

An analysis of long-term winter data on phytoplankton and zooplankton in Neusiedler See, a shallow temperate lake, Austria

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Received: 6 June 2009 / Accepted: 29 July 2009
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Abstract In the last 40 years, the shallow steppe lake, Neusiedler See, was ice covered between 0 and 97 days. The North Atlantic Oscillation (NAO) as well as the Mediterranean Oscillation affected the lake and its conditions during winter. Both climate indices correlated negatively with the duration of ice cover and the timing of ice-out. Average winter phytoplankton biomass increased from less than 0.2 (0.05–0.84) mg FM l⁻¹ in the late 1960s/beginning of 1970s to 3.1 (1.72–5.61) mg FM l⁻¹ in the years 2001–2004. The increase in annual winter biomass of phytoplankton was associated with a significant shift in the composition of the algal assemblage. In the winter 1997/1998, diatoms contributed between 40 and 80% to the phytoplankton biomass while in 2006/2007 cyanoprokaryotes contributed 46%. Mean chlorophyll-*a* concentrations during winter were significantly correlated with those of total phosphorus (P_{tot}). Together with cold-water species (rotifer *Rhinoglena fertöensis*), perennial, eurythermal

ones (copepod *Arctodiaptomus spinosus*) contributed to the zooplankton community. High zooplankton numbers were encountered when rotifers, particularly when densities of *Rhinoglena fertöensis* were high ($r^2 = 0.928$). Zooplankton abundance and biomass varied from year to year but correlated positively with Chl-*a* (biomass – $r^2 = 0.69$; numbers – $r^2 = 0.536$). Winter zooplankton populations were primarily influenced by winter conditions, but in early winter also by survival of autumn populations, i.e., the more adults of *Arctodiaptomus spinosus* survived into winter, the higher was the zooplankton biomass in early winter. Phyto- and zooplankton dynamics in shallow lakes of the temperate region seem to critically depend on the biomass in autumn and on winter conditions, specifically on ice conditions and thus are related to climate signals such as the NAO.

Keywords Polymictic lake · Ice duration · Winter plankton · Abundance · Biomass · *Rhinoglena* · *Arctodiaptomus spinosus*

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Introduction

Limnological measurements during winter have some tradition in high altitude (high mountain) and high latitude (northern boreal) lakes which are usually ice covered for a substantial period of the year (Nauwerck 1963; Pechlaner 1971). Early information on winter

phytoplankton opened conflicting questions about the importance of autotrophic production and the significance of mixotrophic or heterotrophic growth under the ice (Rodhe 1955; Wright 1964). Optimizing light harvesting through active upward migration, a switch to heterotrophic nutrition as well as the period prior and during the melting period turned out to be particularly important for the survival of species under the ice (Phillips and Fawley 2002; Forsström et al. 2007).

In the temperate regions of the world, the winter season has long been believed to be less important, because biological processes are known to cease or run at low rates (Talling 1962). Due to intensified research on permanently ice-covered lakes in the Antarctic and Arctic, the interest in winter limnology also has increased in other parts of the world (e.g., Agbeti and Smol 1995). Investigations of climatic impacts on European lakes (e.g., George 2009) substantiated the importance of winter for the seasonality of the plankton especially in shallow lakes with variable ice cover.

Here, we analyze long-term winter data (December, January, February) on phytoplankton and zooplankton from a shallow, alkaline turbid lake, Neusiedler See, Austria. These data originate from long-term observations conducted on this lake since 1968 mainly by the Biological Station at Illmitz very near Neusiedler See. The study explores the changes in ice duration annually over the past 40 years in relation to climate change. The long-term qualitative and quantitative development of phytoplankton is described in the light of nutrients and changing ice conditions and durations. The long-term development of zooplankton is described and discussed with respect to changing food conditions. Finally, a comparison of winter zooplankton data for 16 European lakes is presented.

Study site

Neusiedler See is the largest (315 km²) lake of Austria, situated in the lowest plain of the country at 116 m a.s.l (Table 1). It is a shallow, well-mixed lake, which is composed of two different habitat types: the open water zone and a *Phragmites* belt (178 km²). Within the reed cover, the water is not turbid due to less exposure to wind and brown in color due to humic substances. Owing to the fine lake

Table 1 Geographical position, morphological and hydrological characteristics of Neusiedler See (116 m a.s.l.)

Latitude	47°38′–47°57′
Longitude	16°41′–16°52′
Elevation (m)	116
Area (km ²)	315
Volume (10 ⁶ m ³)	368
Mean depth (m)	1.2
Maximum depth (m)	1.8
Retention time (year)	1.5
Catchment area (km ²)	1120

sediments, its shallowness and exposure to wind, the open lake is characterized by a high concentration of suspended solids. During winter, when the lake is ice covered, suspended solids decline due to the absence of turbulences. The lake is characterized by large annual variations in temperature ranging from 28°C in summer to 0°C during winter immediately under ice, and by high alkalinity (7.5–14.6 meq l⁻¹) and a conductivity of 130–320 mS m⁻¹ (Löffler 1979).

For the past 40 years, four phases of lake development can be identified from the yearly phenology of total phosphorus, phytoplankton biomass, chlorophyll-*a* and zooplankton (Herzig and Dokulil 2001). In the early 1960s, low to moderate phosphorus levels were associated with average phytoplankton biomass of 500–1500 mg FM (fresh mass) m⁻³ and mean annual chlorophyll-*a* values of 4–8.5 mg m⁻³ (Dokulil 1984). The corresponding mean annual zooplankton biomass ranged between 56 and 126 mg DM (dry mass) m⁻³ (Herzig 1979). In the late 1960s and 1970s, Neusiedler See suffered from high nutrient loadings of anthropogenic origin, mainly from sewage and agriculture. Total phosphorus levels (Total-P) increased dramatically, reaching an annual mean of 160 mg m⁻³ in 1979. While nutrients increased by an order of magnitude, phytoplankton biomass doubled (maximum 3.2 g FM m⁻³ corresponding 18 mg m⁻³ chlorophyll-*a*) which led to a pronounced increase in zooplankton (annual means ranging from 295 to 724 mg DM m⁻³) as well as cyprinid fish biomass (Herzig and Dokulil 2001).

In the mid-1980s, the external restoration measures taken in the catchment area (i.e., sewerage, sewage treatment plants) led to a steady decrease in total phosphorus. This third phase was characterized by a

recovery from eutrophication after 1986 (Herzig and Dokulil 2001). Annual mean total phosphorus concentrations declined to 100 mg m^{-3} finally reaching 50 mg m^{-3} in the late 1990s. At the same time, annual mean chlorophyll-*a* concentration decreased to $7\text{--}8 \text{ mg m}^{-3}$, but still with a pronounced variation. Phytoplankton biomass changed little but zooplankton biomass decreased to a level comparable with the time before eutrophication ($124\text{--}561 \text{ mg DM m}^{-3}$), because planktivorous fish and their predation pressure on zooplankton remained at a very high level. The fourth phase, from the mid-1990s until 2006, was characterized by again increasing total phosphorus concentration, phytoplankton biomass and chlorophyll-*a*, and zooplankton biomass remaining on a low level (range of yearly means for the period 1998–2006: $60\text{--}95 \text{ mg P m}^{-3}$, $3000\text{--}4000 \text{ mg FM m}^{-3}$, $4.3\text{--}8.2 \text{ mg Chl-}a \text{ m}^{-3}$ and $80\text{--}128 \text{ mg DM m}^{-3}$, respectively; Herzig and Dokulil 2001; and Herzig unpublished results).

Methods

Sampling

In Neusiedler See, phytoplankton and zooplankton have been monitored since 1968. Even though sampling in winter is difficult and sometimes virtually impossible because of varying and unsafe ice conditions, we managed to sample during 27 winters of the 40 years investigated. The sampling program and sampling gear are described in detail for the period 1968–1979 in Herzig (1979) and Dokulil (1984). Samples for phytoplankton and zooplankton enumeration were collected with a 5-l Schindler sampler in the years 1986–2007.

During the open water season, zooplankton was concentrated by filtering the water through a $40 \mu\text{m}$ bolting sieve. Samples for the determination of zooplankton biomass were collected with vertical net hauls (mesh size $40 \mu\text{m}$). It resulted in integrated samples (bottom to surface), filtering $50\text{--}120 \text{ l}$ lake water (depending on water depth); as most of the inorganic particles and algae were $<20 \mu\text{m}$ the net was not clogged. In the period of ice cover, the lake was sampled with a 5-l Schindler sampler at three discrete depths from $0\text{--}50$, $50\text{--}100$ and $100\text{--}150 \text{ cm}$.

From 1987 onwards, the lake was sampled weekly at four stations and at 6–10 stations which included the four weekly sampling stations once a month. In the period of ice formation or melting, the sample intervals were sometimes up to 4 weeks. Data obtained from all sampling stations of a sampling date were averaged. All statistical calculations were performed with ln-transformed values because the Kolmogorov–Smirnov test for normality failed. Regression analysis, Spearman rank correlation analysis and ANOVA were performed using Abacus Concepts StatView software (zooplankton) or SigmaStat 3.2 (phytoplankton, chlorophyll-*a*).

Samples for phytoplankton enumeration were preserved with $400 \mu\text{l}$ Lugol's solution in brown 100-ml glass bottles which were stored in the dark at 4°C until counting. Cell numbers were estimated by counting taxonomic units on an inverted microscope using the sedimentation technique developed by Utermöhl (1958). Cell dimensions were measured on at least 20 individuals of each taxon, and cell volumes were calculated using simple geometric approximations (Rott 1981; Hillebrand et al. 1999; Pohlmann and Friedrich 2001). Biovolumes were estimated by multiplying abundances by mean cell volumes. For converting to biomass (FM), we assumed a specific density of one. Chlorophyll-*a* was determined spectrophotometrically after acetone extraction (Lorenzen 1967).

Zooplankton samples were counted under an inverted dissecting microscope. All species, developmental stages and eggs were counted. Total zooplankton biomass was determined from material retained on a $40 \mu\text{m}$ net which was dried at 105°C for 24 h and then weighed.

Population growth rates (r) for the dominant winter rotifer *Rhinoglena fertöensis* were calculated assuming exponential growth, according to

$$r = (\ln N_t - \ln N_0) / t \quad (1)$$

with N_0 equals the initial population size, N_t the final population size and t the time between the two observations. Its birth rates (b) were calculated using Paloheimo's model (1974)

$$b = \ln(E + 1) / D_e \quad (2)$$

where E is the egg ratio (mean number of eggs per female) and D_e is the embryonic development time in days. The embryonic development times were

calculated using the experimentally defined relationship between water temperature (T) and development time (D_e) (for the temperature range of 1–12°C, Herzig 1983b)

$$D_e = 101/(T + 5)^{1.49} \quad (3)$$

The death rates (d) of *Rhinoglena fertöensis* were calculated by the formula

$$d = b - r. \quad (4)$$

Ice development and climatic data

Freezing was defined as the period when >80% of the lake was ice covered including days of temporary ice formation. Ice duration therefore corresponds to the number of days when >80% of the lake was covered with ice.

Temperature data were obtained from the meteorological monitoring by the Biological Station Neusiedler See. Values for the North Atlantic Oscillation (NAO) and the Arctic Oscillation (AO) were taken from <http://www.cpc.noaa.gov/products/precip/CWlink/pna/nao.shtml>. The index of the Mediterranean Oscillation (MOI) was defined according to Sušelj and Bergant (2006), and values were extracted from <http://www.cru.uea.ac.uk/~andrewh/moi.html>.

Results

Winter conditions

Neusiedler See is situated in a region which has a more continental, Pannonian climate compared with other parts of Austria. As a consequence, winter temperatures can be quite low. Over the last 40 years from 1968 to 2008, ice duration ranged from a maximum of 116 days in 1969–1970 to no ice in winter 2006–2007. Average ice duration was 56 (median 51) days. Although inter-annual variation was large, a tendency of ice duration to decline at a rate of ca. 1 day per year could be deduced (Fig. 1). Observations for the period 1928 to 1950, summarized by Eckel (1953), indicate ice duration between 21 and 105 days. Both ice duration and timing of ice-out (Table 2) were significantly influenced by long distance climate signals from the north–west by the North Atlantic Oscillation, NAO, and the Arctic

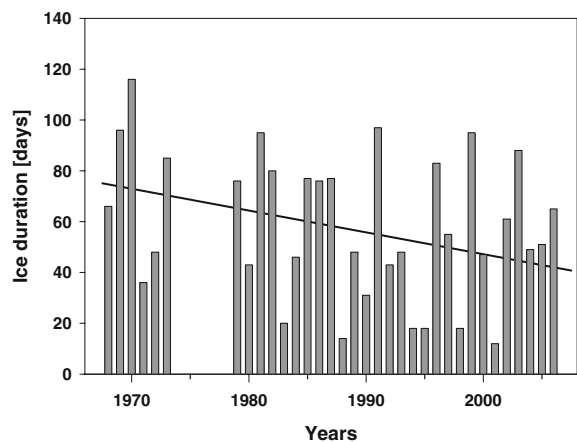


Fig. 1 Duration of ice cover in Neusiedler See for the years 1968–2007. The regression line indicates the general trend (Biological Station Neusiedler See, unpublished data)

Oscillation, AO, but also from the south by Mediterranean Oscillation, MOI (Table 3).

Winter phytoplankton

The number of species in the phytoplankton assemblages during winter did not differ much from those in autumn (Table 4). Total winter phytoplankton fresh biomass considerably increased from 0.1 mg l^{-1} in the late 1960s to around $2 \text{ mg l}^{-1}</math> between 2001 and 2005 (Fig. 2a). The increase in winter phytoplankton biomass was associated with a significant shift in the composition of the algal assemblage from diatom dominated to cyanoprokaryote dominated (Fig. 2b) while flagellated cells remained at almost the same biomass as before. In the winters of 1968–1972, diatom contribution was 40–80% of biomass which since then declined to the recent average of 12%. Contribution of cyanoprokaryotes has increased from an average of <math><1\text{--}4.7\%</math> in the 1980s and early 1990s and finally reached a mean share of 46% between the winters 1997/1998–2006/2007. In these recent winters, the assemblage of the cyanoprokaryotes became dominated by the colonial, small celled species *Aphanocapsa incerta*, a species commonly ascribed to the picoplankton. In addition, thin filamentous cyanobacterial genera, *Oscillatoria* and *Anabaena*, became more significant while centric diatoms declined in importance. Several species of chlorococcalean green-algae such as *Monoraphidium pseudobraunii*, *Oocystis lacustris* or *Pediastrum*$

Table 2 Dates of ice formation and ice-out in Neusiedler See for two observation periods

	1928–1950			1968–2008			Balaton 1932–2006		
	Earliest	Mean	Latest	Earliest	Mean	Latest	Earliest	Mean	Latest
Ice-in	26.11	13.12	08.01	19.10	15.12	12.02	1.12	31.12	19.02
Ice-out	05.12	16.02	26.03	25.12	22.02	24.03	11.01	25.02	28.03

Data for 1928–1950 from Eckel (1953); Data from Lake Balaton 1932–2006 (Vörös et al. 2009; Padisák personal communication) are shown for comparison

Table 3 Relationship between ice conditions in Neusiedler See and Lake Balaton with winter North Atlantic Oscillation (NAO), Arctic Oscillation (AO) and Mediterranean Oscillation Index (MOI)

Lake	Ice	NAO	AO	MOI
Neusiedler See	Duration	−0.451*	NS	−0.503*
	Ice-out	−0.511**	−0.461*	−0.650**
Lake Balaton	Duration	−0.261*	NS	−0.381*
	Ice-out	−0.528***	−0.323**	−0.486**

Significance levels of correlation coefficients *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns not significant

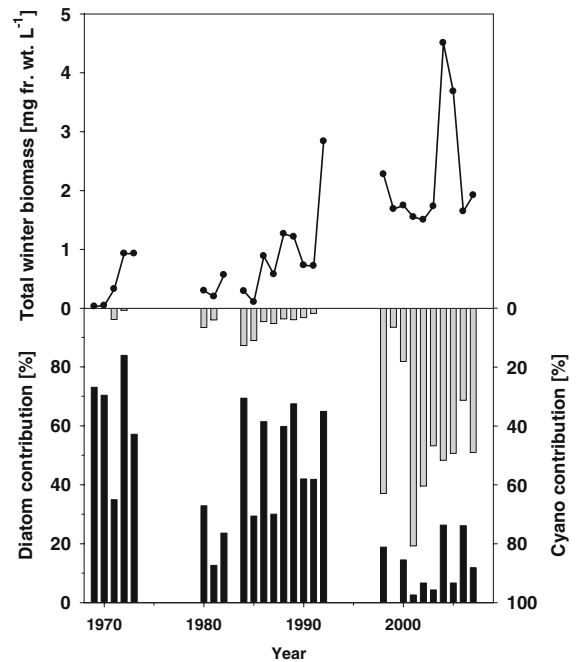
Table 4 Dependence of species number in different algal groups in winter on species number in autumn (September–November); $N = 22$

Algal group	Slope	Adjusted r^2	P
Cyanoprokaryota	0.762	0.55	<0.001
Cryptophyta	0.908	0.58	<0.001
Bacillariophyta	0.886	0.74	<0.001
Chlorophyta	0.803	0.72	<0.001

duplex contributed considerably to green-algal biomass in the winters of 2000/2001–2004/2005.

The maximum phytoplankton biomass of 4.5 mg l^{-1} was observed in the winter 2003/2004. Winter biomass depends inversely on ice duration. It seemed to be highly variable and unpredictable when ice cover lasted for 0–50 days, but duration longer than 50 days led to a significant reduction in total winter biomass (Pearson correlation $r^2 = 0.37$, $n = 17$, $P = 0.01$).

Winter mean chlorophyll-*a* concentrations were significantly related to total phosphorus (P_{tot}) and directly depended on ice duration (Fig. 3). Average concentrations of chlorophyll-*a* in winter was lower when ice cover was <20 days ($\text{Chl-}a = -3.79 + 0.083 P_{\text{tot}}$, $r^2 = 0.97$, $n = 4$, $P = 0.0163$) compared with those in years with ice between 20 and 60 days

**Fig. 2** a Phytoplankton biomass in Neusiedler See for the winters 1968/1969–2006/2007. b Contribution of diatoms (black columns) and cyanoprokaryotes to total biomass (Biological Station Neusiedler See, unpublished data)

($\text{Chl-}a = 3.92 + 0.082 P_{\text{tot}}$, $r^2 = 0.78$, $n = 10$, $P = 0.0002$). At durations longer than 60 days, $\text{Chl-}a$ was highly variable and unpredictable, strongly depending on ice conditions.

Winter zooplankton

Both cold-water species and perennial, eurythermal species contributed to the zooplankton community. Rotifer plankton consisted of 10–15 species. *Brachionus calyciflorus*, *Keratella cochlearis*, *K. quadrata*, *Notholca acuminata*, *Polyarthra dolichoptera*, *Synchaeta tremula-oblonga* group and, above all, *Rhynoglena fertöensis* were generally dominating. Only

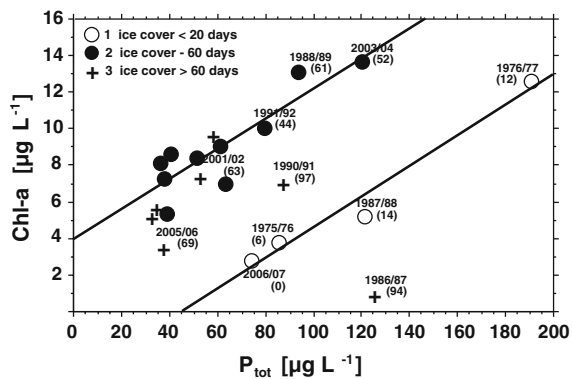


Fig. 3 Relation of winter chlorophyll-*a* on total phosphorus concentrations in Neusiedler See. The ice duration and the corresponding year are indicated in the graph (Biological Station Neusiedler See, unpublished data)

in the years 1968–1972 and 1995–2001, when *Synchaeta tremula-oblonga*, *Keratella quadrata* and *K. cochlearis* dominated, high densities of rotifers in winter coincided with a successful population development of *Rhinoglena* comprising in such winters 86–100% of the rotifer densities.

The crustacean plankton consisted of copepods with the eurythermal *Arctodiaptomus spinosus* attaining 50–96% of individual numbers, and nauplii and copepodid stages of cyclopoids (mainly *Acanthocyclops robustus*).

For comparison, an analysis of zooplankton communities of 16 European lakes from latitudes between 60°N and 44°N revealed the presence of 20–25 species, 2–5 rotifers and 1–3 copepods being the dominant species (Table 5).

Maximum zooplankton numbers occurred in winter 1999/2000 with 439 ind l⁻¹, lowest in winter 2003/2004 with 24 ind l⁻¹. Highest dry biomass was measured in 1987–1988 (183 mg m⁻³), the lowest during 1968–1971 (15 mg m⁻³). Like in the other seasons, a steady increase in densities and biomass ($r^2 = 0.687$; $P < 0.013$) occurred from 1968 to 1979 (Fig. 4). It correlated well with the increase in phytoplankton biomass (Chl-*a*, $r^2 = 0.662$; $P < 0.016$). In 1987–2006 (abundances and) biomasses decreased (Fig. 4) ($r^2 = 0.293$; $P < 0.01$).

In Neusiedler See, a significant positive relationship was found between the autumnal and winter zooplankton biomasses (multiple regression of ln winter zooplankton biomass vs. ln Chl-*a* and ln autumn zooplankton biomass: $r^2 = 0.831$; $P < 0.0001$). Such

Table 5 Relative occurrence (%) of Rotifera and Crustacea in winter zooplankton of European lakes from latitudes 60°N–44°N ($n = 16$ lakes; dominating species in bold)

<i>Keratella cochlearis</i>	93	<i>Eudiaptomus gracilis</i>	92
<i>Polyarthra dolichoptera</i>	87	<i>Cyclops abyssorum</i>	46
<i>Kellicottia longispina</i>	67	<i>Cyclops vicinus</i>	46
<i>Keratella quadrata</i>	60	<i>Cyclops strenuus</i>	23
<i>Synchaeta tremula-oblonga</i>	40	<i>Eudiaptomus graciloides</i>	15
<i>Conochilus unicornis</i>	33	<i>Acanthocyclops robustus</i>	15
<i>Synchaeta pectinata</i>	33	<i>Daphnia</i> spp.	15
<i>Filinia terminalis</i>	20	<i>Eubosmina longispina</i>	15
<i>Notholca</i> spp.	20	<i>Eudiaptomus vulgaris</i>	8
<i>Synchaeta verrucosa</i>	7	<i>Macrocyclus albidus</i>	8
<i>Trichocerca</i> sp.	7	<i>Bosmina longirostris</i>	8
		<i>Ceriodaphnia quadrangula</i>	3

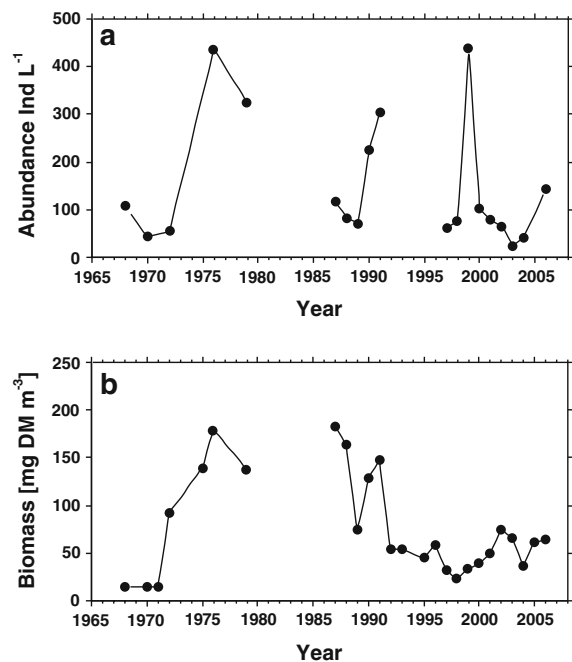


Fig. 4 Mean winter (December–February) zooplankton abundance **a** and dry biomass **b** in Neusiedler See for the years 1968–1980 and 1987–2006 (Biological Station Neusiedler See, unpublished data)

a relationship was less significant for zooplankton numbers ($r^2 = 0.161$; $P < 0.0858$).

High zooplankton numbers were always associated with high abundances of *Rhinoglena*. To detect possible reasons for success or failure of the *Rhinoglena* population, birth and death rates were

Table 6 Spearman rank correlations of the birth and death rates of *Rhinoglena fertöensis* with some environmental factors

	Birth rate	Death rate
$T^{\circ}\text{C}$	0.63***	0.573***
Chlorophyll- <i>a</i>	0.296*	0.188*
Phytoplankton biomass	0.631***	0.145
Nauplii	0.199*	0.521***
Nauplii + Synchaeta	0.221*	0.429***
Cyclopidae (ad + cop)	0.162	0.391**

Levels of significance as in Table 3

calculated and related to temperature, food and potential competitors and predators. According to a Spearman rank correlation analysis (Table 6), water temperature had a highly significant influence on birth and death rates. Below 6°C, an increase in water temperature resulted in a decrease in development times and increase in birth rates. Above 8°C, death rates increased with increasing temperatures. Phytoplankton biomass and *Rhinoglena* birth rates correlated highly significantly reflecting the positive influence of improving food conditions on this rotifer. High numbers of copepod nauplii and *Synchaeta* coincided with higher death rates of *Rhinoglena* pointing to possible competitive advantage during the latter's mortality. A significant correlation between death rates and the occurrence of copepodids and adults of cyclopoids, which are known as potential predators (Brandl 2005) strengthens the idea of predatory impact (Table 6).

Discussion

The dominating algal groups during winter were diatoms and increasingly cyanoprokaryotes represented by small colonial and thin filamentous forms. Variation between years was high because small chlorococcalean chlorophytes were also abundant in certain years possibly due to better light conditions. In shallow lakes, small chrysophytes, dinoflagellates, centric diatoms and chlorophytes contribute significantly to phytoplankton biomass (e.g., Agbeti and Smol 1995; Phillips and Fawley 2002).

Cryptomonas and *Plagioselmis* (*Rhodomonas*) cryptophytes often dominate the phytoplankton assemblage in Neusiedler See during winter. This is partly due to their ability of heterotrophic growth

(e.g., Wright 1964; Danilov and Ekelund 2001; Morabito et al. 2002). On the other hand, under the ice, motility of phytoplankton is advantageous because cells can adjust their position in the water column according to light and nutrient availability (e.g., Nauwerck 1963). However, in Neusiedler See, the contribution of flagellated algal cells in winter did not significantly differ from the other seasons.

A dramatic increase in algal biomass during winter was associated with a change from diatoms and cryptophytes to cyanoprokaryotes similar to that reported for Heiligensee, Germany by Adrian et al. (1995). To a large extent, the increase in algal winter biomass was associated with either milder winters, or shorter ice duration or better light conditions under clear ice. Relative light penetration decreased under the ice (Dokulil 1979) because suspended solids settled out leading to clear water and light penetration to the bottom. The growth of algae during the winter months can be as active as during the summer months (Tryfiates 1960; Reitner et al. 1997). Both planktonic and benthic primary production are quite considerable under clear ice and minimal when the ice is snow covered in Neusiedler See (Dokulil 1984) similar to observations in Lake Balaton (Herodek and Tamás 1975; Dokulil 1984).

Ice duration can strongly influence plankton succession in polymictic lakes like Neusiedler See (e.g., Adrian et al. 1999). Increased chlorophyll-*a* concentration under the ice when the ice cover lasts longer as observed in this study has also been reported by, for example, Leßmann et al. (2003) from lakes in Germany. The large variability of Chl-*a* concentration in Neusiedler See during ice-period >60 days largely reflected variable ice conditions. Patchy snow on the ice will create large spatial differences in under-water light conditions and hence Chl-*a* values (Leppäranta et al. 2003; Leppäranta 2009). Clear ice and hence more available light in the water column can enhance algal growth particularly supporting benthic algae which are usually insignificant during the open water season due to turbidity (Herodek and Oláh 1973; Schiemer 1979; Dokulil 2008).

Ice duration on Neusiedler See is similar to that on Lake Balaton where, on average, there are 52 days of ice cover, which ranges from no ice to a maximum of 110 days (Vörös et al. 2009, Dr. J. Padisák, personal communication). Mean and latest date of ice-out does not differ significantly between the two lakes.

The duration of ice cover and the timing of ice-in/ice-out were strongly influenced by changes in the climate across Europe (Livingstone 2000; Livingstone et al. 2008; Weyhenmeyer et al. 2004) and the Northern Hemisphere (Livingstone 1999; Jensen et al. 2007). Altitude above sea level and latitude also determine the existence or duration of ice cover even in large lakes like Lake Ladoga (Assel and Herche 1998; Šporka et al. 2006; Karetnikov and Naumenko 2008).

Winter zooplankton in Neusiedler See was composed of cold-water and eurythermal species. Species composition and dominance of 16 European lakes with sufficient information about winter plankton correspond quite well with observation on Neusiedler See although the lakes vary markedly in size, depth and trophic status (see Table 5; lakes are presented in Tables 7, 8). Long-term data of rotifer communities for Neusiedler See reveal that each year can be characterized by a few dominant species, which may differ annually (cf. Lago di Mergozzo, Piburger See

and Neusiedler See, Herzig 1987 and present paper; Lake Constance, Walz et al. 1987; Lough Neagh, Andrew and Fitzsimons 1992).

As Neusiedler See has both high alkalinity and high conductivity, its species composition differs from the other European lakes. For example, although the same rotifer species prevail in this lake as in other European lakes, the winter plankton is dominated by the rotifer *Rhinoglena fertöensis*, a cold stenothermic specialist species inhabiting athalassic (i.e., non-marine) saline water bodies, in most years since the 1980s. The dominating calanoid copepod, *Arctodiaptomus spinosus*, is a typical crustacean of sodium lakes and an eurythermal species reproducing at a wide range of temperatures (0.8°C and 28°C: Herzig 1983a).

Winter zooplankton populations are probably primarily influenced by factors operating during winter. Nevertheless, the abundances and biomasses at the beginning of winter also depend on the survival of autumn populations; i.e., the more adult or copepodid stages IV and V of *Arctodiaptomus spinosus* survive

Table 7 Mean abundance (individuals l^{-1}) of rotifer and crustacean zooplankton in some European lakes from latitudes 44°N–60°N with different trophic status in December–February

Lake	Trophic status	Rotifera	Crustacea	Reference
Stechlinsee	Oligo	13	2	Kasprzak and Ronneberger (1982)
Ammersee	Oligo/meso	15	17	Morscheid (1999)
Grundlsee	Oligo	10	5	Herzig (2001)
Lago di Mergozzo, 1948/1950	Oligo	3	2	Herzig (1987)
Lago di Mergozzo, 1969/1970	Oligo	17	1	Herzig (1987)
Lago di Mergozzo 1975	Oligo	37	2	Herzig (1987)
Piburger See 1971/1973	Meso	570	5	Herzig (1987)
Piburger See, 1973/1976	Meso	60	8	Herzig (1987)
Ossiacher See	Meso	19	4	Herzig (2001)
Vortsjärvi	Eu	142	64	Haberman and Virro (2004)
Lough Neagh	Eu	37	17	Fitzsimons and Andrew (1993)
Farmoor I Reservoir	Eu	20	55	Jones et al. (1979)
Mindelsee	Eu	103	45	Einsle (1983)
Fischkalter See	Eu	1266	26	Schrimpf (1994)
Reither See	Eu	160	19	Schrimpf (1994)
Lago d'Endine, 1972/1974	Eu	148	60	Barbanti et al. (1974)
Neusiedler See, 1970	Meso	16	26	Herzig (1987)
Neusiedler See, 1976	Eu	337	99	Herzig (1987)
Neusiedler See, 1988	Meso	10	73	Present paper
Neusiedler See, 1990	Meso	108	118	Present paper
Neusiedler See, 1999	Meso	366	73	Present paper
Neusiedler See, 2004	Meso	3	39	Present paper

Table 8 Mean winter (December–February) zooplankton biomass (μg dry mass l^{-1}) in some European lakes from latitudes 44°N – 56°N with different trophic status in December–February

Lake	Trophic status	Biomass	Reference
Stechlinsee	Oligo	4	Kasprzak and Ronneberger (1982)
Ammersee	Oligo/meso	22	Morscheid (1999)
Grundlsee	Oligo	47	Herzig (2001)
Lago Maggiore	Oligo	11	Ravera (1969)
Ossiacher See	Meso	30	Herzig (2001)
Lake Esrom	Eu	43	Bosselmann (1974)
Frederiksborg Slotssø	Eu	300	Andersen and Jacobsen (1979)
Haussee	Eu	85	Kasprzak and Ronneberger (1982)
Fischkalter See	Eu	180	Schrimpf (1994)
Reither See	Eu	36	Schrimpf (1994)
Lago d'Endine, 1972/1974	Eu	565	Barbanti et al. (1974)
Neusiedler See, 1968–1972	Meso	70	Present paper
Neusiedler See, 1975–1979	Eu	210	Present paper
Neusiedler See, 1987–1991	Meso	147	Present paper
Neusiedler See, 1992–1996	Meso	64	Present paper
Neusiedler See, 1997–2000	Meso	32	Present paper
Neusiedler See, 2001–2006	Meso	59	Present paper

into winter, the higher the early winter biomass. In Neusiedler See, this is indicated by the significant, positive relationship between the autumnal zooplankton biomass and the winter biomass and a less significant relationship for total zooplankton densities.

The stock of rotifers, especially *Rhinoglena fertöensis*, was primarily influenced by the actual winter situation, i.e., mainly food quantity and quality. *Rhinoglena* is a filter feeder which prefers small, unicellular algae such as *Cryptomonas* spp., *Plagioselmis* (*Rhodomonas*) sp., *Chlamydomonas* spp., *Oocystis* sp. or *Scenedesmus* spp. In years, with winter phytoplankton offering such food quality, *Rhinoglena* reached densities of 2000 individuals l^{-1} (Herzig 1980). Since 2001, *Rhinoglena* has not reach comparable high numbers as in the 1980s and 1990s. This seems to be caused by food conditions, i.e., much higher relative contribution of cyanoprokaryotes of the genera *Oscillatoria* and *Anabaena* to the phytoplankton biomass which are less edible for *Rhinoglena* (Herzig 1980).

A comparison of the abundance and biomass of winter zooplankton in Neusiedler See with a number of European lakes of varying area, depth and trophic status (Tables 7, 8) leads us to draw a few generalizations. First, if food quality and quantity are good, i.e., cryptophytes prevail and winter mean Chl-*a* is $>4.5 \text{ mg m}^{-3}$, some cold-water and eurythermal

rotifer species will quickly develop high densities. Moreover, abundance and biomass of zooplankton are quite variable from year to year, e.g., in Piburger See, Neusiedler See, Lago di Mergozzo and Lough Neagh but their values correlate with the trophic status of the lakes. In this respect, an ANOVA (Bonferroni/Dunn test) reveals that oligotrophic and meso/eutrophic lakes significantly differ in the densities of rotifers ($P < 0.0327$) and crustaceans ($P < 0.0001$) as well as zooplankton total biomass ($P < 0.0106$). Unfortunately, detailed phytoplankton and bacterioplankton data are not available for all lakes and years.

We conclude that phytoplankton and zooplankton dynamics in shallow lakes of the temperate region depends on both the biomass in autumn and the winter conditions, specifically ice cover. Ice duration and ice conditions in turn are strongly influenced by climate change. The impact of the winter conditions on biological processes in shallow lakes is critical for the spring situation, but its effect is modified by changes in prevailing weather conditions (Gerten and Adrian 2000).

Acknowledgments The continuous support of the staff of the Biological Station Neusiedler See (especially R. Haider, R. Klein, F. Rauchwarter and R. Schalli) is gratefully acknowledged. We thank H. Krisa who did the phytoplankton counts and biomass calculations since 1995. The comments of the reviewers are acknowledged; they helped to improve the manuscript.

References

- Adrian R, Deneke R, Mischke U, Stellmacher R, Lederer P (1995) A long-term study of the Heiligensee (1975–1992). Evidence for effects of climatic change on the dynamics of eutrophied lake ecosystems. *Arch Hydrobiol* 133:315–337
- Adrian R, Walz N, Hintze T, Hoeg S, Rusche R (1999) Effects of ice duration on plankton succession during spring in a shallow polymictic lake. *Freshwat Biol* 41:621–623
- Agbeti MD, Smol JP (1995) Winter limnology: a comparison of physical, chemical and biological characteristics in two temperate lakes during ice cover. *Hydrobiologia* 304:221–234
- Andersen JM, Jacobsen OS (1979) Production and decomposition of organic matter in eutrophic Frederiksborg Slotssø, Denmark. *Arch Hydrobiol* 85:511–542
- Andrew TE, Fitzsimons EM (1992) Seasonality, population dynamics and production of planktonic rotifers in Lough Neagh, Northern Ireland. *Hydrobiologia* 24:147–164
- Assel RA, Herche LR (1998) Ice-on, ice-off, and ice duration for lakes and rivers with long-term records. In: Shen HT (ed) *Ice in surface waters*. Proc 14th international symposium on Ice, Potsdam, USA, Balkema, Rotterdam, pp 147–151
- Barbanti L, Bonacina C, Calderoni A, Carollo A, de Bernardi R, Guilizzoni P, Nocentini AM, Ruggiu D, Saraceni C, Tonolli L (1974) Indagini ecologiche sul Lago d'Endine. Edizioni dell'Istituto Italiano di Idrobiologia Verbania, Pallanza
- Bosselmann S (1974) The crustacean plankton of Lake Esrom. *Arch Hydrobiol* 74:18–31
- Brandl Z (2005) Freshwater copepods and rotifers: predators and their prey. *Hydrobiologia* 546:475–489
- Danilov RA, Ekelund GA (2001) Phytoplankton communities at different depths in two eutrophic and two oligotrophic temperate lakes at higher latitude during the period of ice cover. *Acta Protozool* 40:197–201
- Dokulil M (1979) Optical properties, colour and turbidity. In: Löffler H (ed) *Neusiedlersee: the limnology of a shallow lake in central Europe*. Monographiae Biologicae, vol 37. Dr. W. Junk bv Publishers, The Hague, pp 151–167
- Dokulil M (1984) Assessment of components controlling phytoplankton photosynthesis and bacterioplankton production in a shallow, alkaline, turbid lake (Neusiedlersee, Austria). *Int Rev ges Hydrobiol* 69:679–727
- Dokulil M (2008) Comparative primary production. In: Likens GE (ed) *Encyclopedia of inland waters*. Elsevier, San Diego in print
- Eckel O (1953) Zur Thermik des Neusiedlersees. *Wetter Leben* 5:72–78
- Einsle U (1983) Die Limnologie des Mindelsees. In: *Der Mindensee bei Radolfzell*. Monographie eines Naturschutzgebietes auf dem Bodanrück, Natur- und Landschaftsschutzgebiete Baden-Württemberg 11:161–218
- Fitzsimons AG, Andrew TE (1993) The seasonal succession of the zooplankton of Lough Neagh. In: Wood RB, Smith RV (eds) *Lough Neagh: the ecology of a multipurpose water resource*, vol 69. Kluwer, Dordrecht, Boston London, pp 281–326 Monographiae Biologicae
- Forsström L, Sorvari S, Rautio M, Sonninen E, Korhola A (2007) Changes in physical and chemical limnology and plankton during the spring melt period in a Subarctic Lake. *Internat Rev Hydrobiol* 30:1–325
- George GE (2009) The impact of climate change on European lakes. Springer, Berlin in print
- Gerten D, Adrian R (2000) Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic oscillation. *Limnol Oceanogr* 45:1058–1066
- Haberman J, Virro T (2004) Zooplankton. In: Haberman J, Pihu E, Raukas A (eds) *Lake Võrtsjärv*. Estonian Encyclopaedia Publishers, Tallin, pp 233–251
- Herodek S, Oláh J (1973) Primary production in the frozen Lake Balaton. *Annal Biol Tihany* 40:197–201
- Herodek S, Tamás G (1975) Phytoplankton production in Lake Balaton. *Symp Biol Hung* 15:29–34
- Herzig A (1979) The zooplankton of the open lake. In: Löffler H (ed) *Neusiedlersee. The limnology of a shallow lake in Central Europe*, vol 37. Dr. W. Junk bv Publishers, The Hague, pp 281–335 Monographiae Biologicae
- Herzig A (1980) Ten years quantitative data on a population of *Rhynchocystis* (*Brachionidae*, Monogononta). *Hydrobiologia* 73:161–167
- Herzig A (1983a) The ecological significance of the relationship between temperature and duration of embryonic development in planktonic freshwater copepods. *Hydrobiologia* 100:65–91
- Herzig A (1983b) Comparative studies on the relationship between temperature and duration of embryonic development of rotifers. *Hydrobiologia* 104:237–246
- Herzig A (1987) The analysis of planktonic rotifer populations: a plea for long-term investigations. *Hydrobiologia* 147:163–180
- Herzig A (2001) Zooplankton. In: Dokulil M, Hamm A, Kohl J-G (eds) *Ökologie und Schutz von Seen*. Facultas UTB, Wien, pp 132–161
- Herzig A, Dokulil M (2001) Neusiedler See—ein Steppensee in Europa. In: Dokulil M, Hamm A, Kohl J-G (eds) *Ökologie und Schutz von Seen*. Facultas UTB, Wien, pp 401–415
- Hillebrand H, Dürselen CD, Kirschtel D, Pollinger U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. *J Phycol* 35:403–424
- Jensen OP, Benson BJ, Magnuson JJ, Card VM, Futter MN, Sorrano PA, Stewart KM (2007) Spatial analysis of ice phenology trends across the Laurentian Great Lakes region during a recent warming period. *Limnol Oceanogr* 52:2013–2026
- Jones HR, Lack TJ, Jones CS (1979) Population dynamics and production of *Daphnia hyalina* var. *lacustris* in Farmoor I, a shallow eutrophic reservoir. *J Plankton Res* 1:45–65
- Karetnikov SG, Naumenko MA (2008) Recent trends in Lake Ladoga ice cover. *Hydrobiologia* 599:41–48
- Kasprzak P, Ronneberger D (1982) Vergleichende Untersuchungen zur Struktur und Dynamik des Zooplanktons im Stechlinsee, Nehmitzsee und Haussee 1978/79. *Limnologica* (Berlin) 14:263–295
- Leppäranta M (2009) Radiation transfer and heat budget during the ice season in Lake Pääjärvi. This volume

- Leppäranta M, Reinart A, Erma A, Arst H, Hussainov M, Sipelgas L (2003) Investigation of ice and water properties and under-ice light fields in fresh and brackish water bodies. *Nord Hydrol* 34:245–266
- Leßmann D, Ender R, Hofmann H, Rücker J, Beulker C, Nixdorf B (2003) Der Einfluß lang dauernder Eisbedeckung auf die Phytoplankton-Entwicklung in sauren Tagauseen. *Dt Ges Limnol (DGL) Tagungsbericht (Köln) Werder* 2003
- Livingstone DM (1999) Ice break-up on southern Lake Baikal and its relationship to local and regional air temperatures in Siberia and to the North Atlantic oscillation. *Limnol Oceanogr* 44:1486–1497
- Livingstone DM (2000) Large-scale climatic forcing detected in historical observations of lake ice break-up. *Verh Internat Verein Limnol* 27:2775–2783
- Livingstone DM, Adrian R, Arvola L, Blenckner T, Dokulil MT, Hari RE, George DG, Jankowski T, Järvinen M, Jennings E, Nöges P, Nöges T, Straile D, Weyhenmayer GA (2008) Regional and supra-regional coherence in limnological variables. In: George DG (ed) *The impact of climate change on European Lakes*. Springer, Berlin in print
- Löffler H (1979) Neusiedlersee: the limnology of a shallow lake in central Europe. *Monographiae Biologicae*, vol 37. Dr. W. Junk Publisher, The Hague, pp 1–543
- Lorenzen CJ (1967) Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnol Oceanogr* 12:343–346
- Morabito G, Ruggio D, Panzani P (2002) Recent dynamics (1995–1999) of the phytoplankton assemblages in Lago Maggiore as a basic tool for defining association patterns in the Italian deep lakes. *J Limnol* 61:129–145
- Morscheid H (1999) Entwicklung und Stellung des Zooplanktons im pelagischen Ökosystem des Ammersees nach der Oligotrophierung (1993–1997). PhD thesis, Univ Vienna
- Nauwerck A (1963) Die Beziehungen zwischen zooplankton und phytoplankton im See Erken. Uppsala, Schweden. *Symp bot Upsal* 17:1–163
- Paloheimo JE (1974) Calculation of instantaneous birth rate. *Limnol Oceanogr* 19:692–694
- Pechlaner R (1971) Factors that control the production rate and biomass of phytoplankton in high mountain lakes. *Mitt Internat Verein Limnol* 19:125–145
- Phillips KA, Fawley MW (2002) Winter phytoplankton community structure in three shallow temperate lakes during ice cover. *Hydrobiologia* 470:97–113
- Pohlmann M, Friedrich G (2001) Bestimmung der Phytoplanktonvolumina—Methodik und Ergebnisse am Beispiel Niederrhein. *Limnologica* 31:229–238
- Ravera O (1969) Seasonal variation of the biomass and bio-coenotic structure of plankton of the Bay of Ispra (Lago Maggiore). *Verh Internat Verein Limnol* 17:237–254
- Reitner B, Herzig A, Herndl G (1997) Microbial activity under the ice cover of the shallow Neusiedler See (Austria, Central Europe). *Hydrobiologia* 357:173–184
- Rodhe W (1955) Can plankton production proceed during winter darkness in subarctic lakes? *Verh Internat Verein Limnol* 12:117–122
- Rott E (1981) Some results from phytoplankton counting intercalibrations. *Schweiz Z Hydrol* 43:35–62
- Schiemer F (1979) The benthic communities of the open lake. In: Löffler H (ed) *Neusiedlersee: the limnology of a shallow lake in central Europe*. *Monographiae Biologicae*, vol 37. Dr. W. Junk bv Publishers, The Hague, pp 337–384
- Schrimpf A (1994) Auswirkungen von Restaurierungsmaßnahmen auf zwei Kleinseen in Bayern und Tirol unter besonderer Berücksichtigung des Zooplanktons. PhD thesis Univ. Innsbruck
- Šporka F, Livingstone DM, Stuchlík E, Turek J, Galas J (2006) Water temperatures and ice cover in lakes of the Tatra Mountains. *Biologia*. Bratislava 61(Suppl. 18):S77–S90
- Sušelj K, Bergant K (2006) Mediterranean oscillation index. *Geophys Res* 8:02145 Abstracts
- Talling JF (1962) Freshwater algae. In: Lewin RA (ed) *Physiology and biochemistry of algae*. Academic Press, New York, pp 743–757
- Tryfiates GW (1960) Algal photosynthesis as measured by absorption of radioactive carbon from water. *Ohio J Sci* 60:77–82
- Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton Methodik. *Mitt Internat Verein Limnol* 9:1–38
- Vörös L, Mózes A, Somogyi B (2009) A five-year study of autotrophic winter picoplankton in Lake Balaton, Hungary. This volume
- Walz N, Elster HJ, Mezger M (1987) The development of the rotifer community structure in Lake Constance during its eutrophication. *Arch Hydrobiol* 74:452–487 *Monogr Beiträge*
- Weyhenmayer GA, Meili M, Livingstone DM (2004) Nonlinear temperature response of lake ice breakup. *Geophys Res Letters* 31:L07203. doi:10.1029/2004GL019530
- Wright RT (1964) Dynamics of a phytoplankton community in an ice covered lake. *Limnol Oceanogr* 9:163–178