

# Response of *Bosmina* to climate variability and reduced nutrient loading in a large lake

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## ABSTRACT

The long-term dynamics of the cladoceran *Bosmina* spp. were analysed in Lake Constance during the study period 1979–1998. During this period the lake ecosystem has been influenced strongly by changes in nutrient inflow (oligotrophication) and by climate variability associated with the North Atlantic Oscillation. *Bosmina* abundances declined strongly during the study period presumably as an indirect consequence of the reduced P loading of the lake. A detailed seasonally resolved analysis of *Bosmina* dynamics revealed that its abundance decline occurred throughout the year with the exception of the spring period. The lack of a population decline during spring may be attributed to the seasonal absence of the factor, e.g., food limitation and/or predation control by invertebrates causing the population decline. Additionally, climate variability had its strongest influence on *Bosmina* dynamics during spring and large climate-associated variability of *Bosmina* may have decreased the power to detect a significant reduction in spring *Bosmina* abundances with oligotrophication. However, when we account for the confounding influence of climate variability, the effects of oligotrophication are revealed more clearly also during the spring period. Likewise, the detectability of the influence of climate variability on spring *Bosmina* dynamics increases when accounting for the reduction of abundances in the course of oligotrophication.

## Introduction

Climate variability associated with the North Atlantic Oscillation (NAO) has been shown to affect the temperature regime of a large variability of lakes across Europe (Blenckner et al., 2007). As a consequence, growth rates and population dynamics of plankton and fish species have been suggested to be linked to the NAO (Weyhenmeyer et al., 1999; Straile, 2000; George et al., 2004; Straile et al., 2007; Blenckner et al., 2007). Among plankton special emphasis was given to *Daphnia* and several studies suggest a strong influence of spring climate variability on the population dynamics of this herbivore (Straile and Adrian, 2000; Straile, 2000, 2002; Hampton et al., 2006; Wagner and Benndorf, 2007). Furthermore, the strong influence of water temperatures in generating interannual variability has been confirmed with mesocosm experiments (Berger et al., 2007) and modelling studies (Scheffer et al., 2001; Schalau et al., 2008).

Much less is known about the response of other freshwater zooplankton to climate variability, although more recently work

on e.g., the response of rotifers (Gerten and Adrian, 2000; Winder and Schindler, 2004; Molinero et al., 2006) and copepod species (Gerten and Adrian, 2002; Seebens et al., 2007, 2009) to climate variability has been analysed.

In addition to the dynamics of phytoplankton and *Daphnia*, Straile and Adrian (2000) analysed the response of small crustacean herbivores, *Bosmina* spp. to NAO variability in two lakes in Germany, Müggelsee and Lake Constance. While this study showed that the *Daphnia* populations in the two lakes showed a similar, coherent response to climate variability (but see Gerten and Adrian, 2000), this did not seem the case for the *Bosmina* populations. In Müggelsee, *Bosmina* dynamics were associated with NAO variability, whereas in Lake Constance this was not the case. However, the failure to detect an influence of climate variability on *Bosmina* dynamics was suggested to be due to the confounding effects of oligotrophication on *Bosmina* (Straile and Adrian, 2000).

In the present study, we re-examine the influence of the NAO on *Bosmina* dynamics in Lake Constance by investigating the effect of climate variability together with the effect of oligotrophication. Our hypotheses are that (a) both factors will have overlapping effects – at least seasonally – on *Bosmina* dynamics, and that (b) a reciprocal consideration of the two factors will increase the power of detecting their effects on *Bosmina* dynamics.

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### Study site, species information and methods

Upper Lake Constance is a large (472 km<sup>2</sup>), deep ( $z_{\max}=254$  m), warm-monomictic lake bordered by Austria, Germany and Switzerland. The lake has been studied intensively during the last few decades with regard to the influences of changes in nutrient inflow (Bäuerle and Gaedke, 1998; Güde et al., 1998) and climate variability associated with the North Atlantic Oscillation (Straile, 2000; Straile et al., 2003, 2007). In Upper Lake Constance two *Bosmina* species coexist, namely *B. coregoni* and *B. longirostris*. These populations are minorities among filter feeding crustaceans in this lake (5% average contribution to crustacean zooplankton biomass (Straile and Geller, 1998)), outnumbered during the warm season by two *Daphnia* species and by *Eudiaptomus gracilis* during the winter months. Nevertheless, both *Bosmina* species apparently are well established in the ecosystem of Lake Constance, with reports dating back to the 1920s (Auerbach et al., 1924; Lauterborn, 1925). With other filter feeders they compete for the same food spectrum: small algae, bacteria and detritus. Filter mesh-sizes (Fig. 1) of the dominating *B. coregoni* were found in the range from 0.4 to 1.6  $\mu\text{m}$ , while those of *B. longirostris* were more narrow, ranging from 0.3 to 0.6  $\mu\text{m}$  (Geller and Müller, 1981; Müller, 1985). Due to these differences there might be a slight preference to small algae of *B. coregoni* and to bacteria of *B. longirostris*. However, two modes of food collection have been reported for *Bosmina*: while some of its feeding appendages act as filters, others can be used to selectively grasp larger particles (DeMott and Kerfoot, 1982).

Niche separation relative to *Daphnia* and to filter feeding copepods is achieved mainly by different patterns of diurnal vertical migration (Geller, 1986). No species migrated in May during the spring maximum of phytoplankton. From June to October, however, both *Bosmina* populations were found to migrate within the hypolimnion between 20 and 40 m, in a way that their position at any time was below the other crustaceans (Müller, 1985; Geller, 1986). Between the two *Bosmina* species no significant vertical separation was observed (Müller, 1985). The morphological characters which separate both species are small and cannot be observed at low magnification. During the monitoring programme, therefore, it was not possible to distinguish

between the two species. Hence we consider in the following both species together, i.e., as one population.

We used two proxy variables to represent the influences of trophic status and climate variability, respectively. As a proxy for the trophic status of the lake in a given year the maximum total phosphorus concentration ( $\text{TP}_{\text{MIX}}$ ) during the winter mixing period (February, March) was used (Fig. 2). The winter (DJFM) index of the North Atlantic Oscillation (NAO-I) represents our proxy for interannual climate variability and was provided by the National Centre of Atmospheric Research, USA (<http://www.cgd.ucar.edu/cas/jhurrell/indices.html>) (Hurrell, 1995). During the study period, there was no covariation between  $\text{TP}_{\text{MIX}}$  and NAO-I ( $r=-0.14$ , ns, Fig. 2).

*Bosmina* samples were taken weekly during the vegetation period and less regularly during winter at the deepest point ( $z_{\max}=147$  m) of a fjordlike appendix of Upper Lake Constance, the "Überlinger See". No samples were taken during 1983. Samples were collected using a Clarke-Bumpus sampler (mesh size 140  $\mu\text{m}$ ) by vertical hauls from 140 m depth. Prior to statistical analyses abundance data were  $\log_{10}(N+10)$  transformed. The relationships between *Bosmina* abundances and  $\text{TP}_{\text{MIX}}$ , respectively, NAO-I were analysed using correlation analyses separately for 7-day periods throughout the year. Only during January and February, 14-day periods were used as a reduced sampling frequency during this period of the year would have resulted in a too low number of observations, i.e. years, in which samples were taken during a specific 7-day period. This analysis allows us to study the effects of oligotrophication and climate variability on *Bosmina* abundances with a high seasonal resolution. In a first approach simple correlation coefficients were calculated between season-specific *Bosmina* abundances and  $\text{TP}_{\text{MIX}}$ , respectively NAO-I. To account for the effect of one environmental factor (e.g.,  $\text{TP}_{\text{MIX}}$ ), when analysing the relationship between *Bosmina* abundances and the other environmental factor (e.g. NAO-I), we used two different methods: (a) we included in a second approach the potentially confounding factor as a partial variable in correlation analysis. This accounts for any linear relationship between *Bosmina* abundances and the potentially confounding factor. (b) in a third approach we removed the effects of the potentially confounding factor from the 7-day period abundance time series by subtracting a LOESS fit to

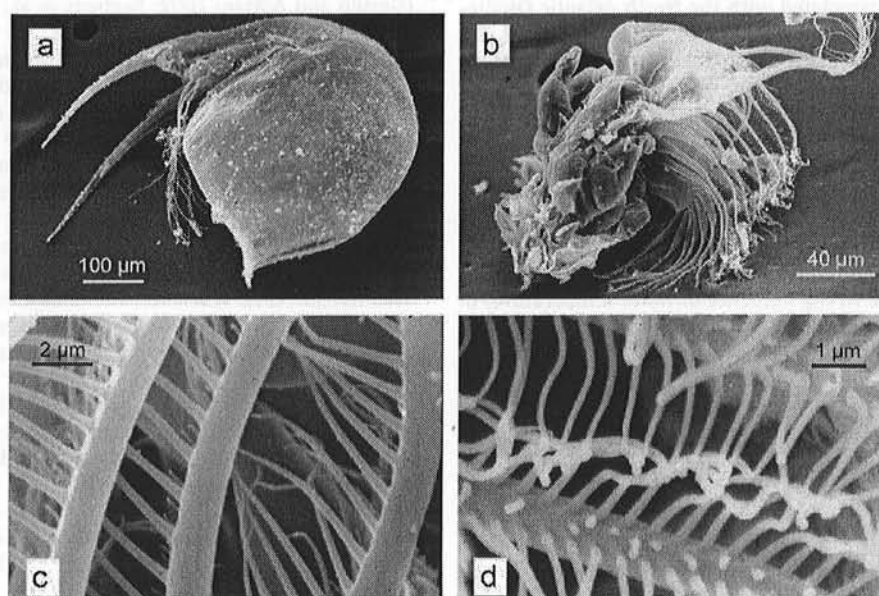


Fig. 1. SEM graphs of *Bosmina coregoni* (a–c) and *B. longirostris* (d). (a) overview; (b) filter comb of limb III (modified from Geller and Müller, 1981); (c, d) filter meshes of limb III (modified from Müller, 1985). Note different scale bars in graphs (c) and (d).

analyze the effects of the variable of interest. The smoothing parameter of the LOESS fit was chosen based on Akaike's information criterion. After removing the effect of the potentially confounding variable, the influence of the variable of interest on *Bosmina* abundances was analysed using Pearson correlation coefficients. This method allows for accounting for non-linear relationships between abundances and the confounding variable. Data analysis was performed with SAS.

## Results

During the study period *Bosmina* abundances were rather stable until the end of the 1980s, declined strongly during the early 1990s and seemed to stabilize at much lower levels towards the end of the 1990s (Fig. 3). Average seasonal dynamics consisted of a strong population increase from April towards June, followed by an exponential population decline until August (Fig. 4). From October onwards the population declined further to reach lowest abundances from January to March. Pearson correlation coefficients revealed that *Bosmina* abundances were strongly related to  $TP_{MIX}$  throughout the year with the exception of two time periods, i.e., from January until February and from mid April until the end of May (Fig. 5a). Accounting for the effects of climate variability either linearly (Fig. 5b) or non-linearly (Fig. 5c) increases correlation coefficients with  $TP_{MIX}$  during April. However, during the start of the year and for two weeks in mid May correlation coefficients with  $TP_{MIX}$  were lower despite accounting for effects of climate variability.

Pearson correlation coefficients of *Bosmina* abundances with the NAO-Index were highest during late May and decreased thereafter (Fig. 5d). Accounting for the effects of  $TP_{MIX}$  increases

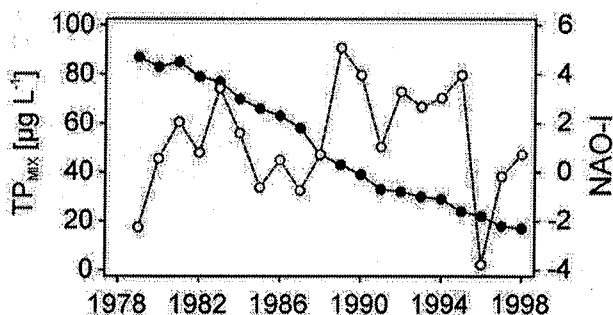


Fig. 2. Development of  $TP_{MIX}$  (filled circles) and NAO-I (open circles) during the study period. There is no covariation between the two time series during the study period ( $r = -0.14$  ns).

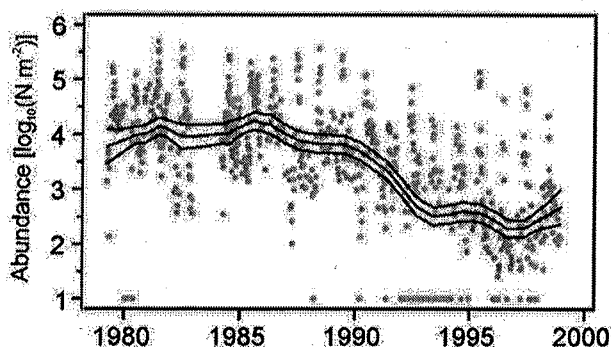


Fig. 3. Long-term dynamics of *Bosmina* ( $\log_{10}(N+10)$  transformed) in Lake Constance. The lines show LOESS fit and 95% confidence intervals based on a smoothing window of 10%.

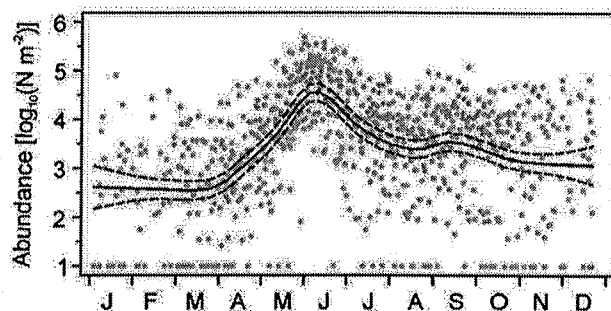


Fig. 4. Average seasonality of *Bosmina* abundances ( $\log_{10}(N+10)$  transformed) in Lake Constance. The lines show LOESS fit and 95% confidence intervals based on a smoothing window of 10%.

correlation coefficients of *Bosmina* abundances with NAO-Index during spring but also during September (Fig. 5e and f). The influence of NAO associated climate variability is further supported by the significant relationship between *Bosmina* population growth rate during April and May and the NAO index (Fig. 6).

## Discussion

Along with other crustacean taxa *Bosmina* biomass was estimated to have strongly increased with eutrophication of Lake Constance (Straile and Geller, 1998). Accordingly, a population decline of this herbivore is also expected with oligotrophication. A decline of annual average abundances as in Lake Constance (Straile and Geller, 1998) was previously also reported for Lake Mjøsa (Løvik and Kjellberg, 2003).

In this study, we show that the striking population decline of *Bosmina* during the 1990s resulted in strong positive correlations of *Bosmina* abundances with  $TP_{MIX}$  almost throughout the season. The lower correlation coefficients obtained during January and February were most likely due to a higher error associated with abundances estimates during this time of the year as abundances were low and no or only few individuals were caught in one vertical haul. In contrast, the lower association of abundances with  $TP_{MIX}$  during April and May may be a combined effect of (1) a seasonally reduced importance of the factors causing the population decline of *Bosmina* with (2) a high interannual variability of *Bosmina* abundances during this time of the year associated with climate variability. The overall decline of *Bosmina* with oligotrophication of Lake Constance might be either a direct effect of a reduced primary productivity or a food-web mediated indirect effect of oligotrophication via e.g. enhanced competition with other herbivores and/or increased predation pressure of invertebrate predators (Straile and Geller, 1998). The literature on competition between *Bosmina* and *Daphnia* has been reviewed by DeMott (1989). According to this overview, competition between both cladocerans is a complex interaction of different abilities, such as growth, resistance to starvation, susceptibility to predation and selective feeding. Notably, competitive advantage could be reversed by changes in environmental conditions, e.g. shifts in food supply, such that the outcome of competition experiments was highly variable. Important factors stabilizing the coexistence between *Daphnia* and *Bosmina* were found to be resource partitioning by different feeding modes and habitat partitioning by depth. The latter was also the case in Lake Constance (Geller, 1986), which might suggest that the decline of *Bosmina* with oligotrophication was unlikely a direct effect of competition.

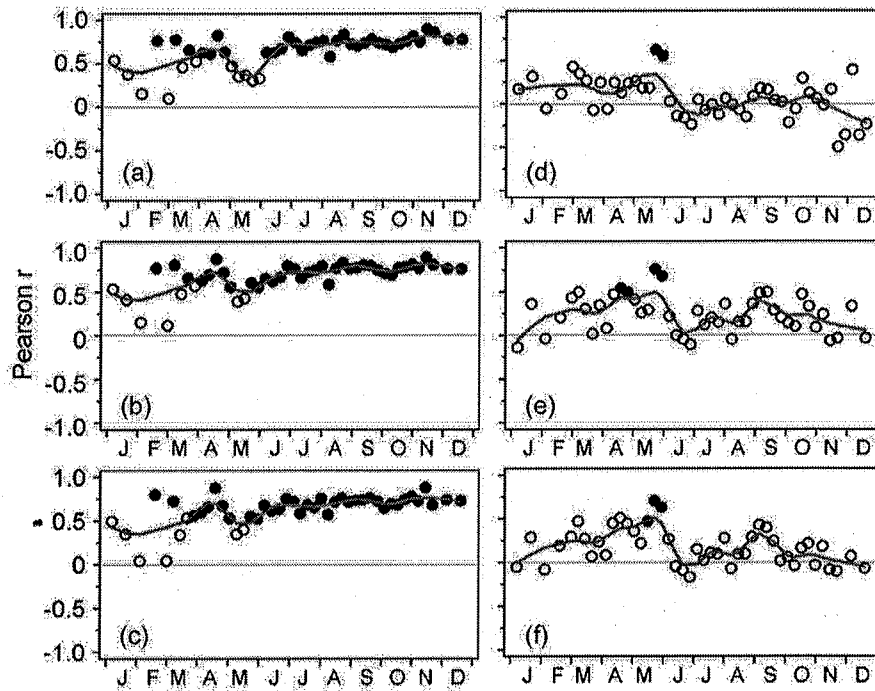


Fig. 5. Seasonality of Pearson correlation coefficients between *Bosmina* abundances in different sampling weeks and the total phosphorous concentration measured during winter mixis (TP<sub>MIX</sub>, a–c) or the winter (DJFM) index of the NAO (d–f). The upper panel (a,d) shows simple correlation coefficients without considering potential effects of the alternative driving force (NAO in the case of the correlation with TP<sub>MIX</sub>, TP<sub>MIX</sub> in the case of the correlations with the NAO index). The middle panel (b,e) shows partial correlation coefficients after partialing out the effects of TP<sub>MIX</sub> and the NAO, respectively. The lower panel (c,f) shows the correlation coefficients when allowing for potentially non-linear effects of the alternative driving forces. Filled circles indicate individual correlation coefficients significant at  $p < 0.05$ .

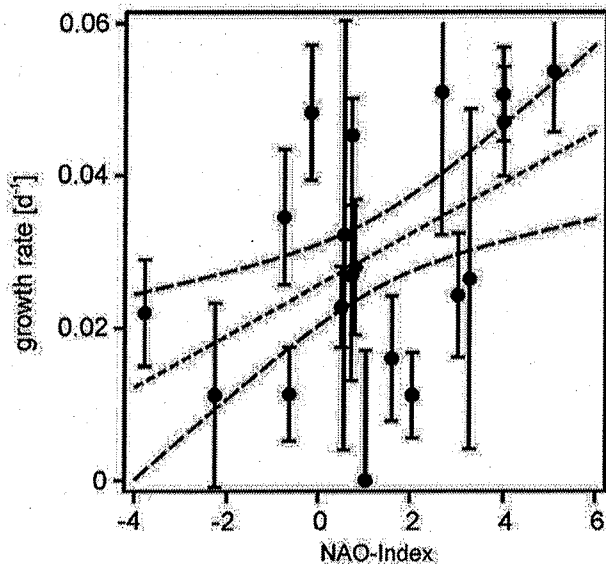


Fig. 6. *Bosmina* growth rate during April and May in relation to the NAO index ( $p < 0.05$ ). Growth rate was calculated as the slope of a linear regression of  $\log_{10}(N+10)$  transformed abundances versus day of the year.

As nutrient concentration declines seasonally, it should be expected that algal productivity during the spring bloom will be not as strongly affected by oligotrophication as algal growth during summer and autumn. In fact, phytoplankton biomass during the study period did not decrease during the spring bloom, but only during summer (Anneville et al., 2005). Likewise,

predation pressure by invertebrate predators such as the cladocerans *Bythotrephes longimanus* and *Leptodora kindtii* is low before June as their abundances usually start to increase from May onwards (Straile and Hälbig, 2000, Straile, unpublished data). Hence, these two processes potentially causing the population decline should be less effective during April and May, i.e., when the lowest correlation coefficients of *Bosmina* abundances with TP<sub>MIX</sub> were observed. The correlation coefficients between *Bosmina* abundances and TP<sub>MIX</sub> during spring are most likely further reduced by high interannual variability of spring water temperatures associated with the NAO (Straile et al., 2003). This is supported by the increase in correlation coefficients when the effects of climate variability are accounted for by using partial correlations or by removing the effects of the NAO by local regression methodology.

Correlation coefficients between *Bosmina* and the NAO-I were only significant during a short period in May. Average May biomasses of *Daphnia* in Lake Constance have also been reported to be strongly related to the NAO-I during the study period 1979–1994 (Straile, 2000). However, without accounting for the effects of oligotrophication, Straile and Adrian (2000) did not detect an association of spring *Bosmina* abundances with the NAO, but found a negative association during July. The analyses presented in this study (1979–1998) suggest that the findings of Straile and Adrian (2000) regarding the *Bosmina* dynamics in Lake Constance were indeed confounded because the effects of oligotrophication on *Bosmina* dynamics were not considered. The inclusion of four additional study years in this study as compared to Straile and Adrian (2000) resulted in a stronger association between spring abundances and the NAO and in the disappearance of the negative association between *Bosmina* abundances in July and the NAO. The latter can be attributed to significant covariation between the NAO-I and TP<sub>MIX</sub> during Straile and Adrian's (2000) study period, i.e.,

1979–1994, ( $r = -0.51$ ,  $p < 0.05$ ), which vanishes when considering the time period from 1979 to 1998 (Fig. 2). Hence, interannual climate variability associated with the NAO resulted in not only coherent *Daphnia* dynamics between Lake Constance and Müggelsee but also coherent *Bosmina* dynamics. The latter however was masked during the period 1979–1994 by the effects of oligotrophication on *Bosmina* dynamics in Lake Constance. When accounting for the effects of oligotrophication ( $TP_{MIX}$ ), the association of *Bosmina* with the NAO is strengthened and correlation coefficients increased throughout April and May. After May, the association with the NAO dropped to zero, but increased slightly again during late August and September. While it seems possible that the NAO effects are transferred further into the season due to, e.g., cohort dynamics (Seebens et al., 2007) or food web interactions (Straile, 2002), the association between late summer *Bosmina* abundances and the winter North Atlantic Oscillation is not strong and its ecological significance remains unclear.

Clearly, all relationships between NAO variability and *Bosmina* abundance represent quite indirect ones involving many intermediate processes. Considering the indirect nature of these relationships it actually seems rather surprising that such a simple index as the NAO-I seems to be able to capture significant variability of ecological processes in many lake ecosystems (Straile, 2002; Blenckner et al., 2007). Indeed, because of this indirectness, it may be assumed that these relationships should be easily disturbed by local processes such as local meteorology unrelated to NAO variability (Gerten and Adrian, 2000) or local changes in e.g. nutrient inflows (this study) or food web structure. Nevertheless, the strong spatial coherence observed for NAO effects in European lakes suggests that the key processes involved in this relationship, e.g., the temperature dependency of cladoceran population growth rates during spring, seem to be also a main driver of interannual ecological variability in many lakes even if they differ strongly in their limnology (Straile, 2002). Furthermore, results of the seasonally resolved regression analyses show that it is possible to disentangle the effects of oligotrophication versus climate variability on plankton dynamics (see also Seebens et al., 2007). Thereby, the two different methods used for accounting for the effects of the potentially confounding factor, i.e. linear versus non-linear, yielded similar results. Furthermore, these analyses showed that by accounting for one potentially confounding factor, the effects of the factor of interest are revealed more clearly. This suggests that climate variability and oligotrophication had additive effects on *Bosmina* dynamics. However, both factors showed a distinct seasonality in their effects on *Bosmina*.

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