

Spatial distribution and filtering efficiency of *Daphnia* in a deep subtropical reservoir*

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Abstract Studies of *Daphnia* distribution and function could help people manage and protect water quality. We investigated how spatial distribution and filtering efficiency of *Daphnia* in the transition and lacustrine zones of the Nanwan Reservoir (China). Samplings were conducted seasonally for 2 years from six sites in the reservoir. *Daphnia* abundance and biomass were significantly higher in the lacustrine zone than in the transition zone. Similar composition and biomass of edible phytoplankton were found in the two zones, suggesting that food quantity could not explain high *Daphnia* distribution in the lacustrine zone. The variations of water velocity and food quality could help explaining *Daphnia* patchy distribution in the reservoir. On the one hand, rapid water velocity can cause the *Daphnia* decrement in the transition zone. On the other hand, the ratio of particulate organic carbon (POC) to chlorophyll *a* (chl *a*) concentration was significantly higher in the transition zone, indicating more allochthonous material constituted the food source for *Daphnia*. The lower quality food likely suppressed *Daphnia* development in the transition zone. A linear regression between *Daphnia* abundance and Secchi depth (SD) may suggest a cause-effect relationship where increased filtering efficiency was responsible for increased water clarity to some extent.

Keyword: *Daphnia*; lacustrine zone; transition zone; water clarity; Nanwan Reservoir

1 INTRODUCTION

Compared to natural lakes, reservoirs experience greater spatial heterogeneity (Kalff, 2002; Han and Liu, 2011) associated with management for water quality. Reservoir zonation occurs longitudinally as water enters from a stream into an impoundment. In a typical reservoir, abiotic and biotic variables (flow rate, depth, trophic state, food resources, transparency, etc.) change along the continuum from the riverine source, through the transition zone into the lacustrine zone. The change in environmental conditions can influence the biota, leading to distinct biological zones. Studies of how differences of zooplankton distribution and function in different zones of a reservoir could, to some extent, help managers protect water quality (Kirk, 2011; Betini et al., 2017).

The “multiple driving forces hypothesis” predicts that, on large spatial scales, physical processes including water temperature and wind have strong control over the spatial distribution organisms; while on small spatial scales, biological drivers (including predation, competition, size of organisms and food sources) are strong (Pinel-Alloul, 1995). At a small spatial scale, a reservoir always is strong controlled by biological drivers over the spatial distribution. For example, Elser et al. (2001) pointed out that the taxonomic composition and distribution of zooplankton is influenced by the food quality.

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Terrestrial carbon inputs partition into different spatial regions of a reservoir and, therefore impact zooplankton distribution. Terrestrial carbon inputs are greater in riverine and transitional zones than in lacustrine zones, leading to growth efficiency variations for zooplankton in the former associated with a decrease in food quality (Brett et al., 2009).

In zooplankton communities, *Daphnia* exerts strong grazing effects on organic particles (phytoplankton and its retinue; e.g., bacterioplankton and associated organic detritus) (Sarnelle, 2005; Altshuler et al., 2011; Effler et al., 2015). Persson et al. (2007) pointed out that *Daphnia* is a keystone genus in freshwater ecosystems, providing a major link in the energy flow between primary producers and secondary consumers in these food webs. They exert greater top-down control over primary producer biomass and water clarity than other zooplankton. As a non-selective filter feeding cladoceran, *Daphnia* has short lifecycles and respond rapidly to changes in the environment (Adrian et al., 2009; Fischer et al., 2011; De Senerpont Domis et al., 2013). The spatial pattern is of considerable interest, because under some conditions, it may influence phytoplankton community and water clarity (Kirk, 2011; Betini et al., 2017). The ability for *Daphnia* to control water clarity through grazing is related to body size as well as taxonomic composition (Cyr and Curtis, 1999). In addition, the maximum size of edible particles depends on body size (Burns, 1968). *Daphnia* with a larger body size has a strong control on phytoplankton and other particle detritus (Sarnelle, 2005). Therefore, knowledge of how *Daphnia* distribution and filtering efficiency in different zones of a reservoir would help explain phytoplankton biomass and protect water quality in reservoir management.

In order to elucidate the *Daphnia* distribution and their filtering efficiency in different zones of a reservoir and provide scientific suggestions for reservoir management, we compared to transition zone to lacustrine zone, both of which are easily modified by anthropogenic withdrawals. We took seasonal samples over two annual cycles from both zones, in a deep and meso-eutrophic reservoir in China to (i) determine the difference in the *Daphnia* distribution and filtering efficiency between the two zones; (ii) evaluate the influence of environmental variability and the strength of environmental factors have on structuring *Daphnia*; and (iii) quantify the interactions between *Daphnia* and water clarity in the two zones.

2 MATERIAL AND METHOD

2.1 Study sites

Samples were collected from Nanwan Reservoir (32°4'N, 113°57'E, Fig.1), which is a deep, monomictic and mesotrophic reservoir, locates in Xinyang, Henan, in central China. It has a watershed area of 1 100 km², water surface area of 4 573 km², the total volume of 16.33×10⁸ m³, and an average depth of 13.5 m (Yu et al., 2009). The reservoir is mainly fed by 3 rivers: Wudao, Dongjia, and Tanjia Rivers. The average concentration (2014–2015 years) of total nitrogen (TN) and total phosphorus (TP) in the reservoir were 822.9 µg/L and 22.1 µg/L, respectively, indicating that the reservoir was meso-eutrophic (Carlson, 1977). The dry season, when precipitation is scarce, spans from October to May and the wet season from June to September during which about 60% of annual precipitation occurs. Silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) have been intensively stocked in the past 15 years, and are the dominant fishes in the reservoir. The samples were collected from three transition sites and three lacustrine sites (Fig.1).

Transition Zone (Sites 1–3): These sites were about 4–6 km below the tributary rivers and chosen as a type of river-reservoir transitional zone. These study sites were shallow (4–8 m), and had a negligible velocity (<0.5 m/s), good light availability (Secchi depth >1 m), and a soft and fine sediment bottom. The riverine watershed is primarily composed of forest and urban land with some agricultural areas.

Lacustrine Zone (Sites 4–6): These sites were characterized by decreased flow rates (<0.1 m/s) and greater depth (8–18 m), resulting in decreased suspended solids, greater light penetration (Secchi depth >2 m), but lower primary productivity (chlorophyll *a* (chl *a*) <15 µg/L) due to decrease nutrient availability.

2.2 Sample collection and analysis

Water temperature (*T*, °C), dissolved oxygen (DO, mg/L) and pH were measured in the water surface by a multi-parameter water quality monitor (YSI incorporated Yellow Springs Ohio, USA). Secchi depth (SD) was recorded as a measure of water clarity. SD, an apparent optical property, is determined by the light-attenuating process of scattering caused by particles, including phytoplankton, bacterioplankton,

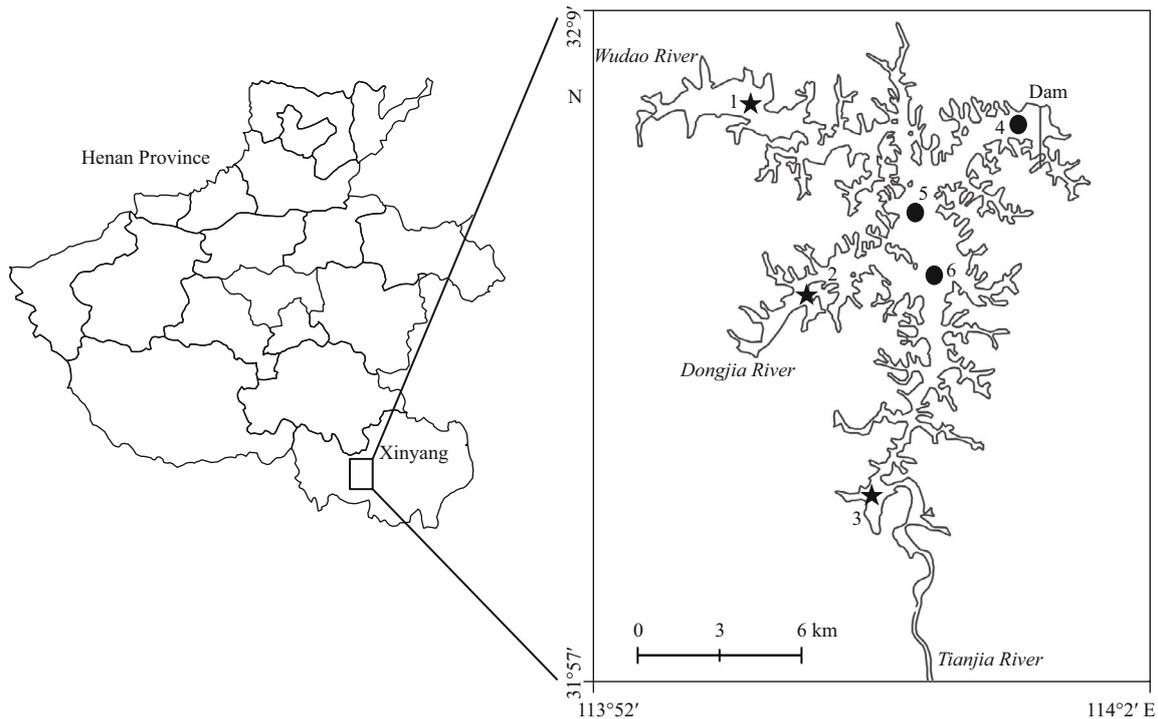


Fig.1 Location of Nanwan Reservoir and the sampling sites

Stars: sites were chosen as transition zone; black dots: sites were chosen as lacustrine zone.

associated organic detritus, and minerogenic particles.

As the major food of zooplankton, phytoplankton always lives in the euphotic zone. Thus, surface water samples for measuring nutrients, chl *a* and phytoplankton were collected with a 5-L iron sampler seasonally from September 21, 2014, to June 31, 2016. Soluble reactive phosphorus (SRP), dissolved inorganic nitrogen (DIN, $\text{NO}_3\text{-N} + \text{NO}_2\text{-N} + \text{NH}_4\text{-N}$), total phosphorus (TP), total nitrogen (TN), and chl *a* concentrations were measured according to the Chinese National Standards for water quality and the USA Environmental Protection Agency standards (APHA, 1989). After filtering 500-mL water samples through a 0.45-mm acetate fiber mesh filter, chl *a* was extracted with acetone and measured by spectrophotometry (Lorenzen, 1967; Lin et al., 2005). Chl *a* concentration is a proxy for estimating phytoplankton biomass, which could be consist of important part of particles in the water column. Samples for particulate organic carbon (POC) concentrations were filtered on pre-combusted (450°C for 4 h) Whatman GF/F glass fiber filters and dried. Then filters were decarbonated with HCl fumes for 4 h, dried, and packed in silver cups. POC concentration was measured using an elemental analyzer (Euro EA 3028).

Phytoplankton samples were preserved with 1% Lugol's solution and 4% formaldehyde and were

stored in cold conditions (4°C). After sedimentation for at least 64 h, the supernatant was siphoned off with a diameter hose. The residue (about 25 mL) was collected and used for counting phytoplankton. At least 300 phytoplankton units placed in a Sedgewick Rafter counting chamber were counted under an optical microscope at 400× magnification (APHA, 1989). Taxa were determined to the species wherever possible. To estimate phytoplankton biomass, at least 25 individuals for each species were measured and then approximations to geometric solids were applied to calculate individual biovolume (Hillebrand et al., 1999). Biomass of phytoplankton was estimated from the individual volume, assuming that $10^6 \mu\text{m}^3$ correspond to $1 \mu\text{g}$ of biomass. In addition, phytoplankton was measured by the length of the greatest axial linear dimension (GALD). Because GALD is related to *Daphnia* edibility, we defined edible phytoplankton as any species with $\text{GALD} < 35 \mu\text{m}$.

Zooplankton was sampled from each of the separate six sampling sites. To estimate the zooplankton biomass in the whole water layer, for each sample, a total of 40 L water was collected from the surface to the bottom at well-spaced intervals according to the different depths (4–18 m) of the sampling sites. Water was filtered through a 45- μm nylon net and concentrated to 10–20 mL. Samples

Table 1 Secchi depth (SD), pH, dissolved oxygen (DO), water temperature, water velocity, dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP) and chl *a* concentration at six sampling sites in the reservoir

Reservoir zone	Sites	SD (m)	pH	DO (mg/L)	Water temperature (°C)	Water velocity (m/s)	DIN (µg/L)	SRP (µg/L)	Chl <i>a</i> (µg/L)
Transition	1	1.95	8.2	7.7	18.4	0.16	238.0	4.5	11.6
	2	2.24	8.0	7.3	18.3	0.11	247.2	7.8	9.3
	3	1.20	8.0	8.3	18.1	0.13	239.5	5.4	11.9
	Mean _T	1.80	8.1	7.8	18.2	0.13	241.6	5.9	10.9
Lacustrine	4	2.65	7.7	6.9	18.5	0.01	203.9	5.6	6.0
	5	2.42	7.9	7.2	18.5	0.01	203.7	5.0	5.1
	6	2.52	8.0	7.8	18.5	0.01	200.7	6.8	5.6
	Mean _L	2.53	7.9	7.3	18.5	0.01	202.8	5.8	5.6

Mean_T: mean values of sites 1–3; mean_L: mean values of sites 4–6.

were preserved with 5% formaldehyde. Since zooplankton species could not be sampled separately, all zooplankton species were sorted and counted using an optical microscope. To estimate the average body length of each zooplankton species, at least 25 specimens were measured. Biomass of each species was estimated from the average individual body length. Individual body wet weight (µg) was estimated following the equations of Zhang and Huang (1991). The zooplankton taxa were classed into three groups: *Daphnia*, other crustaceans, and rotifers + protozoa.

We estimated the *Daphnia* filtering rate as followed (Burns, 1969):

$$F_{B/20} = 4.992L^{2.8},$$

where $F_{B/20}$ is the filtering rate at 20°C (mL/(animal·d)) and L is the body size of the *Daphnia* (mm). The rate at the ambient temperature T is calculated according to an Arrhenius relationship:

$$F_{B/T} = F_{B/20} \Theta^{T-20},$$

where the coefficient Θ was specified as 1.104 8 for *D. galeata* and 0.993 8 for *D. pulex* (Burns, 1969), respectively.

The overall filtering efficiency by *Daphnia* per unit volume of oxie water (F , mL/(L·d)), is calculated as:

$$F = \frac{F_{D/a} \times N_h}{V_{n/DO} \times K_f},$$

where $F_{D/a}$ is the filtering rate of *D. galeata* and consists of more than 90% of total *Daphnia* species. K_f is the net efficiency. A value of $K_f=0.5$ is adopted according to Kasprzak et al. (1999) and Effler et al. (2015). N_h is the number of *Daphnia* collected in the vertical haul. $V_{n/DO}$ is the volume of the vertical haul for the portion of the water column, for which the dissolved oxygen concentration (DO) is >1 mg/L (usually the uppermost 8–10 m).

2.3 Statistical analysis

The mean values from three sites were used to give a value for each region. The Pearson correlation analysis was used to determine relationships between two parameters. Linear regression analysis was followed by the Pearson correlation analysis in case of significant effects. Linear regression analysis was conducted to search for possible cause-effect interactions in further. R^2 , P value and standard error (SE) were estimated in the analyses. The differences in environmental parameters, chl *a* concentration, edible phytoplankton biomass, zooplankton abundance and biomass between the two zones were tested by independent T -test. The assumed significance level was $\alpha=0.05$. The statistical analysis was conducted in SPSS (SPSS for Windows, version 17.0).

After testing runs of detrended correspondence analysis (DCA), our results show that the gradient lengths of the first axis were 2.057. The results indicate that the linear model RDA was suitable for the analysis. Redundancy analysis (RDA) was used to identify the abiotic variables that drove the spatial distribution of the zooplankton groups in the reservoir. The statistical analysis was run with CANOCO (version 4.5).

3 RESULT

3.1 Abiotic conditions

Table 1 shows the actual values of physical and chemical variables at six sampling sites and means values at two zones in the reservoir. The pH and water velocities were significantly higher in the transition zone than those in the lacustrine zone (pH: $P=0.029$; water velocity: $P<0.001$). No differences in DO and

water temperature were found between the transition and lacustrine zones (DO: $P=0.418$; water temperature: $P=0.542$). Significantly higher chl *a* concentrations were found in the transition zone than in the lacustrine zone (t -test, $P=0.005$). DIN and SRP concentrations were often higher in transition zone, but no significant differences were tested (DIN: $P=0.061$; SRP: $P=0.367$).

3.2 Zooplankton community, *Daphnia* distribution, and filtering efficiency

The zooplankton species composition was similar in the two zones. *D. geleata* and *D. pulex* were present in both zones. The dominant *Daphnia* was *D. geleata*, accounting for more than 90% of total *Daphnia* biomass in the two zones (Fig.2e–h). The other cladocerans were represented by *Diaphanosoma leuchtenbergianum*, *Chydorus* sp., *Moina* sp., *Bosmina* sp., *Leptodora kindtii*, followed by copepods *Neurodiaptomus incongruens*, *Mesocyclops leuckarti*, *Thermocyclops taihokuensis* and copepodids. Rotifers (mainly *Filinia* sp., *Trichocerca* sp., *Brachionus urceus*, *Keratella ticinensis*, and *Keratella cochlearis*) and Protozoa (mainly *Diffugia corona*, *Diffugia urceolata*, *Diffugia acuminata*, *Diffugia oblonga*, *Tintinnopsis* sp.) were also present but in very low biomass.

Overall, more *Daphnia* were detected in the lacustrine zone than in the transition zone (t -test, $P<0.001$). In the transition zone, *Daphnia* accounted for only 4% of total zooplankton abundance and 14.3% of total zooplankton biomass (Fig.2a, 2c), whereas *Daphnia* contributed to approximately 10% of total zooplankton abundance and 16.7% of total zooplankton biomass in the lacustrine zone (Fig.2b, 2d). Significantly higher abundance (t -test, $P=0.02$) and biomass (t -test, $P=0.019$) of *Daphnia* were found in the lacustrine zone especially in March (abundance: 42%, biomass: 45% in 2015).

Greater *Daphnia* filtering was often found in lacustrine zone than in the transition zone (t -test, $P=0.05$), especially in March. Overall, *Daphnia* filtration ranged from 0 to 2.1×10^3 mL/(L·d) in the transition zone, and from 0.2 to 6.9×10^3 mL/(L·d) in the lacustrine zone (Fig.3a).

Deeper SD was observed in the lacustrine zone than in the transition zone (t -test, $P=0.02$). The SD ranged from 1.1 m to 2.7 m in the transition zone, and from 1.5 m to 4.5 m in the lacustrine zone (Fig.3b). SD could exceed 2.5 m when *Daphnia* filtering was

above the 2×10^3 mL/(L·d). A positive relationship between the *Daphnia* filtering and SD is supported by the Pearson Correlation Analyses in the lacustrine zone ($R=0.876$, $P=0.004$).

Chl *a* concentration were always higher in the transition zone than in the lacustrine zone (t -test, $P=0.012$). The chl *a* concentration ranged from 0.5 to 21.4 $\mu\text{g/L}$ in the transition zone, and from 0.8 to 15.4 $\mu\text{g/L}$ in the lacustrine zone (Fig.3c).

POC/chl *a* ratios can trace variation in suspended particulate organic matter composition, because POC in water includes terrestrial components whereas chl *a* is specific to autotrophs (Marra, 2002). Significantly higher POC/chl *a* ratios were found in the transition zone than in the lacustrine zone (t -test, $P<0.001$, Fig.3d), indicating more allochthonous material constituted the food source for *Daphnia* in transition zone.

3.3 Edible phytoplankton composition and biomass

During the observation period, 110 taxa were identified for edible phytoplankton (GALD<35 μm), distributing in 8 taxonomic groups: Chlorophyta (64), Bacillariophyta (18), Cyanophyta (16), Euglenophyta (4), Xanthophyta (3), Chrysophyta (3), Cryptophyta (1), Euglenophyta (1). In both of the two zones, Bacillariophyta and Cyanophyta relative biomass had main contribution of the total phytoplankton biomass. Bacillariophyta and Cyanophyta relative biomass had no significant differences in the two zones (t -test, $P>0.05$), indicating that edible phytoplankton community of major taxonomic groups were similar in relative biomass composition between the two zones (Fig.4). No significant difference of GALD<35 μm phytoplankton biomass was found between the two zones (Fig.5), suggesting that edible phytoplankton biomass could not explain high *Daphnia* distribution in lacustrine zone.

3.4 Correlations

The ratio of *Daphnia* biomass to chl *a* concentration ($D/\text{chl } a$ ratio) fluctuated during the study period (Fig.6). Overall, $D/\text{chl } a$ ratios were significantly higher in the lacustrine zone than that in transition zone (t -test, $P=0.002$), indicating a possible enhanced grazing pressure on phytoplankton. In spring, the $D/\text{chl } a$ ratio is high in both transition and lacustrine zones.

To find the main strength of environmental variables for zooplankton community in the two zones, 10

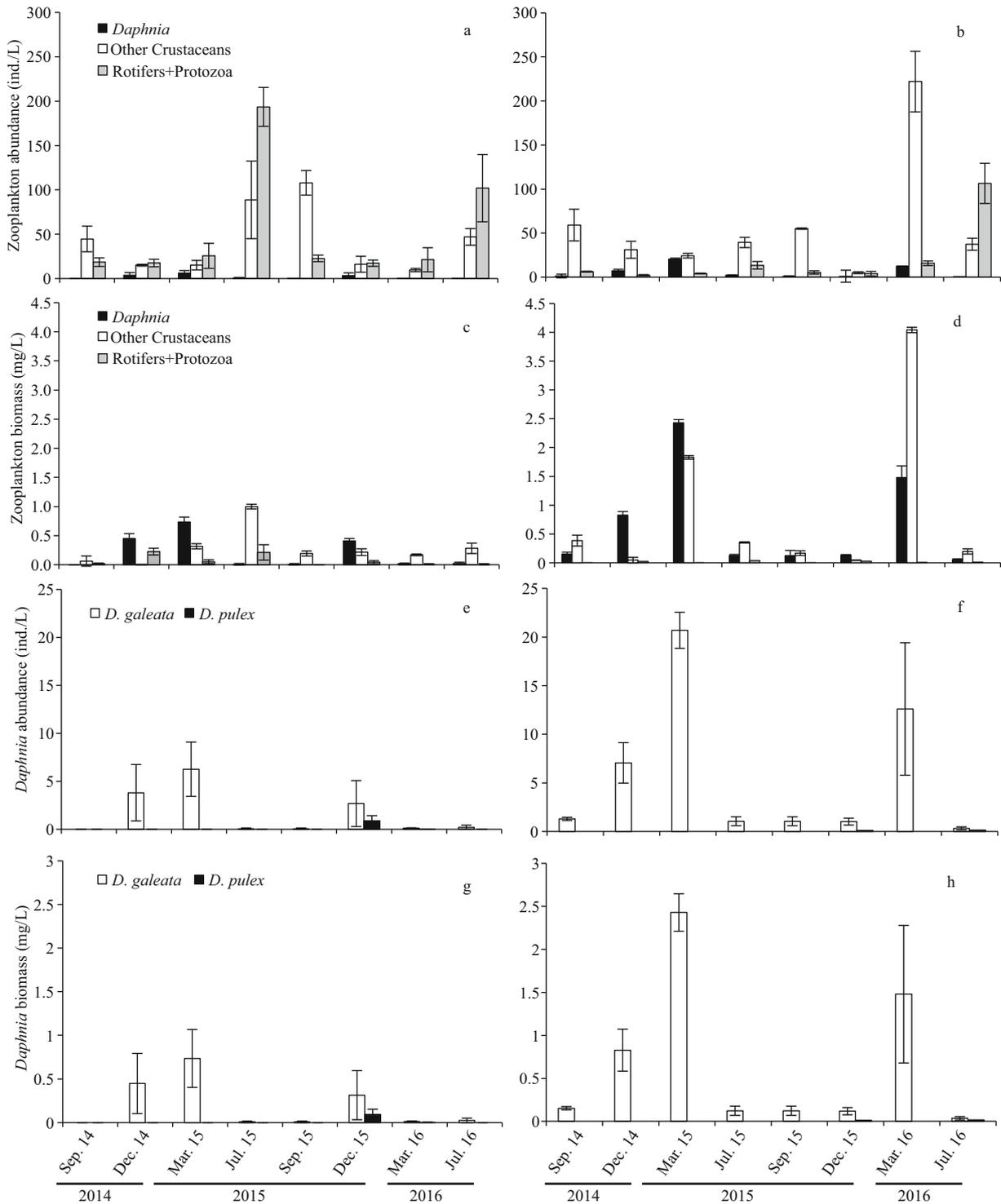


Fig.2 Temporal variation of zooplankton and *Daphnia* (mean values±standard error from all three sites across the zone) during study period

a. zooplankton abundance in transition zone; b. zooplankton abundance in lacustrine zone; c. zooplankton biomass in transition zone; d. zooplankton biomass in lacustrine zone; e. *Daphnia* abundance in transition zone; f. *Daphnia* abundance in lacustrine zone; g. *Daphnia* biomass in transition zone; h. *Daphnia* biomass in lacustrine zone.

different abiotic variables including POC/chl *a*, water velocity, pH, chl *a*, SD, TN, TP, DIN, SRP, and DO were selected to perform the RDA in the reservoir. The results of RDA using all 10 variables are illustrated in

Fig.7. Forward selection indicated that water velocity and POC/chl *a* were responsible for explaining 20.1% and 17.4% of the environmental variables in the first two axes, respectively (Monte Carlo test, *P*<0.05),

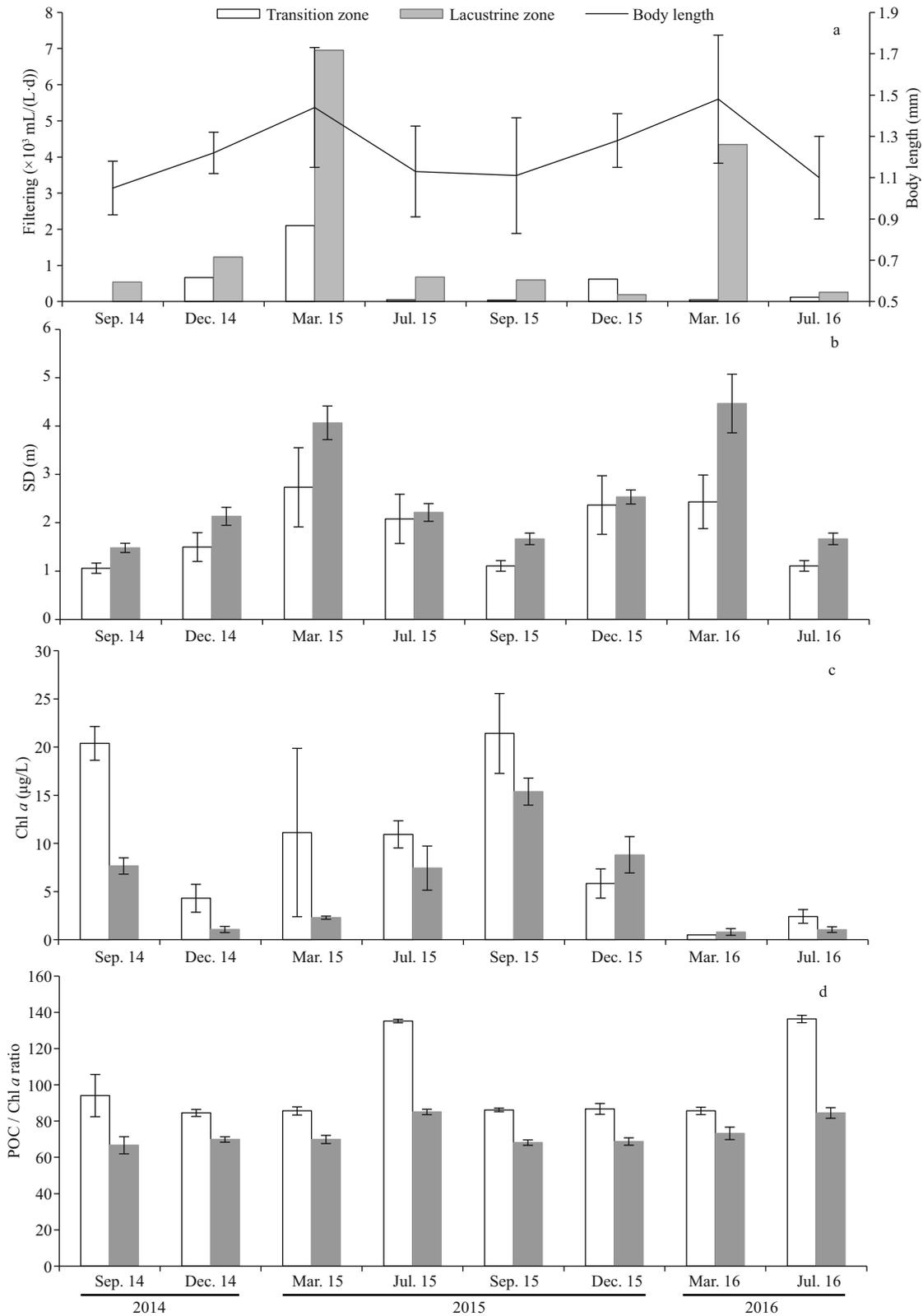


Fig.3 Variables (mean values \pm standard error from all three sites across the zone) related to *Daphnia* filtering efficiency during study period

a. *Daphnia* filtering rates and *Daphnia* body length; b. Secchi depth (SD); c. chl a concentration; d. POC/chl a ratio.

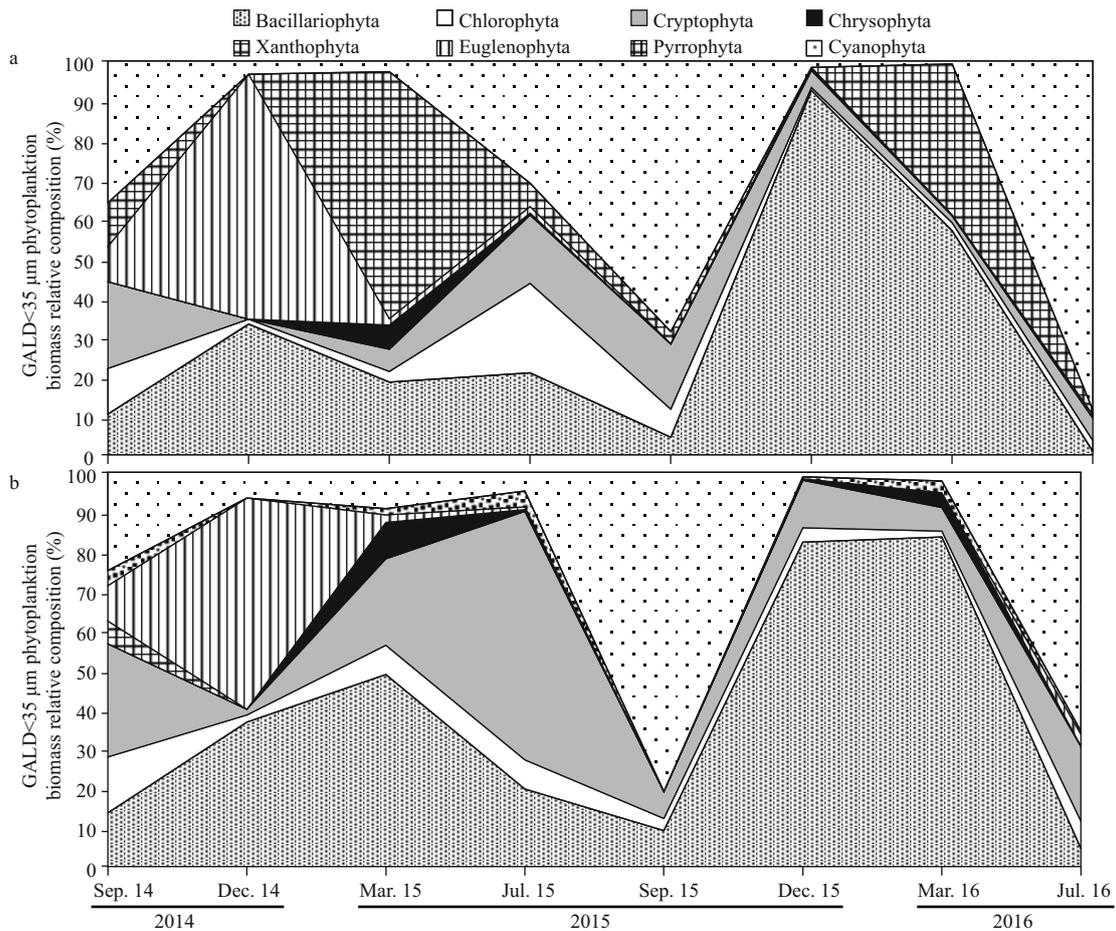


Fig.4 GALD < 35 μm phytoplankton relative biomass composition (mean values from all three sites across the zone) during the study period

a. transition zone; b. lacustrine zone.

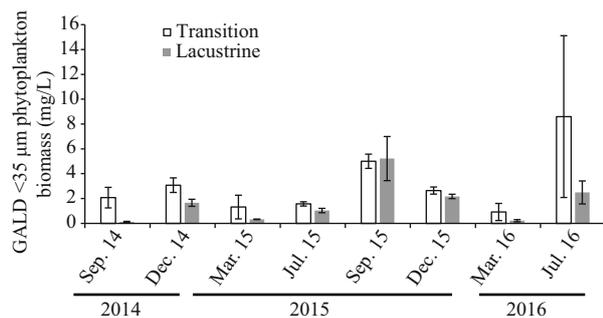


Fig.5 GALD < 35 μm phytoplankton biomass (mean values ± standard error from all three sites across the zone) in the transition and lacustrine zones during the study period

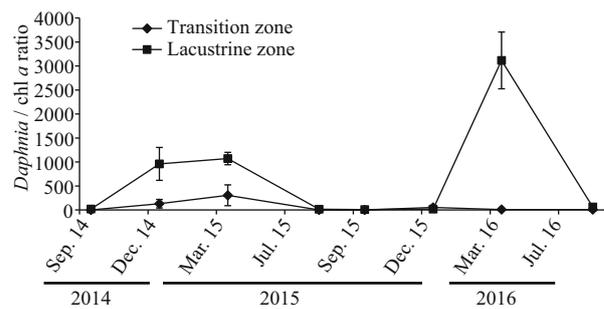


Fig.6 The ratio of *Daphnia* biomass to chl *a* concentration (*D*/chl *a* ratio) (mean values ± standard error from all three sites across the zone) during the study period

indicating that the two environmental variables made significant contributions to the zooplankton abundance. The first two axis account for 91.9% of the variance for the relationship between zooplankton community and environment.

The linear regression analyses help to explain the cause-effect interactions between environmental

parameters and *Daphnia* in further. A positive relationship between the *Daphnia* abundance and SD was supported by the linear regression analysis ($R=0.653$, $P<0.001$, $SE=4.88$). Negative linear correlations were found between the *Daphnia* abundance and water velocity (Fig.8a), and between the *Daphnia* abundance and POC/chl *a* (Fig.8b). In the lacustrine zone, slower water velocity and lower

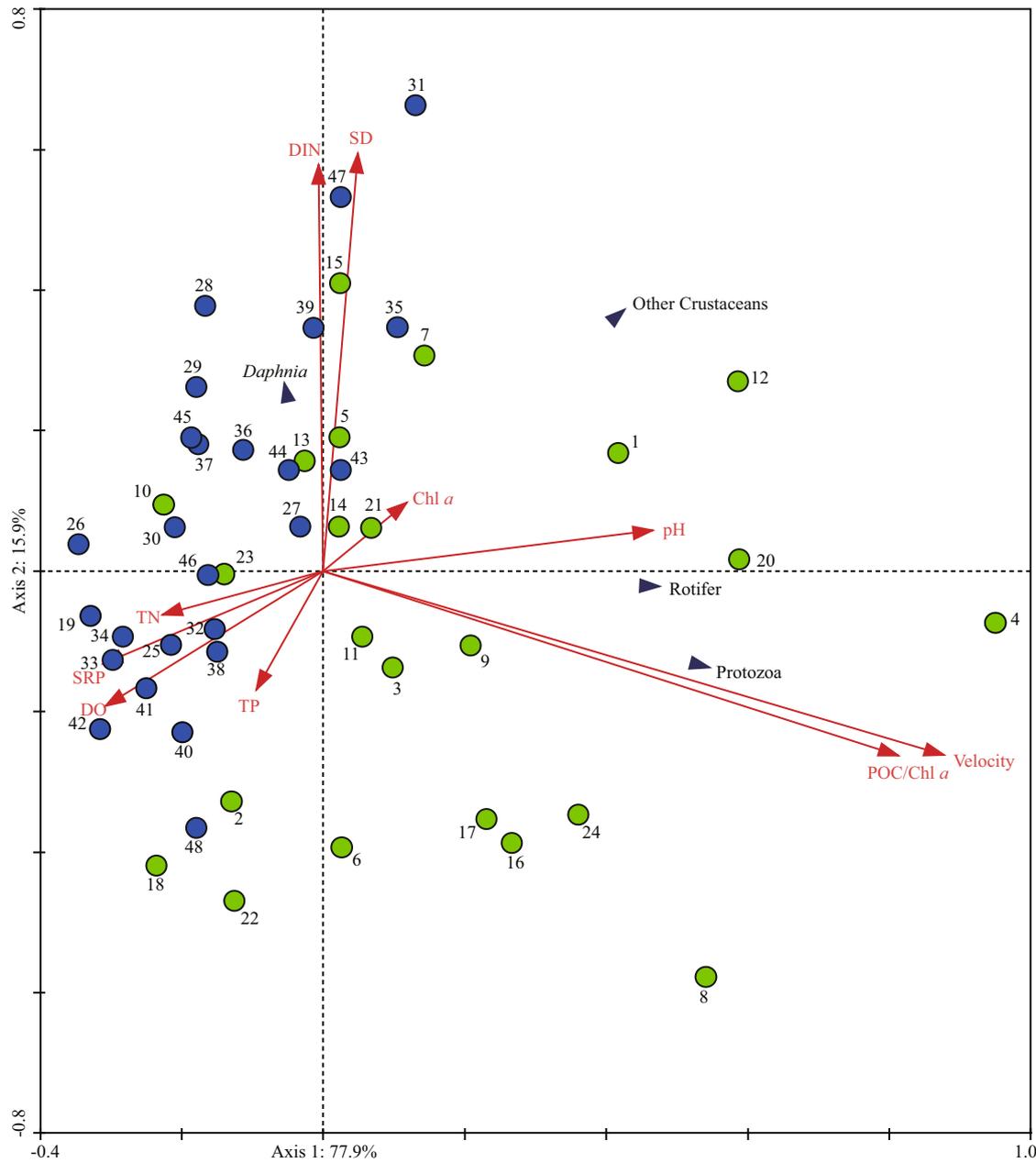


Fig.7 Ordination diagrams of redundancy analysis (RDA) showing variation of the zooplankton groups in relation to environment variability in the reservoir

POC/chl *a*: ratio of particulate organic carbon to chlorophyll-*a* concentration; velocity: water velocity; TN: total nitrogen; TP: total phosphorus; DIN: dissolved inorganic nitrogen; SRP: soluble reactive phosphorus; DO: dissolved oxygen; SD: Secchi depth; chl *a*: chlorophyll *a*. Dots 1–24 (green color) represent the samples in the transition zone; dots 25–48 (blue color) represent the samples in the lacustrine zone.

ratio of POC/chl *a* accompanied by higher abundance of *Daphnia* could explain the deeper SD.

4 DISCUSSION

Conditions in reservoirs are suitable for the development of spatial distribution, promoting variable distribution of species including *Daphnia* (Han and Liu, 2011). Throughout our study, there were significant increases in both *Daphnia* abundance

and biomass in the lacustrine zone compared to the transition zone. Different zones displayed significant differences in abundance and biomass, indicating an extremely patchy distribution at a small spatial scale. Several researchers have reported different reasons for such a patchy distribution. For example, Verreth (1990) found that *Daphnia* was concentrated heavily in the lacustrine zone of a pond, and speculated that wind-induced currents may have displaced them on

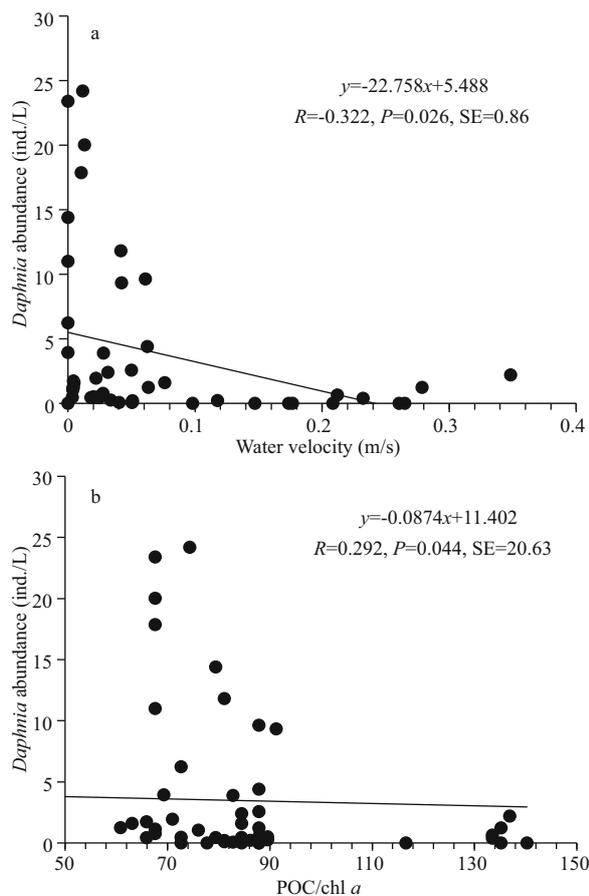


Fig.8 The linear regression showing variations of *Daphnia* abundance in relation to water velocity and POC/chl *a* ratio

a. *Daphnia* abundance vs. water velocity; b. *Daphnia* abundance vs. the ratio of particulate organic carbon to chl *a* concentration (POC/chl *a*).

the down-wind side of the pond. Furthermore, Kvam and Kleiven (1995) found several *Daphnia* swarms with densities up to 4 000 ind./L in Lake Myrvatn because of a predator avoidance. In our study, wind and predator avoidance do not explain the patchy distribution of *Daphnia*, since the three transition sites were connected to the lacustrine zone from different directions. Food quantity could not explain high *Daphnia* distribution in the lacustrine zone either, because no significant differences of edible phytoplankton composition and biomass were found in the two zones.

Rapid water velocity or short retention time can cause the *Daphnia* decrement in the transition zone. The negative relationship between water velocity and *Daphnia* abundance indicate that rapid water velocity could lead to *Daphnia* loss. This agrees with previous studies (Wiedenheft, 1984; Zhang et al., 2013; Da Rosa et al., 2017). Wiedenheft (1984) found lower

Daphnia abundance with fast water velocity in the Missouri River compared to sample sites within a reservoir with longer retention time. Zhang et al. (2013) also pointed out that short retention time induced by increased outflow could remove large crustaceans leading to an increase in phytoplankton biomass and abundance after withdrawal. Thus, slow water velocity is important for maintenance of a healthy *Daphnia* community.

Food quality could explain the patchy distribution of *Daphnia* on the other hand. Previous studies have shown that low food quality could suppress *Daphnia* development (Taipale et al., 2011; McMeans et al., 2015). McMeans et al. (2015) found that higher somatic growth but no viable egg reproduction in *D. magna* exposed to high dissolved organic carbon (t-DOC) concentration and attributed the growth response to the provision of bacteria rather than direct t-DOC utilization. In addition, Taipale et al. (2011) showed that the conversion rate from α -linolenic acid (α -LA) to eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) is low in herbivorous *Daphnia*, and thus *Daphnia* require EPA and DHA directly from their diets. However, terrestrial organic carbon available to support aquatic organism is almost entirely devoid of essential fatty acids and sterols (Brett et al., 2009; Taipale et al., 2014). The POC/chl *a* ratio can distinguish terrestrial detritus (POC/chl *a* greater than 100) from phytoplankton (POC/chl *a* between 30 and 100) (Meybeck et al., 1988). In our study, the POC/chl *a* ratios were constant in the lacustrine zones ranging from 66.7 to 85.1. However, the ratios increased to 84.5–136.3 in the transition zones, especially in summer (Fig.3d). Thus, there was a notable difference in suspended particulate organic matter composition between phytoplankton-derived organic matter in the lacustrine zone and terrestrial organic matter during summer in the transition zone. Rain along with a higher turbidity associated with the inflow water could explain the increase in the terrestrial organic matter during summer in the transition zone. We suggest that these allochthonous resources may allow *Daphnia* to survive but limit population increase. In fact, Wetzel (1995) hypothesized that allochthonous resources might function as a metabolic “lifeboat” by providing low-quality resources that allowed consumers to survive during periods when more nutritious autochthonous resources were not available. Future research on fatty acids of allochthony and *Daphnia* should be considered to elucidate food quality and *Daphnia* abundance.

A number of factors can contribute to spatial variations of *Daphnia* along the water flow in a reservoir. In our study, water velocity and POC/chl *a* ratio may be not the only two factors account for the spatial variation. Even more, factors together could help to explain. However, within the existing environmental factors, those two factors are what we could make sure in analyzing the causes of spatial variation.

The *D*/chl *a* ratio can be used as an indicator of filtering efficiency on phytoplankton in the water column (Muylaert et al., 2003). In our study, the high ratio of *D*/chl *a* in the lacustrine represented strong top-down control on phytoplankton, especially in spring. In addition, there are other explanations for the variation in the ratio. For example, Havens and Beaver (2013) examined crustacean zooplankton from 15 shallow lakes in the south and central Florida and found that short-term and seasonal changes in biomass ratio of zooplankton to phytoplankton in Florida might be controlled by fish predation. However, fish predation could not explain the different *D*/chl *a* ratio in our study because fish can swim throughout the reservoir and have a similar density within the two zones.

In the formula, the filtering rate estimates were strongly correlated with *Daphnia* density and individual body length. The higher *Daphnia* filtering rate could reduce turbidity and lead to the deeper SD in the lacustrine zone. In spring, when *Daphnia* filtering rate was high, there was a long period of high water clarity. *Daphnia* filtering maybe not the only the reason accounting for the water clarity. But undeniable, the *Daphnia* filtering could play important roles in water clarity especially during spring. Tirok and Gaedke (2006) pointed out that high clarity events are commonly attributed to *Daphnia* grazing, although other consumers have also been implicated. Effler et al. (2015) also found that the high clarity events in Onondaga Lake were associated with elevated levels of *Daphnia* grazing.

5 CONCLUSION

In our study, there were significant increases in *Daphnia* abundance and biomass in the lacustrine zone compared to the transition zone. The reasons of water velocity and food quality could help explaining *Daphnia* patchy distribution at a small spatial scale. On the one hand, rapid water velocity can cause the *Daphnia* decrement in the transition zone. On the other hand, a notable difference in suspended

particulate organic matter composition between phytoplankton-derived organic matter in the lacustrine zone and terrestrial organic matter in the transition zone, indicating that food quality difference could explain the patchy distribution of *Daphnia*. The increased *Daphnia* filtering efficiency probably explained the water clarity in the lacustrine zone, especially during spring.

6 DATA AVAILABILITY STATEMENT

The data generated during the current study are available from the corresponding author on reasonable request.

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