the rotifers of the northern part of the lake, *i.e.* Lake Peipus s.str. Attention is focused on two main areas: (1) the seasonal dynamics of the number, biomass and production of rotifers, and their role in the total zooplankton; (2) the seasonal succession of dominant rotifer species.

Materials and methods

For estimating the number, biomass and production of rotifers the plankton of Lake Peipus was investigated from May to October in 1985 and in 1986. For comparison, data from March and November are given as well. Samples of zooplankton were taken with a quantitative Juday net of 85 μm mesh from the central part of the lake (depth 8.3 m). It is generally accepted that plankton nets of this size are too coarse for rotifers. To correct the values for rotifer numbers in net samples, correction coefficients were used. These coefficients, calculated from results of simultaneous net and quantitative water samples, increase the rotifer numbers 1 to 27 times, 8.8 times on the average (Virro, 1989).

The individual weights of rotifers were calculated from average body lengths using the formulae suggested by Ruttner-Kolisko (1977). Rotifer production (P), ration or food consumption (C), respiration (R) and assimilation (A) were calculated using the physiological method (Waters, 1977; Winberg & Lavrentyeva, 1984; Ivanova, 1985). Here, the genus *Asplanchna* is considered as semi-predaceous.

From June 1986 to June 1987 zooplankton samples were taken (4 to 5 times a month) from littoral and pelagial stations (depths 0.5 and 7.0 m respectively) in the north-western part of the lake to ascertain seasonal changes in the rotifer community. Qualitative samples were taken with a cone net. Quantitative samples were taken with a 1-litre Ruttner sampler. The sedimentation method was used to concentrate the samples.

Results and discussion

In total 140 taxa (116 species) of rotifers were identified. The following species dominated: *Anuraeopsis fissa* (Gosse), *Asplanchna priodonta* Gosse, *Conochilus hippocrepis* (Schrank), *C. unicornis* Rousselet, *Kellicottia longispina* (Kellicott), *Keratella cochlearis* (Gosse), *K. quadrata* (Müller), *Notholca squamula* (Müller), *Polyarthra dolichoptera* Idelson, *P. longiremis* Carlin, *P. luminosa* Kutikova, *P. major* Burckhardt, *P. remata* Skorikov, *Synchaeta kitina* Rousselet, *S. oblonga* Ehrenberg, *S. verrucosa* Nipkow, *Trichocerca rousseleti* (Voigt). The composition of this group is typical of eutrophic lakes in the northern temperate zone (Kutikova, 1970).

The number, biomass and production of the zooplankton in Lake Peipus are high and typical of eutrophic lakes (Haberman, 1990). Data from the central area of the lake (Tables 1 and 2) enable us to draw the same conclusion concerning the rotifers. Their contribution to the total zooplankton production is quite high, varying from 13.6% to 89.8% (Fig. 1). Rotifers have two maxima, in May (water temperature 8.3 °C) and August (19.2 °C). In the north-western area, the rotifers also have two maxima, with some development in the winter (Fig. 2). Littoral maxima are in June (1620 ind l^{-1}) and August (1560 ind l^{-1}), pelagial maxima are in June (660 ind l^{-1}) and September (750 ind l^{-1}).

Table 1. Dynamics of the average number (N: 10^3 ind m^{-3}; %N: percent of total zooplankton number) and biomass (B: g m^{-3}; %B: percent of total zooplankton biomass) of rotifers.

Month	N	%N	B	%B
Mar	78.2	94.7	0.081	92.0
May	1841.9	98.3	1.765	85.6
Jun	1726.0	90.2	1.313	31.1
Jul	1109.9	87.0	0.574	27.9
Aug	1680.8	83.8	1.223	50.7
Sep	648.2	80.5	0.444	31.5
Oct	331.2	58.8	0.175	6.2
Nov	134.8	68.4	0.105	10.4

Data reported in Table 2 demonstrate that rotifers are very important in the energy flow of Lake Peipus. The primary production in this lake is 8519 kJ m^{-2} between May and October (Nõges, 1989). Of the primary production, the herbivorous zooplankton consume 49.7%, and the rotifers consume 23.9%. The ration of grazing rotifers constitutes 48.1% of the ration of all grazing zooplankton. The predatory zooplankton consume 53.4% of the production of the herbivorous zooplankton, with the predatory rotifer *Asplanchna* consuming 4.8% of this production. For the normal functioning of all links in the food

Table 2. Average values (kJ m^{-2}) of production (P), ration (C), respiration (R) and assimilation (A) between May and October, 1985 and 1986. Subscripts: Graz – grazers, Pred – predators.

	Rotifers	Total zooplankton	% of rotifers of total zooplankton
P_{Graz}	485.1	861.6	56.3
P_{Pred}	10.0	66.9	14.9
$P_{Graz+Pred}$	495.1	928.5	53.3
C_{Graz}	2035.3	4233.0	48.1
C_{Pred}	41.7	460.3	9.1
$R_{Graz+Pred}$	759.4	1953.4	38.8
$A_{Graz+Pred}$	1254.5	2881.9	43.5

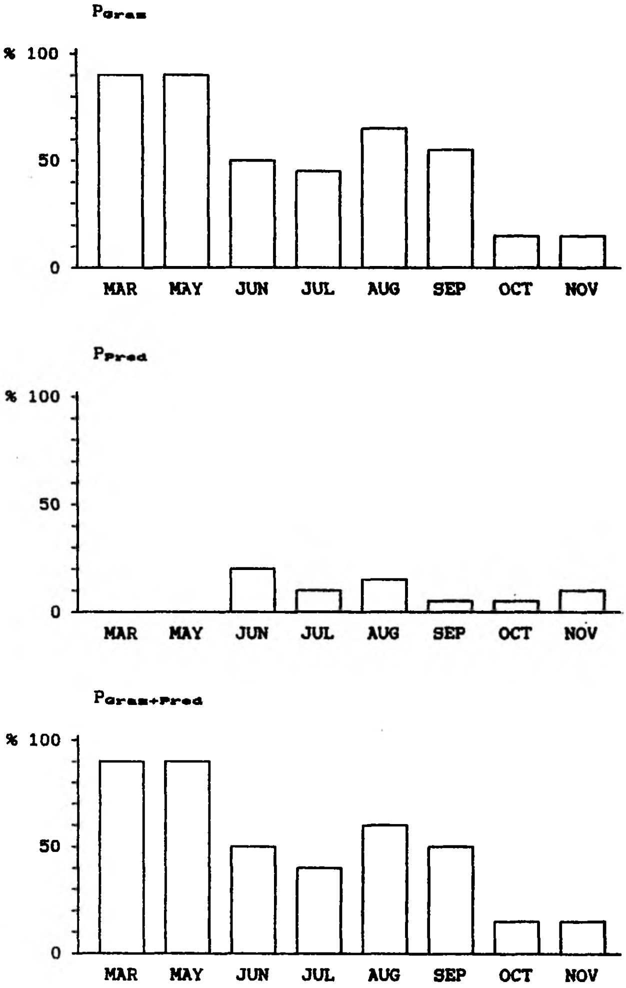


Fig. 1. The contribution (%) of rotifers to total zooplankton production in Lake Peipus. P_{Graz} – grazing rotifers, P_{Pred} – predatory rotifers.

chain, each successive link must not consume more than 60% of the preceding one (Odum, 1959).

Respiration of rotifers is 759.4 kJ m^{-2}. The mean total respiration in Lake Peipus is 17814.9 kJ m^{-2} (Nõges, 1989). The contribution of rotifers to this is 4.3%. Rotifers assimilate 43.5% of all the energy assimilated by the zooplankton.

The seasonal succession of rotifers is illustrated

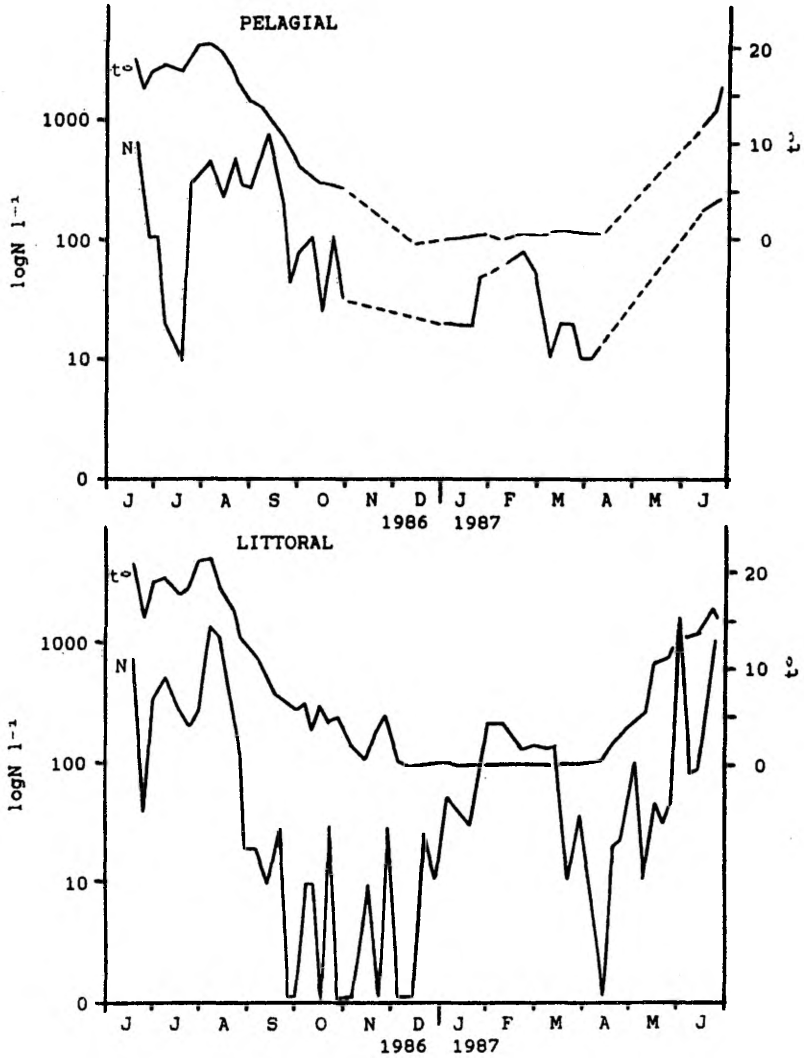


Fig. 2. The seasonal dynamics of rotifers and water temperature (°C) in pelagial and littoral areas of Lake Peipus.

in Figs 3 and 4. *Notholca squamula*, *Polyarthra dolichoptera* and *Synchaeta verrucosa* can be considered thermophobic or winter dominants. *N. squamula* and *S. verrucosa* are distinctly cold stenotherms. *Notholca squamula* is present in the plankton from October until May, at tempera-

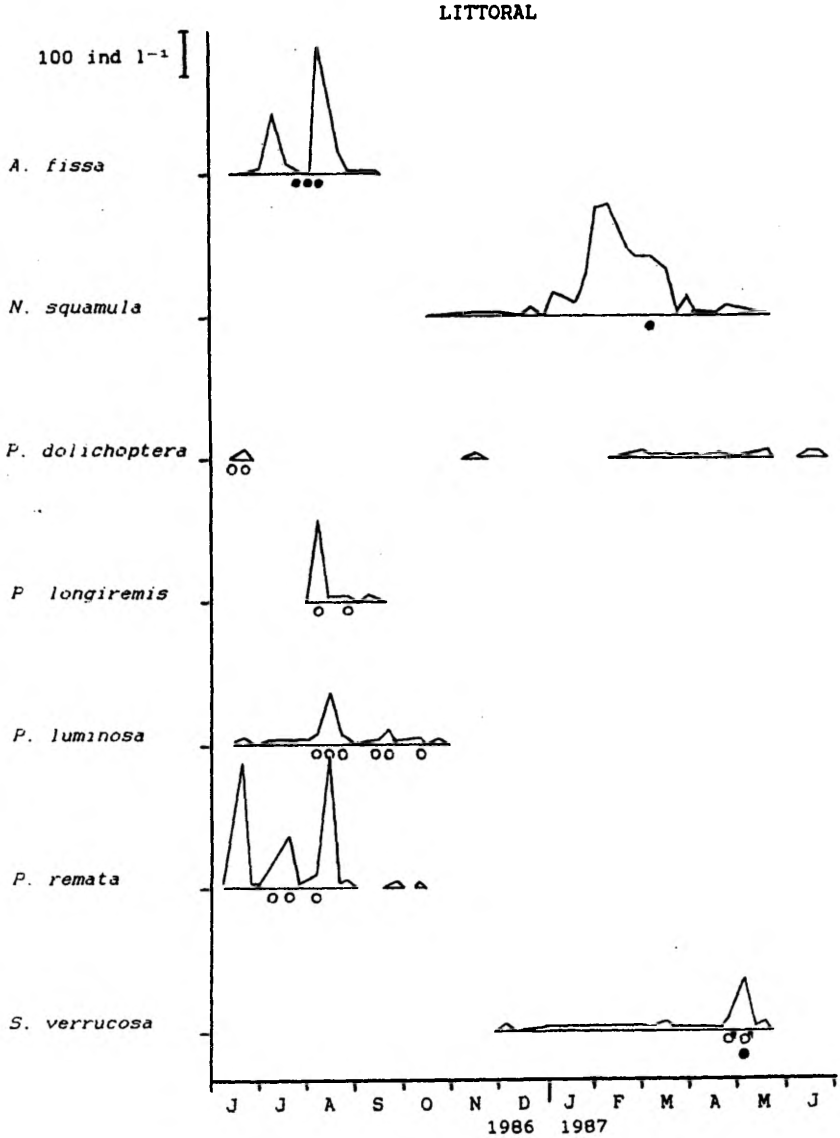


Fig. 3. The seasonal development of dominant rotifers in the littoral zone of Lake Peipus. ♂, o, ● indicate males, haploid eggs, and resting eggs.

tures of 0–11 °C. After the maximum in February (240 ind l^{-1} in littoral), it has sexual reproduction in March. *Polyarthra dolichoptera* appears in October, being more abundant in the pelagial zone. Its development comes to an end in June, soon after the period of sexual reproduction, which coincides with the population maximum in June. *Synchaeta verrucosa* occurs from November until May. Its intensive development starts in early spring and peaks (110 ind l^{-1} in littoral zone) at the beginning of May. *S. verrucosa* disappears at the end of May, when the water temperature rises above 10 °C. Males and resting eggs were encountered just before and at the population maximum.

In May–June the winter complex is replaced by the summer one. Most prominently the seasonal succession of species occurs in the genera *Synchaeta* and *Polyarthra*. In place of *S. verrucosa* come the relatively eurythermal summer dominants *S. oblonga* and *S. kitina*. Synchronously, *S. pectinata* and a warm-water stenotherm, *S. stylata*, occur, but in low numbers. *P. dolichoptera* is replaced by several congeners: *P. longiremis*, *P. luminosa*, *P. major* and *P. remata*. *Polyarthra longiremis* is a warm stenotherm, known to prefer eutrophic conditions (Kutikova, 1970). It occurs in the littoral zone only, in August and September (Fig. 3). Its population maximum (180 ind l^{-1}) and sexual period at the beginning of August coincide with the highest temperature, 21.8 °C. *Polyarthra luminosa* appears in June, reaches maximal numbers in August (in littoral zone 110 ind l^{-1}, in pelagial zone 100 ind l^{-1}), and disappears in October (Figs 3 and 4). Haploid eggs were found attached to females in the middle of August, in September and October. The development of *Polyarthra remata* is somewhat shifted in time in the two different habitats (Figs 3 and 4). In the littoral zone, it occurs from June to September, having a maximum in August (300 ind l^{-1}). In the pelagial zone, the number of *P. remata* begins to rise in August, with a peak in September (50 ind l^{-1}), and declines to zero in October. In the littoral zone, sexual reproduction occurs before the population maximum; in the pelagial zone, it occurs during the decline of the population. *Polyarthra major* has high numbers only in the pelagial zone, where it is one of the main dominants in August and September.

The summer pelagic complex is dominated by *Conochilus hippocrepis* and *C. unicornis*/*C. unicornis* having its maximum in June and *C. hippocrepis* having it in August (110 ind l^{-1}). *Anuraeopsis fissa* is a typical thermophilic dominant in the littoral zone. *A. fissa* starts its development in June, peaks in August (260 ind l^{-1}), at a temperature of 21.8 °C, and practically disappears at the end of August (Fig. 3). The population undergoes sexual reproduction slightly before the maximum.

Keratella cochlearis s.l. is represented in the plankton practically all year round by several seasonally alternating morpho-ecological forms: *hispida*, *macracantha*, *nordica*, *pustulata*, *robusta*, *tecta*, *typica*. In the littoral zone, *K. cochlearis* has maximal numbers in August (540 ind l^{-1}), mainly f. *typica* but also f. *hispida*, f. *pustulata* and f. *tecta*. In the pelagial zone, the maximum is in September (240 ind l^{-1}), mainly f. *hispida*, f. *pustulata* and f. *typica* in equal proportions. *K. cochlearis* f. *macracantha* and f. *nordica* are associated with colder periods, whereas f. *tecta* is associated with warmer ones.

The genus *Asplanchna* is represented by two species: *A. priodonta* and *A. girodi*. The latter never reaches high numbers. *A. priodonta* dominates only sporadically in the pelagial zone. *Keratella quadrata* (mainly *K. quadrata frenzeli*) is also more abundant in this zone. *Kellicottia longispina* has a similar distribution, having a maximum in July.

Two main periods of sexual reproduction seem to occur in the rotifer community of Lake Peipus: in spring or early summer for winter species (*Notholca squamula*, *Polyarthra dolichoptera*, *Synchaeta verrucosa*) and in late summer or autumn for summer ones (*Anuraeopsis fissa*, *Polyarthra longiremis*, *P. luminosa*, *P. remata*). Different life cycle patterns are represented. According to King (1980), we may distinguish: a) early cycle species (*Polyarthra remata* in the littoral zone), initiating sexual reproduction before the population maximum; b) midcycle species

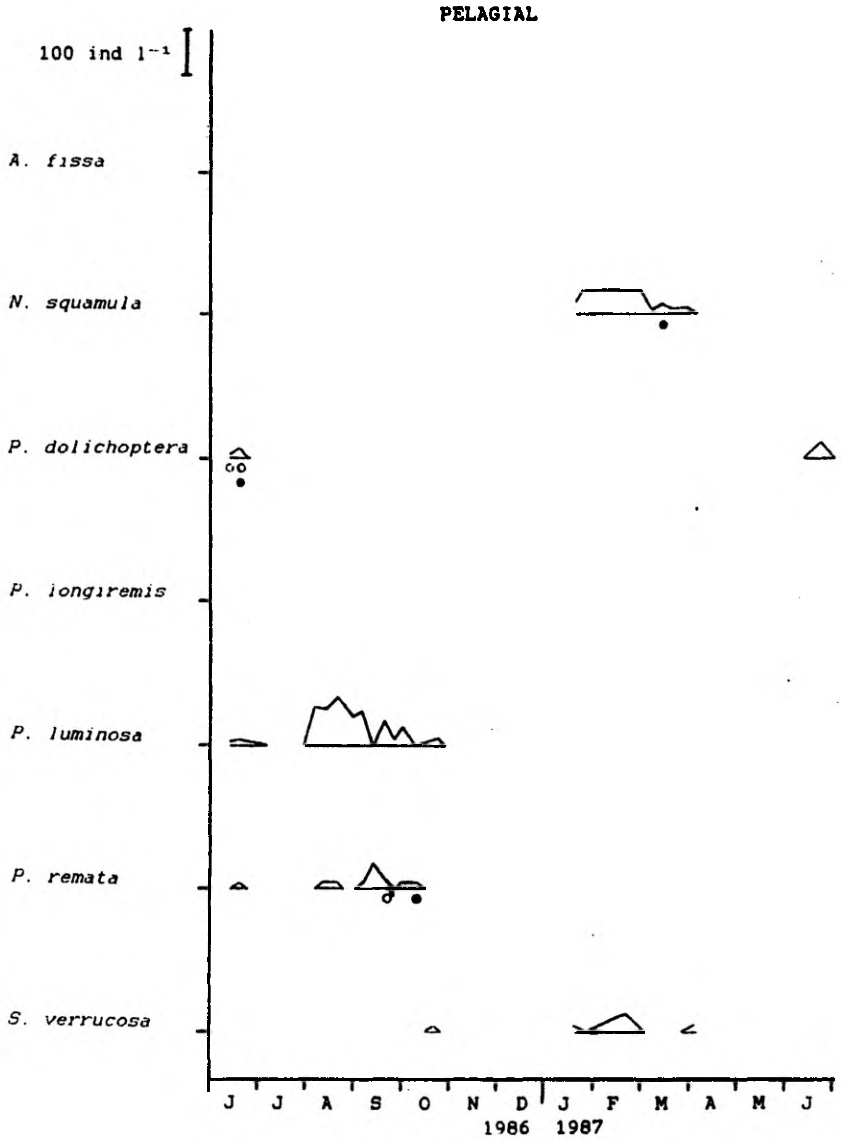


Fig. 4. The seasonal development of dominant rotifers in the pelagial zone of Lake Peipus. ♂, o, ● indicate males, haploid eggs, and resting eggs.

(*Anuraeopsis fissa*, *Polyarthra dolichoptera*, *P. longiremis*, *P. luminosa*, *Synchaeta verrucosa*), which have sexual reproduction at the population maximum; and c) late cycle species (*Notholca squamula*, *Polyarthra remata* in the pelagial zone), having sexual reproduction after the maximum.

References

Haberman, J., 1990. Production of zooplankton in Lake Peipsi. In T. Timm (ed.), State of Lake Peipsi. Eesti TA, Tartu: 115–118. (in Estonian, with English summary).

Ivanova, M. B., 1985. Production of planktonic crustaceans in fresh water. ZIN AN SSSR, Leningrad, 222 pp. (in Russian).

King, C. E., 1980. The genetic structure of zooplankton populations. In W. C. Kerfoot (ed.), Evolution and Ecology of Zooplankton Communities. The University Press of New England, Hanover (N.H.): 315–328.

Kutikova, L. A., 1970. Rotifers of the fauna of the USSR. Nauka, Leningrad, 744 pp. (in Russian).

Lindpere, A., H. Starast, A. Milius, M. Haldna & H. Simm, 1989. Water characteristics of Lake Peipsi-Pihkva in 1985–1987. Proceedings of the Academy of Sciences of the Estonian SSR. Biology 38: 107–118. (in Estonian).

Nõges, T. H., 1989. Ecological relations of the main plankton components in the pelagial of Lake Peipsi. Abstracts of the candidate thesis. Moscow, 17 pp. (in Russian).

Nõges, T., P. Nõges & I. Ott, 1989. Phytoplankton production in the pelagial of Lake Peipsi in 1985–1986. Proceedings of the Academy of Sciences of the Estonian SSR. Biology 38: 123–130. (in Russian).

Odum, E. P., 1959. Fundamentals of ecology. Saunders, Philadelphia, 546 pp.

Ruttner-Kolisko, A., 1977. Suggestions for biomass calculation of planktonic rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 71–76.

Starast, H., A. Lindpere & A. Milius, 1990. Methodological recommendations for the estimation of the trophic state of Lake Peipsi. In T. Timm (ed.), State of Lake Peipsi. Eesti TA, Tartu: 16–19. (in Estonian, with English summary).

Virro, T., 1989. The comparison of sampling methods of planktonic rotifers (Rotatoria) on the example of Lake Peipsi. Proceedings of the Academy of Sciences of the Estonian SSR. Biology 38: 119–122. (in Russian, with English summary).

Waters, T. F., 1977. Secondary production in inland waters. Adv. ecol. Res. 10: 91–164.

Winberg, G. G. & G. M. Lavrentyeva (eds), 1984. Methodical recommendations for collection and analysing materials of hydrobiological studies on fresh water reservoirs. Zooplankton and its production. Leningrad, 33 pp. (in Russian).

Virro, T., 1995.
The genus *Polyarthra* in Lake Peipsi.
Hydrobiologia 313/314 (Dev. Hydrobiol. 109): 351–357.

Hydrobiologia **313/314**: 351–357, 1995.
J. Ejsmont-Karabin & R. M. Pontin (eds), Rotifera VII.
©1995 *Kluwer Academic Publishers. Printed in Belgium.*

The genus *Polyarthra* in Lake Peipsi

Taavi Virro
Institute of Zoology and Hydrobiology, University of Tartu, 46 Vanemuise St., EE 2400 Tartu, Estonia

Key words: Polyarthra, morphometry, seasonal development, bisexual periods, life cycles

Abstract

In Lake Peipsi (Estonia) *Polyarthra* species often dominate the rotifer community, and are represented by 6 species: *Polyarthra dolichoptera* Idelson, *P. longiremis* Carlin, *P. luminosa* Kutikova, *P. major* Burckhardt, *P. remata* Skorikov, *P. vulgaris* Carlin. The highest diversity occurs in August–September, with *P. remata* and *P. luminosa* most abundant. Morphometric data including measurements of body, fins and various types of eggs are given. The seasonal development of the different species and their life cycles are considered.

Introduction

Lake Peipsi (L. Peipus) (surface area 2611 km^2, average depth 8.3 m) is the northern part of Lake Peipsi–Pihkva (L. Peipus–Pskov) (3555 km^2). On the basis of primary production (Nõges *et al.*, 1989), zooplankton production (Haberman, 1990), transparency, nitrogen, phosphorus and chlorophyll-a (Lindpere *et al.*, 1989; Starast *et al.*, 1990), it is eutrophic, with mesotrophic features in the northern region (Lokk *et al.*, 1988).

Species of *Polyarthra* are typical of lakes in the northern temperate zone. The species are quite common in the plankton of Lake Peipsi and often dominate the rotifer community (Denisenko, 1975; Haberman, 1978; Haberman, 1983; Virro & Haberman, 1993).

The aim of the present paper is to discuss the species composition of *Polyarthra* in Lake Peipsi and to characterize their seasonal development and life cycles. Morphometric data of the species are given, as well.

Materials and methods

From June 1986 to March 1988 zooplankton samples were collected (4 to 6 times a month) from a sublittoral station (depth 0.5–1 m) in the north-western part of Lake Peipsi. Qualitative samples were taken with a cone net. Quantitative samples were taken with a 1-litre Ruttner sampler. The sedimentation method was used to concentrate the samples. Samples were fixed with formalin.

Measurements of body, fins, ventral finlets and eggs were taken with an ocular micrometer at 15 × 20 magnification. Specimens with extended corona were used whenever possible. The morphometric data are presented in Tables 1 and 2. Estimated by the index of sample average determination accuracy, the means are representative, the values of the index varying between 1–5%.

The rotifer taxa were identified according to Kutikova (1970) and Koste (1978). The nomenclature of Kutikova (1970) is followed.

Results and discussion

In the present material the genus *Polyarthra* is represented by 6 species:

Polyarthra dolichoptera Idelson, 1925
Polyarthra longiremis Carlin, 1943
Polyarthra luminosa Kutikova, 1962
Polyarthra major Burckhardt, 1900
Polyarthra remata Skorikov, 1896
Polyarthra vulgaris Carlin, 1943

P. luminosa and *P. longiremis* are often referred to as not valid or of uncertain status. Based on the material from Lake Peipsi, these are distinct taxa, differing morphologically and ecologically from other *Polyarthra*

Table 1. Morphometric data of *Polyarthra* species (females only) in Lake Peipsi. B = body; F = fin; VF = ventral finlet; AE = amictic egg; HE = haploid egg; RE = resting egg; *L* = length; *W* = width; Min = minimum value; Max = maximum value; SD = standard deviation; *n* = number of observations; x = character absent; – = not detected. All measurements in μm.

Polyarthra	B		F		VF	AE		HE		RE	
species	*L*	*W*	*L*	*W*	*L*	*L*	*W*	*L*	*W*	*L*	*W*
Dolichoptera											
Min	94	56	105	6	37	62	46	29	26	67	46
Max	141	96	186	10	75	89	58	45	37	93	74
Mean	118.8	77.7	147.8	7.7	56.2	74.4	52.0	37.4	29.5	78.7	58.0
SD	11.8	8.8	19.4	1.3	8.1	4.5	2.8	3.2	2.3	8.2	8.8
n	42	42	42	19	42	57	57	28	28	23	23
Longiremis											
Min	72	41	80	9	39	55	38	35	28		
Max	132	88	153	13	75	72	48	37	30		
Mean	98.2	61.9	110.3	10.5	50.0	66.5	44.4	36.0	29.0	–	–
SD	18.3	12.7	20.7	1.5	10.8	5.5	3.8	1.0	1.0		
n	25	25	25	11	25	8	8	2	2		
Luminosa											
Min	105	58	93	12	29	69	41	27	23		
Max	156	100	136	24	45	87	61	37	28		
Mean	126.0	70.5	118.1	17.4	36.7	78.2	50.3	32.9	25.9	–	–
SD	10.9	7.4	8.8	3.4	3.6	5.2	4.3	2.1	1.4		
n	45	45	45	18	45	41	41	17	17		
Major											
Min	114	58	111	15		78	49	35	29		
Max	199	119	162	40		118	72				
Mean	145.3	83.9	134.3	23.7	x	98.5	62.8			–	–
SD	24.7	14.8	12.5	5.0		8.9	6.2				
n	49	49	49	32		21	21	1	1		
Remata											
Min	68	38	66	4		47	32	28	22	63	50
Max	124	89	137	9		71	50	38	29	76	58
Mean	93.3	54.5	103.9	6.3	x	58.1	39.7	32.8	25.8	71.5	54.3
SD	12.3	9.1	16.5	1.3		4.3	3.9	2.7	2.0	4.6	2.6
n	65	65	65	18		65	65	29	29	6	6
Vulgaris											
Min	100	58	107	12	33						
Max	122	75	135	19	52						
Mean	110.9	68.6	123.8	15.6	44.8	–	–	–	–	–	–
SD	7.7	4.7	9.0	2.1	5.7						
n	13	13	13	12	13						

species. *P. luminosa*, originally described by Kutikova (1962), is distinguishable by its characteristic broad leaf-shaped ventral finlets and rhombic fins in dorsal fin bundles. *P. longiremis* differs from its close congeners *(P. dolichoptera, P. vulgaris)* in trophi structure (Shiel & Koste, 1993).

It should be mentioned that due to extensive overlap (Tables 1 and 2) morphometric criteria, with fin width the most distinctive, are inadequate to distin-

Table 2. Morphometric ratios of *Polyarthra* species (females only) in Lake Peipsi. *BL* = body length; *BW* = body width; *FL* = fin length; *FW* = fin width; Min = minimum value; Max = maximum value; SD = standard deviation; *n* = number of observations.

Polyarthra species	*BL/BW*	*BL/FL*	*FL/FW*
Dolichoptera			
Min	1.3	0.7	14
Max	1.8	1.1	26.8
Mean	1.54	0.81	18.82
SD	0.14	0.09	3.32
n	42	42	19
Longiremis			
Min	1.3	0.7	10.5
Max	1.9	1.1	15
Mean	1.6	0.89	12.55
SD	0.13	0.08	1.45
n	25	25	11
Luminosa			
Min	1.5	0.9	5.1
Max	2.1	1.3	10.8
Mean	1.79	1.07	6.83
SD	0.12	0.09	1.48
n	45	45	18
Major			
Min	1.4	0.9	3.8
Max	2.1	1.3	8.3
Mean	1.74	1.08	5.92
SD	0.17	0.11	0.84
n	49	49	32
Remata			
Min	1.2	0.7	12.6
Max	2.1	1.1	21.8
Mean	1.73	0.91	17.77
SD	0.16	0.10	3.06
n	65	65	18
Vulgaris			
Min	1.4	0.7	5.8
Max	1.9	1.1	10.1
Mean	1.62	0.90	8.05
SD	0.15	0.11	1.33
n	13	13	12

guish *Polyarthra* species. Therefore, both morphological characters such as trophi structure, and ecological features are needed for identification.

In Lake Peipsi, the highest species diversity of *Polyarthra* occurs in August–September, with *P. remata, P. luminosa* and *P. longiremis* most abundant (Fig. 1). This *Polyarthra* assemblage consists of widespread species and reflects the trophic status of this lake.

Compared to the earlier list from Lake Peipsi given by Haberman (1978), *P. dissimulans* and *P. euryptera* were not encountered in our material. These species are considered to be warm stenotherms (Carlin, 1943; Kutikova, 1970; Bērziņš & Pejler, 1989), and may not reach detectable numbers in cool summers. *P. euryptera* prefers eutrophic environments (Ruttner-Kolisko, 1972; Hakkari, 1978), and is probably restricted to the eutrophic southern regions of the lake. *P. remata* was not found by Haberman (1978) in Lake Peipsi, but was present in hypertrophic Lake Võrtsjärv (surface area 270 km^2, average depth 2.8 m, in Estonia). Its appearance in Lake Peipsi is likely connected with increasing eutrophication.

The development of *Polyarthra* species displays a distinct seasonality, related to temperature (Fig. 1). Temperature is one of the main abiotic factors influencing directly (affecting the time of embryonic development) or indirectly (via the other abiotic and biotic factors) the seasonal development of rotifers (Hofmann, 1977; Radwan, 1980; May, 1983; Bērziņš & Pejler, 1989).

Polyarthra dolichoptera is a cold stenothermic species. It appears in October (5°C), or September (13°C), when cooling begins (Fig. 1). Although temperature is favourable, the species is unable to maintain itself during early winter, but ends soon with bisexual development and production of resting eggs. A new rise begins in January, with maximum in March, and comes to an end in June, soon after bisexual reproduction. *Proloba* forms were encountered in samples from February, March and June.

Polyarthra vulgaris occurs in low numbers from December to April, showing a typical cold stenothermal distribution (Fig. 1). This seems contradictory, as *P. vulgaris* is considered to be eurythermal (Carlin, 1943; Pejler, 1956; Ruttner-Kolisko, 1972; Bērziņš & Pejler, 1989). However, it is known that *P. dolichoptera* and *P. vulgaris* have coinciding food niches, which may cause severe competition, suppressing one of them (Stenson, 1983).

Well-defined seasonal succession occurs. In June, the winter complex is replaced by the summer one, consisting of *Polyarthra longiremis, P. luminosa, P. major* and *P. remata*.

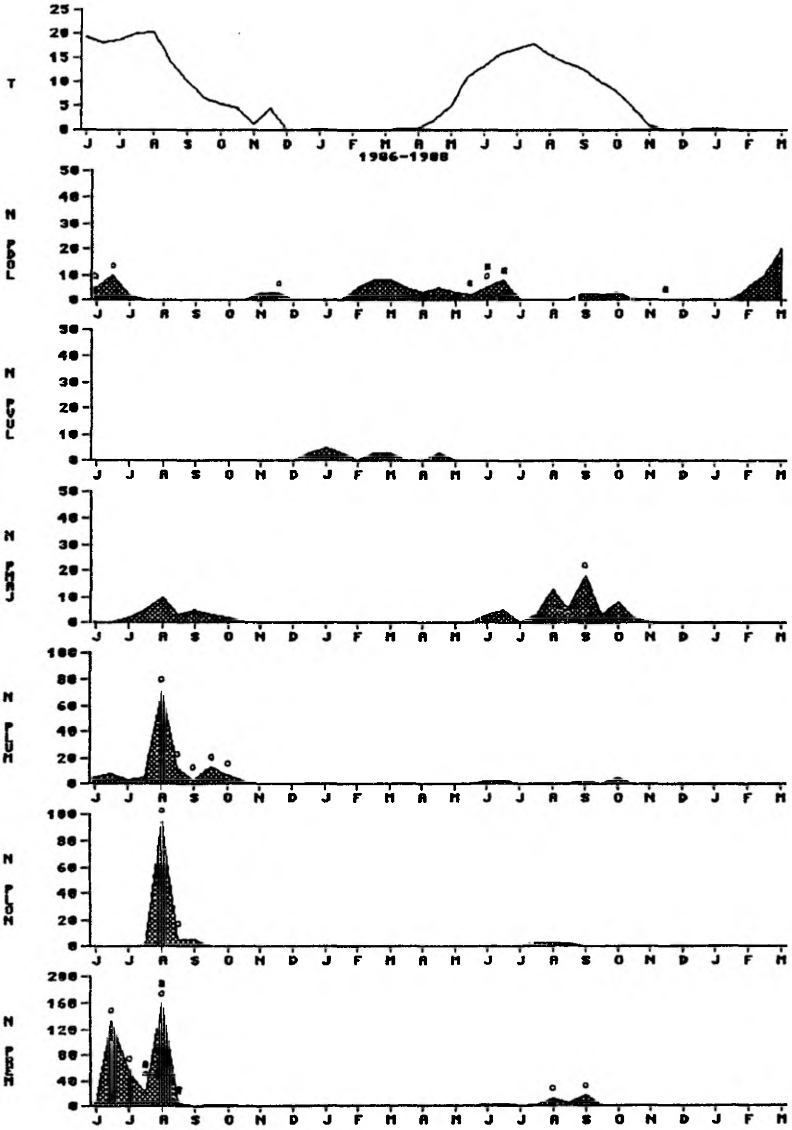


Fig. 1. The seasonal development of *Polyarthra* species and water temperature in Lake Peipsi in 1986–1988. *T* = temperature (°C); *N* = number (ind l^{-1}); PDOL = *P. dolichoptera*; PVUL = *P. vulgaris*; PMAJ = *P. major*; PLUM = *P. luminosa*; PLON = *P. longiremis*; PREM = *P. remata*; o = haploid eggs; ■ = resting eggs.

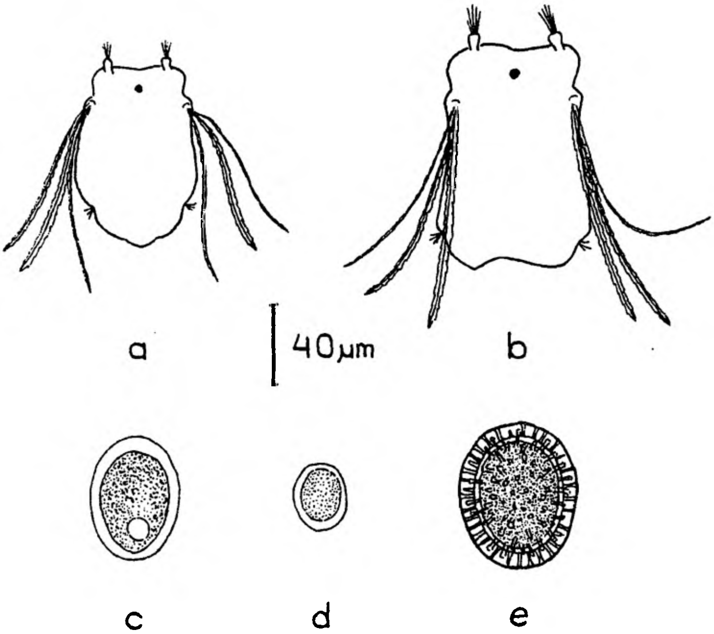


Fig. 2. Polyarthra remata from Lake Peipsi. a: rounded form, habitus, dorsal; b: rectangular form, habitus, dorsal; c: amictic egg; d: haploid egg; e: resting egg.

Polyarthra major is present from May to October, with maxima in August or September (Fig. 1). Females with haploid eggs occur at the population maximum. *P. major* is eurytherm, preferring waters of lower trophy (Ruttner–Kolisko, 1972). *Polyarthra luminosa* appears in May, peaks in August (at the temperature peak, 20.4°C), and disappears in October (Fig. 1). Haploid eggs were found attached to females from August until October. These two congeners, similar in size, have close niches, which excludes their simultaneous mass development (Chuikov, 1985).

Polyarthra longiremis is a warm stenotherm, known to prefer eutrophic conditions (Kutikova, 1970). It is restricted to the littoral of Lake Peipsi (Virro & Haberman, 1993) and occurs from July to September (Fig. 1). Its maximum and bisexual period, in August, coincide with the highest temperature. In shallow and hypertrophic Lake Võrtsjärv the distribution of *P. longiremis* is similar (Kutikova & Haberman, 1986).

Polyarthra remata is an eurythermal and eutrophic species (Bērziņš & Pejler, 1989; Hakkari, 1978) which occurs from June to September/October, with maximum in August or September. Sexual reproduction takes place before the population maximum. Of particular interest is the dimorphism of the females in Lake Peipsi. Two coexisting forms, differing in body outline, were encountered: a rounded form, with rounded posterior end of the body, and a rectangular form, with almost rectangular posterior part (Fig. 2). The latter is similar in habitus to *P. dolichoptera*, but is smaller, and lacks the pair of ventral finlets. The rectangular form is a bit larger than the other. The rounded form appears first, then, in July the rectangular one. Simultaneously with 'normal' rectangular forms, *proloba* forms were encountered in August. The rounded form, had 8 or 4 nuclei in the vitellarium, the rectangular 8. Both forms produce amictic and haploid eggs, but only rectangular forms had resting eggs (Fig. 2). (The measurements of the eggs are given in Table 1). In July an amphoteric female (rectangular) was found, carrying amictic and resting eggs. The structure of the resting eggs is not typical to *P. remata*, described as double-shelled with folded skin between shells (Kutikova, 1970; Ruttner-Kolisko, 1972; Koste, 1978). In our case the resting eggs were double-shelled with spines or 'columns' between them and somewhat bigger in size, resembling those of *P. dolichoptera*. A remarkable polymorphism of resting eggs was mentioned by Bogoslovsky (1967), regarding *P. dolichoptera*. Our data also illustrate this phenomenon in this genus. Wesenberg-Lund (1930) supposed the rounded and rectangular forms to be amictic and mictic females. Considering the egg-carrying variants, we may conclude that our data suit well into his scheme *(op. cit.)*, that the rounded form includes both amictic and mictic females; the latter produce haploid eggs at an early stage. Later, growing up to rectangular habitus, they produce resting eggs. However, there can also be other explanations for the dimorphism. SEM analysis of the trophi of the two forms, desirably combined with DNA sequence analysis, should help to resolve this question.

Analysing the life cycles of *Polyarthra* species we can distinguish two main periods of bisexual reproduction: in spring for thermophobic species *(P. dolichoptera)* and in late summer or autumn for eurythermal and thermophilic ones *(P. major, P. luminosa, P. remata, P. longiremis)*. Different life cycle patterns are present within the genus. According to King (1980), we may distinguish: a) early cycle species *(P. remata)*; b) midcycle species *(P. longiremis, P. luminosa, P. major)*; and c) late cycle species *(P. dolichoptera)*. *P. dolichoptera* seems to be dicyclic, with two bisexual periods per year. However, the resting eggs establishing the second development period, may originate from previous years, not from the first period of the same year. In the case of *P. vulgaris* bisexual reproduction was not detected.

Acknowledgements

I thank the Institute of Ecology, Polish Academy of Sciences and the Stefan Batory Foundation for financial assistance to attend the 7th International Rotifer Symposium at Mikolajki (Poland).

References

Bērzinš, B. & B. Pejler, 1989. Rotifer occurrence in relation to temperature. Hydrobiologia 175: 223–231.

Bogoslovsky, A. S., 1967. Materials to the study of the resting eggs of rotifers 2. Byull. Mosk. Obshch. Isp. Prirody, Ot. Biol. 72: 46–66. (in Russian, with English summary)

Carlin, B., 1943. Die Planktonrotatorien des Motalaström. Zur Taxonomie und Ökologie der Planktonrotatorien. Medd. Lunds Univ. Limn. Inst. 5: 1–256.

Chuikov, Yu. S., 1985. Several data about the ecology of rotifers in eutrophic water-bodies of the Volga delta. In L. A. Kutikova (ed.), Rotifera. Proceedings of the 2nd All-Union rotifer symposium. Nauka, Leningrad: 167–171. (in Russian)

Denisenko, A. I., 1975. The summer zooplankton of the southern part of Lake Chudskoye. In V. P. Krasnopevtsev & N. N. Malashkin (eds), Trudy Pskovskogo otd. Gos NIORH. I. Syryevye resursy Pskovsko–Chudskogo ozera i ikh ratsionalnoye ispolzovaniye. Lenizdat Psk. otd., Pskov: 52–57.

Haberman, J., 1978. Seasonal dynamics of pelagic rotifers of Lakes Peipsi-Pihkva and Võrtsjärv. Proc. Acad. Sci. Est. SSR. Biology 27: 16–30.

Haberman, J., 1983. Comparative analysis of plankton rotifer biomass in large Estonian lakes. Hydrobiologia 104 (Dev. Hydrobiol. 14): 293–296.

Haberman, J., 1990. Production of zooplankton in Lake Peipsi. In T. Timm (ed.), State of Lake Peipsi. Eesti TA, Tartu: 115–118. (in Estonian, with English summary)

Hakkari, L., 1978. On the productivity and ecology of zooplankton and its role as food for fish in some lakes in Central Finland. Biol. Res. Rep. Univ. Jyväskylä 4: 3–87.

Hofmann, W., 1977. The influence of abiotic environmental factors on population dynamics in planktonic rotifers. Arch. Hydrobiol. Beih. Ergebn. Limnol. 8: 77–83.

King, C. E., 1980. The genetic structure of zooplankton populations. In W. C. Kerfoot (ed.), Evolution and Ecology of Zooplankton Communities. The University Press of New England, Hanover (N.H.): 315–328.

Koste, W., 1978. Rotatoria. Die Rädertiere Mitteleuropas. Begründet von Max Voigt, Vol. I, II. Borntraeger, Berlin, 673 pp., 234 pl.

Kutikova, L. A., 1962. Rotifers (Rotatoria) of the genus *Polyarthra* Ehr. of the River Luga (Leningrad region). Trans. Zool. Inst. AN SSSR 31: 453–462. (in Russian)

Kutikova, L. A., 1970. Rotifers of the fauna of the USSR. Nauka, Leningrad, 744 pp. (in Russian)

Kutikova, L. A. & J. Haberman, 1986. Rotifers (Rotatoria) of Lake Võrtsjärv. I. Taxonomical and ecological survey. Proc. Acad. Sci. Est. SSR. Biology 35: 113–121.

Lindpere, A., H. Starast, A. Milius, M. Haldna & H. Simm, 1989. Water characteristics of Lake Peipsi-Pihkva in 1985–1987. Proc. Acad. Sci. Est. SSR. Biology 38: 107–118. (in Estonian, with English summary)

Lokk, S., R. Laugaste & A. Mäemets, 1988. Changes in bacterio-, phyto- and zooplankton of Lake Peipsi-Pihkva. In M. Zobel (ed.), Dynamics and ecology of wetlands and lakes in Estonia. Acad. Sci. Est. SSR, Tallinn: 173–187.

May, L., 1983. Rotifer occurrence in relation to water temperature in Loch Leven, Scotland. Hydrobiologia 104 (Dev. Hydrobiol. 14): 311–315.

Nõges, T., P. Nõges & I. Ott, 1989. Phytoplankton production in the pelagial of Lake Peipsi in 1985–1986. Proc. Acad. Sci. Est. SSR. Biology 38: 123–130. (in Russian, with English summary)

Pejler, B., 1956. Introgression in planktonic Rotatoria with some points of view on its causes and conceivable results. Evolution 10: 246–261.

Radwan, S., 1980. The effect of some biotic and abiotic factors on the fertility of planktonic rotifers species. Hydrobiologia 73 (Dev. Hydrobiol. 1): 59–62.

Ruttner-Kolisko, A., 1972. Rotatoria. In H.-J. Elster & W. Ohle (eds), Die Binnengewässer, 26. Das Zooplankton der Binnengewässer, 1. E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart: 99–234.

Shiel, R. J. & W. Koste, 1993. Rotifera from Australian inland waters. IX. Gastropodidae, Synchaetidae, Asplanchnidae (Rotifera: Monogononta). Trans. r. Soc. S. Aust. 117: 111–139.

Starast, H., A. Lindpere & A. Milius, 1990. Methodological recommendations for the estimation of the trophic state of Lake Peipsi. In T. Timm (ed.), State of Lake Peipsi. Eesti TA, Tartu: 16–19. (in Estonian, with English summary).

Stenson, J. A. E., 1983. Changes in the relative abundance of *Polyarthra vulgaris* and *P. dolichoptera*, following the elimination of fish. Hydrobiologia 104 (Dev. Hydrobiol. 14): 269–273.

Virro, T. & J. Haberman, 1993. The rotifers of Lake Peipus. Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 389–396.

Wesenberg-Lund, C., 1930. Contributions to the biology of the Rotifera. Part II. The periodicity and sexual periods. D. Kgl. Danske Vidensk. Selsk. Skrifter, Naturv. og Mathem. Afd., 9, 2: 3–230.

V

Virro, T., 1996.
Taxonomic composition of rotifers in Lake Peipsi.
Hydrobiologia 338: 125–132.

Hydrobiologia **338:** 125–132, 1996.
T. Timm & T. Nõges (eds), Biology of Lake Peipsi.
©1996 *Kluwer Academic Publishers. Printed in Belgium.*

Taxonomic composition of rotifers in Lake Peipsi

Taavi Virro
Department of Zoology and Hydrobiology, University of Tartu, 46 Vanemuise Street, EE-2400 Tartu, Estonia

Key words: Rotifera, Monogononta, taxonomic composition, eutrophic lake

Abstract

161 rotifer taxa 46 of which are new records for Estonia were identified in the north-western part of Lake Peipsi. The greatest number of taxa occurred in August (93), followed by September (79). In all, 19 families (Monogononta) are represented with 41 genera. The dominant families are Brachionidae (32 taxa) and Synchaetidae (16). The species of *Anuraeopsis, Conochilus, Kellicottia, Keratella, Notholca, Polyarthra* and *Synchaeta* are dominating. The taxonomic composition is analysed in the ecological aspect. Some species of zoogeographic interest, including a supposedly endemic *Ploesoma peipsiense*, are reported.

Introduction

The very first data on the rotifers of Lake Peipsi were presented in the papers based on the samples collected during 1909 and 1912 by Samsonov (1912, 1914). 15 rotifer taxa were listed from the lake. Sokolov (1941) reported 17 rotifer species in the summer zooplankton of Lake Peipsi. Together with complex and extensive limnological studies which started in the 1960s, more data began to accumulate on rotifers. In a series of zooplanktonic works by Mjaèmets (1966), Denisenko (1975) and Jakovleva (1975) about 30 rotifer species were mentioned from Lake Peipsi. The most detailed and comprehensive data, the result of seasonal zooplankton studies in 1964–1966, were published by Haberman (e.g. 1976, 1978, 1983). 43 rotifer taxa were recorded from Lake Peipsi (60 from Lake Peipsi-Pihkva). In 1984–1985 the pelagial of the southern part of the lake was investigated by me (unpublished), with 47 taxa of rotifers being reported. Altogether, approximately 90 rotifer taxa have been recorded in the previous contributions from Lake Peipsi. It should be mentioned that so far mainly the pelagial of the lake has been studied, which leaves the littoral rotifer complex practically uninvestigated. Rotifers are an important component of zooplankton in Lake Peipsi (Haberman, 1978; Virro & Haberman, 1993).

The aim of the present study is to determine the taxonomic composition and its seasonal changes in both the littoral and pelagic rotifer assemblages of Lake Peipsi.

Description of the lake

Lake Peipsi (58°22′N–59°00′N, 26°57′E–27°59′E, surface area 2611 km^2, average depth 8.3 m, maximum depth 12.9 m) represents the northern part of the compound Lake Peipsi-Pihkva (named also L. Peipus-Pskov in some earlier papers; L. Pskovsko-Čudskoe in Russian) (3558 km^2) situated on the eastern border of Estonia.

Considering primary production (Nõges et al., 1989), zooplankton production (Haberman, 1990), transparency, nitrogen, phosphorus and chlorophyll *a* (Lindpere et al., 1989; Starast et al., 1990), L. Peipsi is eutrophic, with mesotrophic features in the northern region (Lokk et al., 1988). During the last 30 years the lake, its northern part to a lesser degree, has been affected by increasing anthropogenic eutrophication. Data on several chemical characteristics are presented in Table 1.

In the phytoplankton of Lake Peipsi diatoms *(Melosira, Stephanodiscus, Cyclotella)*, cyanobacteria *(Aphanothece, Microcystis, Anabaena, Gloeotrichia)*

Table 1. Characteristics of Lake Peipsi.

Characteristic	Period of observation	Range	Mean	Reference
pH	1987 May–Sept.	7.7–8.7	8.3	1
O_2 content (mg l^{-1})	1986–1988	3.8–15.0	12.8	2
Total nitrogen (mg m^{-3})	1987 May–Sept.	380–1330	847.0	1
Total phosphorus (mg m^{-3})	1987 May–Sept.	8–75	31.0	1
Na^+ (mg l^{-1})	1985 June	–	5.4	3
Cl^- (mg l^{-1})	1986–1988	8.2–16.3	11.9	2
Chl *a* (mg m^{-3})	1987 May–Sept.	2.8–30.9	12.8	1

References: 1 = Lindpere et al. (1989); 2 = Saava (1990); 3 = Pihlak et al. (1987).

and green algae *(Scenedesmus)* are dominating (Laugaste, 1983; Nõges et al., 1989). Sandy bottom is characteristic of the littoral areas. Here, the dominant macrophytes are ***Phragmites australis, Schoenoplectus lacustris, Polygonum amphibium, Potamogeton perfoliatus, Elodea canadensis, Stratiotes aloides, Sagittaria sagittifolia*** and ***Chara*** (Mjaèmets, 1983; Mäemets, 1990; Sudnitsõna, 1990). The freezing period lasts from December to April.

Materials and methods

The present paper is based on 335 qualitative and quantitative zooplankton samples collected (4 to 6 times a month) from June 1986 to March 1988 from the littoral (depth 0.5–1 m, sandy bottom with macrophytes) and pelagial (depth 7 m, clayey bottom) stations in the north-western part of Lake Peipsi (Figure 1). Qualitative samples were taken with a cone net (80 μm mesh) by repeated horizontal or vertical hauls. Integrated quantitative samples were collected with a 1-litre Ruttner sampler. 1-litre sub-samples were subsequently taken and concentrated by the sedimentation method after fixation. The samples were fixed with formalin (final concentration 3–4%). Simultaneously, water temperature and transparency (Secchi depth) were measured (Table 2). Several samples from each month were studied alive, focusing on illoricate species which are difficult to identify after fixation.

Rotifers were identified according to the taxonomic works of Lauterborn (1900), Kutikova (1970, 1978), Koste (1978), Mäemets & Kutikova (1979), Stemberger (1979), Koste & Shiel (1987), Shiel & Koste (1993), except for Bdelloidea which remained unidentified. Illoricate rotifers were identified on the basis of their trophi which were dissolved out using a solution of potassium hypochlorite (KClO). With a few exceptions, the taxonomic list followed the nomenclature of Kutikova (1970). Although the application of this nomenclature *(op. cit.)* may be problematic as it attributes a subspecific rank to all infraspecific categories (see Koste & Shiel, 1989), it was preferred for practical considerations, the more so because in most cases the status of the existing infraspecific units was not yet clear.

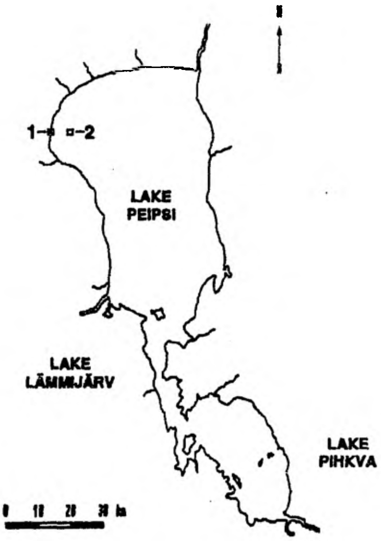


Figure 1. Location of sampling stations in Lake Peipsi. 1 = littoral; 2 = pelagial station.

Table 2. Water temperature and transparency (Secchi disc depth) in the stations studied in the north-western part of Lake Peipsi in 1986–1988. – = no date.

Month	Littoral		Pelagial			
	Temperature (°C)		Temperature (°C)		Transparency (m)	
	Range	Mean	Range	Mean	Range	Mean
Jan.	0.0–0.5	0.2	0.0–0.2	0.1	2.4–3.8	2.9
Feb.	0.1–0.2	0.2	0.2–0.3	0.3	2.3–2.4	2.4
Mar.	0.2–0.3	0.2	0.3–0.4	0.4	2.2–2.4	2.3
Apr.	0.4–3.0	1.4	0.5	0.5	3.0	3.0
May	4.8–11.5	8.7	– –	– –	– –	– –
June	13.0–21.9	16.4	11.9–19.3	16.0	2.5–4.0	3.0
July	16.1–21.4	18.3	15.8–20.4	18.1	2.0–3.8	2.7
Aug.	12.2–21.8	15.6	14.9–20.9	17.2	1.2–3.0	2.1
Sep.	5.8–12.7	9.6	8.0–14.2	11.7	1.8–2.9	2.2
Oct.	1.7–8.4	5.4	5.9–10.4	7.6	0.7–2.0	1.3
Nov.	0.0–5.4	1.7	– –	– –	– –	– –
Dec.	0.0–0.4	0.1	– –	– –	– –	– –

Results and discussion

A total of 161 rotifer taxa were identified (Table 3). Of these, approximately 70 are new in the lake, including 46 new records for Estonia. It is likely that further studies, especially in the littoral regions, will still increase the number of taxa. Compared to the most complete earlier list from Lake Peipsi given by Haberman (1978), 7 species did not re-occur: ***Brachionus diversicornis*** (Daday, 1883), ***Cephalodella stenroosi*** Wulfert, 1937, ***Notholca foliacea*** (Ehrenberg, 1838), ***Polyarthra dissimulans*** Nipkow, 1952, ***P. euryptera*** Wierzejski, 1891, ***Trichocerca (T.) bicristata*** (Gosse, 1887), ***T. (Diurella) similis*** (Wierzejski, 1893). Moreover, ***Asplanchna girodi*** Guerne, 1888 and ***Notommata cyrtopus*** Gosse, 1886 have been encountered in the southern part of the lake by me but are lacking in the present material.

The greatest number of taxa occurred in August (93), followed by September (79) and June (66), the lowest in January (12). In all, 19 families (Monogononta) with 41 genera are represented in the material. The dominant families are Brachionidae (32 taxa) and Synchaetidae (16). The following species are the most abundant: ***Anuraeopsis fissa, Conochilus hippocrepis, C. unicornis, Kellicottia longispina, Keratella cochlearis*** (predominantly ***K. c. cochlearis*** and ***K. c. robusta***), ***K. hispida, K. irregularis (K. i. irregularis, K. i. connectens), K. quadrata (K. q. reticulata, K. q. frenzeli), Notholca cinetura, N. squamula*** (mainly ***N. s. evensi***), ***Polyarthra dolichoptera, P. luminosa, P. major, P. remata, Synchaeta oblonga, S. pectinata, S. stylata, S. verrucosa***. Of these, ***A. fissa, N. cinetura, P. remata*** and ***S. stylata*** predominate only in the littoral, although they are present in the pelagial as well, except for ***A. fissa***. On the other hand, ***K. quadrata*** is dominant only in the pelagial. The composition of the dominating group, as well of the whole rotifer assemblage, is typical of eutrophic lakes in the northern temperate zone (Kutikova, 1970; Bērzinš, 1978).

Several species found are regarded as good indicators of eutrophic environment viz. ***Anuraeopsis fissa, Brachionus angularis, Filinia longiseta, Keratella irregularis, K. tecta, Lecane closterocerca, Pompholyx sulcata, Trichocerca cylindrica*** and ***T. pusilla*** (Bērzinš & Pejler, 1989a; Matveeva, 1991). Some indicators of oligotrophy are also present, viz. ***Ascomorpha ecaudis, Bipalpus hudsoni, Conochilus hippocrepis, C. unicornis, Gastropus stylifer*** and ***Kellicottia longispina*** *(op. cit.)*. As to ***C. unicornis*** and ***K. longispina***, they are more euryecious species which dominate in oligotrophic lakes, though they are found in relatively eutrophic lakes.

Euplanktonic rotifers (*sensu* Kutikova, 1970; Pontin, 1978) constitute about 35% of the taxa encountered, namely from the genera ***Anuraeopsis, Ascomorpha, Asplanchna, Bipalpus, Brachionus, Collotheca, Chromogaster, Filinia, Gastropus, Kellicottia, Keratella, Notholca, Polyarthra*** and ***Synchaeta***. However, several of them occur in the littoral area quite frequently. The representatives of the other genera (e.g. ***Cephalodella, Colurella, Encentrum, Euchlanis,***

Table 3. List of rotifers from Lake Peipsi. L = littoral; P = pelagial station; * = new record for Estonia. Numbers denote the months of occurrence.

1. *Anuraeopsis fissa fissa* (Gosse, 1851). L, 6–9.
2. *Ascomorpha ecaudis* Perty, 1850. L, P, 6, 8.
*3. *A. minima* Hofsten, 1909. P, 6.
4. *A. saltans* Bartsch, 1870. P, 8.
5. *Asplanchna priodonta priodonta* Gosse, 1850. L, P, 2, 6–10.
6. *A. priodonta helvetica* Imhof, 1884. P, 6.
7. Bdelloidea (*indet.*). L, P, 1, 3–12.
8. *Bipalpus hudsoni* (Imhof, 1891). L, P, 6.
9. *Brachionus angularis* Gosse, 1851. L, 7.
10. *B. calyciflorus anuraeiformis* Brehm, 1909. L, 9.
*11. *Cephalodella apocolea* Myers, 1924. L, 8.
12. *C. catellina* (Müller, 1786). L, P, 7–9.
13. *C. exigua* (Gosse, 1886). L, P, 6, 8.
14. *C. gibba gibba* (Ehrenberg, 1832). L, 10.
*15. *C. gibba microdactyla* Koch-Althaus, 1963. L, 6–9, 11.
16. *C. sterea minor* Donner, 1949. L, 7.
17. *C. ventripes ventripes* (Dixon-Nuttall, 1901). L, P, 6–9.
18. *Cephalodella* sp. 1. L, 8.
19. *Cephalodella* sp. 2. L, 11.
20. *Cephalodella* sp. 3. P, 8.
21. *Chromogaster ovalis* (Bergendal, 1892). P, 8.
22. *Collotheca* cf. *balatonica* Varga, 1936. P, 6.
23. *C. mutabilis* (Hudson, 1885). P, 6–10.
24. *C. ornata cornuta* (Dobie, 1849). L, P, 8–10.
25. *C. pelagica* (Rousselet, 1893). P, 6–10.
26. *Colurella adriatica* Ehrenberg, 1831. L, 6–11.
27. *C. colurus colurus* (Ehrenberg, 1830). L, 11.

Table 3. Continued.

*28. *C. colurus compressa* Lucks, 1912. L, 7–9.
*29. *C. uncinata deflexa* (Ehrenberg, 1834). L, 12.
30. *Conochilus hippocrepis* (Schrank, 1803). L, P, 6–10.
31. *C. unicornis* Rousselet, 1892. L, P, 6–10.
*32. *Dicranophorus edestes* Harring et Myers, 1928. P, 8.
33. *Dipleuchlanis propatula* (Gosse, 1886). L, 8.
34. *Encentrum (E.) marinum* (Dujardin, 1841). L, 6.
*35. *E. (E.) putorius putorius* Wulfert, 1936. L, 10, 12.
*36. *E. (E.) putorius armatum* Donner, 1943. L, 9, 11.
*37. *E. (E.) rapax* Donner, 1943. L, 5.
38. *Encentrum (E.)* sp. L, 3.
*39. *E. (Parencentrum)* cf. *spinosum* Koch-Althaus, 1962. L, 8.
*40. *Erignatha clastopis* (Gosse, 1886). L, 12.
41. *Euchlanis deflexa deflexa* Gosse, 1851. L, 6, 7, 9–11.
42. *E. dilatata dilatata* Ehrenberg, 1832. L, 6, 8–11.
43. *E. dilatata macrura* Ehrenberg, 1832. L, 5–8.
44. *E. dilatata unisetata* Leydig, 1854. L, 8.
45. *E. incisa* Carlin, 1939. L, 8, 9.
46. *E. lucksiana* Hauer, 1930. P, 9, 10.
47. *E. lyra lyra* Hudson, 1886. L, 4, 8, 10, 11.
48. *Filinia longiseta longiseta* (Ehrenberg, 1834). L, P, 6–10.
49. *F. longiseta limnetica* (Zacharias, 1893). L, P, 9, 10.
50. *F. terminalis* (Plate, 1886). L, P, 6.
51. *Floscularia?* sp. L, 8.
52. *Gastropus stylifer* Imhof, 1891. P, 6.
53. *Kellicottia longispina longispina* (Kellicott, 1879). L, P, 1–10, 12.
54. *Keratella cochlearis cochlearis* (Gosse, 1851). L, P, 5–12.

Table 3. Continued.

55.	*K. cochlearis macracantha* (Lauterborn, 1898). L, P, 1–10, 12.
56.	*K. cochlearis micracantha* (Lauterborn, 1900). L, P, 6–9.
*57.	*K. cochlearis nordica* Kutikova, 1978. L, P, 6–8.
58.	*K. cochlearis pustulata* (Lauterborn, 1900). L, P, 4, 6–10.
59.	*K. cochlearis robusta* (Lauterborn, 1900). L, P, 1–11.
60.	*K. hiemalis* Carlin, 1943. L, P, 1, 2, 4.
61.	*K. hispida* (Lauterborn, 1898). L, P, 6–10.
62.	*K. irregularis irregularis* (Lauterborn, 1898). L, P, 4, 6–10.
63.	*K. irregularis angulifera* (Lauterborn, 1900). L, P, 6–8, 10.
64.	*K. irregularis connectens* (Lauterborn, 1900). L, P, 2–7, 9, 10.
65.	*K. irregularis wartmanni* (Asper et Heuscher, 1889). L, P, 6–8.
66.	*K. quadrata quadrata* (Müller, 1786). L, P, 8, 9, 11.
67.	*K. quadrata dispersa* Carlin, 1943. L, 10.
68.	*K. quadrata frenzeli* (Eckstein, 1895). L, P, 1–12.
69.	*K. quadrata reticulata* Carlin, 1943. L, P, 1–3, 5–10.
70.	*K. tecta* (Gosse, 1851). L, P, 6–9.
71.	*K. testudo testudo* (Ehrenberg, 1832). L, 5, 6, 8–10.
*72.	*K. testudo gossei* Ahlstrom, 1943. L, 9.
*73.	*K. ticinensis* (Callerio, 1920). L, 10–12.
*74.	*K. valga heterospina* (Klausener, 1908). L, 9, 10.
*75.	*K. valga monospina* (Klausener, 1908). L, 12.
76.	*Lecane (L.) flexilis* (Gosse, 1886). L, 7–9.
*77.	*L. (L.) glypta* Harring et Myers, 1926. L, 9.
*78.	*L. (L.)* cf. *levistyla* (Olofsson, 1917). L, 8.
79.	*L. (L.) luna luna* (Müller, 1776). L, 8, 9.
*80.	*L. (L.) luna balatonica* Varga, 1945. L, 8.
81.	*L. (L.) luna presumpta* Ahlstrom, 1938. L, 7, 8.
*82.	*L. (L.) rhenana* Hauer, 1929. L, 8.
*83.	*L. (L.) verecunda* Harring et Myers, 1926. L, 10.
84.	*L. (Monostyla) arcuata* (Bryce, 1891). L, 7, 9.
85.	*L. (M.) closterocerca* (Schmarda, 1859). L, P, 7–10.
86.	*L. (M.) copeis* (Harring et Myers, 1926). L, 7, 8, 10.
87.	*L. (M.) latvica* (Berzins, 1943). L, 9.
88.	*L. (M.) lunaris* (Ehrenberg, 1832). L, 6, 8–11.
*89.	*L. (M.) opias* Harring et Myers, 1926. L, 8.
90.	*L. (M.) stenroosi* (Meissner, 1908). L, 11.
91.	*Lepadella (L.) acuminata acuminata* (Ehrenberg, 1834). L, 7.
92.	*L. (L.) ovalis* (Müller, 1786). L, 5–10.
93.	*L. (L.) patella patella* (Müller, 1776). L, 5–12.
*94.	*L. (L.) rhomboides lata* Wulfert, 1956. L, 8.
*95.	*Lindia torulosa* Dujardin, 1841. L, 6.
96.	*Lophocharis oxysternon* (Gosse, 1851). L, 5, 7, 8.
*97.	*L. salpina* (Ehrenberg, 1834). L, 2, 5, 6, 9–12.
*98.	*Mytilina crassipes* (Lucks, 1912). L, 5.
99.	*M. mucronata mucronata* (Müller, 1773). L, 9.
100.	*M. mucronata spinigera* (Ehrenberg, 1832). L, 6.
101.	*M. ventralis brevispina* (Ehrenberg, 1832). L, 8.
102.	*Notholca cinetura* Skorikov, 1914, L, P, 1–4, 12.
103.	*N. labis labis* Gosse, 1887. L, 4, 5, 7–11.
104.	*N. squamula squamula* (Müller, 1786). L, 1–5, 7, 9–12.
*105.	*N. squamula evensi* Gillard, 1948. L, P, 1–6, 10, 12.
*106.	*N. squamula mülleri* Focke, 1961. P, 2.

Table 3. Continued.

*107.	*Notommata glyphura* Wulfert, 1935. L, 8.
108.	*Notommata* sp. 1. L, 8.
109.	*Notommata* sp. 2. L, 4.
110.	*Platyias quadricornis quadricornis* (Ehrenberg, 1832). L, 8.
*111.	*Pleurotrocha petromyzon* Ehrenberg, 1830. L, P, 8, 10, 11.
112.	*Ploesoma peipsiense* Mäemets et Kutikova, 1979. L, 8.
113.	*P. truncatum* (Levander, 1894). L, 6–8.
114.	*Polyarthra dolichoptera dolichoptera* Idelson, 1925. L, P, 2–7, 9–11.
115.	*P. longiremis* Carlin, 1943. L, 7–9.
116.	*P. luminosa* Kutikova, 1962. L, P, 6–10.
117.	*P. major* Burckhardt, 1900. L, P, 6–10.
118.	*P. remata* Skorikov, 1896. L, P, 6–10.
119.	*P. vulgaris* Carlin, 1943. L, P, 1–4, 12.
120.	*Pompholyx sulcata* Hudson, 1885. P, 9, 10.
121.	*Proales decipiens* (Ehrenberg, 1832). L, P, 8–12.
*122.	*P.* cf. *globulifera* (Hauer, 1921). L, 5.
*123.	*P. sigmoidea* (Skorikov, 1896). L, 9, 10.
124.	*P. theodora* (Gosse, 1887). L, 6, 11, 12.
125.	*Proales* sp. L, 11.
*126.	*Ptygura melicerta* Ehrenberg, 1832. L, 7.
127.	*Ptygura* sp. L, 8.
*128.	*Sinantherina* sp. L, 9.
129.	*Synchaeta kitina* Rousselet, 1902. L, P, 6–10.
130.	*S. lakowitziana* Lucks, 1912. P, 10.
131.	*S. oblonga* Ehrenberg, 1831. L, P, 5–11.
132.	*S. pectinata* Ehrenberg, 1832. L, P, 5–11.
133.	*S. stylata* Wierzejski, 1893. L, P, 6–9.
134.	*S. tremula* (Müller, 1786). L, P, 9, 11.
135.	*S. verrucosa* Nipkow, 1961. L, P, 1–5, 10–12.

Table 3. Continued.

*136.	*Taphrocampa selenura* Gosse, 1851. P, 8.
*137.	*Testudinella caeca* (Parsons, 1892). L, 9.
*138.	*T. carlini* Bartos, 1951. L, 6.
*139.	*T. elliptica* (Ehrenberg, 1834). L, 6, 11.
*140.	*T. mucronata* (Gosse, 1886). L, 5, 7–9.
141.	*T. patina patina* (Hermann, 1783). L, 5–9, 11.
142.	*T. patina intermedia* (Anderson, 1889). L, 5, 6, 8, 9, 12.
*143.	*T. patina trilobata* (Anderson et Shephard, 1892). L, 6, 11.
*144.	*T. truncata truncata* (Gosse, 1886). L, 5.
145.	*Trichocerca (T.) capucina* (Wierzejski et Zacharias, 1893). L, P, 6, 8, 9.
146.	*T. (T.) cylindrica* (Imhof, 1891). P, 9.
147.	*T. (T.) longiseta* (Schrank, 1802). L, 8. 9.
148.	*T. (T.) pusilla* (Lauterborn, 1898). L, P, 8, 9.
149.	*T. (T.) rattus carinata* (Ehrenberg, 1830). L, 5, 6, 9, 10.
*150.	*T. (Diurella) dixon-nuttalli* (Jennings, 1903). L, 6–8.
*151.	*T. (D.) intermedia* (Stenroos, 1898). L, 5, 9, 11.
*152.	*T. (D.) obtusidens* (Olofsson, 1918). L, 8.
153.	*T. (D.) porcellus porcellus* (Gosse, 1886). L, 7.
154.	*T. (D.) porcellus major* (Hauer, 1935). L, P, 7–11.
*155.	*T. (D.) relicta* Donner, 1950. L, 8.
156.	*T. (D.) rousseleti* (Voigt, 1902). L, P, 6–10.
157.	*T. (D.) taurocephala* (Hauer, 1931). L, 7, 9.
158.	*T. (D.) tenuior* (Gosse, 1886). L, P, 7–10.
159.	*T. (D.) weberi* (Jennings, 1903). L, 8.
160.	*Trichotria pocillum pocillum* (Müller, 1776). L, P, 5–8, 10, 11.
*161.	*Wolga spinifera* (Western, 1894). L, 9.

Lecane, Lepadella, Lophocharis, Mytilina, Notommata, Proales, Testudinella, Trichocerca, Trichotria) and of the class Bdelloidea belong to non-planktonic (periphytic, benthic or plankto-benthic) forms *(op. cit.)* but their invasion into the pelagic zone of lakes is not uncommon.

The majority of the taxa recorded here are more or less eurythermal (Kutikova, 1970; Pontin, 1978; Bērziņš & Pejler, 1989b). Some are restricted to the colder period. *Keratella hiemalis, Notholca cinetura, N. squamula, Polyarthra dolichoptera, P. vulgaris, Synchaeta lakowitziana* and *S. verrucosa* form a typical thermophobic association. As regards *N. squamula* and *P. dolichoptera*, they seem to be more tolerant to higher temperatures. *Asplanchna priodonta, Kellicottia longispina, Keratella cochlearis macracantha, K. cochlearis robusta* and *Keratella quadrata* can be considered as perennial. In May–June, during a rapid increase in water temperature, the winter complex is replaced by the summer community which consists of relatively eurythermal (e.g. *Filinia longiseta, Keratella c. cochlearis, K. irregularis, K. hispida, Polyarthra major, P. remata, Synchaeta oblonga*) or warm stenothermal taxa (e.g. *Anuraeopsis fissa, Polyarthra longiremis, Trichocerca pusilla*).

Nearly all the taxa recorded are rather common with either a cosmopolitan or widespread distribution. Some remarkable taxa can be singled out. *Lecane latvica* has so far been reported only from the Baltic province (Kutikova, 1970; Bērziņš, 1978). Kutikova & Haberman (1986) have found it from the hypertrophic Lake Võrtsjärv (in Estonia), too. However, not all authors accept it as a valid species. Segers (1995) suggests that *L. latvica* is synonymous with *L. closterocerca*. It seems that further revision is needed concerning this point. *Lecane copeis* is another rare species encountered in North and South America, Europe and Australia (Bērziņš, 1978; Segers, 1995). *Lecane verecunda* is even more remarkable, being known only from its type locality in North America and from Moldavia by a single record (Kutikova, 1970; Segers, 1995). The occurrence of *Keratella cochlearis nordica* is also worth mentioning. This subspecies was originally described by Kutikova (1978) from tundra zone lakes in Komi, Russia; it was considered thermophobic and characteristic of Arctic fauna. Haberman & Mäemets (1987) have mentioned it from Finland. Besides, Pejler (1957) has found some forms from the Swedish Lapland, treated by him as variations of *Keratella c. robusta* which seem very similar to *K. c. nordica*. In our material *K. c. nordica* occurs from June to August (at 15.5–19.3 °C).

The local fauna includes a supposed endemic species *Ploesoma peipsiense* described by Mäemets & Kutikova (1979). In the present material *P. peipsiense* occurs in August in the littoral (at 13.2 °C); it was more frequent in the more eutrophic southern part of the lake from July to September (at 14.6–19.0 °C). Our data confirm the supposition of Mäemets & Kutikova (1979) that *P. peipsiense* is a stenotherm living at medium temperatures and preferring eutrophic habitats.

Acknowledgements

This work was supported by grant No. 728 of the Estonian Science Foundation.

References

Bērziņš, B., 1978. Rotatoria. In J. Illies (ed.), Limnofauna Europaea. Gustav Fischer Verlag, Stuttgart-New York, Swets & Zeitlinger B.V., Amsterdam: 54–91.

Bērziņš, B. & B. Pejler, 1989a. Rotifer occurrence and trophic degree. Hydrobiologia 182: 171–180.

Bērziņš, B. & B. Pejler, 1989b. Rotifer occurrence in relation to temperature. Hydrobiologia 175: 223–231.

Denisenko, A. I., 1975. Letnij zooplankton južnoj časti Čudskogo ozera. In V. P. Krasnopevcev & N. N. Malaškin (eds), Syr'evye resursy Pskovsko-Čudskogo ozera i ih racional'noe ispol'zovanie, Trudy Pskovskogo otdelenija GosNIORH 1: 52–57. [The summer zooplankton of the southern part of Lake Peipsi. In Russian].

Haberman, J., 1976. An ecological characterization of the rotifers dominating in the pelagic region of Lakes Peipsi-Pihkva and Võrtsjärv. In H. Haberman, J. Haberman & K. Elberg (eds), Productivity of Estonian fresh waters, Estonian Contributions to the International Biological Programme, 10. Tartu: 35–59.

Haberman, J., 1978. Seasonal dynamics of pelagic rotifers of Lakes Peipsi-Pihkva and Võrtsjärv. Proc. Acad. Sci. Estonian SSR, Biol. 27: 16–30.

Haberman, J., 1983. Comparative analysis of plankton rotifer biomass in large Estonian lakes. Hydrobiologia 104: 293–296.

Haberman, J., 1990. Peipsi zooplanktoni produktsioon. In T. Timm (ed.), Peipsi järve seisund. Eesti Teaduste Akadeemia, Tartu: 115–118.

Haberman, J. & A. Mäemets, 1987. On the zooplankton of some Evo forest lakes. Lammi Notes 14: 1–5.

Jakovleva, N. A., 1975. O vidovom sostave i količestvennom razvitii zooplanktona Pskovsko-Čudskogo ozera. In V. P. Krasnopevcev & N. N. Malaškin (eds), Syr'evye resursy Pskovsko-Čudskogo ozera i ih racional'noe ispol'zovanie, Trudy Pskovskogo otdelenija GosNIORH 1: 64–71. [On the species composition and quantitative development of the zooplankton of Lake Peipsi-Pihkva. In Russian].

Koste, W., 1978. Rotatoria. Die Rädertiere Mitteleuropas. (Überordnung Monogononta). Gebrüder Borntraeger, Berlin-Stuttgart, 673 pp., 234 pl.

Koste, W. & R. J. Shiel, 1987. Rotifera from Australian inland waters. II. Epiphanidae and Brachionidae (Rotifera: Monogononta). Invert. Taxon. 7: 949–1021.

Koste, W. & R. J. Shiel, 1989. Classical taxonomy and modern methodology. Hydrobiologia 186/187 (Dev. Hydrobiol. 52): 279–284.

Kutikova, L. A., 1970. Kolovratki fauny SSSR (Rotatoria). Podklass Eurotatoria (otrjady Ploimida, Monimotrochida, Paedotrochida). Nauka, Leningrad, 744 pp. [Rotifers of the fauna of the USSR. In Russian].

Kutikova, L. A., 1978. Kolovratki. In O. S. Zvereva (ed.), Flora i fauna vodoemov Evropejskogo Severa (na primere ozer Bol'šezemel'skoj tundry). Nauka, Leningrad: 48–51, 168–170. [Rotifers. In Russian].

Kutikova, L. & J. Haberman, 1986. Rotifers (Rotatoria) of Lake Võrtsjärv. 1. Taxonomical and ecological survey. Proc. Acad. Sci. Estonian SSR, Biol. 35: 113–121.

Laugaste, R., 1983. Fitoplankton. In A. A. Sokolov (ed.), Gidrometeorologičeskij režim ozer i vodohranilišč SSSR. Čudsko-Pskovskoe ozero. Gidrometeoizdat, Leningrad: 126–128. [Phytoplankton. In Russian].

Lauterborn, R., 1900. Der Formenkreis von *Anuraea cochlearis*. Ein Beitrag zur Kenntnis der Variabilität bei Rotatorien. I. Teil: Morphologische Gliederung des Formenkreises. Verhandl. d. heidelb. naturhist.-med. Vereins 6: 412–448.

Lindpere, A., H. Starast, A. Milius, M. Haldna & H. Simm, 1989. Peipsi-Pihkva järve vee omadused aastail 1985–1987. Proc. Acad. Sci. Estonian SSR, Biol. 38: 107–118.

Lokk, S., R. Laugaste & A. Mäemets, 1988. Changes in bacterio-, phyto- and zooplankton of Lake Peipsi-Pihkva. In M. Zobel (ed.), Dynamics and ecology of wetlands and lakes in Estonia. Acad. Sci. Est. SSR, Tallinn: 173–187.

Matveeva, L. K., 1991. Planktonnye kolovratki kak indikatory trofnosti. Bjull. mosk. Obščestva Ispytatelej Prirody, otdelenie biol. 96: 54–62. [Planktonic rotifers as indicators of trophic level. In Russian].

Mäemets, A(are) & L. Kutikova, 1979. A new rotifer *Ploesoma peipsiense* sp. nov. in Lake Peipsi. Proc. Acad. Sci. Estonian SSR, Biol. 28: 98–101.

Mäemets, A(ime), 1990. Eutrofeerumisega seotud nähtudest Peipsi-Pihkva järve ja selle sissevoolude suurtaimestikus. In T. Timm (ed.), Peipsi järve seisund. Eesti Teaduste Akadeemia, Tartu: 91–94.

Mjaèmets, A. A., 1983. Vysšaja vodnaja rastitel'nost'. In A. A. Sokolov (ed.), Gidrometeorologičeskij režim ozer i vodohranilišč SSSR. Čudsko-Pskovskoe ozero. Gidrometeoizdat, Leningrad: 125–126. [Water macrophytes. In Russian].

Mjaèmets, A. H., 1966. O letnem zooplanktone Pskovsko-Čudskogo ozera. In Hydrobiology and fisheries of Lake Peipsi-Pskov, Hydrobiological Researches 4. Tallinn: 80–96. [On summer zooplankton of Lake Peipsi-Pskov. In Russian].

Nõges, T., P. Nõges & I. Ott, 1989. Produkcija fitoplanktona v pelagiali Čudskogo ozera v 1985–1986 gg. Proc. Acad. Sci. Estonian SSR, Biol. 38: 123–130. [Phytoplankton production in the pelagial of Lake Peipsi in 1985–1986. In Russian].

Pejler, B., 1957. On variation and evolution in planktonic Rotatoria. Zool. Bidr. Upps. 32: 1–66.

Pihlak, A., E. Maremäe, A. Lindpere, A. Milius & H. Starast, 1987. Gidrohimičeskoe sostojanie vod Pskovsko-Čudskogo ozera v ijune 1985 g. Proc. Acad. Sci. Estonian SSR, Biol. 36: 133–145. [Hydrochemical state of Lake Peipsi-Pihkva in June 1985. In Russian].

Pontin, R. M., 1978. A key to the freshwater planktonic and semi-planktonic Rotifera of the British Isles, Freshwater Biol. Assoc. sci. Publ. 38. Titus Wilson & Son Ltd., Kendal, 178 pp.

Saava, A., 1990. Peipsi järve kui joogiveeallika hügieeniline hinnang. In T. Timm (ed.), Peipsi järve seisund. Eesti Teaduste Akadeemia, Tartu: 68–71.

Samsonov, N. A., 1912. Plankton Pskovskogo vodoema. I. Zimnij plankton. Trudy promyslovo-naučnoj èkspedicii po izučeniju Pskovskogo vodoema 1(1): 15–30. [Plankton of Pskov lake system. I. Winter plankton. In Russian].

Samsonov, N. A., 1914. Plankton Pskovskogo vodoema. II. Vesennij i letnij plankton. Trudy promyslovo-naučnoj èkspedicii po izučeniju Pskovskogo vodoema 1(4): 1–18. [Plankton of Pskov lake system. II. Spring and summer plankton. In Russian].

Segers, H., 1995. Rotifera. Vol. 2: The Lecanidae (Monogononta). Guides to the identification of the microinvertebrates of the continental waters of the world 6. SPB Academic Publishing bv, The Hague, 226 pp.

Shiel, R. J. & W. Koste, 1993. Rotifera from Australian inland waters. IX. Gastropodidae, Synchaetidae, Asplanchnidae (Rotifera: Monogononta). Trans. r. Soc. S. Aust. 117: 111–139.

Sokolov, A. A., 1941. Čudsko-Pskovskoe ozero. Gidrometizdat, Leningrad-Moskva, 224 pp. [Lake Peipsi-Pihkva. In Russian].

Starast, H., A. Lindpere & A. Milius, 1990. Metoodilised soovitused Peipsi troofsuse hindamiseks. In T. Timm (ed.), Peipsi järve seisund. Eesti Teaduste Akadeemia, Tartu: 16–19.

Stemberger, R. S., 1979. A guide to rotifers of the Laurentian Great Lakes. US EPA Publication EPA-600/4-79-021. Cincinnati, 185 pp.

Sudnitsõna, D. N., 1990. Peipsi-Pihkva järve kõrgem veetaimestik. In T. Timm (ed.), Peipsi järve seisund. Eesti Teaduste Akadeemia, Tartu: 87–90.

Virro, T. & J. Haberman, 1993. The rotifers of Lake Peipus. Hydrobiologia 255/256 (Dev. Hydrobiol. 83): 389–396.

VI

Virro, T.
Taxonomic problems in the genus *Polyarthra* from Lake Peipsi.
Proc. Estonian Acad. Sci. Biol. Ecol. (Submitted).

TAXONOMIC PROBLEMS
IN THE GENUS *POLYARTHRA* FROM LAKE PEIPSI

Taavi Virro

Department of Zoology and Hydrobiology,
University of Tartu, 46 Vanemuise Street, 51014 Tartu, Estonia;
e-mail: tvirro@ut.ee

Abstract. The genus *Polyarthra* is one of the dominant rotifer genera in Lake Peipsi (Estonia). The genus appeared to be quite interesting taxonomically. Two confusing *Polyarthra* morphotaxa, camouflaging each other morphologically and ecologically and coexisting with *P. remata,* were found in the summer rotifer community. Previously these were supposed to be rectangular morphotypes of *P. remata*, but thorough analysis of morphology and trophi revealed that actually two distinct species were involved: *P.* cf. *dolichoptera* and *P.* cf. *vulgaris*. Both are atypical forms without ventral finlets, the latter moreover shows *proloba* variation.

In the present study the range of variation in external and trophi morphology of these forms is examined to clarify their status.

Key words: *Polyarthra*, taxonomy, morphology

INTRODUCTION

In general, rotifers are characterized by extensive intraspecific variability, which is the main reason for many taxonomic problems in this group. Identification to species level, so far based mainly on phenotypic characters, may be difficult, particularly in illoricate taxa, as illustrated by the genus *Polyarthra*. Due to the wide variability and presence of transitional forms (e.g. Pejler, 1956), the external morphological features are not always reliable for species discrimination. The calculation of indices of fin length : body length and fin length : fin width has been recommended (Ruttner-Kolisko, 1972; Koste, 1978; Shiel & Koste, 1993). In some cases biometrical analysis has been used with success (Guiset, 1977; Stemberger, 1979). However, it should be mentioned that due to an extensive overlap, morphometric criteria are often inadequate to distinguish *Polyarthra* species (Koste & Shiel, 1989; Shiel & Koste, 1993; Virro, 1995). Therefore, trophi analysis is indispensable to avoid misidentifications. Rotifer trophi appear to be species-specific and are considered extremely valuable taxonomic discriminators (Koste, 1978; Markevich, 1985; Koste & Shiel, 1989; Shiel & Koste, 1993). Sanoamuang (1993) showed that trophi structure of *Filinia* was not affected by temperature unlike body measurements. Trophi analysis was used successfully by Guiset (1977) to separate *Polyarthra* species.

In my earlier study on the genus *Polyarthra* in Lake Peipsi (Virro, 1995), I found two taxonomically confusing *Polyarthra* forms co-occurring with typical *Polyarthra remata* in summer. Both forms lacked ventral finlets and were quite similar in size to *P. remata*. In contrast with the latter, showing a typical rounded posterior and 4 nuclei in the vitellarium, the other two forms had an almost rectangular posterior and 8 nuclei in the vitellarium. One of these showed a normally positioned mastax; the other had the mastax tilted characteristic of *proloba* variation (Virro, *op. cit.*). I supposed them to be rectangular forms of *P. remata* (Virro, *op. cit.*).

The aim of the present study is to determine the range of morphological variation of the three forms involved, and to clarify their status by the analysis of their trophi and body morphology.

THE LAKE

Lake Peipsi (58°22'N–59°00'N, 26°57'E–27°59'E, surface area 2611 km^2, average depth 8.3 m, maximum depth 12.9 m) is the northern part of the compound Lake Peipsi–Pihkva (named also L. Peipus–Pskov in some earlier papers) (3558 km^2) situated on the eastern border of Estonia. It is eutrophic, with mesotrophic features in the northern region. See, e.g. Nõges *et al.* (1996) for the general description of L. Peipsi–Pihkva, and Virro (1996) for the taxonomic composition of rotifers of L. Peipsi.

MATERIALS AND METHODS

The material dealt with in the present paper derived from qualitative and quantitative zooplankton samples collected from June 1986 till March 1988 (4 to 6 times a month) from the littoral (depth 0.5–1 m) and pelagial (depth 7 m) stations in the north-western part of Lake Peipsi. Qualitative samples were taken with a cone net (80 µm mesh). Quantitative samples were collected with a 1-litre Ruttner sampler and concentrated by the sedimentation method after fixation. The samples were fixed with formaldehyde (3–4%). Water temperature was measured at the moment of sampling.

Measurements of body and fins, and trophi were taken with an ocular micrometer at 400×, and 900× magnification respectively, using a compound microscope. Estimated by the index of sample average determination accuracy (Aarma & Vensel, 1996), the means of morphometric characters are representative, the value of the index varying between 1–5%. For trophi analysis, the trophi were isolated using a solution of sodium hypochlorite (NaClO). Photomicrographs were taken with a Wild MPS 51S camera mounted on a Leitz Laborlux D microscope at 500× magnification. Drawings were made using a camera lucida.

The rotifer taxa were identified according to Kutikova (1970), Ruttner-Kolisko (1972), Koste (1978), Stemberger (1979) and Shiel & Koste (1993).

RESULTS

Thorough study of the trophi and external morphological features revealed that actually populations of three distinct *Polyarthra* species are involved, causing the seeming and confusing polymorphism of *Polyarthra remata* in Lake Peipsi. These are *Polyarthra remata* Skorikov, 1896, and atypical forms of *P. dolichoptera* Idelson, 1925 and *P. vulgaris* Carlin, 1943, here referred to as *P.* cf. *dolichoptera* and *P.* cf. *vulgaris*, respectively. Comparative morphometric measurements of these forms and their trophi are presented in Tables 1 and 2, and described below:

Polyarthra remata (Figs 1a-b)

Typical form with rounded posterior end of body and 4 nuclei in vitellarium. It corresponds in all taxonomically significant features, including trophus morphology (Fig. 2a-b), to the descriptions by, e.g. Kutikova (1970), Koste (1978) and Shiel & Koste (1993).

P. remata occurs in Lake Peipsi from June to October at water temperatures of 6.4–21.9°C. It has maxima in August or September (Virro, 1995, 1996). Bisexual reproduction, indicated by the presence of haploid eggs, occurs from June to September.

Polyarthra cf. *dolichoptera* (Figs 1c-e)

Unlike the typical *P. dolichoptera* this form lacks the pair of ventral finlets. It is smaller than the typical form (BL 94–141 μm, FL 105–186 μm) from L. Peipsi (Virro, 1995). Otherwise it is *dolichoptera*-like in habitus displaying an almost rectangular, sometimes slightly lobed, posterior. Narrow fins longer than body, with distinct median rib; lateral ribs absent or faint (Fig. 1e). Lateral antennae located at posterior corners. Vitellarium with 8 nuclei. Resting eggs similar to those of *P. dolichoptera* (double-shelled with spines or columns between) (Virro, 1995: Fig. 2). *P.* cf. *dolichoptera* may be confused with smaller individuals of *P. major*, a species also lacking ventral finlets and having 8 nuclei in vitellarium. These two taxa are easily separated by fin morphology. The fins of *P. major* are shorter than the body, wide (15–40 μm), coarsely serrate, leaflike with lateral ribs and stemlike proximal part, median rib fading distally (Kutikova, 1970; Shiel & Koste, 1993; Virro, 1995). In *P. major* lateral antennae are inserted before posterior corners.

Trophi analysis showed (Fig. 2c-d) that this form without ventral finlets belongs to *P. dolichoptera*, having, according to Shiel & Koste (1993), the characteristic hatchet-like ramus with a single tooth on the inner margin fitting into a groove on the opposite ramus, and long rodlike fulcrum. The trophi of *P. major* resemble those of *P. dolichoptera*. Rami of *P. major* have similar opposite rami teeth, but, unlike the knobbed or lobed rami tips in *P. dolichoptera*, the rami tips in *P. major* are serrated (Shiel & Koste, *op. cit.*).

P. cf. *dolichoptera* was encountered in the littoral from July to September at temperatures 12.6–21.9°C, and in the pelagial from September to October (6.4–14.2°C). It has a bisexual period (haploid and resting eggs found) in July–August.

Polyarthra cf. *vulgaris* (Figs 1f-h)

This form was different from the typical *P. vulgaris* in two respects. First, the entire population belonged to the *proloba* morphotype with tilted mastax. Second, it was also lacking the pair of ventral finlets. Although, having the rectangular habitus similar to

P. vulgaris, this form is smaller than typical *P. vulgaris* (BL 100–122 µm, FL 107–135 µm) from Lake Peipsi (Virro, 1995). Fins (Fig. 1h) are characteristic of *P. vulgaris*: broader than in *P. dolichoptera*, lanceolate, with medial and lateral ribs and serrate margins. Lateral antennae are near the posterior corners. It also has 8 nuclei in vitellarium.

The trophi of this *P.* cf. *vulgaris* (Fig. 2e-f) are similar to that of typical *P. vulgaris*. In accordance with Koste (1978) and Shiel & Koste (1993), the trophus showed a single tooth on the right ramus, fitting between two large teeth on the left ramus. Unlike the typical *P. vulgaris* the fulcrum of this *proloba* form is curved at an angle of almost 45°, resembling a boomerang in lateral view.

This atypical form of *P. vulgaris* occurred in the littoral only, during August at 16.5–21.9°C.

Due to extensive overlap in most morphometric criteria (Fig. 3, Tables 1 and 2) the three forms are difficult to distinguish by morphometric data only. Trophi analysis proved to be the most valuable tool in the discrimination of these taxonomically confusing forms of *Polyarthra*.

DISCUSSION

Considering the above-mentioned results, the supposed polymorphism of *Polyarthra remata* regarding rectangular phenotypic variations, as was described by Wesenberg-Lund (1930) and Virro (1995), should be excluded in our case where two additional morphotaxa are involved. Donner (1978) has mentioned *P. dolichoptera* and *P. vulgaris proloba* forms lacking ventral finlets, and coexisting with *P. remata*. He supposed that certain unidentified environmental or internal factors were producing similar variations in several *Polyarthra* species along two lines: 1) the disappearance of ventral finlets, and 2) appearing of *proloba* variation of mastax. Relying on our results, water temperature cannot be this crucial factor, as the temperature ranges of the forms under discussion were overlapping. The populations of these species probably include different ecotypes. It is likely that these ecotypes are based on genotypically different demes. This possibility was proposed by Pejler (1957) and Bērziņs & Pejler (1989). It has been proved experimentally (King, 1972, 1977) that the rotifer populations consist of temporally restricted, genotypically distinct and practically discrete demes adapted to different environmental conditions.

The patterns of seasonal development of the two forms of *P. dolichoptera* in Lake Peipsi refer to ecological and reproductive segregation. The typical *P. dolichoptera* has two periods of occurrence: from January to June, and from September to November, both with bisexual reproduction (Virro, 1995). The development of the atypical form occupies the interval between these periods. The occurrence of *P.* cf. *vulgaris* is also separated from the typical form, the latter being present from December to April (Virro, 1995).

Considering the differences in morphology and seasonal occurrence, the possibility that these forms are sibling species or species *in statu nascendi* cannot be excluded either. Further study of, e.g. trophi ultrastructure using SEM, and culture experiments starting from eggs of atypical and typical forms of *P. dolichoptera* and *P. vulgaris* found in Lake Peipsi are necessary to solve the above mentioned problems.

ACKNOWLEDGEMENTS

This work was supported by grant No. 2478 of the Estonian Science Foundation. I also thank Mr Siimo Virro for his helpful technical assistance and Mr Harri Virro for financial support to attend the 8th International Rotifer Symposium at Collegeville (U.S.A.) where the results of this project were presented.

REFERENCES

Aarma, A. & Vensel, V. 1996. *Statistika teooria põhikursus*. Külim, Tallinn.

Bērziņs, B. & Pejler, B. 1989. Rotifer occurrence in relation to temperature. *Hydrobiologia*, **175**, 223–231.

Donner, J. 1978. Material zur saprobiologischen Beurteilung mehrerer Gewässer des Donau-Systems bei Wallsee und in der Lobau, Österreich, mit besonderer Berücksichtung der litoralen Rotatorien. *Arch. Hydrobiol., Suppl.*, **52**, 117–228.

Guiset, A. 1977. Some data on variation in three planktonic genera. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **8**, 237–239.

King, C. E. 1972. Adaptation of rotifers to seasonal variation. *Ecology*, **53**, 408–418.

King, C. E. 1977. Genetics of reproduction, variation, and adaptation in rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, **8**, 187–201.

Koste, W. 1978. *Rotatoria. Die Rädertiere Mitteleuropas. (Überordnung Monogononta)*. Gebrüder Borntraeger, Berlin–Stuttgart.

Koste, W. & Shiel, R. J. 1989. Classical taxonomy and modern methodology. *Hydrobiologia*, **186/187**, 279–284.

Kutikova, L. A. 1970. *Rotifers of the fauna of the USSR (Rotatoria). Subclass Eurotatoria (Orders Ploimida, Monimotrochida, Paedotrochida)*. Nauka, Leningrad (in Russian).

Markevich, G. I. 1985. The main trends of idioadaptive evolution of rotifers. Jaws. *In Rotifera. Proceedings of the 2nd All-Union rotifer symposium* (Kutikova, L. A., ed.). Nauka, Leningrad, 17–37 (In Russian).

Nõges, T., Haberman, J., Jaani, A., Laugaste, R., Lokk, S., Mäemets, A., Nõges, P., Pihu, E., Starast, H., Timm, T. & Virro, T. 1996. General description of Lake Peipsi–Pihkva. *Hydrobiologia*, **338**, 1–9.

Pejler, B. 1956. Introgression in planktonic Rotatoria with some points of view on its causes and conceivable results. *Evolution*, **10**, 246–261.

Pejler, B. 1957. On variation and evolution in planktonic Rotatoria. *Zool. Bidr. Upps.*, **32**, 1–66.

Ruttner-Kolisko, A. 1972. Rotatoria. In *Die Binnengewässer, 26. Das Zooplankton der Binnengewässer, 1* (Elster, H.-J. & Ohle, W., eds.). E. Schweizerbartsche Verlagsbuchhandlung, Stuttgart, 99–234.

Sanoamuang, L. 1993. The effect of temperature on morphology, life history and growth rate of *Filinia terminalis* (Plate) and *Filinia* cf. *pejleri* Hutchinson in culture. *Freshwat. Biol.*, **30**, 257–267.

Shiel, R. J. & Koste, W. 1993. Rotifera from Australian inland waters. IX. Gastropodidae, Synchaetidae, Asplanchnidae (Rotifera: Monogononta). *Trans. r. Soc. S. Aust.*, **117**, 111–139.

Stemberger, R. S. 1979. *A guide to rotifers of the Laurentian Great Lakes*. US EPA Publication EPA-600/4-79-021, Cincinnati.

Virro, T. 1995. The genus *Polyarthra* in Lake Peipsi. *Hydrobiologia*, **313/314** (Dev. Hydrobiol. 109), 351–357.

Virro, T. 1996. Taxonomic composition of rotifers in Lake Peipsi. *Hydrobiologia*, **338**, 125–132.

Wesenberg-Lund, C. 1930. Contributions to the biology of the Rotifera. Part II. The periodicity and sexual periods. *Kgl. danske vidensk. Selsk. Skrifter, nat. math. Afd.*, **9**, 2, 1–230.

PEREKOND *POLYARTHRA* TAKSONOOMILISED PROBLEEMID PEIPSI JÄRVES

Taavi Virro

Perekond *Polyarthra* on üks domineerivaid keriloomaperekondi Peipsi järves. Samas on siinsed *Polyarthra* liigid ka taksonoomiliselt üsna huvipakkuvad. Suvises keriloomakoosluses esinevad koos liigiga *P. remata* kaks taksoniliselt kuuluvuselt segast vormi. Morfoloogilise ja ökoloogilise sarnasuse põhjal võis algul oletada, et tegemist on *P. remata* kandilise tagakehaga morfotüüpidega. Väliste morfoloogiliste tunnuste ja lõugade põhjalikum analüüs näitas aga, et need vormid kuuluvad tegelikult kahte erinevasse liiki: *P.* cf. *dolichoptera* ja *P.* cf. *vulgaris*. Mõlemad vormid on ebatüüpilised, ilma kõhtmiste jätketeta. Lisaks on vormil *P.* cf. *vulgaris* normaalsest asendist kõrvale kaldunud mastaks (nn. *proloba* teisend).

Käesoleva töö eesmärk on uurida nende kolme vormi morfoloogilise muutlikkuse ulatust ja selgitada nende staatus väliste morfoloogiliste tunnuste ning lõugade ehituse põhjal.

Table 1. Morphometric data of the *Polyarthra* forms (females only) in Lake Peipsi. BL = body length; BW = body width; FL = fin length; FW = fin width; SD = standard deviation; n = number of observations; NNV = number of nuclei in vitellarium. All measurements in µm

		P. remata	*P.* cf. *dolichoptera*	*P.* cf. *vulgaris*
BL	Range	78–101	86–124	83–111
	Mean	89.9	103.5	97.0
	SD	4.9	7.9	4.5
	n	40	40	40
BW	Range	45–56	55–71	60–69
	Mean	50.2	65.0	64.9
	SD	2.8	3.6	2.1
	n	40	40	40
FL	Range	86–113	95–137	90–112
	Mean	97.4	117.2	105.0
	SD	6.9	9.7	5.3
	n	40	40	40
FW	Range	4–7	6–9	9–14
	Mean	5.4	7.8	11.0
	SD	0.8	0.9	1.3
	n	40	40	40
BL/FL	Range	0.8–1.1	0.7–1.1	0.8–1.1
	Mean	0.93	0.89	0.93
	SD	0.08	0.07	0.04
	n	40	40	40
FL/FW	Range	13.9–24.5	11.2–21.7	7.6–11.7
	Mean	18.32	15.36	9.62
	SD	2.75	2.36	0.99
	n	40	40	40
NNV		4	8	8

Table 2. Trophi measurements of the *Polyarthra* forms in Lake Peipsi. TR = trophus length; RA = rami length; FU = fulcrum length; MA = manubria length; SD = standard deviation; n = number of observations. All measurements in µm

		P. remata	*P.* cf. *dolichoptera*	*P.* cf. *vulgaris*
TR	Range	36–49	40–62	45–72
	Mean	43.4	53.8	60.5
	SD	3.6	6.1	8.7
	n	19	16	14
RA	Range	18–27	23–38	27–44
	Mean	23.7	32.3	36.1
	SD	2.8	4.2	5.7
	n	18	16	14
FU	Range	19–23	16–26	20–29
	Mean	21.1	22.1	26.0
	SD	1.0	2.7	2.9
	n	19	17	15
MA	Range	18–32	23–33	27–34
	Mean	24.3	29.4	31.0
	SD	3.8	3.4	2.3
	n	14	14	9
TR/FU	Range	1.7–2.4	2.2–2.8	1.9–2.8
	Mean	2.06	2.44	2.34
	SD	0.18	0.17	0.23
	n	19	16	14

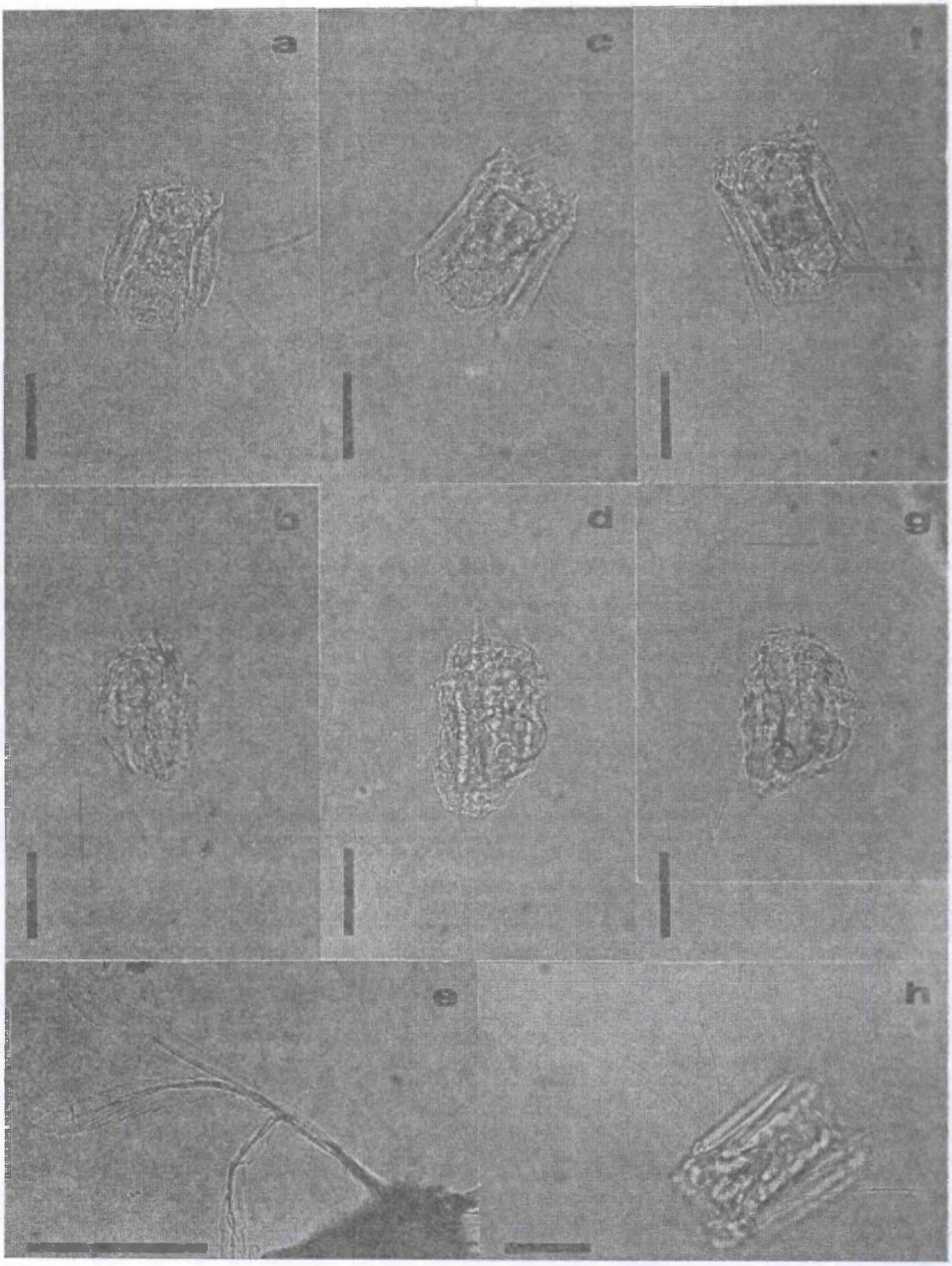


Fig. 1. *Polyarthra remata* (a-b), *P.* cf. *dolichoptera* (c-e) and *P.* cf. *vulgaris* (f-h) from Lake Peipsi; dorsal (a, c), ventral (f), lateral (b, d, g), fin morphology (e, h). Scale bars 50 µm.

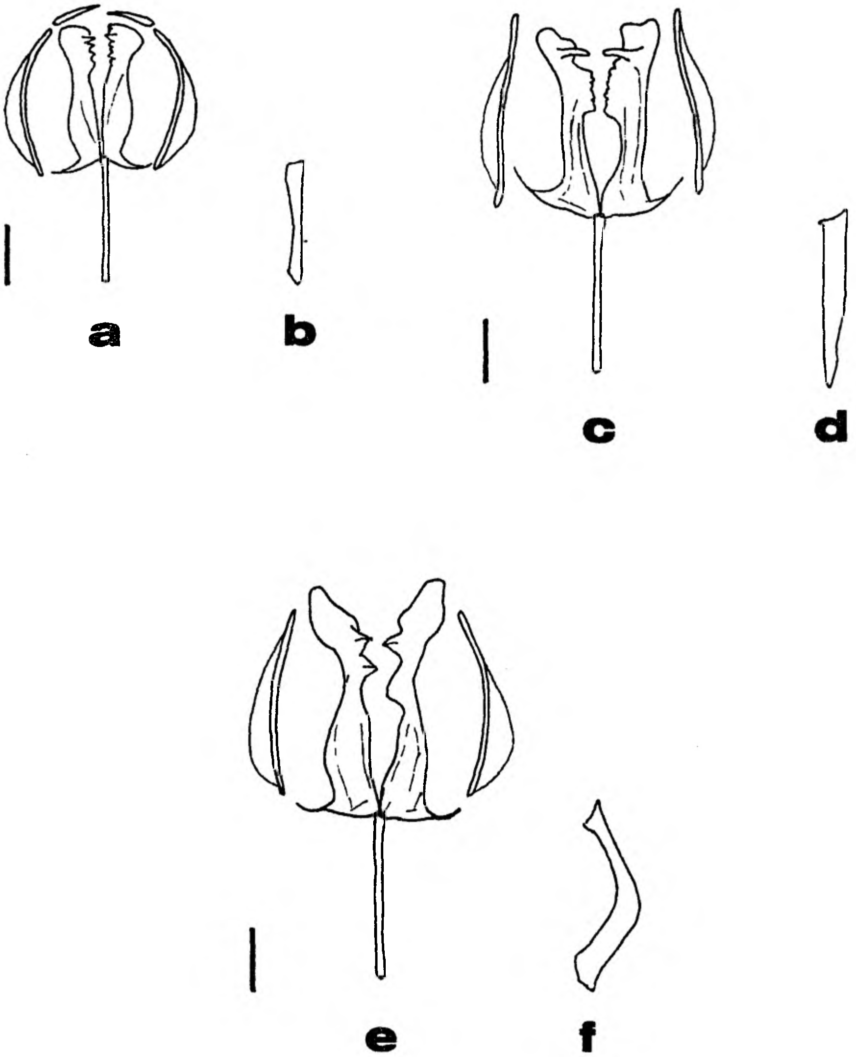


Fig. 2. Trophi of *Polyarthra remata* (a-b), *P.* cf. *dolichoptera* (c-d) and *P.* cf. *vulgaris* (e-f); (b, d, f): fulcri, lateral. Scale bars 10 µm.

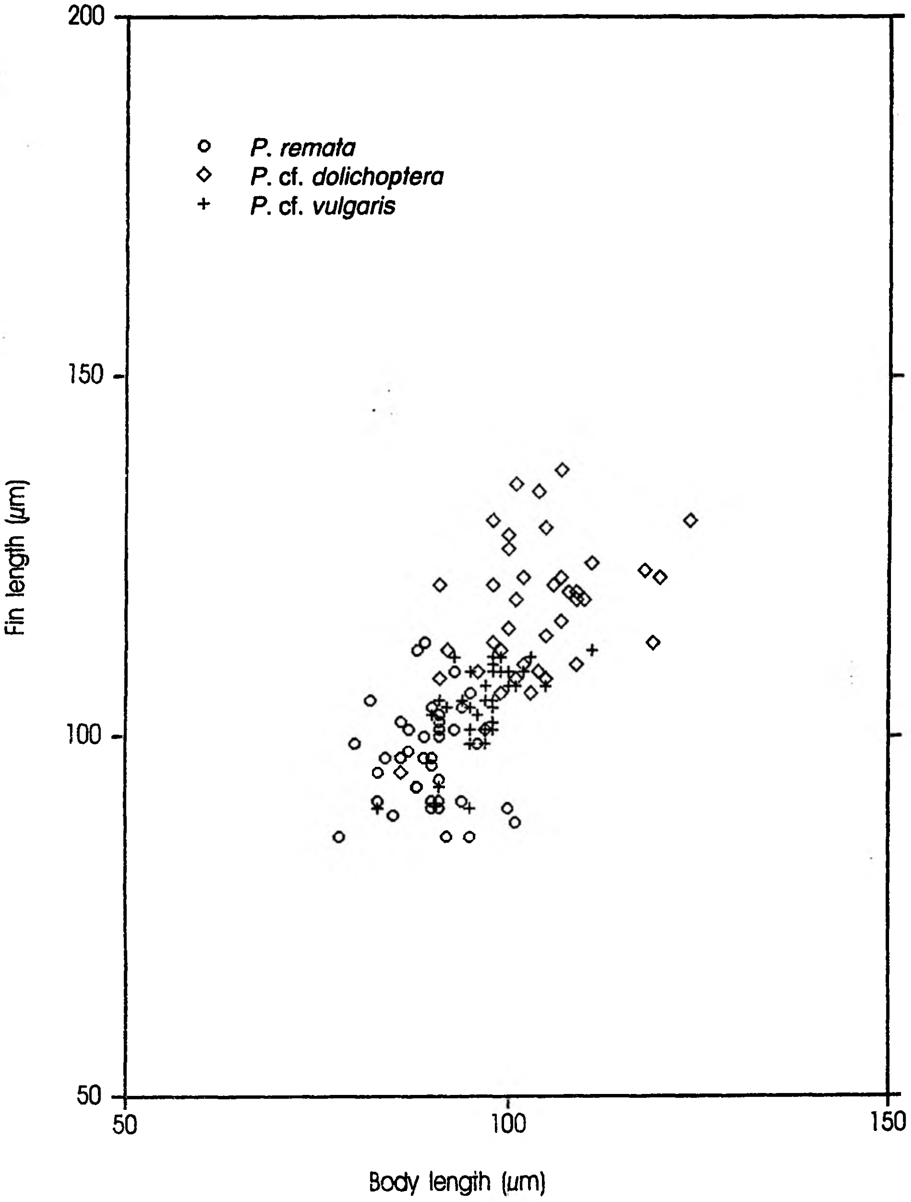


Fig. 3. Relationship between body length and fin length of *Polyarthra remata*, *P.* cf. *dolichoptera* and *P.* cf. *vulgaris*.

CURRICULUM VITAE

TAAVI VIRRO

Date and place of birth:	November 18, 1961, in Tartu (Estonia)
Citizenship:	Estonian
Marital status:	Married (two sons in family)
Address:	Department of Zoology and Hydrobiology, University of Tartu, Vanemuise St. 46, Tartu 51014, Estonia
Phone:	+372 7 375835
Fax:	+372 7 375830
E-mail:	tvirro@ut.ee
Current employment:	University of Tartu, Department of Zoology and Hydrobiology, assistant

Education

1969–1980	Tartu Secondary School No. 7
1980–1985	University of Tartu, biology-hydrobiology-ichtyology, *cum laude*
1985–1988	post-graduate course, Institute of Zoology and Botany of the Estonian Academy of Sciences
1992–1996	doctoral course, University of Tartu, Department of Zoology and Hydrobiology

Professional experience

1985, 1988–1989	Institute of Zoology and Botany of the Est. Acad. Sci., Department of Hydrobiology, research assistant
1989–1991	Institute of Zoology and Botany of the Est. Acad. Sci., Department of Hydrobiology, junior researcher
1996–	University of Tartu, Department of Zoology and Hydrobiology, assistant
Foreign languages:	English, Russian

Scientific work

Fields of research:	Systematics, faunistics and ecology of rotifers (Ph. Rotifera)
Number of scientific publications:	13

The results have been presented at International Rotifer Symposia:
1991 Banyoles, Spain; 1994 Mikolajki, Poland; 1997 Collegeville, U.S.A.

Grants:

1991	Grant from the Open Estonia Foundation for participation in the 6th International Rotifer Symposium in Banyoles, Spain
1994–1995	Estonian Science Foundation grant No. 728
1994	Grant from the Stefan Batory Foundation (Poland) and Polish Academy of Sciences for participation in the 7th International Rotifer Symposium in Mikolajki, Poland
1996–1997	Estonian Science Foundation grant No. 2478

CURRICULUM VITAE

TAAVI VIRRO

Sünniaeg ja -koht:	18. november 1961 Tartus (Eesti)
Kodakondsus:	Eesti
Perekonnaseis:	abielus (peres kaks poega)
Aadress:	zooloogia ja hüdrobioloogia instituut, Tartu Ülikool, Vanemuise 46, Tartu 51014, Eesti
Tel.:	+372 7 375835
Faks:	+372 7 375830
E-post:	tvirro@ut.ee
Praegune töökoht:	Tartu Ülikool, zooloogia ja hüdrobioloogia instituut, assistent

Haridus

1969–1980	Tartu 7. Keskkool
1980–1985	Tartu Ülikool, bioloog-hüdrobioloog-ihtüoloog, *cum laude*
1985–1988	aspirantuuris Eesti Teaduste Akadeemia Zooloogia ja Botaanika Instituudis
1992–1996	doktorantuuris Tartu Ülikooli zooloogia ja hüdrobioloogia instituudis

Teenistuskäik

1985, 1988–1989	Eesti Teaduste Akadeemia Zooloogia ja Botaanika Instituudi hüdrobioloogia osakond, insener
1989–1991	Eesti Teaduste Akadeemia Zooloogia ja Botaanika Instituudi hüdrobioloogia osakond, nooremteadur
1996–	Tartu Ülikooli zooloogia ja hüdrobioloogia instituut, assistent

Võõrkeeled:	inglise, vene

Teadustegevus

Uurimisvaldkonnad: keriloomade (Ph. Rotifera) süstemaatika, faunistika ja ökoloogia

Teaduspublikatsioonide arv: 13

Töö tulemusi on esitatud rahvusvahelistel keriloomade-alastel sümpoosionidel: 1991 Banyolesis, Hispaanias; 1994 Mikolajkis, Poolas; 1997 Collegevilleis, Ameerika Ühendriikides

Grandid:

1991	Avatud Eesti Fondi grant osavõtuks 6. rahvusvahelisest keriloomade-alasest sümpoosionist Banyolesis, Hispaanias
1994–1995	Eesti Teadusfondi grant nr. 728
1994	Stefan Batory Fondi (Poola) ja Poola Teaduste Akadeemia grant osavõtuks 7. rahvusvahelisest keriloomade-alasest sümpoosionist Mikolajkis, Poolas
1996–1997	Eesti Teadusfondi grant nr. 2478

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets**. Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet**. Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
3. **Kristjan Zobel**. Epifüütsete makrosamblike väärtus õhu saastuse indikaatoritena Hamar-Dobani boreaalsetes mägimetsades. Tartu, 1992, 131 lk.
4. **Andres Mäe**. Conjugal mobilization of catabolic plasmids by transposable elements in helper plasmids. Tartu, 1992, 91 p.
5. **Maia Kivisaar**. Studies on phenol degradation genes of *Pseudomonas* sp. strain EST 1001. Tartu, 1992, 61 p.
6. **Allan Nurk**. Nucleotide sequences of phenol degradative genes from *Pseudomonas sp.* strain EST 1001 and their transcriptional activation in *Pseudomonas putida.* Tartu, 1992, 72 p.
7. **Ülo Tamm**. The genus *Populus* L. in Estonia: variation of the species biology and introduction. Tartu, 1993, 91 p.
8. **Jaanus Remme**. Studies on the peptidyltransferase centre of the *E.coli* ribosome. Tartu, 1993, 68 p.
9. **Ülo Langel**. Galanin and galanin antagonists. Tartu, 1993, 97 p.
10. **Arvo Käärd**. The development of an automatic online dynamic fluorescense-based pH-dependent fiber optic penicillin flowthrought biosensor for the control of the benzylpenicillin hydrolysis. Tartu, 1993, 117 p.
11. **Lilian Järvekülg**. Antigenic analysis and development of sensitive immunoassay for potato viruses. Tartu, 1993, 147 p.
12. **Jaak Palumets**. Analysis of phytomass partition in Norway spruce. Tartu, 1993, 47 p.
13. **Arne Sellin**. Variation in hydraulic architecture of *Picea abies* (L.) Karst. trees grown under different enviromental conditions. Tartu, 1994, 119 p.
13. **Mati Reeben**. Regulation of light neurofilament gene expression. Tartu, 1994, 108 p.
14. **Urmas Tartes**. Respiration rhytms in insects. Tartu, 1995, 109 p.
15. **Ülo Puurand**. The complete nucleotide sequence and infections *in vitro* transcripts from cloned cDNA of a potato A potyvirus. Tartu, 1995, 96 p.
16. **Peeter Hõrak**. Pathways of selection in avian reproduction: a functional framework and its application in the population study of the great tit (*Parus major*). Tartu, 1995, 118 p.
17. **Erkki Truve**. Studies on specific and broad spectrum virus resistance in transgenic plants. Tartu, 1996, 158 p.
18. **Illar Pata**. Cloning and characterization of human and mouse ribosomal protein S6-encoding genes. Tartu, 1996, 60 p.

19. **Ülo Niinemets**. Importance of structural features of leaves and canopy in determining species shade-tolerance in temperature deciduous woody taxa. Tartu, 1996, 150 p.
20. **Ants Kurg**. Bovine leukemia virus: molecular studies on the packaging region and DNA diagnostics in cattle. Tartu, 1996, 104 p.
21. **Ene Ustav**. E2 as the modulator of the BPV1 DNA replication. Tartu, 1996, 100 p.
22. **Aksel Soosaar**. Role of helix-loop-helix and nuclear hormone receptor transcription factors in neurogenesis. Tartu, 1996, 109 p.
23. **Maido Remm**. Human papillomavirus type 18: replication, transformation and gene expression. Tartu, 1997, 117 p.
24. **Tiiu Kull**. Population dynamics in *Cypripedium calceolus* L. Tartu, 1997, 124 p.
25. **Kalle Olli**. Evolutionary life-strategies of autotrophic planktonic microorganisms in the Baltic Sea. Tartu, 1997, 180 p.
26. **Meelis Pärtel**. Species diversity and community dynamics in calcareous grassland communities in Western Estonia. Tartu, 1997, 124 p.
27. **Malle Leht**. The Genus *Potentilla* L. in Estonia, Latvia and Lithuania: distribution, morphology and taxonomy. Tartu, 1997, 186 p.
28. **Tanel Tenson**. Ribosomes, peptides and antibiotic resistance. Tartu, 1997, 80 p.
29. **Arvo Tuvikene**. Assessment of inland water pollution using biomarker responses in fish *in vivo* and *in vitro*. Tartu, 1997, 160 p.
30. **Urmas Saarma**. Tuning ribosomal elongation cycle by mutagenesis of 23S rRNA. Tartu, 1997, 134 p.
31. **Henn Ojaveer**. Composition and dynamics of fish stocks in the gulf of Riga ecosystem. Tartu, 1997, 138 p.
32. **Lembi Lõugas**. Post-glacial development of vertebrate fauna in Estonian water bodies. Tartu, 1997, 138 p.
33. **Margus Pooga**. Cell penetrating peptide, transportan, and its predecessors, galanin-based chimeric peptides. Tartu, 1998, 110 p.
34. **Andres Saag**. Evolutionary relationships in some cetrarioid genera (Lichenized Ascomycota). Tartu, 1998, 196 p.
35. **Aivar Liiv**. Ribosomal large subunit assembly *in vivo*. Tartu, 1998, 158 p.
36. **Tatjana Oja**. Isoenzyme diversity and phylogenetic affinities among the eurasian annual bromes (*Bromus* L., Poaceae). Tartu, 1998, 92 p.
37. **Mari Moora**. The influence of arbuscular mycorrhizal (AM) symbiosis on the competition and coexistence of calcareous crassland plant species. Tartu, 1998, 78 p.
38. **Olavi Kurina**. Fungus gnats in Estonia (*Diptera: Bolitophilidae, Keroplatidae, Macroceridae, Ditomyiidae, Diadocidiidae, Mycetophilidae*). Tartu, 1998, 200 p.
39. **Andrus Tasa**. Biological leaching of shales: black shale and oil shale. Tartu, 1998, 98 p.

40. **Arnold Kristjuhan.** Studies on transcriptional activator properties of tumor suppressor protein p53. Tartu, 1998, 86 p.
41. **Sulev Ingerpuu.** Characterization of some human myeloid cell surface and nuclear differentiation antigens. Tartu, 1998, 163 p.
42. **Veljo Kisand.** Responses of planktonic bacteria to the abiotic and biotic factors in the shallow lake Võrtsjärv. Tartu, 1998, 118 p.
43. **Kadri Põldmaa.** Studies in the systematics of hypomyces and allied genera (Hypocreales, Ascomycota). Tartu, 1998, 178 p.
44. **Markus Vetemaa.** Reproduction parameters of fish as indicators in environmental monitoring. Tartu, 1998, 117 p.
45. **Heli Talvik.** Prepatent periods and species composition of different *Oesophagostomum* spp. populations in Estonia and Denmark. Tartu, 1998, 104 p.
46. **Katrin Heinsoo.** Cuticular and stomatal antechamber conductance to water vapour diffusion in *Picea abies* (L.) karst. Tartu, 1999, 133 p.
47. **Tarmo Annilo.** Studies on mammalian ribosomal protein S7. Tartu, 1998, 77 p.
48. **Indrek Ots.** Health state indicies of reproducing great tits (*Parus major*): sources of variation and connections with life-history traits. Tartu, 1999, 117 p.
49. **Juan Jose Cantero.** Plant community diversity and habitat relationships in central Argentina grasslands. Tartu, 1999, 161 p.
50. **Rein Kalamees.** Seed bank, seed rain and community regeneration in Estonian calcareous grasslands. Tartu, 1999, 107 p.
51. **Sulev Kõks.** Cholecystokinin (CCK) — induced anxiety in rats: influence of environmental stimuli and involvement of endopioid mechanisms and erotonin. Tartu, 1999, 123 p.
52. **Ebe Sild.** Impact of increasing concentrations of O_3 and CO_2 on wheat, clover and pasture. Tartu, 1999, 123 p.
53. **Ljudmilla Timofejeva.** Electron microscopical analysis of the synaptonemal complex formation in cereals. Tartu, 1999, 99 p.
54. **Andres Valkna.** Interactions of galanin receptor with ligands and G-proteins: studies with synthetic peptides. Tartu, 1999, 103 p.

TARTU ÜLIKOOL
UNIVERSITAS TARTUENSIS
1632

ISSN 1024–6479
ISBN 9985–56–448–0