UNIVERSITY OF PARMA

PhD in Ecology

XXIV cycle

Zooplankton dynamics in a lowland river along temporal and spatial gradients

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1. General introduction

1.1 Zooplankton assemblages in lowland rivers – State of the art and open questions

Studies on zooplankton ecology have traditionally dealt with lentic systems, while research on lotic assemblages has lagged far behind (Lair, 2006). It is especially in the last decades that riverine zooplankton has become the focus of an increasing number of investigations, showing that large lowland rivers often host extremely rich and abundant zooplankton communities, particularly when extensive nutrient input from the catchment stimulates algal growth (Bergfeld et al., 2008). One of the characteristics of metazoan plankton in rivers is that rotifers usually represent the dominant component in terms of density and biomass (e.g. Saunders & Lewis, 1988a; Ferrari et al., 1989; de Ruyter van Steveninck et al., 1992; Thorp et al., 1994; Marneffe et al., 1996; Basu & Pick, 1997; Reckendorfer et al., 1999; Viroux, 1999; Burger et al., 2002). This is due to their shorter development times, lower susceptibility to physical damage during downstream transport and lower vulnerability of their feeding apparatus to high concentrations of suspended solids in comparison to microcrustaceans (Kirk & Gilbert, 1990; Jack et al., 1993; Sluss et al., 2008). Among crustaceans though, cladocerans appear to be better adapted to lotic conditions than copepods, thanks to their shorter development times and the possibility of reproducing parthenogenetically (Dole-Olivier et al., 2000). Copepods, on the contrary, tend to have lower growth rates and longer life cycles as they reproduce sexually, and turbulence may represent a relevant obstacle for encountering and mating with conspecifics (loc. cit.).

Surveys conducted in rivers all over the world highlighted the major role played by abiotic constraints in regulating the spatio-temporal dynamics of zooplankton assemblages in large rivers. In particular, abiotic factors which have proven to influence potamoplankton dynamics are water temperature (as determined by climatic conditions), hydrological regime and water residence time, turbulence and turbidity, presence of discontinuities along the river, availability of inshore retention zones and lateral connectivity with the floodplain (Saunders & Lewis, 1988b; Thorp et al., 1994; van Dijk & van Zanten, 1995; Reckendorfer et al., 1999; Welker & Walz, 1999; Aoyagui & Bonecker, 2004; Guelda et al., 2005; Wahl et al., 2008; Havel et al., 2009; see Chapter 3.1).

Fewer studies have dealt with the role of biotic factors (see Chapter 3.2), revealing the importance of phytoplankton abundance and composition, food availability and presence of planktivorous fish and benthic filter-feeders in structuring riverine zooplankton communities (Thorp & Casper, 2003 and references therein).

Despite this growing amount of research, questions still remain to be answered regarding the origin of river plankton and how these communities are able to persist in the current although facing continuous downstream transport.

Zooplankton assemblages found in the main channel of large rivers are usually made up of both truly planktonic taxa and littoral/epibenthic forms (Lair, 2006). These latter are often subjected to dislodgement from the bottom and the river banks, or may derive from inshore retention zones, backwaters and tributaries (Schmid-Araya, 1998; Casper & Thorp, 2007; Wahl et al., 2008). The role played by low-flow shoreline habitats, reservoirs and connected lentic water bodies as inocula of organisms for the main river channel has been investigated by relatively few studies and may change according to the degree of hydraulic regulation and anthropogenic modification to which the river has been subjected (Reynolds, 2000; Wahl et al., 2008; see Chapter 5).

While the intrinsic spatio-temporal variability of lotic ecosystems and the heterogeneity of available microhabitats promote the development of highly diverse zooplankton communities, when comparing the taxonomic composition of the assemblages found in large rivers all over the world strong similarities emerge (Kobayashi et al., 1998). This may be attributed to the selection operated by hydraulic constraints related to water movement, which tend to favour small taxa with short generation times (see above). In particular, the monogonont rotifer families Brachionidae, Synchaetidae, Lecanidae, Trichocercidae and Asplanchnidae are usually dominant in terms of abundance. Bdelloid rotifers can also attain remarkable densities, while the families Notommatidae, Dicranophoridae and Lepadellidae are often present with a high number of sporadic or occasional species (Lair, 2006).

As for the crustacean component, small cladoceran taxa belonging to the families Bosminidae and Chydoridae and cyclopoid larval stages are the most common microcrustaceans found among river plankton (loc. cit.).

Large herbivore zooplankters are thus often absent in the main current of rivers and this poses questions regarding the true impact of zooplankton on the riverine food web. In fact, zooplankton can play a pivotal role in the trophic dynamics of rivers by representing a crucial link between primary producers and secondary consumers, and rotifers and crustaceans are undoubtedly important prey items for many invertebrates and young fish (King, 2005; Ning et al., 2010). Nonetheless, the nature and magnitude of carbon flows between primary producers and consumers in rivers remains a relevant issue. In fact, it is still technically very difficult to measure the grazing effect of zooplankton on algae, protozoans and bacteria in flowing water. Authors therefore often use indirect measurements and some papers have shown a considerable impact of grazing by zooplankton (e.g. Lair & Reyes-Marchant, 1997) whereas others highlighted a more modest influence (e.g. Admiraal et al., 1994; Basu & Pick, 1997). A few attempts were made to assess the effect of zooplankton grazing on phytoplankton through *in situ* or *ex situ* grazing measurements, mainly suggesting that zooplankton can significantly control phytoplankton especially during low-flow conditions, when rotifers, early copepod stages and small cladocerans are abundant (Gosselain et al., 1994; Gosselain et al., 1996; Kobayashi et al., 1996; Gosselain et al., 1998a,b; Ietswaart et al., 1999). The role played by rotifers in energy and carbon transfers within riverine food webs is thus still open to debate and a better understanding of lotic zooplankton ecology is a crucial step to improve present knowledge on the functioning of river ecosystems.

1.2 Questions and Answers: aims of this work and thesis outline

The present work deals with different aspects of the ecology of zooplankton assemblages in a large river. The leading questions on which the research was developed are hereby presented, together with a brief outline of the main related hypotheses.

- What are the main abiotic and biotic factors controlling the spatial and temporal dynamics of zooplankton abundance and composition in the potamal reach of a lowland river? What is the effect of potential disturbance events like floods on zooplankton community structure? Does the community exhibit regular successional patterns?

  These research topics are addressed in Chapter 3.1, where results of a two-year sampling campaign carried out in the potamal reach of the Po River are presented. Seasonality and hydrology are hypothesized to be the major drivers of zooplankton temporal patterns. More specifically, a negative effect of river flow on community abundance and diversity is expected. The work also aims at verifying whether regular successional patterns within the zooplankton can be detected, despite the peculiar instability of advective environments and the disturbance events to which river assemblages are periodically exposed.

- Can biotic interactions (predation/competition) within the zooplankton become crucial drivers of community abundance and composition under advective conditions?

  Chapter 3.2 presents the results of a short-term, high-frequency survey carried out during summer 2005 in the potamal stretch of the Po River. The main goal is to test the hypothesis that biotic interactions within the zooplankton can significantly affect community structure even under conditions of turbulence that are naturally found in the main channel of a large river. This is achieved by means of a multi-level approach combining different methods for the analysis of community dynamics from time series of species abundances collected in the field.

- What are the main changes within the plankton community during its downstream transport and how can the observed longitudinal dynamics be explained? What is the contribution of the major tributaries to the main channel zooplankton assemblage?

These questions are addressed in Chapter 4, which contains the results of a Lagrangian sampling experiment carried out on a 330-km river stretch. The general hypotheses underlying this work are that zooplankton should display little or no downstream increase and a rather homogeneous longitudinal composition during spring conditions, because of the relatively high discharge rates (and low water residence time) due to seasonal snowmelt and rainfall. On the contrary, under summer low-discharge levels a gradual downstream increase in abundance and diversity is expected, thanks to the higher water residence time. Influence of the major tributaries on community abundance and diversity is a completely unexplored issue in this river. However, due to the low discharge rates of the tributaries, in comparison to the Po, and to their hydrogeomorphological features, a minor effect on the Po River assemblage is hypothesized.
Unfortunately, results of the summer sampling campaign could not be added to the present work as the survey had to be postponed to August 2011 because of adverse hydro-meteorological conditions. Time was then not sufficient to carry out a complete elaboration of the dataset and only a brief overview on some of the hydrochemical variables is reported.

- Does the presence of an hydrological discontinuity along the river course, such as a man-made reservoir, induce relevant changes in zooplankton composition and abundance? Are there significant differences in community structure along cross-channel transects (middle channel versus river banks) or is the river a completely well-mixed environment with homogeneously distributed plankton assemblages?

Chapter 5 provides the results of a sampling campaign carried out during summer 2009 at four stations respectively upstream, inside (mid-channel vs. shore) and downstream of the artificial impoundment of Isola Serafini, located in the middle reach of the Po River. The bottom-line hypothesis of this work is that a shift of the lotic environment towards “more lentic” conditions is expected immediately above the dam and near the shores. As a result, zooplankton growth and particularly the development of microcrustaceans at the expenses of rotifers should be enhanced, in comparison to the truly riverine assemblage.

In Chapter 6 a taxonomic account is given on 24 species of monogonont rotifers new to Italy that have been found in the Po River.

2. Study Area

2.1 The Po River

The Po is the main Italian river, both in terms of length (652 km) and catchment surface (70700 km^2). It originates in the Cottian Alps (44° 42' N; 7° 5' E), at an altitude of 2022 m a.s.l., and it flows through a delta (44° 58' N; 12° 32' E) into the Adriatic Sea, about 60 km south of the city of Venice (Fig. 2.1). It is fed by 141 tributaries originating from the Alps and the Northern Apennines.

The natural meandering course of the river has been radically modified and straightened over the years, so that the middle and lower reaches are now completely confined within artificial banks, resulting in a low hydrological connectivity between the main river channel and floodplain backwaters (AdBPo, 2006).

At the closing station of Pontelagoscuro, located just upstream of the river delta, the mean annual discharge (period 1918-2003) is 1525 $m^3 s^{-1}$ (Syvitski & Kettner, 2007).

The annual hydrological regime is strongly influenced by the seasonal pattern of precipitation, with low-water levels (down to 200 $m^3 s^{-1}$) usually occurring during summer, and floods (up to over 10000 $m^3 s^{-1}$) in late fall and spring (Zanchettin et al., 2008).

In the last years extreme hydrological events, such as severe floods and protracted drought periods, have been repeatedly reported (Allodi & Pecora, 2003; Mazzarella & Rapetti, 2004).

Seventeen million people inhabit the river catchment area, which sustains the largest proportion of the national agricultural and industrial production (Viaroli et al., 2010). In particular, the population equivalent treated by wastewater facilities in the basin reaches 23.5 millions, while the total livestock population amounts to 61.3 millions and the surface used for cultivation is about 30440 km^2 (AdBPo, 2006). High nutrient loads arising from urbanisation and human activities support high levels of primary production in the lowland river section, especially during summer, when chlorophyll-*a* concentrations typically reach values up to 75 µg L^{-1} (Rossetti et al., 2009).

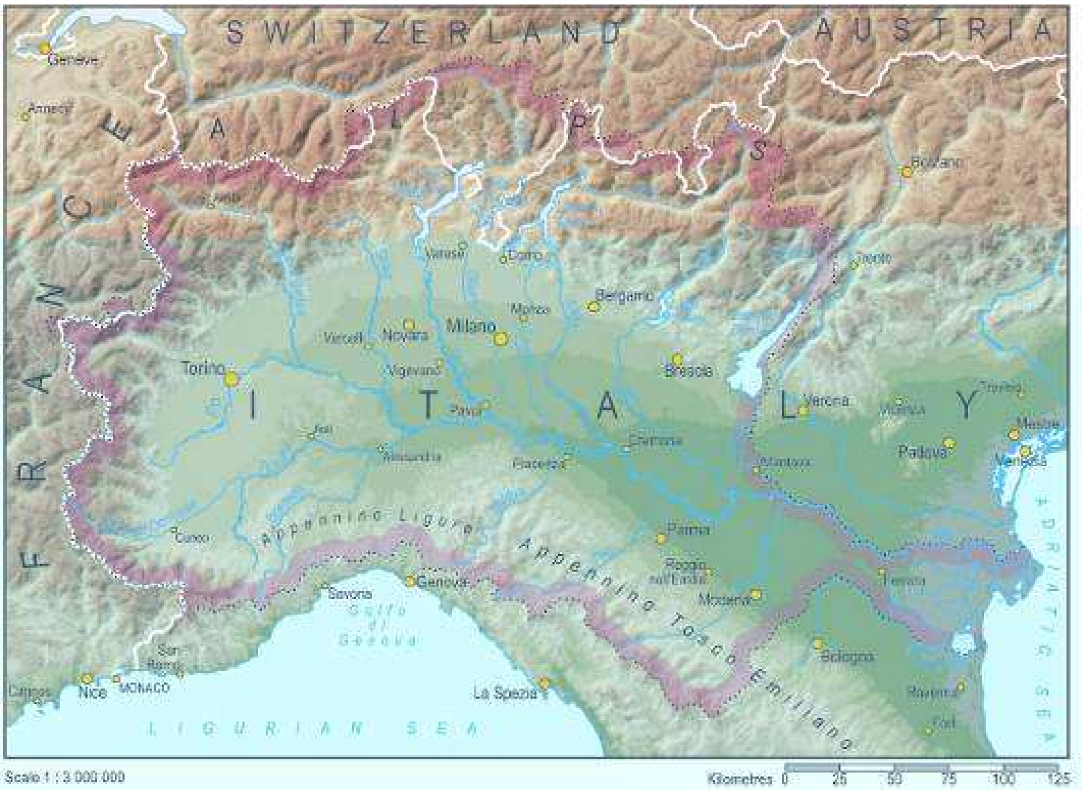


Fig. 2.1 - Map of the Po River Basin

2.2 Zooplankton in the Po River – Present knowledge

The first documented studies on the zooplankton assemblage of the Po middle reach date back to the beginning of the 20th century, when a short list of rotifer taxa found in a few samples collected near the city of Ferrara was compiled by Padovani (1911).

In the 1970s, the construction of a nuclear power plant near Isola Serafini stimulated a series of investigations on the river water quality in that area. In particular, a seven-year survey (1974-1982) was conducted in order to provide a characterization of the riverine planktonic community and examine the seasonal dynamics of the main crustacean species (Rossaro, 1976; Rossaro & Cotta Ramusino, 1976; Rossaro, 1981; Rossaro, 1988). Strong weekly, seasonal and annual variations of community abundance and composition were highlighted and densities of several taxa were significantly related to water temperature and river discharge, pointing towards hydrological, physical and climatic constraints as the key drivers of microcrustacean temporal patterns. Nevertheless, a large proportion of the observed variability remained unexplained. During this first set of studies rotifers were generally excluded from analyses, mainly because of the sampling techniques which did not allow quantitative sampling of small-sized animals.

However, in 1980 a 15-day survey was carried out to investigate the short-term population dynamics and interactions among some rotifer taxa in an experimental canal connected to the Po River (Ferrari et al., 1984). The results emphasized the role of the predator *Asplanchna* gr. *girodi-brightwellii* in controlling densities of the dominant herbivorous rotifer species, thus enhancing community diversity and evenness. Similar short-term studies were conducted in the summer of 1985 and 1988 at a station near the town of Viadana, in the middle reach of the river, to analyse daily fluctuations of the major zooplankton taxa in relation to variations in hydrological and physico-chemical variables (Ferrari & Mazzoni, 1989; Ferrari et al., 1989). Both studies revealed that rotifers accounted for more than 99% of the total zooplankton density and their abundance was negatively related to river flow. These results were then examined by means of Caswell's neutral model, suggesting that during low water phases the rotifer community was able to show a marked stability, keeping its structure constant over time (De Leo & Ferrari, 1993). Abrupt flow increases acted as a destabilizing factor, leading to higher diversity as a consequence of drastic drops in the density of the dominant taxa. Yet the community showed a tendency towards a rapid recovery of its structure and composition after disturbance events.

During a severe drought in the summer of 2003, a new short-term study was carried out at the same station to describe the development of riverine zooplankton at very reduced flow rates (Ferrari et al., 2006). The assemblage showed lower abundances but an higher equitability in comparison to what had been reported by previous studies carried out in the same river segment under comparable summer low-flow conditions. The authors hypothesized that the exceptional persistence of a low discharge regime might have significantly enhanced the effectiveness of biological interactions in regulating community temporal patterns.

The influence of abiotic and biotic constraints on zooplankton abundance and diversity in the Po River was also the main subject of a more extensive research carried out from June 2000 to June 2002 at two stations in the middle river reach (Rossetti et al., 2009). Zooplankton abundance was positively correlated to water temperature and chlorophyll-*a* concentration, and only in warmer months inversely correlated to river flow. Rotifer richness showed a peak at intermediate discharge values. In fact, at very low flow rates, community diversity seemed to be limited by the strong dominance of a few competitively superior taxa under “*quasi*-lentic” conditions. On the other hand, more turbulent and turbid conditions at higher discharge values could have a negative impact on rotifer feeding, survival and reproduction abilities. The authors proposed a simple descriptive model illustrating the main successional phases of the zooplankton in the river, distinguishing between a “favourable” and an “unfavourable” phase to zooplankton growth (from late spring to early autumn and from late autumn to early spring, respectively), suggesting how temporal changes in community structure mainly depended on water temperature and trophic conditions.

Finally, research on zooplankton conducted in lentic systems located within the Po River floodplain showed a low similarity in species composition when compared to the main channel, probably due to the extremely low hydrological connectivity between the river and the adjacent floodplain (Viaroli et al., 2002; Rossetti et al., 2003).

3. Factors regulating zooplankton dynamics in the Po River

3.1 Abiotic vs. biotic constraints

3.1.1 Introduction

Although a growing number of studies have focussed on the abiotic and biotic factors regulating plankton development in large rivers, the major mechanisms involved are still incompletely understood (Lair, 2006).

Constraints related to hydrology, such as river discharge and water residence time, have long been recognised as fundamental drivers of zooplankton dynamics in rivers (Margalef, 1960; Winner, 1975). In numerous rivers plankton abundance and/or biomass have been inversely correlated to discharge (e.g. Saunders & Lewis, 1988a; Pace et al., 1992; Thorp et al., 1994; Basu & Pick, 1996; Kobayashi et al., 1998). In fact, besides the negative effects related to dilution and enhanced advective losses, increases in river flow bring about an increment in turbulence and turbidity, which impose stressful conditions on zooplankters, e.g. by interfering with feeding efficiency, reducing phytoplankton production by light limitation and modifying competition interactions (Reynolds & Descy, 1996; Miquelis et al., 1998; Sluss et al., 2008). As a result, survival and reproduction can be severely impaired by rises in water level and flow velocity, and Rzoska (1978) found that reproduction of zooplankton in rivers is rarely observed at velocities over 0.4 m s^{-1}.

On the other hand, an increase in water level may enhance resuspension of organisms from the river bottom and/or littoral zones as well as recruitment of individuals from adjacent water bodies into the main channel (Binford, 1978; Van den Brink et al., 1994). The significance of these phenomena depends of course on the degree of regulation and artificialization to which the river has been subjected, which in turn affects the connectivity level between the main channel and the surrounding floodplain (Lair, 2006). Inundation of the adjacent floodplain habitats during floods is more likely to occur in unregulated rivers, where plankton wash-out from off-channel sources into the river has been reported (Saunders & Lewis, 1988b; Wahl et al., 2008).

While several studies have dealt with the relationship between discharge and zooplankton abundance, the effect of fluctuations in the hydrological regime on community diversity has been documented much less frequently and while some works have found a positive relationship between river flow and zooplankton diversity (Saunders & Lewis, 1988a; Pace et al., 1992; Wahl et al., 2008), others reported the opposite (Vásquez & Rey, 1989). The role played by hydrology may thus be difficult to predict, especially as other factors interact with it in influencing riverine zooplankton dynamics. Temperature has been reported as a positive correlate of plankton density in many rivers (Thorp et al., 1994; Kobayashi et al., 1998) but not in all (Holden & Green, 1960; Greenberg, 1964; Basu & Pick, 1997), and several large rivers in the temperate zone show a typical seasonal pattern of zooplankton abundance, with low densities in winter, a spring peak and relatively high densities during summer (van Dijk & van Zanten, 1995).

High zooplankton abundances are generally associated with high chlorophyll-*a* concentrations, suggesting that food availability may also be a key factor (van Dijk & van Zanten, 1995; Basu & Pick, 1996; Kobayashi et al., 1998). Bacteria and protozoans have also been shown to make up a significant proportion of the rotifers' diet in large rivers, especially when phytoplankton concentrations decrease below the incipient limiting level (Kim et al., 2000; Joaquim-Justo et al., 2006).

The development patterns of zooplankton in large rivers appear thus to be the result of a combination of hydrological, geomorphological and trophic constraints, whose relative importance is likely to vary among species, seasons and river type. Such heterogeneous conditions, together with the intrinsic variability of lotic ecosystems, make it difficult to disentangle the actual role played by the different factors. As a result, while descriptive models have been developed for plankton successional events in lakes, the processes that govern riverine zooplankton remain rather difficult to predict as substantial gaps still affect our knowledge on the basic ecology of these communities (Reynolds, 2000; Lair, 2006).

The present chapter reports the results of a two-year survey conducted in the potamal reach of the Po River in order to explore the major mechanisms involved in regulating the spatio-temporal dynamics of the zooplankton community.

3.1.2 Materials and Methods

3.1.2.1 Field sampling and laboratory analyses

A sampling campaign was carried out at three stations along the potamal reach of the Po River: Mortizza (45° 05’ N, 9° 45’ E), Viadana (44°18' N, 10°22' E) and Serravalle (44° 58’ N, 12° 02’ E), which are located 338, 438 and 602 km from the river source, respectively (Fig. 3.1.1). A two-year fortnightly survey was conducted at the station of Viadana (January 2008 - April 2010), while a one-year monthly survey was carried out at the stations of Mortizza and Serravalle (July 2009 - August 2010). The stations were fixed at floating pontoons, which enabled to reach the main current flow in the river channel. *In situ* measurements of surface water temperature and electric conductivity at 25°C were carried out using a multiparametric probe (YSI Model 85).

Surface water for hydrochemical analyses was collected by lowering a plastic bottle into the river. pH was determined with a pH-meter (Radiometer TIM 90), using a GK 2401 C combined electrode (Radiometer). Dissolved oxygen was measured by means of the Winkler method (APHA, 1998). Total alkalinity was determined only on the samples collected in 2009 and 2010 by potentiometric end-point titration and linearization according to Rodier (1978). A known volume of water was filtered, and the filters retained for chlorophyll-*a* (Chl-*a*) and suspended particulate matter (SPM) analyses. Chl-*a* concentration was determined spectrophotometrically after acetone extraction (Golterman et al., 1978). SPM was determined after drying filters at 70°C (APHA, 1998). Aliquots of filtered water were stored for determination of nitrate (NO_3-N), nitrite (NO_2-N), ammonium (NH_4-N), soluble reactive phosphorus (SRP) and dissolved reactive silica (DRSi). Total nitrogen (TN) and phosphorous (TP) were determined on unfiltered water. Standard spectrophotometric analyses were applied for TN and TP (Valderrama, 1981), SRP (Valderrama, 1977), DRSi (Golterman et al., 1978) and nitric, nitrous and ammonium nitrogen (APHA, 1998).

At the station of Viadana sampling and hydrochemical analyses for the year 2008, as well as analyses of Chl-*a*, NO_3-N, NO_2-N, NH_4-N, TN, SRP, TP and DRSi for the period March 2009 – March 2010 were performed by Enrica Pierobon, another PhD student at the Department of Environmental Sciences. Hydrochemical data are therefore reported in detail in her PhD thesis (Pierobon, 2010) and partly in a recently published paper (Tavernini et al., 2011). They are nonetheless provided in this work in order to give a characterisation of the studied system and as explanatory variables in the interpretation and discussion of zooplankton data.

Mean daily values of the Po River discharge at Piacenza (45° 03’ N, 9° 42’ E; 6 km upstream of Mortizza), Boretto (44° 54’ N, 10° 33’ E; 2 km downstream of Viadana) and Pontelagoscuro (44° 52’ N, 11° 36’ E; 40 km upstream of Serravalle), the gauging stations respectively closest to the three sampling sites, were provided by the Environmental Agency of the Emilia Romagna Region.

Zooplankton samples were taken by lowering a 15 L bucket into the river; water was then passed through a 50 µm net until reaching a volume of 90 L. Smaller volumes of water (30-60 L) were filtered during floods, in order to avoid clogging of the plankton net due to high levels of suspended solids. Two replicate samples were collected and immediately preserved in a 4% buffered formalin solution.

Zooplankton samples were analysed under an optical microscope at a magnification of up to 100x. Rotifers and microcrustaceans were identified to the lowest possible taxonomic level, except for bdelloid rotifers, harpacticoids and juvenile stages of copepods, these latter assigned either to nauplii or copepodites, separately for calanoids and cyclopoids. The following references were used for taxa identification: Gurney (1933), Kiefer (1968), Dussart (1969), Dussart & Defaye (1995), Einsle (1996), Karaytug (1999) and Ueda & Reid (2003) for copepods, Margaritora (1985) and Alonso (1996) for cladocerans, Ruttner- Kolisko (1974), Koste (1978), Braioni & Gelmini (1983), Segers (1994, 1995a, 1995b), Segers et al. (1994), Nogrady et al. (1995), De Smet (1996), De Smet & Pourriot (1997) and De Smet & Gibson (2008) for monogonont rotifers.

Quantitative analysis of each zooplankton sample was performed by counting a series of 1-ml sub-samples taken with a Hensen-Stempel pipette from the original sample previously concentrated to a known volume. Sub-samples were dispensed on a Thalassia plexiglass slide with 1-mm wide vertical counting fields and counted under an optical microscope until 1/10 of the concentrated sample volume was reached. Metazoans other than rotifers, cladocerans and copepods were also enumerated and grouped into broad taxonomic categories (bivalve veligers, insect larvae, oligochaetes, nematodes, cnidarians, tardigrades, gastrotrichs, hydrachnids and ostracods).

The total number of individuals for each taxon was then converted to a density value by multiplying it by a coefficient obtained with the following formula:

$$\frac{\text{CV (ml)} * 1000}{\text{n° subs (ml)} * \text{FV (L)}}$$

where:

CV: known volume to which the original sample was concentrated
1000: conversion factor from L to m³
n° subs: total number of 1-ml sub-samples counted
FV: volume of river water filtered for each sample.

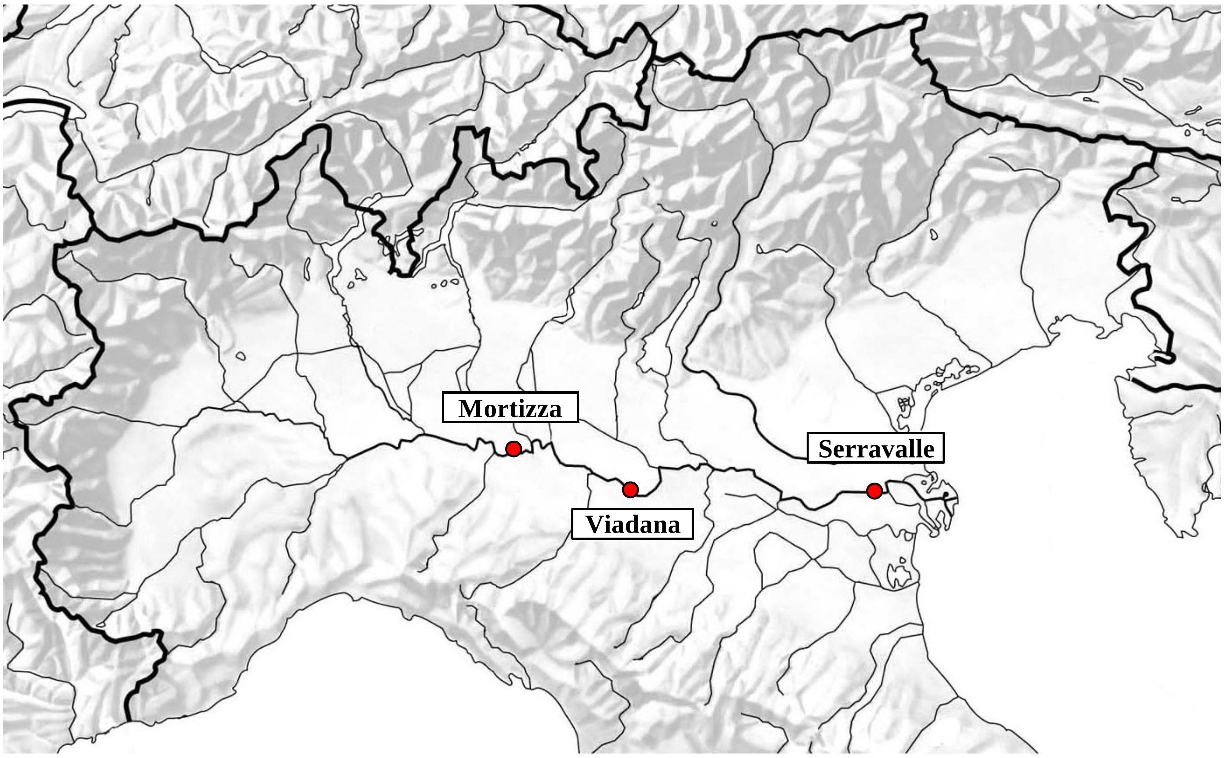


Fig. 3.1.1 - Location of the three sampling stations surveyed between 2008 and 2010.

3.1.2.2 Data elaboration

For each hydrochemical variable outliers were identified as those values outside 1.5 times the interquartile range from 1st to 3rd quartile of the whole dataset for that variable and excluded from analyses.

The Shannon Diversity Index and the Shannon Equitability Index (Shannon Diversity divided by the logarithm of the number of taxa) for the rotifer component were calculated using the package PAST version 1.06 (Hammer et al., 2001).

Ordination of zooplankton taxa according to environmental data was examined by Canonical Correspondence Analysis (CCA) using CANOCO version 4.5 (ter Braak & Šmilauer, 2002). Due to the tendency of rare forms to distort the analysis, only taxa which attained a minimum density of 1 ind L^{-1} in at least one sampling date were included into the analysis. Microcrustacean taxa other than cyclopoid nauplii and copepodites were thus discarded because of their very low abundances throughout the whole study period. Rotifer densities and environmental variables, except for pH, were log(x+1)-transformed prior to the analysis. Monte Carlo permutation tests were used to assess the significance of the canonical axes and of the environmental variables that were selected in a forward selection procedure; only variables found to be significant (499 permutations, $p < 0.05$) were included in the model.

3.1.3 Results

3.1.3.1 Hydrology

Values of mean daily river discharge recorded between January 2008 and April 2010 at the station of Boretto are presented in Fig. 3.1.2. In 2008 the highest discharge value was observed on December 18 (4835 $m^3 s^{-1}$), while in 2009 a maximum of 8819 $m^3 s^{-1}$ was reached on May 1. The two years show remarkable differences in the hydrological regime: during the late winter-early spring of 2009 (January-April) river flow was generally higher in comparison to the same period of the previous year, with peaks of up to 4000 $m^3 s^{-1}$. Moreover, while in 2009 the typical spring flood took place in the beginning of May, in 2008 it was delayed by one month, with a peak of 4711 $m^3 s^{-1}$ on June 2. Finally, no severe summer drought occurred in any of the two years, with summer flow values never dropping below 582 $m^3 s^{-1}$.

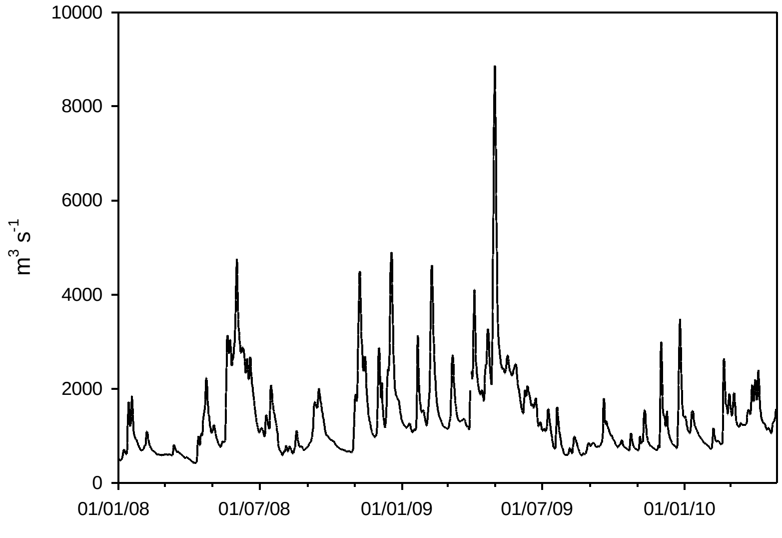


Fig. 3.1.2 - Mean daily river discharge measured at the gauging station of Boretto in the period January 2008 - April 2010.

The aforementioned 2009 spring flood peaked on April 29 at the most upstream gauging station of Piacenza, reaching a maximum of 6747 m^3 s^{-1}, while at the most downstream station of Pontelagoscuro the highest value was recorded on May 2 (7472 m^3 s^{-1}; Fig. 3.1.3). River flow tended then to gradually decrease, with the lowest summer values recorded on August 2 at Piacenza (446 m^3 s^{-1}) and on August 1 at Pontelagoscuro (773 m^3 s^{-1}).

The period between September 2009 and April 2010 was characterized by a few discharge peaks that did not exceeded 2555 m^3 s^{-1} (December 1, 2009) at Piacenza and 4166 m^3 s^{-1} (December 27, 2009) at Pontelagoscuro. Two remarkable spring floods then occurred in the beginning of May and in middle June, respectively, with values above 4000 m^3 s^{-1} at Piacenza and over 5000 m^3 s^{-1} at Pontelagoscuro. A sharp decrease in river flow was then recorded, down to minima of 358 m^3 s^{-1} (July 29) at Piacenza and 677 m^3 s^{-1} (July 24) at Pontelagoscuro, until a new peak occurred in the first half of August, up to values of 2433 m^3 s^{-1} (August 16) at Piacenza and 2968 m^3 s^{-1} (August 18) at Pontelagoscuro.

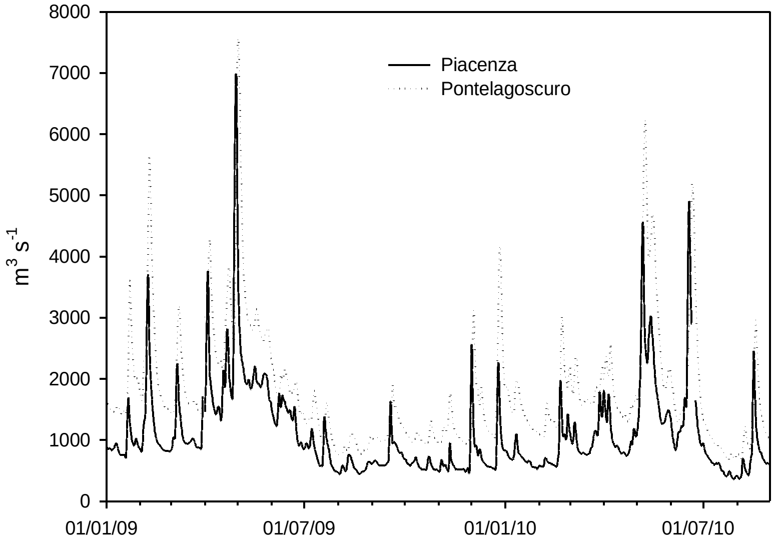
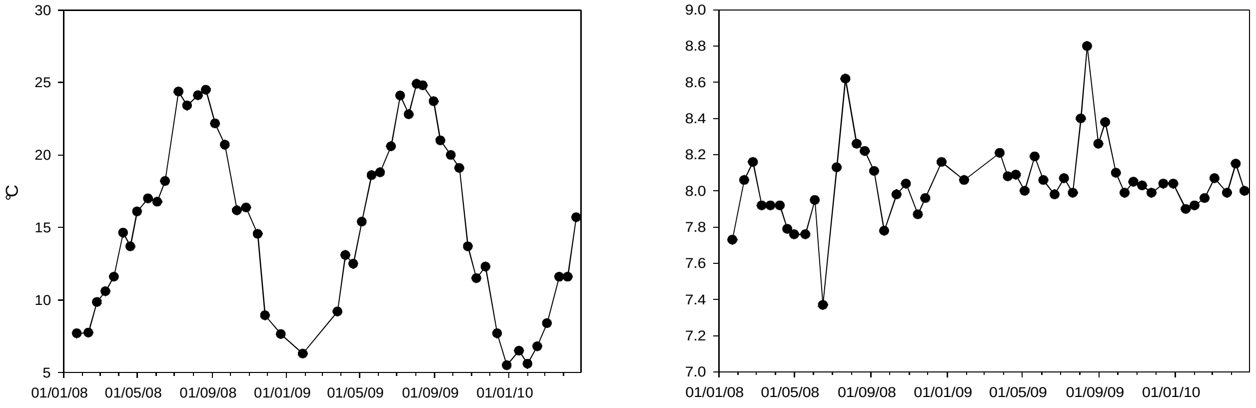


Fig. 3.1.3 - Mean daily river discharge measured at the gauging stations of Piacenza (upstream) and Pontelagoscuro (downstream) in the period January 2009 - August 2010.

3.1.3.2 Hydrochemistry

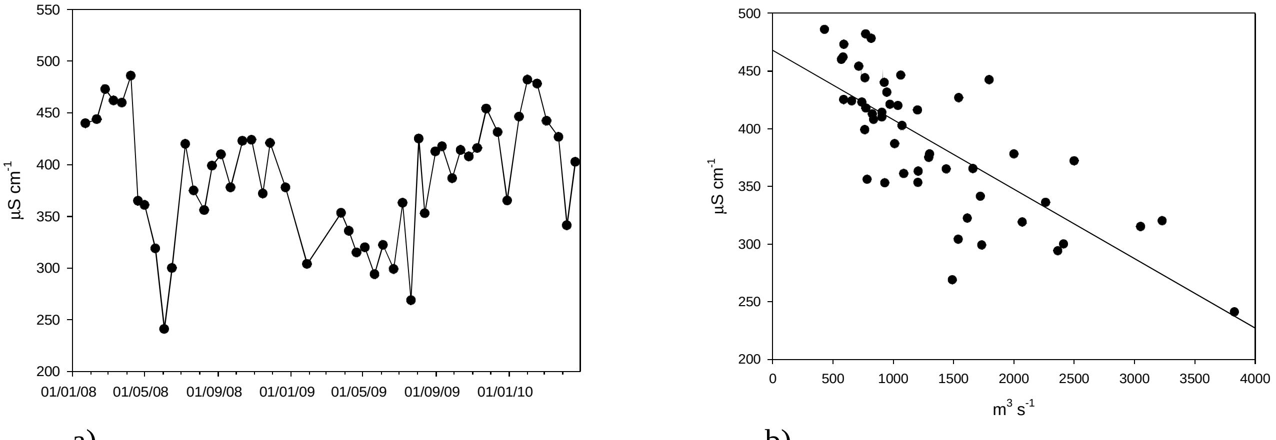
Viadana

Water temperature followed a regular seasonal pattern, with maxima of about 25°C in summer and minima around 7°C in winter (Fig. 3.1.4a). pH values were always above 7, with a minimum of 7.3 on June 16, 2008 and a maximum of 8.8 on August 13, 2009 (Fig. 3.1.4b). Conductivity varied between 241 and 486 µS cm^{-1}, with low values at high discharge rates and peaks during summer low flow conditions (Fig. 3.1.5a). This pattern is confirmed by the significant negative relationship between this variable and river discharge ($R^2 = 0.57$, $p < 0.01$; Fig. 3.1.5b). Total alkalinity was measured only in 2009 and 2010 and it varied between 1.61 meq L^{-1} (July 21, 2009) and 4.15 meq L^{-1} (April 21, 2009; Fig. 3.1.6a). Conductivity was significantly related to alkalinity ($R^2 = 0.88$, $p < 0.01$; Fig. 3.1.6b). Oxygen content underwent marked fluctuations, with prevailing conditions of slight undersaturation, down to a value of 54% on December 23, 2008. Oxygen oversaturation typically occurred during summer low discharge rates (Fig. 3.1.7). NO_3-N concentrations varied between 1012 µg L^{-1} (April 20, 2008) and 2837 µg L^{-1} (February 25, 2008; Fig. 3.1.8a). Although no clear trend emerged, in both years flood events were generally associated with marked drops in nitrate values. NO_2-N never exceeded 30 µg L^{-1} (Fig. 3.1.8b), while NH_4-N showed irregular fluctuations between a minimum of 15 µg L^{-1} (July 8 and 22, 2008) and a maximum of 177 µg L^{-1} (January 23, 2008; Fig. 3.1.9a). SRP peaked in April of both years, with values of 145 µg L^{-1} (April 8, 2008) and 155 µg L^{-1} (April 21, 2009), respectively. Concentrations tended to decrease in the subsequent months of both years, with minima during summer (17 µg L^{-1} on July 22, 2008 and 32 µg L^{-1} on July 21, 2009; Fig. 3.1.9b). DRSi ranged between 1369 µg L^{-1} (August 13, 2009) and 5866 µg L^{-1} (August 9, 2008), with sharp decreases in association with phytoplankton summer peaks (Fig. 3.1.10a). SPM varied between 11.8 mg L^{-1} (August 13, 2009) and 178.7 mg L^{-1} (May 5, 2009), with the exceptions of three isolated peaks of 333.7 mg L^{-1} (June 3, 2008), 233.0 mg L^{-1} (November 15, 2008) and 1067.3 mg L^{-1} (April 21, 2009; Fig. 3.1.10b). A significant, positive linear relationship was found between SPM and river discharge (R^2 = 0.40, $p < 0.01$; Fig. 3.1.11a). Chl-*a* content reached the highest values in summer of both years (71.6 µg L^{-1} on July 8, 2008 and 76.3 µg L^{-1} on August 13, 2009), while in the remaining seasons it never exceeded 20 µg L^{-1} (Fig. 3.1.11b). A linear negative relationship between log-transformed Chl-*a* and river discharge was detected only in the period more favourable to algal growth (March-September) of 2009 (R^2 = 0.60, $p < 0.01$).



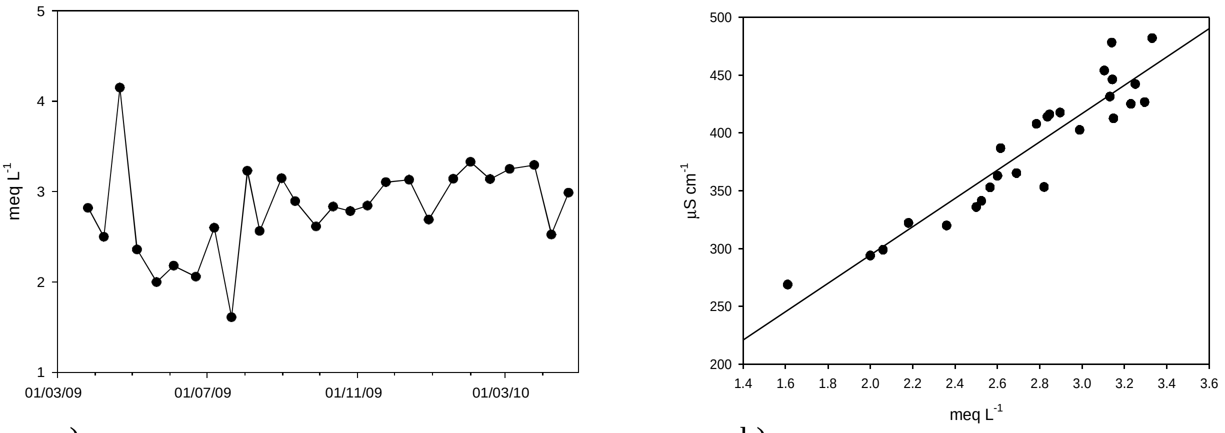
a) b)

Fig. 3.1.4 - Water temperature (a) and pH (b) measured at the station of Viadana in the study period.



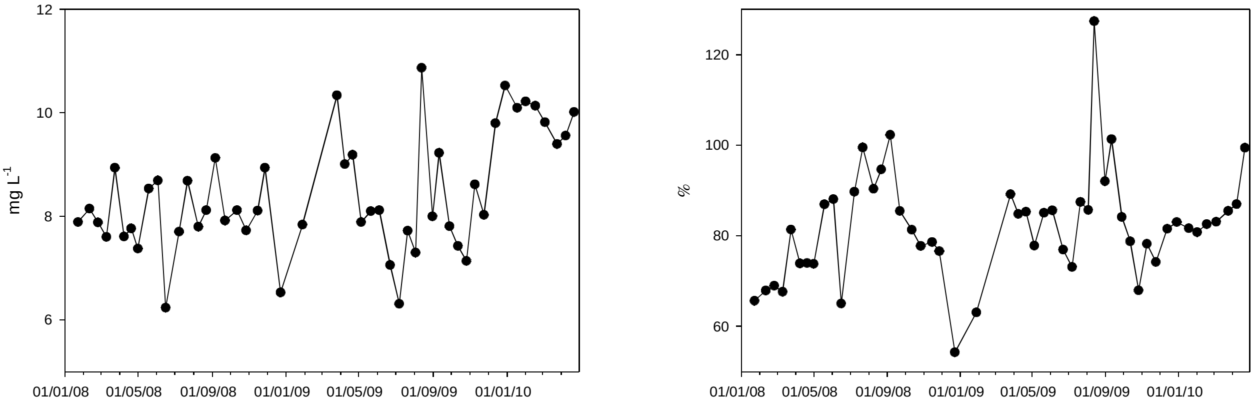
a) b)

Fig. 3.1.5 - Electric conductivity at 25°C measured at the station of Viadana in the study period (a) and relationship between conductivity and mean daily river discharge (b).



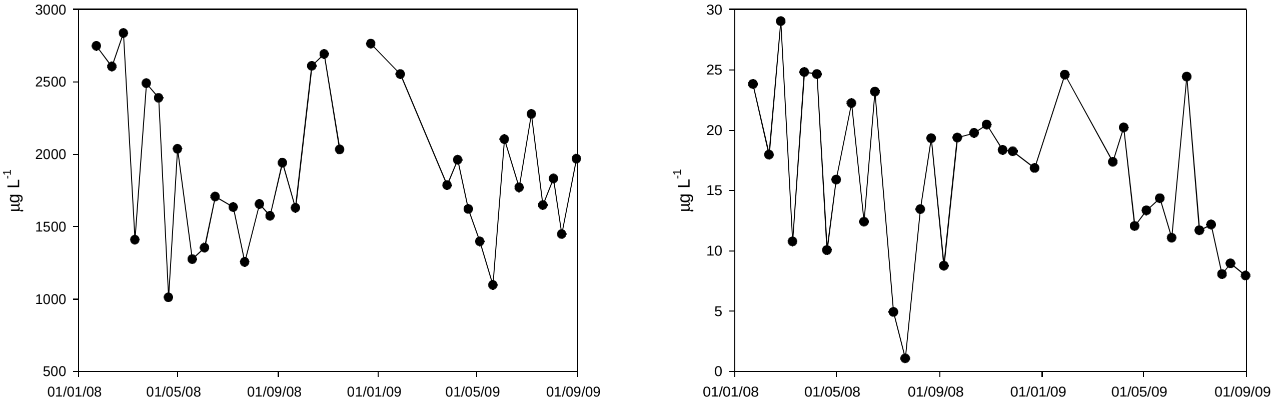
a) b)

Fig. 3.1.6 - Total alkalinity measured at the station of Viadana in the period March 2009 - April 2010 (a) and relationship between conductivity and total alkalinity (b). The alkalinity value of 4.15 meq L^{-1} (April 21, 2009) was identified as an outlier and excluded from the analysis.



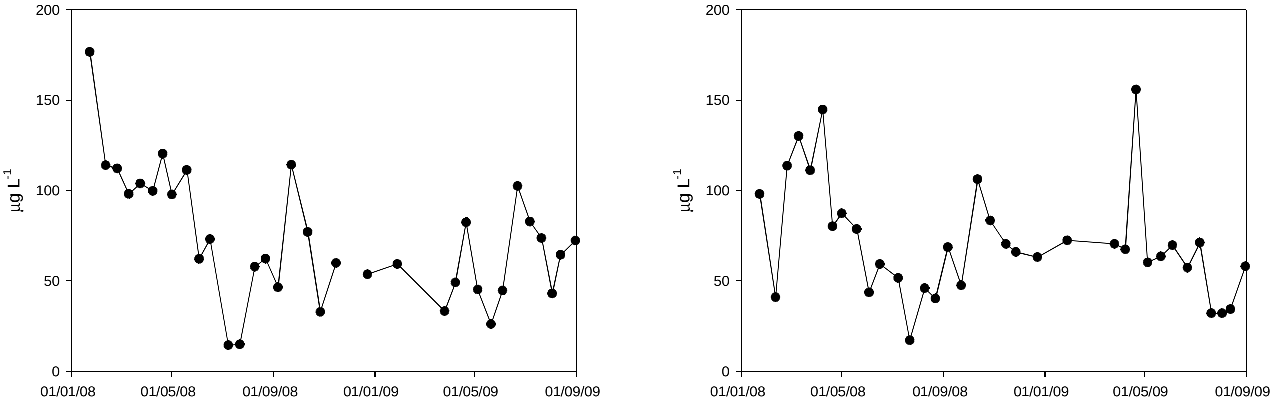
a) b)

Fig. 3.1.7 - Dissolved oxygen concentration (a) and percentage saturation (b) measured at the station of Viadana in the study period.



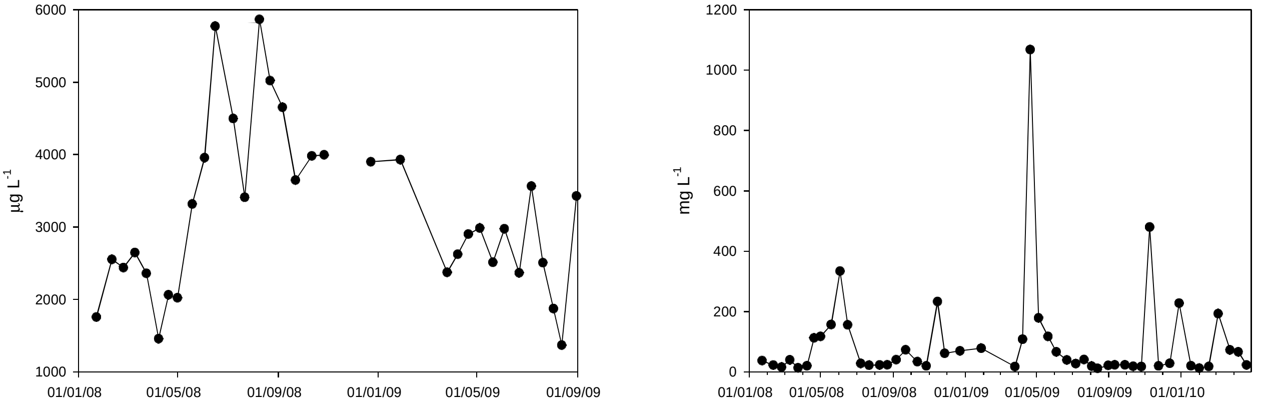
a) b)

Fig. 3.1.8 - Nitrate (a) and nitrite (b) concentration measured at the station of Viadana in the period January 2008 - August 2009.



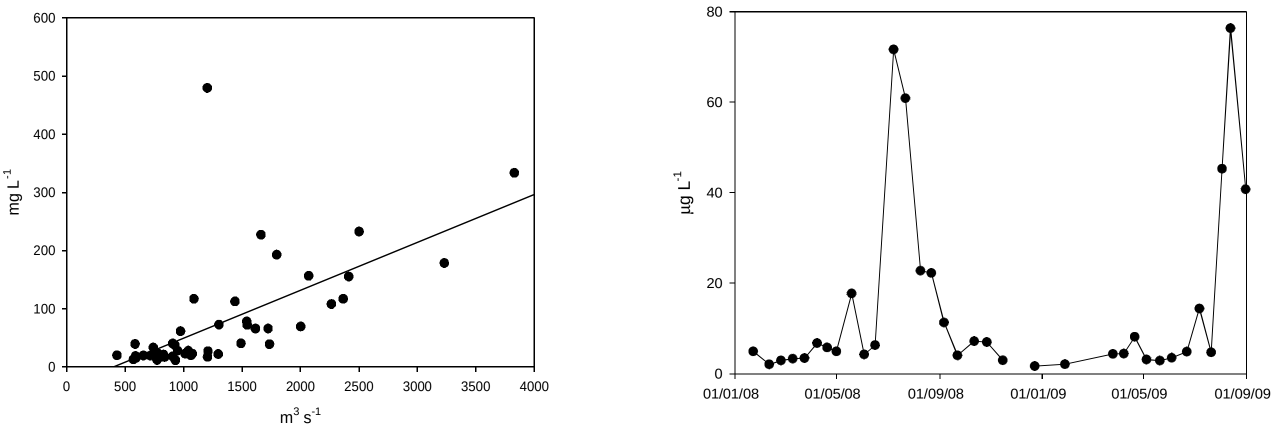
a) b)

Fig. 3.1.9 - Ammonium (a) and soluble reactive phosphorus (b) concentration measured at the station of Viadana in the period January 2008 - August 2009.



a) b)

Fig. 3.1.10 - Dissolved reactive silica concentration measured at the station of Viadana in the period January 2008 - August 2009 (a) and suspended particulate matter concentration measured at the station of Viadana in the study period (b).



a) b)

Fig. 3.1.11 - Relationship between suspended particulate matter and mean daily river discharge (a) and chlorophyll-*a* concentration measured at the station of Viadana in the period January 2008 - August 2009 (b). The exceptionally high SPM value of 1067 mg L^{-1} (April 21, 2009) was identified as an outlier and excluded from the analysis.

Mortizza

Water temperature reached summer maxima between 24.0 and 25.4°C, while in winter it dropped down to 6.3°C (Fig. 3.1.12a). pH values varied between a minimum of 7.7 in March 2010 and a maximum of 8.3 in August 2010 (Fig. 3.1.12b). Conductivity ranged between 326 and 465 µS cm^{-1} (Fig. 3.1.13a) and it was not significantly related to river discharge. Total alkalinity varied between 2.21 meq L^{-1} (May 2010) and 3.73 meq L^{-1} (March 2010; Fig. 3.1.13b). Conductivity was significantly related to alkalinity ($R^2 = 0.43$, $p < 0.05$; Fig. 3.1.14a).

Dissolved oxygen content was comprised between 6.8 and 10.3 mg L^{-1} (Fig. 3.1.15a). Percentage saturation fluctuated between 70 and 90%, with oversaturation peaks of 113 and 120% in August of 2009 and 2010, respectively (Fig. 3.1.15b).

NO_3-N concentrations showed an increasing trend from August 2009 (minimum of 1211 µg L^{-1}) to February 2010 (maximum of 2459 µg L^{-1}), followed by a gradual decrement (Fig. 3.1.16a).

A TN peak of 6465 µg L^{-1} was recorded in September 2009. During the rest of the study period concentrations were comprised between 1902 µg L^{-1} (April 2010) and 3110 µg L^{-1} (July 2009), with a decreasing pattern in the first months of 2010 and a subsequent rise in late spring and summer (Fig. 3.1.16b).

SRP increased progressively from a concentration of 18 µg L^{-1} in July 2009 to a peak of 80 µg L^{-1} in December 2009. It then started to gradually decrease down to a minimum of 5 µg L^{-1} in August 2010 (Fig. 3.1.17a). TP did not show any clear seasonal pattern, with concentrations irregularly fluctuating between 77 and 155 µg L^{-1} (Fig. 3.1.17b).

SPM varied between 14.2 mg L^{-1} (January 2010) and 114.9 mg L^{-1} (March 2010; Fig. 3.18a). A significant, positive linear relationship was found between SPM and river discharge ($R^2 = 0.56$, $p < 0.01$; Fig. 3.1.19a). Chl-*a* reached the highest values in August of both years (96.9 µg L^{-1} in 2009 and 54.1 µg L^{-1} in 2010), while between October and June it never exceeded 10 µg L^{-1} (Fig. 3.18b).

Serravalle

The lowest water temperature was recorded in January 2010 (6.3°C), while the highest values were measured in August of both years (26.4 and 25.0°C in 2009 and 2010, respectively; Fig. 3.1.12a). pH fluctuated around 8.0 for most of the study period, while in the summer months it increased to values up to 8.7 (September 2009; Fig. 3.1.12b). Conductivity gradually rose from 394 µS cm^{-1} in July 2009 to a maximum of 548 µS cm^{-1} in February 2010. A marked drop then occurred in the following months, down to a minimum of 372 µS cm^{-1} in May 2010 (Fig. 3.1.13a). No relationship was detected between this variable and river discharge. Total alkalinity showed the same temporal pattern as conductivity, with a peak of 3.77 meq L^{-1} in March 2010 and a minimum of 2.55 meq L^{-1} in May 2010 (Fig. 3.1.13b). Conductivity was significantly related to alkalinity ($R^2 = 0.78$, $p < 0.01$; Fig. 3.1.14b).

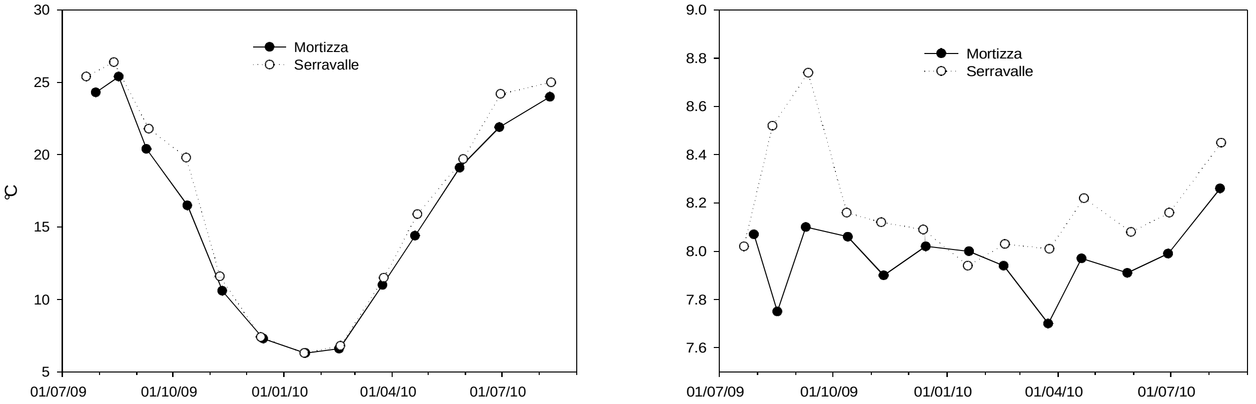
Dissolved oxygen concentrations varied between 7.8 and 11.1 mg L^{-1} (Fig. 3.1.15a). Percentage saturation was comprised between 80 and 90% for most of the sampling period. Oversaturation occurred in April 2010 (107%) and in the summer months of both years, with a maximum of 130% in August 2010 (Fig. 3.1.15b).

In August 2009 a NO_3-N concentration of 1458 µg L^{-1} was recorded. It then progressively increased up to a maximum of 3441 µg L^{-1} in February 2010, while in the following months it dropped again to values around 2000 µg L^{-1} (Fig. 3.1.16a).

TN exhibited an increasing trend from September 2009 (2280 µg L^{-1}) to December 2009 (3870 µg L^{-1}). A subsequent decrease was observed during the rest of the study period, down to a minimum of 1786 µg L^{-1} in August 2010 (Fig. 3.1.16b).

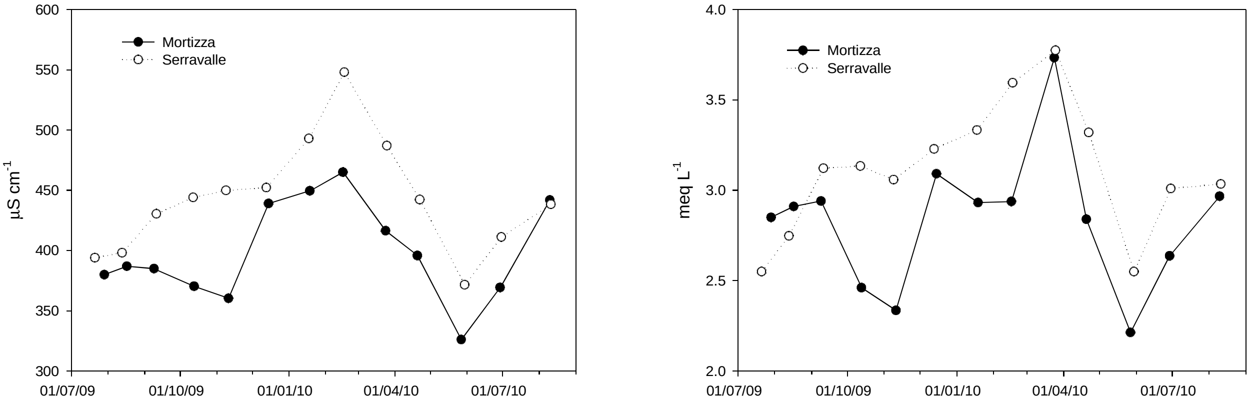
SRP varied between 17 µg L^{-1} (May 2010) and 78 µg L^{-1} (October 2009), with the highest values generally recorded in autumn and winter (Fig. 3.1.17a). TP fluctuated between 42 µg L^{-1} (September 2009) and 136 µg L^{-1} (March 2010; Fig. 3.1.17b).

SPM ranged between 15.7 mg L^{-1} (August 2010) and 67.2 mg L^{-1} (May 2010), with the exception of three peaks of 87.2, 114.0 and 76.9 mg L^{-1} recorded in December 2009, March 2010 and June 2010, respectively (Fig. 3.18a). A significant, positive linear relationship was found between SPM and river discharge ($R^2 = 0.53$, $p < 0.01$; Fig. 3.1.19b). Chl-*a* concentrations ranged between 1.7 µg L^{-1} (December 2009) and 45.4 µg L^{-1} (August 2010; Fig. 3.18b).



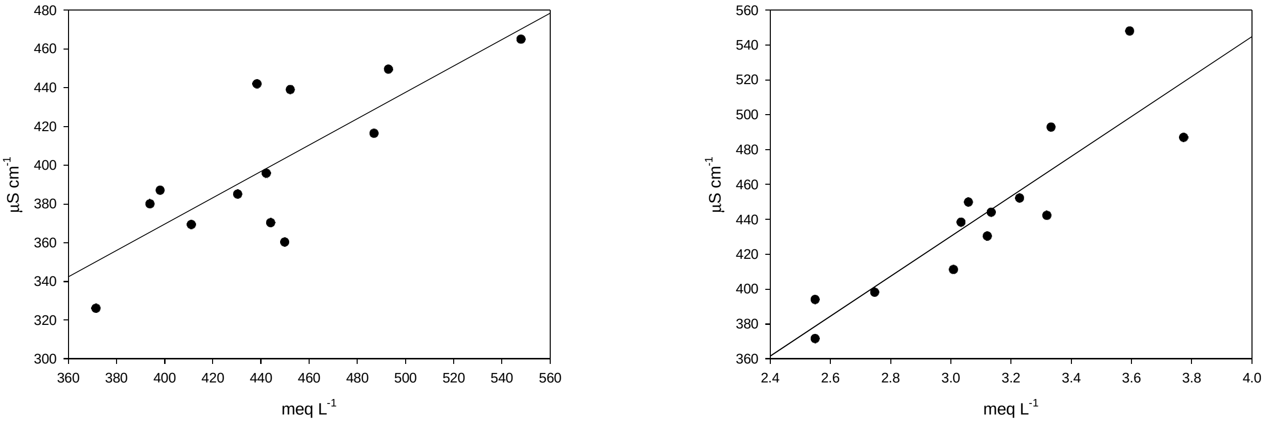
a) b)

Fig. 3.1.12 - Water temperature (a) and pH (b) measured at the stations of Mortizza and Serravalle in the period July 2009 - August 2010.



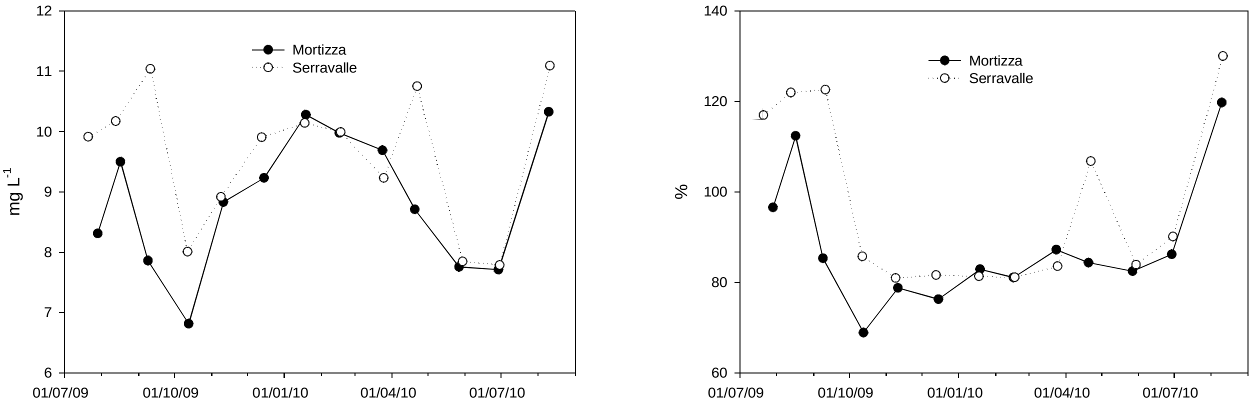
a) b)

Fig. 3.1.13 - Electric conductivity at 25°C (a) and total alkalinity (b) measured at the stations of Mortizza and Serravalle in the period July 2009 - August 2010.



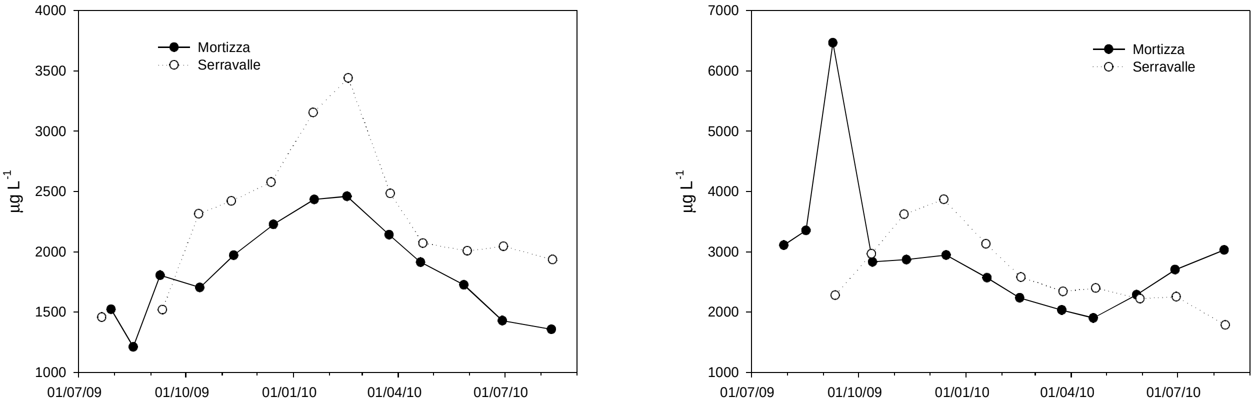
a) b)

Fig. 3.1.14 - Relationships between conductivity and alkalinity measured at the stations of Mortizza (a) and Serravalle (b) in the period July 2009 - August 2010.



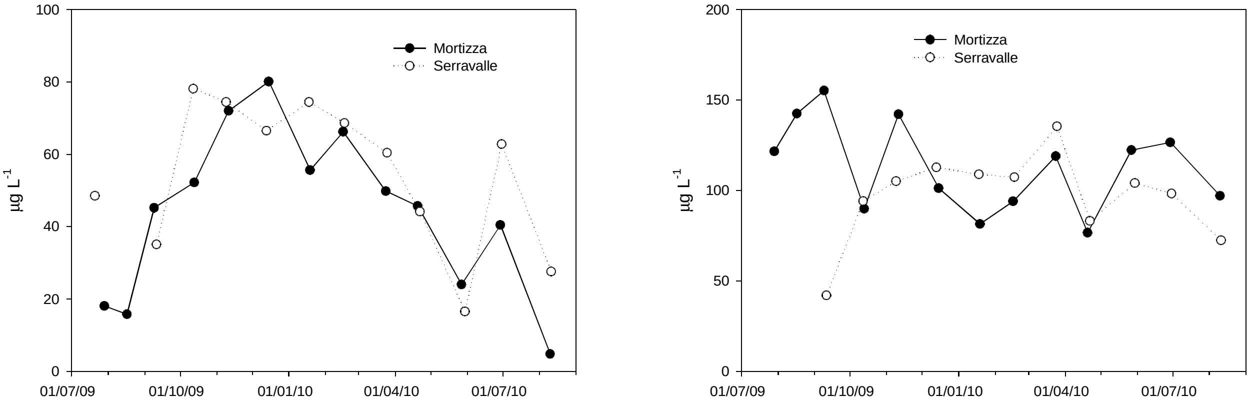
a) b)

Fig. 3.1.15 - Dissolved oxygen concentration (a) and percentage saturation (b) measured at the stations of Mortizza and Serravalle in the period July 2009 - August 2010.



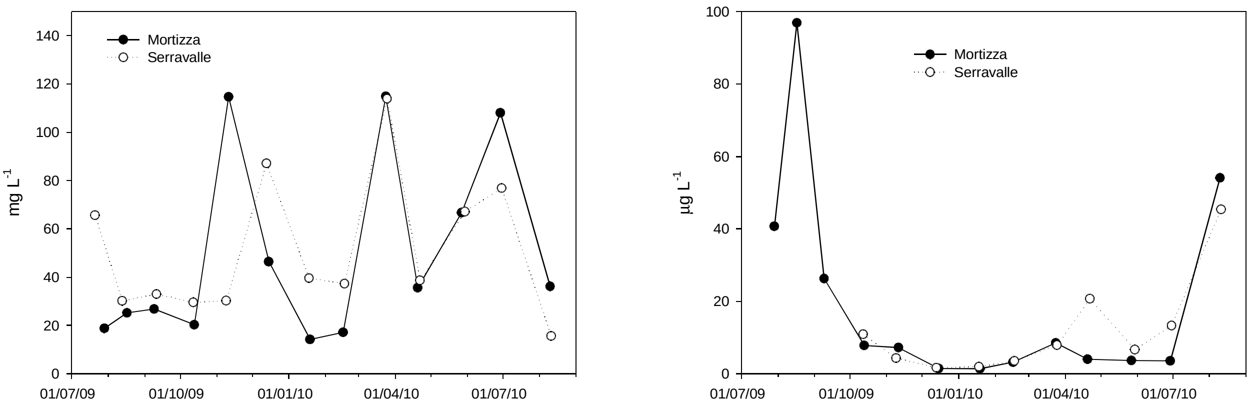
a) b)

Fig. 3.1.16 - Nitrate (a) and total nitrogen (b) concentration measured at the stations of Mortizza and Serravalle in the period July 2009 - August 2010.



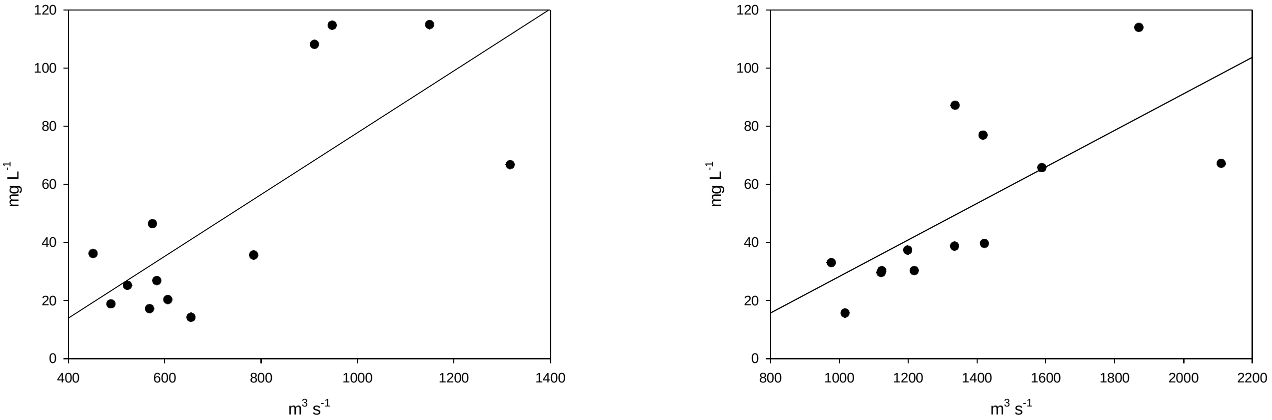
a) b)

Fig. 3.1.17 - Soluble reactive phosphorus (a) and total phosphorus (b) concentration measured at the stations of Mortizza and Serravalle in the period July 2009 - August 2010.



a) b)

Fig. 3.1.18 - Suspended particulate matter (a) and chlorophyll-*a* (b) concentration measured at the stations of Mortizza and Serravalle in the period July 2009 - August 2010.



a) b)

Fig. 3.1.19 - Relationships between suspended particulate matter and mean daily discharge recorded at the stations of Mortizza (a) and Serravalle (b) in the period July 2009 - August 2010.

3.1.3.3 Zooplankton assemblage

Viadana

The analysis of samples collected at the station of Viadana led to the identification of 172 zooplankton taxa: 139 rotifers, 15 copepods and 18 cladocerans (see Annex 1). Temporal patterns of total zooplankton abundance showed marked differences between the two years. In 2008 no summer peak in total zooplankton density was detected, with values never exceeding 45 ind L^{-1}. On the contrary, a maximum of 400 ind L^{-1} was recorded in August 2009 (Fig. 3.1.20). Total zooplankton density was positively related to water temperature ($R^2 = 0.32$, $p < 0.01$) and chlorophyll-*a* concentrations ($R^2 = 0.36$, $p < 0.01$). On the other hand, zooplankton abundance revealed contrasting patterns of variation in relation to river discharge during the growing season (March-September) of the two years. In fact, while in 2008 moderate flood events were followed by a net increment in the assemblage abundance, in 2009 total zooplankton density showed a negative pattern of variation with river flow (Fig. 3.1.21).

As for the composition of the assemblage, rotifers were by far the most abundant group (Figs. 3.1.22 and 3.1.23). The summer peak in 2009 was dominated by the rotifer species *Brachionus calyciflorus* and, secondarily, *Brachionus bennini* and *Brachionus quadridentatus* (Figs. 3.1.24 and 3.1.25a and b). These three species all reached their highest densities on August 3, with 173, 98 and

70 ind L^{-1}, respectively. Similar temporal patterns, although with much lower abundances, were followed by *Keratella cochlearis* f. *tecta* (Fig. 3.2.25c) and *Synchaeta* gr. *stylata-pectinata* (Fig. 3.1.25d), which attained maxima of 12 and 17 ind L^{-1}, respectively, in August 2009. *Keratella cochlearis* peaked in May-June of both years, with abundances up to 8 ind L^{-1}, while *Synchaeta* gr. *tremula-oblonga* tended to increase during summer months of both years, up to 9 ind L^{-1} in August 2009. Among the species of the genus *Lecane*, the most abundant were *L. fadeevi*, *L. closterocerca* and *L. tenuiseta*, with occasional spring-summer peaks of about 4-8 ind L^{-1} (Fig. 3.1.25e). Bdelloid rotifers showed irregular fluctuations during the study period but never exceeded 11 ind L^{-1} (Fig. 3.1.25f).

Copepod abundances were mainly sustained by cyclopoid nauplii, which tended to increase in the period May-August of both years, reaching densities of up to 13 ind L^{-1} (August 31, 2009; Fig. 3.1.26).

Cladocerans very rarely exceeded an overall abundance of 1 ind L^{-1}, with *Bosmina longirostris*, *Moina micrura* and *Macrothrix laticornis* as the most frequently recorded species.

Diversity of the rotifer assemblage, as measured by the Shannon Diversity Index, showed a strong seasonality in both years, with an increasing trend during spring, maxima in summer and a substantial drop in autumn and winter (Fig. 3.1.27a). In fact, a significant, positive linear relationship was detected between this variable and water temperature ($R^2 = 0.34$, $p < 0.01$).

No distinct relationship emerged between rotifer diversity and river discharge. Nevertheless, when considering the growing season (March-September) of both years, diversity seemed to peak at intermediate discharge values, while further increases in river flow corresponded to marked drops in community diversity (Fig. 3.1.27b). Similarly, intermediate discharge values were associated with a more even composition of the assemblage in terms of loricate and illoricate rotifers, while loricate taxa tended to dominate at very low or very high flow rates (Figs. 3.1.28 and 3.1.29).

Non-planktonic organisms were mainly represented by cnidarians, nematodes, insect larvae, gastrotrichs, tardigrades, ostracods, hydrachnids and oligochaetes. They were present in the water column during the whole study period, but their percentage share in terms of abundance increased during flood events (Fig. 3.1.23). A positive linear relationship was found between the density of non-planktonic taxa and river discharge ($R^2 = 0.29$, $p < 0.001$).

Contrarily to the previous year, during summer 2009 a substantial development of bivalve veligers was observed, with a maximum density of 34 ind L^{-1} on August 3 (Fig. 3.1.30).

CCA ordination of the most abundant zooplankton taxa and of environmental variables is reported in Fig. 3.1.31. The Monte Carlo permutation test indicated that all the canonical axes were significant ($p < 0.01$). Water temperature (permutation test: $F = 5.08$, $p < 0.01$, Lambda $A = 0.18$), river discharge (permutation test: $F = 3.32$, $p < 0.01$, Lambda $A = 0.11$), pH (permutation test: $F = 2.24$, $p < 0.01$, Lambda $A = 0.07$), chlorophyll-*a* (permutation test: $F = 0.09$, $p < 0.05$, Lambda $A = 0.05$) and SRP (permutation test: $F = 0.09$, $p < 0.05$, Lambda $A = 0.06$) were the environmental variables that significantly contributed to explain taxa occurrence. In particular, brachionid rotifers dominated during summer low-flow conditions, when temperature and Chl-*a* content were high. On the contrary, taxa like *Kellicottia longispina*, *Hexarthra fennica*, *Trichocerca porcellus* and *Notholca* gr. *acuminata-labis* were typically associated with spring high-flow conditions, when water temperature and Chl-*a* were still relatively low. *Proales theodora* and *Keratella* gr. *quadrata* tended to peak during spring as well, but under lower discharge levels. The remaining taxa did not show any clear seasonal pattern, although it is worth noting that some closely related taxa like *Lecane closterocerca* and *L. fadeevi*, or *Keratella cochlearis* and *K. cochlearis* f. *tecta*, are located in opposite quadrants of the biplot.

The CCA ordination of samples showed a seasonal separation into three clusters, one including summer samples, one including spring-autumn samples and one with samples collected in winter 2008 (Fig. 3.1.32).

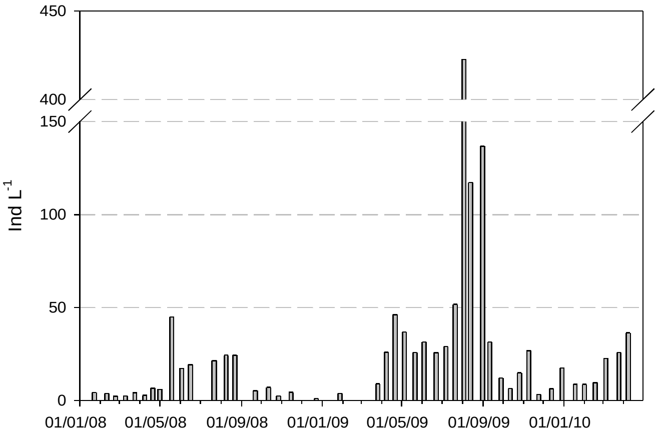


Fig. 3.1.20 - Total zooplankton density measured at the station of Viadana in the study period.

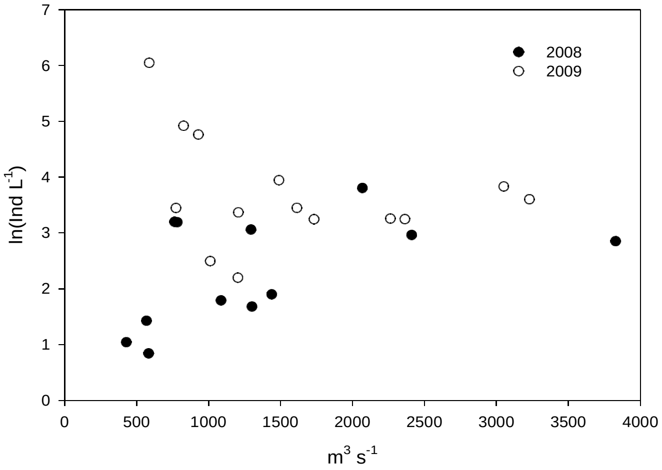


Fig. 3.1.21 - Patterns of variation of total zooplankton density in relation to mean daily river discharge in the March-September period of 2008 and 2009 at the station of Viadana.

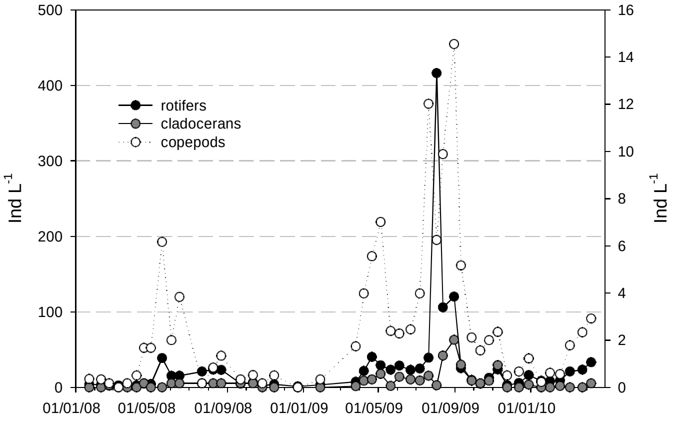
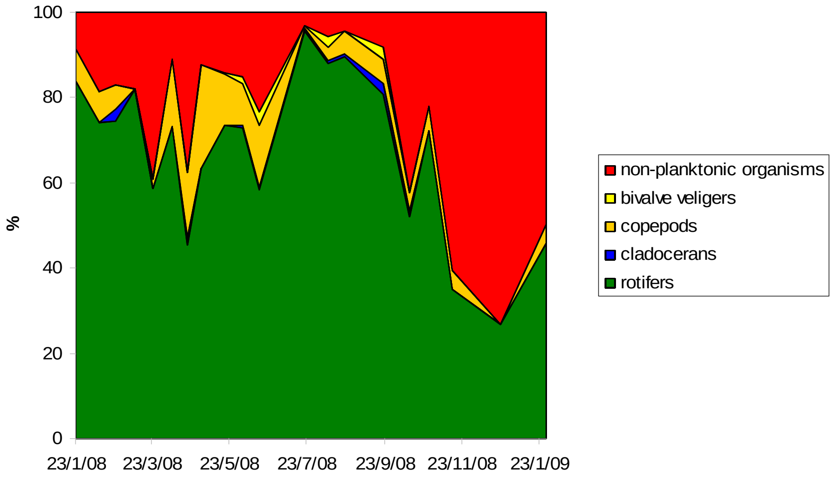
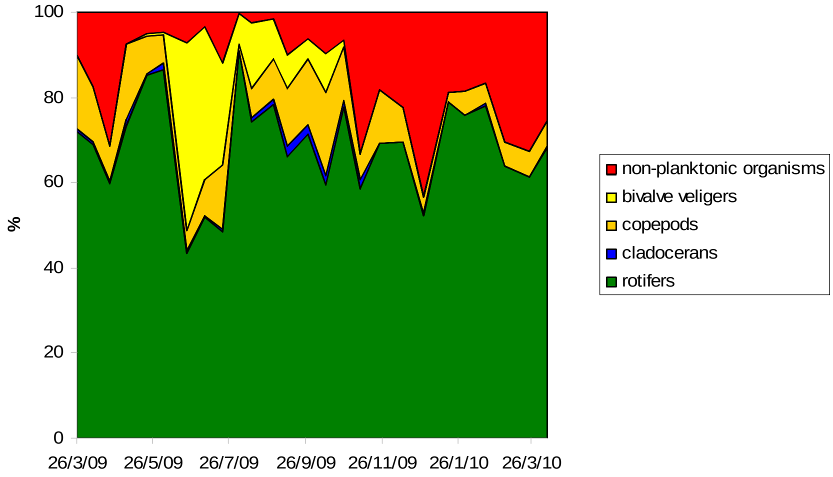


Fig. 3.1.22 - Total rotifer (left axis), cladoceran (right axis) and copepod (right axis) density measured at the station of Viadana during the study period.



a) 2008



b) 2009-2010

Fig. 3.1.23 - Percentage composition of the metazoan assemblage recorded in 2008 (a) and 2009-2010 (b) at the station of Viadana during the study period.

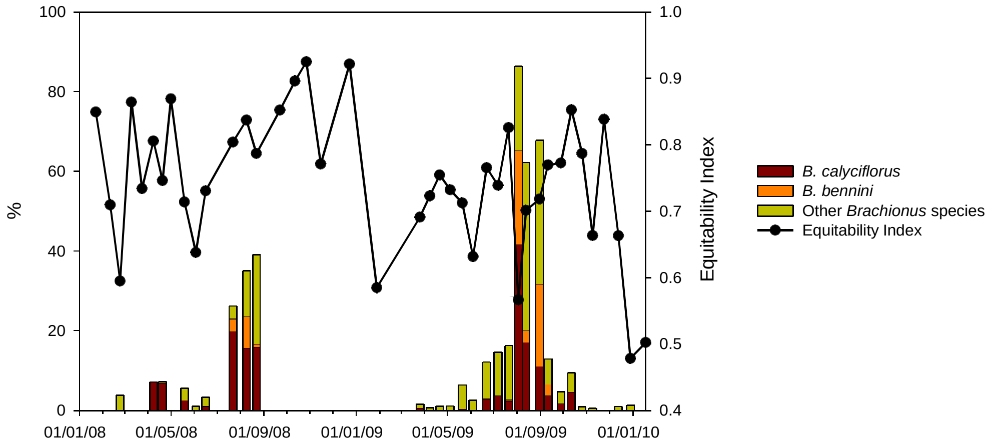


Fig. 3.1.24 - Percentage occurrence of the species of the genus *Brachionus* (left axis) and Equitability Index calculated for the rotifer assemblage (right axis) at the station of Viadana during the study period.

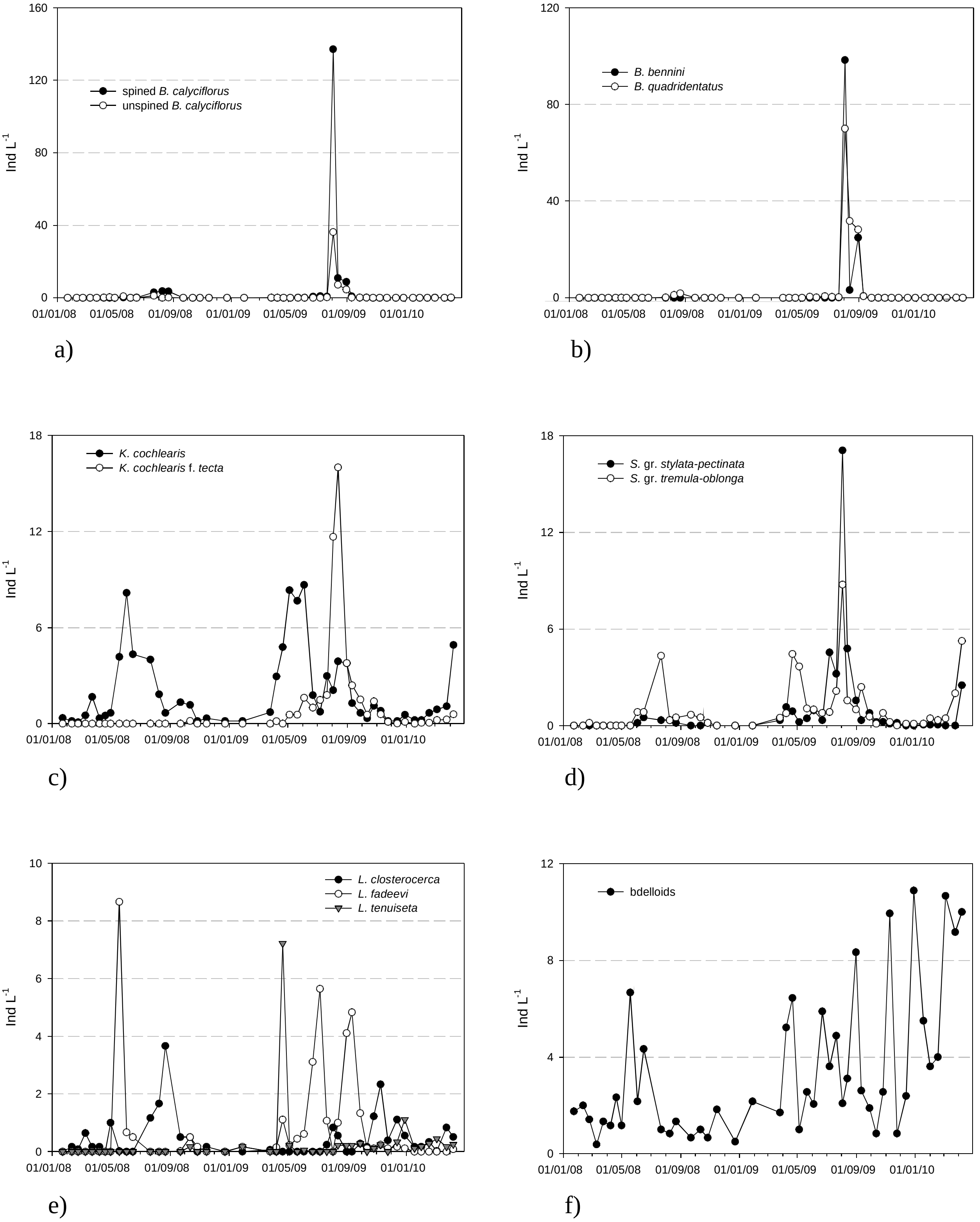


Fig. 3.1.25 - Density of some rotifer taxa found at the station of Viadana during the study period: spined and unspined *Brachionus calyciflorus* (a), *B. bennini* and *B. quadridentatus* (b), *Keratella cochlearis* and *K. cochlearis* f. *tecta* (c), *Synchaeta* gr. *tremula-oblonga* and *S.* gr. *stylata-pectinata* (d), *Lecane closterocerca*, *L. fadeevi* and *L. tenuiseta* (e), bdelloids (f).

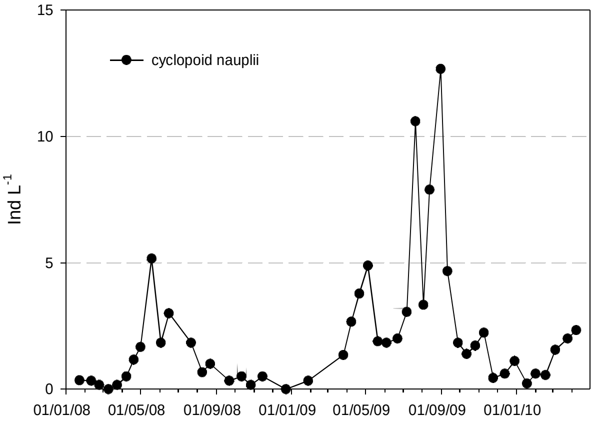
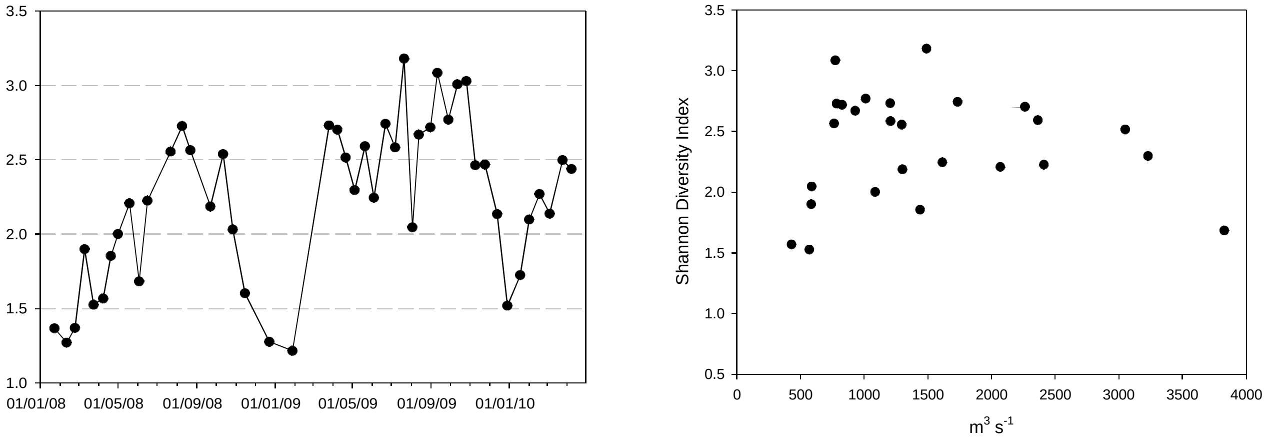


Fig. 3.1.26 - Density of cyclopoid nauplii recorded at the station of Viadana in the study period.



a) b)

Fig. 3.1.27 - Shannon Diversity Index calculated for the rotifer assemblage in the study period (a) and pattern of variation of rotifer diversity in relation to mean daily river discharge in the March-September period of 2008 and 2009 at the station of Viadana (b).

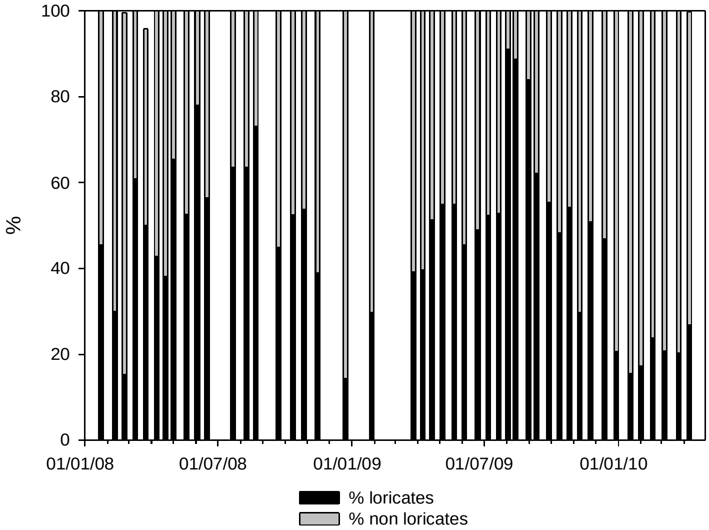


Fig. 3.1.28 - Percentage composition of the rotifer assemblage in terms of loricate and illoricate taxa recorded at the station of Viadana in the study period.

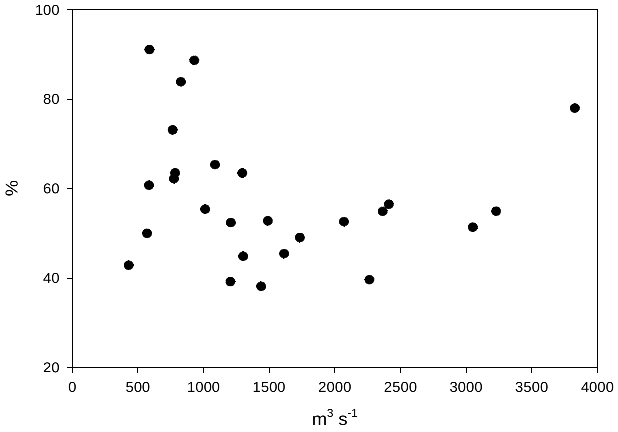


Fig. 3.1.29 - Variation in the percentage of loricate rotifer taxa in relation to mean daily river discharge in the March-September period of 2008 and 2009 at the station of Viadana.

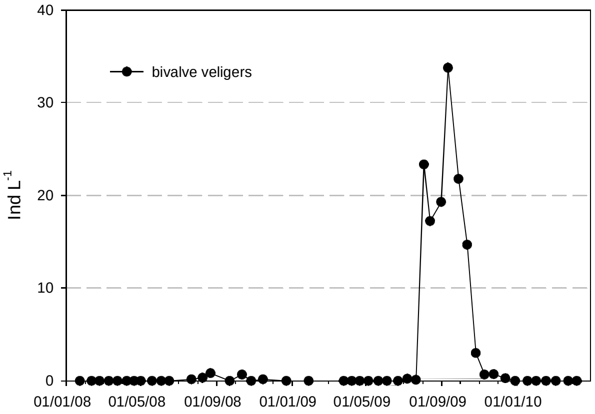


Fig. 3.1.30 - Density of bivalve veligers recorded at the station of Viadana during the study period.

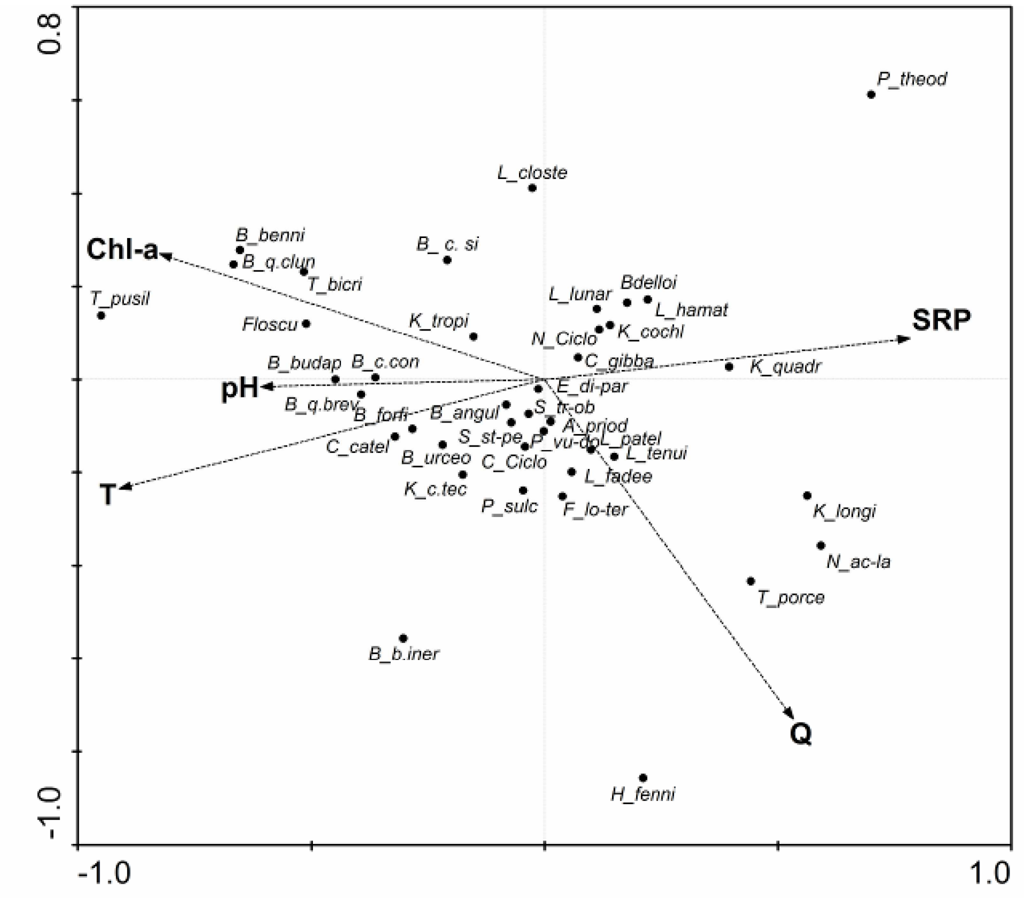


Fig. 3.1.31 - CCA biplot of rotifer taxa and environmental variables measured at the station of Viadana in the period January 2008 – August 2009. Only significant variables ($p < 0.05$) are displayed. (A_priod: *Asplanchna priodonta;* Bdelloi: bdelloids; B_angul: *Brachionus angularis*; B_benni: *B. bennini*; B_b.iner: *B. bidentatus* f. *inermis;* B_budap: *B. budapestinensis;* B_c.con: spined *B. calyciflorus*; B_c.sin: unspined *B. calyciflorus*; B_forfi: *B. forficula*; B_q.brev: *B. quadridentatus* f. *brevispinus;* B_q.cluni: *B. quadridentatus* f. *cluniorbicularis;* B_urceo: *B. urceolaris*; C_catel: *Cephalodella catellina;* C_gibba: *C. gibba;* E_di-par: *Euchlanis* gr. *dilatata-parva;* F_lo-ter: *Filinia* gr. *longiseta-terminalis*; Floscu: unidentified Flosculariidae; H_fenni: *Hexarthra fennica*; K_longi: *Kellicottia longispina;* K_cochl: *Keratella cochlearis;* K_c.tec: *K. cochlearis* f. *tecta;* K_quadr: *K.* gr. *quadrata;* K_tropi: *K. tropica*; L_hamat: *Lecane hamata;* L_closte: *L. closterocerca*; L_fadee: *L. fadeevi;* L_lunar: *L.* gr. *lunaris;* L_tenui: *L. tenuiseta;* L_patel: *Lepadella patella;* N_ac-la: *Notholca* gr. *acuminata-labis;* P_vu-do: *Polyarthra* gr. *vulgaris-dolichoptera;* P_sulca: *Pompholyx sulcata;* P_theod: *Proales theodora;* S_st-pe: *Synchaeta* gr. *stylata-pectinata;* S_tr-ob: *S.* gr. *tremula-oblonga;* T_bicri: *Trichocerca bicristata;* T_porce: *T. porcellus;* T_pusil: *T.* cfr. *pusilla;* N_Ciclo: cyclopoid nauplii; C_Ciclo: cyclopoid copepodites).

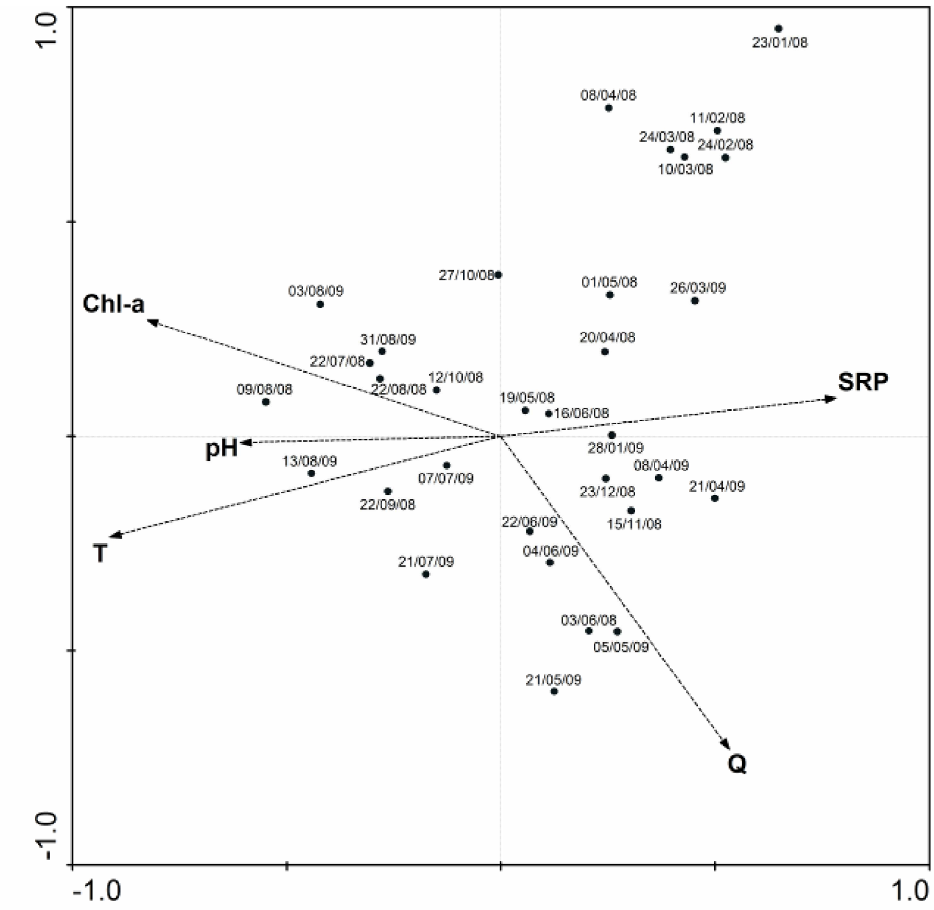


Fig. 3.1.32 - CCA biplot of samples collected at the station of Viadana in the period January 2008 - August 2009.

Mortizza

A total of 107 zooplankton taxa were identified at the station of Mortizza: 98 rotifers, 1 copepod and 8 cladocerans (see Annex 1). Total zooplankton abundance varied between 10 and 61 ind L^{-1}, with the maximum value recorded in August 2010 (Fig. 3.1.33). No significant relationship was found between zooplankton density and water temperature, chlorophyll-*a* content or river discharge. The assemblage was dominated by rotifers, whose share in terms of density ranged between 49 and 95% (Figs. 3.1.34a and 3.1.35a). *Brachionus quadridentatus* was the rotifer species reaching the highest abundance, with a peak of 21 ind L^{-1} in August 2009, thereby making up 56% of the whole assemblage (Figs. 3.1.36b and 3.1.38a). It then never exceeded 3 ind L^{-1} for the rest of the sampling period. *Brachionus calyciflorus*, *B. bennini* and *B. budapestinensis* showed a temporal pattern similar to that of *B. quadridentatus*, with the highest densities recorded in summer (Fig. 3.1.35a-b). Other taxa peaked in the spring months, such as *Keratella cochlearis* and *Polyarthra* gr. *vulgaris-dolichoptera* (Fig. 3.1.36c), which together made up 30 and 36% of the community in May and April 2010, respectively (Fig. 3.1.38a). Up to 45% of total rotifer abundance in late autumn and winter was sustained by bdelloids, reaching a peak of 9 ind L^{-1} in November 2009 (Fig. 3.1.36e).

As for the three most abundant *Lecane*, namely *L. fadeevi*, *L. closterocerca* and *L. tenuiseta*, their highest densities were recorded between autumn and winter, with the peak of each species following the decline of the previous one (Fig. 3.1.36d).

While in summer months the rotifer assemblage was largely dominated by loricate taxa, their share gradually decreased over autumn and winter, with the maximum percentage of illoricate taxa (82%) recorded in March 2010 (Fig. 3.1.39a). The percentage of littoral/epibenthic rotifers, as opposed to the truly planktonic ones, ranged between 36% (August 2009 and 2010) and 94% (December 2009), with the highest values generally found in autumn and winter (Fig. 3.1.40a).

Cladocerans were extremely rare and copepods, mainly cyclopoid nauplii, reached a maximum of 11 ind L^{-1} in August 2010, while they never exceeded 3 ind L^{-1} in the rest of the study period (Fig. 3.1.34a).

The Shannon Diversity Index calculated for the rotifer assemblage varied between 2.01 (January 2010) and 3.02 (August 2010; Fig. 3.1.41). No relationship was found between diversity and river discharge.

Non-planktonic organisms fluctuated between less than 1 ind L^{-1} (August 2009) and 21 ind L^{-1} (March 2010; Fig. 3.1.42a). Bivalve veligers were absent in most of the samples and never went over 2 ind L^{-1} (Fig. 3.1.42b).

Serravalle

The one-year survey at the station of Serravalle led to the identification of 105 zooplankton taxa: 85 rotifers, 4 copepods and 6 cladocerans (see Annex 1). Total zooplankton density reached the highest values during summer, with a peak of 2310 ind L^{-1} in August 2009, while the lowest abundances were recorded in winter (down to 5 ind L^{-1} in December 2009; Fig. 3.1.33). Zooplankton density was positively related to water temperature ($R^2 = 0.85$, $p < 0.01$) and chlorophyll-*a* concentration ($R^2 = 0.77$, $p < 0.01$), while no clear relationship could be found with river discharge.

Rotifers were the dominant group in terms of abundance, reaching a share of 64-99% of the whole community (Figs. 3.1.34b and 3.1.35b).

Species of the genera *Brachionus*, *Keratella*, *Synchaeta* and *Polyarthra* were the most abundant and they all showed the same temporal pattern, with the highest densities during summer low-flow conditions (Figs. 3.1.37 and 3.1.38b). In particular, summer peaks were largely dominated by *Brachionus calyciflorus*, which made up over 60% of the whole rotifer assemblage in August 2009 (Fig. 3.1.37a). *Brachionus budapestinensis* was the second most abundant Brachionid in summer, while in autumn and spring the share of the genus *Brachionus* was strongly reduced in favour of that of *Keratella cochlearis*, *K. cochlearis* f. *tecta* and *Synchaeta* gr. *tremula-oblonga* (Fig. 3.1.37c-d). The winter assemblage was mainly dominated by bdelloids, which reached their highest densities in January 2010 (Fig. 3.1.37f). This is reflected by the temporal trend of the percentage of loricate and illoricate taxa in the community, showing that the share of illoricate taxa increased in winter months (Fig. 3.1.39b). A similar pattern emerges when separating littoral/epibenthic rotifers from truly planktonic ones, with the former tending to dominate the assemblage only in winter (Fig. 3.1.40b).

The microcrustacean component was dominated by cyclopoid larval stages, which tended to increase in summer. In particular, cyclopoid nauplii reached a maximum of 15 ind L^{-1} in August 2009. In the same month cladocerans also attained their highest abundance (1 ind L^{-1}), but in most of the sampling dates their presence was only occasional (Fig. 3.1.34b).

The Shannon Diversity Index calculated for the rotifer assemblage ranged between 1.45 (August 2009) and 2.65 (September 2009; Fig. 3.1.41). No clear relationship was found between this variable and river discharge.

Non-planktonic organisms never exceeded 4 ind L^{-1}, with the highest densities recorded in winter and spring (Fig. 3.1.42a).

A marked increase in abundance of bivalve veligers was observed in summer, with a peak of 60 ind L^{-1} in August 2009 (Fig. 3.1.42b).

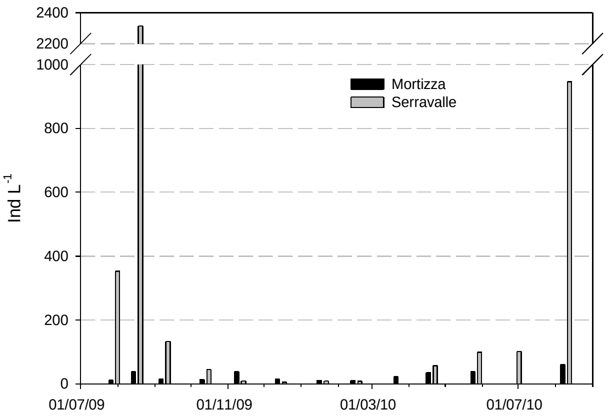
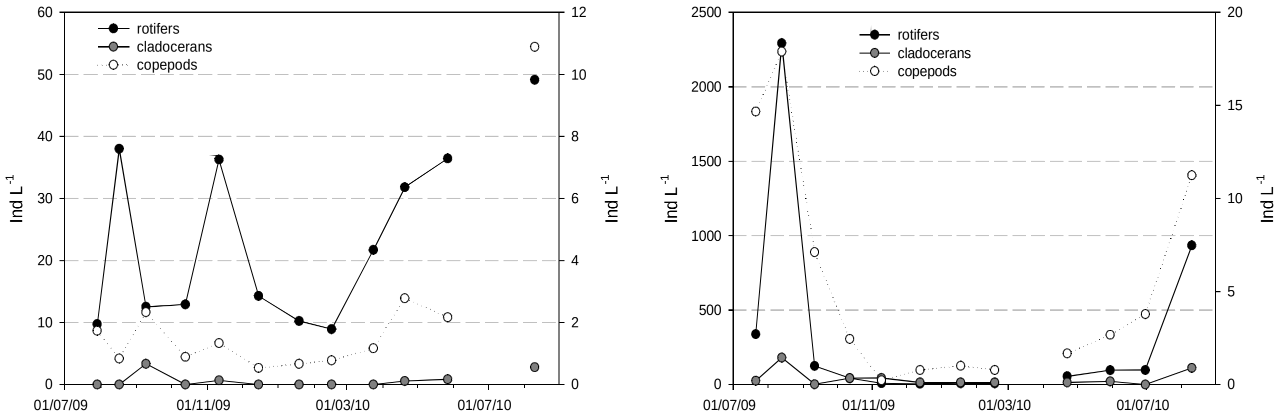
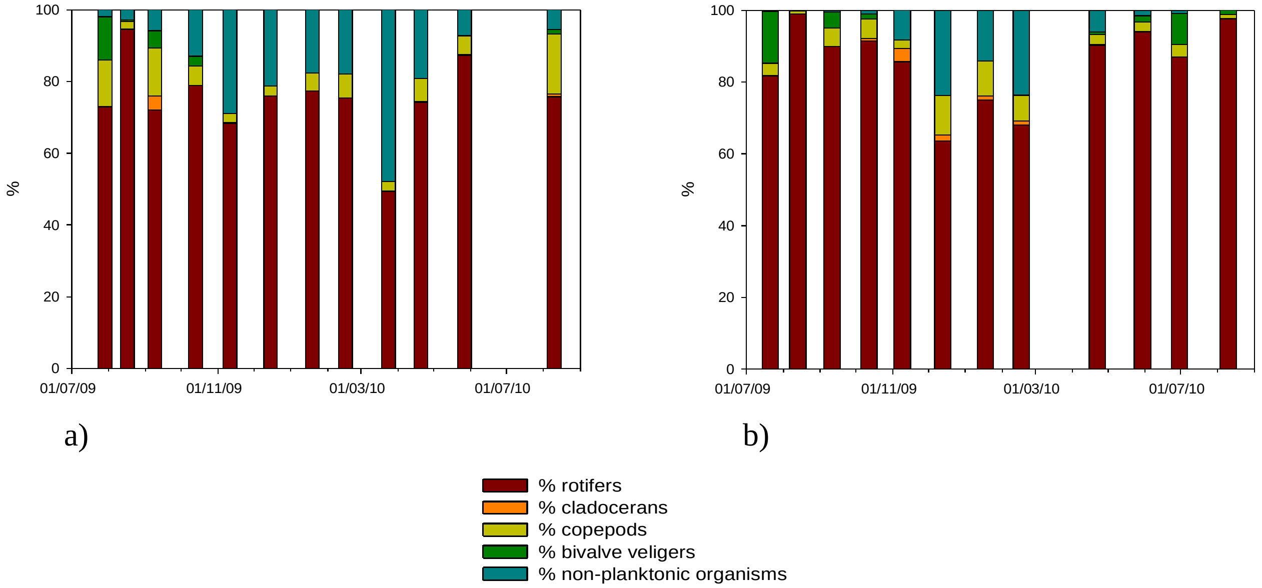


Fig. 3.1.33 - Total zooplankton abundance recorded at the stations of Mortizza and Serravalle in the period July 2009 - August 2010.



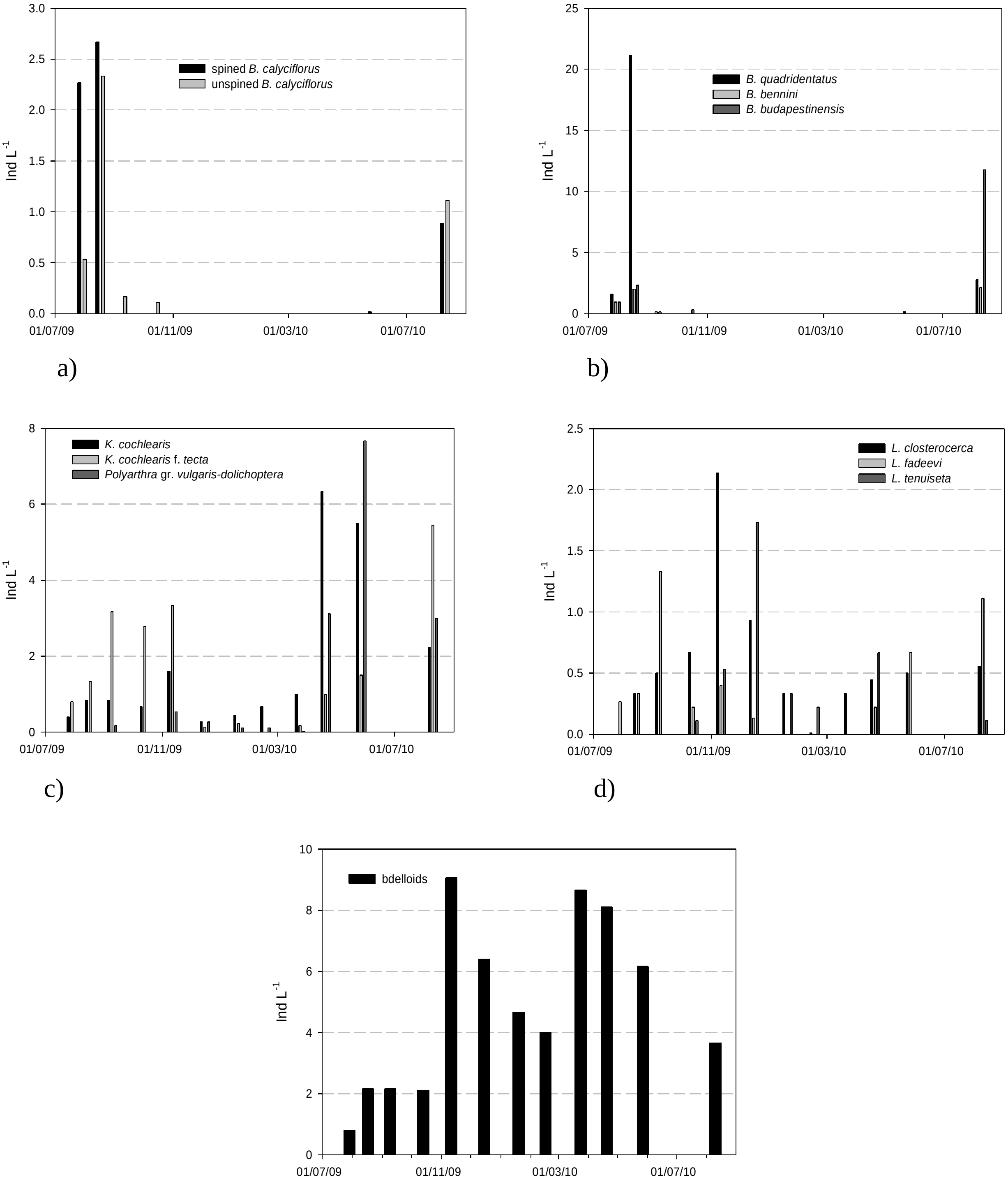
a) b)

Fig. 3.1.34 - Total rotifer (left axis), cladoceran (right axis) and copepod (right axis) density measured at the stations of Mortizza (a) and Serravalle (b) in the period July 2009 - August 2010.



a) b)

Fig. 3.1.35 - Percentage composition of the metazoan assemblage found at the stations of Mortizza (a) and Serravalle (b) in the period July 2009 - August 2010.



a)

b)

c)

d)

e)

Fig. 3.1.36 - Density of some rotifer taxa found at the station of Mortizza: spined and unspined *Brachionus calyciflorus* (a), *B. quadridentatus*, *B. bennini* and *B. budapestinensis* (b), *Keratella cochlearis*, *K. cochlearis* f. *tecta* and *Polyarthra* gr. *vulgaris-dolichoptera* (c), *Lecane closterocerca*, *L. fadeevi* and *L. tenuiseta* (d) and bdelloids (e).

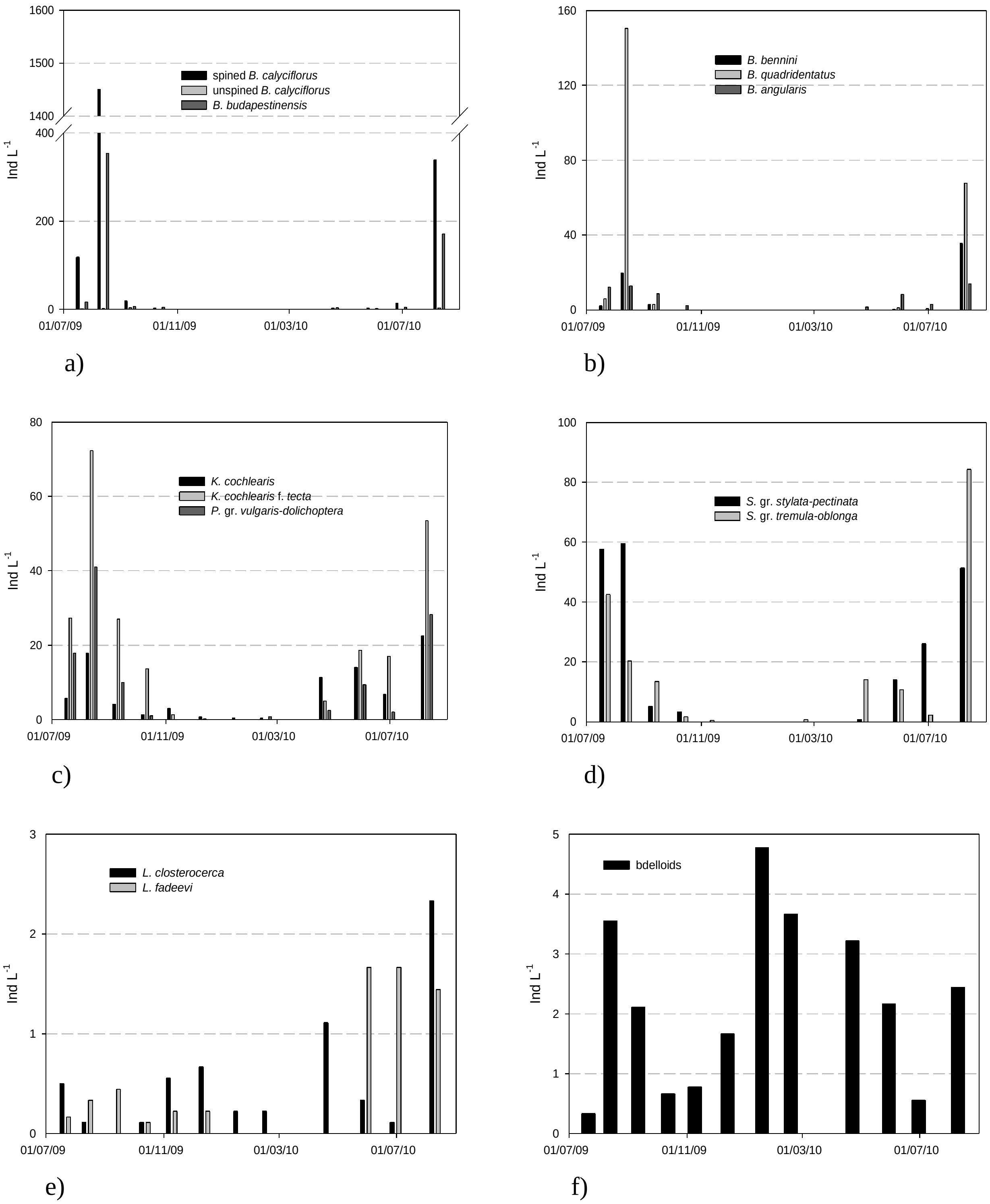
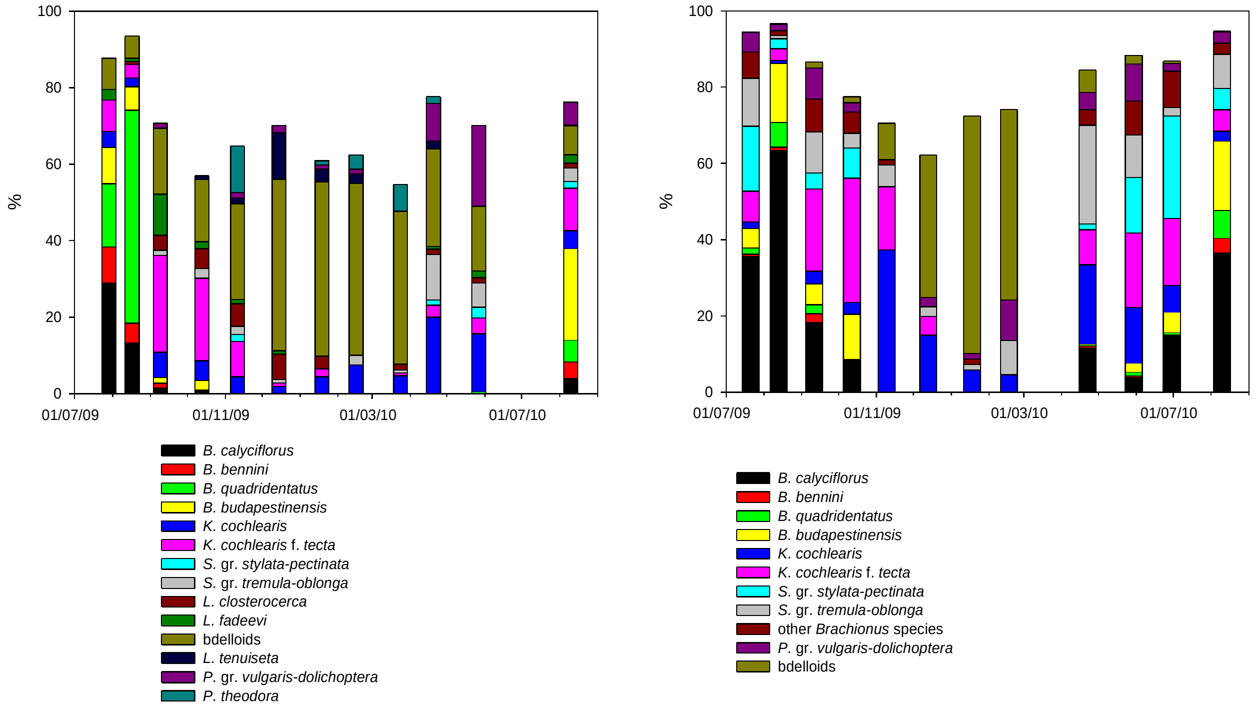
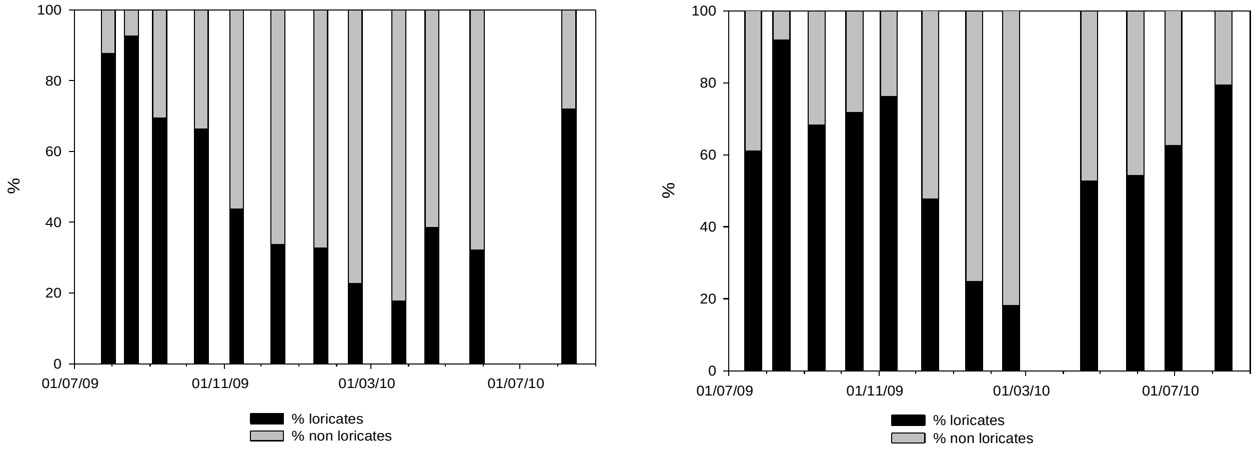


Fig. 3.1.37 - Density of some rotifer taxa found at the station of Serravalle: spined and unspined *Brachionus calyciflorus* and *B. budapestinensis* (a), *B. bennini*, *B. quadridentatus* and *B. angularis* (b), *Keratella cochlearis*, *K. cochlearis* f. *tecta* and *Polyarthra* gr. *vulgaris-dolichoptera* (c), *Synchaeta* gr. *stylata-pectinata* and *S.* gr. *tremula-oblonga* (d), *Lecane closterocerca* and *L. fadeevi* (e) and bdelloids (f).



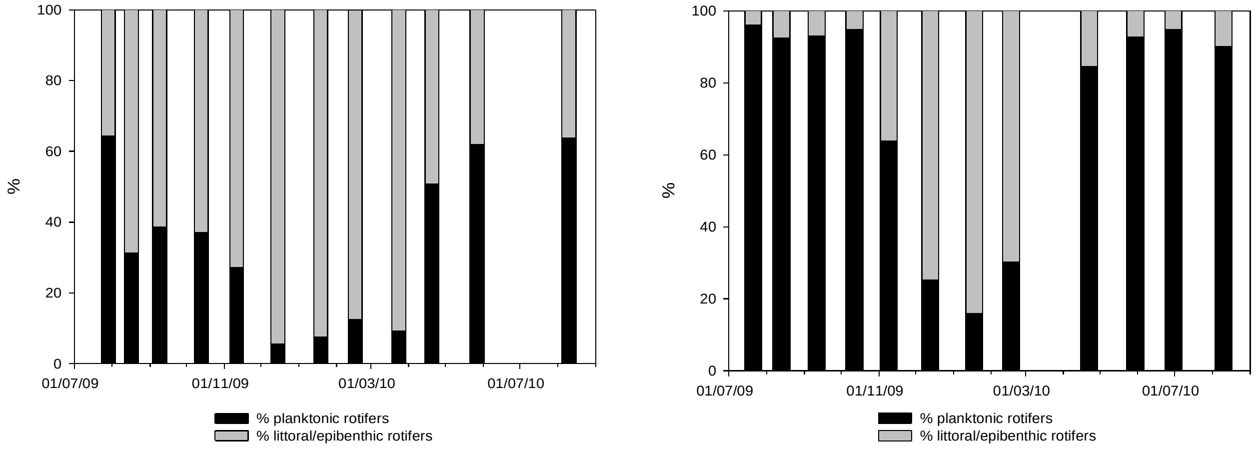
a) b)

Fig. 3.1.38 - Percentage composition of the rotifer assemblage in terms of the most abundant taxa found at the stations of Mortizza (a) and Serravalle (b).



a) b)

Fig. 3.1.39 - Percentage composition of the rotifer assemblage in terms of loricate and illoricate taxa at the stations of Mortizza (a) and Serravalle (b).



a) b)

Fig. 3.1.40 - Percentage composition of the rotifer assemblage in terms of planktonic and littoral/epibenthic taxa at the stations of Mortizza (a) and Serravalle (b).

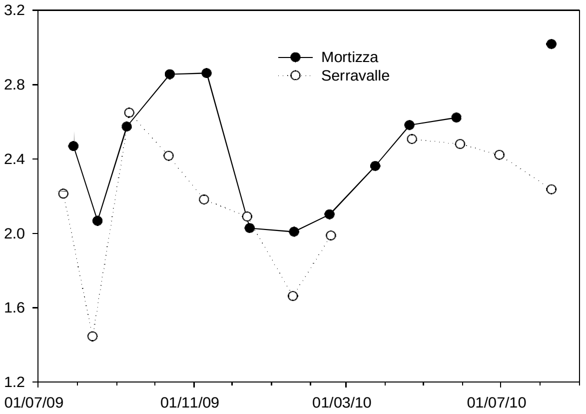
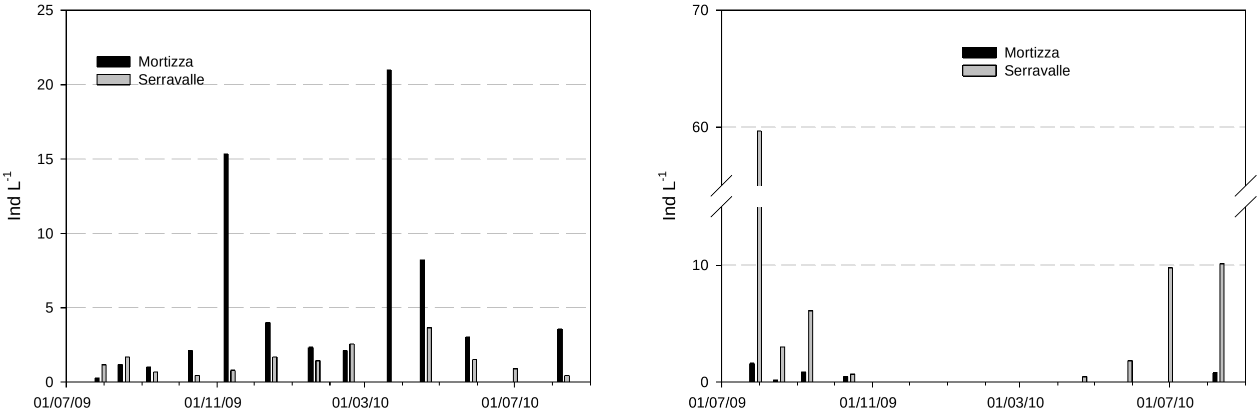


Fig. 3.1.41 - Shannon Diversity Index calculated for the rotifer assemblage at the stations of Mortizza and Serravalle.



a) b)

Fig. 3.1.42 - Density of non-planktonic organisms (a) and bivalve veligers (b) recorded at the stations of Mortizza and Serravalle.

3.1.4 Discussion and Conclusions

Viadana

The two studied years showed remarkable differences in the hydrological regime, with the typical spring flood delayed by one month in 2008 compared to the following year, so that by mid-July 2008 river flow was still as high as 2000 $m^3 s^{-1}$. A clear seasonality was observed for some variables like temperature and chlorophyll-*a* content, the latter being also influenced by the discharge rate, as it is suggested by the peaks occurring only during summer low flow levels (see below). Other variables that revealed a strong dependence on the hydrological regime were conductivity and suspended particulate matter. Flood events generally brought about a dilution effect that resulted in a significant decrease in conductivity (Fig. 3.1.5b). The correlation of this variable to alkalinity also suggests that conductivity was substantially affected by carbonate weathering (Fig. 3.1.6b).

The increase in SPM with river flow (Fig. 3.1.11a) is due to runoff and sediment resuspension typically associated with floods (Naldi et al., 2010). Exceptionally high SPM values, like the one measured during the April 2009 flood event, have occasionally been recorded also in previous studies carried out in the potamal reach of the river (loc. cit.).

Frequent oxygen undersaturation conditions are probably caused by decomposition of large loads of organic matter. Nevertheless, during summer low water phases these processes seem to be offset by phytoplankton primary production, as shown by oxygen oversaturation and high pH values associated with chlorophyll-*a* peaks (Figs. 3.1.4b, 3.1.7b and 3.1.11b).

High inorganic nutrient levels are mainly attributable to intensive agricultural activities in the watershed (AdBPo, 2006). In particular, nitrate and ammonium concentrations are comparable to those recorded in other European large lowland rivers with an heavily human-impacted watershed (Rhine: Ietswaart et al., 1999; Meuse: Gosselain et al., 1998; Loire: Lair et al., 1999; Elbe: Deutsch et al., 2009).

Floods tend to exert a dilution effect on inorganic nutrients, with a consequent drop in nitrate concentrations, while the slight decreasing trend in nitrates and especially ammonium observed during summer might be partly due to assimilation by phytoplankton (Figs. 3.1.8a and 3.1.9a). Nutrient control potential by phytoplankton is far more evident when looking at the temporal patterns of SRP and DRSi. Concentrations of both nutrients showed in fact marked drops during summer algal blooms, which were dominated by diatoms (Tavernini et al., 2011).

The DRSi levels measured in 2008 were higher than those reported for other European rivers (Rhine: Admiraal et al., 1994; Meuse: Gosselain et al., 1998; Elbe: Deutsch et al., 2009), while in 2009 concentrations were substantially lower and comparable to those recorded in the aforementioned studies.

On the contrary, SRP values and Chl-*a* summer peaks were somewhat lower than those measured in other large European watercourses (Loire: Lair & Reyes-Marchant, 1997; Rhine: Admiraal et al., 1994; Danube: Bothár & Kiss, 1990).

As previously mentioned, these western-central Europe large lowland rivers are comparable to the Po in terms of anthropogenic pressures on the watershed, and they also share a similar flow regime, which is generally characterized by high flow rates in winter and spring, and low discharge levels during summer (cf. Kristensen & Hansen, 1994).

Completely different features are displayed by European rivers with a typical Alpine flow regime, like the Adige (second longest river in Italy), where high flow rates are recorded in spring and summer, while low water phases usually occur in autumn and winter (Salmaso & Zignin, 2010). Despite being artificially regulated by several dams and affected by water withdrawals for drinking and irrigation purposes, the impact of agricultural activities in the Adige watershed is less marked when compared to the Po, resulting in much lower concentrations of inorganic nutrients (Salmaso & Braioni, 2008; Salmaso & Zignin, 2010). Nevertheless, it was demonstrated that nutrient levels in the Adige are not sufficiently low to represent a limiting factor for algal growth, physical constraints related to the hydrological regime being the main cause for the relatively low phytoplankton abundances found in this river (loc. cit.). Bottom-up limitation is therefore even less likely to occur in the Po, where inorganic nutrients reach extremely higher concentrations. In fact, even though nutrient levels were rather high throughout the years, chlorophyll-*a* maxima were recorded only during summer low-flow, high-temperature conditions, suggesting that constraints related to hydrology and seasonality are the main factors influencing phytoplankton development.

As for the metazoan plankton assemblage, rotifers represented the dominant group in terms of abundance, thanks to their fast generation times, as it is usually the case in rivers (Lair, 2006).

The density peak recorded in August 2009 was well below summer maxima reported by previous studies carried out in the same river trait (Ferrari & Mazzoni, 1989: > 6600 ind L^{-1}; Ferrari et al., 1989: > 2400 ind L^{-1}; Ferrari et al., 2006: > 1100 ind L^{-1}; Rossetti et al., 2009: > 1100 ind L^{-1}).

Zooplankton abundance and biomass was found to be positively related to water residence time, temperature and chlorophyll-*a* concentration in many large rivers around the world (Saunders & Lewis, 1988a; Thorp et al., 1994; van Dijk & van Zanten, 1995; Basu & Pick, 1996). These findings were also confirmed by a survey carried out in the years 2000-2002 in the potamal stretch of the Po River (Rossetti et al., 2009) as well as by results of the present study for the year 2009. On the other hand in 2008, when no summer increase in zooplankton was detected, moderate floods were followed by an increment of the community, probably due to drift, resuspension of organisms from the river bottom and/or inocula of new individuals from adjacent water bodies. The occurrence of such phenomena is further supported by the positive relationship between river flow and the abundance of non-planktonic/benthic organisms in the water column. These processes were probably sufficient to compensate for the loss of the scarce resident assemblage as a result of flushing and dilution, thereby determining a net positive variation of zooplankton density with river discharge (Fig. 3.1.19). This positive effect was apparently not detectable in 2009, when the community reached much higher abundances during summer low-flow conditions and a negative relationship between discharge and density emerged (Fig. 3.1.19).

The causes of the very limited zooplankton development in summer 2008 are difficult to disentangle, due to the multitude of factors potentially involved. The relatively high discharge values recorded until mid-July are likely to have played a role in limiting zooplankton growth. On the other hand, the high chlorophyll-*a* concentrations detected in July indicate that hydrology did not affect algal development. This may however be explained by the generally faster growth rates of phytoplankton in comparison to zooplankton, which allow algae to grow even under hydrological conditions that are too severe for metazoans (Basu & Pick, 1996).

No significant differences in the taxonomic composition of the community were found with respect to previous studies carried out in the same river reach (e.g. Rossetti et al., 2009), confirming the extremely high biodiversity that often characterizes zooplankton assemblages in large lowland rivers (Lair, 2006). Fluctuations in the hydrological regime seemed to act as a disturbance factor, promoting diversity via inhibition of competitive exclusion exerted by the dominant taxa under low-flow conditions. This positive effect occurs up to a “catastrophic” threshold, over which destructive processes on the community prevail (Fig. 3.1.27b), in agreement with the Intermediate Disturbance Hypothesis (Connell, 1978). Accordingly, Fig. 3.1.24 shows how the summer 2009 zooplankton peak was mainly sustained by two rotifer species of the genus *Brachionus*, which made up over 60% of the rotifer assemblage in terms of abundance. Community equitability dropped as a consequence. On the contrary in 2008, when the hydrological regime was less favourable, dominance by these *Brachionus* species was markedly reduced and community equitability did not show any decreasing trend during summer.

Despite these strong interannual differences in both hydrological regime and zooplankton development, some regular successional patterns mainly related to seasonality emerged. CCA ordination of samples shows how summer samples of both years tend to cluster separately with respect to spring-autumn samples (Fig. 3.1.32). In particular, spring-autumn conditions are generally characterized by moderate to high discharge rates, low temperatures and Chl-*a* concentrations as well as high inorganic nutrient levels. Some rotifer taxa appear to be favoured under these conditions, such as *Proales theodora, Notholca* gr. *acuminata-labis, Hexarthra fennica* and *Kellicottia longispina.* These are the taxa that typically constitute the rotifer community at its early stages of development, that is in the beginning of the growing season. With the onset of summer low-flow conditions, high water temperatures and phytoplankton blooms, brachionid rotifers increase their abundances and tend to dominate the community. Finally, other taxa seem to be less related to environmental conditions and do not show any clearly regular pattern of occurrence in the river (Fig. 3.1.31).

To sum up, results of the present study confirmed the key role of seasonality, hydrological regime, trophic conditions and their interactions in regulating the development of riverine zooplankton. In particular, the comparison of two hydrologically rather different years suggested how the uncoupling between seasonality and hydrology can significantly influence abundance, diversity and temporal patterns of the zooplankton community. Despite favourable conditions in terms of temperature and food resources, hydrological regime may still severely limit plankton growth. Nevertheless, the widely accepted assumption of a negative impact of flow increases on zooplankton abundance was partly contraddicted by results of this study. The net effect of discharge fluctuations depends in fact on the interplay of antagonist processes like flushing/dilution of the resident community vs. enrichment due to resuspension and recruitment of organisms from lentic areas. In this respect, the degree of connectivity to adjacent floodplain habitats might also play a crucial role in influencing composition and abundance of riverine plankton, especially during floods. Finally, in spite of the commonly held view that lotic environments are intrinsically unstable, the zooplankton community clearly showed some regular successional patterns and a remarkable resilience even after extreme hydrological events.

Mortizza and Serravalle

A comparison of results obtained at Viadana with those from the additional survey carried out at the stations of Mortizza and Serravalle provided insight on the spatial heterogeneity of the zooplankton assemblage along the river longitudinal dimension.

In autumn and winter comparable zooplankton abundances were recorded at all stations, with a marked dominance of bdelloid rotifers. On the contrary, in summer months a progressive downstream increase in community density was observed, as it is often reported in the potamal reach of lowland rivers (Zimmermann-Timm et al., 2007; de Ruyter van Steveninck et al., 1992).

The most upstream station of Mortizza was generally characterized by a much higher share of littoral/epibenthic rotifer taxa and by a higher diversity in summer, as a result of the faster current speed and higher turbulence in comparison to the downstream stations. Moreover, zooplankton abundance remained quite low throughout the year and it did not seem to be influenced by water temperature or chlorophyll-*a* content. On the other hand, these variables were significantly related to zooplankton density at the downstream stations, where a clear effect of seasonality in the temporal development of the community was detected.

A shift in the relative importance of hydrodynamic forcings and seasonality/trophic conditions as major drivers of zooplankton development occurred thus in the downstream direction, together with a gradual increase in the degree of predictability of community dynamics.

In this view, despite the continuum provided by downstream transport, during summer low-flow conditions upstream and downstream riverine assemblages may be relatively uncoupled with respect to the type of constraints that regulate them and their overall “functioning”. In fact, while the upstream assemblage shared the features of a mere aggregation of organisms mainly transported to the water column from other habitats, a downstream change towards a true planktonic community was evident.

Reynolds (2000) formulated the hypothesis that the linkage between upstream and downstream plankton populations may be rather indirect, so that the plankton observed in the river may have different characters determined by local hydroecological features. Furthermore, Thorp et al. (1994) drew attention on the still debated topic whether potamoplankton assemblages constitute independent, reproducing communities, or they are merely assortments of transient organisms. The results of the present survey, together with those reported in the following chapters, suggest that the answer to this question might not be univocal and it might change along the temporal as well as the spatial dimension of the river system.

3.2 Do biotic interactions within the zooplankton influence community structure in rivers?

3.2.1 Introduction

The ecology of zooplankton communities in rivers has been the focus of an increasing number of studies in the last decades (Lair, 2006). Nevertheless, the vast majority of such investigations have addressed the influence of abiotic constraints, while a comparatively much smaller amount of research has dealt with biotic interactions, which are generally thought to play a minor role in the main channel of rivers (Pace et al., 1992; Basu & Pick, 1996; Reckendorfer et al., 1999; Baranyi et al., 2002). This was actually found to be the case in many large rivers, where abiotic factors like water temperature, hydrological regime and current velocity (Saunders & Lewis, 1988a; Thorp et al., 1994; van Dijk & van Zanten, 1995; Dickerson et al., 2010), presence of discontinuities along the river course (Welker & Walz, 1999; Havel et al., 2009), availability of inshore retention zones (Reckendorfer et al., 1999; Schiemer et al., 2001; Casper & Thorp, 2007) and connectivity with the adjacent floodplain (Aoyagui & Bonecker, 2004; Wahl et al., 2008) were shown to be key drivers of zooplankton dynamics (see Chapters 3.1, 4 and 5 for further details). Most of these surveys, though, rely on fortnightly or monthly sampling frequencies, which are too low to detect the outcome of potential interactions among organisms with high growth rates like rotifers, that usually represent the dominant component of metazoan plankton in rivers, both in terms of density and biomass (Lair, 2006; Vadadi-Fülöp et al., 2010). In many of these field investigations, the analysis of biological interactions is thus limited to relations between zooplankton and phytoplankton/protozooplankton abundance and composition over time (Lair & Reyes-Marchant, 1997; Kobayashi et al., 1998; Kim & Joo, 2000; Lair, 2005; Bergfeld et al., 2009).

On the other hand, among the relatively fewer works specifically dealing with the role of biotic factors in structuring riverine zooplankton communities, most of the research has focussed on the impact of planktivorous fish and benthic bivalves on plankton assemblages or on the grazing potential of zooplankton. These studies were carried out both by means of field surveys (Basu & Pick, 1997; Welker & Walz, 1998; Chang et al., 2008; Pace et al., 2010) and *ex-situ* or *in-situ* experiments (Gosselain et al., 1998a & b; Ietswaart et al., 1999; Jack & Thorp, 2000 & 2002; Kim et al., 2000; Thorp & Casper, 2003; Joaquim-Justo et al., 2006; Ning et al., 2010; Davis & Gobler, 2011). On the contrary, few studies have investigated the significance of biotic interactions within the zooplankton community itself (De Leo & Ferrari, 1993; Lair et al., 1999; Guelda et al., 2005). Furthermore, surveys on biological constraints are generally carried out in river slackwaters or retention zones with increased water residence time and typically very low or null current compared to the main channel (Ferrari et al., 1984; Pollard et al., 1998; Baranyi et al., 2002), which makes these habitats more similar to lentic than lotic environments. Similarly, experimental studies are mainly based on *in-situ* enclosures, which inevitably impair or alter the effect of natural river hydrology.

Although the importance of these investigation approaches in understanding the ecology of river communities is indisputable, the intrinsic difficulties in simulating lotic conditions should lead to substantial caution in extending results to what actually happens in main river channels. This is especially true for planktonic organisms, whose feeding activities, growth rates and ultimately competitive interactions proved to be significantly affected by turbulence and turbidity (Miquelis et al., 1998; Sluss et al., 2008).

This lack of knowledge on the role of biotic interactions within lotic zooplankton traditionally led to considering it as an assemblage of taxa subjected to downstream transport and solely driven by external abiotic forces, therefore lacking internal, self-regulating properties of a true community in its strict sense, contrary to what has been acknowledged in lentic systems (Agustì et al., 1990; Pahl-Wostl, 2004; Roy, 2009). As a result, the actual influence of biological control on community dynamics might be underestimated, ultimately leading to an incomplete understanding of the functioning of lotic systems.

The main goal of this study is therefore to assess whether biotic interactions among metazooplankton are crucial drivers of community structure even under conditions of turbulence and turbidity that are naturally found in the main channel of rivers. To answer this question, a short-term, high frequency sampling campaign was carried out during summer 2005 in the potamal reach of the Po River. Previous surveys in the same area (Ferrari & Mazzoni, 1989; Ferrari et al., 1989) postulated the importance of biotic interactions as a driver of community dynamics based on data analysis by means of Caswell's neutral model (De Leo & Ferrari, 1993), but no further investigation was undertaken, especially on the nature of the biological processes involved. Following an approach that has been successfully adopted in studies dealing with compensatory dynamics in plankton communities (Klug et al., 2000; Fischer et al., 2001), a variance ratio test (Schluter, 1984; Frost et al., 1995) was applied to the time series of zooplankton abundances to detect negative or positive temporal associations among individual species or functional groups. Whenever association patterns which may be indicative of biotic interactions were found, time series were further analysed by means of first order multivariate autoregressive models, in order to quantify potential interactions among species (or groups of species) and describe the biological processes that might be responsible for the observed patterns. Additionally, a specific case of predator-prey interaction, involving the most abundant predator and the dominant filter-feeder in the assemblage, was investigated in further detail, to assess its influence on community structure and dynamics.

3.2.2 Materials and methods

3.2.2.1 Field sampling

Sampling was carried out at the station of Viadana (see Chapter 3.2.1.2).

A total of 27 zooplankton samples were collected from July 16 to September 3 2005 from a floating pontoon that enabled to reach the main current flow in the river channel. Sampling frequency ranged between 1-4 days, with the exception of the last but one sample, that was collected 6 days after the previous one. Samples were taken by throwing a 15-L bucket into the main channel and passing the water through a 50 μm net until 60 L were filtered. Preservation in 4% buffered formalin followed immediately.

Surface water temperature was measured by means of a thermistor (Delta Ohm, HD 9215) and water samples for chlorophyll-*a* determination were collected on four occasions (August 2, 9, 16 and 25). Daily data on river discharge, recorded at a gauging station approximately 2 km downstream of the sampling site, were provided by the Environmental Agency of the Emilia Romagna Region. The latter also made a long-term dataset available (1970-2008) of current velocity measurements performed at the same station, which were plotted against the relative discharge values in order to derive the mean current speed corresponding to the flow levels observed during the survey.

3.2.2.2 Laboratory analyses

Chlorophyll-*a* concentration was determined following the spectrophotometric method reported by A.P.H.A. (1998). Zooplankton samples were analysed as explained in Chapter 3.1.2.1.

The dominant rotifer taxon, *Brachionus calyciflorus*, was present in the river with two morphotypes, one with a pair of posterolateral spines (hereafter referred to as “spined” *B. calyciflorus*) and one lacking those spines (referred to as “unspined” *B. calyciflorus*).

Whenever present in sufficient numbers, morphometric measurements of 30 randomly selected adult individuals of spined and unspined *B. calyciflorus* were carried out.

Since ovigerous females were generally rare due to detachment of eggs from the rotifers caused by formalin fixation, a criterion had to be adopted to discriminate adult from immature rotifers. Individuals were therefore designated as adults if they were larger than the smallest ovigerous female found in that sampling date or in the closest one.

For each individual, body length (BL) as well as the lengths of the anterolateral (AL) and posterolateral (PL) spines, these latter in the case of the spined morph, were measured with a calibrated ocular micrometer at a 400x magnification, according to Gilbert (1967). Whenever a female carrying parthenogenetic eggs was found, egg length (EL) was also measured.

Brachionus calyciflorus diploid subitaneous eggs, haploid male eggs and resting eggs were also counted. Since ovigerous females were rare (see above), the number of each type of egg found loose in sub-samples was recorded until at least 100 had been counted. The sample collected on August 9 was not well preserved at the time of the morphometric and egg analysis and had thus to be discarded. Shape and size of *B. calyciflorus* diploid subitaneous and resting eggs allowed to easily distinguish them from the eggs of other *Brachionus* species present in the community, except from the ones produced by *Brachionus quadridentatus*, which are very similar. Therefore, the densities of diploid subitaneous and resting eggs belonging to *B. calyciflorus* or to *B. quadridentatus* were estimated to be proportional to the abundance of the two species on each date, i.e. assuming a similar reproductive effort. The same calculations were applied to estimate the densities of *B. calyciflorus* haploid male eggs, as it was impossible to unequivocally distinguish them from *B. quadridentatus* male eggs as well as from parthenogenetic eggs of *B. bennini*, *B. angularis* and *B. budapestinensis.* Egg ratio (number of eggs per female) was calculated for each type of egg as the ratio of egg density to the total density of the taxa having similar eggs.

Whenever present in sufficient numbers, stomach content analysis of 20-30 randomly selected females of the predatory rotifer *Asplanchna brightwellii* was performed by dissolving the rotifer's tissues with sodium hypochlorite under an optical microscope in order to extract the food items. Eaten prey were identified to the lowest possible taxonomic level and counted. Algal cells were also enumerated but no taxonomic analysis was undertaken. A similar analysis was not performed on *A. priodonta* because its predatory impact was assumed to be negligible, both because of the extremely low densities and the less predacious nature of its diet (Chang et al., 2010).

3.2.2.3 Relationships between community abundance/equitability and river discharge

Community density data were log-transformed and linear regression analysis between density and mean daily river discharge was performed for the whole sampling period as well as on two separate phases, before (July 16 – August 4) and after (August 6 – September 3) a sudden, short-lasting increase in river discharge, hereafter referred to as “pre-peak” and “post-peak” phase, respectively.

Equitability was calculated as the Shannon Equitability Index (Shannon Diversity divided by the natural logarithm of the number of taxa). As for the relationship between discharge and community equitability, a quadratic function of the form $y = a + b*x + c*x^2$ was fitted to untransformed data in the post-peak phase and the Mitchell-Olds and Shaw’s test (MOS test; Mitchell-Olds & Shaw, 1987) was performed to assess whether the maximum equitability value fell within the observed range of discharge values. Analyses were performed using the *vegan* package (Oksanen et al., 2011) in R (R Development Core Team, 2005).

3.2.2.4 Functional groups

In order to explore potential trophic interactions such as predation and competition within the community, zooplankton taxa were combined into functional groups with similar feeding ecology based on their body and feeding apparatus size and morphology (Table 3.2.1). Following a recently proposed classification of rotifers into feeding guilds (Obertegger et al., 2010), two groups were firstly created, one for species with malleate, malleoramate or ramate trophi (microphagous) and one for species with virgate trophi (raptorials). Since the microphagous group contained a very wide range of body sizes, and food size preferences are often related to body size even within genera (Rothhaupt, 1990), it was further divided into three groups (large, medium and small) according to rotifer body size. A fifth group included only two species of the polyphagous genus *Asplanchna*, namely *A. priodonta* and *A. brightwellii*, with the latter making up 80 to 100% of the whole group density in the pre-peak phase. Microcrustaceans were discarded from the analysis because of their low densities during most of the sampling period, as it is often the case in rivers. An exception was made for cyclopoid nauplii, which reached relatively high densities and were thus assigned to the medium size group because of their dimensional range and feeding ecology (Böttjer et al., 2010).

Table 3.2.1 – Zooplankton taxa assigned to five functional groups according to their feeding strategies and body size, following the classification proposed by Obertegger et al. (2010).

Functional group	Component taxa
1 – Malleate trophi, large body size	*Brachionus bennini; Brachionus bidentatus; Brachionus calyciflorus; Brachionus diversicornis; Brachionus falcatus; Brachionus quadridentatus; Brachionus leydigii; Plationus patulus; Euchlanis* gr. *dilatata-parva*
2 – Malleate, malleoramate and ramate trophi, medium body size + cyclopoid nauplii	*Brachionus angularis; Brachionus budapestinensis; Brachionus forficula; Lophocharis salpina; Trichotria pocillum; Trichotria tetractis;* unidentified Bdelloidea; unidentified Flosculariidae; cyclopoid nauplii
3 – Malleate trophi, small body size	*Anuraeopsis fissa; Colurella* spp.*; Filinia cornuta* f. *brachiata; Filinia* gr. *longiseta-terminalis; Filinia opoliensis; Hexarthra mira; Keratella cochlearis; Keratella cochlearis* f. *tecta; Keratella* gr. *quadrata; Keratella tropica; Lecane bulla; Lecane fadeevi; Lecane hamata; Lecane luna; Lecane* gr. *lunaris; Lecane quadridentata; Lecane papuana; Lepadella patella; Pompholyx sulcata*
4 – Virgate trophi, raptorials	*Cephalodella gibba; Gastropus stylifer; Polyarthra* spp.*; Synchaeta* spp.*; Trichocerca bicristata; Trichocerca elongata; Trichocerca porcellus; Trichocerca pusilla; Trichocerca similis; Trichocerca* sp.
5 – Incudate trophi, carnivorous (*Asplanchna* spp.)	*Asplanchna brigthwellii; Asplanchna priodonta*

3.2.2.5 Patterns of covariance within and among functional groups

Biotic interactions like predation or competition may result in positive or negative associations among temporal patterns of species abundances (Schluter, 1984). For example, the decline of a species may be followed by the increase of a weaker competitor after release from competition, so that the two species show negatively covarying abundance fluctuations. In order to test for the presence of positive or negative associations within and among functional groups, a variance ratio test was applied, defined as the ratio of the temporal variance of total species abundance to the sum of the variances of individual species (Schluter, 1984; Frost et al., 1995). A variance ratio <1 results when species covary negatively, while a ratio >1 denotes positive covariance among species. When species fluctuate independently the variance ratio is ~1. This technique has been used to detect compensatory dynamics within communities in previous studies (Klug et al., 2000; Fischer et al., 2001; Vinebrooke et al., 2003), to which I also refer for a more extensive account of its statistical properties. It is important to note that the variance ratio only tests for the existence of patterns of positive or negative covariance among species (or groups of species), which may be indicative of biotic interactions, but it does not provide evidence of the actual occurrence of such interactions. The variance ratio was calculated both within and among functional groups for the whole sampling period, as well as for the pre- and post-peak phase separately. Data were untransformed prior to calculations. Statistical significance of the variance ratio was assessed by means of a boostrap method (phase scrambling) which accounts for temporal autocorrelation within the time series of species abundances (Solow & Duplisea, 2007). For each species in a functional group, 1000 random time series were generated according to the expression provided by Solow & Duplisea (2007). The corresponding 1000 within-group variance ratios were calculated, in order to create a distribution of ratios under the null hypothesis of independently fluctuating species abundances. The significance level of the observed variance ratio for that group was then assigned as the proportion of values in the distribution created that were less (in case of negative covariance) or greater (in case of positive covariance) than it. In case of among-group variance ratios, the whole functional groups instead of the individual species were used to generate the random time series. Analyses were performed using R (R Development Core Team, 2005).

3.2.2.6 Multivariate autoregressive models

Since I was interested in potential competitive or predatory interactions in the community, in cases where a variance ratio less than 1 was obtained, which may indicate negative biotic interactions, first order vector autoregressive models (VAR) were applied to describe the processes that might have been responsible for such patterns of negative covariance, following Klug et al. (2000).

Considering n species (or species groups), a first order VAR model is an n-equation linear model that relates the abundance of each species at time t to its abundance, as well as to the abundances of the other n-1 species, at time t-1. Covariates can also be added to the model, so that it assumes the general form:

$$Y_t = A + BY_{t-1} + CV_{t-1} + W_t \qquad (1.1)$$

where Y_t is a n x 1 vector of species abundances at time t, A is a n x 1 vector of constants, B is a n x n matrix whose elements b_{ij} give the effect of species j on the abundance pattern of species i, V_{t-1} is a v x 1 vector containing the values of v covariates at time t-1, C is a n x v matrix whose elements c_{ij} give the effect of covariate j on species i and W_t is a n x 1 vector of process errors that represent unexplained variability (Ives et al., 2003). Autoregression coefficients quantify the mutual effect of two species on their respective abundance fluctuations, therefore providing insights on potential interactions that may affect community dynamics (Beisner et al., 2003).

As a variance ratio <1 was only found among functional groups in the pre-peak phase, a VAR model of the form (1.1) was fitted with the first four functional groups as variates and limiting the time series to the ten sampling dates before the flow peak. The *Asplanchna* group was included in the model as a covariate, because the main focus was on the effects of predation by this rotifer on other groups rather than the reverse. This choice also allowed to decrease the number of parameters to be estimated by the model, which is a relevant issue when dealing with short time series, in order to avoid overparameterisation (Ives et al., 2003). Data were log(x + 1) transformed prior to the analysis. River discharge and water temperature were not included in the model because they remained quite stable in the pre-peak phase and regression analysis showed no significant relationship between any of the two variables and zooplankton density or equitability when only that phase is taken into account.

Autoregressive models require time series to be regularly distributed in time. Nonetheless, samples were treated as evenly spaced in time since differences in sampling frequency remained well within the time scale of rotifer development times (e. g., Fontaine & Gonzalez, 2005; Gillooly, 2000; Guo et al., 2011). No *a priori* constraint was set to the model coefficients, because interactions among all functional groups were biologically plausible. Model parameters were estimated using conditional least squares (CLS) and the 95% confidence intervals for the parameter estimates were obtained by bootstrapping the model (2000 iterations; Ives et al., 2003). Total and conditional R^2 were computed to assess model fit. Analyses were performed in Matlab with the LAMBDA package (Viscido & Holmes, 2010).

3.2.2.7 Statistical analyses on *Brachionus calyciflorus* morphometric data

The Kruskal-Wallis Test and Dunn's Post-Hoc Test for multiple comparisons were used to test for significant differences among the morphometric variables measured on *Brachionus calyciflorus* on different dates. The Mann-Whitney Rank Sum Test was applied to compare the egg length to body length ratio and the number of eggs per female between the two morphotypes. The Spearman Rank Correlation Coefficient (rho) was calculated to explore potential linear relationships between some of the morphometric variables. Analyses were performed using R (R Development Core Team, 2005).

3.2.3 Results

3.2.3.1 Community structure and role of abiotic factors

On July 3 river discharge was 291 m^3 s^{-1}. It then started to increase in the following days, culminating with a maximum of 564 m^3 s^{-1} on July 13, just before the beginning of our survey, during which it ranged between 210 and 1026 m^3 sec^{-1}, with a mid-summer peak of 642 m^3 sec^{-1} at the beginning of August (Fig. 3.2.1). Under the discharge levels observed in the pre- and post-peak phases, current velocity generally ranges between 0.6-0.8 m s^{-1} in this river segment, with values up to 1.1 m s^{-1} during flow maxima. Water temperature varied between 25.1 and 27.4°C in the pre-peak phase, it then dropped to 23.0°C with the aforementioned mid-summer flow peak and stayed around this value until the end of August. Chlorophyll-*a* concentrations measured on August 2, 9, 16 and 25 reached values of 39.2, 80.5, 94.4 and 25.3 µg L^{-1},respectively.

Zooplankton density varied between 41 and 1474 ind L^{-1}, with a marked drop coinciding with the mid-summer flow peak (Fig. 3.2.1). Rotifers made up more than 90% of the total density in most of the samples, with 48 identified taxa (see Annex 1). Species of the genus *Brachionus* were numerically prevailing throughout the sampling period, *B. calyciflorus* being the dominant species (up to 950 ind L^{-1}). Species of the genera *Keratella*, *Lecane*, *Synchaeta*, *Polyarthra*, *Filinia* and *Asplanchna* were also abundant. Twenty-nine microcrustacean taxa were found, but they never exceeded 72 ind L^{-1}, with a clear prevalence of cyclopoid nauplii (up to 53 ind L^{-1}).

Community equitability varied between 0.30 and 0.79, showing increasing trends in both phases, separated by a minimum occurring a few days after the mid-summer discharge peak. Although no relationships were found between community density or equitability and water temperature, a linear negative relationship was found between river discharge and log-transformed zooplankton density during the whole study period ($R^2 = 0.60$, $p < 0.01$). The regression fit improves if only the post-peak phase is taken into account ($R^2 = 0.86$, $p < 0.01$). On the contrary, if only the pre-peak phase is considered, river discharge remained quite stable and showed no significant relationship to zooplankton abundance. Similarly, no distinct pattern emerged between discharge and community equitability if the whole study period or only the pre-peak phase was considered, while in the second phase a hump-shaped relationship was observed, with the quadratic hump falling within the observed discharge interval, as indicated by the MOS test ($p < 0.05$; Fig. 3.2.2).

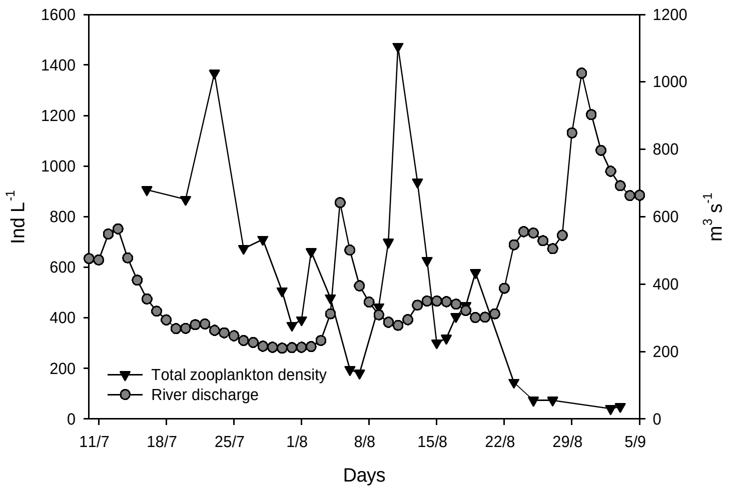


Fig. 3.2.1 - River discharge (right y-axis) and total zooplankton density (left y-axis) in the study period. Pre-peak phase: July 16 – August 4; post-peak phase: August 6 – September 3.

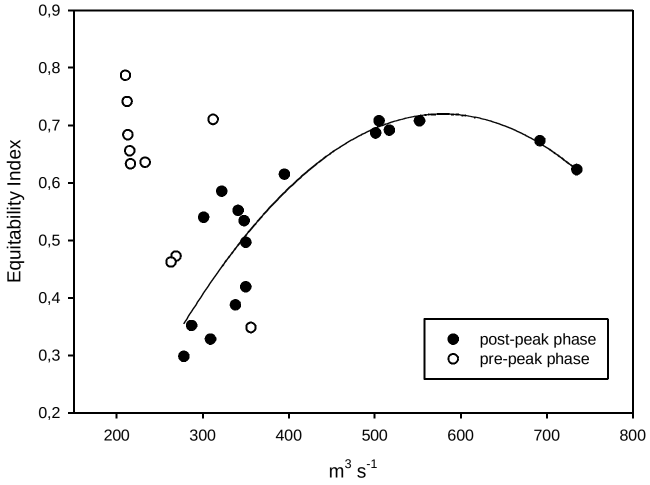


Fig. 3.2.2 – Relationship between community equitability and river discharge (post-peak phase: $R^2 = 0.74$, $p < 0.01$ for both the linear and quadratic term).

3.2.3.2 Role of biotic interactions: variance ratio and multivariate autoregressive analysis applied to zooplankton functional groups

Density trends of the five functional groups are presented in Fig. 3.2.3, while abundances of the dominant taxa within each group are shown in Fig. 3.2.4 (a-e). Within-group variance ratios were either not statistically different from one or greater than one for most of the groups when considering either the whole sampling period or the two discharge phases separately (Table 3.2.2). As for the among-group variance ratios, while the value for the entire period was not significantly different from one, the pre- and post-peak phases showed contrasting situations. In fact, a ratio <1 resulted in the first phase, even though slightly exceeding the significance limit (p = 0.06), while a value >1 was obtained in the second phase. The coefficients of the autoregressive model fitted to the pre-peak time series, with their 95% confidence intervals, are reported in Table 3.2.3, together with total and conditional R^2 values, which ranged between 0.73-0.97 and 0.63-0.93, respectively. All interactions were retained when performing the analysis but only the coefficients significantly different from zero are reported. As for the first four groups, which were included as variates, the model detected a negative effect of group 1 on group 2, while group 2 showed negative effects on both itself and group 3. Positive coefficients were estimated for the influence of group 3 on itself as well as on group 2. The *Asplanchna* group, added to the model as a covariate, had a negative effect on group 1 but a positive influence on group 2.

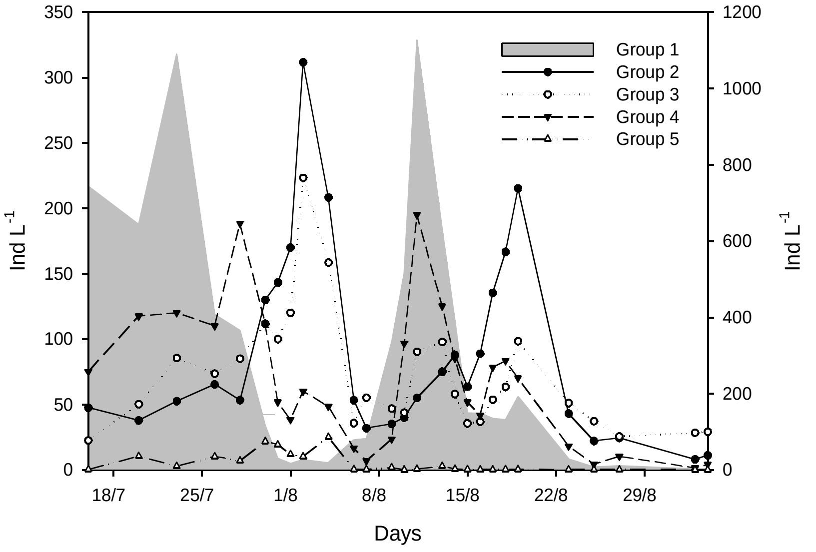
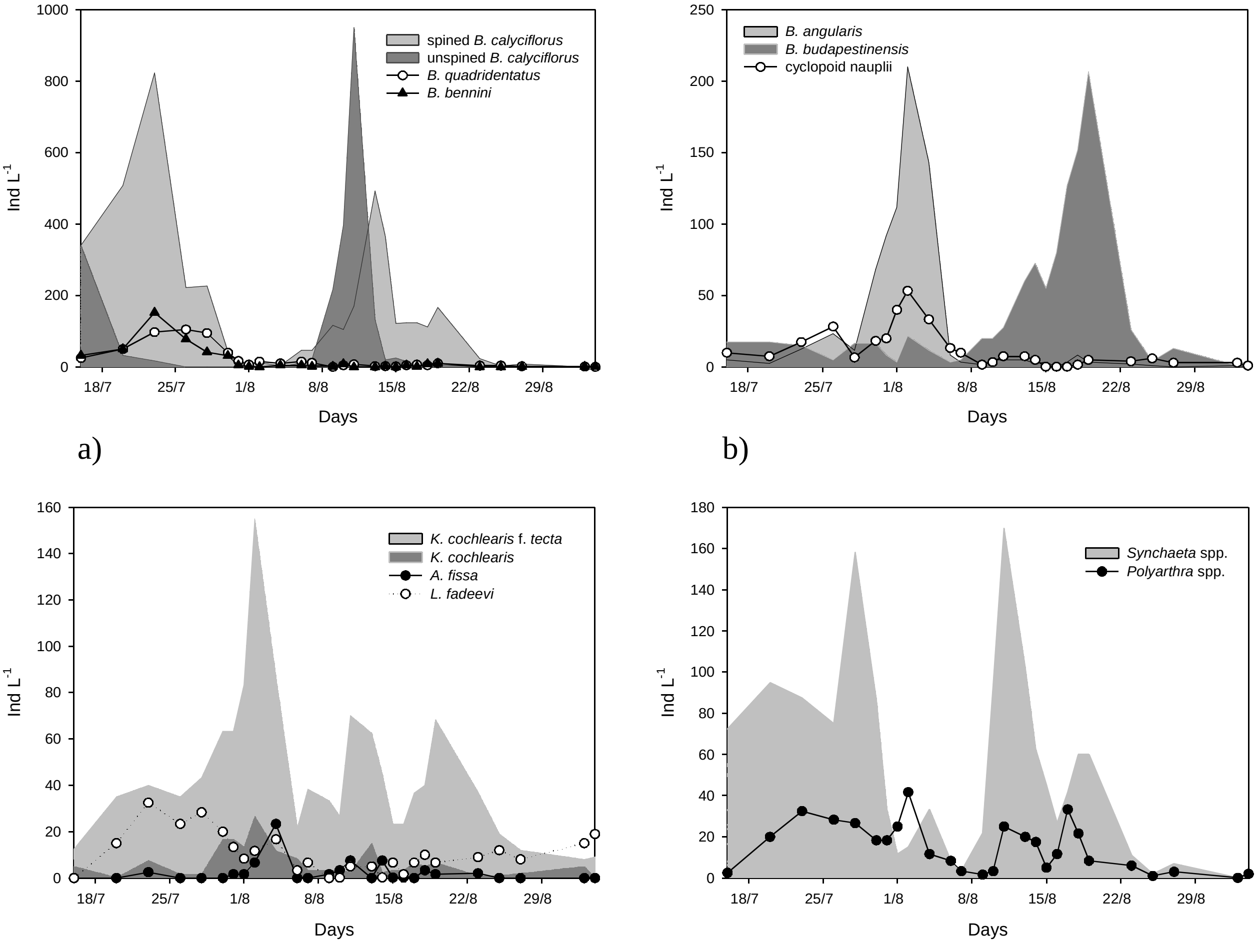


Fig. 3.2.3 - Density patterns of the five functional groups during the study period (Group 1 refers to right y-axis, all other groups to left y-axis).

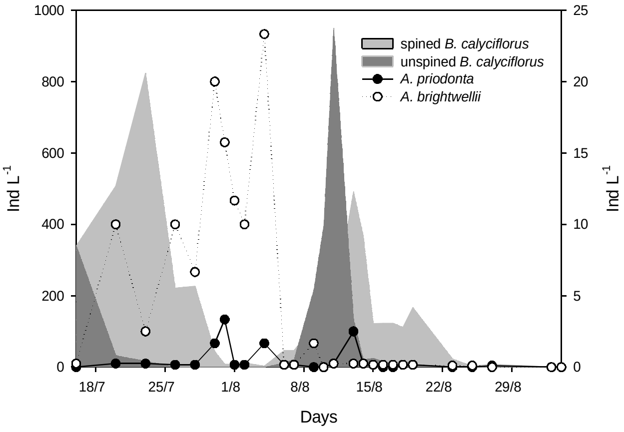


a)

b)

c)

d)



e)

Fig. 3.2.4 - Temporal patterns of the dominant taxa within each of the five functional group (a: Group 1; b: Group 2; c: Group 3; d: Group 4; e: Group 5 with *B. calyciflorus* (left y-axis)).

Table 3.2.2 – Within- and among-group variance ratios calculated for the entire sampling period as well as for the pre-peak (July 16 - August 4) and the post-peak (August 6 – September 3) phase. Asterisk indicates values significantly different from 1 with $p < 0.05$.

Functional groups	Whole period	Pre-peak phase	Post-peak phase
1	1.29	1.58*	1.16
2	0.98	1.50*	0.89
3	1.82*	1.72*	1.27
4	1.23	1.00	1.26*
5	1.14*	1.20*	1.00
Among groups	1.16	0.60	1.49*

Table 3.2.3 - Coefficients of the first-order multivariate autoregressive model fitted to the first four functional groups for the pre-peak phase (July 16 - August 4) and adding the group 5 (*Asplanchna* spp.) as a covariate. Bootstrapped 95% confidence intervals are shown in brackets. Only coefficients whose confidence intervals do not encompass zero are reported. Each coefficient quantifies the effect of the column-group on the corresponding row-group.

	Variates				Covariate		
	Group 1	Group 2	Group 3	Group 4	Group 5	Tot. R^2	Cond. R^2
Group 1					-0.80 (-1.51, -0.11)	0.96	0.84
Group 2	- 0.56 (-0.92, -0.21)	-1.11 (-1.49, -0.68)	0.69 (0.11, 1.27)		0.39 (0.08, 0.66)	0.97	0.92
Group 3		-0.67 (-1.02, -0.28)	0.58 (0.02, 1.07)			0.93	0.93
Group 4						0.73	0.63

3.2.3.3 *Asplanchna brightwellii* and *Brachionus calyciflorus*: population dynamics and predator-prey interactions

The population of *Brachionus calyciflorus* showed a bimodal growth pattern, with two distinct peaks of 840 (July 23) and 1120 (August 11) ind L^{-1} (Fig. 3.2.4a). While on July 16 the population was made up of equal proportions of both morphs, the unspined one rapidly disappeared and the first density peak was completely sustained by spined individuals. After a subsequent period of very low densities, the second peak was largely made up of unspined specimens, whose dominance was very short though and quickly taken over by the spined morph again (Fig. 3.2.4a). Changes in population abundance were consistent with the temporal pattern of egg production. Both diploid and male eggs reached the highest densities during the phases of population growth. In particular, diploid eggs reached maxima of 481 (July 16) and 651 eggs L^{-1} (August 11), while male eggs showed peaks of 374 (July 23) and 341 eggs L^{-1} (August 11). On the contrary, the lowest densities (well below 10 eggs L^{-1} for both types of eggs) were associated with the *B. calyciflorus* decreasing phases. Resting eggs were produced only during the first population decline, with a maximum of 34 eggs L^{-1} on July 26. The number of parthenogenetic diploid eggs per female ranged between 0.24 and 0.74 until August 23, with the lowest values corresponding to the low-density phase between the two population peaks (Fig. 3.2.5). It then sharply increased to values close to 2 by the end of the sampling period, when the whole community showed extremely low abundances. Male egg ratio ranged between 0.05 and 0.68. The resting egg ratio was ~ 0 on most of the dates, with the highest values (up to 0.42) when population abundance was lowest.

The rapid decline of the *B. calyciflorus* unspined morph at the beginning of the survey matched with the appearance of the rotifer *Asplanchna brightwellii*, which reached densities of up to 20 ind L^{-1} in the first part of the study (Fig. 3.2.4e), despite a slight decline associated with the production of males (up to 13 ind L^{-1}). Coinciding with the early August discharge peak, *Asplanchna* abruptly disappeared and was unable to recover thereafter. Considering therefore only the pre-peak phase, when the predator was present, a significant linear negative relationship was found between its densities and the log-transformed densities of *B. calyciflorus* ($R^2 = 0.56$, $p < 0.05$), while community equitability was positively related to *A. brightwellii* abundance ($R^2 = 0.65$, $p < 0.01$). The gut content analysis confirmed that rotifers made up the largest proportion of the predator's diet, with 6 taxa (spined *B. calyciflorus*, *B. bennini*, *B. angularis*, *Synchaeta* spp., *Polyarthra* spp. and *Anuraeopsis fissa*) reaching over 50% of the total prey abundance found in stomachs on each date (Fig. 3.2.6). Their relative proportions in the *Asplanchna* gut contents generally followed the temporal trends of their abundance in the river. In particular, during its dominance phase, spined *B. calyciflorus*, both as developed individuals and parthenogenetic eggs, made up 20 to 40% of the diet, with a mean number of ingested individuals and parthenogenetic eggs per *Asplanchna* ranging between 0.47-0.84 and 0.41-0.67, respectively. Its abundance in the diet gradually decreased as its population declined in the river and *Asplanchna* shifted to other prey which increased their density in the meantime, e.g. *Synchaeta* spp. Other prey occasionally found in the predator's guts were *Trichocerca* spp., *B. quadridentatus*, *B. budapestinensis*, *Cephalodella* spp., *Lecane fadeevi*, *Keratella* spp., bdelloids and cyclopoid nauplii. Cannibalism was also sporadically observed.

As for the morphometric measurements on *B. calyciflorus*, only results of the analyses performed on the left anterolateral and posterolateral spines are reported (from here on denoted as ALsx and PLsx, respectively), since for each specimen no significant differences ever emerged between the lengths of left and right spines.

A clear increasing trend in the mean posterolateral spine length to body length ratio of spined *B. calyciflorus* was observed between July 16 and August 4, with a maximum of 0.47 ± 0.06 on August 2 (Fig. 3.2.7a). After August 4 a marked drop occurred and mean ratio values fluctuated between 0.20 ± 0.10 and 0.28 ± 0.19 for the rest of the sampling campaign. Significant differences were detected among the ratios recorded on the different dates (Kruskal-Wallis Test, $p < 0.01$). In particular, the multiple comparisons revealed that the ratios measured on August 1, 2 and 4 were not statistically different from those recorded between July 26 and 31, but were different from those measured in the first three sampling dates and after August 4 (Dunn's Post-Hoc Test, $p < 0.05$). On the contrary, no differences emerged among ratios measured after August 4, with the exception of one date (August 23). The very same applies to the anterolateral spine length to body length ratio (Fig. 3.2.7b).

An increase in body length of the spined morph was also observed, from a minimum of 189 ± 18 µm (July 16) to a maximum of 252 ± 12 µm (August 2; Fig. 3.2.7c). Once again, after August 4 values rapidly decreased and ranged between 179 ± 18 µm and 199 ± 25 µm. Values measured between July 30 and August 4 were different from those recorded afterwards, which on the contrary did not differ significantly from each other (Kruskal-Wallis Test, $p < 0.01$ and Dunn's Post-Hoc Test, $p < 0.05$).

The mean anterolateral spine length to body length ratio of the unspined morph varied between 0.09 ± 0.03 (August 11) and 0.15 ± 0.04 (August 23; Fig. 3.2.8a). The mean ratio measured on August 11 resulted significantly different from all other values, except from that recorded on August 10 (Kruskal-Wallis Test, $p < 0.01$ and Dunn's Post-Hoc Test, $p < 0.05$). The mean ratios found on August 10 and 15 were different from some of the others (Kruskal-Wallis Test, $p < 0.01$ and Dunn's Post-Hoc Test, $p < 0.05$), but the majority of the recorded values did not differ significantly from each other. Body length of the unspined morphotype varied between 173 ± 9 µm (August 19) and 191 ± 15 µm (July 20; Fig. 3.2.8b). Significant differences among some of the dates were detected but no clear trend emerged (Kruskal-Wallis Test, $p < 0.01$).

A positive linear relationship was found between PLsx/BL and BL for spined *B. calyciflorus* ($R^2 = 0.86$; $p < 0.01$).

No significant difference was found between the egg length to body length ratio or the number of eggs per female of the two morphotypes (Mann-Whitney Rank Sum Test; Fig. 3.2.9).

For both morphotypes a positive correlation was detected between EL and BL (spined: Spearman rho = 0.37; $p < 0.01$; unspined: Spearman rho = 0.43; $p < 0.01$), while a negative relationship emerged between the EL/BL ratio and BL (spined: Spearman rho = - 0.65; $p < 0.01$; unspined: Spearman rho = - 0.35; $p < 0.05$). Finally, EL was positively related to PLsx (Spearman rho = 0.45; $p < 0.01$) and to the PLsx/BL ratio (Spearman rho = 0.43; $p < 0.01$) for the spined morph.

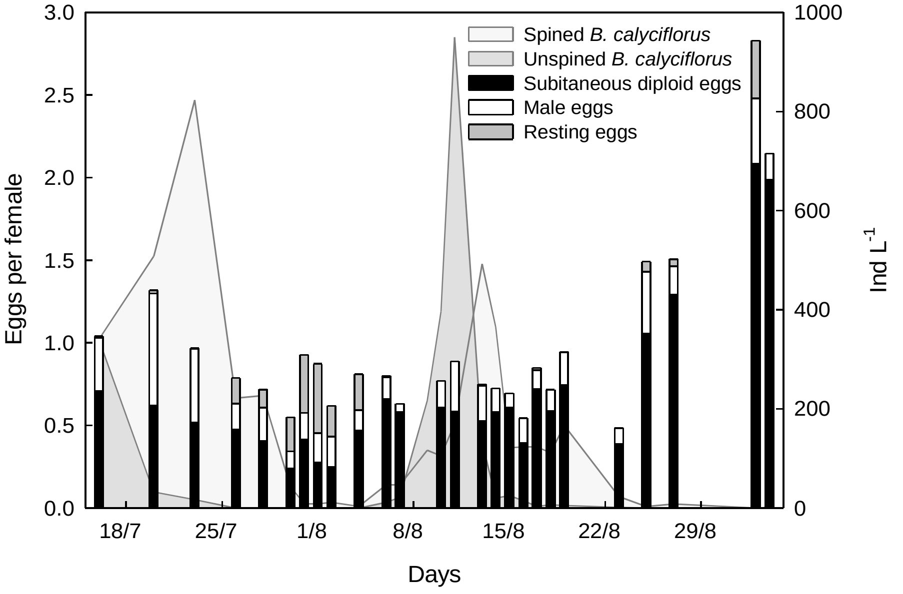


Fig. 3.2.5 - Number of subitaneous diploid, male and resting eggs per *Brachionus calyciflorus* female (left y-axis), with density of the spined and unspined *B. calyciflorus* morphs superimposed (right y-axis).

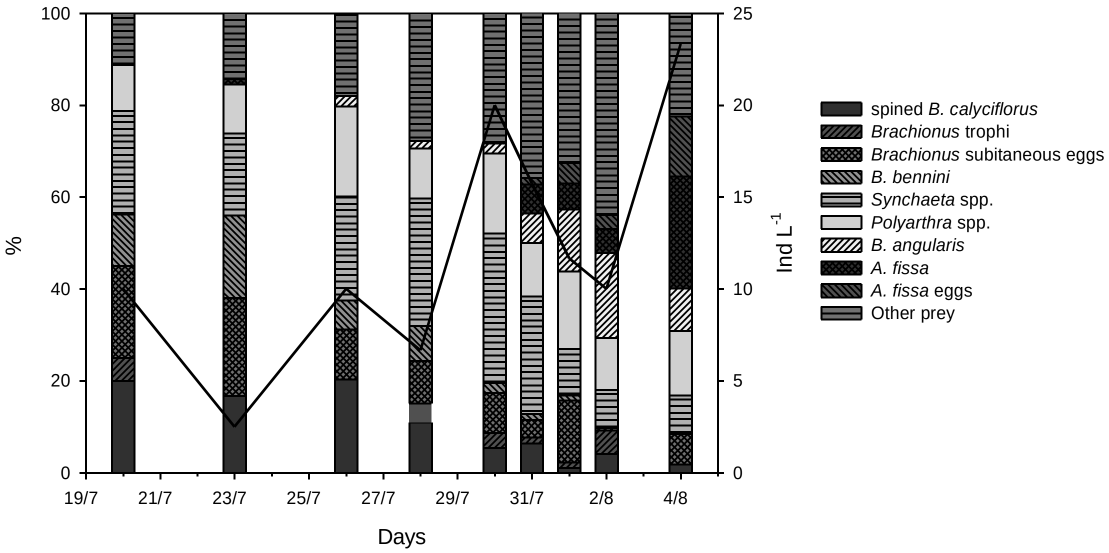
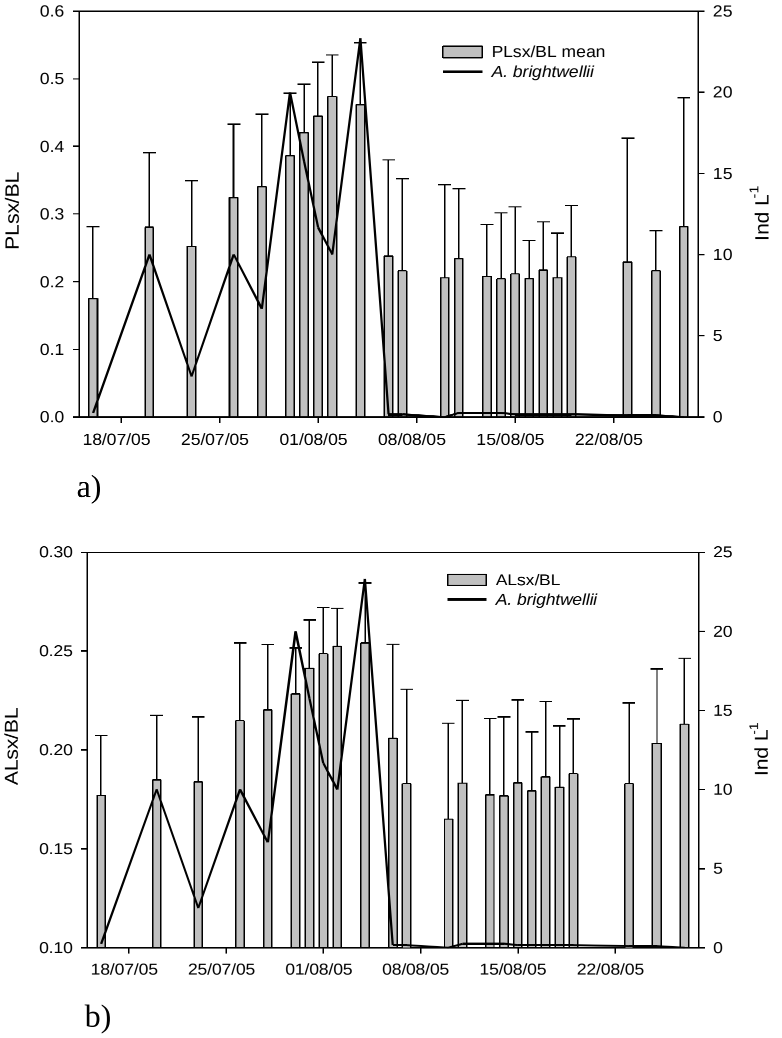
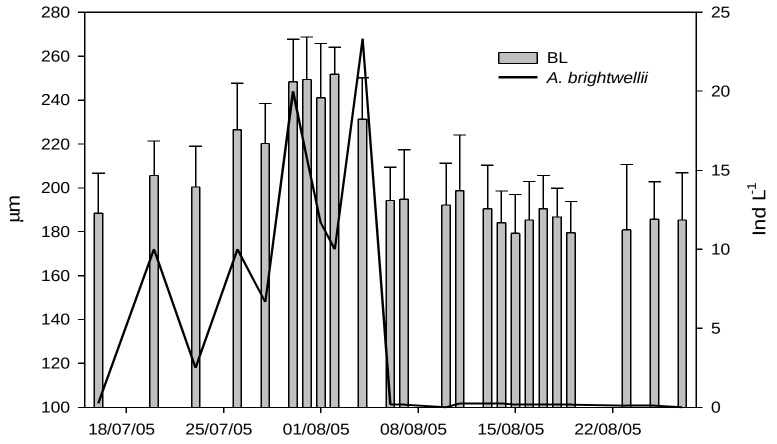


Fig. 3.2.6 - Percentage composition of stomach contents of *Asplanchna brightwellii* females in each sampling date (black line shows *A. brightwellii* density (right y-axis)).



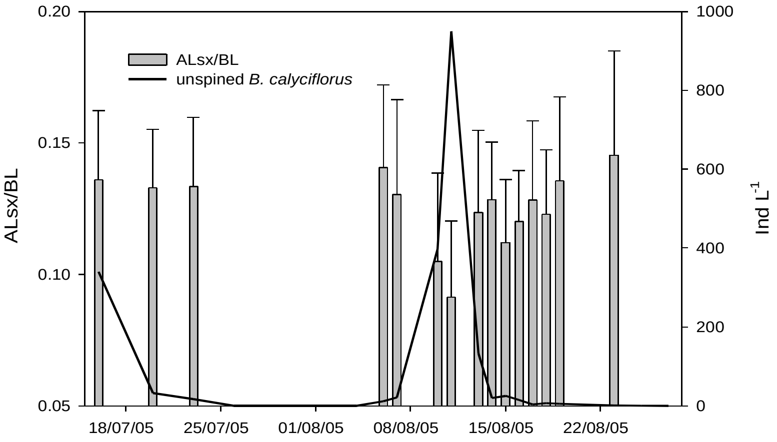
a)

b)

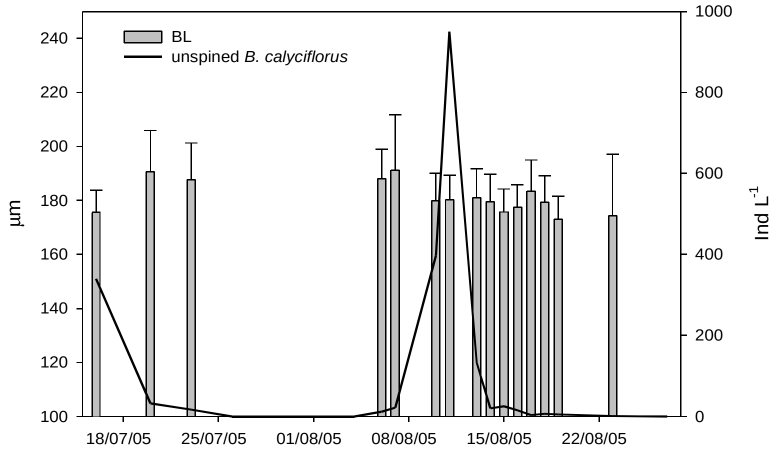


c)

Fig. 3.2.7 - Temporal trend of mean posterolateral spine length to body length ratio (a), anterolateral spine length to body length ratio (b) and body length of spined *B. calyciflorus*. The black line represents the density of *A. brightwellii* (right y-axis).

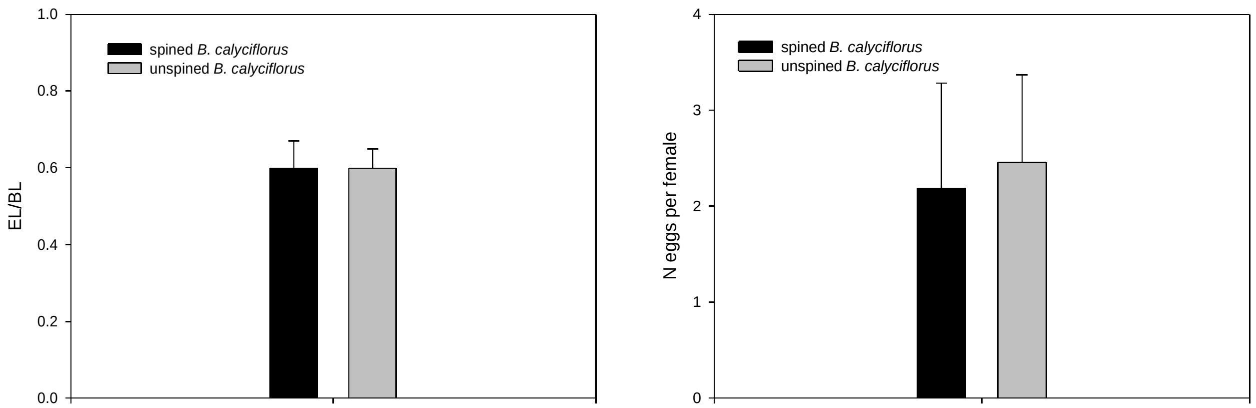


a)



b)

Fig. 3.2.8 - Temporal trend of mean anterolateral spine length to body length ratio (a) and body length of unspined *B. calyciflorus*, with its population density showed by the black line (right y-axis).



a) b)

Fig. 3.2.9 - Mean egg length to body length ratio (a) and mean number of eggs per female (b) recorded for spined and unspined *B. calyciflorus* over the whole study period.

3.2.4 Discussion and conclusions

To my knowledge, this is the first time that the role of biotic interactions within riverine zooplankton has been investigated by means of a multi-level approach, combining different tools for the study of community ecology from field data: assessment of the impact of abiotic factors, coupling of a trait-based approach with statistical modelling for estimating potential biotic interactions from time series data and biological analyses on a specific case of predator-prey interaction as well as on prey population dynamics. While these methods have been largely applied to the study of zooplankton in lentic systems (Urabe 1992; Ives et al., 1999; Klug et al. 2000; Beisner et al., 2003), their employment in lotic environments has lagged far behind, mainly because of the widespread consensus that riverine plankton are primarily abiotically constrained.

3.2.4.1 Pre-peak phase: potential role of biotic interactions

The key role of abiotic factors related to hydrology in shaping lotic zooplankton is indisputable, as it has been shown in rivers globally and this was also observed in the post-peak phase of this survey (see below). Nevertheless, results related to the pre-peak phase suggest that biotic interactions may become the primary driver of zooplankton dynamics even in a system that, although under low-flow rates, still retains the hydrological features of a truly lotic, advective environment. In fact, despite the low and relatively stable discharge levels observed in the pre-peak phase (Fig. 3.2.1), current velocities were well above the values commonly reported as the thresholds above which plankton growth and reproduction are severely impaired (0.4 m s^{-1} for zooplankton (Rzoska 1978) and 0.48 m s^{-1} for phytoplankton (Reynolds 1988)), meaning that physical constraints related to water movement and turbulence were far from negligible for planktonic organisms. Under these conditions, the variance ratio test revealed significant synchronous dynamics among taxa within most functional groups, while negative covariance emerged among functional groups, which might be suggestive of negative interactions (Table 3.2.2). This pattern of negative covariance in the pre-peak phase was mainly due to strong compensatory dynamics between group 1 and the rest of the herbivorous groups (Fig. 3.2.3). Group 1 was dominated by *Brachionus calyciflorus* and, secondarily, by *B. bennini* and *B. quadridentatus* (Fig. 3.2.4a), which are the closest to *B. calyciflorus* in terms of body and feeding apparatus size and morphology. The discharge increase right before the start of our survey, to which high loads of nutrients and organic matter are generally associated (Naldi et al., 2010), probably ensured favourable trophic conditions for the mid-July rapid development of *B. calyciflorus*. However, when environmental conditions become favourable for a certain species, taxa with similar ecological requirements are expected to increase as well, if resources are not limiting. This seemed to be the case for the synchronous increase showed by the three aforementioned brachionids in the beginning of the survey (Fig. 3.2.4a). These three taxa are the largest among the filter-feeder rotifers that usually attain significant densities in this river. Their food size spectrum is then likely to overlap to a certain extent with those of other rotifers, including also larger particle sizes (Rothhaupt 1990). Hence, as long as they maintained high population densities, they might have been capable of controlling a large portion of available resources, thus preventing other species from developing significantly. Indeed, right after their decline, all other groups of potential competitors showed a marked and rapid increase (Fig. 3.2.3), with a concurrent increase in community equitability.

Community dynamics in the pre-peak phase appeared thus to be primarily regulated by temporal trends of the dominant taxon, *B. calyciflorus*, and, to a lesser extent, of the co-dominant large brachionids, as it is also suggested by the significant negative effect of group 1 on group 2 detected by the autoregressive model (Table 3.2.3). Competitive interactions most likely occurred to a certain degree among other groups too, as it is hinted by the negative autoregressive coefficient of group 2 on group 3 (Table 3.2.3), but the decline of *B. calyciflorus* probably made sufficient resources available to allow a synchronous increase of species in all other groups (Fig. 3.2.3; Table 3.2.2). The question then arises as to what might have determined the decline of *B. calyciflorus* and, secondarily, of *B. bennini* and *B. quadridentatus* in the pre-peak phase.

3.2.4.2 Large brachionids population dynamics and predation impact by *Asplanchna*

In previous surveys carried out in the same river segment and under comparable summer conditions, the *B. calyciflorus* density drop coincided with a sudden increase in river discharge, which caused a sharp decline of all taxa in the community (De Leo & Ferrari 1993). During the present survey, on the contrary, the decline of *B. calyciflorus* and *B. bennini* occurred in the middle of a phase of stable discharge (Figs 3.2.1 and 3.2.4a). The immediately subsequent density increase of other rotifer taxa additionally proves that conditions were still favourable for zooplankton development in the river, both in terms of hydrology and resource availability. It cannot be ruled out that the decline of the large brachionids of group 1 may have been related, at least partially, to the depletion of their optimal food supply, with a consequent shift in the quality of available resources in favour of other functional groups. Nevertheless, the autoregressive analysis detected a significant negative effect of group 5 on group 1 (Table 3.2.3), which could be explained by *Asplanchna* predation on the dominant taxa of group 1. This hypothesis is well supported by gut content analysis, revealing that *A. brightwellii* preyed significantly upon *B. bennini* and both individuals and subitaneous eggs of spined *B. calyciflorus* (Fig. 3.2.6). As for the third large brachionid, *B. quadridentatus*, its avoidance by the predator allowed it to maintain relatively high densities even when the other two were already starting to decrease, hence showing a decline phase delayed by a few days in comparison to them (Fig. 3.2.4a).

Even though both autoregressive analysis and stomach content observations point towards a significant effect of predation, a more detailed examination of *B. calyciflorus* population dynamics highlighted other important aspects. The production of resting eggs and the concurrent decrease in the diploid subitaneous egg ratio observed during the decline phase (Fig. 3.2.5) are typical density-dependent self-regulation mechanisms in response to crowding, as it was observed in laboratory populations of *B. calyciflorus* under non-limiting food conditions (Gilbert, 2003). The relative importance of predation by *A. brightwellii* and crowding is difficult to determine, the most likely scenario being a combined effect of both, considering that the production of resting eggs may also be enhanced, among other factors, as a defence mechanism against predation (Gliwicz, 2004).

Control of prey population density by predation is not the only kind of interaction that may occur between *B. calyciflorus* and *A. brightwellii*. Induction of spine and body elongation on *B.*

calyciflorus by *Asplanchna* kairomones as a defence mechanism has been well documented by laboratory experiments (Gilbert, 1966; Gilbert, 1967) as well as, to a lesser extent, by field surveys (Gilbert & Waage, 1967; Green & Lan, 1974).

The rapid disappearance of the unspined morphotype and the gradual increment in the spine length to body length ratios of the spined morph with increasing *Asplanchna* densities strongly point towards a significant effect of the predator on the prey's morphology. This hypothesis is further supported by the fact that, after the collapse of the *Asplanchna* population, a peak in the unspined morph was recorded, together with a marked drop in the spine length to body length ratios and in the body length of the spined morphotype. Nevertheless, the shift of the spined *Brachionus* population towards individuals with larger bodies and longer spines might also be the result of the selective predation by *Asplanchna* on smaller and shorter-spined prey phenotypes (Gilbert, 1980; Nandini et al., 2003).

None of the two mechanisms can thus be excluded, spine and body elongation through chemical induction or selective predation, but in both cases predator-prey interactions appear to play a major role in influencing population dynamics of the dominant rotifer in the river community.

Other factors that have been shown to induce non-genetic polymorphism in *B. calyciflorus* are water temperature and food shortage (Buchner et al., 1957; Rauh, 1963; Stemberger, 1990). A sharp decrease in water temperature has been observed to provoke spine elongation in some *B. calyciflorus* strains (Buchner et al., 1957; Rauh, 1963), but temperatures measured in the Po River were far above those used in the aforementioned studies and they kept increasing in the phase when maximum values in spine to body length ratios were recorded.

No measures of chlorophyll-*a*, a proxy for resource levels, are available for the phase when *Asplanchna* was present and as previously discussed, the decline in *B. calyciflorus* may have also been partly related to intra-population density-dependent regulation processes. Nonetheless, these self-regulation mechanisms were shown to be triggered by population crowding, irrespective of food levels (Gilbert, 2003). Moreover, as already mentioned, the decline in *B. calyciflorus* was followed by a subsequent density increase of other rotifer taxa, suggesting that conditions were still favourable in the river in terms of resource availability. Finally, starvation has been shown to have no effect, or a negative one, on body size and it generally induces much shorter posterolateral spines in comparison to those induced by *Asplanchna* kairomones (Halbach, 1970; Stemberger, 1990).

3.2.4.3 Post-peak phase: switch from biotic to abiotic control of community dynamics

The development of other functional groups after the suppression of large brachionids in the end of July was disrupted by the sudden discharge peak in early August (Figs 3.2.1 and 3.2.3). Not all taxa were able to recover after this disturbance event, and in most functional groups a single taxon made up the largest proportion of the whole group density and therefore of the total temporal variance in the post-peak phase (Fig. 3.2.4a-e). Under these conditions, the within-group ratios ~1 (Table 3.2.2) do not necessarily indicate independent fluctuations among taxa, but rather result from the fact that numerator and denominator in the variance ratio formula were mainly affected by a single taxon. On the other hand, the significant synchronous dynamics detected among groups in the post-peak phase (Table 3.2.2) appeared to be mainly related to fluctuations in river flow rather than potential biotic interactions. In fact, the discharge peak presumably transported an additional input of resources to the system, as shown by the extremely high chlorophyll-*a* concentrations recorded in the subsequent days, which allowed all herbivorous groups to at least partially recover, despite the strong dominance of *B. calyciflorus* once again (Fig. 3.2.3).

Moreover, the following decrease observed for all groups in mid-August coincided with a slight increase in river discharge (Figs 3.2.1 and 3.2.3). During this phase, the *B. calyciflorus* egg ratio remained constant, suggesting that at least its decline was not due to a reduction in the population reproductive effort (Fig. 3.2.5). The primary influence of river hydrology in regulating community dynamics in the post-peak phase is supported by the negative relationship between discharge and zooplankton density. In addition, the hump-shaped relation between river flow and community equitability (Fig. 3.2.2) shows how increases in river discharge promote community equitability up to a threshold above which disruptive effects seem to prevail, in agreement with the Intermediate Disturbance Hypothesis (Connell 1978). A similar threshold effect of flow regime on community structure was also observed in different studies carried out in the same river segment (De Leo & Ferrari 1993; Rossetti et al., 2009; this study).

3.2.4.4 Concluding remarks

The present study did not take into account top-down interactions like the potential impact of planktivorous fish or benthic bivalves, which have been shown to significantly affect zooplankton abundance and structure in several large rivers (e.g. Jack & Thorp 2000; Ning et al. 2010). However, the short-term zooplankton dynamics hereby described were far too rapid to be ascribed to interactions with organisms characterized by considerably longer life cycles and whose effects on the zooplankton would manifest on a larger time scale than the one actually considered. In this regard, the high sampling frequency was fundamental to capture short-term dynamics that are inevitably overlooked by surveys carried out at longer time intervals. Moreover, the synthesis of detailed taxonomic analyses by means of a trait-based approach proved to be useful to simplify a complex community, thus facilitating the detection of potential interactions among groups of similar taxa.

While the multivariate models only suggest that competition among functional groups may be a driver of community dynamics, but do not represent a test for the actual occurrence of such interactions, statistical and biological analyses point towards a significant effect of predation within rotifer taxa. The view of riverine zooplankton as a mere assortment of taxa mainly abiotically controlled is therefore oversimplified. On the contrary, under certain conditions river zooplankton may behave like a true community, exhibiting internal, self-regulating properties and with biotic interactions becoming as important as in lentic systems in driving community dynamics. Biological control within riverine zooplankton may therefore be more effective than previously thought even in the main current and should not be ignored in order to improve our understanding of river ecology.

4. Longitudinal dynamics of river zooplankton during downstream transport: a Lagrangian sampling approach

4.1 Introduction

The vast majority of field studies dealing with zooplankton ecology in rivers has generally adopted an Eulerian reference frame, which is based on measuring the flux of objects through or within a spatially bounded area (Doyle & Ensign, 2009). These surveys rely on a traditional sampling design, involving the collection of samples at one or more stations at fixed time intervals, without accounting for water travel time from one station to the next. An alternative approach is to virtually follow a water parcel as it travels downstream (Lagrangian reference frame). This method has been used to describe longitudinal changes in water quality and/or phytoplankton communities in different large rivers (see Table 4.1), as it allows to study hydrochemical/biological processes occurring during downstream transport in a much more direct way, and apparent plankton growth rates can be estimated. Nevertheless, this approach has rarely been applied to the investigation of river zooplankton dynamics (see Table 4.1), probably because of the considerable logistic difficulties involved in carrying out this kind of studies. In particular, most of the extant work has been carried out on the River Rhine, where different Lagrangian surveys have been performed through the years on a >600-km river trait, considering both the metazoan and the microbial component of the plankton community, as well as phytoplankton (de Ruyter van Steveninck et al., 1992; Ietswaart et al., 1999; Scherwass et al., 2010). A clear downstream increase in some of the hydrochemical variables was observed, such as water temperature, conductivity, turbidity, nitrate, phosphate and silicate. Chlorophyll-*a* concentration, as well as rotifer and microcrustacean abundances, showed contrasting longitudinal patterns according to the season and the hydrological conditions. While a significant downstream shift in the taxonomic composition of the phytoplankton assemblage was recorded, no data were reported regarding the composition and/or diversity of the zooplankton component.

The study conducted on a 500-km trait of the River Elbe, on the contrary, focussed on the taxonomic composition of the phyto- and zooplankton assemblages, which both increased in density during downstream transport (Zimmermann-Timm et. al., 2007). Nevertheless, no significant longitudinal change in the rotifer community structure was observed, except for a higher relative abundance of brachionids in the lower parts of the river.

Finally, surveys conducted on the River Spree (Germany) cannot easily be compared to those reported above, as they were carried out on a much shorter river trait (21 km) just below a lake, and a significant effect of benthic bivalves on the longitudinal zooplankton dynamics was detected (Welker & Walz, 1998). As a result, a downstream decrease in both rotifers and crustaceans was observed, even though relative abundances of dominant taxa remained constant.

To sum up, some contrasting patterns emerge regarding longitudinal dynamics of zooplankton in large lowland rivers, mainly as a result of the different hydrological conditions, times of the year and especially peculiar characteristics of the river system in which the surveys were carried out. Moreover, even though a downstream increase in plankton abundance is reported by most of the studies, only very little information is available on the qualitative changes occurring within the communities over space, both from a taxonomic and/or a functional point of view.

Based on that, two Lagrangian experiments were carried out on the zooplankton of the Po River in the frame of this PhD work. It is the first time that large-scale longitudinal surveys are performed I n this river, as all previous studies focussed on a very restricted river trait (see Chapter 2.2).

Only the results of the first survey are presented here, while just a brief overview on some of the hydrochemical variables measured during the second survey is reported, as the analyses of zooplankton and hydrochemical samples could not be finished because of time constraints.

Table 4.1 - Overview of the extant studies on river water quality and/or plankton communities adopting a Lagrangian sampling strategy. Asterisk indicates surveys involving analysis of the zooplankton component.

River	**Considered Trait Length**	**N° Surveys**	**N° Stations**	**Tributaries / Backwaters**	**Simulation of water transport time**	**Reference**
Elbe	500 km	4 (Oct 1996, Aug 1997, Sep 1998 and Apr 1999)	10	4 tributaries	German Federal Institute of Hydrology	Guhr et al., 2003
Elbe *	500 km	1 (Jul 2000)	16	5 tributaries, 3 channels and 9 backwaters	QSIM Model	Zimmermann-Timm et al., 2007
Elbe	600 km	1 (Jul-Aug 2005)	9	4 tributaries and 6 sewage treatement plants	HYDRAX Model	Deutsch et al., 2009
Mississippi	> 1500 km	2 (Jun 1997 and Apr 1998)	5	3 tributaries	DAFLOW/BLTM Model	Battaglin et al., 2001
Ohio	122 km	13 (May-Oct 1998 and May-Oct 1999)	4	1 tributary	HEC-RAS 2.2	Sellers & Bukaveckas, 2003
Rhine *	> 600 km	3 (May, Jul and Sep 1990)	8	3 tributaries	Alarmmodel für den Rhine	de Ruyter van Steveninck et al., 1992
Rhine *	> 600 km	2 (Apr and Sep 1995)	9	3 tributaries	Alarmmodel für den Rhine	Ietswaart et al., 1999
Rhine	160 km	Every 2-3 weeks in Feb 1999-Jan 2000	2	/	Alarmmodel für den Rhine	Weitere & Arndt, 2002
Rhine *	> 600 km	1 (May 2000)	16	8 tributaries	Alarmmodel für den Rhine	Scherwass et al., 2010
Spree *	21 km	5 (Jun, Jul, Aug and Sep 1994)	11	/	/	Welker & Walz, 1998
Spree	28 km	Every other week in Mar-Sep 1995	2	/	tracer experiments	Köhler & Bosse, 1998
Spree and Warnow	S1: 20 km S2: 30 km W: 20 km	S1: 13 (Mar-Sep 1995); S2: 7 (Apr-Aug 1998); W: 2 (Jun 1998 and 1999);	S1: 3 S2: 3 W: 6	/	tracer experiments	Köhler et al., 2002
St. Lawrence	250 km	4 (May, Aug, Nov 1991 and Apr 1992)	3	2 fluvial lakes	/	Hudon et al., 1996

4.2 Materials and Methods

4.2.1 Modelling water transport time: the forecasting system of the Emilia-Romagna Environmental Protection Agency

In order to follow water as it moved downstream and ideally sample the same water parcel travelling from one station to the next, water transport time along the river was simulated through the operational forecasting system of the Emilia-Romagna Environmental Protection Agency (ARPA Emilia-Romagna). A collaboration was started with the staff of the Hydro-Meteo-Climate Section of the PA, who have developed a forecasting system over the years to support ordinary planning and management activities in the Po River basin as well as the organization of flood control and soil defence measures during extraordinary emergency events.

The system (Fig. 4.1) is based on both real time hydrometeorological data collected by a monitoring network spread over the whole river basin (Fig. 4.2) and on forecasted meteorological conditions provided by a non-hydrostatic model with a time horizon of 3 days, the LAMI (Limited Area Model Italy). These data feed three hydrological and hydrodynamic chains, each one coupling a rainfall/runoff model and a hydrodynamic model and finally producing forecasting scenarios of river discharge and water travel time.

Simulations of water travel time under different hydrological conditions were performed by the staff of the Protection Agency and it was decided to use the output values of the second chain because, based on their experience, it is the one providing the most reliable simulations of water velocity in the Po River. Based on these simulations the ARPA staff was able to provide a schedule of the day and time at which sampling should have taken place at each station in order to follow an ideal water parcel under the forecasted hydrological conditions.

The degree of accuracy of the simulations was assessed by comparing simulated and observed discharge values at six gauging stations along the considered river stretch.

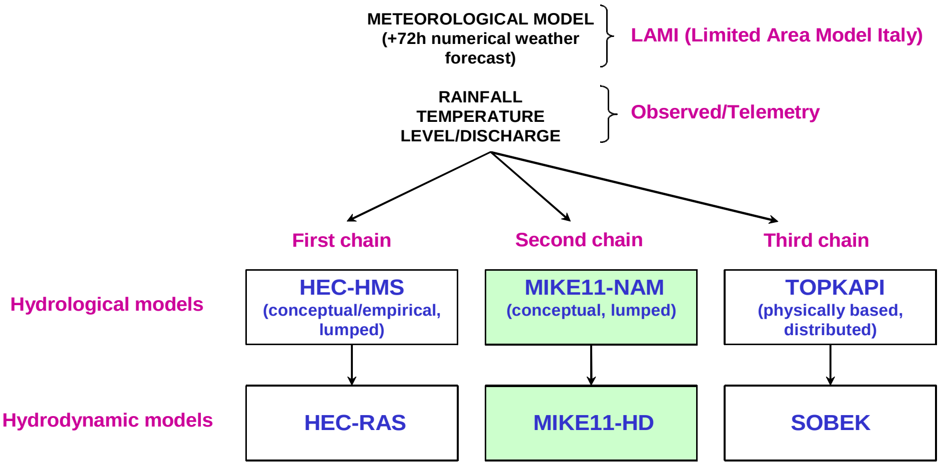


Fig. 4.1 - Schematic overview of the operational forecasting system used by the Emilia-Romagna Environmental Protection Agency to simulate water transport time along the Po River.

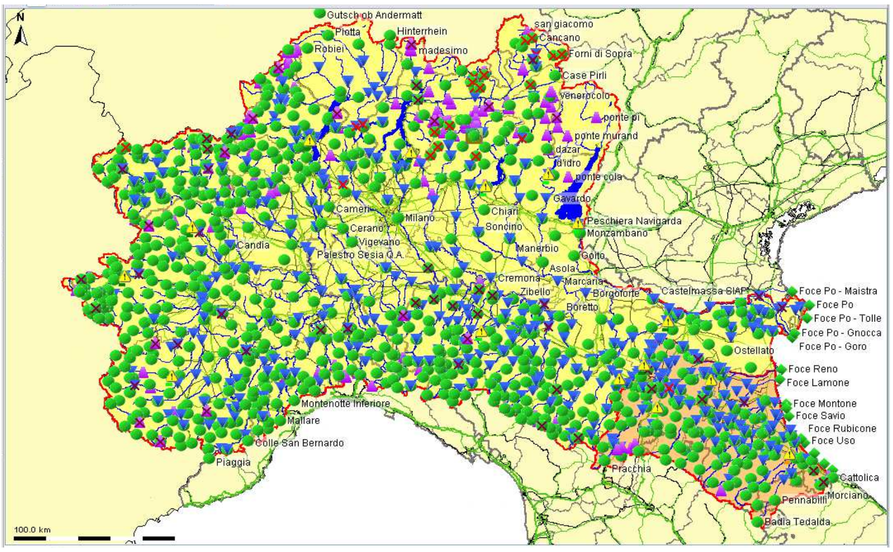


Fig. 4.2 - Overview of the monitoring network on the river basin collecting real time data that feed the ARPA forecasting system. Blue triangles: 588 water level gauges; green dots: 1014 rain gauges

and 756 thermometers; violet triangles: 187 dams. (Source: Hydro-Meteo-Climate Section, ARPA Emilia-Romagna).

4.2.2 Field sampling and laboratory analyses

Twelve sampling stations were selected along a 330-km stretch of the Po River lowland section (Fig. 4.3). The most upstream station (Rea) is located 269 km from the river source. Distance between consecutive stations varies between 13 and 36 km, with the exception of the two most downstream stations (Pontelagoscuro and Serravalle), which are 68 and 41 km far from the preceding one, respectively. Additionally, the four major tributaries along the considered river stretch were also sampled, namely the Ticino, Adda, Oglio and Mincio (Fig. 4.4), choosing a station as close as possible to their confluence with the Po River.

Two surveys were carried out, one in May 2010 and one in August 2011, in order to compare two situations under markedly different meteorological and hydrological conditions.

According to the simulations of water travel time provided by ARPA Emilia-Romagna, the first survey began on May 26, 2010 at 9:00 am and finished on May 31, 2010 at 13:20 pm, while the second survey started on August 19, 2011 at 7:30 am and finished on August 27, 2011 at 4:30 am (Table 4.2).

The presence of the Isola Serafini dam was taken into account considering that about 2/3 of the river discharge is generally diverted into a 11-km artificial canal, while the rest of the water flows through the natural river meander (see Chapter 5, in particular Fig. 5.1). Water travel times along the artificial canal and the natural meander up to the point where the two branches rejoin are different. It was decided to follow water travel time along the artificial canal, since most of the river discharge is diverted into it.

At each station samples were taken from floating pontoons that allowed to reach the main current in the river channel. Field collection and laboratory analyses of both water and zooplankton samples were carried out following the same methods provided in Chapter 3.1.2, with the only difference that a volume of 60 L of water was filtered for zooplankton samples.

Daily data of the Po River discharge at five gauging stations along the considered river trait (Table 4.2) were provided by the Hydro-Meteo-Climate Section, ARPA Emilia-Romagna.

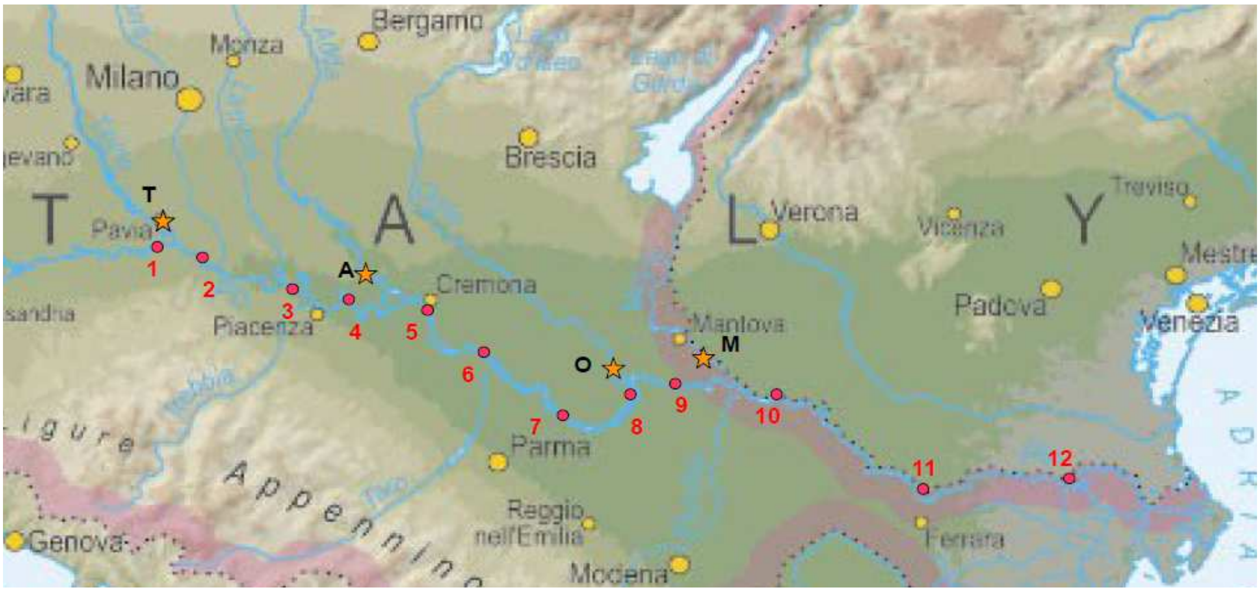


Fig. 4.3 - Map of the sampling stations selected for the Lagrangian surveys.
1: Rea: 45° 07' 28.36" N 9° 09' 31.97" E; **2**: Portalbera: 45° 06' 03.65" N 9° 20' 38.42" E; **3**: Corte S. Andrea: 45° 07' 52.00" N 9° 33' 16.18" E; **4**: Mortizza: 45° 05' 04.14" N 9° 45' 15.00" E; **5**: Cremona: 45° 07' 33.49" N 10° 00' 02.18" E **6**: Stagno: 45° 01' 22.75" N 10° 13' 36.62" E; **7**: Viadana: 44° 54' 48.24" N 10° 32' 11.88"

E; **8**: Riva di Suzzara: 44° 59' 43.01" N 10° 41' 52.55" E; **9**: Borgoforte: 45° 02' 48.07" N 10° 45' 29.20" E; **10**: Sacchetta: 45° 04' 08.94" N 10° 59' 42.33" E; **11**: Pontelagoscuro: 44° 53' 22.52"; N 11° 36' 21.64" E; **12**: Serravalle: 44° 58' 28.58" N 12° 02' 47.53" E; **T**: Ticino River: Vaccarizza: 45° 08' 56.19" N 9° 13' 07.33" E; **A**: Adda River: Crotta d'Adda: 45° 09' 25.42" N 9° 51' 11.11" E; **O**: Oglio River: Torre d'Oglio: 45° 02' 28.60" N 10° 39' 02.95" E; **M**: Mincio River: Governolo: 45° 04' 58.82" N 10° 57' 23.17" E.

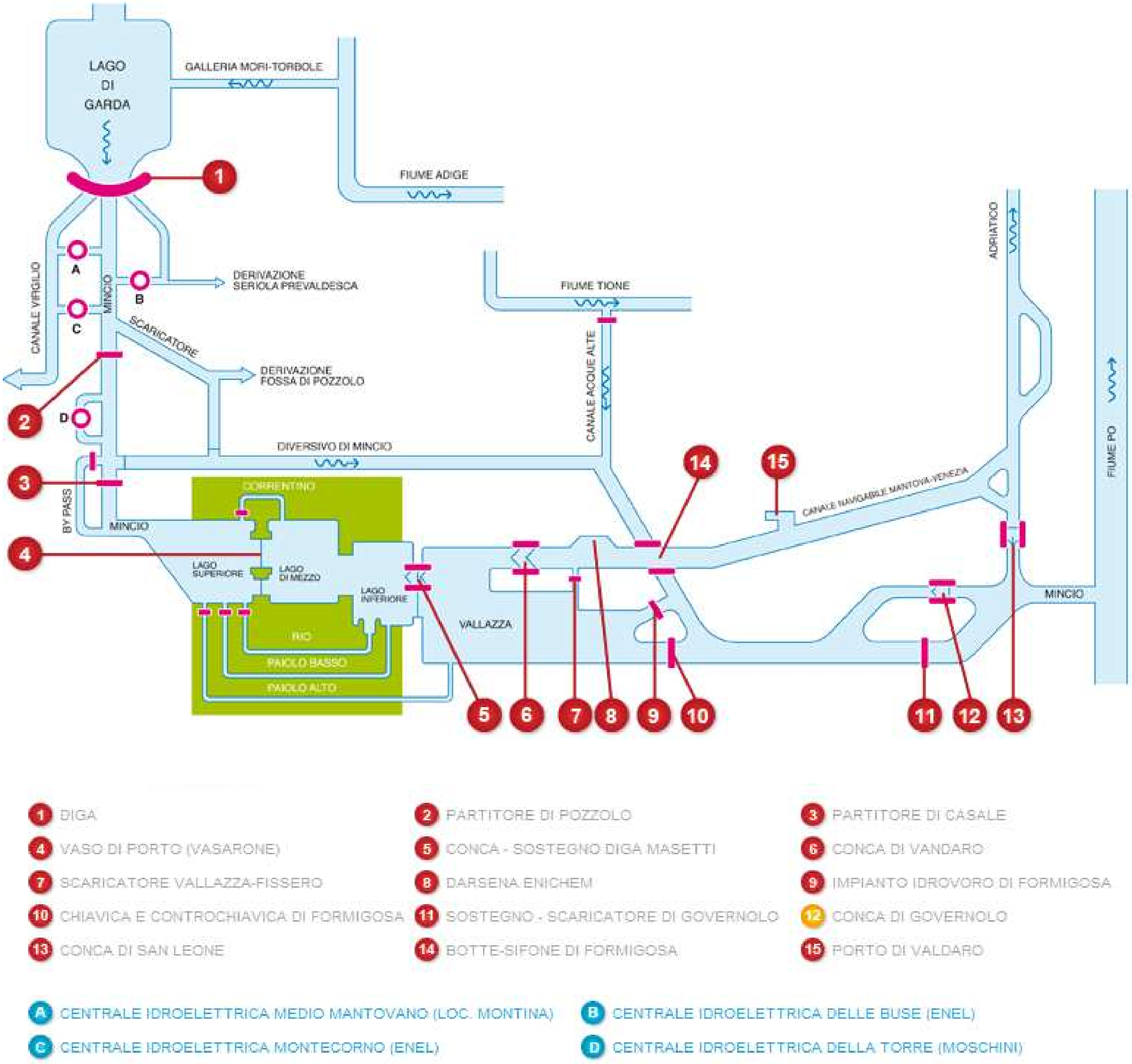


Fig. 4.4 - Hydraulic scheme of the Mincio River below the Garda Lake outlet (modified from www.parcodelmincio.it).

Table 4.2 - Sampling sites and time schedule of the Lagrangian surveys. Stations in bold are the gauging stations. Spessa, Piacenza and Boretto gauging stations are located few km upstream of COR, MOR and RIV sampling sites, respectively. Cremona, Borgoforte and Pontelagoscuro gaugin stations are located at the corresponding sampling sites.

	Abbreviation	Distance km	Cumulated distance km	Date of sampling	Hour of sampling	Date of sampling	Hour of sampling
1. Rea	REA	0	0	26/05/10	09:00	19/08/11	07:30
Ticino River	TIC			26/05/10	11:30	19/08/11	10:30
2. Portalbera	POR	17.99	17.99	26/05/10	15:40	19/08/11	19:56
Spessa							
3. Corte S.Andrea	COR	24.59	42.58	26/05/10	22:45	20/08/11	07:17
Piacenza							
4. Mortizza	MOR	26.48	69.06	27/05/10	06:00	20/08/11	22:49
Adda River	ADD			27/05/10	09:30	21/08/11	10:30
5. Cremona	CRE	33.96	103.02	27/05/10	19:15	22/08/11	21:06
6. Stagno	STA	28.53	131.55	28/05/10	03:00	23/08/11	10:33
7. Viadana	VIA	36.23	167.78	28/05/10	13:50	24/08/11	01:23
Boretto							
8. Riva di Suzzara	RIV	18.65	186.43	28/05/10	18:10	24/08/11	08:11
Oglio River	OGL			28/05/10	20:40	24/08/11	10:40
9. Borgoforte	BOR	12.82	199.25	28/05/10	23:10	24/08/11	15:10
Mincio River	MIN			29/05/10	09:00	24/08/11	17:30
10. Sacchetta	SAC	1.22	223.33	29/05/10	05:45	25/08/11	00:38
11. Pontelagoscuro	PON	67.97	291.30	30/05/10	00:50	26/08/11	05:30
12. Serravalle	SER	40.76	332.06	30/05/10	13:20	27/08/11	04:30

4.3 Results

4.3.1 Hydrology

Spring survey: May 2010

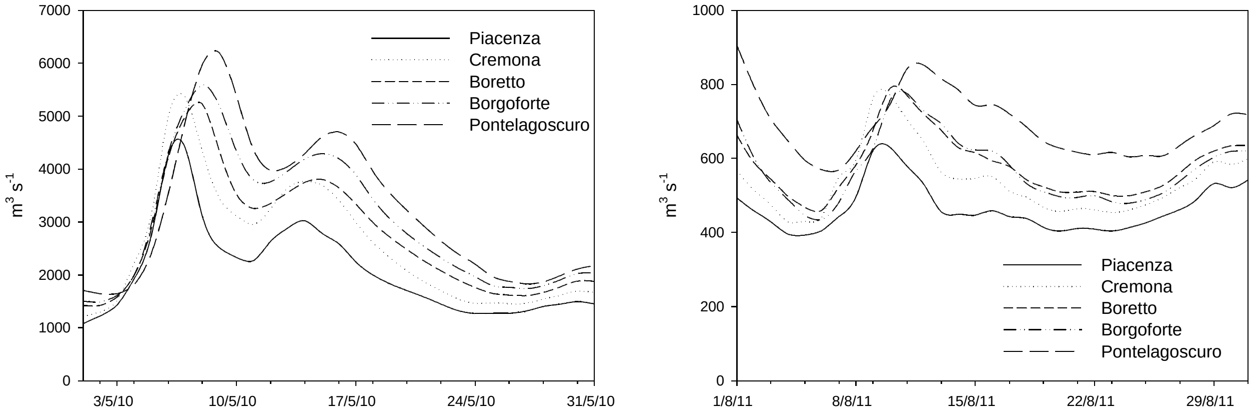
In early May a flood occurred, with peaks of 4397 m^3 s^{-1} on May 7 at Piacenza, 5592 m^3 s^{-1} on May 8 at Borgoforte and 6195 m^3 s^{-1} on May 9 at Pontelagoscuro (Fig. 4.5a). A subsequent, though smaller, increase in discharge took place around the middle of the month, after which river flow steadily decreased until the beginning of sampling. During the survey discharge remained relatively stable, showing only a slight increasing trend, so that from the beginning to the end of the study values rose from 1275 to 1451 m^3 s^{-1} at Piacenza, from 1762 to 2038 m^3 s^{-1} at Borgoforte and from 1874 to 2175 m^3 s^{-1} at Pontelagoscuro.
Fig. 4.6a compares discharge values measured at six gauging stations with the corresponding simulated values on which estimates of water travel time were based. The percentage error between observed and simulated values ranges between -5.52% and 0.42%, with a mean of -0.15%.

Summer survey: August 2011

An increase in river discharge was recorded in the first half of August, with maxima of 630 m^3 s^{-1} on August 10 at Piacenza, 775 m^3 s^{-1} on August 11 at Borgoforte and 851 m^3 s^{-1} on August 12 at Pontelagoscuro (Fig. 4.5b). A gradual decrease in flow rates took place in the following days and on August 19, when the sampling began, values of 414, 510 and 646 m^3 s^{-1} were observed at the stations of Piacenza, Borgoforte and Pontelagoscuro, respectively. Discharge remained then relatively constant for most of the study period. It started to slightly increase on August 24 at

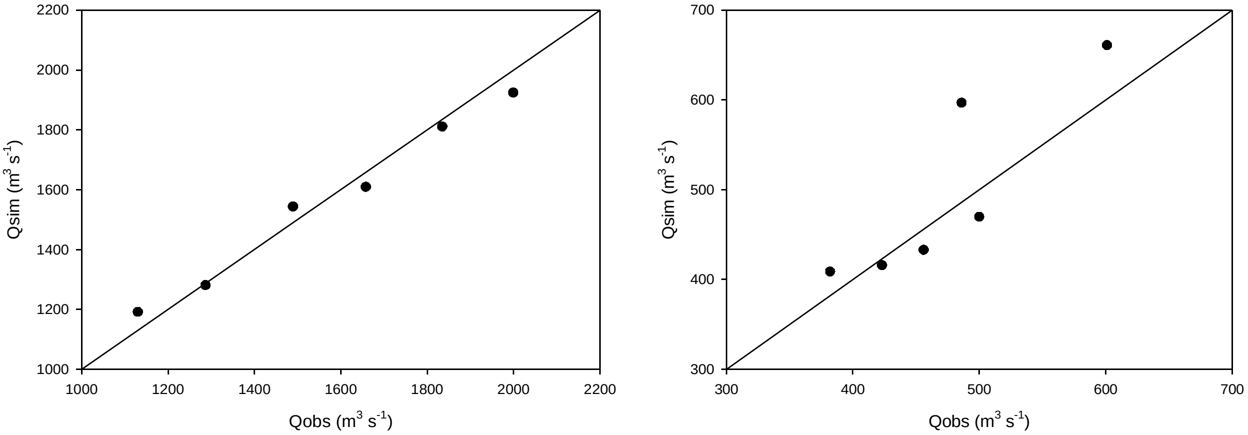
Piacenza and with a one-day delay at the following stations, so that on August 27 (last day of the survey) values of 462, 539 and 635 m^3 s^{-1} were recorded at the three aforementioned stations, respectively.

The percentage error between observed and simulated flow values ranges between -6.00% and 22.84%, with a mean of 4.53% (Fig. 4.6b).



a) b)

Fig. 4.5 - Mean daily values of river discharge measured at five gauging stations along the middle reach of the Po River during May 2010 (a) and August 2011 (b). Note the different scales on the y-axis.



a) b)

Fig. 4.6 - Comparison between simulated (Qsim: y-axis) and observed (Qobs: x-axis) discharge values at six gauging stations along the Po River during the Lagrangian surveys in May 2010 (a) and August 2011 (b). The hour selected for comparison is the time at which water was assumed to pass by each gauging station according to model simulations. The line represents the y=x line.

4.3.2 Hydrochemistry

Spring survey: May 2010

Water temperature measured along the Po River ranged between 18.6°C (Rea) and 19.9°C (Por), while in the tributaries it varied between 16.5°C (Ticino) and 22.2°C (Mincio; Fig. 4.7a). pH was around 8 at all sites, with the lowest value measured in the Ticino River (7.9) and the highest in the Mincio River (8.2; Fig. 4.8a). Conductivity reached 345 µS cm^{-1} at the two most upstream Po stations, it then dropped to 317 µS cm^{-1} at the following site (Cor), and then showed a slight increasing trend moving downstream, up to values around 371 µS cm^{-1} at the last four sites (Fig. 4.9a). The tributaries showed markedly different conductivity levels, with a minimum of 210 µS cm^{-1} in the Ticino River, and a maximum of 504 µS cm^{-1} in the Oglio River (Fig. 4.9a). Total alkalinity ranged between 2.21 meq L^{-1} (Por and Cor) and 2.70 meq L^{-1} (Bor) along the Po River (Fig. 4.10a), and it was significantly related to conductivity ($R^2 = 0.79$, $p < 0.01$). Once again, the minimum alkalinity value among the tributaries was recorded in the Ticino River (1.50 meq L^{-1}), while the maximum was measured in the Oglio River (3.86 meq L^{-1}; Fig. 4.10a). Dissolved oxygen in the Po River varied between a minimum of 7.8 mg L^{-1} at Mor and a maximum of 9.6 mg L^{-1} at Via (Fig. 4.11a), with corresponding saturation levels of 82% and 102%, respectively (Fig. 4.12a). Oxygen saturation was close to 90% in the tributaries, with the exception of the Mincio, where oversaturation conditions were found (111%; Fig. 4.12a).

NO_3-N concentrations measured in the Po River fluctuated between 1352 µg L^{-1} at Sta and 2144 µg L^{-1} at Bor, and although they did not show any clear longitudinal trend, the highest values were recorded at the most downstream stations (Fig. 4.13). Concentrations in the tributaries were comparable to those recorded in the Po, with the exception of the Oglio River, where a NO_3-N content of 4321 µg L^{-1} was detected (Fig. 4.13). NO_2-N exceeded 30 µg L^{-1} only in two tributaries, the Mincio (31 µg L^{-1}) and the Oglio (42 µg L^{-1}; Fig. 4.14). The highest NH_4-N content in the Po River was recorded at the uppermost station (Rea, 53 µg L^{-1}), while the lowest value was measured at Riv (6 µg L^{-1}; Fig. 4.15). As for the tributaries, concentrations varied between 41 µg L^{-1} in the Ticino River and 77 µg L^{-1} in the Mincio River (Fig. 4.15).

SRP fluctuated between 29 µg L^{-1} (Cor) and 12 µg L^{-1} (Riv) along the Po, but the lowest SRP concentration was found in the Mincio River (8 µg L^{-1}; Fig. 4.16)

Chl-*a* content in the Po River varied between 2.4 µg L^{-1} (Sta) and 6.7 µg L^{-1} (Ser), with the most downstream stations tending to show the highest values (Fig. 4.17). Concentrations in the tributaries ranged between minima of 1.6 and 1.0 µg L^{-1} (Ticino and Adda, respectively), and a maximum of 20.9 µg L^{-1} measured in the Mincio River.

SPM peaked at the two most upstream Po River sites, with values of 83.4 mg L^{-1} and 95.7 mg L^{-1}, respectively; at the remaining stations values ranged between 45.5 mg L^{-1} (Bor) and 67.2 mg L^{-1} (Ser; Fig. 4.18a). The two uppermost tributaries (Ticino and Adda) showed SPM levels below 20 mg L^{-1}, while in the Mincio and Oglio values of 26.8 mg L^{-1} and 65.7 mg L^{-1} were detected, respectively (Fig. 4.18a).

Summer survey: August 2011

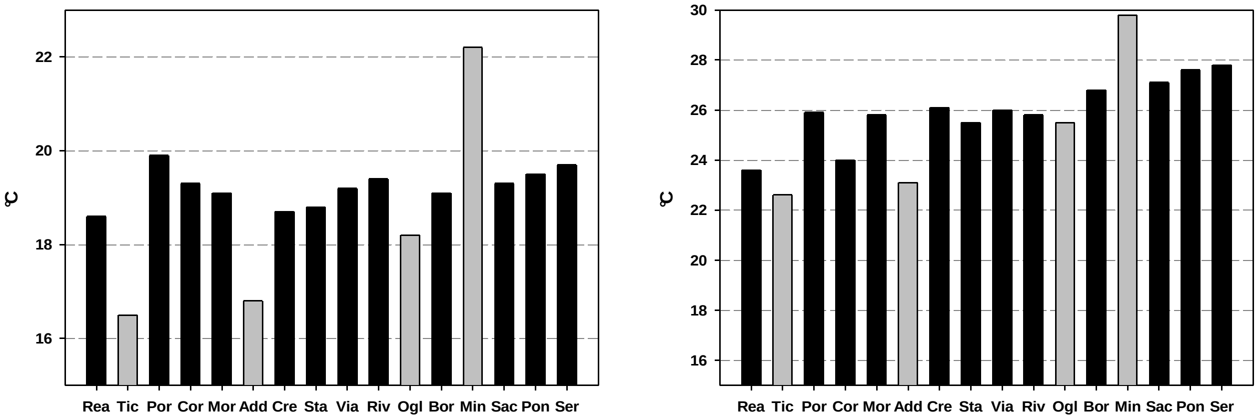
The only hydrochemical variables currently available are water temperature, pH, conductivity, alkalinity, dissolved oxygen and suspended particulate matter.

Water temperature showed a downstream increase along the Po River, from a minimum of 23.6°C at the uppermost station to a maximum of 27.8°C at the most downstream one (Fig. 4.7b). While the two uppermost tributaries had lower temperatures than those measured in the Po River (22.6 and 23.1°C, respectively), the Oglio River exhibited a value comparable to those found in the Po (25.5°C). In the Mincio River, on the contrary, a peak of 29.8°C was observed. pH ranged between 7.9 (Rea) and 8.4 (Bor) in the Po, with no clear longitudinal pattern (Fig. 4.8b). As for the tributaries, the lowest pH value was measured in the Ticino River (7.6) while the highest was recorded in the Oglio River (8.1). Conductivity decreased along the first four Po stations, from a maximum of 541 µS cm^{-1} at Rea to a minimum of 436 µS cm^{-1} at Mor (Fig. 4.9b). It then increased again and fluctuated within 460-485 µS cm^{-1} at the remaining sites. The lowest conductivity among the tributaries was measured in the Ticino River (278 µS cm^{-1}), while in the Oglio River a value of 600 µS cm^{-1} was observed. Total alkalinity varied between 2.97 meq L^{-1} (Mor) and 3.96 meq L^{-1} (Rea) in the Po, with a longitudinal pattern similar to that of conductivity (Fig. 4.10b). A significant positive relationship was found between these two variables ($R^2 = 0.87$, $p < 0.01$). Once again, the

Ticino exhibited the lowest alkalinity value (2.08 meq L^{-1}) while the Oglio had the highest (4.62 meq L^{-1}).

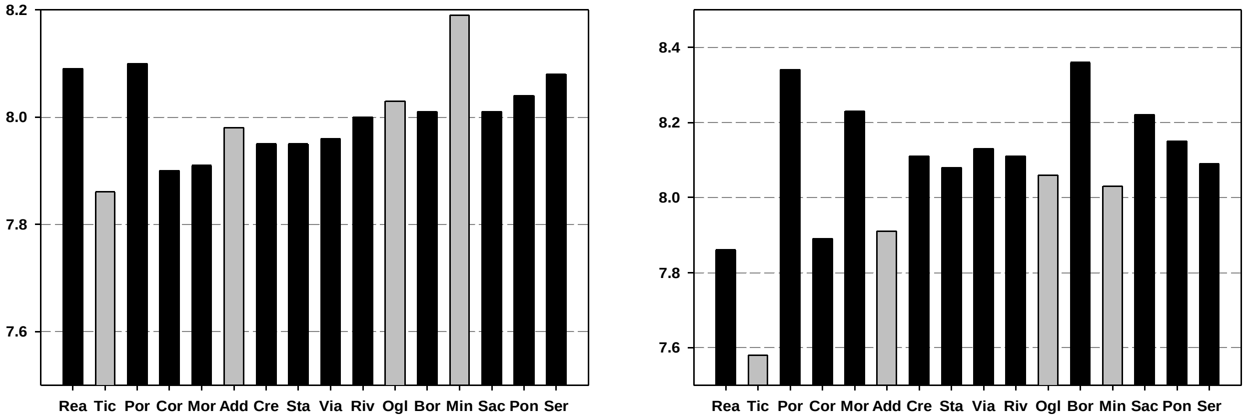
Dissolved oxygen fluctuated between 7.2 and 12.8 mg L^{-1} in the Po River (Fig. 4.11b), with a corresponding percentage saturation varying between 89 and 153% (Fig. 4.12b). While no clear longitudinal trend was observed in the Po River, the tributaries showed progressively increasing oxygen contents from the uppermost one (Ticino: 6.8 mg L^{-1}, 77%) to the most downstream one (Mincio: 9.9 mg L^{-1}, 125%).

SPM varied between 18.6 mg L^{-1} (Mor) and 41.5 mg L^{-1} (Bor; Fig. 4.18b). The most downstream stations tended to exhibit the highest values, with the exception of the last one, where SPM dropped to 24.2 mg L^{-1}. The lowest SPM levels were recorded in the Ticino and Adda (6.3 and 10.4 mg L^{-1}, respectively), while the Oglio River showed the highest value (52.1 mg L^{-1}).



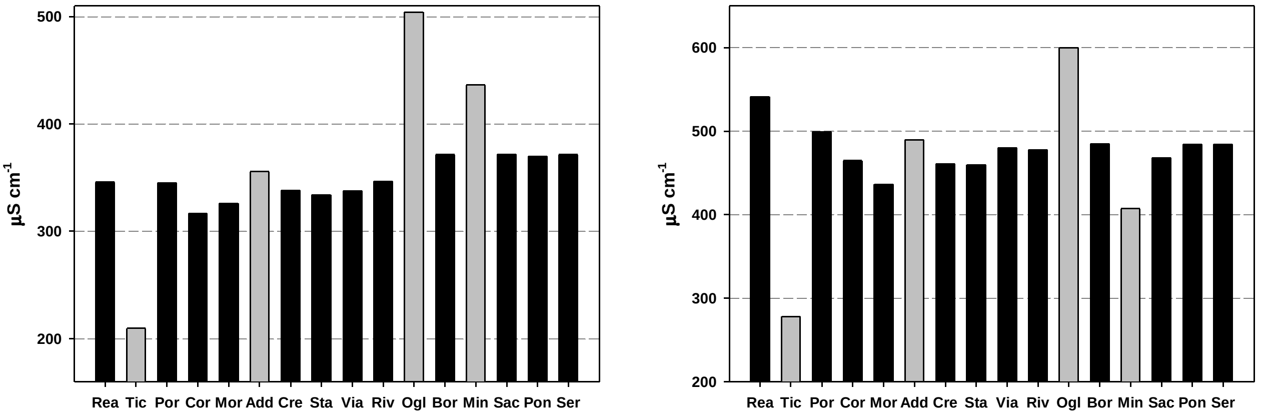
a) b)

Fig. 4.7 - Water temperature measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010 (a) and August 2011 (b). Note the different scales on the y-axis.



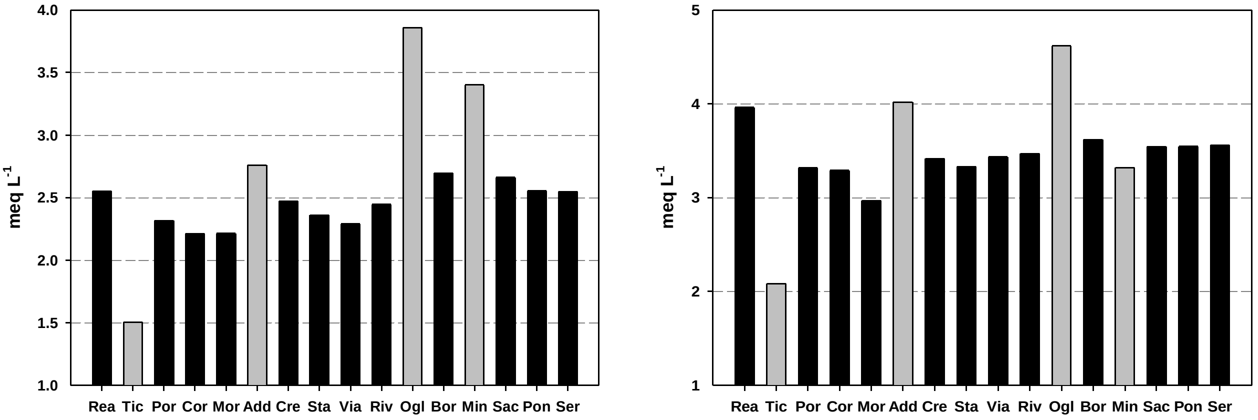
a) b)

Fig. 4.8 - pH values measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010 (a) and August 2011 (b). Note the different scales on the y-axis.



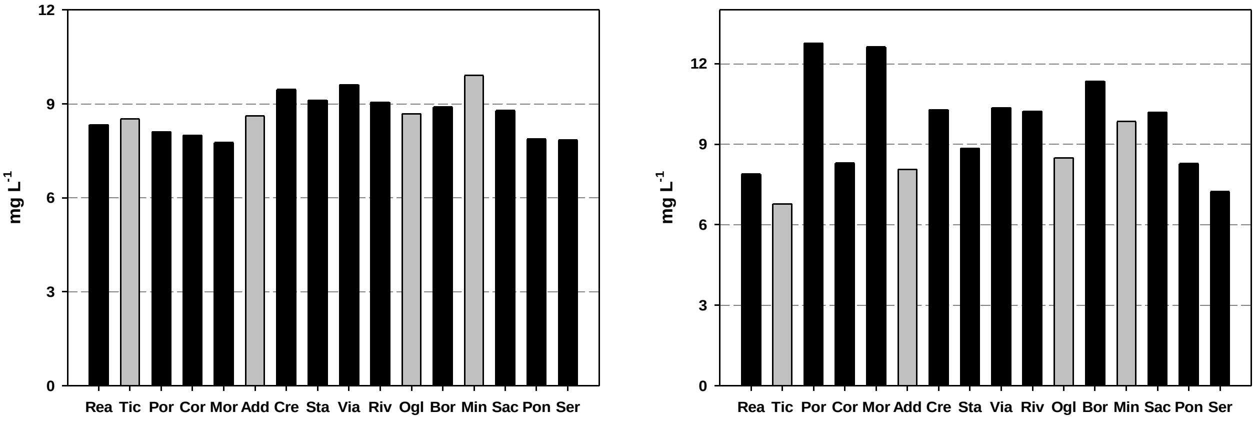
a) b)

Fig. 4.9 - Electric conductivity at 25°C measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010 (a) and August 2011 (b). Note the different scales on the y-axis.



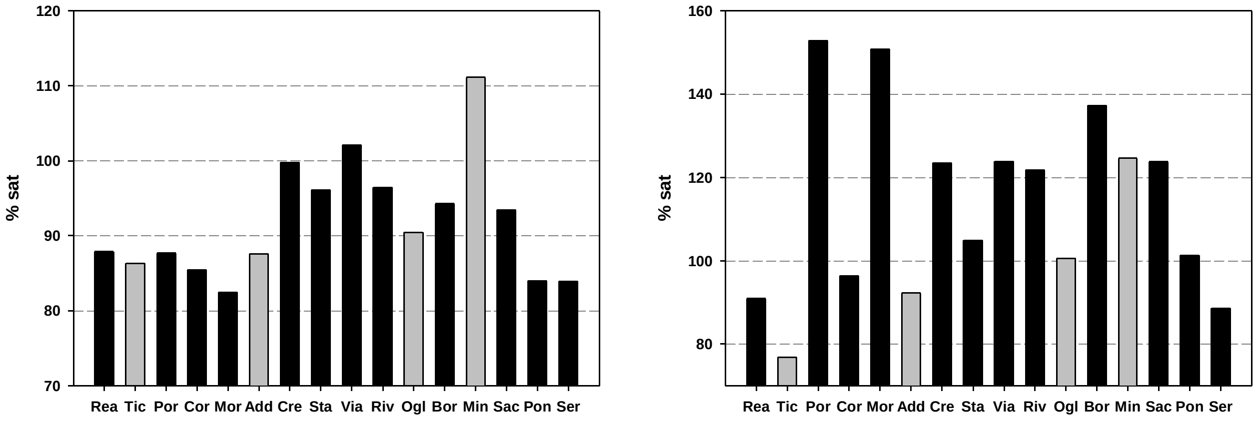
a) b)

Fig. 4.10 - Total alkalinity measured at 12 stations on the Po River (black bars) and in four tributaries (grey bars) in May 2010 (a) and August 2011 (b). Note the different scales on the y-axis.



a) b)

Fig. 4.11 - Dissolved oxygen concentration measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010 (a) and August 2011 (b). Note the different scales on the y-axis.



a) b)

Fig. 4.12 - Dissolved oxygen percentage saturation measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010 (a) and August 2011 (b). Note the different scales on the y-axis.

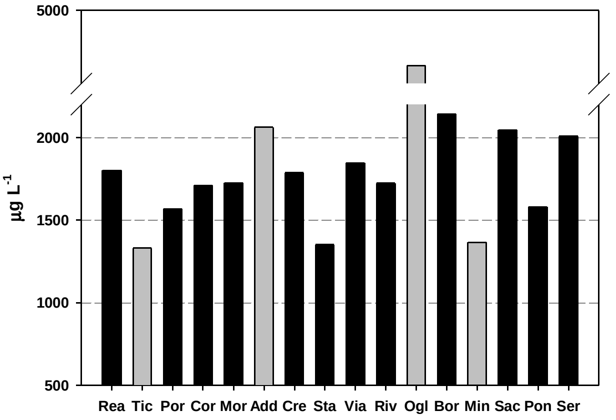


Fig. 4.13 - Nitrate concentrations measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

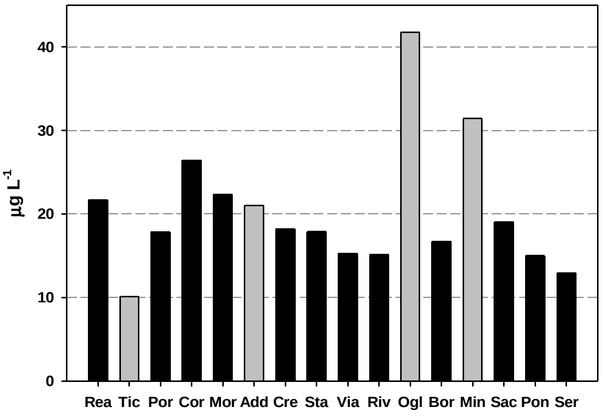


Fig. 4.14 - Nitrite concentrations measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

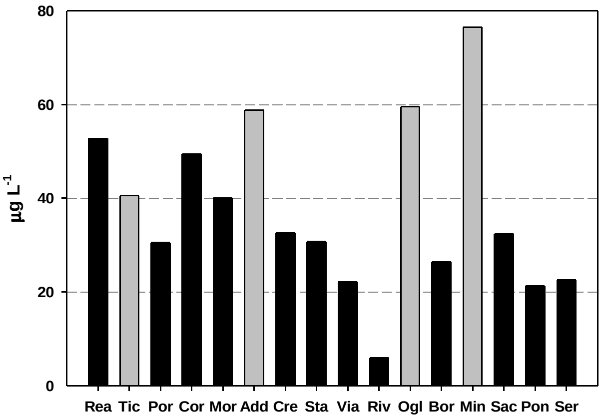


Fig. 4.15 - Ammonium concentrations measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

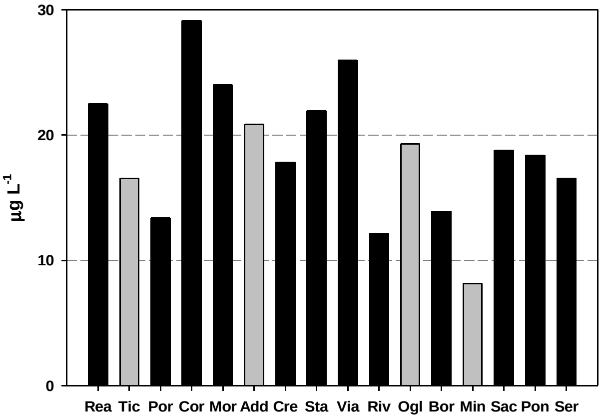


Fig. 4.16 - Soluble reactive phosphorus concentrations measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

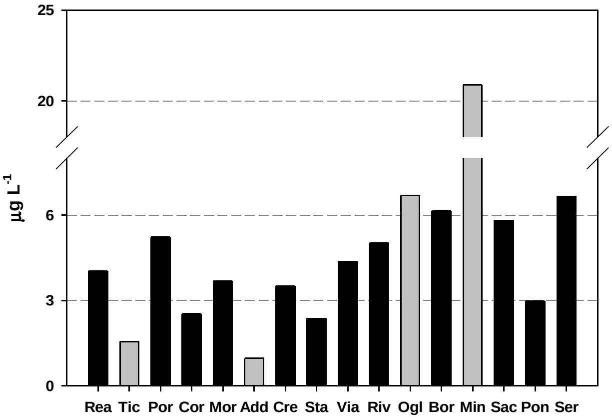
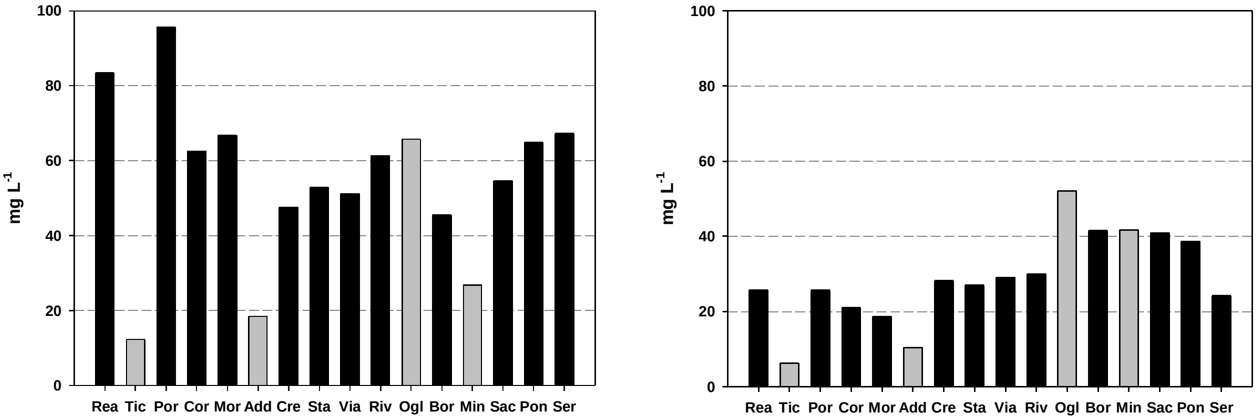


Fig. 4.17 - Chlorophyll-*a* concentrations measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.



a) b)

Fig. 4.18 - Suspended particulate matter concentrations measured at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010 (a) and August 2011 (b).

4.3.3 Zooplankton assemblage

Spring survey: May 2010

A total of 117 zooplankton taxa were identified: 99 rotifers, 13 cladocerans and 5 copepods (see Annex 1). Total zooplankton density fluctuated around 30 ind L^{-1} along the first eight stations in the Po River, it then increased to 52 ind L^{-1} at Bor, peaked at the Sac station (165 ind L^{-1}) and decreased to values around 100 ind L^{-1} at the two most downstream sites (Fig. 4.19a). The first two tributaries showed zooplankton densities comparable to those recorded in the uppermost segment of the Po River. In the Oglio River a total zooplankton abundance of 65 ind L^{-1} was found, while in the Mincio River a peak of 747 ind L^{-1} was detected.

Zooplankton density was mainly sustained by rotifers (Fig. 4.19b), which made up over 90% of the whole community at all sites.

Loricate taxa made up 29 to 43% of the rotifer assemblage in the first eight Po stations and in the Ticino and Adda Rivers, while in the two most downstream tributaries and in the last four Po sites their share increased to around 60% (Fig. 4.20).

The share of truly planktonic rotifer taxa against the littoral/epibenthic ones showed a gradual downstream increase, from a minimum of 46% at Rea to a maximum of 90% at Ser (Fig. 4.21). While in the Adda River littoral/epibenthic species tended to dominate, with a share of 56%, in the other tributaries the situation was reversed, with planktonic taxa making up 63 to 98% of the whole assemblage.

The percentage composition of the rotifer component in terms of the most abundant taxa remained quite similar in the first nine stations along the Po River (Fig. 4.22). In particular, bdelloids, *Keratella cochlearis*, *K. cochlearis* f. *tecta* and *Polyarthra* gr. *vulgaris-dolichoptera* made up a large proportion of the whole community in the Po sites as well as in the first three tributaries. In the Mincio River and at the Po stations downstream of its confluence, the share of bdelloids and *Polyarthra* was reduced in favour of that of *K. cochlearis* f. *tecta*, *Asplanchna priodonta*, *Brachionus angularis* and *Synchaeta* gr. *stylata-pectinata*.

This is reflected by the longitudinal abundance patterns of some rotifer taxa. Species like *Asplanchna priodonta*, *Brachionus angularis*, *B. budapestinensis*, *B. calyciflorus*, *Keratella cochlearis*, *K. cochlearis* f. *tecta* and *Filinia* gr. *longiseta-terminalis* showed low abundances along most of the studied river stretch and then sharply peaked in the Mincio River and in the following stations in the Po River (Fig. 4.23). On the contrary, some taxa showed a clear decreasing pattern in the downstream direction, e.g. *Lecane luna*, *Lepadella patella*, *Hexarthra fennica*, *Trichocerca* *porcellus* and bdelloid rotifers (Fig. 4.24). Finally, no clear longitudinal trend emerged for some taxa, such as *Lecane closterocerca* and *Brachionus quadridentatus* f. *brevispinus* (Fig. 4.25).

The rest of the zooplankton community consisted mainly of copepod larval stages, with abundances varying between <2 ind L^{-1} (Cre) and 4 ind L^{-1} (Pon; Fig. 4.26a). Densities observed in the first three tributaries did not differ significantly from those measured in the Po River. On the contrary, in the Mincio River copepods reached an abundance of 13 ind L^{-1}. Cladocerans occurred only occasionally in the Po and in the two uppermost tributaries, never exceeding 1 ind L^{-1} (Fig. 4.26b). In the Oglio and Mincio, total cladoceran abundances over 1 and 2 ind L^{-1} were found, respectively.

The Shannon Diversity Index ranged between 2.56 (Ser) and 3.06 (Rea); despite some exceptions (especially Via and Bor), a declining trend in the downstream direction emerged (Fig. 4.27). In the tributaries, diversity ranged between 2.14 (Ticino) and 2.91 (Oglio).

Non-planktonic organisms, mainly nematodes, reached the highest abundances in the most upstream stations, with a maximum of about 5 ind L^{-1} at Cor; on the contrary, the lowest value was recorded at the most downstream site (Ser, ca. 2 ind L^{-1}; Fig. 4.28a).

Bivalve veligers started to occur in plankton samples only at the station of Cre (<1 ind L^{-1}). They tended to slightly increase moving downstream, with maximum abundances of about 2 ind L^{-1} at the two last sampling sites (Fig. 4.28b).

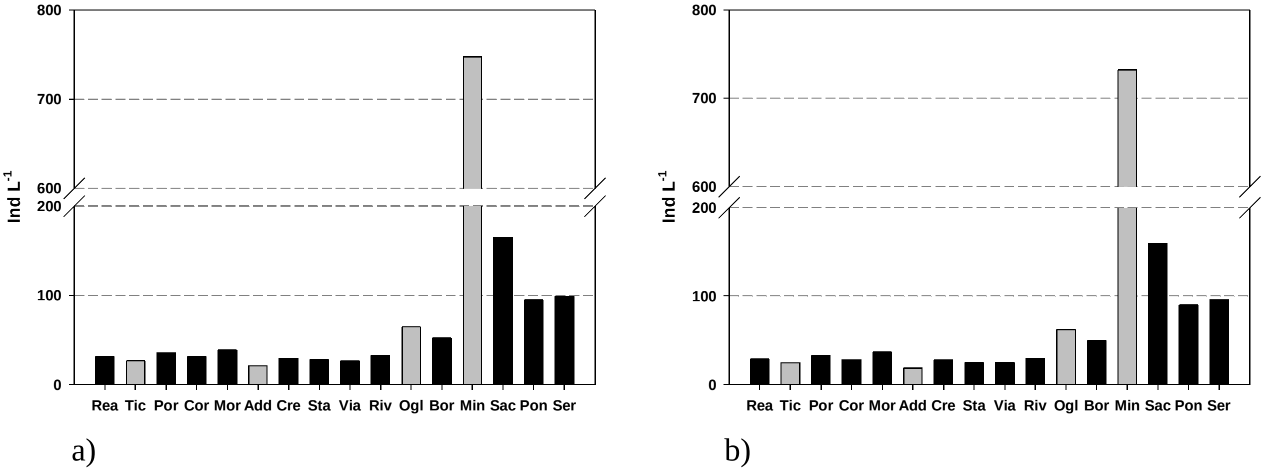


Fig. 4.19 - Total zooplankton density (a) and total rotifer density (b) recorded at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

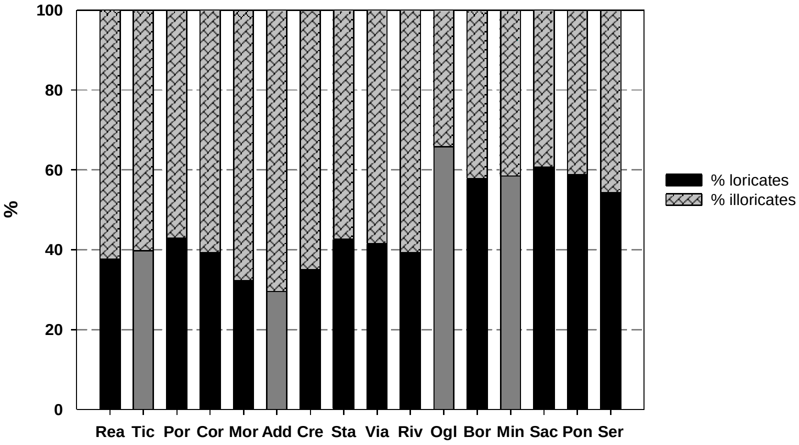


Fig. 4.20 - Percentage of loricate vs. illoricate rotifer taxa recorded at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

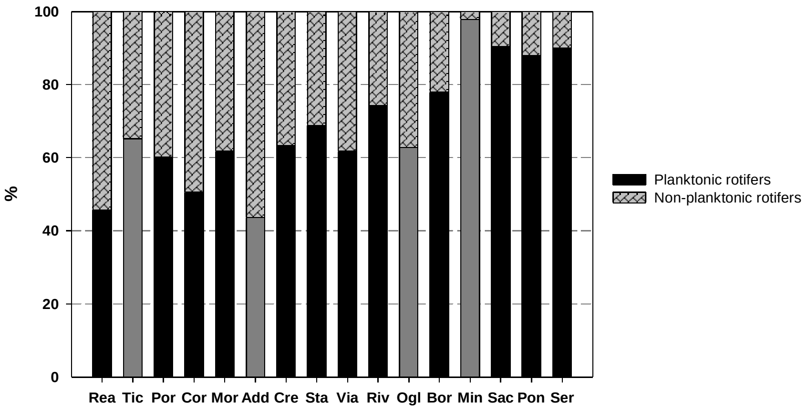


Fig. 4.21 - Percentage of planktonic vs. littoral/epibenthic rotifer taxa recorded at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

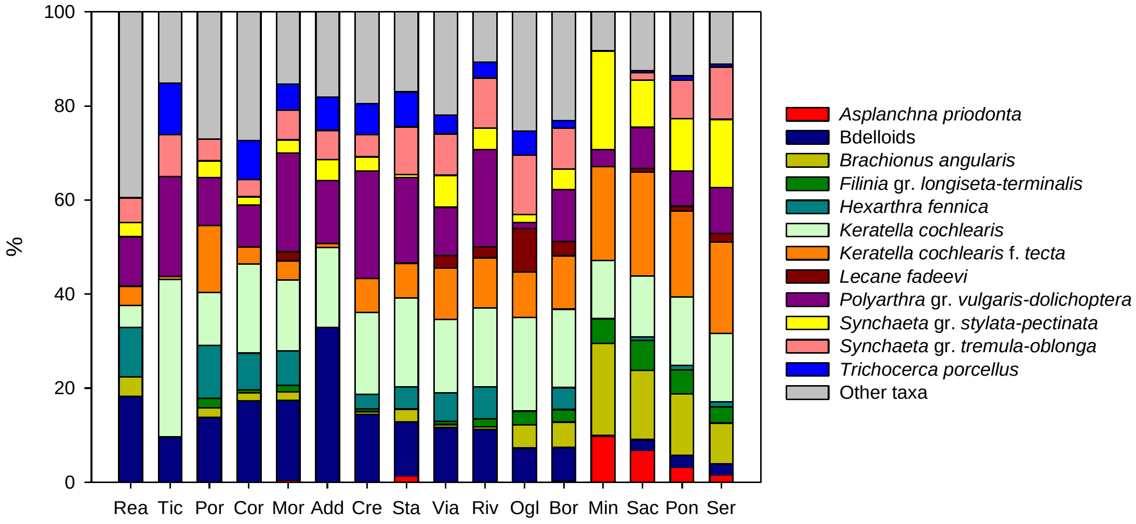
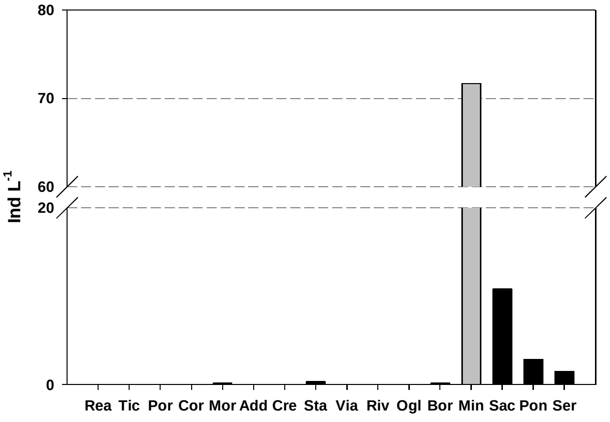
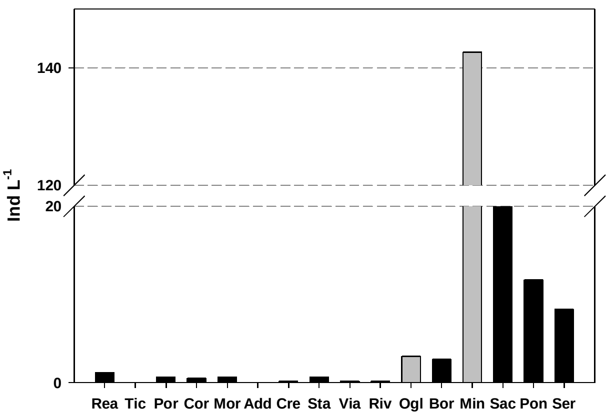


Fig. 4.22 - Percentage composition of the rotifer assemblage recorded at 12 stations along the Po River and in four tributaries in May 2010.



a)



b)

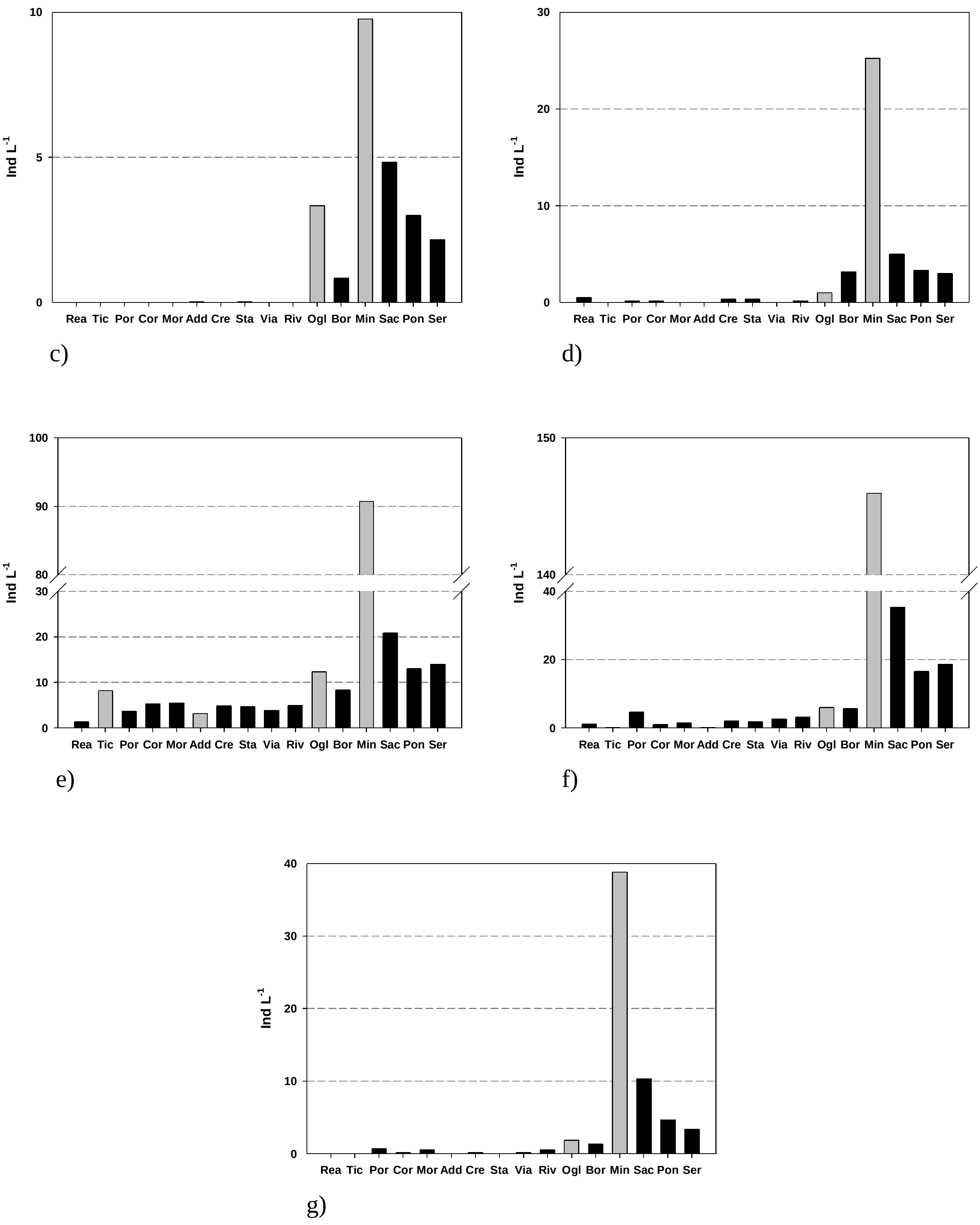


Fig. 4.23 - Density of some rotifer taxa recorded at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010; a) *Asplanchna priodonta*; b) *Brachionus angularis*; c) *B. budapestinensis*; d) spined *B. calyciflorus*; e) *Keratella cochlearis*; f) *K. cochlearis* f. *tecta*; g) *Filinia* gr. *longiseta-terminalis*.

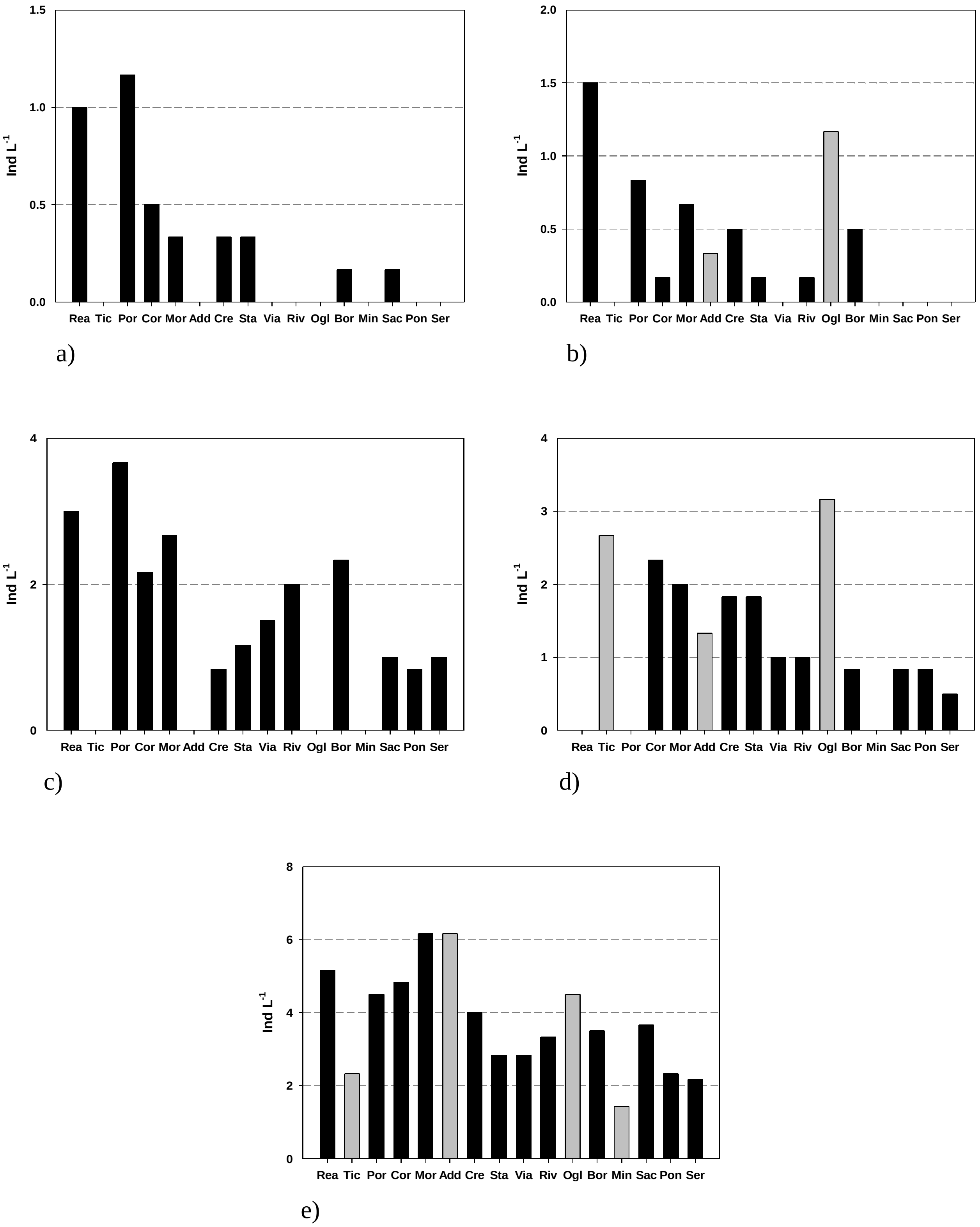
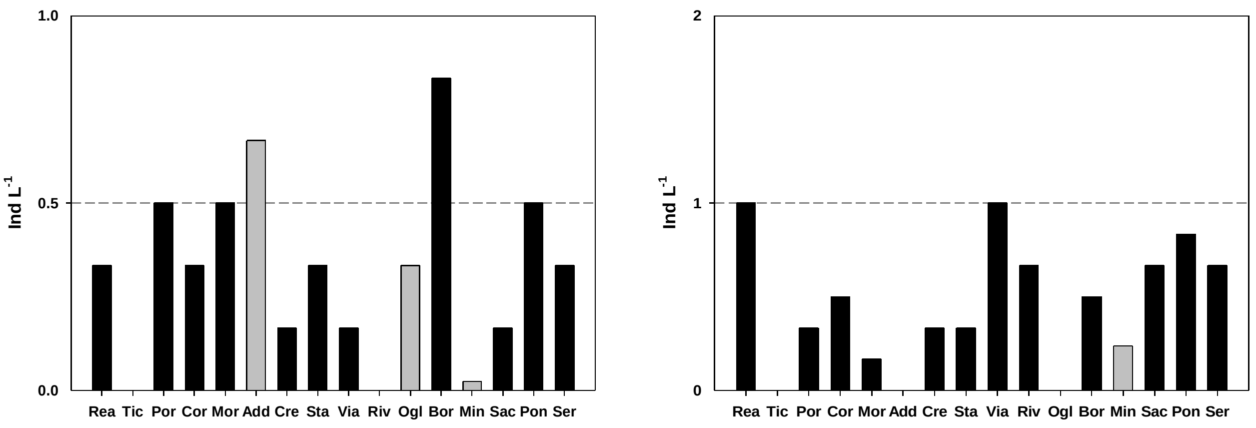
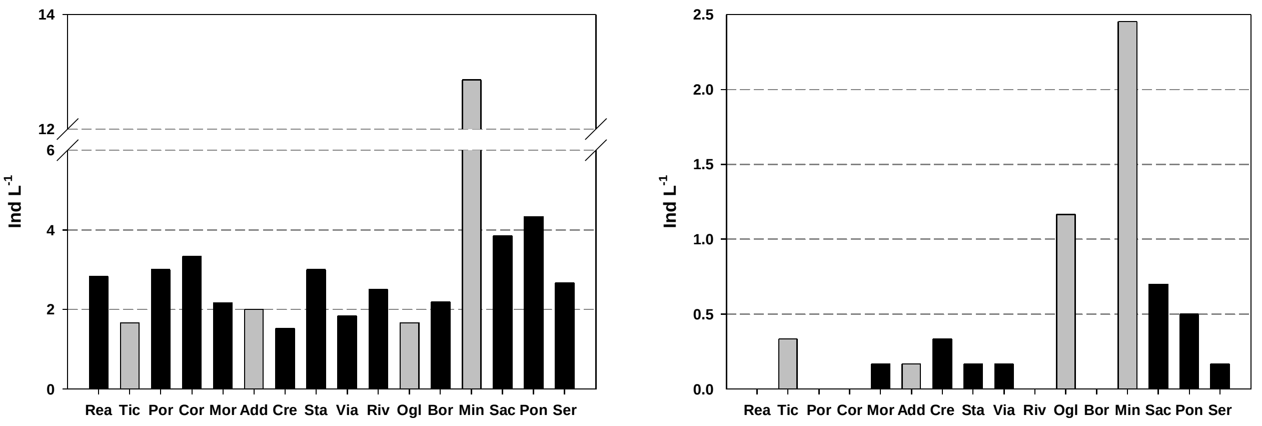


Fig. 4.24 - Density of some rotifer taxa recorded at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010; a) *Lecane luna*; b) *Lepadella patella*; c) *Hexarthra fennica*; d) *Trichocerca porcellus*; e) bdelloids.



a) b)

Fig. 4.25 - Density of some rotifer taxa recorded at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010; a) *Lecane closterocerca*; b) *Brachionus quadridentatus* f. *brevispinus*.



a) b)

Fig. 4.26 - Total copepod (a) and cladoceran (b) density recorded at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

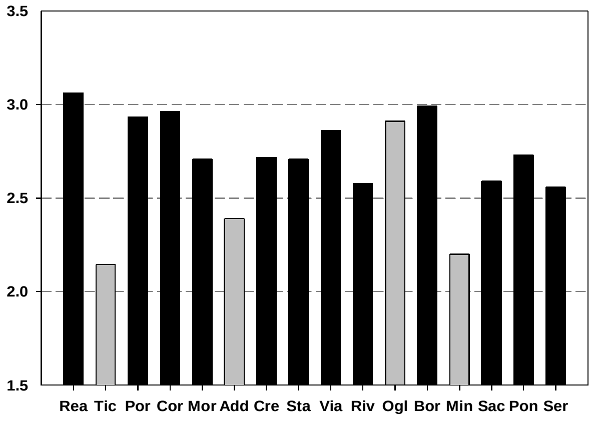
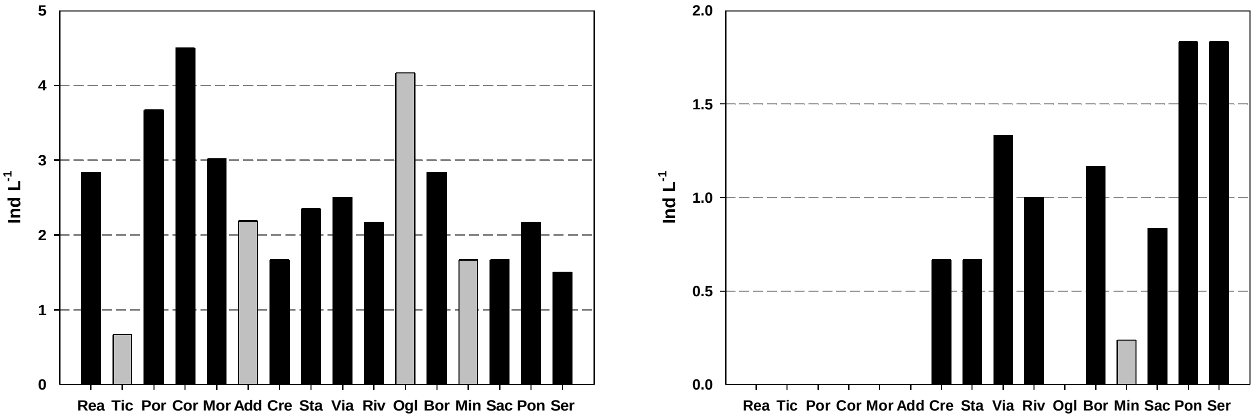


Fig. 4.27 - Shannon Diversity Index calculated for the zooplankton assemblage at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.



a) b)

Fig. 4.28 - Density of non-planktonic organisms (a) and bivalve veligers (b) recorded at 12 stations along the Po River (black bars) and in four tributaries (grey bars) in May 2010.

4.4 Discussion and Conclusions

Discharge peaks in the order of magnitude of those recorded in the first half of May 2010 are often observed in the Po River as a result of spring snowmelt and heavy rainfall events (Zanchettin et al., 2008). Nonetheless, no precipitation occurred in the days immediately preceding and during the sampling experiment, and flow rates remained relatively stable around values comparable to the monthly average discharge measured in May in the period 1918-2002 (~ 2000 m^3 s^{-1} at Pontelagoscuro; Syvitski & Kettner, 2007). The same long-term monthly average calculated for August is about 1000 m^3 s^{-1} at Pontelagoscuro, where base-flow conditions are typically in the range of 700-800 m^3 s^{-1} (loc. cit.). Accordingly, the August 2011 survey was carried out during a drought phase, an event that typically occurs in summer due to low precipitation and massive water withdrawals for agricultural irrigation. A recent analysis of long-term hydrometeorological data on the Po River Basin has revealed that prolonged summer droughts are becoming more and more frequent, likely as a result of a downward shift in precipitation and a concurring upward shift in evapotranspiration since the 1920s (Zanchettin et al., 2008).

While for the May 2010 survey a very close agreement between observed and simulated discharge values was obtained (Fig. 4.5a), in August 2011 an overestimation of actual discharge occurred in the final stations (Fig. 4.5b). This was most likely due to unexpected management activities on the deep sub-alpine lakes that can considerably influence flow variability but are not taken into account by model simulations. Nevertheless, there is no direct proportionality between river discharge and water velocity, so that a rise in the former generally translates in a correspondent lower increase in the latter. Consequently, the entity of the error between actual and simulated water velocities can be assumed to be lower than that recorded between observed and simulated discharge values.

No evident longitudinal pattern could be detected for most of the hydrochemical variables during the May survey, and for some of them, such as water temperature and oxygen content, fluctuations appeared to be more related to the time of the day in which sampling took place. Water residence time during spring conditions (less than five days to cover a 330-km distance) is probably too short to allow local biogeochemical processes to significantly affect water quality during downstream transport, resulting in relatively homogeneous longitudinal hydrochemical features. Nevertheless, a slight downstream increase in conductivity was observed, as it is often the case in large rivers with heavily human-impacted watersheds (e.g. Ietswaart et al., 1999). The four tributaries exhibited rather contrasting hydrochemical characteristics. The uppermost tributary, the Ticino River, had lower water temperature, conductivity and alkalinity as well as lower chlorophyll-*a* and suspended particulate matter in comparison to the values measured in the Po River. The Adda River also had lower temperature and suspended matter than the Po, but comparable values of conductivity, alkalinity and main inorganic nutrients. Nevertheless, those differences did not seem strong enough to have a detectable effect on the Po water chemistry, probably because of the relatively low average discharge levels of the two tributaries (350 and 190 m^3 s^{-1}, respectively) when compared to those of the Po itself. The Oglio River had strikingly higher conductivity and nitrate concentrations than the Po, which might be the reason for the slight increase in both variables observed immediately downstream of the Oglio confluence (Figs. 4.9a and 4.13), despite an average discharge of only 135 m^3 s^{-1}. Finally, the Mincio River stood out for its peculiar characteristics: the high loads of inorganic nutrients, combined with high water temperature and low suspended particulate matter, as a result of negligible current velocity in the lower trait of the river (see below), created favourable conditions for algal production, as shown by the high pH and chlorophyll-*a* content and by the oxygen oversaturation conditions (Figs. 4.8a, 4.12a and 4.17).

Contrary to what has been observed in spring, a clear downstream increase in water temperature was detected in August, even after accounting for daily fluctuations, together with an increase in the concentration of suspended particulate matter, as it is often reported in the potamal trait of large rivers (Zimmermann-Timm et al., 2007; Scherwass et al., 2010). pH and oxygen saturation levels were mainly related to the daytime of sampling, with the highest values generally recorded in the afternoon or early evening, when primary production was at its peak or just after it. Accordingly, the lowest values were measured during the night or early morning.

Total zooplankton abundance remained constant along the Po until the confluence of the Mincio River. This tributary hosted an exceptionally abundant zooplankton community, which resulted in a significant increase in total zooplankton densities in the Po River downstream of its inflow. The Mincio lower course is highly regulated and artificially modified. In particular, below the Garda lake outlet four hydroelectric power plants were constructed and downstream of them the river enters the city of Mantova and forms three artificial reservoirs (Fig. 4.4). Moreover, along its course a large number of dams, spillways, shiplocks and other hydraulic engineering structures aimed at regulating water level were built. The result is a system where current is extremely impaired and slowed down, creating favourable conditions for phytoplankton and zooplankton massive development. As a consequence, despite an average discharge of only 50 m^3 s^{-1}, the influence of this tributary on the Po River zooplankton was still detectable as far as 100 km downstream of its mouth (Fig. 4.19). The Mincio did not only affect zooplankton abundance in the Po River, but also its taxonomic composition, which once again remained rather constant until the Mincio confluence, while after it some major changes in the relative dominance of the most abundant taxa occurred (Fig. 4.22). As a result, the community composition recorded downstream of the Mincio inflow was more similar to the assemblage found in the tributary than to that found in the upstream stations of the Po River itself.

To a lesser extent, the Oglio seemed to affect the Po River community composition too, as shown by the increase in the share of loricate taxa downstream of its mouth (Fig. 4.20). This was mainly due to the higher abundances attained by species of the genus *Brachionus* in the Oglio and later in the Mincio (Fig. 4.23). In particular, in the Mincio River a few taxa made up a large proportion of the rotifer assemblage, that is *B. angularis*, *K. cochlearis* f. *tecta* and *Synchaeta* gr. *stylata-pectinata*, resulting in a reduced overall diversity (Fig. 4.27). On the contrary, the Oglio hosted a more diverse and even assemblage, probably due to the higher turbulence and turbidity that acted as disturbance factors, preventing the development of a structured community with few taxa dominating over the others (De Leo & Ferrari, 1993). As a consequence, a marked increase in community diversity was observed just downstream of the Oglio confluence, but in general, diversity tended to decrease in the downstream direction (Fig. 4.27). This pattern, together with the clear downstream shift from a dominance of benthic/periphytic taxa to the prevalence of pelagic ones (Fig. 4.21), can probably be ascribed to the progressive longitudinal decrease in turbulence, resulting in both a reduction of resuspension of organisms from the bottom and more favourable conditions for the development of a truly planktonic community (Zhou et al., 2008.).

To sum up, zooplankton abundance and composition did not show significant changes during downstream transport along the considered river stretch until the confluence of the Mincio River, similarly to what has been reported in previous Lagrangian studies conducted on the River Rhine under comparable hydrometeorological conditions (de Ruyter van Steveninck et al., 1992; Ietswaart et al., 1999). Spring flow rates appear thus to be unsuitable for plankton growth in the main channel, as a result of low water residence times and unfavourable physico-chemical conditions. The extremely high zooplankton densities found in the Mincio River are most likely due to "*quasi*-lentic" conditions caused by dams and other hydraulic retention structures that strongly alter river hydrology.

River regulation and artificialization may thus deeply affect also biotic components of the riverine system that are often neglected by standard monitoring programs, although they can play a significant role in the functioning of lotic ecosystems.

The analysis of samples collected in August 2011 should shed some light on plankton longitudinal dynamics under summer low flow rates, when doubled water residence times, higher primary production and lower turbulence and turbidity are expected to provide suitable conditions for actual growth of zooplankters in the main channel.

5. Role of hydrological discontinuities and inshore retention habitats: impacts of a main-channel dam on the riverine zooplankton assemblage (the Isola Serafini case study)

5.1 Introduction

Dams have been built along most of the world's large rivers for hydroelectric power production, flood control, navigation, water supply and irrigation (World Commission on Dams, 2000). As a consequence, riverine ecosystems face deep alterations, such as reduction in current velocity and increase in water residence time, enhanced sedimentation rates, thermal stratification of the water column, impairment of fish migration to spawning grounds, increase in primary production and overall alteration of the biogeochemical processes that regulate nutrient cycles (Stanford & Ward, 1979; Friedl & Wuest, 2002; Allan & Castillo, 2007). Consequently, the impact of dam construction on river systems has received increasing attention by the scientific community (Hart & Poff, 2002). However, most surveys have focussed on biogeochemistry, macroinvertebrates, fish and macrophytes, while zooplankton have been investigated in relatively few studies (Allan & Castillo, 2007). Even though some works did not detect any significant effect related to the presence of dams along a river on the resident zooplankton community (Thorp et al., 1994), most of the relevant studies reported an increase in zooplankton abundance and in the relative contribution of microcrustaceans in dam reservoirs as a result of decreased water velocity and enhanced residence time (Pourriot et al., 1997; Havel et al., 2009; Kentzer et al., 2010). Since zooplankton represent a fundamental resource for larval fish (King, 2004), a shift from rotifer to crustacean dominance could have a significant impact on the river food-web downstream of the reservoir by affecting the diet of size-selective fish (Havel et al., 2009).

Nevertheless, while zooplankton drifting from reservoirs were shown to be an important food resource for downstream invertebrate and vertebrate predators (Chang et al., 2008; Welker & Walz, 1998), microcrustaceans exported from artificial impoundments were often observed to dramatically decrease once they enter the main river channel (Akopian et al., 2002; Havel et al., 2009). This is not only due to predation but also to their poor adaptation to conditions of turbulence and turbidity commonly found in the free-flowing sections of large rivers (see General Introduction in Chapter 1).

Significant shifts in plankton abundance and composition can be determined not only by longitudinal discontinuities along the river course, such as main-stem dams, but also by the lateral heterogeneity of the river channel (Thorp et al., 2006). Generally, most studies on river zooplankton have focussed on large-scale longitudinal changes, based on samples taken from the main stream, while few have considered small-scale transverse variations in community structure (Viroux, 1999 and references therein).

According to the Inshore Retention Concept, formulated by Schiemer et al. (2001), inshore zones with increased water residence time are critical areas for the development of abundant zooplankton and fish populations, and they may function as inocula of organisms to the main channel, when water exchange is enhanced. A similar concept was developed for phytoplankton by Reynolds & Descy (1996). Shoreline slackwaters are in fact often characterized by slower current speed, higher temperature and presence of macrophytes that might represent effective refugia for zooplankton from predators (Schiemer et al., 2001). These differences in habitat characteristics between inshore and mid-channel zones depend on the river geomorphology and hydrological regime and may result in contrasting patterns of zooplankton abundance and diversity. For example, examining the lateral distribution of river plankton in the Meuse, Marneffe et al. (1996) observed the maxima in algae and zooplankton close to the banks. Similarly, Thorp et al. (1994) recorded higher zooplankton densities in the littoral zone of the Ohio River than in the mid-channel during low-flow conditions, while Shiel et al. (1982) found the opposite trend in the River Murray in Australia. Reckendorfer et al. (1999) identified potential storage zones in the Danube River that may affect zooplankton growth rates and distribution, while Viroux (1999) found a marked heterogeneity in the transversal distribution of zooplankton in the rivers Moselle and Meuse.

In order to explore the role played by a longitudinal discontinuity along the river as well as that of shoreline habitats in influencing zooplankton abundance and diversity, this chapter presents the results of a survey carried out on the Po River at the Isola Serafini dam (see below) during summer 2009. The work was conducted in collaboration with other researchers at the Department of Environmental Sciences in the frame of a broader project ("Assessment of pollutant transport and changes in ecological connectivity under damming scenarios in the lowland stretch of the Po River") funded by ARPA Emilia-Romagna and aimed at assessing hydrological, hydrochemical and biological alterations induced by the presence of the Isola Serafini impoundment on the Po River.

As part of the project, the focus of the present PhD work was on the zooplankton community, while hydrochemical analyses have been carried out by another PhD student (Pierobon, 2010).

5.2 Study site: the Isola Serafini dam

The Isola Serafini dam was constructed in the beginning of the 1960s on the Po River, near the town of Monticelli d'Ongina (45° 05' N; 9° 56' E), to generate hydroelectric energy and regulate river flow. The gate-structure dam, built on the natural river bed, diverts water to the hydroelectric power plant along a 11-km artificial canal that rejoins the natural river course downstream of the power plant (Fig. 5.1). The resulting reservoir has a surface area of about 240 ha and hydraulic retention times ranging from 36 h at minimum river discharge (100 $m^3 s^{-1}$) to about 5 h at mean river discharge (~700 $m^3 s^{-1}$ at the dam site; Rossaro, 1988). The maximum diverted flow is 1200 $m^3 s^{-1}$, the useful hydraulic head ranges between 3.5 and 11 m. The power plant has 4 generators with Kaplan turbines, for an overall electric power of 76 MW and a mean annual electric production of about 480 GWh (Brunelli et al., 2003).

Between 1972 and 1982 a series of hydrobiological studies was carried out in this area, focussing on the microcrustacean component of the zooplankton assemblage (Cotta Ramusino & Rossaro, 1974; Rossaro & Cotta Ramusino, 1976; Rossaro, 1976, 1981 & 1988; see Chapter 2.2).

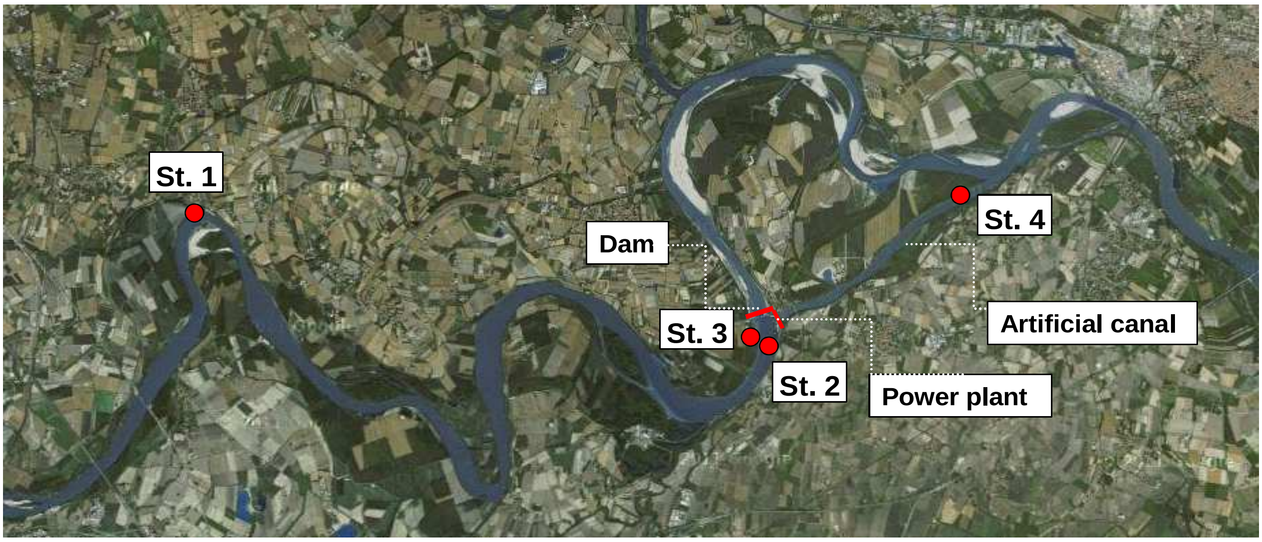


Fig. 5.1 - The Po River at the Isola Serafini dam. Sampling sites are indicated by red circles (Source: Google Maps).

5.3 Materials and Methods

5.3.1 Field sampling and laboratory analyses

Four surveys, at roughly fortnightly intervals, were carried out in July and August 2009, that is in the period when low-flow conditions favourable to biological processes are typically expected.

Samples for analyses of hydrochemistry, phytoplankton and zooplankton were collected at four stations: upstream of the reservoir (station 1); in the center and near the shore of the reservoir (stations 2 and 3, respectively); downstream of the reservoir (station 4; Fig. 5.1). Station 1 was located about 20 km upstream of the reservoir, a distance that was considered sufficient to assume a negligible upstream influence of the impoundment. Station 3 was close to the left shore of the reservoir and it was characterized by lower depth and slower water current in comparison to the center of the artificial basin. The shore was covered by riparian vegetation and macrophytes that especially thrive under summer low-flow conditions. Station 4 was located about 5 km downstream of the dam, in the artificial canal, before the confluence with the natural river meander.

Physico-chemical analyses were performed by another PhD student at the Department of Environmental Sciences and a comprehensive account on the used methods is given in her PhD thesis (Pierobon, 2010).

As for the zooplankton component, which is the focus of this thesis, on each sampling date and at each station two replicate samples were taken from a boat. Collection methods and laboratory analyses were carried out as provided in Chapter 3.1.2. 60 L of water were filtered for each sample.

Daily data of the Po River discharge at the gauging stations of Piacenza (45° 03' N, 9° 42' E; ~ 6 km upstream of station 1), and Cremona (45° 08' N, 12° 02' E; ~ 4 km downstream of station 3) were provided by the Environmental Agency of the Emilia Romagna Region.

5.4 Results

5.4.1 Hydrology

River discharge fluctuated between 446 m^3 s^{-1} (August 2) and 1767 m^3 s^{-1} (June 8) at the station of Piacenza and between 496 m^3 s^{-1} (August 21) and 2006 m^3 s^{-1} (June 11) at the station of Cremona (Fig. 5.2). In particular, peaks exceeding 1000 m^3 s^{-1} were recorded through most of June and in two occasions in the first half of July. Flow levels then remained well below 1000 m^3 s^{-1} until mid-September.

Current speed was halved in the reservoir compared to st. 1, where it ranged between 0.34 and 0.68 m s^{-1}. The highest values (up to 1.13 m s^{-1}) were always recorded at st. 4.

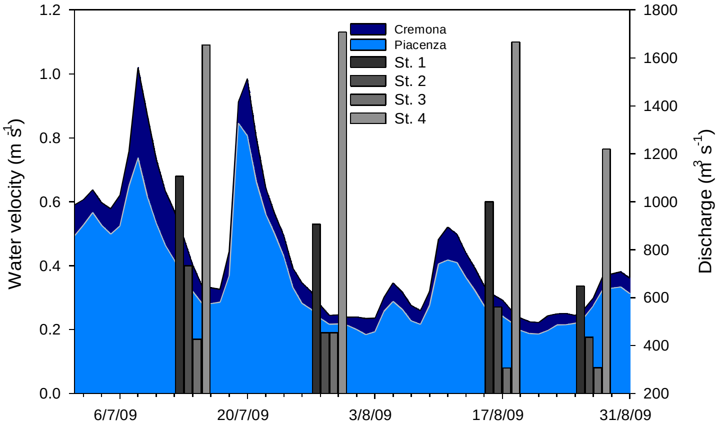


Fig. 5.2 - Mean daily river discharge at the gauging stations of Piacenza and Cremona and water velocity measured at the sampling sites.

5.4.2 Hydrochemistry

Hydrochemical analyses were performed as part of another PhD work (Pierobon, 2010), from which Table 5.1 has been drawn. A brief summary of the main hydrochemical results will be given, in order to support the interpretation of zooplankton data. A far more detailed report and discussion on these data can be found in Pierobon (2010).

Water temperature in the reservoir (st. 2) ranged between 24.1 and 26.1°C and it generally was 0.4-0.7°C higher than that recorded in the upstream site (st. 1). Downstream of the reservoir (st. 4), a further increase of about 0.2-0.4°C was observed. Near the reservoir shore (st. 3) in July water temperature was comparable to that measured in the center, while in August it was about 1°C higher. No thermal stratification in the reservoir was ever detected.

At st. 1 pH varied between 7.8 and 8.3, while at all the other stations a peak of 8.7-8.8 was reached on August 17.

At all sites a progressive increase in oxygen content was observed from July to August. While on July 14 oxygen concentrations were relatively similar at all sites, ranging between 7.3 and 7.7 mg L^{-1}, on the other sampling dates they were consistently higher at st. 2 than at st. 1. Similarly, concentrations at st. 3 were always higher than those recorded at st. 2, with a peak of 16.6 mg L^{-1} on August 17. Values measured at st. 4 were comparable to those of st. 2.

DIN fluctuated between 2210 and 1377 µg L^{-1}, with no remarkable differences among stations. TN ranged between 3110 and 5761 µg L^{-1} at st. 1, while at st. 2 it was comprised between 2689 and 4403 µg L^{-1}, with a reduction of 1359 µg L^{-1} at st. 2 in comparison to st. 1 on August 17. At st. 3 and 4 TN was generally lower than at st. 1.

SRP varied between 10 and 57 µg L^{-1} at all stations. TP concentrations were generally 10-15 µg L^{-1} lower at st. 2 than at st. 1. TP tended then to increase again at st. 4, reaching values similar to those measured at st. 1.

DRSi levels in the range 2478-4141 µg L^{-1} were measured at st. 1. Consistently lower concentrations were found at st. 2, especially in August, with a difference of 379-440 µg L^{-1}. St. 3 and 4 showed values comparable to those recorded at st. 2.

A decrease in SPM of up to 80% was observed in the reservoir with respect to the upstream site.

Chl-*a* content sharply increased over time at all sites, with maxima on August 17. Values recorded at st. 1 and 2 were comparable in the first three dates, while on August 27 concentrations of 36.3 and 50.0 µg L^{-1} were measured at st. 1 and 2, respectively. At st. 3 a peak of 104.8 µg L^{-1} was detected on August 17 while at st. 4 values were similar to those recorded at st. 2 (Fig. 5.3).

Table 5.1 - Hydrochemical variables measured during summer 2009 at the Isola Serafini sampling sites (modified from Pierobon, 2010).

St. 1 – upstream

Date	**Temp.**	**Cond.**	**pH**	**DO**	**SPM**	**DRSi**	**SRP**	**TP**	**DIN**	**TN**	**Chl-*a***
	℃	µS cm^{-1}		mg L^{-1}	mg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}
14/07/09	23.7	380.0	7.8	7.34	34.50	4141	51.0	160.1	2210	3569	7.4
29/07/09	24.3	380.0	8.1	8.31	18.83	3146	18.1	121.6	1599	3110	40.7
17/08/09	25.4	387.0	7.8	9.50	25.20	2478	15.8	142.5	1279	3353	96.9
27/08/09	24.7	400.0	8.3	8.14	10.08	3604	14.3	129.2	1502	5762	36.3

St. 2 – reservoir

Date	**Temp.**	**Cond.**	**pH**	**DO**	**SPM**	**DRSi**	**SRP**	**TP**	**DIN**	**TN**	**Chl-*a***
	℃	µS cm^{-1}		mg L^{-1}	mg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}
14/07/09	24.1	376.0	7.8	7.56	6.07	4141	56.1	149.2	2082	3937	10.4
29/07/09	24.8	381.0	8.4	10.37	7.97	2857	9.3	109.9	1707	2689	39.7
17/08/09	26.1	377.0	8.7	13.05	16.47	2038	12.8	128.3	1391	3251	87.7
27/08/09	25.4	403.0	8.4	10.29	8.43	3225	12.2	115.8	1503	4403	50.0

St. 3 – reservoir shore

Date	**Temp.**	**Cond.**	**pH**	**DO**	**SPM**	**DRSi**	**SRP**	**TP**	**DIN**	**TN**	**Chl-*a***
	°C	µS cm^{-1}		mg L^{-1}	mg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}
14/07/09	23.9	376.0	7.8	7.75	19.55	3903	51.1	148.4	2086	3569	16.2
29/07/09	25.2	378.0	8.6	11.16	11.57	2695	13.1	103.2	1435	2534	37.7
17/08/09	27.2	355.0	8.8	16.62	35.83	1991	13.4	150.1	1181	3090	104.8
27/08/09	26.3	397.0	8.4	11.61	66.25	2973	14.9	165.1	1377	3184	38.5

St. 4 – downstream

Date	**Temp.**	**Cond.**	**pH**	**DO**	**SPM**	**DRSi**	**SRP**	**TP**	**DIN**	**TN**	**Chl-*a***
	°C	µS cm^{-1}		mg L^{-1}	mg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}	µg L^{-1}
14/07/09	24.3	380.0	7.8	7.59	14.05	4165	56.5	134.2	2155	3314	9.7
29/07/09	25.2	384.0	8.6	10.52	10.87	2919	17.6	115.8	1554	2833	36.6
17/08/09	26.6	375.0	8.7	12.76	20.87	2230	13.8	143.4	1478	2586	96.0
27/08/09	25.2	399.0	8.3	9.41	21.07	3097	15.3	123.3	1455	2947	46.1

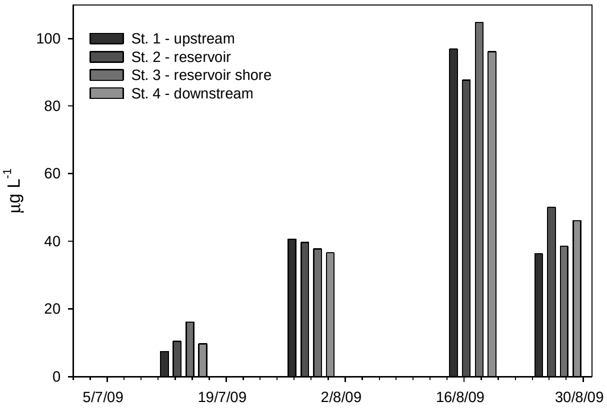


Fig. 5.3 - Chlorophyll-*a* concentrations recorded at the Isola Serafini stations during summer 2009.

5.4.3 Zooplankton assemblage

A total of 78 zooplankton taxa were found: 65 rotifers, 8 cladocerans and 5 copepods (see Annex 1). Total zooplankton density increased with time at all sites, with maxima during August (Fig. 5.4a). Abundances varied between 10 and 80 ind L^{-1} at st. 1 and 3, while at st. 2 and 4 densities ranged between 6 and 160 ind L^{-1}. Rotifers were always the dominant component in terms of abundance and their share tended to increase with time, reaching peaks of over 90% on August 17 (Figs. 5.4b and 5.6a). Copepod densities varied between less than 1 ind L^{-1} (August 17, st. 1) and 6 ind L^{-1} (August 27, st. 1) at the first three stations, with the highest values recorded in August (Fig. 5.5a); at st. 4 copepods showed a clear increasing trend with time, reaching a peak of 15 ind L^{-1} on August 27.

Cladocerans were absent or only occasionally found in July, while in August abundances ranged between <1 and 3 ind L^{-1}, except for a peak of ca. 5 ind L^{-1} detected at st. 3 on August 17 (Fig. 5.5b).

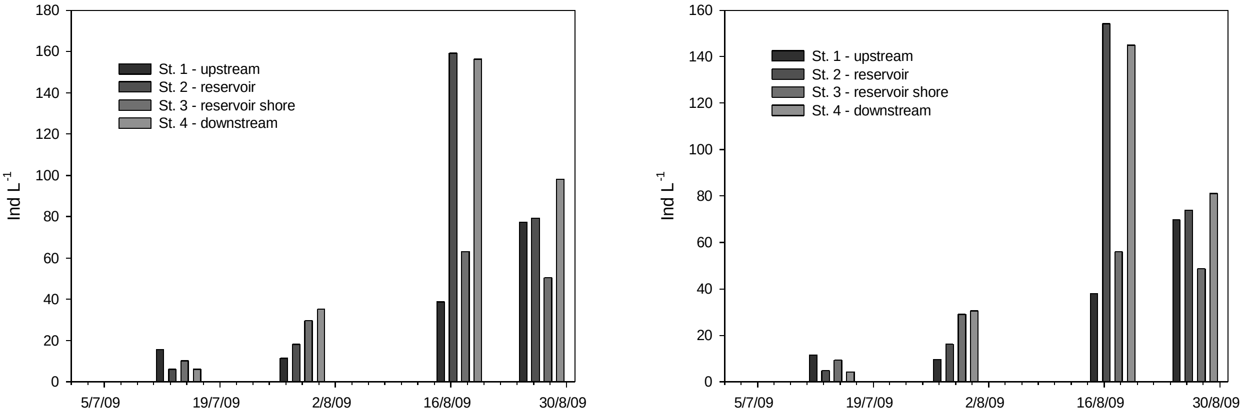
As for the rotifer component, percentage of loricate taxa varied between 35 and 76% at the four stations on July 14. It then increased with the advancing season, reaching values of 76-97% in August (Fig. 5.6b). The same temporal trend was observed for the total number of zooplankton taxa, which ranged between 10 and 30 at st. 1, 2 and 4, while at st. 3 species richness was comprised between 32 and 48 (Fig. 5.7a). The Shannon Diversity Index ranged between 1.91 and 2.64 at st. 1, 2 and 4, with st. 4 tending to show the lowest diversity, while at st. 3 values fluctuated between 2.18 and 2.85 (Fig. 5.7b).

Fig. 5.8 shows the percentage composition of the rotifer assemblage in terms of the most abundant taxa.

Samples collected in July displayed the most evident differences among the stations. On July 14 the rotifer assemblage at st. 1 and 4 was dominated by bdelloids and *Lecane* species, while in the reservoir *Keratella cochlearis* and *K. cochlearis* f. *tecta* accounted for up to 52% of the community (Fig. 5.8a). On July 29 species of the genus *Brachionus* made up the largest proportion of the assemblage at st. 1 and 4, while in the reservoir their share was reduced in favour of that of *K. cochlearis* (Fig. 5.8b). In August *Brachionus quadridentatus* largely dominated at st. 1, 2 and 4, while st. 3 showed a more even composition of the rotifer assemblage (Figs. 5.8c-d).

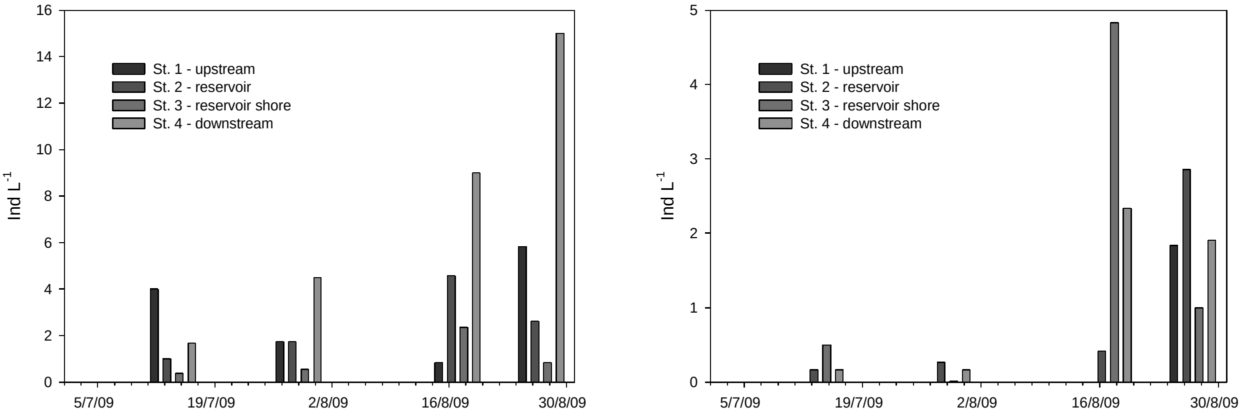
Non-planktonic organisms, mainly insect larvae and nematodes, tended to be most abundant at st. 1 and 4, with maxima of about 1 and 3 ind L^{-1}, respectively (Fig. 5.9a). Nevertheless, a value of about 3 ind L^{-1} was recorded in the reservoir on August 17.

Bivalve veligers never exceeded 2 ind L^{-1} at st. 1, 2 and 3, while at st. 4 a peak of 13 ind L^{-1} was recorded on August 17 (Fig. 5.9b).



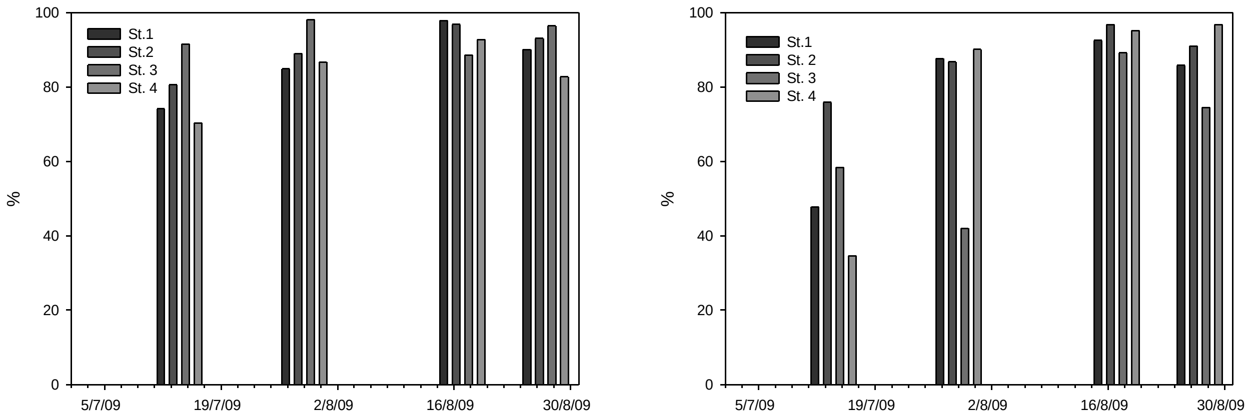
a) b)

Fig. 5.4 - Total zooplankton (a) and total rotifer (b) density recorded at the Isola Serafini stations during summer 2009.



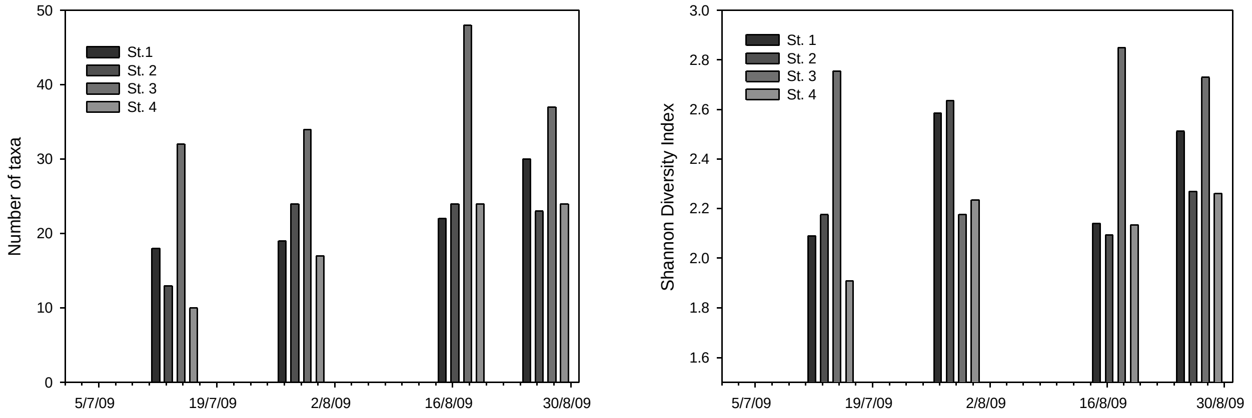
a) b)

Fig. 5.5 - Total copepod (a) and total cladoceran (b) density recorded at the Isola Serafini stations during summer 2009.



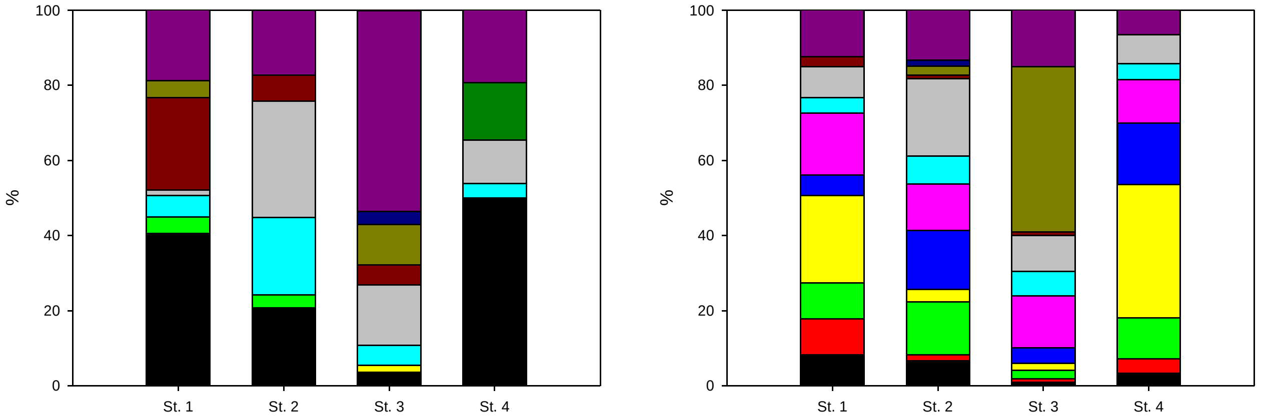
a) b)

Fig. 5.6 - Percentage occurrence of rotifers in the zooplankton (a) and percentage of loricate taxa over the total rotifer assemblage (b) at the Isola Serafini stations during summer 2009.

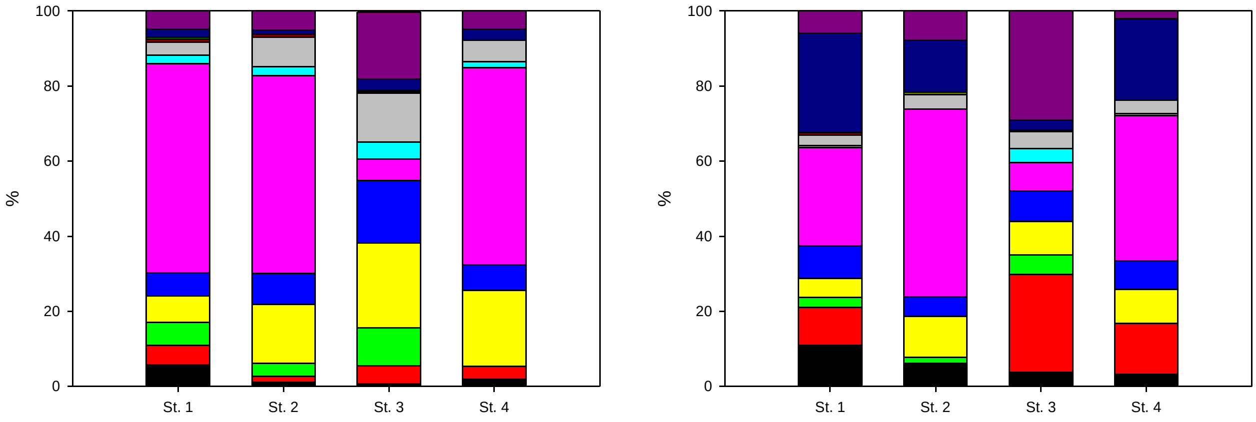


a) b)

Fig. 5.7 - Total number of zooplankton taxa (a) and Shannon Diversity Index (b) at the Isola Serafini stations during summer 2009.



a) b)



c) d)

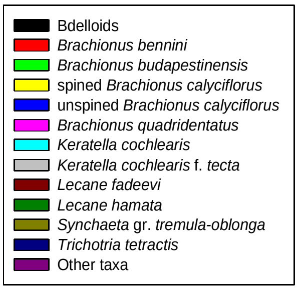
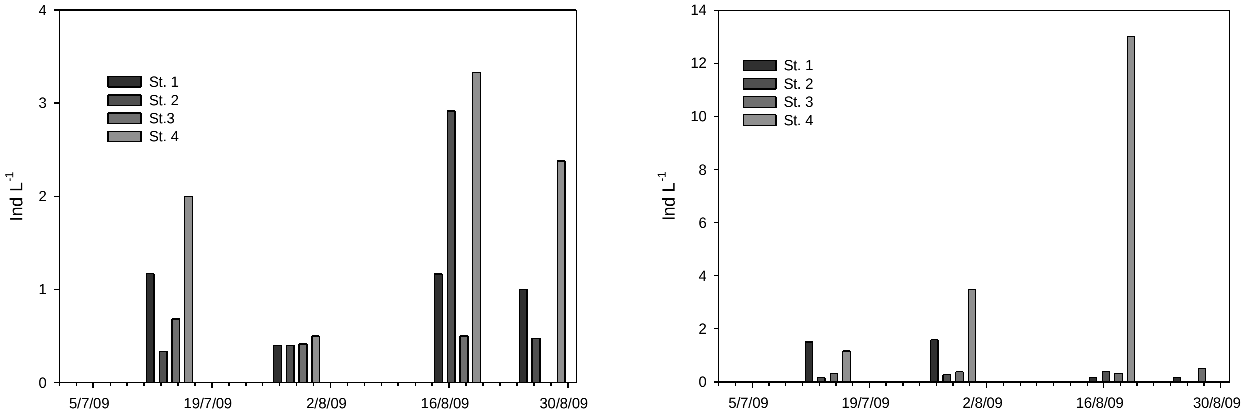


Fig. 5.8 - Percentage composition of the rotier assemblage recorded at the Isola Serafini stations on July 14 (a), July 29 (b), August 17 (c) and August 27 (d).



a) b)

Fig. 5.9 - Density of non-planktonic organisms (a) and bivalve veligers (b) recorded at the Isola Serafini stations during summer 2009.

5.5 Discussion and Conclusions

The presence of the dam strongly reduced current velocity in the reservoir, with a consequent decrease in the concentration of total suspended solids and a slight increase in water temperature (Table 5.1). A shift in the physico-chemical characteristics of the riverine environment towards "more lentic" conditions has often been shown to enhance phytoplankton and zooplankton production (Reynolds & Descy, 1996; Akopian et al., 1999; Zhou et al., 2008). Nevertheless, chlorophyll-*a* concentrations in the reservoir center were generally comparable to those found upstream of it and only in the end of August the reservoir and the artificial canal exhibited a higher chlorophyll-*a* content than that measured at the upstream station (Table 5.1 and Fig 5.3). This might be due to the fact that samples were collected near the surface and especially under reduced turbulence and turbidity algae might tend to avoid the uppermost layers under mid-day high irradiance conditions. Nonetheless, in the last three dates clorophyll-*a* was measured in deeper layers as well and it was always not significantly different from surface concentrations (data not shown), which, together with the lack of thermal stratification, points towards a well-mixed water column (Pierobon, 2010). Despite the reduction in current velocity, water residence time probably remained too high in the reservoir for most of the season to further promote phytoplankton growth, and only during the low water phase that occurred in the end of August the hydraulic retention time decreased sufficiently to exert a detectable positive effect on algal production. This is also supported by zooplankton data, showing that only under August low discharge rates a more than three fold increase in rotifer density and a slight increase in the microcrustacean component occurred both in the reservoir and in the artificial canal, compared to the upstream site (Figs. 5.4 and 5.5). Previous studies have reported a substantial enhancement of zooplankton production in artificial impoundments along the course of large rivers, and a shift from an upstream dominance of rotifers to an increased contribution of microcrustaceans (Pourriot, 1997; Akopian et al., 2002; Havel et al., 2009; Kentzer et al., 2010), but contrary to what had been hypothesized, no massive development of microcrustaceans was observed above the Isola Serafini dam. This once again suggests that, despite favourable conditions in terms of food availability and reduced turbulence and turbidity, water residence time played a major role in impairing the development of organisms with relatively low growth rates such as cladocerans and copepods.

Contrary to what has been reported by other studies, where an increase in community diversity and a shift from benthic to pelagic taxa has been observed in artificial impoundments (Zhou et al., 2008; Kentzer et al., 2010), in the present survey species richness and overall diversity did not appear to be influenced by the presence of the dam (Fig. 5.7). As for the taxonomic composition of the rotifer assemblage, even during low-flow phases no major changes in the relative abundances of the dominant taxa could be detected (Fig. 5.8). Only in July a remarkable decrease in the share of bdelloids and *Lecane* species in favour of that of species of the genus *Keratella* occurred in the reservoir, probably as a result of the dampening of resuspension of benthic organisms due to reduced turbulence.

Surveys aimed at evaluating the mortality rate of planktonic organisms passing through the turbines of hydroelectric power plants revealed that contact with mechanical structures and cavitation in the turbines may result in the death of a significant portion of zooplankters, especially microcrustaceans (Postoev, 1997; Dubovskaia et al., 2004). However, no such effect could be detected in the present work, as abundances of the different components of the zooplankton assemblage in the artificial canal were always comparable to those found in the reservoir center.

Compared to the reservoir center, the shoreline zone exhibited consistently higher water temperature and decreased water velocity (Table 5.1), thus providing a theoretically more favourable habitat for phytoplankton and zooplankton growth (Thorp et al., 1994; Marneffe et al., 1996; Reynolds & Descy, 1996; Ning et al., 2009). Nonetheless, only in two of the four sampling dates an increment in chlorophyll-*a* concentration near the shore was observed when compared to the reservoir center (Table 5.1 and Fig. 5.3).

Moreover, contrary to what has been reported by most of previous studies dealing with lateral complexity of riverine zooplankton (e.g. Thorp et al., 1994; Schiemer et al., 2001; Casper & Thorp, 2007; Ning et al., 2009), rotifer abundance in the shore habitat was comparable or even lower than that found in the middle of the reservoir (Fig. 5.4b). Similar results were obtained by Holst et al. (2002) during a transversal survey on the River Elbe and a possible explanation may be an increased predation rate in lentic shore habitats that are used as refugia by fish larvae (Schiemer et al., 2001). Nonetheless, this hypothesis contrasts with the peak of cladocerans recorded in August near the shore and mainly sustained by the small species *Macrothrix laticornis* (Fig. 5.5b). Increased competition due to massive development of microcrustaceans has been invoked as one of the possible mechanisms responsible for the decrease in the rotifer share in riverine slackwaters

(Reckendorfer et al., 1999; Baranyi et al., 2002). However this does not seem to be the case here as chlorophyll-*a* values remained extremely high during most of the study period and zooplankton densities were not sufficient to determine a significant depletion in food resources, especially in a highly productive river as the Po. In spite of the difficulties in interpreting the observed lateral patterns in zooplankton abundance, it is evident that the assemblage in the shore habitat differed substantially from that found in the mid-channel (Fig. 5.8). A higher share of illoricate rotifer taxa, less adapted to advective conditions (Lair, 2006), was generally found near the shore (Fig. 5.6b) and both species richness and Shannon Diversity were greater than those measured in the main current (Fig. 5.7). This may be attributed to reduced hydrodynamic constraints and to the availability of different microhabitats in the littoral zone, promoting the development of highly diverse invertebrate assemblages (Ward & Tockner, 2001; Ning et al., 2009).

To sum up, results of this work show that the presence of the dam may affect zooplankton growth by disrupting river hydrodynamics, which often represents the major constraint to potamoplankton development. However, the entity of the impact strongly depends on factors such as the hydrological regime and the reservoir hydraulic retention time.

In a deeply channelized river like the Po, the influence of lateral complexity on abundance and diversity of planktonic communities is expected to be rather low and this is assumed to be the case along the free-flowing rectified traits of the potamal reach. However, transversal differences in zooplankton density and composition could be detected in the impounded section, highlighting the role of inshore zones as habitats capable of hosting extremely diverse assemblages. More extensive surveys are needed though, including a greater number of near-shore sites and a higher sampling frequency, together with a quantification of the volume occupied by inshore zones in relation to that of the main channel, in order to determine the actual contribution of lateral habitats and local small-scale hydrogeomorphic variability to the overall riverine biodiversity and plankton biomass.

6. Monogonont rotifers in the Po River: new records for the Italian fauna

6.1 Introduction

Rotifers have long been recognised as a critical component of freshwater ecosystems, yet information on their ecology and distribution is still limited (Wallace et al., 2006). This is due to issues like inadequate taxonomic and molecular knowledge on the phylum, identification difficulties related to phenotypic plasticity and cryptic speciation as well as insufficiency of reliable biogeographical studies, especially in developing countries (Segers, 2008). With approximately 1600 known species, the group Monogononta is the most diverse of rotifers (Segers, 2007). Of them, only about 200 species or species-groups belonging to 46 genera in 20 families are reported in the checklist of the Italian fauna (Braioni & Ricci, 1995). Sixty-five species were reported by earlier studies but not included in the aforementioned checklist (De Ridder & Segers, 1997). In addition to that, 58 more species were recorded by subsequent works (Fontaneto & Melone, 2003; Rossetti et al., 2003; Fontaneto et al., 2004; De Smet, 2007; Fontaneto et al., 2008; Bertani et al., 2009; De Smet, 2009; Rossetti et al., 2009).

In Italy, extensive field research has traditionally been carried out on monogonont rotifers in lentic ecosystems, while a comparatively smaller amount of studies have focussed on lotic communities (e.g. Braioni, 1981; Ferrari et al., 1989; Rossetti et al., 2009). Nevertheless, as it was shown in the present work, rotifer richness is especially enhanced in high-order rivers; this is due to the influence of abiotic constraints like fluctuations in the hydrological regime, that may act as a disturbance factor, promoting equitability and diversity of plankton assemblages. Moreover, the hydrogeomorphic complexity of fluvial systems often provides an extremely diverse array of substrates and microhabitats that favour the development of rich benthic-periphytic assemblages (Ricci & Balsamo, 2000; Thorp et al., 2006). These latter may be subjected to dislodgement and resuspension, especially during high water phases, further enriching the truly planktonic community (Braioni, 1981; Schmid-Araya, 1998). Accordingly, assemblages found in the main current of rivers often derive from a mixture of planktonic organisms and inocula from benthic and periphytic substrates, inshore retention zones, backwaters, periodically inundated floodplain habitats and tributaries. Thus, these assemblages can be considered as representative of the aquatic biodiversity of a much broader area than the sole main river channel.

6.2 Taxonomic account

Surveys carried out in the frame of this PhD work led to the discovery of 24 species of monogonont rotifers new to Italy (i.e. not included in the checklist compiled by Braioni & Ricci, 1995). Among the 17 listed genera, six (*Aspelta*, *Enteroplea*, *Kostea*, *Paradicranophorus*, *Parencentrum* and *Wolga*) are new for the Italian fauna, while three species are new records for the Palaearctic region (Segers, 2007; Tab. 6.1). A summary on the ecology of each species based on the available literature is given below. Most of the records refer to a single or a limited number of specimens occasionally found in plankton samples. Information on temporal patterns, abundance and site of occurrence of each species is provided in Table 6.2 and Fig. 6.3.

Table 6.1 - Taxonomic account and global distribution (*Afr*: Afrotropical region; *Ant*: Antarctic region; *Aus*: Australian region; *Nea*: Nearctic region; *Neo*: Neotropical region; *Ori*: Oriental region; *Pac*: Pacific region; *Pal*: Palaearctic region) of the rotifer taxa reported in this study (according to Segers, 2007). Asterisks indicate new records for the Palaearctic region.

Family	Species	Distribution
Brachionidae	*Brachionus durgae* Dhanapathi, 1974	*Afr, Neo, Ori, Pal*
Epiphanidae	*Rhinoglena frontalis* Ehrenberg, 1853	*Ant, Aus, Nea, Ori, Pal*
Lecanidae	*Lecane elegans* Harring, 1914	*Afr, Neo, Ori, Pac, Pal*
	Lecane fadeevi (Neiswestnova-Shadina, 1935)	*Pal*
	Lecane hastata (Murray, 1913)	*Afr, Aus, Nea, Neo, Ori, Pac, Pal*
	Lecane pyriformis (Daday, 1905)	*Afr, Aus, Nea, Neo, Ori, Pac, Pal*
Lepadellidae	*Lepadella (Xenolepadella) astacicola* Hauer, 1926	*Neo, Pal*
	Lepadella (Lepadella) biloba Hauer, 1958	*Afr, Aus, Neo, Pal*
Notommatidae	**Cephalodella* cfr. *hollowdayi* Koste, 1986	*Neo*
	Cephalodella theodora Koch-Althaus, 1961	*Nea, Pal*
	Cephalodella trigona (Rousselet, 1895)	*Pal*
	Enteroplea lacustris Ehrenberg, 1830	*Aus, Nea, Neo, Ori, Pal*
	Eosphora anthadis Harring & Myers, 1922	*Aus, Nea, Neo, Ori, Pal*
	Notommata cyrtopus cyrtopus Gosse, 1886	*Afr, Ant, Aus, Nea, Neo, Ori, Pac, Pal*

Table 6.1 (cont.)

	**Resticula anceps* Harring & Myers, 1924	*Nea*
Dicranophoridae	*Aspelta circinator* (Gosse, 1886)	*Aus, Nea, Neo, Pal*
	Dicranophorus luetkeni (Bergendal, 1892)	*Afr, Aus, Nea, Neo, Ori, Pal*
	Encentrum wiszniewskii Wulfert, 1939	*Pal*
	Kostea wockei (Koste, 1961)	*Afr, Neo, Pal*
	Paradicranophorus hudsoni (Glascott, 1893)	*Aus, Pal*
	Parencentrum lutetiae (Harring & Myers, 1928)	*Ori, Pal*
Trichocercidae	**Trichocerca braziliensis* (Murray, 1913)	*Afr, Aus, Neo, Ori,*
	Trichocerca tenuior (Gosse, 1886)	*Afr, Aus, Nea, Neo, Ori, Pac, Pal*
Trichotriidae	*Wolga spinifera* (Western, 1894)	*Afr, Aus, Nea, Neo, Ori, Pal*

Brachionus durgae Dhanapathi, 1974 (Fig. 6.1A)

Brachionus durgae was originally described from India (Dhanapathi, 1974). A redescription of the taxon, together with updated information on its distribution, was provided by Segers et al. (1994). It was typically found during summer low-flow conditions in the Po River, although with very modest abundances (less than 1000 ind m^{-3} at both Isola Serafini and Viadana). The species was also found in samples previously collected in the same river reach (summer 2005) and re-examined during this work; this suggests that *B. durgae* has been present in the Po River for many years and was probably confused with similar congenerics in previous surveys. This species has been reported from lakes, permanent and temporary ponds (Segers et al., 1994).

Rhinoglena frontalis Ehrenberg, 1853

The genus *Rhinoglena* comprises four described species (De Smet & Gibson, 2008). Among them, only *R. tokioensis* has been recorded in Italy so far, in a small wetland in the Po River floodplain (Rossetti et al., 2003). *Rhinoglena frontalis* is a cold stenotherm and widespread species (Koste, 1978; De Smet & Gibson, 2008) that typically inhabits small, shallow ponds and temporary floodplain habitats (Schröder, 2005 and refs. therein). It is described as exclusively phytophagous, feeding mainly on unicellular algae (Koste, 1978; Pourriot, 1977) and showing rather slow swimming movements (Ruttner-Kolisko, 1974; Koste, 1978).

Lecane elegans Harring, 1914 (Fig. 6.1B)

Published data on the ecology of this species are lacking. It is reported in rivers (e.g. Koste, 1978; Wang et al., 2009) and floodplain habitats (e.g. Sanoamuang, 1998; Serafim et al., 2003).

Lecane fadeevi (Neiswestnowa-Shadina, 1935) (Fig. 6.1C)

Lecane fadeevi was found at the sampling sites of Viadana (Fig. 6.3) and Isola Serafini. In the latter case, a maximum of 2833 ind m^{-3} was recorded in July 2009, while in the rest of the sampling dates abundances never exceeded 1250 ind m^{-3}.

The record of *L. fadeevi* is of particular interest because it has previously been reported only from two rivers in the Moscow region (Russia) and one in Poland, where it was found living in the interstitial of sandy sediments or among the shore vegetation (Segers, 1994 and refs. therein). The lorica and head aperture shape is very similar to that of its close relative *L. closterocerca*. Nevertheless, they can be distinguished by the toe shape, bulging medially in *L. fadeevi*, parallel-sided and tapering to a sharp, spiniform tip in *L. closterocerca* (Segers, 1994 & 1996). This similarity to the cosmopolitan *L. closterocerca* is probably the reason why *L. fadeevi* has not been reported from previous surveys in the Po River. In fact, a re-examination of samples collected during summer 2005 in the same river trait revealed the overlooked presence of the species.

Previous records from Central and Eastern European rivers report the co-occurrence of the two closely related species (Segers, 1994). At Viadana both species were present too, but they exhibited asynchronous fluctuations in population abundance. In fact, a similar pattern was observed in 2008 and 2009, with the peaks of *L. closterocerca* always immediately following the decline of *L. fadeevi* (Fig. 6.3).

Lecane hastata (Murray, 1913) (Fig. 6.1D)

Lecane hastata is described in the literature as a cosmopolitan species that can be found in the periphyton and psammon of both brackish and freshwater habitats (Koste, 1978; Segers, 1995; Turner, 1996).

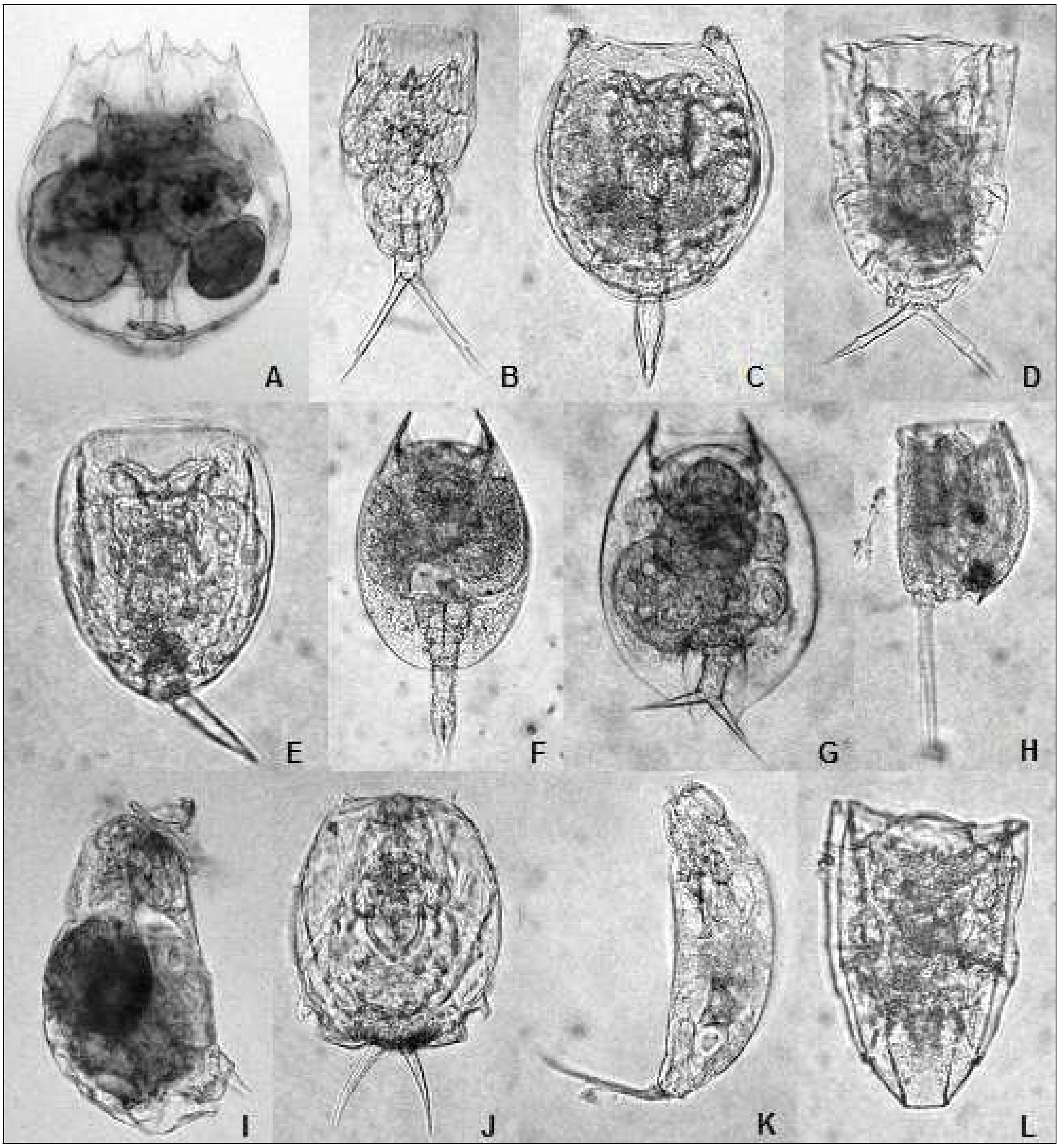


Fig. 6.1 - Microphotographs (not to scale) of rotifer species found in this study. Some soft-bodied specimens are contracted due to formalin fixation. A: *Brachionus durgae*; B: *Lecane* elegans; C: *Lecane fadeevi*; D: *Lecane hastata*; E: *Lecane pyriformis*; F: *Lepadella (Xenolepadella) astacicola*; G: *Lepadella (Lepadella) biloba*; H: *Cephalodella trigona*; I: *Encentrum wiszniewskii*; J: *Kostea wockei*; K: *Trichocerca tenuior;* L: *Wolga spinifera*.

Lecane pyriformis (Daday, 1905) (Fig. 6.1E)
Lecane pyriformis is a cosmopolitan littoral rotifer that generally lives in the periphyton of standing and running waters (Koste, 1978; Segers, 1995). It is also reported from slightly to highly saline water bodies (Walsh et al., 2008; Kaya et al., 2010).

Lepadella (Xenolepadella) astacicola Hauer, 1926 (Fig. 6.1F)

Despite being reported as living in the branchial cavities of freshwater crayfish such as *Astacus fluviatilis*, *A. leptodactylus* and *Cambarus affinis* (Koste, 1978), this species has also been found in plankton samples of both standing and running waters (Ejsmont-Karabin & Kruk, 1998; Sarma & Elías-Gutiérrez, 1999; De Manuel, 2000).

Lepadella (Lepadella) biloba Hauer, 1958 (Fig. 6.1G)

This cosmopolitan taxon was originally considered a subspecies of *L. patella*, but later elevated to the species rank by Segers & De Meester (1994). It commonly inhabits the littoral of ponds, like the majority of its congeners; the genus *Lepadella* comprises in fact mainly benthic-periphytic forms, occasionally to be found in plankton but often present in the drift of running waters (Koste, 1978; Pejler & Bērziņš, 1993).

Cephalodella cfr. *hollowdayi* Koste, 1986 (Fig. 6.2A)

Originally described from the floodplain of Rio Paraguay (Koste, 1986), to my knowledge this is the first record of the taxon outside the Neotropical region (Segers, 2007). It is reported from both lentic and lotic water bodies (Nogrady et al., 1995; Keppeler & Hardy, 2004; Janetzky et al., 1995).

Cephalodella theodora Koch-Althaus, 1961 (Fig. 6.2B)

Cephalodella theodora has been found in both backwaters and main channels of streams and rivers (Zsuga, 1997; Bjørklund, 2009). It is a rare benthic-periphytic rotifer, usually inhabiting the littoral of water bodies, especially among macrophytes and algal mats (Jersabek & Bolortsetseg, 2010).

Cephalodella trigona (Rousselet, 1895) (Fig. 6.1H)

Bērziņš (1954) reported the presence of *C. trigona* in Southern Italy, but his record was omitted by Braioni & Ricci (1995). Having a heavier lorica than most *Cephalodella* species and dorsal keels, the habitus of *C. trigona* may appear similar to that of a *Mytilina*. Nonetheless, the granulated lorica and especially the virgate trophi (malleate in *Mytilina*) are diagnostic features of the genus and species (Nogrady et al., 1995). Sparse information is available on the ecology of this taxon, which is described as inhabiting small ephemeral ponds (Nogrady et al., 1995).

Enteroplea lacustris Ehrenberg, 1830 (Fig. 6.2C)

Although previously recorded from Italy by Mola (1931) and Taticchi (1968), this species is not included in the checklist of the Italian fauna (Braioni & Ricci, 1995). This could be due to the fact that such records are questionable. This is especially the case for those by Mola (1931), whose rotifer descriptions are of a quality that does not enable recognition of the taxon recorded (see list of "*species inquirendae*" in Segers, 1995). *Enteroplea lacustris* is the only species known for this genus (Segers, 2007). It is described in the literature as cosmopolitan but rare, typically found in shallow or ephemeral ponds (Nogrady et al., 1995). It is a predatory rotifer feeding on bdelloids, as observed both in laboratory cultures (Pourriot, 1965) and field populations (José de Paggi, 2001).

Eosphora anthadis Harring & Myers, 1922 (Fig. 6.2D)

Among the seven species of this genus (Segers, 2007), only *E. najas* and *E. ehrenbergi* have so far been recorded from Italy (Taticchi, 1968; Bērziņš, 1978; Fontaneto & Melone, 2003). *Eosphora anthadis* is a cosmopolitan but rare predatory rotifer, which was observed preying upon peritrich ciliates (Kusuoka & Watanabe, 1989; Nogrady et al., 1995).

Notommata cyrtopus cyrtopus Gosse, 1886

The first record of *N. cyrtopus* for the Italian fauna dates back to the work of Mola (1930), but the species is not listed by Braioni & Ricci (1995), possibly for the same reason as for his record of *E.*

lacustris. It is a cosmopolitan rotifer, common in the periphyton and littoral of both standing and running waters (Koste, 1978; Nogrady et al., 1995).

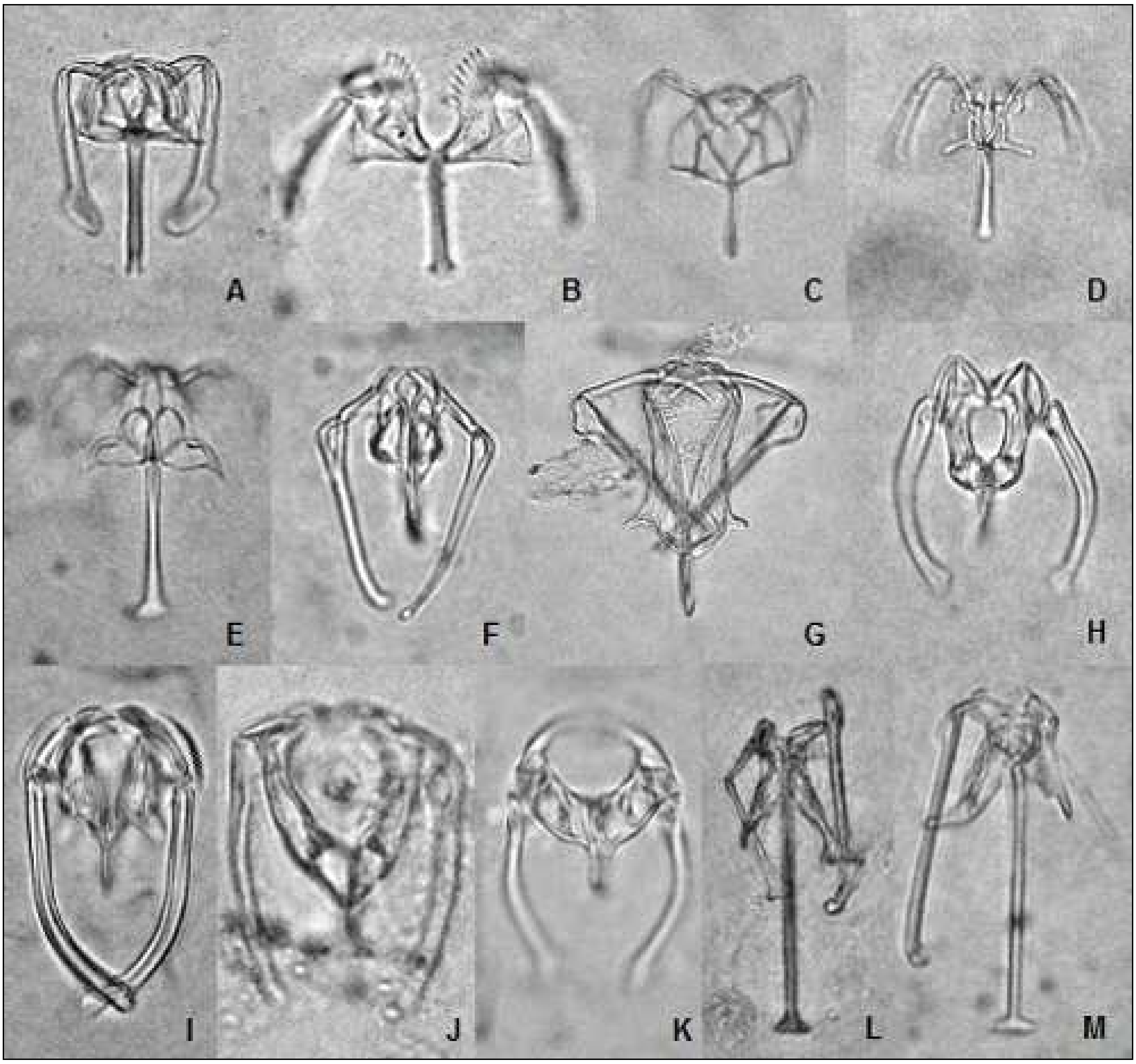


Fig. 6.2 - Microphotographs of trophi (not to scale) belonging to rotifer species found in this study. A: *Cephalodella* cfr. *hollowdayi*; B: *Cephalodella theodora*; C: *Enteroplea lacustris*; D: *Eosphora anthadis*; E: *Resticula anceps*; F: *Aspelta circinator*; G: *Dicranophorus luetkeni*; H: *Encentrum wiszniewskii*; I: *Kostea wockei*; J: *Paradicranophorus hudsoni*; K: *Parencentrum lutetiae*; L: *Trichocerca braziliensis*; M: *Trichocerca tenuior*.

Resticula anceps Harring & Myers, 1924 (Fig. 6.2E)
The genus *Resticula* comprises seven known species (Segers, 2007), of which only *R. gelida* and *R. nyssa* have been found in Italy so far (Braioni & Ricci, 1995; Bertani et al., 2009). No information is available on the ecology of *R. anceps*; it is a rare species that has previously been reported only from the Nearctic region (Segers, 2007).

Aspelta circinator (Gosse, 1886) (Fig. 6.2F)
Despite the record of *Aspelta aper* by Bērziņš in Italy (1978), the genus *Aspelta* is not listed by Braioni & Ricci (1995). *Aspelta circinator* is a widespread taxon, although sporadic (De Smet &

Pourriot, 1997). It lives in the mud over different substrates such as mosses; it is found also in acidic waters (Koste, 1978), among submerged vegetation and in the littoral psammon of lakes and rivers (De Smet & Pourriot, 1997; Jersabek & Bolortsetseg, 2010). Like the majority of its congeners, it is carnivorous and feeds on other rotifers, ciliates and nematodes (De Smet & Pourriot, 1997).

Dicranophorus luetkeni (Bergendal, 1892) (Fig. 6.2G)
This cosmopolitan rotifer is commonly found in the littoral of both lotic and lentic water bodies, especially in the periphyton and psammon, among macrophytes and in the interstitial of streams (De Smet & Pourriot, 1997; Jersabek & Bolortsetseg, 2010). It feeds on diatoms and other rotifers (Jersabek, 1998).

Encentrum wiszniewskii Wulfert, 1939 (Figs. 6.1I and 6.2H)
Sporadic individuals of *E. wiszniewskii* were found in samples collected at Viadana throughout the summer and autumn of 2009. It is reported in the literature as a typical inhabitant of the river psammon (Turner, 1996; De Smet & Pourriot, 1997).

Kostea wockei (Koste, 1961) (Figs. 6.1J and 6.2I)
The genus *Kostea* was specifically established by De Smet (1997) to contain the species formerly designated as *Paradicranophorus wockei*. *Kostea wockei* is reported as a littoral rotifer, often inhabiting sandy and muddy sediments of both standing and running waters. It feeds on small rotifers and nematodes as well as on algae (Koste, 1978; De Smet, 1997).

Paradicranophorus hudsoni (Glascott, 1893) (Fig. 6.2J)
The genus *Paradicranophorus* includes six known species (Segers, 2007). Sparse individuals of *P. hudsoni* were found in spring of each year (Tab. 6.2), but in November 2009 an isolated peak of 1926 ind m^{-3} was observed. This cosmopolitan rotifer lives both in freshwater and marine habitats and although it can occasionally be found in plankton or in the drift of running waters, it is a littoral species typically associated with muddy bottoms and shores (Koste, 1978; De Smet & Pourriot, 1997).

Parencentrum lutetiae (Harring & Myers, 1928) (Fig. 6.2K)
Only two known species belong to the genus *Parencentrum* (Segers, 2007). *Parencentrum lutetiae* can be found in muddy sediments of both lentic and running waters (De Smet & Pourriot, 1997). Information on its ecology and distribution is scarce. Outside of Europe it has been recorded only in Laos (Segers & Sanoamuang, 2007).

Trichocerca braziliensis (Murray, 1913) (Fig. 6.2L)
This is the first record of *T. braziliensis* for the Palaearctic region, even though confusion with the similar *T. rattus* might have led to an underestimation of its actual distribution in temperate regions (Segers & De Meester, 1994). *Trichocerca braziliensis* seems to prefer warm waters and so far it has mainly been reported from tropical and subtropical regions, where it is relatively widespread (Segers & De Meester, 1994; Segers, 2003).

Trichocerca tenuior (Gosse, 1886) (Figs. 6.1K and 6.2M)
Despite being a cosmopolitan taxon (Segers, 2003), this is the first record of *T. tenuior* for Italy (Braioni & Ricci, 1995). Like most of the species belonging to this genus, *T. tenuior* typically lives in detritus, periphyton and psammon of standing waters as well as in the littoral of streams, occurring only occasionally in open water habitats; it is also found in bogs (Koste, 1978).

Wolga spinifera (Western, 1894) (Fig. 6.1L)

Wolga spinifera, the only species of the genus *Wolga* according to Segers (2007), has been recorded from Sicily (Southern Italy) by Bērziņš (1954), although it is not included in the checklist of the Italian fauna (Braioni & Ricci, 1995). It is a widespread benthic-periphytic rotifer that is commonly found among macrophytes and on muddy sediments in lentic water bodies, rice fields, streams and rivers (Koste, 1978; Jersabek & Bolortsetseg, 2010).

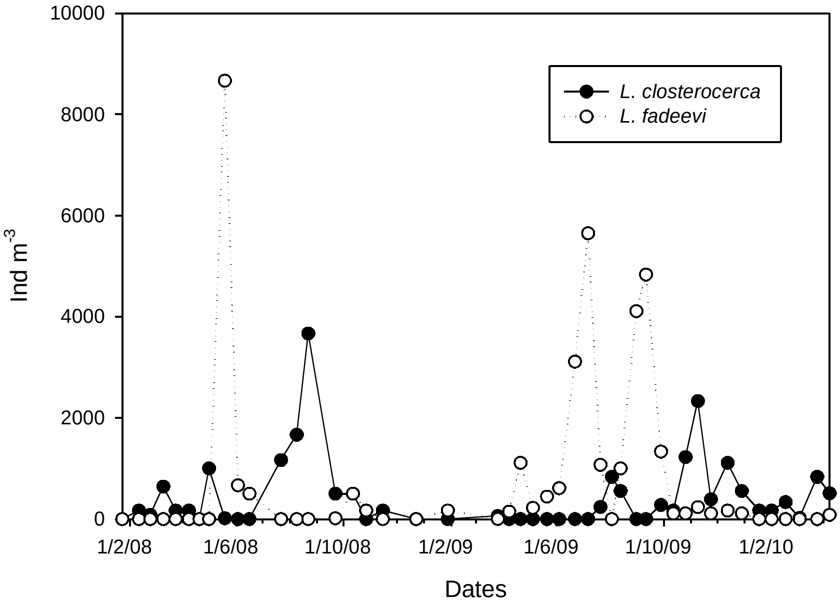


Fig. 6.3 - Abundances of *Lecane closterocerca* and *Lecane fadeevi* recorded between February 2008 and April 2010 at the station of Viadana.

Table 6.2 - Occurrence of rotifer taxa in the Po River. Unless otherwise specified (see notes below), data refer to the station of Viadana. Symbols indicate abundances as follows: ■ ≤ 200 ind m^{-3}; ● 200-500 ind m^{-3}; ◆ > 500 ind m^{-3}. In cases where a species was found on more than one sampling date in the same month, the highest recorded abundance is reported. For the occurrence of *Lecane fadeevi* see text and Fig. 6.3.
(1): the record of July 2009 refers to Isola Serafini; in August 2009 the species was found with similar abundances (see text) at both Viadana and Isola Serafini stations. (2): the record refers to Isola Serafini. (3): the record of August 2009 refers to Isola Serafini.

	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
	2008											2009												2010			
Brachionus durgae (1)																		●	◆	■							
Rhinoglena frontalis																											■
Lecane elegans																					■						
Lecane hastata																			■								
Lecane pyriformis																	■		●	■							
Lepadella (Xenolepadella) astacicola															■												
Lepadella (Lepadella) biloba														■								■					
Cephalodella cfr. *hollowdayi* (2)																			●								
Cephalodella theodora																						◆				■	
Cephalodella trigona																										■	
Enteroplea lacustris																				■							
Eosphora anthadis																		■		■	■						
Notommata cyrtopus cyrtopus																					■				■	■	■
Resticula anceps																	■	■	■								
Aspelta circinator																						■					■
Dicranophorus luetkeni (3)																			■			■			■		
Encentrum wiszniewskii																	■	●	●		■	●					
Kostea wockei																■						■		■			
Paradicranophorus hudsoni			■	■										■	■							◆			■	●	■
Parencentrum lutetiae																											■
Trichocerca braziliensis																		■									
Trichocerca tenuior																		■	■		■		■			■	
Wolga spinifera																■			■								

6.3 Conclusions

Most of the recorded species are reported in the literature as littoral and/or benthic-periphytic. This probably explains why they occurred only sporadically in plankton samples collected in the main river channel. Nevertheless, their finding further supports the notion of large lowland rivers and their floodplain as capable of sustaining extremely rich and diverse rotifer assemblages (Segers et al., 1993; Lair, 2006; this work) and the need to investigate all types of heterogeneous environments, substrates and microhabitats that contribute to the overall biodiversity of riverine ecosystems (Ward & Tockner, 2000).

The record of species previously reported only from other biogeographical regions once again emphasizes how substantial gaps still affect our understanding of rotifer species' chorology. Taxa that are considered rare or endemic of certain areas might be much more widespread than currently assumed.

To sum up, while being a contribution to the present knowledge on the distribution of monogonont rotifers, these results indicate that much remains to be done to get a reliable picture on the biogeography and ecology of this group.

7. General Conclusions

This PhD work has dealt with the study of several aspects of the ecology of riverine zooplankton, a component that has often been neglected in lotic systems. A multi-level approach was adopted, combining different surveys carried out at distinct spatial and temporal resolutions, which proved to be fundamental to investigate abiotic and biotic processes that inevitably act on different scales, both in space and time.

The two-year survey at the station of Viadana confirmed the role of abiotic constraints related to seasonality and hydrology, together with that of trophic conditions, as the major drivers of zooplankton dynamics in a large lowland river. The comparison of two hydrologically different years suggested that the uncoupling between seasonality and hydrology can significantly influence community density, diversity and temporal patterns. The relationship between discharge and zooplankton abundance is not univocally negative, as increases in river flow may at times bring about a net increment of the assemblage, when resuspension of organisms from the river bottom and/or littoral zones prevails over advective losses. Discharge fluctuations strongly affect zooplankton diversity too, both taxonomical and functional (loricate vs. illoricate rotifers), with higher diversity values associated with increases in river flow, up to a threshold over which destructive effects dominate.

However, the impact of hydrodynamic forcings in shaping lotic zooplankton appears to lose importance in favour of that of seasonality and trophic state when moving down the longitudinal dimension of the river system, as suggested by the comparison of results obtained at Viadana with those from the additional surveys at the stations of Mortizza and Serravalle. While at the upstream site the zooplankton assemblage is generally closer to a mere collection of tychoplanktonic organisms, a clear downstream shift towards a truly planktonic community occurs, especially during summer low-flow conditions.

The downstream changes in zooplankton abundance and composition that are often observed in rivers have generally been associated with the longer time available to grow and reproduce. Nonetheless, growing populations may not only be a phenomenon related to downstream transport time. Longitudinal and lateral discontinuities, such as dams and reservoirs, inshore retention zones and habitats with slow-moving water, may significantly affect the development of potamoplankton.

The role of large-scale longitudinal changes as opposed to that of local processes acting at a relatively smaller spatial scale was thus investigated in further detail by means of different sampling strategies. The Lagrangian experiment carried out in May 2010 highlighted how water residence time under spring conditions is too short to allow longitudinal development of zooplankton, which is merely transported downstream without significant changes in abundance and composition. The increase in density observed at the most downstream stations was actually related to the influence of a tributary rather than to growth processes within the main current.

On the contrary, in-channel growth appears to take place at low-flow conditions, as hinted by the increase in density detected in summer along the three stations monitored monthly as well as by results of the short-term survey carried out at Viadana in 2005, when massive egg production was observed for the dominant rotifer taxon.

Nevertheless, during summer conditions the role of local environmental complexity is also enhanced, as shown by the survey carried out at the Isola Serafini dam. Focussing on a finer spatial scale, the study revealed that longitudinal and lateral hydrogeomorphic heterogeneity may affect community abundance and diversity, so that the assemblage found at one site along the river may also be related to local hydroecological features and not only to processes taking place further upstream. However, in a rectified and channelized river like the Po, this appears to be the case only at extremely low discharge rates and high water residence time. Under these conditions, biotic interactions within the zooplankton community are also expected to gain importance, as it is actually suggested by results of the high-frequency sampling campaign performed at Viadana in summer 2005. The view of riverine zooplankton as a mere assemblage of taxa exclusively abiotically controlled is therefore oversimplified, as internal, self-regulatory mechanisms may become major drivers of community dynamics also in the main current of a large river, under certain conditions, similarly to what is commonly observed in lentic systems. Moreover, the combination of results from the present long- and short-term surveys and the comparison with those carried out in the past in the same river stretch highlight the occurrence of clear regular successional patterns in both community abundance and composition, despite the strong intrinsic variability of the river system.

Finally, results of the studies carried out along extremely artificialized traits of both the Po River (Isola Serafini dam) and its tributaries (lower section of the Mincio River) show how anthropogenic modifications of the river's natural hydrogeomorphic features may have strong impacts also on biotic components that are usually overlooked by standard monitoring programs, even though their role in the functioning of lotic systems is still not completely understood.

Future research should take into account the multidimensionality of rivers and the different spatial and temporal scales at which the studied processes take place.

Long-term monitoring programs are fundamental to investigate the behaviour of an ecosystem as well as that of the communities that dwell in it, and they allow to build a solid dataset on which further analyses on the system's temporal evolution can be based.

Nonetheless, other approaches need to be integrated too. A Lagrangian reference frame, as opposed to the traditional Eulerian one, seems to be more appropriate to investigate processes that occur in flowing water, but still few studies are going into that direction. The challenge of experimental works in large rivers has also been met relatively rarely, mainly because of huge logistic difficulties, but it appears necessary to simplify a complex system in order to understand the basic mechanisms involved in its functioning.

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References

Admiraal W., Breebaart L., Tubbing G.M.J., van Zanten B., de Ruyter van Steveninck E.D. & Bijkerk R., 1994. Seasonal variation in composition and production of planktonic communities in the lower River Rhine. *Freshwater Biology* 32: 519-531.

Agustì S., Duarte C.M. & Canfield Jr.D.E., 1990. Phytoplankton abundance in Florida lakes: Evidence for the frequent lack of nutrient limitation. *Limnology and Oceanography* 35: 181-188.

Allan J.D. & Castillo M.M., 2007. *Stream ecology: structure and function of running waters. 2nd Ed.*, Springer, Berlin.

Allodi A. & Pecora S., 2003. On the winter low water of the Po River in the year 2002. *L'Acqua* 4: 23–32 (in Italian with English summary).

Alonso M., 1996. *Crustacea, Branchiopoda*. Fauna Ibérica Vol. 7. Museo Nacional de Ciencias Naturales, CSIS, Madrid (in Spanish).

Aoyagui A.S.M. & Bonecker C.C., 2004. Rotifers in different environments of the Upper Paranà River floodplain (Brazil): richness, abundance and the relationship with connectivity. *Hydrobiologia* 522: 281-290.

A.P.H.A., A.W.W.A., W.E.F., 1998. *Standard Methods for the Examination of Water and Wastewater, 20th Ed.* American Public Health Association, Washington DC.

Autorità di Bacino del Fiume Po, 2006. *Caratteristiche del bacino del fiume Po e primo esame dell'impatto ambientale delle attività umane sulle risorse idriche*. Autorità di Bacino del Fiume Po, Parma (in Italian).

Baranyi C., Hein T., Holarek C., Keckeis S. & Schiemer F., 2002. Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. *Freshwater Biology* 47: 473-482.

Basu B.K. & Pick F.R., 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. *Limnology and Oceanography* 41: 1572-1577.

Basu B.K. & Pick F.R., 1997. Phytoplankton and zooplankton development in a lowland, temperate river. *Journal of Plankton Research* 19: 237-253.

Battaglin W.A., Kendall C., Chang C.C.Y., Silva S.R. & Campbell D.H., 2001. Chemical and isotopic evidence of nitrogen transformation in the Mississippi River, 1997–98. *Hydrological Processes* 15: 1285-1300.

Beisner B.E., Ives A.R. & Carpenter S.R., 2003. The effects of an exotic fish invasion on the prey communities of two lakes. *Journal of Animal Ecology* 72: 331-342.

Bergfeld T., Scherwass A., Ackermann B., Arndt H. & Schöl A., 2009. Comparison of the components of the planktonic food web in three large rivers (Rhine, Moselle and Saar). *River Research and Applications* 25: 1232-1250.

Bertani I., Segers H. & Rossetti G., 2009. Monogonont rotifers (Rotifera: Monogononta) from Northern Apennine lakes: new and rare taxa for Italy. *Studi Trentini di Scienze Naturali - Acta Biologica* 86: 71-74.

Bērziņš B., 1954. Zur Rotatorienfauna Siziliens. *Hydrobiologia* 6: 309-320 (in German).

Bērziņš B., 1978. Rotatoria. In Illies J. (ed.), *Limnofauna Europaea*. Gustav Fischer Verlag, Stuttgart, New York; Swets and Zeitlinger B.V., Amsterdam, pp. 54-91 (in German).

Binford M.W., 1978. Copepoda and cladocera communities in a river-swamp system. *Verhandlungen des Internationalen Verein Limnologie*, 20: 2524-2530.

Bjørklund B.G., 2009. Freshwater rotifers from Hordaland, western Norway, with a survey of freshwater rotifers previously found in Norway. *Fauna Norvegica* 29: 11-54.

Bothár A. & Kiss K.T., 1990. Phytoplankton and zooplankton (Cladocera, Copepoda) relationship in the eutrophicated River Danube (Danubialia Hungarica, CXI). *Hydrobiologia* 191: 165-171.

Böttjer D., Morales C.E. & Bathmann U., 2010. Trophic role of small cyclopoid copepod nauplii in the microbial food web: a case study in the coastal upwelling system off central Chile. *Marine Biology* 157: 689-705.

Braioni M.G., 1981. The drift of Rotifers in the River Adige: preliminary communication. *Bollettino di Zoologia* 48: 305-310.

Braioni M.G. & Gelmini D., 1983. *Rotiferi Monogononti (Rotatoria: Monogononta)*. Consiglio Nazionale delle Ricerche AQ/1/200, Roma (in Italian).

Braioni M.G. & Ricci C., 1995. *Rotifera*. In Minelli A., Ruffo S. & La Posta S. (eds.), *Checklist delle specie della fauna italiana*, *8th Ed*. Calderini, Bologna, pp. 1-11 (in Italian).

Brunelli A., Caputo D., Chillè F. & Maugliani V., 2003. The bump of a boat into a gate-structure dam: An unusual risk scenario. In Llanos J.A., Yague J., Sanz de Ormijana F., Cabrera M. & Penas J. (eds.), *Dam Maintenance and Rehabilitation: Proceedings of the International Congress on Conservation and Rehabilitation of Dams, Madrid, Spain, 11–13 November 2002*. Taylor & Francis, pp. 145-146.

Buchner H., Mulzer F. & Rauh F., 1957. Untersuchungen über die Variabilität der Rädertiere. I. Problemstellung und vorläufige Mitteilung über die Ergebnisse. *Biologischen Zentralblatt* 76: 289-315 (in German).

Casper A.F. & Thorp J.H., 2007. Diel and lateral patterns of zooplankton distribution in the St. Lawrence River. *River Research and Applications* 23: 73-85.

Chang K.H., Doi H., Imai H., Gunji F. & Nakano S., 2008. Longitudinal changes in zooplankton distribution below a reservoir outfall with reference to river planktivory. *Limnology* 9: 125-133.

Chang K.H., Doi H., Nishibe Y. & Nakano S., 2010. Feeding habits of omnivorous *Asplanchna*: comparison of diet composition among *Asplanchna herricki*, *A. priodonta* and *A. girodi* in pond ecosystems. *Journal of Limnology* 69: 209-216.

Connell J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Davidson N.L., Kelso W.E. & Rutherford D.A., 2000. Characteristics of cladoceran and copepod communities in floodplain habitats of the Atchafalaya River Basin. *Hydrobiologia* 435: 99-107.

Davis T.W. & Gobler C.J., 2011. Grazing by mesozooplankton and microzooplankton on toxic and non-toxic strains of *Mycrocystis* in the Transquaking River, a tributary of Chesapeake Bay. *Journal of Plankton Research* 33: 415-430.

De Leo G.A. & Ferrari I., 1993. Disturbance and diversity in a river zooplankton community: a neutral model analysis. *Coenoses* 8: 121-129.

De Manuel J., 2000. The Rotifers of Spanish reservoirs: ecological, systematical and zoogeographical remarks. *Limnetica* 19: 91-167.

De Ridder M. & Segers H., 1997. Rotifera Monogononta in six zoogeographical regions after publications between 1960 and 1992. In Van Goethem J. (ed.), *Studiedocumenten van het Koninklijk Belgisch Instituut voor Natuurwetenschappen 88.*

De Smet W.H., 1996. *Rotifera. Vol. 4 : The Proalidae (Monogononta).* SPB Academic Publishing, Amsterdam.

De Smet W.H., 2009. A review of the marine and brackish-water species of *Testudinella* (Rotifera: Monogononta, Testudinellidae), with the description of two new species. *Zootaxa* 2092: 1-20.

De Smet W.H. & Gibson J.A.E., 2008. *Rhinoglena kutikovae* n.sp. (Rotifera: Monogononta: Epiphanidae) from the Bunger Hills, East Antarctica: a probable relict species that survived Quaternary glaciations on the continent. *Polar Biology* 31: 595-603.

De Smet W.H. & Pourriot R., 1997. *Rotifera. Vol. 5 : The Dicranophoridae (Monogononta).* SPB Academic Publishing, Amsterdam.

de Ruyter van Steveninck E.D., Admiraal W., Breebaart L., Tubbing G.M.J. & van Zanten B., 1992. Plankton in the River Rhine: structural and functional changes observed during downstream transport. *Journal of Plankton Research* 14: 1351-1368.

Descy J.P., Everbecq E., Gosselain V., Viroux L. & Smitz J.S., 2003. Modelling the impact of benthic filter-feeders on the composition and biomass of river plankton. *Freshwater Biology* 48: 404-417.

Deutsch B., Voss M. & Fischer H., 2009. Nitrogen transformation processes in the Elbe River: Distinguishing between assimilation and denitrification by means of stable isotope ratios in nitrate. *Aquatic Sciences* 71: 228-237.

Dhanapathi M.V.S.S.S., 1974. Rotifers from Andhra Pradesh, India - I. *Hydrobiologia* 45: 357-352.

Dickerson K.D., Medley K.A. & Havel J.E., 2010. Spatial variation in zooplankton community structure is related to hydrologic flow units in the Missouri River, USA. *River Research and Applications* 26: 605-618.

Dole-Olivier M.-J., Galassi D.M.P., Marmonier P. & Creuzé des Châtelliers M., 2000. The biology and ecology of lotic microcrustaceans. *Freshwater Biology* 44: 63-91.

Doyle M.W. & Ensign S.H., 2009. Alternative reference frames in river system science. *BioScience* 59: 499-510.

Dubovskaia O.P., Gladyshev M.I. & Makhutova O.N., 2004. Limnetic zooplankton run-off a high-head dam and their fate in a river with high current velocity (case of the Krasnoiarsk hydroelectric power station on the Yenisei river). *Zhurnal obshcheĭ biologii* 65: 81-93 (in Russian with English summary).

Dussart B.H., 1969. *Les Copépodes des eaux continentales d'Europe occidentale. 1. Calanöides et Harpacticöides; 2. Cyclopöides et Biologie*. Boubée & Cie., Paris (in French).

Dussart B.H. & Defaye D., 1995. *Copepoda: Introduction to the Copepoda*. SPB Academic Publishing, Amsterdam.

Einsle U., 1996. *Copepoda: Cyclopoida. Genera* Cyclops, Megacyclops, Acanthocyclops. SPB Academic Publishing, Amsterdam.

Ejsmont-Karabin J. & Kruk M., 1998. Effects of contrasting land use on free-swimming rotifer communities of streams in Masurian Lake District, Poland. *Hydrobiologia* 387-388: 241-249.

Ferrari I., Caleo A., Mazzocchi M.G. & Matteucci G., 1984. Dynamics of planktonic rotifer populations in an experimental canal. *Atti 4° Simposio Dinamica Popolazioni:* 51-57.

Ferrari I., Farabegoli A. & Mazzoni R., 1989. Abundance and diversity of planktonic rotifers in the Po River. *Hydrobiologia* 186/187: 201-208.

Ferrari I. & Mazzoni R., 1989. Zooplankton in the Po River during the summer of 1985. *Toxicological and Environmental Chemistry* 20/21: 39-48.

Ferrari I., Viglioli S., Viaroli P. & Rossetti G., 2006. The impact of the drought event of summer 2003 on the zooplankton of the Po River (Italy). *Verhandlungen des internationalen Verein Limnologie* 29: 2143-2149.

Fischer J.M., Frost T.M. & Ives A.R., 2001. Compensatory dynamics in zooplankton community responses to acidification: measurement and mechanisms. *Ecological Applications* 11: 1060-1072.

Fontaine C. & Gonzalez A., 2005. Population synchrony induced by resource fluctuations and dispersal in an aquatic microcosm. *Ecology* 86: 1463-1471.

Fontaneto D. & Melone G., 2003. On some rotifers new for the Italian fauna. *Italian Journal of Zoology* 70: 253-259.

Fontaneto D., Segers H. & Melone G., 2004. Epizoic rotifers (Rotifera: Monogononta, Bdelloidea) from the gill chambers of *Potamon fluviatile* (Herbst, 1785). *Journal of Natural History* 38: 1225-1232.

Fontaneto D., Segers H. & Melone G., 2008. Marine rotifers from the Northern Adriatic Sea, with description of *Lecane insulaconae* sp. nov. (Rotifera: Monogononta: Lecanidae). *Journal of the Marine Biological Association of the United Kingdom* 88: 253-258.

Friedl G. & Wuest A., 2002. Disrupting biogeochemical cycles - consequences of damming. *Aquatic Sciences* 64: 55-65.

Frost T.M., Carpenter S.M., Ives A.R. & Kratz T.K., 1995. Species compensation and complementarity in ecosystem function. In Jones C.G. & Lawton J.H. (eds), *Linking species and ecosystems*. Chapman and Hall, New York, pp. 224-239.

Gilbert J.J., 1966. Rotifer ecology and embryological induction. *Science* 151: 1234-1237.

Gilbert J.J., 1967. *Asplanchna* and postero-lateral spine production in *Brachionus calyciflorus*. *Archiv für Hydrobiologie* 64: 1-62.

Gilbert J.J., 1980. Feeding in the rotifer *Asplanchna*: behaviour, cannibalism, selectivity, prey defenses and impact on rotifer communities. In Kerfoot W.C. (ed.), *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hannover, pp. 158-172.

Gilbert J.J., 2003. Specificity of crowding response that induces sexuality in the rotifer *Brachionus*. *Limnology and Oceanography* 48:1297-1303.

Gilbert J.J. & Waage J.K., 1967. *Asplanchna*, *Asplanchna*-substance, and posterolateral spine length variation of the rotifer *Brachionus calyciflorus* in a natural environment. *Ecology* 48: 1027-1031.

Gillooly J.F., 2000. Effect of body size and temperature on generation time in zooplankton. *Journal of Plankton Research* 22: 241-251.

Gliwicz Z.M., 2004. Zooplankton. In O'Sullivan P.E. & Reynolds C.S. (eds.), *The Lakes Handbook. Limnology and Limnetic Ecology*. Blackwell Science, Oxford, pp. 461-516

Golterman H.L., Clymo R.S. & Ohnstand M.A.M., 1978. *Methods for Physical and Chemical Analysis of Freshwaters, IBP Handbook No. 8*. Blackwell Science, Oxford.

Gosselain V., Descy J.P. & Everbecq E., 1994. The phytoplankton community of the river Meuse, Belgium: seasonal dynamics (year 1992) and the possible incidence of zooplankton grazing. *Hydrobiologia* 289: 179-191.

Gosselain V., Descy J.P., Viroux L., Joaquim-Justo C., Hammer A., Métens A. & Schweitzer S., 1998a. Grazing by large river zooplankton: a key to summer potamoplankton decline? The case of the Meuse and Moselle rivers in 1994 and 1995. *Hydrobiologia* 369/370: 199-216.

Gosselain V., Joaquim-Justo C., Viroux L., Mena M., Métens A., Descy J.P. & Thomé J.P., 1996. Laboratory and in situ grazing rates of freshwater rotifers and their contribution to community grazing rates. *Archiv für Hydrobiologie, Supplement 113, Large Rivers* 10: 353-361.

Gosselain V., Viroux L. & Descy J.P., 1998b. Can a community of small-bodied grazers control phytoplankton in rivers? *Freshwater Biology* 39: 9-24.

Green J. & Lan O.B., 1974. *Asplanchna* and the spines of *Brachionus calyciflorus* in two Javanese sewage ponds. *Freshwater Biology* 4: 223-226.

Greenberg A.E., 1964. Plankton of the Sacramento River. *Ecology* 45: 40-49.

Guelda D.L., Koch R.W., Jack J.D. & Bukaveckas P.A., 2005. Experimental evidence for density-dependent effects and the importance of algal production in determining population growth rates of riverine zooplankton. *River Research and Applications* 21: 595-608.

Guhr H., Spott D., Bormki G., Baborowski M. & Karrasch B., 2003. The Effects of Nutrient Concentrations in the River Elbe. *Acta Hydrochimica et Hydrobiologica* 31: 282-296.

Guo R., Snell T. & Yang J., 2011. Ecological strategy of rotifer (*Brachionus calyciflorus*) exposed to predator- and competitor-conditioned media. *Hydrobiologia* 658: 163-171.

Gurney R., 1933. *British Fresh-Water Copepoda, Vol. 3. Cyclopoida*. Adlard and Son, London.

Halbach U., 1970. Die Ursachen der Temporalvariation von *Brachionus calyciflorus* Pallas (Rotatoria). *Oecologia* 4: 262-318 (in German with English summary).

Hammer Ø., Harper D.A.T. & Ryan P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 9.

Hart D.D. & Poff N., 2002. A special section on dam removal and river restoration. *BioScience* 52: 653–655

Havel J.E., Medley K.A., Dickerson K.D., Angradi T.R., Bolgrien D.W., Bukaveckas P.A. & Jicha T.M., 2009. Effect of main-stem dams on zooplankton communities of the Missouri River (USA). *Hydrobiologia* 628: 121-135.

Holden M.J. & Green J., 1960. The hydrology and plankton of the river Sokoto. *Journal of Animal Ecology* 29: 65-84.

Holst H., Zimmermann-Timm H. & Kausch H., 2002. Longitudinal and Trasversal Distribution of Plankton Rotifers in the Potamal of the River Elbe (Germany) during Late Summer. *International Review of Hydrobiology* 87: 267-280.

Hudon C., Paquet S. & Jarry V., 1996. Downstream variations of phytoplankton in the St. Lawrence River (Québec, Canada). *Hydrobiologia* 337: 11-26.

Ietswaart T., Breebaart L., van Zanten B. & Bijker R., 1999. Plankton dynamics in the river Rhine during downstream transport as influenced by biotic interactions and hydrological conditions. *Hydrobiologia* 410: 1-10.

Ives A.R., Carpenter S.R. & Dennis B., 1999. Community interaction webs and zooplankton responses to planktivory manipulations. *Ecology* 80: 1405-1421.

Ives A.R., Dennis B., Cottingham K.L. & Carpenter S.R., 2003. Estimating community stability and ecological interactions from time-series data. *Ecological Monographs* 73: 301-330.

Jack J.D., Fang W. & Thorp J.H., 2006. Vertical, lateral and longitudinal movement of zooplankton in a large river. *Freshwater Biology* 51: 1646-1654.

Jack J.D. & Thorp J.H., 2000. Effects of the benthic suspension feeder *Dreissena polymorpha* on zooplankton in a large river. *Freshwater Biology* 44: 569-579.

Jack J.D. & Thorp J.H., 2002. Impacts of fish predation on an Ohio River zooplankton community. *Journal of Plankton Research* 24: 119-127.

Jack J.D., Wickham S.A., Toalson S. & Gilbert J.J., 1993. The effects of clays on a freshwater plankton community: an enclosure experiment. *Archiv für Hydrobiologie* 127: 257-270.

Janetzky W., Koste W. & Vareschi E., 1995. Rotifers (Rotifera) of Jamaican inland waters. A synopsis. *Ecotropica* 1: 31-40.

Jersabek C.D., 1998. Dicranophoridae (Rotifera) from the Alps. *Hydrobiologia* 387/388: 63-77.

Jersabek C.D. & Bolortsetseg E., 2010. Mongolian rotifers (Rotifera, Monogononta) - a checklist with annotations on global distribution and autecology. *Proceedings of the Academy of Natural Sciences of Philadelphia* 159: 119-168.

Joaquim-Justo C., Pirlot S., Viroux L., Servais P., Thomé J.P. & Descy J.P., 2006. Trophic links in the lowland River Meuse (Belgium): assessing the role of bacteria and protozoans in planktonic food webs. *Journal of Plankton Research* 28: 857-870.

José de Paggi S., 2001. Diversity of Rotifera (Monogononta) in wetlands of Río Pilcomayo National Park, Ramsar Site (Formosa, Argentina). *Hydrobiologia* 462: 25-34.

Karaytug S., 1999. *Copepoda: Cyclopoida. Genera* Paracyclops, Ochridacyclops *and Key to the Eucyclopinae.* Backhuys Publishers, Leiden.

Kaya M., Fontaneto D., Segers H. & Altindag A., 2010. Temperature and salinity as interacting drivers of species richness of planktonic rotifers in Turkish continental waters. *Journal of Limnology* 69: 297-304.

Kentzer A., Dembowska E., Giziński A. & Napiorkówski P., 2010. Influence of the Włocławek Reservoir on hydrochemistry and plankton of a large, lowland river (the lower Vistula River, Poland). *Ecological Engineering* 36: 1747-1753.

Keppeler E.C. & Hardy E.R., 2004. Abundance and composition of Rotifera in an abandoned meander lake (Lago Amapá) in Rio Branco, Acre, Brazil. *Revista Brasileira de Zoologia* 21: 233-241.

Kiefer F., 1968. Versuch einer Revision der Gattung *Eudiaptomus* Kiefer (Copepoda Calanoida). *Memorie Istituto Italiano Idrobiologia* 24: 9–160 (in German).

Kim H.W., Hwang S.J. & Joo G.J., 2000. Zooplankton grazing on bacteria and phytoplankton in a regulated large river (Nakdong River, Korea). *Journal of Plankton Research* 22: 1559-1577.

Kim H.W. & Joo G.J., 2000. The longitudinal distribution and community dynamics of zooplankton in a regulated large river: a case study of the Nakdong River (Korea). *Hydrobiologia* 438: 171-184.

King A.J., 2004. Density and distribution of potential prey for larval fish in the main channel of a floodplain river: pelagic versus epibenthic meiofauna. *River Research and Applications* 20: 883-897.

King A.J., 2005. Ontogenetic dietary shifts of fishes in an Australian floodplain river. *Marine and Freshwater Research* 56: 215-225.

Kirk K.L. & Gilbert J.J., 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. *Ecology* 71: 1741-1755.

Klug J.L., Fischer J.M., Ives A.R. & Dennis B., 2000. Compensatory dynamics in planktonic community responses to pH perturbations. *Ecology* 81: 387-398.

Kobayashi T., Gibbs P., Dixon P.I. & Shiel R.J., 1996. Grazing by a river zooplankton community: importance of microzooplankton. *Marine and Freshwater Research* 47: 1025-1036.

Kobayashi T., Shiel R.J., Gibbs P. & Dixon P.I., 1998. Freshwater zooplankton in the Hawkesbury-Nepean River: comparison of community structure with other rivers. *Hydrobiologia* 377: 133-145.

Koste W., 1978. *Rotatoria*. Gebrüder Borntraeger, Berlin (in German).

Koste W., 1986. Über die Rotatorienfauna in Gewässern südöstlich von Concepción, Paraguay, Südamerika. *Osnabrücker Naturwissenschaftliche Mitteilungen* 12: 129-155 (in German).

Köhler J., Bahnwart M. & Ockenfeld K., 2002. Growth and Loss Processes of Riverine Phytoplankton in Relation to Water Depth. *International Review of Hydrobiology* 87: 241-254.

Köhler J. & Bosse S., 1998. Growth and losses of phytoplankton studied with a new dialysis chamber technique along the river Spree. *Archiv für Hydrobiologie* 142: 1-19.

Kristensen P. & Hansen H.O., 1994. *European Rivers and Lakes. Assessment of Their Environmental State*. European Environment Agency, EEA Environmental Monographs 1, Copenhagen.

Kusuoka Y. & Watanabe Y., 1989. Distinction of emigration by telotroch formation and death by predation in peritrich ciliates: SEM observations on the remaining stalk ends. *FEMS Microbiology Letters* 62: 7-12.

Lair N., 2005. Abiotic vs. biotic factors: lessons drawn from rotifers in the Middle Loire, a meandering river monitored from 1995 to 2002, during low flow periods. *Hydrobiologia* 546: 457-472.

Lair N., 2006. A review of regulation mechanisms of metazoan plankton in riverine ecosystems: aquatic habitat versus biota. *River Research and Applications* 22: 567-593.

Lair N., Jacquet V. & Reyes-Marchant P., 1999. Factors related to autotrophic potamoplankton, heterotrophic protists and micrometazoan abundance, at two sites in a lowland temperate river during low water flow. *Hydrobiologia* 394: 13-28.

Lair N. & Reyes-Marchant P., 1997. The potamoplankton of the Middle Loire and the role of the «moving littoral» in downstream transfer of algae and rotifers. *Hydrobiologia* 356: 33-52.

Mandal S., Ray S. & Roy S.K., 2009. Study of biocomplexity in an aquatic ecosystem through ascendency. *BioSystems* 95: 30-34.

Margalef R., 1960. Ideas for a synthetic approach to the ecology of running waters. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 45: 133-153.

Margaritora F.G., 1985. *Cladocera. Fauna d'Italia*. Calderini, Bologna (in Italian).

Marneffe Y., Descy J.P. & Thomé J.P., 1996. The zooplankton of the lower river Meuse, Belgium: seasonal changes and impact of industrial and municipal discharges. *Hydrobiologia* 319: 1-13.

Marneffe Y., Comblin S. & Thomé J.P., 1998. Ecological water quality assessment of the Bütgenbach lake (Belgium) and its impact on the River Warche using rotifers as bioindicators. *Hydrobiologia* 387/388: 459-467.

Mazzarella A. & Rapetti F., 2004. Scale-invariance laws in the recurrence intervals of extreme floods: an application to the upper Po River valley (Northern Italy). *Journal of Hydrology* 288: 264-271.

Miquelis A., Rougier C. & Pourriot R., 1998. Impact of turbulence and turbidity on the grazing rate of the rotifer *Brachionus calyciflorus* (Pallas). *Hydrobiologia* 386: 203-211.

Mitchell-Olds T. & Shaw R.G., 1987. Regression analysis of natural selection: statistical influence and biological interpretation. *Evolution* 41: 1149-1161.

Mola P., 1930. Fauna rotatoria italiana delle acque dolci. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 23: 428-477 (in Italian).

Mola P., 1931. Addenda ed alcune errata-corrige alla „Fauna rotatoria italiana delle acque dolci". *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 26: 143-162 (in Italian).

Naldi M., Pierobon E., Tornatore F. & Viaroli P., 2010. Relationships between flood events and formation and variability of nitrogen and phosphorous loads in the Po river. *Biologia Ambientale* 24: 59-69 (in Italian with English summary).

Nandini S., Pérez-Chávez R. & Sarma S.S.S., 2003. The effect of prey morphology on the feeding behaviour and population growth of the predatory rotifer *Asplanchna sieboldii*: a case study using five species of *Brachionus* (Rotifera). *Freshwater Biology* 48: 2131-2140.

Ning N.S.P., Nielsen D.L., Hillman T.J. & Suter P.J., 2010. The influence of planktivorous fish on zooplankton communities in riverine slackwaters. *Freshwater Biology* 55: 360-374.

Nogrady T., Pourriot R. & Segers H., 1995. *Rotifera. Vol. 3: The Notommatidae and The Scaridiidae*. SPB Academic Publishing, Amsterdam.

Obertegger U., Smith H.A., Flaim G. & Wallace R.L., 2011. Using the guild ratio to characterize pelagic rotifer communities. *Hydrobiologia* 662: 157-162.

Oksanen J., Blanchet F.G., Kindt R., Legendre P., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H. & Wagner H., 2011. Vegan: Community Ecology Package. R package version 1.17-7 (http://vegan.r-forge.r-project.org/).

Pace M.L., Findlay S.E.G. & Lints D., 1992. Zooplankton in advective environments: The Hudson River community and a comparative analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1060-1069.

Pace M.L., Strayer D.L., Fischer D. & Malcom H.M., 2010. Recovery of native zooplankton associated with increased mortality of an invasive mussel. *Ecosphere* 1(1):art3. doi:10.1890/ES10-00002.1

Padovani C., 1911. Il plancton del fiume Po, contributo allo studio del plancton fluviale. *Zoologischer Anzeiger* 37: 99-104 (in Italian).

Pahl-Wostl C., 2004. Self-Regulation of Limnetic Ecosystems. In O'Sullivan P.E. & Reynolds C.S. (eds.), *The Lakes Handbook. Limnology and Limnetic Ecology*. Blackwell Science, Oxford, pp. 583-608.

Pejler B. & Bērziņš B., 1993. On the ecology of Colurellidae (Rotifera). *Hydrobiologia* 263: 61-64.

Picard V. & Lair N., 2005. Spatio-temporal investigations on the planktonic organisms of the Middle Loire (France), during the low water period: biodiversity and community dynamics. *Hydrobiologia* 551: 69-86.

Pierobon, E., 2010. Alterazioni nel regime idrogeologico nel fiume Po: analisi delle implicazioni nella composizione e nelle trasformazioni dei carichi di N e P. PhD Thesis, University of Parma (in Italian).

Pollard A.I., Gonzàlez M.J., Vanni M.J. & Headworth J.L., 1998. Effects of turbidity and biotic factors on the rotifer community in an Ohio reservoir. *Hydrobiologia* 387/388: 215-223.

Postoev V.S., 1997. Loss of plankton in the turbines of hydroelectric power stations and a method of its protection. *Water Resources (Vodnye Resursy)* 2: 186-191.

Pourriot R., 1965. Recherches sur l'ecologie des rotifères. *Vie et Milieu* 21(suppl.): 1-224 (in French).

Pourriot R., 1977. Food and feeding habits of Rotifera. *Archiv für Hydrobiologie* 8: 243-260.

Pourriot R., Rougier C. & Miquelis A., 1997. Origin and development of river zooplankton: example of the Marne. *Hydrobiologia* 345: 143-148.

R Development Core Team, 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (available at: http://www.r-project.org/).

Rauh F., 1963. Untersuchungen über die Variabilität der Rädertiere. III. Die Experimentelle Beeinflussung der Variation von *Brachionus calyciflorus* und *Brachionus capsuliflorus*. *Zeitschrift für Morphologie und Okologie der Tiere* 53: 61-106 (in German).

Reckendorfer W., Keckeis H., Winkler G. & Schiemer F., 1999. Zooplankton abundance in the River Danube, Austria: the significance of inshore retention. *Freshwater Biology* 41: 583-591.

Reynolds C.S., 1988. Potamoplankton: paradigms, paradoxes and prognoses. In Round F.E. (ed.), *Algae and the Aquatic Environment*. Biopress, Bristol, pp. 285-311.

Reynolds C.S., 2000. Hydroecology of river plankton: the role of variability in channel flow. *Hydrological Processes* 14: 3119-3132.

Reynolds C.S & Descy J.P., 1996. The production, biomass and structure of phytoplankton in large rivers. *Archiv für Hydrobiologie, Supplement 113, Large Rivers* 10: 161-187.

Ricci C. & Balsamo M., 2000. The biology and ecology of lotic rotifers and gastrotrichs. *Freshwater Biology* 44: 15-28.

Rodier J., 1978. *L'analyse de l'eau*. Dunod, Orleans (in French).

Rossaro B., 1976. Lo «zooplancton» del Po a Caorso. *Istituto Lombardo Rendiconti Scientifici B* 110: 35-54 (in Italian).

Rossaro B., 1981. Il carico biologico del medio Po presso Caorso (Piacenza): la sua composizione specifica e le relazioni con le proprietà dell'acqua esaminate mediante l'analisi delle componenti principali. *Rivista di Idrobiologia* 20: 153-163 (in Italian with English summary).

Rossaro B., 1988. Mid-Po River zooplankton. A seven year study. *Hydrobiologia* 160: 97-105.

Rossaro B. & Cotta Ramusino M., 1976. I copepodi del Po a Isola Serafini. *Rivista di Idrobiologia* 15: 187-203 (in Italian with English summary).

Rossetti G., Tireni F., Viglioli S. & Ferrari I., 2003. Ricerche ecologiche in un ambiente acquatico della golena del Po nei pressi di Casalmaggiore. *Studi Trentini di Scienze Naturali - Acta Biologica* 80: 193-200 (in Italian with English summary).

Rossetti G., Viaroli P. & Ferrari I., 2009. Role of abiotic and biotic factors in structuring the metazoan plankton community in a lowland river. *River Research and Applications* 25: 814-835.

Rothhaupt K.O., 1990. Differences in particle size-dependent feeding efficiencies of closely related rotifer species. *Limnology and Oceanography* 35: 16-23.

Roy S., 2009. Do phytoplankton communities evolve through a self-regulatory abundance-diversity relationship? *BioSystems* 95: 160-165.

Ruttner-Kolisko A., 1974. *Planktonic Rotifers: biology and taxonomy. Die Binnengewässer (Supplement) 26*. Schweizerbart, Stuttgart.

Rzoska J., 1978. *On the nature of rivers*. Dr. W. Junk, The Hague.

Salmaso N. & Braioni M.G., 2008. Factors controlling the seasonal development and distribution of the phytoplankton community in the lowland course of a large river in Northern Italy (River Adige). *Aquatic Ecology* 42: 533-545.

Salmaso N. & Zignin A., 2010. At the extreme of physical gradients: phytoplankton in highly flushed, large rivers. *Hydrobiologia* 639: 21-36.

Sanoamuang L-o., 1998. Rotifera of some freshwater habitats in the floodplain of the River Nan, northern Thailand. *Hydrobiologia* 387/388: 27-33.

Sarma S.S.S. & Elías-Gutiérrez M., 1999. Rotifers (Rotifera) from four natural water bodies of Central Mexico. *Limnologica* 29: 475-483.

Saunders J.F. & Lewis W.M., 1988a. Zooplankton abundance and transport in a tropical white-water river. *Hydrobiologia* 162: 147-155.

Saunders J.F. & Lewis W.M., 1988b. Zooplankton abundance in the Caura River, Venezuela. *Biotropica* 20: 206-214.

Schiemer F., Keckeis H., Reckendorfer W. & Winkler G., 2001. The "inshore retention concept" and its significance for large rivers. *Archiv für Hydrobiologie, Supplement 135, Large Rivers* 12: 509-516.

Schluter D., 1984. A variance test for detecting species associations, with some example applications. *Ecology* 64: 998-1005.

Schmid-Araya J.M., 1998. Rotifers in interstitial sediments. *Hydrobiologia* 387/388: 231-240.

Schram M.D., Brown A.V. & Jackson D.C., 1990. Diel and seasonal drift of zooplantkon in a headwater stream. *American Midland Naturalist* 123: 135-143.

Schram M.D., Gunter J.M. & Engle D.B., 1998. Diurnal vertical distribution and drift of zooplankton in an Ozark headwater stream pool. *Journal of Freshwater Ecology* 13: 47-54.

Schröder T., 2005. Diapause in monogonont rotifers. *Hydrobiologia* 546: 291-306.

Segers H., 1994. Redescription of *Lecane fadeevi* (Neiswestnowa-Shadina, 1935) (Rotifera, Lecanidae). *Bulletin de l'Institut Royal de Sciences Naturelles de Belgique, Biologie* 64: 235-238.

Segers H., 1995a. *Rotifera. Vol. 2: The Lecanidae (Monogononta)*. SPB Academic Publishing, Amsterdam.

Segers H., 1995b. A reappraisal of the Scaridiidae (Rotifera, Monogononta). *Zoologica Scripta* 24: 91-100.

Segers H., 1996. The biogeography of littoral *Lecane* Rotifera. *Hydrobiologia* 323: 169-197.

Segers H., 2003. A biogeographical analysis of rotifers of the genus *Trichocerca* Lamarck, 1801 (Trichocercidae, Monogononta, Rotifera), with notes on taxonomy. *Hydrobiologia* 500: 103-114.

Segers H., 2007. Annotated checklist of the rotifers (Phylum Rotifera), with notes on nomenclature, taxonomy and distribution. *Zootaxa* 1564: 1-104.

Segers H., 2008. Global diversity of rotifers (Rotifera) in freshwater. *Hydrobiologia* 595: 49-59.

Segers H. & De Meester L., 1994. Rotifera of Papua New Guinea, with a description of a new *Scaridium* Ehrenberg, 1830. *Archiv für Hydrobiologie* 131: 111-125.

Segers H., Nwadiaro C.S. & Dumont H.J., 1993. Rotifera of some lakes in the floodplain of the River Niger (Imo State, Nigeria) II. Faunal composition and diversity. *Hydrobiologia* 250: 63-71.

Segers H. & Sanoamuang L-o., 2007. Note on a highly diverse rotifer assemblage (Rotifera: Monogononta) in a Laotian rice paddy and adjacent pond. *International Review of Hydrobiology* 92: 640-646.

Segers H., Sarma S.S.S., Ovie S.I. & Mbogo D.K., 1994. Note on the taxonomy and distribution of *Brachionus durgae* Dhanapathi, 1974 (Rotifera: Brachionidae). *Journal of African Zoology* 108: 397-400.

Sellers T. & Bukaveckas P.A., 2003. Phytoplankton production in a large, regulated river: a modeling and mass balance assessment. *Limnology and Oceanography* 48: 1476-1487.

Serafim M.Jr., Bonecker C.C., Rossa D.C., Lansac-Tôha F.A. & Costa C.L., 2003. Rotifers of the Upper Paraná River floodplain: additions to the checklist. *Brazilian Journal of Biology* 63: 207-212.

Shiel R.J., Walker K.F. & Williams W.D., 1982. Plankton of the Lower River Murray, South Australia. *Australian Journal of Marine and Freshwater Research* 33: 301-327.

Sládecek V., 1983. Rotifers as indicators of water quality. *Hydrobiologia* 100: 169-201.

Sluss T.D., Cobbs G.A. & Thorp J.H., 2008. Impact of turbulence on riverine zooplankton: a mesocosm experiment. *Freshwater Biology* 53: 1999-2010.

Solow A.R. & Duplisea D.E., 2007. Testing for compensation in a multi-species community. *Ecosystems* 10: 1034-1038.

Stanford J.A. & Ward J.V., 1979. Stream regulation in North America. In Ward J.V. & Stanford J.A. (eds.), *The Ecology of Regulated Rivers*. Plenum Press, New York, pp 215–236.

Stemberger R.S., 1990. Food limitation, spination, and reproductin in *Brachionus calyciflorus*. *Limnology and Oceanography* 35: 33-44.

Syvitski J.P.M. & Kettner A.J., 2007. On the flux of water and sediment into the Northern Adriatic Sea. *Continental Shelf Research* 27: 296-308.

Tavernini S., Pierobon E. & Viaroli P., 2011. Physical factors and dissolved reactive silica affect phytoplankton community structure and dynamics in a lowland eutrophic river (Po river, Italy). *Hydrobiologia* 669: 213-225.

Taticchi M.I., 1968. Vicende stagionali delle comunità litoranee del Lago Trasimeno (1963-1965). *Rivista di Idrobiologia* 7: 195-302 (in Italian).

ter Braak C.J.F. & Šmilauer P., 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power, Ithaca.

Thorp J.H., Black A.R. & Haag K.H., 1994. Zooplankton assemblages in the Ohio River: Seasonal, tributary and navigation dam effects. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1634-1643.

Thorp J.H. & Casper A.F., 2003. Importance of biotic interactions in large rivers: an experiment with planktivorous fish, dreissenid mussels and zooplankton in the St. Laurence River. *River Research and Applications* 19: 265-279.

Thorp J.H., Thoms M.C. & Delong M.D., 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* 22: 123-147.

Turner P.N., 1996. Preliminary data on rotifers in the interstitial of the Ninnescah river, Kansas, USA. *Hydrobiologia* 319: 179-184.

Ueda H. & Reid J.W., 2003. *Copepoda: Cyclopoida. Genera* Mesocyclops *and* Thermocyclops. Backhuys Publishers, Leiden.

Urabe J., 1992. Midsummer succession of rotifer plankton in a shallow eutrophic pond. *Journal of Plankton Research* 14: 851-866.

Vadadi-Fülöp C., Hufnagel L. & Zsuga K., 2010. Effect of sampling effort and sampling frequency on the composition of the planktonic crustacean assemblage: a case study of the river Danube. *Environmental Monitoring and Assessment* 163: 125-138.

Valderrama J.C., 1977. Methods used by the hydrographical department of the National Board of Fisheries. In Grasshof K. (ed.), *Report of the Baltic Intercalibration Workshop. Annex, Interim Commission for the Protection of the Environment of the Baltic Sea*. Goteborg, Sweden, pp. 13-40.

Valderrama J. C., 1981. The simultaneous analysis of total nitrogen and total phosphorus in natural water. *Marine Chemistry* 10: 109-122.

Van den Brink F.W.B., Van Katwijk M.M. & Van der Velde G., 1994. Impact of hydrology on phyto- and zooplankton community composition in floodplain lakes along the Lower Rhine and Meuse. *Journal of Plankton Research* 16: 351-373.

van Dijk G.M. & van Zanten B., 1995. Seasonal changes in zooplankton abundance in the lower Rhine during 1987-1991. *Hydrobiologia* 304: 29-38.

Vásquez E. & Rey J., 1989. A longitudinal study of zooplankton along the Lower Orinoco River and its Delta (Venezuela). *Annales de Limnologie* 25: 107-120.

Viaroli P., Ferrari I. & Rossetti G., 2002. Long-term limnological research in a quarry lake of the Po River, Italy. *Verhandlungen des internationalen Verein Limnologie* 28: 576-581.

Viaroli P., Puma F. & Ferrari I., 2010. Aggiornamento delle conoscenze ecologiche sul bacino idrografico padano: una sintesi. *Biologia Ambientale* 24: 7-19 (in Italian).

Vinebrooke R.D., Schindler D.W., Findlay D.L., Turner M.A., Patterson M. & Mills K.H., 2003. Trophic dependence of ecosystem resistance and species compensation in Experimentally Acidified Lake 302S (Canada). *Ecosystems* 6: 101-13.

Viroux L., 1999. Zooplankton distribution in flowing waters and its implications for sampling: case studies in the River Meuse (Belgium) and the River Moselle (France, Luxembourg). *Journal of Plankton Research* 21: 1231-1248.

Viscido S.V. & Holmes E.E., 2010. Statistical modelling of communities and ecosystems using the LAMBDA software tool. *Environmental Modelling & Software* 25: 1905-1908.

Wahl D.H., Goodrich J., Nannini M.A., Dettmers J.M. & Soluk D.A., 2008. Exploring riverine zooplankton in three habitats of the Illinois River ecosystem: where do they come from? *Limnology and Oceanography* 53: 2583-2593.

Wallace L.R., Snell T.W., Ricci C. & Nogrady T., 2006. *Rotifera. Vol. 1: Biology, Ecology and Systematics (2nd edition)*. Backhuys Publishers, Leiden.

Walsh E.J., Schröder T., Wallace R.L., Ríos-Arana J.V. & Rico-Martínez R., 2008. Rotifers from selected inland saline waters in the Chihuahuan Desert of México. *Saline Systems* 4: 1-11.

Walz N. & Welker M., 1998. Plankton development in a rapidly flushed lake in the River Spree system (Neuerdorfer See, Northeast Germany). *Journal of Plankton Research* 20: 2071-2087.

Wang Q., Yang Y. & Chen J., 2009. Impact of environment on the spatio-temporal distribution of rotifers in the tidal Guangzhou segment of the Pearl River estuary, China. *International Review of Hydrobiology* 94: 688-705.

Ward J.V., 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8: 2-8.

Ward J.V. & Tockner K., 2000. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology* 46: 807-819.

WCD, World Commission on Dams, 2000. *Dams and development: a new framework for decision-making*. Earthscan Publications Ltd, London; Sterling VA, USA.

Weitere M. & Arndt H., 2002. Top-down effects on pelagic heterotrophic nanoflagellates (HNF) in a large river (River Rhine): do losses to the benthos play a role? *Freshwater Biology* 47: 1437-1450.

Welker M. & Walz N., 1998. Can mussels control the plankton in rivers? - a planktological approach applying a Lagrangian sampling strategy. *Limnology and Oceanography* 43: 753-762.

Welker M. & Walz N., 1999. Plankton dynamics in a river-lake system - on continuity and discontinuity. *Hydrobiologia* 408/409: 233-239.

Williams L.G., 1966. Dominant planktonic rotifers of major waterways of the United States. *Limnology and Oceanography* 11: 83-91.

Winner J.M., 1975. Zooplankton. In Whitton B.A. (ed.), *River Ecology*. Blackwell, Oxford, pp. 155-169.

Zanchettin D., Traverso P. & Tomasino M., 2008. Po River discharges: a preliminary analysis of a 200-year time series. *Climatic Change* 89: 411-433.

Zhou S., Tang T., Wu N., Fu X. & Cai Q., 2008. Impact of a small dam on riverine zooplankton. *International Review of Hydrobiology* 93: 297-311.

Zimmermann-Timm H., Holst H. & Kausch H., 2007. Spatial dynamics of rotifers in a large lowland river, the Elbe, Germany: How important are retentive shoreline habitats for the plankton community? *Hydrobiologia* 593: 49-58.

Zsuga K., 1997. The ecological condition of the Criş/Körös catchment area on the basis of planktonic fauna. In Sárkány-Kiss A. & Hamar J. (eds.), *The Criş/Körös Rivers' Valleys. A study of the geography, hydrobiology and ecology of the river system and its environment.* Tiscia Monograph Series 2. Szolnok, Szeged, Târgu Mureş, pp. 135-152.

ANNEX 1

List of zooplankton taxa found during the different surveys presented in this work. (VIA0810: samples collected at Viadana in the period Jan 2008 - Apr 2010; VIA05: samples collected at Viadana in the period Jul - Sep 2005; LAGR: samples collected during the Lagrangian survey in May 2010; I.SER: samples collected at Isola Serafini in summer 2009; MOR: samples collected at Mortizza in the period Jul 2009 - Aug 2010; SER: samples collected at Serravalle in the period Jul 2009 - Aug 2010).

	VIA0810	**VIA05**	**LAGR**	**I.SER.**	**MOR**	**SER**
Rotifera						
Order Bdelloidea						
Bdelloidea n.i.	*x*	*x*	*x*	*x*	*x*	*x*
Order Monogononta						
Family Epiphanidae						
Genus *Epiphanes* Ehrenberg, 1832						
Epiphanes brachionus spinosa (Rousselet, 1901)	*x*		*x*			
Epiphanes macroura (Barrois & Daday, 1894)	*x*					*x*
Epiphanes senta (Müller, 1773)	*x*				*x*	
Genus *Rhinoglena* Ehrenberg, 1853						
Rhinoglena frontalis Ehrenberg, 1853	*x*					
Genus *Cyrtonia* Rousselet, 1894						
Cyrtonia tuba (Ehrenberg, 1834)			*x*			
Genus *Mikrocodides* Bergendal, 1892						
Mikrocodides chlaena (Gosse, 1886)					*x*	
Family Brachionidae						
Genus *Brachionus* Pallas, 1766						
Brachionus angularis Gosse, 1851	*x*	*x*	*x*	*x*	*x*	*x*
Brachionus bennini Leissling, 1924	*x*		*x*	*x*	*x*	*x*
Brachionus bidentatus Anderson, 1889	*x*	*x*				*x*
Brachionus budapestinensis Daday, 1885	*x*	*x*	*x*	*x*	*x*	*x*
Brachionus calyciflorus Pallas, 1766	*x*	*x*	*x*	*x*	*x*	*x*
Brachionus diversicornis (Daday, 1883)	*x*	*x*	*x*			*x*
Brachionus durgae Dhanapathi, 1974	*x*			*x*	*x*	*x*
Brachionus falcatus Zacharias, 1898	*x*	*x*		*x*	*x*	*x*
Brachionus forficula Wierzejski, 1891	*x*	*x*	*x*	*x*	*x*	*x*
Brachionus leydigii Cohn, 1862	*x*					
Brachionus quadridentatus Hermann, 1783	*x*		*x*	*x*	*x*	*x*
Brachionus rubens Ehrenberg, 1838	*x*		*x*	*x*	*x*	*x*
Brachionus gr. *urceolaris* sensu Koste, 1978	*x*	*x*	*x*		*x*	*x*
Genus *Plationus* Segers, Murugan & Dumont, 1993						
Plationus patulus (Müller, 1786)		*x*				
Genus *Keratella* Bory de St. Vincent, 1822						
Keratella cochlearis (Gosse, 1851)	*x*	*x*	*x*	*x*	*x*	*x*
Keratella cochlearis f. *tecta* (Gosse, 1851)	*x*	*x*	*x*	*x*	*x*	
Keratella quadrata sensu Ruttner-Kolisko, 1974	*x*	*x*	*x*		*x*	*x*
Keratella spp.	*x*					
Keratella ticinensis (Callerio, 1921)			*x*			
Keratella tropica (Apstein, 1907)	*x*	*x*	*x*	*x*	*x*	*x*
Genus *Notholca* Gosse, 1886						
Notholca gr. a*cuminata-labis* sensu Ruttner-Kolisko, 1974	*x*		*x*		*x*	*x*
Notholca foliacea (Ehrenberg, 1838)	*x*				*x*	
Notholca squamula (Müller, 1786)	*x*		*x*		*x*	*x*
Genus *Anuraeopsis* Lauterborn, 1900						
Anuraeopsis fissa Gosse, 1851	*x*	*x*		*x*		
Anuraeopsis sp.			*x*		*x*	*x*
Genus *Kellicottia* Ahlstrom, 1938						

	VIA0810	VIA05	LAGR	I.SER.	MOR	SER
Kellicottia longispina (Kellicott, 1879)	*x*		*x*		*x*	*x*
Family Euchlanidae						
Genus *Euchlanis* Ehrenberg, 1832						
Euchlanis gr. *deflexa-lyra* sensu Ruttner-Kolisko, 1974	*x*		*x*		*x*	*x*
Euchlanis gr. *dilatata-parva* sensu Ruttner-Kolisko, 1974	*x*	*x*	*x*	*x*	*x*	*x*
Family Mytilinidae						
Genus Mytilina Bory de St. Vincent, 1826						
Mytilina bisulcata (Lucks, 1912)	*x*					
Mytilina sp.	*x*					
Genus *Lophocharis* Ehrenberg, 1838						
Lophocharis salpina (Ehrenberg, 1834)		*x*	*x*		*x*	
Family Trichotriidae						
Genus *Trichotria* Bory de St. Vincent, 1827						
Trichotria pocillum (Müller, 1776)	*x*	*x*	*x*		*x*	
Trichotria tetractis (Ehrenberg, 1830)	*x*	*x*	*x*	*x*	*x*	*x*
Genus *Wolga* Skorikov, 1903						
Wolga spinifera (Western, 1894)	*x*		*x*		*x*	
Family Lepadellidae						
Genus *Colurella* Bory de St. Vincent, 1824						
Colurella adriatica Ehrenberg, 1831	*x*					
Colurella colurus (Ehrenberg, 1830)	*x*					
Colurella spp.	*x*		*x*	*x*	*x*	
Colurella uncinata (Müller, 1773)	*x*	*x*	*x*	*x*	*x*	*x*
*Colurella uncinata bicuspidata (*Ehrenberg, 1832)	*x*		*x*		*x*	*x*
Genus *Lepadella* Bory de St. Vincent, 1826						
Lepadella acuminata (Ehrenberg, 1834)	*x*		*x*		*x*	*x*
Lepadella biloba Hauer, 1958	*x*				*x*	*x*
Lepadella patella (Müller, 1786)	*x*	*x*	*x*	*x*	*x*	*x*
Lepadella rhomboides (Gosse, 1886)	*x*		*x*		*x*	*x*
Lepadella sp.			*x*	*x*	*x*	
Lepadella (Xenolepadella) astacicola Hauer, 1926	*x*					
Genus *Squatinella* Bory de St. Vincent, 1826						
Squatinella mutica (Ehrenberg, 1832)	*x*					
Family Lecanidae						
Genus *Lecane* Nitzsch, 1827						
Lecane bulla (Gosse, 1851)	*x*	*x*	*x*	*x*	*x*	*x*
Lecane closterocerca (Schmarda, 1859)	*x*	*x*	*x*	*x*	*x*	*x*
Lecane cornuta (Müller, 1786)	*x*		*x*		*x*	*x*
Lecane elegans Harring, 1914	*x*				*x*	
Lecane fadeevi (Neiswestnova-Shadina, 1935)	*x*		*x*	*x*	*x*	*x*
Lecane flexilis (Gosse, 1886)	*x*		*x*		*x*	*x*
Lecane hamata (Stokes, 1896)	*x*	*x*	*x*	*x*	*x*	*x*
Lecane hastata (Murray, 1913)	*x*					
Lecane incospicua Segers & Dumont, 1993	*x*					
Lecane ivli (Wiszniewski, 1935)	*x*					
Lecane ludwigii (Eckstein, 1883)					*x*	
Lecane luna (Müller, 1776)	*x*	*x*	*x*	*x*	*x*	*x*
Lecane gr. *lunaris* (Ehrenberg, 1832)	*x*	*x*	*x*	*x*	*x*	*x*
Lecane papuana (Murray, 1913)	*x*	*x*	*x*	*x*	*x*	*x*
Lecane pyriformis (Daday, 1905)	*x*					*x*
Lecane quadridentata (Ehrenberg, 1830)	*x*	*x*			*x*	
Lecane sp.	*x*					
Lecane stenroosi (Meissner, 1908)	*x*			*x*		*x*
Lecane subtilis Harring & Myers, 1926	*x*					
Lecane tenuiseta Harring, 1914	*x*		*x*	*x*	*x*	*x*
Family Proalidae						
Genus *Proales* Gosse, 1886						
Proales sigmoidea (Skorikov, 1896)	*x*					
Proales sp.			*x*	*x*		

	VIA0810	**VIA05**	**LAGR**	**I.SER.**	**MOR**	**SER**
Proales theodora (Gosse, 1887)	*x*				*x*	*x*
Family Lindiidae						
Genus *Lindia* Dujardin, 1841						
Lindia torulosa Dujardin, 1841	*x*				*x*	
Family Notommatidae						
Notommatidae n.i.		*x*				
Genus *Resticula* Harring & Myers, 1924						
Resticula anceps Harring & Myers, 1924	*x*					
Resticula gelida (Harring & Myers, 1922)	*x*					
Resticula sp.			*x*			
Genus *Enteroplea* Ehrenberg, 1830						
Enteroplea lacustris Ehrenberg, 1830	*x*					
Genus *Eosphora* Ehrenberg, 1830						
Eosphora anthadis Harring & Myers, 1922	*x*			*x*		
Eosphora ehrenbergi Weber & Montet, 1918	*x*			*x*	*x*	
Eosphora najas Ehrenberg, 1830				*x*		
Genus Monommata Bartsch, 1870						
Monommata sp.				*x*		
Genus *Notommata* Ehrenberg, 1830						
Notommata cyrtopus cyrtopus Gosse, 1886	*x*			*x*	*x*	
Notommata glyphura Wulfert, 1935	*x*		*x*		*x*	
Notommata cfr. *pachyura* (Gosse, 1886)	*x*			*x*	*x*	
Notommata pseudocerberus de Beauchamp, 1908	*x*		*x*	*x*	*x*	*x*
Notommata spp.	*x*		*x*	*x*	*x*	
Genus *Pleurotrocha* Ehrenberg, 1830						
Pleurotrocha petromyzon (Ehrenberg, 1830)	*x*		*x*	*x*	*x*	*x*
Genus *Cephalodella* Bory de St. Vincent, 1826						
Cephalodella catellina (Müller, 1786)	*x*		*x*	*x*	*x*	*x*
Cephalodella forficula (Ehrenberg, 1830)	*x*		*x*	*x*	*x*	
Cephalodella gibba (Ehrenberg, 1830)	*x*	*x*	*x*	*x*	*x*	*x*
Cephalodella cfr. *hollowdayi* Koste, 1986			*x*	*x*		*x*
Cephalodella cfr. *innesi* Myers, 1924	*x*					
Cephalodella megalocephala (Glascott, 1893)	*x*		*x*	*x*		*x*
Cephalodella spp.	*x*		*x*	*x*	*x*	*x*
Cephalodella stenroosi Wulfert, 1937			*x*		*x*	
Cephalodella theodora Koch-Althaus, 1961	*x*					
Cephalodella trigona (Rousselet, 1895)	*x*					*x*
Cephalodella ventripes (Dixon-Nuttall, 1901)	*x*					
Cephalodella xenica Myers, 1924					*x*	*x*
Family Scaridiidae						
Genus *Scaridium* Ehrenberg, 1830						
Scaridium longicaudum (Müller, 1786)	*x*		*x*	*x*	*x*	
Family Trichocercidae						
Genus *Trichocerca* Lamarck, 1801						
Trichocerca bicristata (Gosse, 1887)	*x*	*x*			*x*	
Trichocerca braziliensis (Murray, 1913)	*x*					
Trichocerca elongata (Gosse, 1886)		*x*				
Trichocerca insignis (Herrick, 1885)				*x*		
Trichocerca porcellus (Gosse, 1851)	*x*	*x*	*x*		*x*	*x*
Trichocerca pusilla (Jennings, 1903)		*x*				
Trichocerca rattus (Müller, 1776)	*x*		*x*			
Trichocerca similis (Wierzejski, 1893)	*x*	*x*	*x*			*x*
Trichocerca spp.	*x*	*x*	*x*	*x*	*x*	*x*
Trichocerca tenuior (Gosse, 1886)	*x*		*x*	*x*	*x*	*x*
Family Gastropodidae						
Genus *Gastropus* Imhof, 1898						
Gastropus hyptopus (Ehrenberg, 1838)	*x*		*x*		*x*	
Gastropus stylifer (Imhof, 1891)	*x*	*x*				
Genus *Ascomorpha* Perty, 1850						

	VIA0810	**VIA05**	**LAGR**	**I.SER.**	**MOR**	**SER**
Ascomorpha ovalis (Bergendal, 1892)	*x*		*x*		*x*	
Ascomorpha saltans Bartsch, 1870	*x*		*x*		*x*	*x*
Family Synchaetidae						
Genus *Synchaeta* Ehrenberg, 1832						
Synchaeta gr. *stylata-pectinata* sensu Ruttner-Kolisko, 1974	*x*		*x*	*x*	*x*	*x*
Synchaeta gr. *tremula-oblonga* sensu Ruttner-Kolisko, 1974	*x*		*x*	*x*	*x*	*x*
Synchaeta sp.	*x*	*x*	*x*	*x*	*x*	
Genus *Polyarthra* Ehrenberg, 1834						
Polyarthra major Burckhardt, 1900	*x*		*x*	*x*	*x*	*x*
Polyarthra gr. *vulgaris-dolichoptera* sensu Ruttner-Kolisko, 1974	*x*	*x*	*x*	*x*	*x*	*x*
Family Asplanchnidae						
Genus *Asplanchna* Gosse, 1850						
Asplanchna brightwellii Gosse, 1850	*x*	*x*	*x*	*x*		*x*
Asplanchna priodonta Gosse, 1850	*x*	*x*	*x*	*x*	*x*	*x*
Asplanchna sieboldii (Leydig, 1854)			*x*			*x*
Family Ituridae						
Genus *Itura* Harring & Myers, 1928						
Itura gr. *aurita* sensu Koste, 1978	*x*		*x*		*x*	*x*
Itura myersi Wulfert, 1935	*x*					*x*
Family Dicranophoridae						
Genus *Dicranophorus* Nitzsch, 1827						
Dicranophorus cfr. *epicharis* Harring & Myers, 1928				*x*		
Dicranophorus forcipatus (Müller, 1786)	*x*		*x*			
Dicranophorus luetkeni (Bergendal, 1892)	*x*			*x*	*x*	*x*
Dicranophorus spp.	*x*		*x*		*x*	
Genus *Dicranophoroides* De Smet, 1997						
Dicranophoroides caudatus (Ehrenberg, 1834)	*x*					*x*
Genus *Paradicranophorus* Wiszniewski, 1929						
Paradicranophorus hudsoni (Glascott, 1893)	*x*				*x*	
Paradicranophorus sp.				*x*		
Genus *Encentrum* Ehrenberg, 1838						
Encentrum cfr. *gibbosum* Wulfert, 1936	*x*					
Encentrum incisum Wulfert, 1936		*x*				
Encentrum cfr. *putorius* Wulfert, 1936	*x*		*x*		*x*	*x*
Encentrum saundersiae (Hudson, 1885)	*x*		*x*		*x*	*x*
Encentrum spp.	*x*					
Encentrum uncinatum (Milne, 1886)	*x*					*x*
Encentrum wiszniewskii Wulfert, 1939	*x*		*x*		*x*	
Genus *Parencentrum* Wiszniewski, 1953						
Parencentrum lutetiae (Harring & Myers, 1928)	*x*					*x*
Genus *Aspelta* Harring & Myers, 1928						
Aspelta circinator (Gosse, 1886)	*x*				*x*	
Aspelta sp.			*x*			
Genus *Kostea* De Smet, 1997						
Kostea wockei (Koste, 1961)	*x*		*x*			
Family Testudinellidae						
Genus T*estudinella* Bory de St. Vincent, 1826						
Testudinella caeca (Parsons, 1892)			*x*		*x*	
Testudinella elliptica (Ehrenberg, 1834)	*x*					
Testudinella gr. *incisa* sensu Ruttner-Kolisko, 1974	*x*				*x*	
Testudinella mucronata (Gosse, 1886)	*x*					
Testudinella patina (Hermann, 1783)	*x*		*x*	*x*		*x*
Testudinella truncata (Gosse, 1886)	*x*					
Genus *Pompholyx* Gosse, 1951						
Pompholyx sulcata Hudson, 1885	*x*	*x*	*x*	*x*	*x*	*x*
Family Flosculariidae						
Flosculariidae n.i.	*x*	*x*	*x*	*x*	*x*	*x*
Family Conochilidae						
Genus *Conochilus* Ehrenberg, 1834						

	VIA0810	**VIA05**	**LAGR**	**I.SER.**	**MOR**	**SER**
Conochilus dossuarius Hudson, 1885	*x*					*x*
Family Hexarthridae						
Genus *Hexarthra* Schmarda, 1854						
Hexarthra fennica (Levander, 1892)	*x*		*x*		*x*	*x*
Hexarthra mira (Hudson, 1871)		*x*				
Family Filiniidae						
Genus F*ilinia* Bory de St. Vincent, 1824						
Filinia brachiata (Rousselet, 1901)		*x*	*x*			
Filinia gr. *longiseta-terminalis* sensu Ruttner-Kolisko, 1974	*x*	*x*	*x*	*x*	*x*	*x*
Filinia opoliensis (Zacharias, 1898)	*x*	*x*		*x*	*x*	*x*
Family Collothecidae						
Genus *Collotheca* Harring, 1913						
Collotheca sp.	*x*		*x*	*x*		*x*
Cladocera						
Family Sididae						
Genus *Diaphanosoma* Fischer, 1850						
*Diaphanosoma brachyurum (*Liévin, 1848)		*x*				
Family Bosminidae						
Genus *Bosmina* Baird, 1845						
Bosmina coregoni Baird, 1857			*x*		*x*	
Bosmina longirostris (Müller, 1785)	*x*	*x*	*x*	*x*	*x*	*x*
Family Daphniidae						
Genus *Ceriodaphnia* Dana, 1853						
Ceriodaphnia reticulata (Jurine, 1820)	*x*					
Ceriodaphnia sp.			*x*			
Genus *Scapholeberis* Schödler, 1858						
Scapholeberis mucronata (Müller, 1776)	*x*	*x*	*x*			*x*
Genus *Simocephalus* Schödler, 1858						
Simocephalus vetulus (Müller, 1776)		*x*				
Genus *Daphnia* (Müller, 1785)						
Daphnia ambigua Scourfield, 1947		*x*				
Daphnia cucullata Sars, 1862			*x*			
Daphnia galeata Sars, 1864		*x*	*x*			*x*
Daphnia gr. *longispina* (Müller, 1776)	*x*					
Daphnia sp.	*x*	*x*	*x*	*x*		
Family Moinidae						
Genus *Moina* Baird, 1850						
Moina brachiata (Jurine, 1820)	*x*					
Moina micrura Kurz, 1874	*x*	*x*	*x*	*x*		*x*
Family Macrothricidae						
Genus *Ilyocryptus* Sars, 1862						
Ilyocryptus agilis Kurz, 1878	*x*				*x*	
Ilyocryptus sordidus Liévin, 1848		*x*	*x*		*x*	
Genus Macrothrix Baird, 1843						
Macrothrix laticornis (Jurine, 1820)	*x*	*x*		*x*	*x*	*x*
Macrothrix rosea (Jurine, 1820)	*x*					
Macrothrix sp.			*x*			
Family Chydoridae						
Genus *Pleuroxus* Baird, 1843						
Pleuroxus denticulatus Birge, 1879		*x*				
Genus *Phrixura* Müller, 1867						
Phrixura leei (Chien, 1970)	*x*	*x*		*x*	*x*	*x*
Genus *Leydigia* Kurz, 1875						
Leydigia acanthocercoides (Fischer, 1854)	*x*	*x*				
Leydigia leydigi (Schödler, 1862)	*x*	*x*				
Genus *Chydorus* Leach, 1816						
Chydorus sphaericus Müller, 1785	*x*		*x*	*x*		

	VIA0810	**VIA05**	**LAGR**	**I.SER.**	**MOR**	**SER**
Genus *Alona* Baird, 1843						
Alona affinis (Leydig, 1860)		*x*				
Alona guttata Sars, 1862	*x*	*x*	*x*			
Alona quadrangularis (Müller, 1776)	*x*	*x*	*x*	*x*	*x*	
Alona rectangula Sars, 1862	*x*	*x*			*x*	
Alona sp.	*x*					
Genus *Alonella* Sars, 1862						
Alonella nana (Baird, 1843)			*x*			
Copepoda						
Order Calanoida						
Family Centropagidae						
Genus *Boeckella* De Guerne & Richard, 1889						
Boeckella triarticulata Thomson, 1882		*x*				
Family Diaptomidae						
Genus *Eudiaptomus* Kiefer, 1932						
Eudiaptomus gracilis (Sars, 1863)	*x*					
Eudiaptomus sp.	*x*	*x*				
Eudiaptomus padanus (Burckhardt, 1900)	*x*					
Order Cyclopoida						
Family Cyclopidae						
Genus *Eucyclops* Kiefer, 1957						
Eucyclops macrurus (Sars, 1863)		*x*				
Eucyclops sp.	*x*	*x*		*x*	*x*	*x*
Eucyclops serrulatus (Fischer, 1851)	*x*	*x*				
Genus *Paracyclops* Claus, 1893						
Paracyclops fimbriatus (Fischer, 1853)	*x*	*x*				
Paracyclops sp.	*x*			*x*		
Genus *Cyclops* Müller, 1776						
Cyclops sp.	*x*		*x*			
Cyclops strenuus Fischer, 1851	*x*					
Genus *Acanthocyclops* Kiefer, 1927						
Acanthocyclops sp.	*x*		*x*			
Acanthocyclops gr. *vernalis-robustus* sensu Kiefer, 1976	*x*	*x*	*x*	*x*		
Genus *Macrocyclops* Claus, 1893						
Macrocyclops fuscus (Jurine, 1820)		*x*				
Macrocyclops albidus (Jurine, 1820)			*x*			
Genus *Mesocyclops* Sars, 1914						
Mesocyclops sp.	*x*					
Genus *Microcyclops* Claus, 1893						
Microcyclops varicans (Sars, 1863)						*x*
Genus *Thermocyclops* Kiefer, 1937						
Thermocyclops crassus (Fischer, 1853)		*x*				
Thermocyclops sp.	*x*			*x*		*x*
Genus *Tropocyclops* Kiefer, 1927						
Tropocyclops prasinus (Fischer, 1860)				*x*		
Genus *Graeteriella* Brehm, 1926						
Graeteriella sp.	*x*					
Order Harpacticoida						
Harpacticoida n.i.	*x*		*x*			*x*