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Research Article

Water residence time as a driving force of zooplankton structure and succession

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Abstract. We studied zooplankton dynamics in a groundwater-fed, montane lake during four consecutive years and assessed the importance of water residence time for zooplankton dynamics. Crustacean abundance and biomass were significantly correlated with water residence time and temperature, but showed no significant correlation with phytoplankton biovolume. We hypothesised that temperature depended on water residence time (τ), and therefore we further investigated the functional relationship of crustacean dominance with the latter by logistic regression analysis. Water residence time values above a threshold value ($\tau = 193$ days) determined crustacean biomass dominance while values below determined rotiferan dominance. Our results indicated that water residence time was an important factor structuring zooplankton succession in this lake that showed large fluctuations of τ values (median 263 days; range 23 – 786 days for the four year period) compared to other lakes. We suggest that crustacean biomass was directly controlled through water residence time as found for riverine systems, whereas rotifer biomass was controlled through exploitative competition with crustaceans for phytoplankton. The importance of water residence time may have been underestimated in lakes when explaining zooplankton community structure and succession, because studies usually focus on other factors such as temperature, predation, or food limitation.

Key words. Lakes; rotifers; crustaceans; competition; hydrology.

Introduction

Zooplankton are a fundamental component of the pelagic food web in lakes, linking primary producers to higher consumers, and limnological research has a long tradition in investigating the mechanisms that govern zooplankton diversity and species succession. While single species often show stochastic patterns,

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seasonal succession of larger taxonomic units is fairly predictable (Sommer et al., 1986). In temperate lakes, zooplankton community succession usually shows an early spring maximum of rotifers followed by a maximum of crustaceans, and then a zooplankton decline in summer (Hutchinson, 1967; Wetzel, 2001). Traditionally, this succession has largely been explained by the short generation time of rotifers, the competitive advantage of crustaceans in exploiting resources, and fish predation (Sommer et al., 1986), whereas hydrological features are usually not considered as an important factor in lakes (Pace et al., 1992).

Plankton studies in rivers, reservoirs, and ponds, however, have shown that hydrological aspects such as water-level fluctuations, length of wet phase, water residence time, or flow rate influence zooplankton dynamics and determine the dominance of small taxa such as ciliates, rotifers, and small crustaceans over large crustaceans (e.g. rivers: Basu and Pick, 1996; 1997; Thorp and Mantovani, 2005; reservoirs: Naselli-Flores and Barone, 1997; Campbell et al., 1998; Geraldes and Boavida, 2006; ponds: Girdner and Larson, 1995; Brucet et al., 2005). The zooplankton community in flood plains and rapidly flushed lakes shows similarities with those of rivers, with a rotifer or crustacean dominance in lotic and lentic conditions, respectively (Walz and Welker, 1998; Baranyi et al., 2002). Moreover, several authors have related zooplankton community structure in dimictic lakes to spring inflow (Jassby et al., 1990) and precipitation (Romare et al., 2005).

To our knowledge, zooplankton structure in natural lakes has not been found to be driven by water residence time, a parameter that summarises different hydrological aspects such as inflow, water-level fluctuations, precipitation, and evaporation. In this study, we anticipated that i) an increase in water residence time would be more favourable to crustacean biomass, ii) crustaceans outcompete rotifers by exploitative competition, and iii) water residence time and temperature are important zooplankton community structuring forces. We tested these hypotheses in Lake Tovel because its peculiar hydrology (Borsato and Ferretti, 2006), i.e. large water-level fluctuations and a major inflow through isothermal underground springs, allowed us to test the effects of rapidly changing water residence times on zooplankton structure. In addition, we considered the importance of other factors such as algal biomass and predation for zooplankton community structure and dynamics.

Materials and methods

Study site

Lake Tovel (46°15'N, 10°57'E; area = 38 ha, volume = 7.4×10^6 m^3, maximum depth = 39 m, mean depth = 19 m) is located 1178 m above sea level (a.s.l.) in the Adamello Brenta Natural Park (Trentino, Italy) and has a watershed area of 40.6 km^2. The oligotrophic lake has a small and shallow (4 m) SW basin and a larger, deeper (39 m) NE basin (Fig. 1) and is ice-covered from December to April. Secchi disk transparency in this lake is high with an annual average of 11 m (range 7–21 m) (Borghi et al., 2006). The fish fauna of Lake Tovel consists of two littoral species, minnow (*Phoxinus phoxinus* L.) and stone loach (*Othrias barbatula* L.), and one pelagic species, arctic charr (*Salvelinus alpinus* L.) present in low abundance (Betti, 2003).

Sampling and sample processing

Sampling was done at biweekly (2002) or monthly (2003, 2004, and 2005) intervals. Vertical profiles of water temperature and dissolved oxygen (Hydrolab DS4a multiprobe) were taken at each sampling occasion. Zooplankton samples ($n = 400$) were collected with a 3-L Kemmerer-like sampler at the surface, and at 1, 2, 5, 10, 15, 20, 25, 30, and 35 m depth in the NE basin of the lake, filtered through a 10 μm plankton net, and fixed with formalin (1 % v/v final concentration). Species composition and biomass were determined as described in Obertegger et al. (2006). Briefly, the whole sample was counted with a stereoscope (model Wild Macroscope M420) due to the low zooplankton abundance (< 250 specimens per sample). Quantitative integrated zooplankton samples were also taken by vertical net hauls (70 μm) from 35 m depth to the surface. Species identification was according to Braioni and Gelmini (1983) and Dumont (2002). Rotifer biovolume was calculated and transformed to dry weight according to Bottrell et al. (1976). Crustacean dry weight was estimated according to Bottrell et al. (1976) and Rosen et al. (1981).

Whereas the bottle sampler is adequate for sampling rotifers, it is not always considered adequate for estimating crustacean abundance (de Bernardi, 1984). However, comparison of the crustacean abundance obtained by the two sampling methods showed good agreement (*Bosmina longirostris* O.F. Müller: $R^2 = 0.76$; $p < 0.001$; *Daphnia longispina* O.F. Müller: $R^2 = 0.59$; $p < 0.001$), and therefore data analysis was based on bottle sampling. *Cyclops strenuus* Fischer, however, was a rare species making accurate abundance estimates difficult.

Phytoplankton samples were collected at the same depths as zooplankton samples using a 3-L Kemmerer-like sampler. Subsamples were fixed with acid Lugol's solution, and algae were counted with an inverted microscope according to the Uthermöhl technique (1958); algal biovolume was estimated from cell dimensions.

Zooplankton ability to ingest algae may depend on cell size; thus, algal biomass was separated by the greatest axial linear dimension (GALD) into an edible ($\leq 30\ \mu m$) and non-edible fraction ($> 30\ \mu m$) according to Naselli-Flores and Barone (1997).

Hydrology of Lake Tovel

The lake is characterised by a very limited surface inflow (Rislà stream, annual mean 23 L s^{-1}) and a predominant underground inflow through porous aquifers. The main aquifer (Pozzol) is located in porous carbonate debris deposits into which the tributary (Santa Maria Flavona stream) disappears about 1 km upstream of the lake (Fig. 1). The Pozzol aquifer feeds the lake through several perilacustrine springs in the SW basin, as demonstrated by tracing tests that also allowed estimating the permeability coefficient of the aquifer (Borsato and Ferretti, 2006). The inflow of the perilacustrine springs fed by the Pozzol aquifer was estimated by direct gauging of the Santa Maria Flavona tributary, and quantified by applying Darcy's law for open aquifers (Stokes and Evans, 1997):

$$\text{inflow}_{\text{underground}} = K \times H \times L \times I, \quad (1)$$

where K is the coefficient of permeability, H is the mean height of the aquifer, L is the mean length of the aquifer perpendicular to the direction of water flow, and I is the hydraulic gradient H/L between the two piezometers (datalogger Ejkelkamp-DIVER) located at 1183 m and 1204 m a.s.l., respectively. The hydrological budget of the lake was complemented by rain gauging, direct continuous measurements of the surface inflow from the Rislà stream and of the outflow from the Tresenga stream, and by quantifying water loss by surface evaporation and downing through the porous lake bottom. Continuous lake level measurements were taken with a datalogger placed on the lake bottom (Ejkelkamp-DIVER). Values of lake volume as a function of lake level were obtained by a hypsographic curve. The hydrological budget shows that the Pozzol aquifer contributes 81 % of the total inflow, whereas the smaller porous aquifers, surface inflow, and precipitation on the lake surface contribute about 12 %, 5 %, and 2 %, respectively (Borsato and Ferretti, 2006). When the water level is over the threshold value for the outflow (Fig. 2), 45 % of water loss is through the Tresenga stream and bottom seepage accounts for the rest; otherwise all outflow is through bottom seepage (Borsato and Ferretti, 2006).

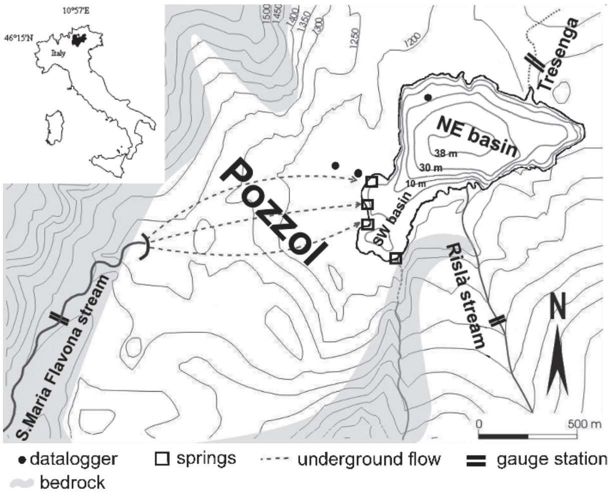

Figure 1. Lake Tovel with part of its watershed showing location of dataloggers and gauge. Left panel shows geographical location.

The theoretical water residence time of a lake is generally calculated by relating the annual amount of water passing through the lake to the volume of the whole basin (George and Hurley, 2003). However, water residence time (τ) values can vary in different strata dependent on stratification and surface outflow (Ambrosetti et al., 2003). This has implications for assessing the functional relationship between τ and zooplankton, because varying τ values in different strata affect specimens in different ways. In this deep lake (39 m), thermal stratification usually showed an atypical pattern with the epilimnion having a maximum depth of only 2 m (Fig. 2). This upper layer accounted for *ca.* 10 % of the lake volume, and τ values calculated with the lower layer (2 m downwards) did not change substantially compared to those calculated with the whole water column. Moreover, stratification in this lake was limited to a short period per year (*ca.* 4 months; Fig. 2). Surface outflow through the Tresenga stream accounted for water loss from the lake only for limited periods: usually following snowmelt (May-June) or in rainy summers (2002, 2005) (Fig. 2). Stratification and surface outflow coincided for about 11 months ($< 25\,\%$), and WRT values calculated with the epilimnion would obviously be much smaller than those of the lower layer.

In any case, pattern of zooplankton diel vertical migration (DVM) in this lake indicated that migrating species generally stayed in the lower layers during the day but showed a nocturnal migration to the upper layers, therefore spending an approximately equal amount of time in both layers, whereas non-migrating species were in the lower layer (Obertegger et al., unpubl. data). Therefore, we suggest that for assessing

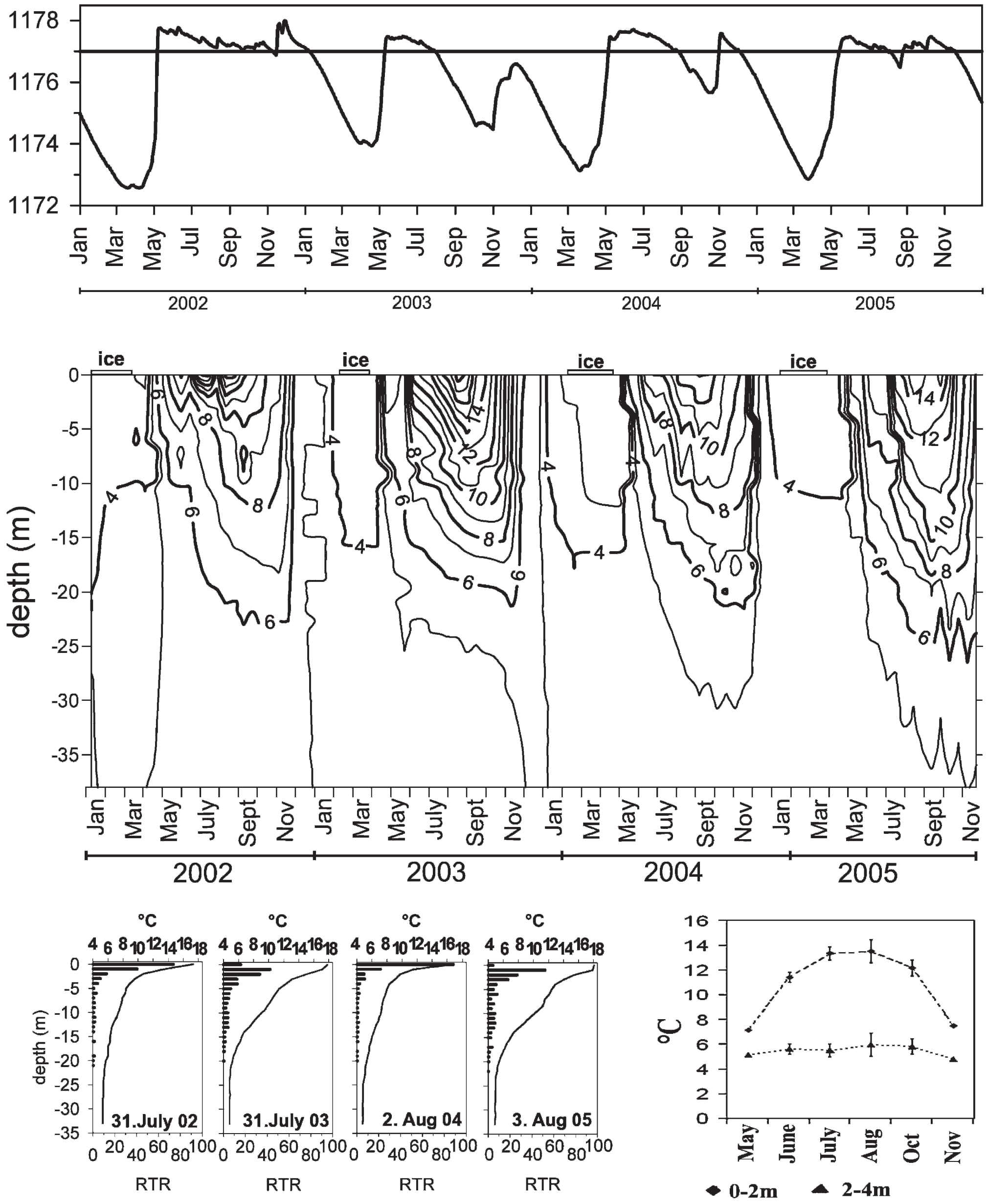

Figure 2. Upper panel: water level fluctuations for the study period. Horizontal line indicates the threshold level for the water outflow. Middle panel: depth-time diagram of isotherms (°C) for the study period. Lower left panel: relative thermal resistance (RTR) for summer days in 2002–2005. Lower right panel: temperature comparison of the upper layer (surface–2 m depth) and the upper layer (<2 m -4 m) of the shallow SW basin (maximum depth 4 m).

the functional relation between water residence time and zooplankton, estimating τ values for the whole water column instead of separately for the upper and lower layer was the better approach, considering that stratification and surface outflow were temporarily and spatially limited and that zooplankton spent equal amounts in the upper and lower layer. We consequently calculated the mean daily water residence time (τ) as the ratio between the lake volume and the water inflow based on mean daily data (24 measurements per day).

Data analysis

Analyses of temperature and plankton data were based on volume-weighted means. The percentage of crustacean abundance ($\%\text{crust}_{\text{ind}}$) or biomass ($\%\text{crust}_{\mu g}$) at each sampling date was calculated as the

$$\Sigma \text{ crustaceans} / \Sigma \text{ (crustaceans} + \text{rotifers) x } 100 \qquad (2)$$

Crustaceans indicated the sum of *B. longirostris*, *D. longispina,* and *C. strenuus* (adults, copepodites, and nauplii) and 'rotifers' indicated all pelagic rotifer species. Crustacean biomass values exceeding 50 % were assigned the value 1 whereas lower values were assigned the value 0. On the basis of this coding, we sorted τ values into two classes based on the dominance of either crustacean (i.e. 1) or rotifer biomass (i.e. 0). The difference between these classes was investigated by non parametric Mann-Whitney Rank Sum test. Correlation analysis of plankton biomass or abundance with τ and temperature data was carried out using non-parametric Spearman (r_S) (STATISTICA 6.0, StatSoft 2003). Additionally, the binary coding was used in a logistic regression analysis to investigate the sole effect of water residence time on zooplankton dominance by a multi-step procedure. Firstly, we investigated the effect of τ on zooplankton biomass, and secondly, we derived the value of τ corresponding to equal probability of crustacean or rotifer dominance from the first calculated regression equation, and set this value as the threshold for the third step. In this step, we counted the number of days showing a water residence time value above (positive values) or below (negative values) the equal dominance threshold, always beginning with the value one when the sign changed. Finally, the number (τ_T) reached at the sampling date was used in the second logistic regression analysis to investigate the delayed effect of water residence time on zooplankton succession. The logistic regression equations were obtained using R (www.r-project.org). As our data were time series, we performed Chi^2 goodness of fit statistics instead of showing p values and F statistics.

Results

In Lake Tovel, water residence time was very variable during the four years (median 263 days; range 23–786 days; Fig. 3). Correlation analysis showed that mean water temperature and edible algal biovolume were correlated with τ (Table 1), while algae were not correlated with crustacean or rotiferan biomass. Anoxia was never found in Lake Tovel (data not shown).

Table 1. Spearman rank correlations (r_S) of different parameters (abundance (ind), biomass (µg), biovolume (vol)), with temperature and water residence time (τ). *** $\alpha = 0.001$; ** $\alpha = 0.01$; * $\alpha = 0.05$.

	temperature	τ	$\text{algae}_{\text{vol}}$
temperature	–	0.35*	–0.02
τ	0.35*	–	–0.34*
$\text{algae}_{\text{vol}}$	–0.02	–0.34*	–
$\text{crustaceans}_{\text{ind}}$	0.50***	0.64***	–0.139
$\text{crustaceans}_{\mu\text{g}}$	0.48***	0.57***	–0.182
$\text{rotifers}_{\text{ind}}$	0.12	0.15	–0.073
$\text{rotifers}_{\mu\text{g}}$	0.11	–0.10	–0.034

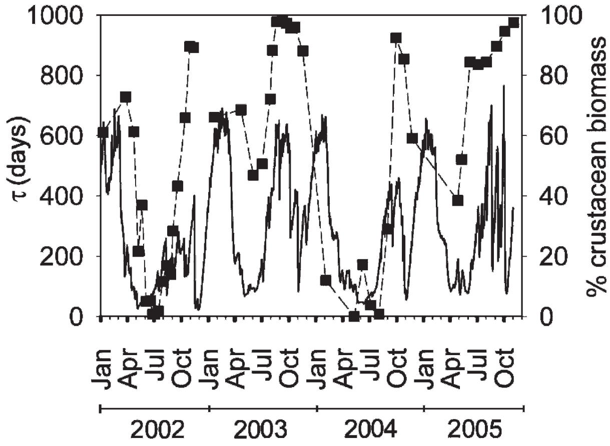

Figure 3. Temporal changes of crustacean biomass (expressed as the percentage of total zooplankton biomass, % $\text{crust}_{\mu\text{g}}$) and water residence time (τ) in Lake Tovel. Continuous line indicates τ and filled squares indicate crustacean biomass (%).

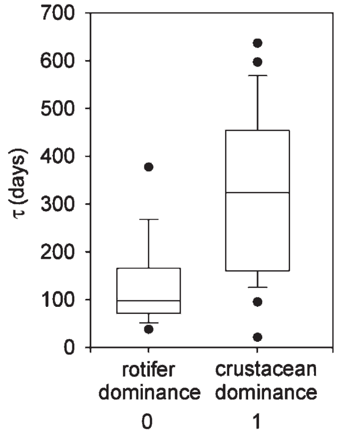

Figure 4. Boxplot for mean water residence time (τ) values for the sampling dates sorted by crustacean (i.e. > 50 % total zooplankton biomass, coded as 1) or rotifers biomass dominance (i.e. < 50 % total zooplankton biomass, coded as 0) in Lake Tovel. Dots represent extreme values, lines represent the 10 %, 25 %, 50 %, 75 %, and 90 % percentiles.

Crustacean and rotifer abundance showed different seasonal patterns in the years investigated. Crustaceans mainly consisted of *B. longirostris* (range of abundance for the whole study period was <1–37 individuals L^{-1}), whereas *D. longispina* (<1–6 individuals L^{-1}) and nauplii, copepodites, and adults of *C. strenuus* (<1–7 individuals L^{-1}) were present in lower abundances. Crustacean abundance and biomass showed a significant correlation with τ and temperature, whereas rotifer did not (Table 1). Rotifer abundance (range 5–193 individuals L^{-1}) was always higher than crustacean abundance and never below 60 %. On the other hand, rotifer and crustacean biomass showed an alternate dominance (range of biomass for the whole study period was 0.2–102 mg

Table 2. Summary of regression analyses between hydrological parameters and crustacean dominance according to biomass (μg L^{-1}). See text for explanation on calculations of τ and τ_T.

variables		function	goodness of fit		
x	y	logistic regression	residual deviance	df	5 % significance limit
τ	crustacean dominance (0 or 1)	$y = -1.54 + 0.009\ \tau$	48.607	45	61.6
τ_T	crustacean dominance (0 or 1)	$y = 0.71 + 0.023\ \tau_T$	48.145	45	61.6

L^{-1} for rotifers, and 0.1–50 mg L^{-1} for crustaceans). Rotifer biomass dominated in spring and summer 2002 and 2004, coinciding with high water inflow and a relatively short water residence time, while crustacean biomass dominated for the rest of the study period when water residence time was longer (Fig. 3). There was a significant difference at the $\alpha = 0.001$ level (Mann-Whitney rank sum $T = 405$, $p = 0.006$) between the "crustacean dominance" and "rotifer dominance" classes according to τ (Fig. 4). The logistic regression between crustacean dominance and τ indicated that an equivalent crustacean and rotiferan biomass could be found at $\tau = 193$ days (Table 2, Fig. 5). Accordingly, crustacean biomass dominated when $\tau > 193$ days, while rotifer biomass did so when $\tau < 193$ days (Fig. 5). On the basis of this threshold value ($\tau = 193$ days), the number of days with lower or higher water residence values was accounted for each sampling date (τ_T). The logistic regression between crustacean dominance and τ_T indicated that an equivalent crustacean and rotiferan biomass could be found found at $\tau_T = -31$ (Table 2, Fig. 5).

Total phytoplankton biovolume for the whole study period was almost twice than that of edible phytoplankton (range 73–1006 $mm^3\ m^{-3}$ and 39–738 $mm^3\ m^{-3}$, respectively). Edible algal biovolume showed a negative correlation with τ (Table 1). Diatoms made the major contribution to edible phytoplankton biovolume (range 2–1227 $mm^3\ m^{-3}$), followed by chrysophytes (16–565 $mm^3\ m^{-3}$), and dinoflagellates (11–354 $mm^3\ m^{-3}$).

Discussion

Our results showed that τ influenced zooplankton biomass succession by favouring crustacean or rotifer dominance. Several studies in rivers, riverine systems, and reservoirs have shown that wash-out effects regulate crustacean and rotifer abundance and biomass (Campbell et al., 1998; Walz and Welker, 1998; Baranyi et al., 2002). Thus, zooplankton biomass is usually higher in lakes than in rivers (Pace et al., 1992). In Lake Tovel, a threshold value ($\tau = 193$ days) determining equivalent crustacean and rotifer biomass was found that was higher than the values of τ usually found (<20 days) for rivers or rapidly flushed lakes (Walz and Welker, 1998; Baranyi et al., 2002). We suggest that possible reasons for this discrepancy (193 *vs.* 20 days of τ as the threshold value of crustacean dominance) were based on two reasons: i) selective wash-out, and ii) population recruitment in lakes as opposed to rivers. Low τ values result in general wash-out (Walz and Welker, 1998; Baranyi et al., 2002), while higher values could affect various life stages differently. In fact, juveniles have reduced swimming capacities compared to adults as indicated by Maar et al. (2003) for copepods and by Dodson and Ramcharan (1991) for *Daphnia pulex*. This suggests that wash-out could be selective with juveniles not being able to resist low τ values, leading to a

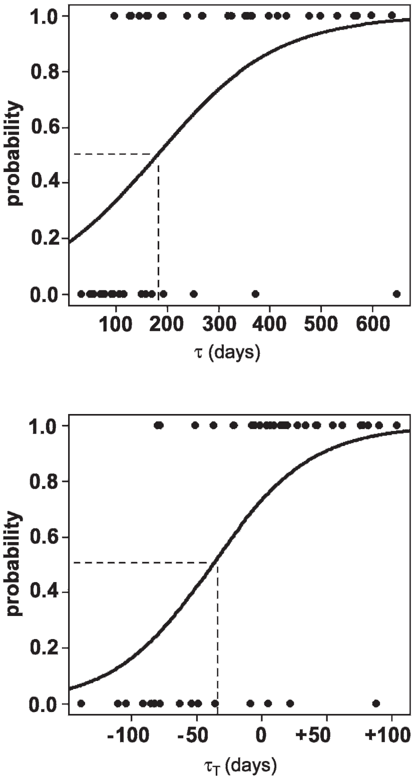

Figure 5. Upper panel: logistic regression between residence time (τ) and the probability of crustacean dominance (i.e. 1). The dashed line indicates a 0.5 probability of crustacean dominance. Lower panel: logistic regression between the time period (days) of water residence time above or below 193 days (τ_T) and the probability of crustacean dominance (i.e. 1). The dashed line indicates a 0.5 probability of crustacean dominance.

progressive decrease in population due to lack of juveniles and adult mortality. Zooplankton recruitment in rivers and rapidly flushed lakes is related to a constant input of individuals transported from upstream (Walz and Welker, 1998). However, in Lake Tovel, recruitment might be negligible from inflowing waters, especially since they pass through an underground aquifer that acts as a natural filter. Therefore in this lake, the (re)establishment of the population might be only from resting eggs in the sediments or isolated patches inside the lake leading to a slower recruitment of populations than seen in rivers or riverine systems.

Furthermore, we found that the zooplankton community in Lake Tovel was continuously "reset" by changes in water residence time with respect to the threshold value ($\tau = 193$ days), but the reset signal depended on the temporal permanence of the change (τ_T). Equivalent rotifer and crustacean biomass was found at $\tau_T = -31$ days (i.e. a period of 31 days with $\tau < 193$ days; Fig. 5), which corresponded to the time needed to observe a shift from crustacean to rotifers dominance. We calculated the theoretical time of crustacean biomass decline assuming an average survival rate of 80 % (Wetzel and Likens, 2000) and a sampling threshold values of 5 individuals m^{-3}. This gave us a theoretical time interval of 40 days to observe a decrease from the highest crustacean abundance found (38 individuals L^{-1}) to 0.005 crustacean L^{-1}. Therefore, we suggest that the time delay ($\tau_T = -31$ days) observed by us could be reasonably attributed to continuous dying of adult crustaceans and a lack of juveniles. A similar delayed effect of water level fluctuations on zooplankton size structure has already been observed by Badosa et al. (2007). By contrast, rotifer biomass did not seem to be influenced by τ (Table 1). The decisive advantage of rotifers over crustaceans is their short generation times and fast development rates at comparable temperatures (Nogrady et al., 1993) that allow them to respond rapidly to changes in water residence time. The importance of generation time as a regulating factor for the dominance of crustaceans or rotifers is recognised in reservoirs (Campbell et al., 1998), rivers (Basu and Pick, 1996), ponds (Girdner and Larson, 1995), and flood plains (Baranyi et al., 2002). We suggest that the shorter generation time of rotifers (5–7 days at 10 °C; Girdner and Larson, 1995) with respect to crustaceans (3–4 weeks for cladocerans at 10 °C; Girdner and Larson, 1995; and up to > 1 year for copepods; Wetzel, 2001) compensated for their advective loss and resulted in their dominance at relatively low τ values (Fig. 5).

The above considerations give evidence that water residence time was an important factor in structuring the zooplankton community in this lake. We showed how rotifer and crustacean dominance was influenced both by an intensity (τ) and a delayed effect (τ_T) of water residence time. However, other factors such as temperature, food availability, and predation could interact with water residence time. In this regard, water temperature is an important factor governing zooplankton dynamics in lakes (Gyllström et al., 2005; Romare et al., 2005), mainly because it determines the length of zooplankton generation time (Gillooly et al., 2002). Crustacean abundance showed a significant correlation with temperature, whereas rotifer abundance did not (Table 1). Crustaceans mainly consisted of one summer species (*Bosmina longirostris*), so the positive effect of higher temperatures was evident. On the other hand, rotifers were represented both by winter and summer species, which probably cancelled out their correlation with temperature. In Lake Tovel, the main inflows are underground springs (Borsato and Ferretti, 2006) showing a stable water temperature of about 5.4 ± 0.1 °C throughout the year (Fig. 2). The influence of these cold inflowing waters on thermal structure is supported by the positive correlation found between temperature and τ, implying that with low τ values surface water temperature was lower than expected for a lake at this altitude. Temperature surely affected zooplankton dynamics in Lake Tovel, and it might be difficult to distinguish between the influence of τ and temperature on zooplankton. However, we suggest that τ determined the temperature evolution in Lake Tovel, and therefore the influence of temperature on zooplankton was an indirect effect of water residence time.

Another important factor governing zooplankton dynamics in lakes is exploitative competition between crustaceans and rotifers for phytoplankton (Nogrady et al., 1993). In Lake Tovel, biomass of edible phytoplankton decreased at high τ-values (Table 1), implying that exploitative competition probably increased during these periods. In fact, crustaceans have a higher clearance rate than rotifers, and are favoured under limited food conditions (Herzig, 1987).

Crustaceans were dominated by *Bosmina* and its abundance seemed to be particularly influenced by τ as indicated by the positive correlation found (Table 1), even if its numerical dominance might suggest top-down control. Fish predation can structure the zooplankton community by favouring smaller taxa such as *B. longirostris* and rotifers (Brooks and Dodson, 1965). While fish predation can not be excluded in our study as a zooplankton structuring force, its influence might be limited because of the low fish production rate (< 1.8 g m^{-2} $year^{-1}$) and a preference of arctic charr for benthic food sources in this lake (Betti, 2003). Invertebrate predation pressure also affects population dynamics of zooplankton (Williamson, 1983), but predators such as

Chaoborus sp. and *Leptodora kindtii* were never found in Lake Tovel. Moreover, the impact of *Cyclops strenuus* seemed negligible because of its very low abundance and its rare occurrence.

Considerations

The importance of hydrology (water residence time, water-level fluctuations, flow rate, etc.) as a zooplankton regulating factor in rivers, reservoirs, ponds, and floodplains has been recognized, but its influence in lakes has been often neglected. Our results showed that water residence time is an important factor determining crustacean or rotiferan dominance. Hydrological aspects such as water residence time should be considered when explaining zooplankton community structure and succession in lakes. Moreover, the importance of hydrology *sensu latu* will increase with society's increasing need of freshwater: changes in lake water-level and water inflow will change τ-values and consequently causing an altered zooplankton community.

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