

Salinity shapes zooplankton communities and functional diversity and has complex effects on size structure in lakes

María Florencia Gutierrez · Ülkü Nihan Tavşanoğlu · Nicolas Vidal · Jinlei Yu · Franco Teixeira-de Mello · Ayşe Idil Çakiroglu · Hu He · Zhengwen Liu · Erik Jeppesen

Received: 17 July 2017 / Revised: 26 January 2018 / Accepted: 28 January 2018
© Springer International Publishing AG, part of Springer Nature 2018

Abstract Changes in zooplankton community structure and function were analyzed in 24 lakes covering a wide salinity gradient (from 0.5 to 115 g l⁻¹) in a semiarid region in northwest China. We hypothesized that species richness (*S*), species diversity (*H*), functional diversity (FD), biomass, and size of zooplankton would decrease with increasing salinity. We found that *S*, *H*, and FD did decrease with increasing salinity, whereas zooplankton sizes, size range, and biomasses did not. In fact, the sizes of microcrustaceans were

mainly regulated by the abundance of small fish. Besides the impoverishment of FD, the zooplankton functional groups also varied along the salinity gradient. A shift occurred from selective raptorial to more generalist microphagous rotifers, from selective to more generalist filter feeder cladocerans, and from dominance of microphagous herbivorous copepods to microphagous carnivores. Our study indicates that the ongoing salinization of lakes with climate warming will result in important changes in the zooplankton, affecting not only the structure but also the functioning of this community. A weakened top-down control by zooplankton on phytoplankton at moderate high salinities may be an indirect consequence, leading to a worsening of eutrophication symptoms. Loss of fish at high salinities may, however, counteract this effect.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10750-018-3529-8>) contains supplementary material, which is available to authorized users.

Handling editor: Karl E. Havens

M. F. Gutierrez (✉)
Instituto Nacional de Limnología, CONICET-UNL,
Ciudad Universitaria, 3000 Santa Fe, Argentina
e-mail: fgutierrez@inali.unl.edu.ar

Ü. N. Tavşanoğlu
Limnology Laboratory, Department of Biology, Middle
East Technical University, 06800 Ankara, Turkey

N. Vidal · E. Jeppesen
Department of Bioscience, Aarhus University, Vejløvej
25, 8600 Silkeborg, Denmark

N. Vidal · E. Jeppesen
Sino-Danish Centre for Education and Research (SDC),
Beijing, China

N. Vidal · F. Teixeira-de Mello
Departamento de Ecología y Gestión Ambiental, CURE,
Universidad de la República, Tacuarembó s/n Maldonado,
Montevideo, Uruguay

J. Yu · H. He · Z. Liu
State Key Laboratory of Lake Science and Environment,
Nanjing Institute of Geography and Limnology, Chinese
Academy of Sciences, Nanjing 210008, China

A. I. Çakiroglu
Biofluids and Cardiovascular Engineering Laboratory,
Mechanical Engineering Department, Koc University,
Istanbul, Turkey

Keywords Functional classification · Salinity gradient · Taxon diversity · Taxon richness · Zooplankton size

Introduction

Climate warming may lead to an increase in salinity in lakes due to increasing temperatures and reduced net precipitation, not least in arid and semiarid regions of the world (Brucet et al., 2010). High evaporation together with enhanced soil erosion following more extreme rainfall events increases lake salinity and the concentrations of other harmful substances, affecting the aquatic biota (Jeppesen et al., 2015). Some studies have suggested that salinity per se has only a minor effect on zooplankton community structure and trophic dynamics in saline lakes (Williams, 1998; Waterkeyn et al., 2008). However, others have revealed salinity to be an important environmental filter that may change zooplankton richness and diversity, causing a decline at high salinities (Schalenberg et al., 2003; Jeppesen et al., 2007; Brucet et al., 2009; Jeppesen et al., 2015). Taxon richness and diversity are, however, also affected by a number of other variables such as productivity, dispersal limitations (Declerck et al., 2005), and trophic interactions (e.g., high richness at lower trophic levels may be promoted by high richness at high trophic levels) (Jeppesen et al., 2000). Thus, richness and diversity (as structural attributes of a community) can be considered highly sensitive to biological and environmental changes, even more than the ecological role (function) of species, since sensitive species may be replaced by tolerant ones with similar functions (Schindler, 1990; Ruesink & Srivastava, 2001; Mano & Tanaka, 2016). Loss of taxon richness and biodiversity can have negative consequences for the overall functioning of the ecosystem (Flöder & Hillebrand, 2012; Ding et al., 2017) and such an impoverishment of functional diversity (FD) might result in decreased resilience, not least in an already perturbed system (Vandermeer et al., 1998; Flöder & Hillebrand, 2012). Considering that environmental filtering processes

particularly affect species traits and not so much the taxonomic structure (Heino, 2008), a classification based on organism traits associated with their specific function in the ecosystem may provide key information on the effects of salinity on lakes, linking ecosystem function and biodiversity (Schmera et al., 2009).

In recent years, an increasing number of studies have been conducted to classify aquatic communities based on their functional characteristics in order to examine FD patterns as well as to find appropriate functional indicators of environmental changes (McGill et al., 2006; Barnett et al., 2007; Heino, 2008; Heino et al., 2013; Mason et al., 2013). For example, phytoplankton trait-based approaches have been used to characterize lake trophic levels (Reynolds et al., 2002; Kruk et al., 2010) and to elucidate how environmental conditions determine community dynamics (Longhi & Beisner, 2010; Gallego et al., 2012). For aquatic plants, functional classifications and life-history traits have been used to assess the effects of eutrophication and drought disturbances in lakes (Grime, 1973; Nielsen, 2003). It has been found that increasing productivity selects for the more competitive species, resulting in decreased functional richness and dispersion (Arthaud et al., 2012). Invertebrate functional approaches have also been used to assess the structuring effects of lake size and habitat complexity (Heino, 2008) as well as to find appropriate indicators of stream conditions for biomonitoring purposes (Ding et al., 2017). These studies indicate that functional and taxonomic approaches are often highly correlated, providing rather similar information about ecosystem functioning, and that a reduction in taxa richness could result in a decline in their functional components (Heino, 2008; Ding et al., 2017).

Relatively little information exists on how increasing salinity levels may act as an environmental filter on the whole zooplankton community from a taxonomic and functional perspective. A recent study documented that salinity was one of the main predictors of the spatial patterns and FD of zooplankton (Helenius et al., 2016). However, this work refers to brackish coasts and the functional classification was performed only for crustaceans.

The size structure and biomass of the different zooplankton organisms can also be used as a surrogate of the community function (Obertegger & Flaim,

Z. Liu
Institute of Hydrobiology, Jinan University,
Guangzhou 510632, Guangdong, China

2015). Recent studies conducted along a salinity gradient have demonstrated a shift from dominance of large and more efficient filter-feeding cladoceran species at low salinities to dominance of copepods and small cladoceran species at higher salinities (Jeppesen et al., 2007; Brucet et al., 2009; Jensen et al., 2010). Accordingly, it has been suggested that species replacement may weaken top-down control by zooplankton on phytoplankton at high salinities, leading to a worsening of eutrophication symptoms (Brucet et al., 2009). Besides the shift of species ranges and the seasonal shifts in life cycle events (Daufresne et al., 2009), this size reduction pattern has been considered as the third universal response to warming for ectotherm organisms. It is therefore possible that an increasing salinity scenario produced by climate change may create the same size-decline trend as warming since the general mechanisms in both cases include metabolic shifts and energy reallocation (Sheridan & Bickford, 2011).

The objective of this study was to evaluate the role of salinity in shaping the zooplankton community from both a taxonomic and a functional perspective by analyzing 24 lakes along a wide salinity gradient encompassing freshwater (0.5 g l^{-1}) to hypersaline lakes (115 g l^{-1}) in a semiarid region in northwest China. All lakes are located in the surroundings of Lake Ulungur ($47^{\circ}16'N$, $87^{\circ}20'E$), covering an area of 7900 km^2 approximately, at 480–550 m altitude in the Altay region of the Xinjiang province. This large-scale study including species sharing the same biogeographical range (i.e., exposed to similar co-evolutionary processes and environmental filters) allowed us not only to elucidate the effects of salinity on system structure and functioning but also to predict possible changes in semiarid shallow lakes associated with climate change. Our hypothesis was that zooplankton species richness (S), specific diversity (H), and FD would decrease with increasing salinity because only tolerant species would be able to survive in high-salinity lakes, leading to an impoverishment of species interaction. We further hypothesized that with increasing salinity, zooplankton size and biomass would decrease together with changes in species composition and due to physiological constraints (e.g., the energy requirements for osmoregulation would reduce the energy input for individual growth). However, at high-salinity levels, the disappearance of fish (their main predators) would expectedly favor the occurrence of

other competitively superior zooplankters, and hence high size ranges, leading to an increase in size and biomass.

Methods

Study site

The sampling was performed during July 2014 along a wide salinity gradient in the Ulungur Lake area (from $47^{\circ}40'$ to $46^{\circ}30'N$ and $86^{\circ}50'$ to $88^{\circ}20'E$). This area is located at an altitude ranging from 480 to 550 m in the Altay region of the Xinjiang province in northwest China. Twenty-four shallow and deep lakes were sampled, encompassing freshwater (0.5 g l^{-1}) to hypersaline systems (115 g l^{-1}). Lake area and mean depth ranged from 0.02 to 24 km^2 and 0.5 and 15 m , respectively.

Chemical and environmental analyses

Salinity (g l^{-1}), water temperature ($^{\circ}\text{C}$), conductivity (mS cm^{-1}), pH, turbidity (NTU), chlorophyll- a ($\mu\text{g l}^{-1}$), and dissolved oxygen (mg l^{-1}) were measured in situ at the deepest point of each lake using a YSI multiprob (YSI 6500, YSI Company, USA). Secchi disc depth (cm) was also measured in the limnetic area. Three replicates of water samples (220 ml) were taken and frozen for posterior analysis of total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorus (TP), total dissolved phosphorus (TDP), nitrate (NO_3^-), ammonium (NH_4^+), nitrite (NO_2^-), and orthophosphate (PO_4^{3-}). All these parameters were measured according to the Chinese Standard Methods for Monitoring Lake Eutrophication (Jin & Tu, 1990), which is similar to the US standards (APHA, 1998). Another water sample (1–2 l) was taken and filtered through a GF/C glass fiber filter using an electric pump for measurement of the chlorophyll- a (Chl- a) concentration. In the laboratory, the Chl- a concentration was determined using a 90% (v/v) acetone/water solution extraction, followed by spectrophotometry and calculated without correcting for phaeophytin interference (USEPA, 2002).

Fish

In each lake, survey fishing was undertaken using gillnets with seven mesh sizes (7, 10, 15, 20, 25, 30, and 40 mm from knot to knot), each section being 10 m long and 1.5 m high, comprising in total 91.5 m². The gillnets were located perpendicular to the littoral zones. Fish density and biomass were calculated as CPUE (Capture Per Unit Effort) (number of fish net⁻¹ h⁻¹) and Biomass Per Unit Effort (BPUE) (g net⁻¹ h⁻¹). The fish were determined to species level and then the standard length (0.1 cm) and weight (0.1 g) of each fish were measured. For the analysis, the fish were classified into three size ranges in length: small (< 10 cm), medium (10–25 cm), and large (> 25 cm), considering that their feeding habits usually change during their growth and that small-sized fish are typically zooplanktivorous. Fish size diversity was calculated using individual size measurements (Brucet et al., 2006; Quintana et al., 2008, 2015) and following the non-parametric methodology of Quintana et al. (2008). Size diversity is related to the Shannon diversity index but adapted for continuous variables (i.e., fish length) (Quintana et al., 2008). Size diversity integrates the amplitude of the size range and the size evenness, and it therefore condenses different aspects of the size structure into a single comparable value (Brucet et al., 2006; Quintana et al., 2008).

Zooplankton

In all lakes, zooplankton sampling was performed at one station in the pelagic area and at one station in the littoral region to obtain an integrated and representative sample of each lake. Zooplankton samples were collected with a Patalas sampler encompassing a water column of approximately 1.5–5 m, depending on the lake depth. Water samples sized between 15 and 50 l (depending on the characteristics of the lake) were filtered through a 20- μ m mesh net. The animals retained on the mesh were pooled and fixed with 4% Lugol's solution and stored in 100 ml plastic bottles.

Counting was performed in the laboratory following standard methodologies using specific keys (e.g., Koste, 1978; Korínek, 1981, 2002; Korovchinsky, 1992; Alekseev, 2002). At least three (or more) homogeneous aliquots were taken from the sample to obtain 100 individuals of the dominant taxa. For

each sample, countings of every aliquot were averaged after correcting for the amount of water filtered in order to calculate individual abundances (ind. l⁻¹) and. Zooplankton larger than 140 μ m were counted in a 5 ml Bogorov counting chamber at 10 \times magnification using a stereomicroscope (Nikon Eclipse, E100), while subsamples between 20 and 140 μ m were counted in a 1 ml Sedgewick-Rafter chamber at 40 \times magnification.

In the analysis, some species were classified at genus level because of morphological ambiguities of preserved species (e.g., *Mesocyclops*, *Acroperus*, *Alona*, *Trichocerca*, *Synchaeta*, *Polyarthra*, *Collothea*). When possible, 20–30 individuals of each taxon were measured in each sample. After obtaining length data, biomasses were calculated using length–weight relationships available from the literature (Dumont et al., 1975; Bottrell et al., 1976; Ojaveer et al., 2001). If no information was available (e.g., for some rotifers), geometric shapes were used instead.

For the functional characterization, the different zooplankton taxa were divided into different groups (Table 1) based on several traits such as their feeding strategies, predator avoidance, and growth according to Barnett et al. (2007) and Obertegger & Manca (2011). Rotifers were separated into raptorial (*Ascomorpha*, *Asplanchna*, *Collothea*, *Gastropus*, *Ploesoma*, *Polyarthra*, *Synchaeta*, and *Trichocerca*) and microphagous (*Brachionus*, *Conochilus*, *Euchlanis*, *Filinia*, *Keratella*, *Lecane*, *Notholca*, *Testudinella*, and *Trichotria*). Cladocerans and copepods were classified into filtering Ctenopoda (*Diaphanosoma* and *Pseudosida*), filtering Anomopoda (*Daphnia*, *Simocephalus*, *Ceriodaphnia*, and *Moina*), selective filter feeders (*Bosmina* and *Bosminopsis*), filtering scrapers (Chydoridae and Macrotrichidae), microphagous herbivores (*Sinocalanus*, *Arctodiaptomus*, Calanoidea copepodites), and microphagous carnivores (*Mesocyclops*, Cyclopoidea copepodites). A FD index was calculated for each lake by using the eight functional groups mentioned above and the same formulae as for the Shannon–Wiener diversity index (Shannon & Weaver, 1964). In addition, the proportion of microphagous rotifers to raptorial rotifers (microphagous:raptorial ratio) (Obertegger et al., 2011) was calculated in order to identify possible replacement of rotifer FGs along the salinity gradient.

Table 1 Functional characterization of the different zooplankton taxa based on several traits such as their feeding strategies, predator avoidance, and growth

Rotifera	Raptorial	<i>Ascomorpha</i>	<i>Synchaeta</i>		
		<i>Asplanchna</i>	<i>Trichocerca</i>		
		<i>Collotheca</i>	<i>Polyarthra</i>		
		<i>Ploesoma</i>			
	Microphagous	<i>Brachionus</i>	<i>Filinia</i>		
		<i>Conochilus</i>	<i>Keratella</i>		
		<i>Euchlanis</i>	<i>Lecane</i>		
		<i>Notholca</i>	<i>Testudinella</i>		
		<i>Trichotria</i>			
		Cladocera	Filtering Ctenopoda	<i>Diaphanosoma</i>	
				<i>Pseudosida</i>	
			Filtering Anomopoda	<i>Daphnia</i>	
				<i>Ceriodaphnia</i>	
				<i>Simocephalus</i>	
	Selective filter feeders	<i>Moina</i>			
		<i>Bosmina</i>			
		<i>Bosminopsis</i>			
	Filtering scrapers	<i>Chydoridae</i>			
		<i>Macrotrichidae</i>			
Copepods	Microphagous herbivorous	<i>Sinocalanus</i>			
		<i>Arctodiaptomus</i>			
		Calanoidae copepodites, etc.			
	Microphagous carnivores	<i>Mesocyclops</i>			
			Cyclopoidea copepodites, etc.		

Modified from Barnett et al. (2007) and Obertegger & Manca (2011)

Statistical analyses

All 24 lakes were grouped according to salinity following the classification of Hammer (1986) but unifying two categories for high-saline lakes: subsaline (Sub; 0.5–3 g l⁻¹), which included seven lakes, hyposaline (Hypo; 3–20 g l⁻¹), which included 13 lakes, and meso-hypersaline (Meso-hyper: > 20 g l⁻¹), including 4 lakes. Differences in environmental characteristics and zooplankton FD among these three salinity categories were assessed using the non-parametric Kruskal–Wallis with Dunn post hoc test ($\alpha = 0.05$).

The similarity analysis was used to compare the taxonomic composition among lake categories through the Bray–Curtis dissimilarity index. Results were displayed in a dendrogram following the method unweighted pair-group with arithmetic mean (UPGMA). A similarity percentage procedure (SIMPER) with 9999 permutations was performed on the Bray–Curtis triangular matrix to determine taxonomic differences among the lakes. A posteriori non-

parametric multivariate analysis of variance (NPMA-NOVA) was performed to analyze whether those differences were statistically significant. For this analysis, eight taxa were used, which included *Asplanchna*, *Brachionus*, *Hexarthra*, *Lecane*, *Daphnia*, *Diaphanosoma*, Calanoidea, and Cyclopoidea. In addition, beta (β) diversity index or global replacement of taxa between systems was calculated based on presence–absence data according to Whittaker (1972), using the following formula: $bw = (S/\alpha) - 1$, where S is the total number of species recorded for the lakes and α is the average number of species found within lakes.

From an initial set of twenty environmental (physical, chemical, and biological) variables, a correlation matrix (Spearman non-parametric correlations, ρ) was calculated in order to detect highly correlated variables. A correlation factor of 0.6 was considered strong, and from each correlation pair only the variable with the lowest VIF (Lepš & Šmilauer, 1998) was retained to diminish the chance of spurious correlations in the successive steps. Then, a subset of

explanatory variables known to influence the zooplankton was selected (Jeppesen et al., 1994, 1996; Kalf, 2002; Schallenberg et al., 2003; Bruce et al., 2006, 2012; Moss, 2009; Helenius et al., 2016). Thus, the following explanatory variables were considered in the analyses: lake depth, salinity, temperature, pH, concentration of $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, and *Chl-a*, abundance of small fish (10–25 cm SL), mean total fish biomass, and fish size diversity.

Multiple generalized linear models (GLM) were used to find the model that best explained the variations in H, FD, S, total zooplankton size (TZS), and total zooplankton biomass (TZB). From the above-mentioned considered variables, we selected three explanatory variables for each response variable due to the small sample size ($n=24$), and different models with all possible combinations were compared in a set of preliminary analyses. Following the information theoretic approach, we used the Akaike's Information Criterion corrected for small sample size (AICc) to evaluate the models that best fitted the data (Burnham & Anderson, 2002). The difference between the lowest AICc value and AICc from all other models (ΔAICc) was also calculated in order to rank the potential models (Burnham & Anderson, 2002). Also, the AICc weight of a model (w_i) was calculated based on all candidate models (Burnham & Anderson, 2002). For each response variable, an exploratory analysis was performed, including verification of normality, homoscedasticity, and sub- or over-dispersion. According to that, S, H, TZS, and TZB were analyzed using GLM with a Poisson error distribution and a logarithmic link function, while FD was analyzed using GLM with a Gaussian error distribution and an identity link function. The selected explanatory variables used to model S, H, and TZS were: salinity, depth, and abundance of small fish. However, in the first case (for S), the quadratic value of salinity was also incorporated in the model to include the distant values. To model FD, we used salinity, depth, and fish size diversity as explanatory variables, and to model TZB, the selected explanatory variables were salinity, depth, and fish biomass.

Different multivariate analyses such as canonical correspondence analysis (CCA) or redundancy analyses (RDA) were performed to explore the controlling factors of zooplankton composition in the lakes. The choice of CCA or RDA was based on a previously conducted detrended correspondence analysis (DCA):

when the response of the biological data was unimodal we used CCA and when it was linear we used RDA (ter Braak, 1994). All zooplankton functional groups were included as response variables. The following biotic and abiotic variables were used as explanatory ones: lake depth, salinity, temperature, pH, concentration of $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, and *Chl-a*. Response and explanatory variables were transformed, when necessary, and standardized by norm. The explanatory variables retained in the models were based on forward stepwise selection ($\alpha = 0.05$) and only those that had an acceptable VIF value (< 20) were finally considered (Lepš & Šmilauer, 1998). The significance of each variable and the combination of all canonical axes were determined using the Monte Carlo permutation test (999 permutations).

To analyze the relative importance of environmental and biological factors in shaping the zooplankton FD, the variance partitioning procedure was used (Borcard et al., 1992). We used partial CCA since the response was unimodal. The whole variation of the zooplankton matrix was partitioned into “biological factors,” which included mean fish biomass (CPUE), abundance of small fish (< 10 cm length, CPUE), *Chl-a* concentration, and “environmental factors,” which included salinity, depth, $\text{PO}_4\text{-P}$, and $\text{NH}_4\text{-N}$. The significance of these components was evaluated with a Monte Carlo permutation test.

All statistical analyses were performed using R software v0.99.903 (R Development Core Team, 2011) with the MASS, MuMIn, vegan, and Biodiversity packages, and CANOCO 5 software (ter Braak & Šmilauer, 2002).

Results

A total of 70 (1–27 per lake) zooplankton taxa were identified within the groups Rotifera (52 taxa), Cladocera (12 taxa), and Copepoda (6 taxa). The diversity index (Shannon–Wiener) ranged between 0.11 (at a salinity level of 21 g l^{-1}) and 2.26 (at a salinity level of 2.1 g l^{-1}).

The lake salinity categories (Sub, Hypo, and Meso-hyper) differed in depth, DO, TN, TP, and K; high-salinity lakes were, in general, deeper and had low DO, and higher values of TN, TP, and K were recorded. In contrast, lake area, Secchi disc depth, concentrations of *Chl-a*, $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, and pH

remained practically similar among the three groups (Table 2). According to the Bray–Curtis dissimilarity index, subsaline and hyposaline lakes showed the most

Table 2 Differences in environmental characteristics (Kruskal–Wallis with Dunn post hoc test) among the three lake systems classified according to salinity (modified from Hammer, 1986)

	<i>H</i>	<i>P</i>	Post hoc tests		
			Sub	Hypo	Meso-hyper
Depth	7.83	0.019*			
Sub				0.36	0.01
Hypo			1.00		0.03
Meso-hyper			0.03	0.08	
DO	8.74	0.012*			
Sub				0.81	0.01
Hypo			1.00		0.01
Meso-hyper			0.03	0.02	
NT	14.92	<0.001*			
Sub				<0.01	0.01
Hypo			0.01		0.01
Meso-hyper			0.03	0.02	
TP	7.82	0.019*			
Sub				0.48	0.02
Hypo			1.00		0.01
Meso-hyper			0.05	0.04	
<i>K</i>	18.7	<0.001*			
Sub				<0.01	0.01
Hypo			<0.01		<0.01
Meso-hyper			0.03	0.01	
pH	0.6	0.74			
Lake area	0.85	0.652			
Secchi	3.92	0.14			
Chl- <i>a</i>	1.43	0.49			
NH ₄ -N	3.22	0.19			
PO ₄ -P	2.18	0.33			

Sub subsaline (0.5–3 g l⁻¹), *Hypo* hyposaline (3–20 g l⁻¹), *Meso-hyper* mesosaline and hypersaline grouped lakes (> 20 g l⁻¹)

For the comparison within lake categories, the statistic *Q* is given in italics and the *P* values from the Dunn post hoc test are shown in bold. Asterisks indicate statistical differences (*P* < 0.05)

similar zooplankton taxa composition, from which the meso-hypersaline lakes differed (cophenetic correlation: 0.981; NPMANOVA, *P* = 0.042). Mean beta-diversity (Whittaker index) was 0.53, meso-hyper and subsaline lakes showed the largest replacement of taxa (0.38), followed by sub- to hyposaline lakes (0.25). Only 9 taxa were responsible for 90% of the variation mentioned above, namely the rotifer genera *Brachionus*, *Hexarthra*, *Polyarthra*, *Keratella*, *Filinia*, and *Lecane*, the cladoceran *Moina*, and calanoid copepods (all species) (SIMPER, *P* < 0.05). A significant positive correlation was found between Shannon–Wiener taxonomic diversity and FD ($\rho = 0.43$, *P* = 0.04).

The multiple GLM analyses showed that salinity was the most significant variable explaining the variation in species richness (*S*) and FD. In both cases, an inverse relationship was observed, where salinity negatively affected each analyzed variable (*S* and FD). Using the AIC method and the inference of multiple models, we obtained sixteen candidate models to consider *S* (Table 3). The relative importance (*w_i*) of the variable salinity was 0.99 and that of its quadratic term (salinity)² was 0.91. From these values and the obtained coefficients, the selected final model included both variables as the main predictors of zooplankton species richness (Table 4). In the case of FD, eight candidate models were obtained (Table 3), but only salinity was retained in the final model as a significant variable (*w_i* = 0.75) (Table 4). Although for *H*, any explanatory variables were statistically significant from the GLM, a significant negative relation was found between *H* and log-transformed salinity values ($\rho = -0.45$; *P* = 0.027).

For TZS and TZB, none of the explanatory variables included in the GLM were significant predictors. In addition, no influence of salinity was observed on either microcrustacean mean size ($r = -0.23$, *P* = 0.278 and $r = -0.02$, *P* = 0.92, for cladocerans and copepods, respectively) or on rotifer mean size ($r = -0.288$, *P* = 0.182). However, we found a significant positive correlation between salinity and TZB (Fig. 1a, b) and that the size range of zooplankton (maximum size minus minimum size observed per lake) was highly variable and high also at high salinities (Fig. 2). Among the explanatory variables included, total fish biomass and abundance of small fish correlated negatively with TZB (Fig. 1c, d). Besides, the particular analysis of

Table 3 Statistics of the GLM

Candidate models	<i>K</i>	AICc	ΔAICc	<i>w_i</i>
Richness				
sal + sal ²	3	130.13	0	0.55
absmallfish + sal + sal ²	4	132.63	2.5	0.16
area + sal + sal ²	4	132.73	2.6	0.15
absmallfish + area + sal + sal ²	5	135.44	5.31	0.04
sal + sal ²	2	135.55	5.43	0.04
absmallfish + sal	3	136.16	6.03	0.03
Area + sal	3	137.48	7.35	0.01
absmallfish + area + sal	4	138.11	7.98	0.01
absmallfish + sal ²	3	140.17	10.04	0
sal ²	2	141.21	11.08	0
absmallfish	2	141.87	11.74	0
absmallfish + area + sal ²	4	141.94	11.81	0
Area + sal	3	143.03	12.9	0
absmallfish + area	3	143.45	13.32	0
Null	1	145.35	15.22	0
Area	2	147.07	16.94	0
FD				
sal	3	20.62	0	0.44
fishzd + sal	4	22.56	1.94	0.17
Null	2	23.38	2.75	0.11
Area + fishzd	4	23.52	2.9	0.1
fishzd	3	23.85	3.23	0.09
area + fishzd + sal	5	25.78	5.15	0.03
Area	3	25.99	5.37	0.03
Area + fishzd	4	26.74	6.11	0.02

sal salinity, *absmallfish* abundance of small fish, *fishzd* fish size diversity

Summary of model selection results for candidate models explaining species richness (*S*) and functional diversity (FD). Null model and models with strong support ($\Delta\text{AICc} \leq 2$) are provided and listed in decreasing order of importance. *K* (no. of estimated parameters), AICc (Akaike information criterion corrected for small sample size), ΔAICc (difference between the lowest AICc value and AICc from all other models), and *w_i* (AIC weights) for all candidate models are presented

cladoceran and copepod sizes excluding lakes without fish (i.e., with salinities above 14 g l⁻¹) revealed a decline in microcrustacean size with increasing fish abundance (Fig. 3). Fishless lakes were characterized by the presence of relatively large and salt-tolerant zooplankton species such as *Daphnia magna* Straus, 1820, *Moina micrura* Kurz, 1874, *Arctodiaptomus salinus* (Daday, 1885), *Sinocalanus tenellus* (Kikuchi

K., 1928), and large *Brachionus plicatilis* Müller, 1786.

The functional classification of zooplankton taxa showed a clear segregation along the salinity gradient (Fig. 4). Among the cladocerans, selective filter feeders and filtering scrapers were restricted to the lower salinities, filtering Ctenopoda occupied an intermediate niche, whereas filtering Anomopoda were abundant at high salinities. Within the Copepoda, calanoids were highly tolerant to salinity, while cyclopoids disappeared at salinities > 7.6 g l⁻¹. As regards to rotifers, a bimodal distribution was observed for raptorial within a salinity range of 0.5–12 g l⁻¹, while microphagous species dominated at salinity concentrations over 12 g l⁻¹ ($r = 0.56$, $P = 0.008$, Fig. 4). The segregation of raptorial and microphagous was represented by a replacement from species of *Ascomorpha*, *Asplanchna*, *Polyarthra*, *Synchaeta*, and *Trichocerca* genera to species of *Brachionus* (being dominant), *Conochilus*, *Euchlanis*, *Filinia*, *Keratella*, and *Lecane* genera (Fig. 5).

Moreover, within the raptorial rotifers, *Asplanchna* was usually the dominant genus in subhaline lakes; however, at higher salinities they disappeared and raptorial such as *Polyarthra* and *Hexarthra*, mainly *H. oxyurus* (Zernov 1903), became dominant.

Among the three salinity groups, freshwaters and hyposaline lakes hosted on average 6.6 (± 1.5) and 3.7 (± 1.2) functional groups, respectively; while high-salinity lakes had on average 2.5 (± 2) functional groups: All three groups differed significantly ($F = 13$, $P < 0.001$). Also, the calculated FD Index differed substantially between the two low-salinity lakes and meso-hypersaline lakes (Fig. 6). Variance partitioning indicated that both biological and environmental factors influenced zooplankton FD. The overall explained variation in this analysis was 20.3% (environment alone: 8.1%; biological alone: 2.1%; environment \times biological: 10.1%). Monte Carlo test results were significant for environment \times biological factors ($F = 1.16$, $P = 0.034$) but not for each factor alone ($F = 1.5$, $P = 0.088$, and $F = 0.8$, $P = 0.646$ for environment and biological factors, respectively).

The first two axes of the RDA accounted for 58.3% of the variation in total zooplankton FD (axis 1: 33.6%; axis 2: 24.7%) (Fig. 7). Among the copepods, microphagous herbivores and microphagous carnivores were mainly correlated with the salinity gradient and fish variables (size and diversity). Salinity was

Table 4 Weight of each variable in the final models explaining species richness (S) and functional diversity (FD) using GLM

Explanatory variables	w_i	Estimated variables	SE	P
Richness				
Intercept		2824	83.56	$<2e-16^{***}$
Salinity	0.99	- 35.9	10.11	0.000381***
Salinity ²	0.91	0.259	0.09175	0.004763**
FD				
Intercept		- 0.20813	0.28982	$<2e-16^{***}$
Salinity	0.75	- 0.01484	0.01635	0.0352*

Estimated variables, standard errors (SE), and significance values (P) are presented

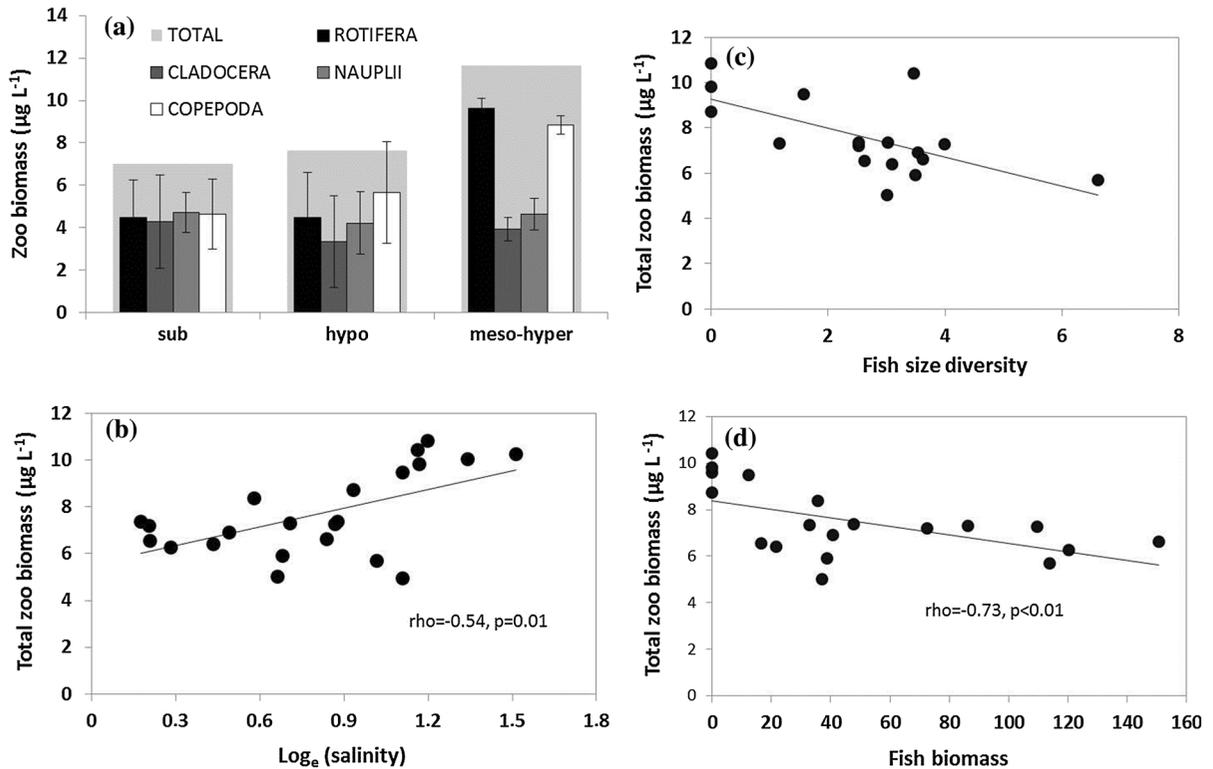


Fig. 1 Means (\pm SD) of total and within-zooplankton group biomasses in the four salinity categories: *Sub* subsaline ($0.5\text{--}3\text{ g l}^{-1}$), *Hypo* hyposaline ($3\text{--}20\text{ g l}^{-1}$), *Meso-hyper* mesosaline, and hypersaline ($> 20\text{ g l}^{-1}$) (a). Relationship between total zooplankton biomass (log-transformed values) and salinity (log-transformed values) (b). Relationship between

total zooplankton biomass (log-transformed values) and fish parameters: small fish (fork length between 10 and 25 cm) abundance (c) and fish biomass (d). Spearman correlation coefficients (ρ) and P significance values are given for each correlation graph

also the factor that correlated (negatively) with most raptorial cladocerans and rotifer abundances. Microphagous copepods (calanoids) and filtering anomopods (*Daphnia*, *Moina*) were positively correlated with fish size diversity and average fish biomass, indicating high sensitivity to fish predation pressure in the lakes. Among all lakes, the sub- and hypohaline ones were characterized by the presence of fish, raptorial rotifers,

macrophagous copepods, and most cladocerans (Fig. 7).

Discussion

Zooplankton constitutes a key component in aquatic food webs and is highly important in the transfer of

Fig. 2 Mean and range size (in mm) of zooplankton for each lake along the salinity gradient. Fishless lakes are shown as light bars and lakes with fish as dark gray bars

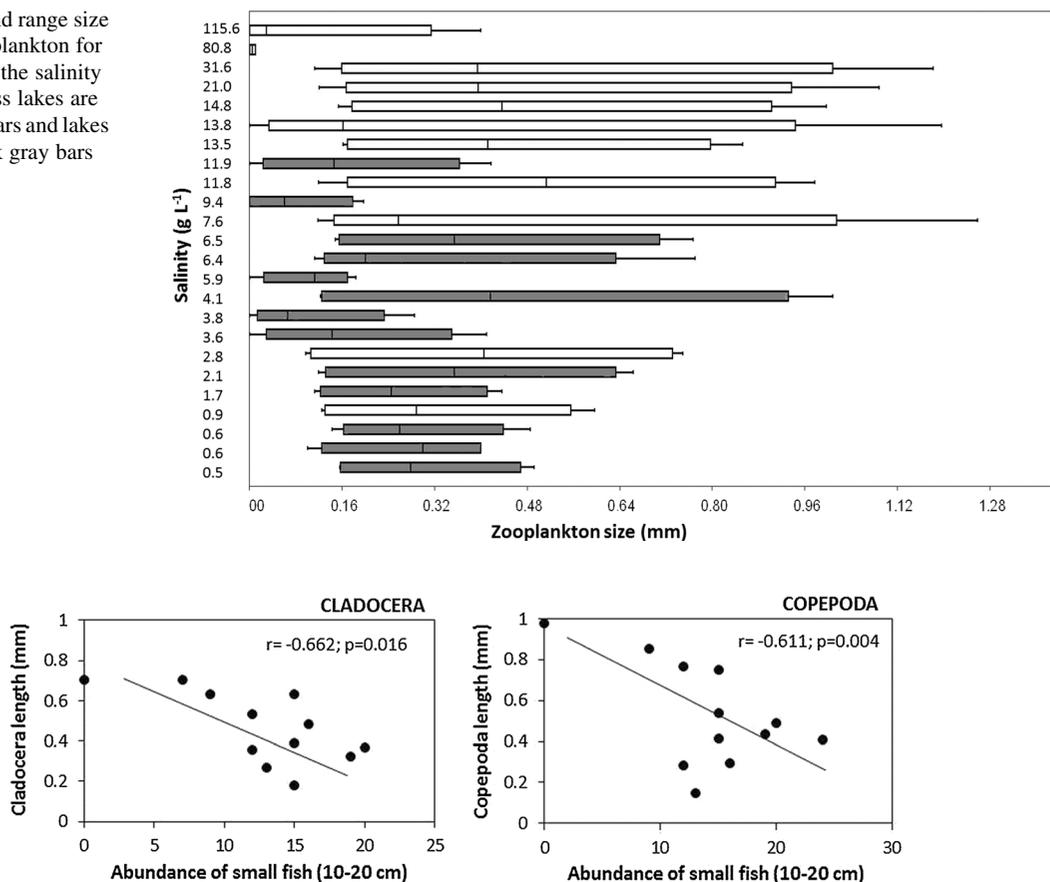


Fig. 3 Relationship between Cladocera and Copepoda lengths and the abundance of small fish (standard length between 10 and 25 cm). Pearson correlation coefficient (r) and P significance

energy and matter from primary producers to higher trophic levels. Therefore, changes in their structure and function as a result of salinity fluctuations would have serious consequences for ecosystem functioning. As expected, we found that zooplankton richness (S), specific diversity (H), and FD decreased with increasing salinity, as in previous studies on zooplankton (Boix et al., 2008; Bruce et al., 2009; Jensen et al., 2010; Tavsanoglu et al., 2015), fish (Harrison & Whitfield, 2006), macroinvertebrates (Bruce et al., 2012), and macrophytes (Rodríguez-Gallego et al., 2015). Furthermore, we found that subsaline and hyposaline lakes had the most similar zooplankton taxa composition but differed from the meso-hyper-saline lakes, the salinity group in which the largest replacement of taxa occurred along the salinity gradient. Salinity-tolerant species, such as the Branchiopod *Artemia* sp., the copepod *A. salinus*, and the

rotifers *B. plicatilis*, *H. oxyurus*, and *Colurella* sp., dominated the zooplankton community in the high-salinity lakes, which agrees with the findings in other field and experimental studies (Toruan, 2012; Paturej & Gutkowska, 2015; Tavsanoglu et al., 2015). Calanoid copepods are considered to be salt-tolerant taxa because of their marine origin (Sarma et al., 2006), which explains their high tolerance to salinity, not only in the lake region studied here but also in other parts of the world (Bruce et al., 2009). By contrast, rotifers may be limited by salinity because of their freshwater origin (De Deckker, 1983); however, *B. plicatilis*, *H. oxyurus*, and *Colurella* spp. such as *C. uncinata* (Müller, 1773) are salt-tolerant species and frequently occur in highly saline systems (Toruan, 2012; Paturej & Gutkowska, 2015), confirming our first hypothesis that only salt-tolerant species are able to survive in high-salinity lakes.

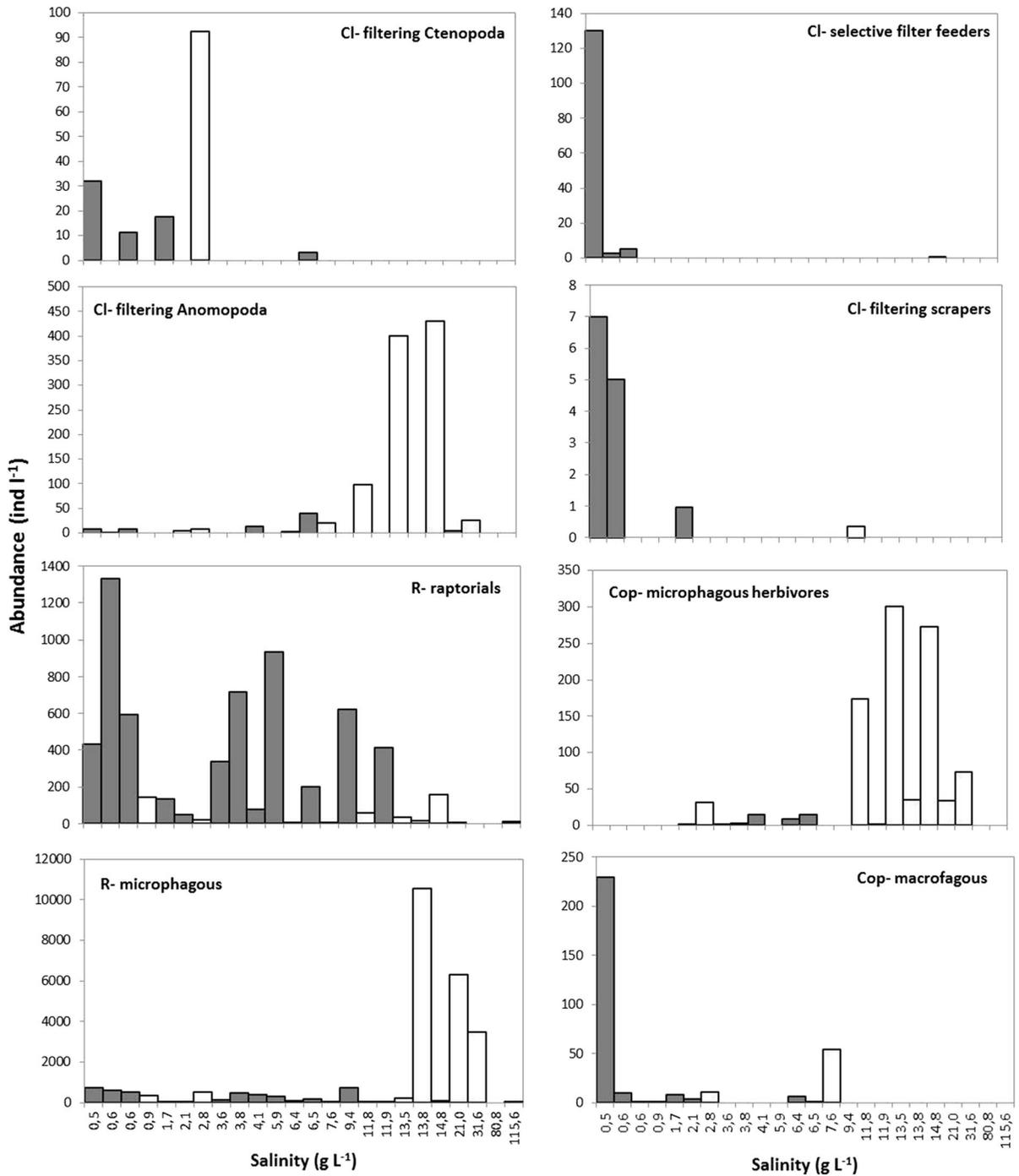


Fig. 4 Abundance (ind. l⁻¹) and distribution of each zooplankton functional group along the salinity gradient in the study lakes. Fishless lakes are shown with light gray bars and lakes with fish are shown with dark gray bars

Functional and species diversity declined together since a significant positive correlation was found between the Shannon–Wiener index and the FD index.

Among the three salinity categories, freshwater lakes hosted significantly more functional groups than hyposaline and meso-hypersaline categories. The

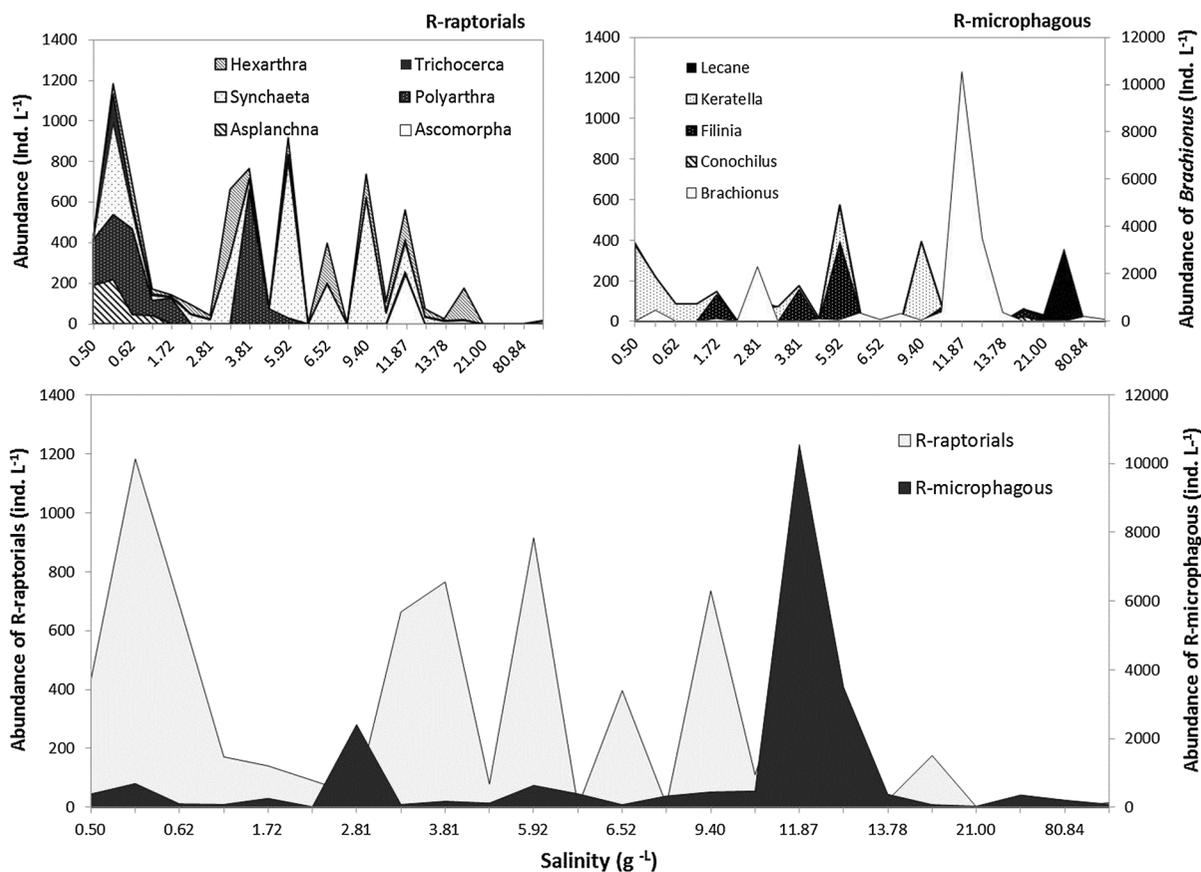


Fig. 5 Abundances of the main raptorial genera (upper left panel), abundances of the main microphagous genera (upper right panel), and abundances of total raptorial and microphagous rotifers (lower panel) along the salinity gradient

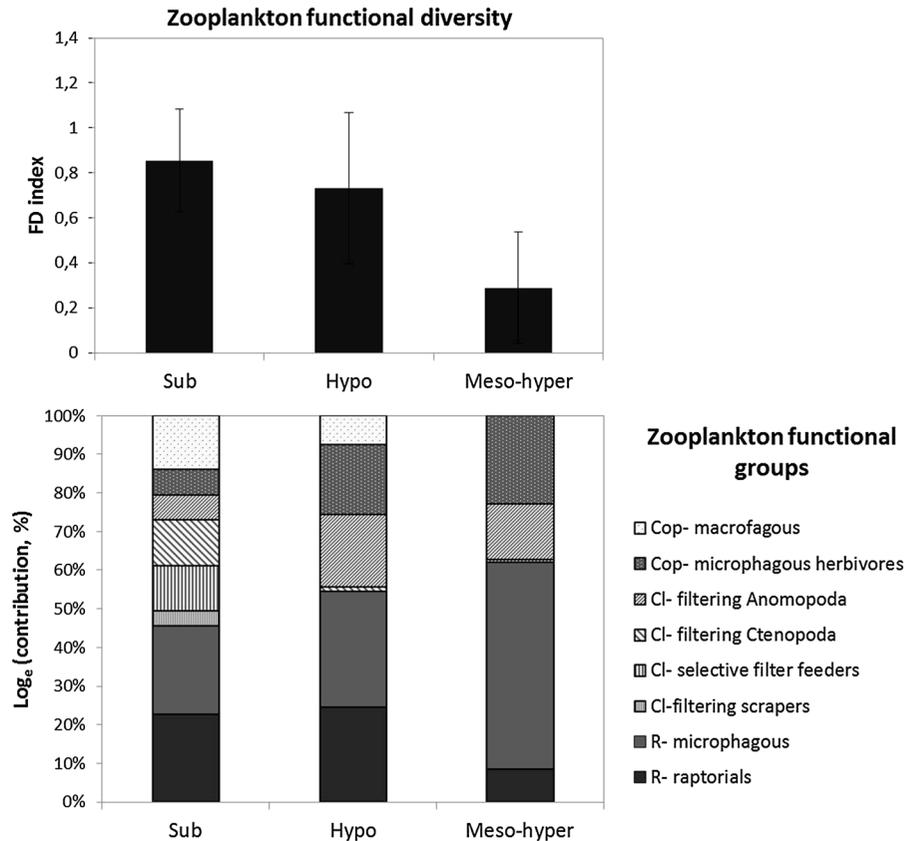
filtering scrapers, filtering Ctenopoda, and microphagous copepods, were lost in the last categories. However, there was not only a loss of FGs with increasing salinity, for rotifers but also the relative balance of the FGs changed. While microphagous and raptorial were equally represented in the low-salinity lakes, a disproportional increase of microphages occurred in the most salty lakes. The differences in food acquisition and processing mechanisms of microphagous and raptorial might favor their coexistence in the low-salinity lakes (Obertegger et al., 2011). However, in high-salinity lakes, the increase of microphages may be explained by their stronger competition ability for food in stressing environments (Alva-Martínez et al., 2009), and probably because they are better adapted to salinity than other rotifers (Viayeh & Špoljar, 2012).

Both the imbalances and the decrease in FD may not only result in less control of phytoplankton as

previously suggested (Helenius et al., 2016), but they may also lead to less efficient nutrient cycling and lower quality of the supply of food for invertebrates and small fish at higher trophic levels (Barnett et al., 2007; Obertegger & Manca, 2011).

The ‘compensation hypotheses’ (Schindler, 1990; Ruesink & Srivastava, 2001; Mano & Tanaka, 2016) suggest that sensitive species can be replaced by more tolerant ones in stress situations, in this way maintaining the stability of ecosystem functioning (Ruesink & Srivastava, 2001; Mano & Tanaka, 2016). However, the replacements we observed both within and between FGs in our study partly contradict these hypotheses. We found that *Asplanchna* sp., a dominant genus in subsaline lakes, disappeared at higher salinities, while species such as *Polyarthra* sp., *Synchaeta* sp., and *H. oxyurus* became dominant (Fig. 5). Although *Polyarthra* sp., *Synchaeta* sp., and *Hexarthra* are raptorial and members of the same FG

Fig. 6 Zooplankton functional diversity index (upper panel) and the contribution of each functional group to the total zooplankton community (lower panel) within the four lake systems, classified according to salinity. *Sub* subsaline ($0.5\text{--}3\text{ g l}^{-1}$), *Hypo* hyposaline ($3\text{--}20\text{ g l}^{-1}$), *Meso-hyper* meso-hypersaline ($> 20\text{ g l}^{-1}$). Lowercase letters indicate significant differences



as *Asplanchna*, these genera can have quite different effects on phytoplankton and the microbial web due to their different sizes, feeding habits, and swimming behaviors. Apart from the coronal activity, *Polyarthra* sp. and *Hexarthra* possess unusual appendages that facilitate quick locomotion or saltation movements, allowing efficient avoidance of predator attacks (e.g., from cyclopoid copepods, invertebrates, and small fish) (Hochberg & Gurbuz, 2008). *Asplanchna* spp. has a relatively wide food size spectrum and prey diversity (Chang et al., 2010) compared with the other two genera. Its diet includes particulate matter, phytoplankton, protozoans, bacteria, and even dinoflagellates (Chang et al., 2010). Thus, the replacement of *Asplanchna* by *Polyarthra* sp., *Synchaeta* sp., and *Hexarthra* along the salinity gradient would promote a change in the ecological role of the raptorial FG, with potential consequences for the ecosystem functioning.

Considering the replacements between FGs, we found that selective raptorial diminished, while microphagous rotifers increased along the salinity

gradient. This may have implications for the sizes of the ingested particles since the former consume large and the latter smaller-sized particles (between 15 and 20 μm) (Obertegger & Manca, 2011). Among cladocerans, a gradual shift occurred from an assemblage including *Bosmina* sp. and chydorids to one composed almost exclusively of *Moina micrura* and *Daphnia magna* at intermediate salinity levels. Although the latter are mostly generalist feeders and feed on a wide spectrum of food types and sizes (Jeppesen et al., 1996), they are more sensitive to toxic cyanobacteria and large filament sizes than other groups such as chydorids (Tönno et al., 2016). This constraint may have ecological implications since increased salinity, apart from causing osmotic stress in the organisms, may generate blooms of salt-tolerant cyanobacteria (Paerl & Huisman, 2009) such as *Microcystis aeruginosa* (Tonk et al., 2007), *Anabaenopsis* sp., and *Nodularia* sp. (Moisander et al., 2002). Thus, the efficiency of cladocerans as a controller of phytoplankton might change at increasing salinities, leading to a worsening of eutrophication symptoms (Jeppesen

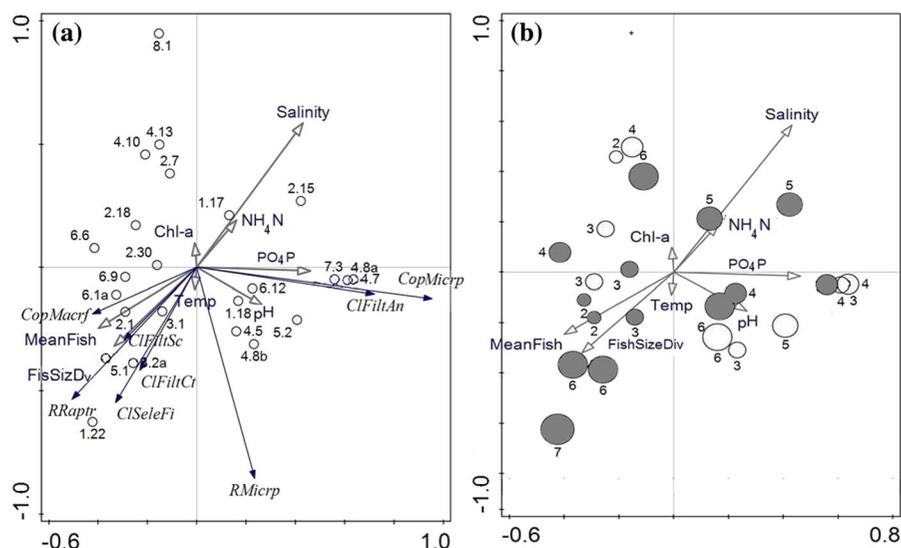


Fig. 7 First two axes of the RDA based on zooplankton functional groups (FG) (axis 1 explaining 33.6% and axis 2 explaining 24.7% of the total variation). Zooplankton functional groups are indicated with blue arrows, explanatory (environmental and biological) variables with gray arrows (**a**, **b**), and the ordination of lakes with circles (**b**). In the right panel, the circle sizes are proportional to the abundance of each FG within each lake. Fishless lakes are shown as white circles, lakes with fish as gray circles. *RRaptr*: raptorial rotifers (*Ascomorpha*, *Asplanchna*, *Collotheca*, *Gastropus*, *Ploesoma*, *Polyarthra*, *Synchaeta*, and *Trichocerca*); *RMicrp*: microphagous rotifers

(*Brachionus*, *Conochilus*, *Euchlanis*, *Filinia*, *Keratella*, *Lecane*, *Notholca*, *Testudinella*, and *Trichotria*); *ClFiltCr*: cladoceran filtering Ctenopoda (*Diaphanosoma* and *Pseudosida*), *ClFiltAn*: cladoceran filtering Anomopoda (*Daphnia*, *Simocephalus*, *Ceriodaphnia*, and *Moina*), *ClSeleFi*: cladoceran-selective filter feeders (*Bosmina* and *Bosminopsis*), *ClFiltSc*: filtering scrapers (Chydoridae and Macrotrichidae), *CopMicr*: microphagous herbivores (*Sinocalanus*, *Arctodiaptomus*, Calanoidea copepodites, etc.) *CopMacrf*: microphagous carnivores (*Mesocyclops*, Cyclopoidea copepodites, etc.)

et al., 2015). Among the copepods, calanoids (microphagous herbivores) remained highly tolerant to salinity, whereas cyclopoids (microphagous carnivores) disappeared at salinities $> 7.6 \text{ g l}^{-1}$, as also seen in other salinity-gradient studies (Bruce et al., 2009; Jeppesen et al., 2015). This shift may have implications for other related trophic levels such as primary producers. In fact, we found that phytoplankton biomass (measured as Chl-a concentration) remained almost constant along the salinity gradient, which was probably controlled by the joint pressure of large calanoids and other microphagous herbivores favored by the absence of carnivorous cyclopoids.

Our second hypothesis was that zooplankton size and biomass would decrease due to physiological constraints with increasing salinity. Yet, contrary to our expectation, we found that zooplankton mean sizes, size ranges, and biomasses did not decrease with increasing salinity. Actually, we found increased size ranges and biomasses in high-salinity lakes compared with subsaline and hyposaline ones. This contradicts a

previous study in brackish lakes which revealed no effect of salinity on zooplankton size and biomass (Gao et al., 2008) or a decrease in the mean size of zooplankton with increasing salinity, affecting the capacity of grazing zooplankton to control phytoplankton (Moss & Leah, 1982; Jeppesen et al., 1994, 2007). Our study, however, covered a larger gradient in salinity ($0.5\text{--}115 \text{ g l}^{-1}$) where fish were absent when salinity exceeded 14 g l^{-1} , allowing the presence of large-sized zooplankton species such as *Artemia* sp. and calanoid copepods (e.g., *A. salinus*, *S. tenellus*) (Pennak, 1991; Tolomeev et al., 2010). We found that copepod and cladoceran sizes correlated negatively with the abundance of small fish and total fish biomass in the lakes with fish. This result indicates that fish predation rather than salinity was the key factor determining abundance, biomass, and size of zooplankton, which is in agreement with previous studies undertaken in shallow brackish lakes (Bruce et al., 2010; Jensen et al., 2010).

We conceptually summarize the observed responses of the zooplankton to increasing salinity created by a combination of direct (physiological constraints) and indirect factors (fish predation pressure) from both a structural (taxonomic) and a functional perspective (Fig. 8). In accordance with Helenius et al. (2016), we found that salinity acted as a primary physiological filter structuring species richness and diversity, while predation was the main biological driving factor defining the species size structure. While high abundances of small fish tend to reduce the overall size of the zooplankton, favoring smaller taxa such as *B. longirostris* and rotifers

(Brooks & Dodson, 1965), high salinity, if resulting in loss of fish, promotes the presence of large and more saline-tolerant zooplankton species such as *D. magna*, *Moina* spp., large copepods, and large brachionid rotifers.

Moreover, we found that the distribution and abundance of each FG depended on the interactions between different factors (e.g., the turnover between raptorial and microphagous rotifers responded to changes in salinity, turbidity, and TP), resembling the pattern observed in previous works (Litchman et al., 2013; Vogt et al., 2013).

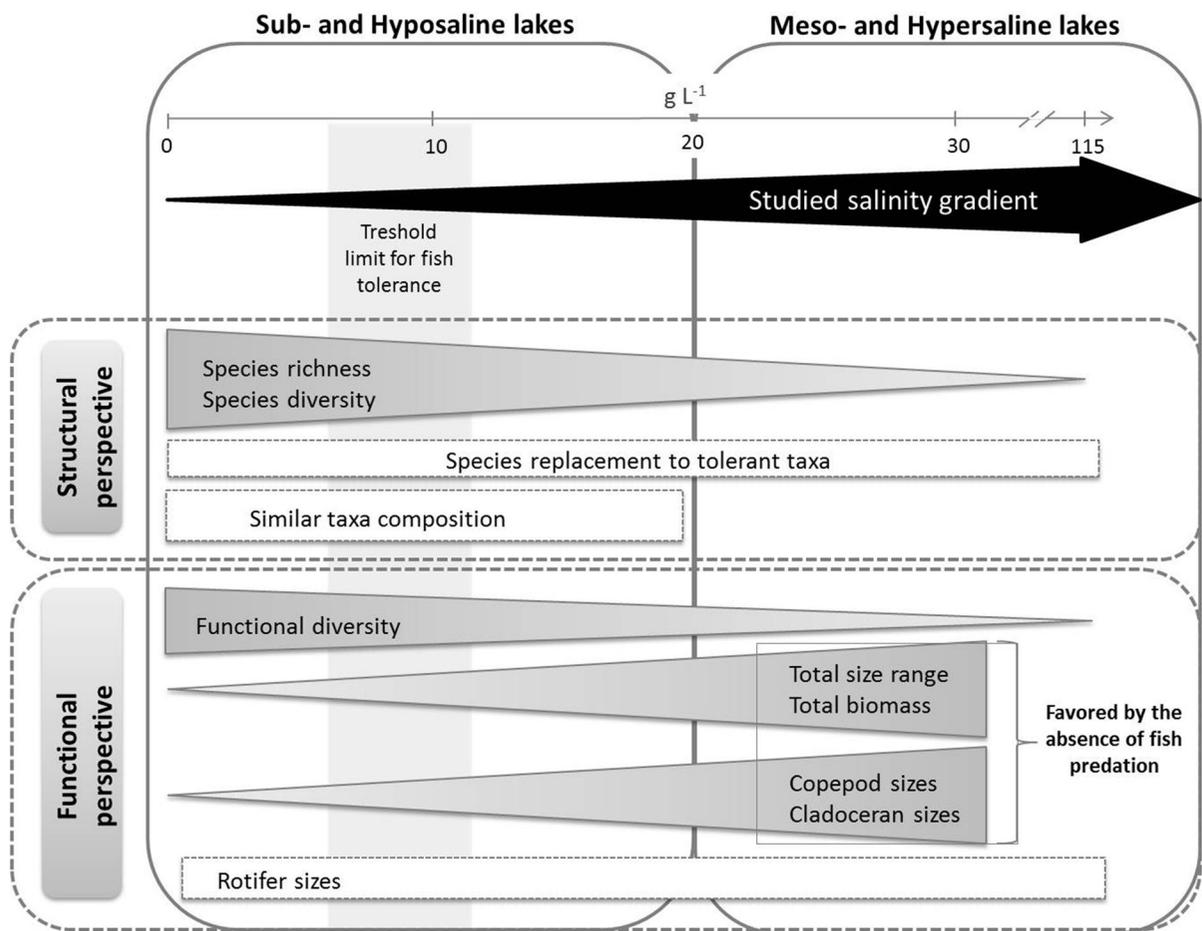


Fig. 8 Schematic summary of the observed responses of the zooplankton to increasing salinity induced by a combination of direct (physiological constraints) and indirect factors (predation pressure). Considering taxonomy, zooplankton richness (S) and specific diversity (H) decreased from freshwater to hypersaline lakes. Sensitive species were replaced by more tolerant ones, and subsaline and hyposaline lakes ($< 20 \text{ g l}^{-1}$) had the most

similar zooplankton taxa composition. A functional approach revealed that the number of functional groups (FD) diminished from subsaline to meso-hypersaline lakes. Zooplankton size and biomass increased as a consequence of an increase in copepod and cladoceran sizes, which were favored by the absence of fish predation. Rotifer sizes did not depend on the salinity gradient since no relation was found between these two variables

It can be concluded that for the zooplankton community, species diversity (H) and species richness (S) can be seriously affected by increased salinities with potential effects on the trophic structure. Functional diversity (FD, based on the differentiation between functional groups proposed in this work) and size structure diminished from subsaline to meso-hypersaline lakes, suggesting that both attributes may be appropriate indicators of changes in ecosystem functioning related to changes in salinity (Fig. 7). More diverse functional groups and wider size structures may promote more complex and balanced trophic structures, more productive systems, and more resistant communities under extreme environmental variations (Vandermeer et al., 1998; Vaughn, 2010; Flöder & Hillebrand, 2012). It is evident from our study that the expected salinity increase in lakes in arid and semiarid climate zones in a warmer world (e.g., Jeppesen et al., 2015) will cause adverse effects on biodiversity and functioning. However, our conclusions should be interpreted with caution because other factors may also influence the species responses such as, among others, their physiological adaptation to salinity, different biological interactions, and degree of eutrophication.

Acknowledgements We want to thank the technical staff at the Department of Bioscience in Silkeborg and NIGLAS in Nanjing for help with the study in the field and the laboratory, Drs. Juan Paggi and Susana José de Paggi for help with zooplankton species identification, A. M. Poulsen for editorial assistance, and Mariana Meerhoff for her kind encouragement and valuable comments on an early version of the manuscript. The staff at the Agriculture Department of Fuhai is gratefully acknowledged for fieldwork assistance. This research was funded by the Sino-Danish Centre for Education and Research (SDC), Aarhus University (AU). J. L. Y. was supported by the National Natural Science Foundation of China (31400400). F. T. M. was supported by SNI-ANII (Uruguay). E. J. was supported by the MARS project (Managing Aquatic ecosystems and water Resources under multiple Stress) funded under the 7th EU Framework Programme, Theme 6 (Environment including Climate Change), Contract No.: 603378) and the AU Centre for Water Technology.

References

- Alekseev, V. R., 2002. Copepoda. In Fernando, C. H. (ed.), A Guide to Tropical Freshwater Zooplankton: Identification, Ecology and Impact on Fisheries. Backhuys Publishers, Leiden: 123–188.
- Alva-Martínez, A. F., R. Fernández, S. S. S. Sarma & S. Nandini, 2009. Effect of mixed toxic diets (Microcystis and Chlorella) on the rotifers *Brachionus calyciflorus* and *Brachionus havanaensis* cultured alone and together. *Limnologia – Ecology and Management of Inland Waters* 39: 302–305.
- APHA, 1998. Standard Methods for the Examination of Water and Wastewater, 20th edn. APHA, Washington DC.
- Arthaud, F., D. Vallod, J. Robin & G. Bornette, 2012. Eutrophication and drought disturbance shape functional diversity and life-history traits of aquatic plants in shallow lakes. *Aquatic Sciences* 74: 471–481.
- Barnett, A. J., K. Finlay & B. E. Beisner, 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology* 52: 796–813.
- Boix, D., S. Gascón, J. Sala, A. Badosa, S. Brucet, R. López-Flores, M. Martinoy, J. Gifre & X. D. Quintana, 2008. Patterns of composition and species richness of crustaceans and aquatic insects along environmental gradients in Mediterranean water bodies. *Hydrobiologia* 597: 53–69.
- Borcard, D., P. Legendre & P. Drapeau, 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045–1055.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Węgleńska, 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24: 419–456.
- Brooks, J. L., S. I. Dodson, 1965. Predation, body size, and composition of plankton. *Science* 150: 28–35.
- Brucet, S., D. Boix, R. López-Flores, A. Badosa & X. D. Quintana, 2006. Size diversity and species diversity of zooplankton communities in fluctuant Mediterranean salt marshes. *Estuarine, Coastal and Shelf Science* 67: 424–432.
- Brucet, S., D. Boix, S. Gascón, J. Sala, X. D. Quintana, A. Badosa, M. Søndergaard, T. L. Lauridsen & E. Jeppesen, 2009. Species richness of crustacean zooplankton and trophic structure of brackish lagoons in contrasting climate zones: north temperate Denmark and Mediterranean Catalonia (Spain). *Ecography* 32: 692–702.
- Brucet, S., D. Boix, X. D. Quintana, E. Jensen, L. W. Nathansen, C. Trochine, M. Meerhoff, S. Gascón & E. Jeppesen, 2010. Factors influencing zooplankton size structure at contrasting temperatures in coastal shallow lakes: implications for effects of climate change. *Limnology and Oceanography* 55: 1697.
- Brucet, S., D. Boix, L. W. Nathansen, X. D. Quintana, E. Jensen, D. Balayla, M. Meerhoff & E. Jeppesen, 2012. Effects of temperature, salinity and fish in structuring the macroinvertebrate community in shallow lakes: implications for effects of climate change. *PloS one* 7: e30877.
- Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, NY.
- Chang, K. H., H. Doi, Y. Nishibe & S. I. Nakano, 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.

- Daufresne, M., K. Lengfellner & U. Sommer, 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences* 106: 12788–12793.
- De Deckker, P., 1983. Notes on the ecology and distribution of non-marine ostracods in Australia. *Hydrobiologia* 106: 223–234.
- Declerck, S., J. Vandekerkhove, L. Johansson, K. Muylaert, J. M. Conde-Porcuna, K. Van Der Gucht, C. Pérez-Martínez, T. Lauridsen, K. Schwenk, G. Zwart, W. Rommens, J. López-Ramos, E. Jeppesen, W. Vyverman, L. Brendonck & L. De Meester, 2005. Multi-group biodiversity in shallow lakes along gradients of phosphorus and water plant cover. *Ecology* 86: 1905–1915.
- Ding, N., W. Yang, Y. Zhou, I. González-Bergonzoni, J. Zhang, K. Chen, N. Vidal, E. Jeppesen & B. Wang, 2017. Different responses of functional traits and diversity of stream macroinvertebrates to environmental and spatial factors in the Xishuangbanna watershed of the upper Mekong River Basin, China. *Science of the Total Environment* 574: 288–299.
- Dumont, H. J., I. Van de Velde & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19: 75–97.
- Flöder, S. & H. Hillebrand, 2012. Species traits and species diversity affect community stability in a multiple stressor framework. *Aquatic Biology* 17(3): 197–209.
- Gallego, I., T. A. Davidson, E. Jeppesen, C. Pérez-Martínez, P. Sánchez-Castillo, M. Juan, F. Fuentes-Rodríguez, D. León, P. Peñalver, J. Toja & J. J. Casas, 2012. Taxonomic or ecological approaches? Searching for phytoplankton surrogates in the determination of richness and assemblage composition in ponds. *Ecological Indicators* 18: 575–585.
- Gao, Q., Z. Xu & P. Zhuang, 2008. The relation between distribution of zooplankton and salinity in the Changjiang Estuary. *Chinese Journal of Oceanology and Limnology* 26: 178–185.
- Grime, J. P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344–347.
- Hammer, U. T., 1986. *Saline Lake Ecosystems of the World*. Junk, Dordrecht.
- Harrison, T. D. & A. K. Whitfield, 2006. Temperature and salinity as primary determinants influencing the biogeography of fishes in South African estuaries. *Estuarine, Coastal and Shelf Science* 66: 335–345.
- Heino, J., 2008. Patterns of functional biodiversity and function-environment relationships in lake littoral macroinvertebrates. *Limnology and Oceanography* 53: 1446–1455.
- Heino, J., D. Schmera & T. Erős, 2013. A macroecological perspective of trait patterns in stream communities. *Freshwater Biology* 58: 1539–1555.
- Helenius, L. K., E. Leskinen, H. Lehtonen & L. Nurminen, 2016. Spatial patterns of littoral zooplankton assemblages along a salinity gradient in a brackish sea: a functional diversity perspective. *Estuarine, Coastal and Shelf Science*. <https://doi.org/10.1016/j.ecss.2016.08.031>.
- Hochberg, R. & O. A. Gurbuz, 2008. Comparative morphology of the somatic musculature in species of Hexarthra and Polyarthra (Rotifera, Monogononta): its function in appendage movement and escape behavior. *Zoologischer Anzeiger-A Journal of Comparative Zoology* 247: 233–248.
- Jensen, E., S. Brucet, M. Meerhoff, L. Nathansen & E. Jeppesen, 2010. Community structure and diel migration of zooplankton in shallow brackish lakes: role of salinity and predators. *Hydrobiologia* 646: 215–229.
- Jeppesen, E., M. Søndergaard, E. Kanstrup, B. Petersen, R. B. Eriksen, M. Hammershøj, E. Mortensen, J. P. Jensen & A. Have, 1994. Does the impact of nutrients on the biological structure and function of brackish and fresh-water lakes differ? *Hydrobiologia* 275: 15–30.
- Jeppesen, E., M. Søndergaard, J. P. Jensen, E. Mortensen & O. Sortkjær, 1996. Fish-induced changes in zooplankton grazing on phytoplankton and bacterioplankton: a long-term study in shallow hypertrophic Lake Søbygaard. *Journal of Plankton Research* 18: 1605–1625.
- Jeppesen, E., T. L. Lauridsen, S. F. Mitchell, K. Christoffersen & C. W. Burns, 2000. Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *Journal of Plankton Research* 22: 951–968.
- Jeppesen, E., M. Søndergaard, A. R. Pedersen, K. Jürgens, A. Strzelczak, T. L. Lauridsen & L. S. Johansson, 2007. Salinity induced regime shift in shallow brackish lagoons. *Ecosystems* 10: 47–57.
- Jeppesen, E., S. Brucet, L. Naselli-Flores, E. Papastergiadou, K. Stefanidis, T. Nöges, P. Nöges, J. L. Attayde, T. Zohary, J. Coppens, T. Bucak, R. Fernandes Menezes, F. R. Sousa Freitas, M. Kernan, M. Søndergaard & M. Beklioğlu, 2015. Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity. *Hydrobiologia* 750: 201–227.
- Jin, X. C. & Q. Y. Tu, 1990. *Survey Specification for Lake Eutrophication*. Environmental Science Press, Beijing.
- Kalf, J., 2002. *Limnology: Inland Water Ecosystems*.
- Kořínek, V., 1981. *Diaphanosoma birgei* n. sp. (Crustacea, Cladocera). A new species from America and its widely distributed subspecies *Diaphanosoma birgei* ssp. *lacustris* n. ssp. *Canadian Journal of Zoology* 59: 1115–1121.
- Kořínek, V., 2002. Cladocera. In Fernando, C. H. (ed.), *A Guide to Tropical Freshwater Zooplankton*. Leiden, Backhuys Publishers, pp. 69–122.
- Korovchinsky, N. M., 1992. *Sididae & Holopediidae* (Crustacea: Daphniiformes). SPB Academic Publishing, The Hague.
- Koste, W., 1978. *Rotatoria. Die Rädertiere Mitteleuropas*. Gebr. Borntraeger, Berlin, Stuttgart: 673 pp. 234 plates.
- Kruk, C., V. I. M. Huszar, E. T. H. Peeters, S. Bonilla, L. Costa, M. Lürling, C. S. Reynolds & M. Scheffer, 2010. A morphological classification capturing functional variation in phytoplankton. *Freshwater Biology* 55: 614–627.
- Lepš, J., & P. Šmilauer, 1998. *Multivariate Analysis of Ecological Data*. Faculty of Biological Sciences, University of South Bohemia České Budejovice, Czech Republic: 110 pp.
- Litchman, E., M. D. Ohman & T. Kiørboe, 2013. Trait-based approaches to zooplankton communities. *Journal of Plankton Research* 35: 473–484.
- Longhi, M. L. & B. E. Beisner, 2010. Patterns in taxonomic and functional diversity of lake phytoplankton. *Freshwater Biology* 55: 1349–1366.

- Mano, H. & Y. Tanaka, 2016. Mechanisms of compensatory dynamics in zooplankton and maintenance of food chain efficiency under toxicant stress. *Ecotoxicology* 25: 399–411.
- Mason, N. W., F. Bello, D. Mouillot, S. Pavoine & S. Dray, 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science* 24: 794–806.
- McGill, B. J., B. Enquist, E. Weiher & M. Westoby, 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.
- Moisaner, P. H., E. McClinton & H. W. Paerl, 2002. Salinity effects on growth, photosynthetic parameters, and nitrogenase activity in estuarine planktonic cyanobacteria. *Microbial Ecology* 43: 432–442.
- Moss, B. R., 2009. *Ecology of Fresh Waters: Man and Medium, Past to Future*. Wiley.
- Moss, B. & R. T. Leah, 1982. Changes in the ecosystem of a guantrophic and brackish shallow lake in eastern England: potential problems in its restoration. *Internationale Revue der Gesamten Hydrobiologie* 67: 625–659.
- Nielsen, K. J., 2003. Nutrient loading and consumers: agents of change in open-coast macrophyte assemblages. *Proceedings of the National Academy of Sciences USA* 100: 7660–7665.
- Obertegger, U. & G. Flaim, 2015. Community assembly of rotifers based on morphological traits. *Hydrobiologia* 753: 31–45.
- Obertegger, U. & M. Manca, 2011. Response of rotifer functional groups to changing trophic state and crustacean community. *Journal of Limnology* 70: 231–238.
- Obertegger, U., H. A. Smith, G. Flaim & R. L. Wallace, 2011. Using the guild ratio to characterize pelagic rotifer communities. *Hydrobiologia* 662: 157–162.
- Ojaveer, H., L. A. Kuhns, R. P. Barbiero & M. L. Tuchman, 2001. Distribution and population characteristics of *Cerropagis pengoi* in Lake Ontario. *Journal of Great Lakes Research* 27: 10–18.
- Paerl, H. W. & J. Huisman, 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environmental Microbiology Reports* 1: 27–37.
- Paturej, E. & A. Gutkowska, 2015. The effect of salinity levels on the structure of zooplankton communities. *Archives of Biological Sciences* 67: 483–492.
- Pennak, R., 1991. *Fresh-Water Invertebrates of the United States*. Wiley Interscience, USA: 628.
- Quintana, X. D., S. Brucet, D. Boix, R. López-Flores, S. Gascón, A. Badosa, J. Sala, R. Moreno-Amich & J. J. Egozcue, 2008. A non-parametric method for the measurement of size diversity, with emphasis on data standardisation. *Limnology and Oceanography: Methods* 6: 75–86.
- Quintana, X. D., M. Arim, A. Badosa, J. M. Blanco, D. Boix, S. Brucet, J. Compte, J. J. Egozcue, E. de Eyto, U. Gaedke, S. Gascón, L. Gil de Solá, K. Irvine, E. Jeppesen, T. L. Lauridsen, R. López-Flores, T. Mehner, S. Romo & M. Søndergaard, 2015. Predation and competition effects on the size diversity of aquatic communities. *Aquatic Sciences* 77: 45–57.
- R Development Core Team, 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Reynolds, C. S., V. Huszar, C. Kruk, L. Naselli-Flores & S. Melo, 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research* 24: 417–428.
- Rodríguez-Gallego, L., V. Sabaj, S. Masciadri, C. Kruk, R. Arocena & D. Conde, 2015. Salinity as a major driver for submerged aquatic vegetation in coastal lagoons: a multi-year analysis in the subtropical Laguna de Rocha. *Estuaries and Coasts* 38: 451–465.
- Ruesink, J. L. & D. S. Srivastava, 2001. Numerical and per capita responses to species loss: mechanisms maintaining ecosystem function in a community of stream insect detritivores. *Oikos* 93: 221–234.
- Sarma, S. S. S., S. Nandini, J. Morales-Ventura, I. Delgado-Martínez & L. González-Valverde, 2006. Effects of NaCl salinity on the population dynamics of freshwater zooplankton (rotifers and cladocerans). *Aquatic Ecology* 40: 349–360.
- Schallenberg, M., C. J. Hall & C. W. Burns, 2003. Consequences of climate-induced salinity increases on zooplankton abundance and diversity in coastal lakes. *Marine Ecology Progress Series* 251: 181–189.
- Schindler, D. W., 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* 57: 25–41.
- Schmera, D., T. Erős & J. Podani, 2009. A measure for assessing functional diversity in ecological communities. *Aquatic Ecology* 43: 157–167.
- Shannon, C. E. & W. Weaver, 1964. *The Mathematical Theory of Communication*. University Illinois Press, Urbana, IL.
- Sheridan, J. A. & D. Bickford, 2011. Shrinking body size as an ecological response to climate change. *Nature Climate Change* 1: 401–406.
- Tavsanoglu, U. N., R. Maleki & N. Akbulut, 2015. Effects of salinity on the zooplankton community structure in two marine lakes and one freshwater lake in the Konya closed basin, Turkey. *Ekoloji* 24: 25–32.
- Ter Braak, C. J., 1994. Canonical community ordination. Part I: basic theory and linear methods. *Ecoscience* 1: 127–140.
- Ter Braak, C. J., & P. Smilauer, 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination, version 4.5*. www.canoco.com.
- Tolomeev, A. P., N. N. Sushchik, R. D. Gulati, O. N. Makhutova, G. S. Kalacheva & T. A. Zotina, 2010. Feeding spectra of *Arctodiaptomus salinus* (Calanoida, Copepoda) using fatty acid trophic markers in seston food in two salt lakes in South Siberia (Khakasia, Russia). *Aquatic Ecology* 44: 513–530.
- Tonk, L., K. Bosch, P. M. Visser & J. Huisman, 2007. Salt tolerance of the harmful cyanobacterium *Microcystis aeruginosa*. *Aquatic Microbial Ecology* 46: 117–123.
- Tönno, I., H. Agasild, T. Kõiv, R. Freiberg, P. Nõges & T. Nõges, 2016. Algal diet of small-bodied crustacean zooplankton in a cyanobacteria-dominated eutrophic lake. *PLoS one* 11: e0154526.
- Toruan, R. L., 2012. Zooplankton community emerging from fresh and saline wetlands. *Ecology & Hydrobiology* 12: 53–63.
- USEPA, 2002. National primary drinking water regulations. US Environmental Protection Agency, Washington, DC.

- Vandermeer, J., M. van Noordwijk, J. Anderson, C. Ong & I. Perfecto, 1998. Global change and multi-species agroecosystems: concepts and issues. *Agriculture, Ecosystems & Environment* 67: 1–22.
- Vaughn, C. C., 2010. Biodiversity losses and ecosystem function in freshwaters: emerging conclusions and research directions. *BioScience* 60: 25–35.
- Viayeh, R. M. & M. Špoljar, 2012. Structure of rotifer assemblages in shallow waterbodies of semi-arid northwest Iran differing in salinity and vegetation cover. *Hydrobiologia* 686: 73–89.
- Vogt, M., T. Hashioka, M. R. Payne, E. T. Buitenhuis, C. L. Quéré, S. Alvain, M. N. Aita, L. Bopp, S. C. Doney, T. Hirata, I. Lima, S. Sailley & Y. Yamanaka, 2013. The distribution, dominance patterns and ecological niches of plankton functional types in Dynamic Green Ocean Models and satellite estimates. *Biogeosciences Discussions* 10: 17193–17247.
- Waterkeyn, A., P. Grillas, B. Vanschoenwinkel & L. Brendonck, 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshwater Biology* 53: 1808–1822.
- Whittaker, R. H., 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–251.
- Williams, W. D., 1998. Salinity as a determinant of the structure of biological communities in salt lakes. *Hydrobiologia* 381: 191–201.