The response of *Daphnia* to changes in trophic status and weather patterns: a case study from Lake Constance

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Relationships between changes in trophic status and weather patterns and biomass of *Daphnia* in Lake Constance were analysed by comparing three long-term records conducted at approximately 30-year intervals. These describe the zooplankton of Lake Constance in its oligotrophic (1920–1924), mesotrophic (1952–1962), and finally meso/eutrophic (1979–1995) state. Biomass increased approximately 30-fold from the 1920s to the 1950/60s and 6-fold from the 1950/60s to the 1980/90s. The former increase was evident throughout the season, the latter was restricted to the second half of the year. Daphnid biomass has not yet shown any response to the re-oligotrophication process of Lake Constance during the 1980/90s. Within the period 1979–1995, biomass in May was significantly correlated with the North Atlantic Oscillation, whereas the annual average showed no response. The magnitude of inter-annual variation in spring biomass due to climate variability was as large as the long-term response to eutrophication. Because of the key role of daphnids in freshwater ecosystems, even a temporally restricted response to climate forcing might have important consequences for the ecosystem.

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"Wir wissen jetzt aus unseren über einen Zeitraum von fünf Jahren sich erstreckenden Untersuchungen, daß die Planktonmenge, Zusammensetzung, Verteilung und saisonales Auftreten in den einzelnen Jahren sehr wechseln kann. . . . Also nur systematische Arbeit, monatlich mehrmals jedes ganze Jahr hindurch ist einwandfrei, und verfahre ich so mehrere Jahre hintereinander, so kann ich mir zum Schluß ein Bild machen, wie die Planktonverhältnisse, während dieser ganzen Untersuchungsperiode im Durchschnitt waren."
Auerbach *et al.* (1926)

Introduction

Understanding the causes of variability in species abundance is one of the major goals of ecological science. Depending on the temporal and/or spatial scales of interest, a large number of biotic and abiotic factors have to be considered as potentially important in influencing the abundance of a population under study.

The importance of the relative densities of predator and prey in determining the abundance of zooplankton has been discussed intensively within the last decade (Carpenter and Kitchell, 1993). Anthropogenic changes in nutrient concentrations have required a deeper understanding of the dependence of zooplankton biomass and species composition on the trophic state of lakes. During recent years, there has been renewed interest and an increasing recognition of the role that meteorological factors play in influencing the abundance of planktonic organisms (George and Taylor, 1995; Karl *et al.*, 1995). Meteorological factors may alter the abundance of organisms directly via, for example, temperature-dependent metabolic rates, and/or indirectly via changes in the abundance of potential prey, competitors, or predators. The impact of these external forces on individual populations may be dampened or enhanced by food–web interactions. This restricts the use of laboratory and mesocosm studies when predicting the response of *in situ* populations to environmental changes and demands the analysis of natural food webs, despite their complexity, although the different external factors
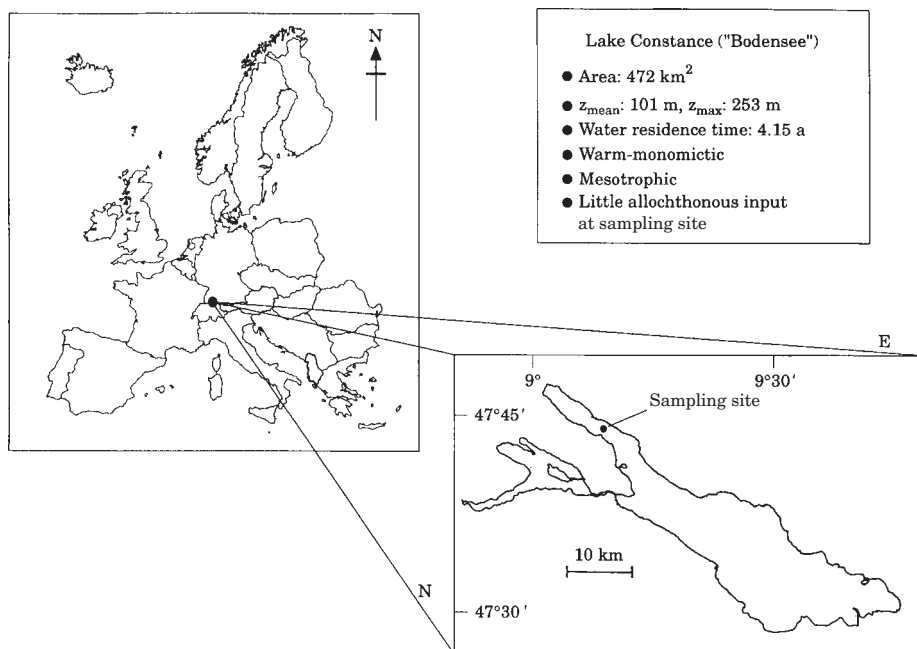
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Figure 1. Geographical setting and morphological data (upper lake only; z: depth) of Lake Constance.

may vary simultaneously. Lack of control frequently complicates the identification of causal mechanisms underlying observed changes of field populations.

Zooplankton research in Lake Constance has a long tradition and scientific investigations date back to the last century (Weismann, 1876; Hofer, 1896). The analysis of the resulting long-term time series may be used to distinguish between the influence of changes in trophy and weather patterns on zooplankton populations. We explored the effect of eutrophication on the biomass and population dynamics of daphnids by analysing results from three periods conducted at approximately 30-year intervals. The first period comprises five years of investigation (1920–1924) when Lake Constance was oligotrophic (Auerbach *et al.*, 1924, 1926). The second period covers 10 years (1952–1962) during which the first signs of eutrophication were recognized (Muckle and Muckle-Rottengatter, 1976). Finally, crustacean zooplankton has been sampled since 1979. This last period of 17 years encompasses the peak of eutrophication and the return towards more oligotrophic conditions. For a detailed picture of the trophic history of Lake Constance, see Güde *et al.* (in press), Gaedke (in press), and Straile and Geller (in press).

The potential influence of climatic variability on daphnid population dynamics is analysed for the years 1979–1995. The weather regime over much of Europe is influenced by the North Atlantic Oscillation (NAO), a large-scale pressure variation between subtropical high and sub-polar low surface pressures (Lamb and Peppler,

1987; Hurrell, 1995). The occurrence of warm winters in northern and central Europe during the late 1980s and early 1990s is associated with anomalously low pressures in the region of the Icelandic Low, and with pressures higher than normal at lower latitudes, corresponding to a highly positive NAO Index (Hurrell, 1995). The objective of this contribution is to analyse the response of daphnids to changes in trophic status and weather patterns, such as the NAO, and to compare the magnitude and seasonality of the respective responses in a large continental lake.

Study site and methods

Lake Constance (or "Bodensee") is a large and deep temperate lake at approximately 47°40′N 9°20′E (Fig. 1). Owing to its large size and often steep banks, the lake has a well-mixed epilimnion and a true pelagic zone. Mixis of the total water column occurs usually in late February or March. The natural history of the lake and the population dynamics of all important biota have been examined in detail (see Bäuerle and Gaedke, in press). Data on phosphorus concentrations during winter mixis were provided by the International Commission for the Protection of Lake Constance (IGKB, 1997).

Daphnids were sampled at least once per month during 1920–1924 and 1952–1962 with a Nansen closing net with mesh sizes of 50 μm and 130/200 μm, respectively. From 1979 to 1995, a Clarke–Bumpus Sampler (mesh size 140 μm) was used to obtain weekly
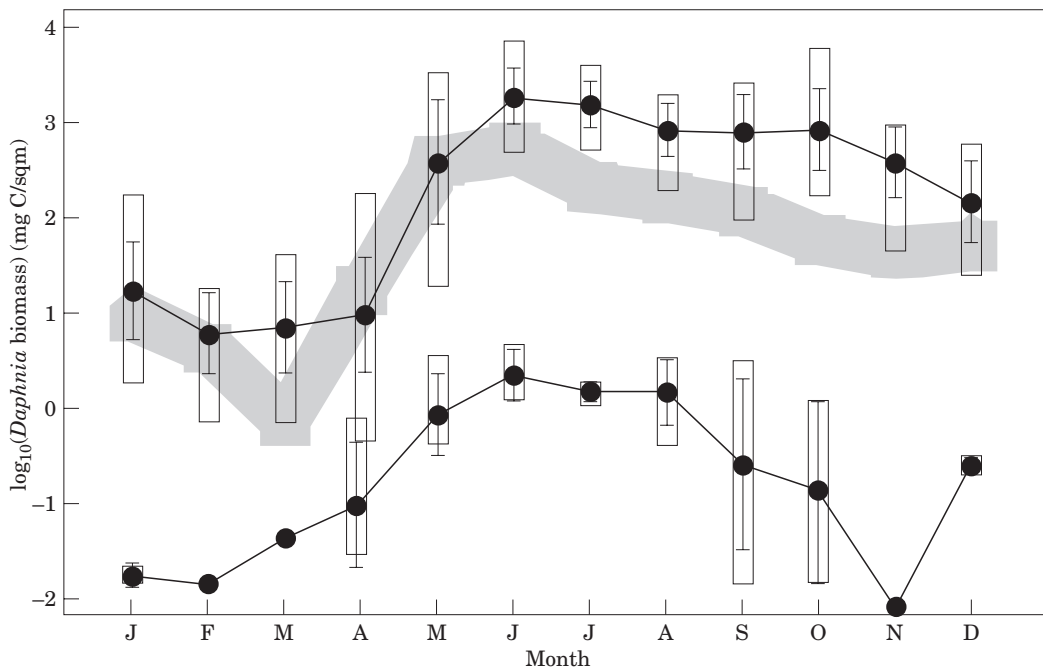
Figure 2. Average monthly development of daphnid biomass in Lake Constance during 1920–1924 (lower curve), 1952–1962 (grey band), and 1979–1995 (upper curve). Standard deviations and ranges (bars) are shown for the first and last periods; data for individual years from 1952–1962 are not available.

(biweekly in winter) measurements of the abundances of crustacean zooplankton. Biomass during 1979–1995 was calculated from species-specific length–dry-weight relationships established for Lake Constance (Geller and Müller, 1985) and a carbon to dry weight conversion factor of 0.5 (Berberovic, 1990). Daphnid biomass in 1920–1924 and 1952–1962 was calculated from abundances and average carbon weights obtained during 1979–1995 by assuming that average carbon weights did not change between the study periods (for more details, see Straile and Geller, in press).

Results

On average, biomass of daphnids increased approximately 30-fold from the early 1920s to the 1950/60s and approximately 6-fold from the 1950/60s to the 1980/90s, i.e., by two orders of magnitude over the total time range. The increase between the 1920s and the 1950/60s is expressed in higher biomass values throughout the year (Fig. 2). Only during April, there is no difference between these time periods (T-test, p>0.05). The reason for the extremely low value in November 1920–1924 is not clear and may at least partly be attributed to a low sampling frequency. However, total crustacean biomass did not show this biomass gap (Straile and Geller, in press). Biomass levels in the 1950/60s to the 1980/90s are roughly

similar during the first 5 months of the year, but differences become increasingly larger from June until October. Mean biomasses differ significantly between the two time periods within the second half of the year (T-test, p<0.05). Thus, the biomass response of daphnids, which dominate crustacean zooplankton during this time, is restricted to the second half of the year.

In contrast to the apparent strong response to eutrophication since the 1920s, daphnid biomass did not decline during the period of re-oligotrophication since 1979 (Fig. 3). While total phosphorus during winter mixis decreased by a factor of about 3, average daphnid biomass was remarkably constant during these years (Pearson correlation coefficients between phosphorus concentration and annual or summer/autumn biomass values were not significant; r= − 0.22 and − 0.09, respectively). This, however, does not hold for Daphnia population dynamics. In particular in spring, population growth, and consequently the date of maximum biomass, exhibits strong inter-annual variability (Fig. 4). The two years were selected to represent the slowest (1987) and fastest (1990) population growth in spring observed between 1979 and 1995. Starting from roughly similar biomasses in late March and early April, maximum biomass may occur in May or in July. These differences in growth rates during April and May result in large inter-annual differences in average biomasses in
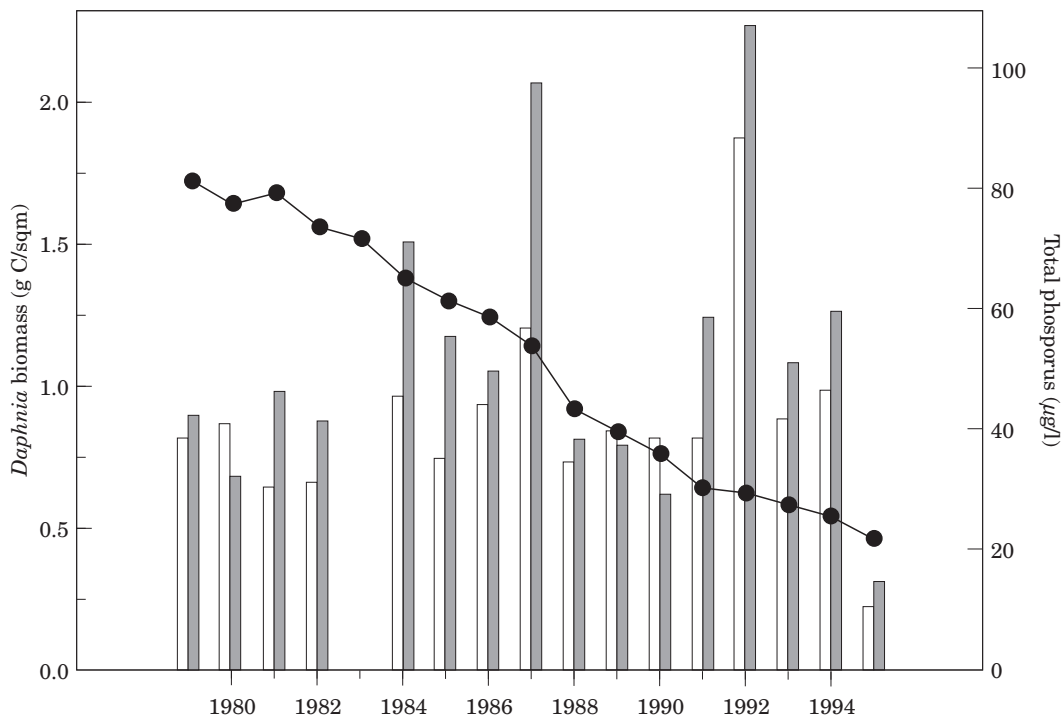
Figure 3. Total phosphorus concentrations during winter mixis (dots), annual average daphnid biomass (white bars), and average biomass during July through December (grey bars), 1979–1995 (no zooplankton data available for 1983).

May. Growth rates of daphnids in individual years, estimated as the slope of a linear increase of log (*Daphnia* biomass) with day number, and average biomass of daphnids (Fig. 5) were correlated with the NAO ($r=0.53$, $p<0.05$, and $r=0.64$, $p<0.05$, respectively). In contrast, maximum biomasses achieved each year are not related to the NAO ($r=0.22$, $p>0.05$). This implies that during years with a high NAO index population growth is fast and restricted to a short period of time, whereas in other years net population increase is slow but continues over a longer time span.

Discussion

The analysis of potential effects of eutrophication on Lake Constance zooplankton is partially hampered by methodological changes between study periods, the effects of which on the observed biomass changes are difficult to assess. For example, a mesh size of 50 µm (Auerbach *et al.*, 1924, 1926) should lead to enhanced clogging of the net due to particulate organic matter (POM) and a reduced sampling efficiency as compared to larger mesh sizes used during later studies. However, during the 1920s the much lower POM concentrations should reduce the difference in clogging due to different mesh sizes. The biomass increase of phytoplankton and of rotifers is estimated to be of similar magnitude

as the biomass increase of zooplankton (Walz *et al.*, 1987).

The relative increase in daphnid biomass was more pronounced than the relative increase in other zooplankton taxa, and total crustacean biomass went up approximately 50-fold (Straile and Geller, in press). These relative increase patterns are typical for many lakes undergoing eutrophication (Ravera, 1980), where daphnids have been shown to benefit from eutrophication more than other zooplankton species, e.g., in Lago Lugano (Polli and Simona, 1992), Lago Maggiore (De Bernardi *et al.*, 1988), and Lough Neagh (Fitzsimons and Andrew, 1993).

Phosphorus concentrations declined from 87 µg l^{-1} in 1979 to 24 µg l^{-1} in 1995 and begin now to approach values of the late 1950s and early 1960s. Despite the strong response of daphnids to eutrophication, no decline in biomass either as an annual mean nor for the second half of the year was observed in the course of the re-oligotrophication of Lake Constance. This stands in contrast to the decline of summer phytoplankton biomass since 1979 (Gaedke and Schweizer, 1993). However, the algal decline is to a large extent due to large and hardly edible species (Gaedke, in press). Biomass of small and edible phytoplankton, the main diet of herbivorous zooplankton, has remained fairly constant during the last two decades. In addition, the decrease
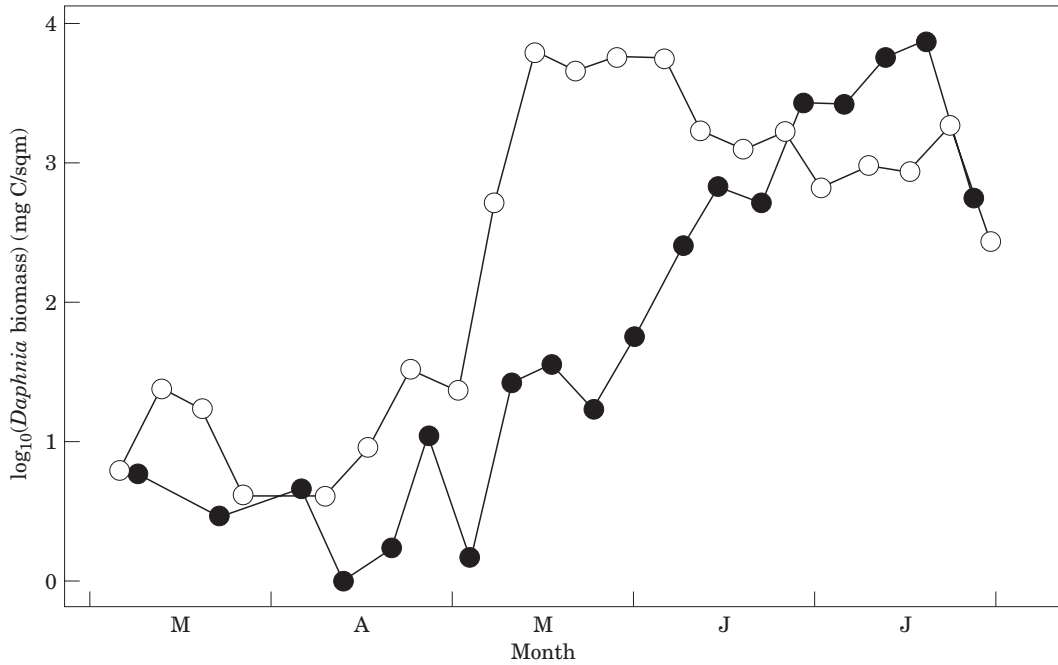
Figure 4. Development of daphnid biomass during the spring months of 1987 (dots) and 1990 (circles).
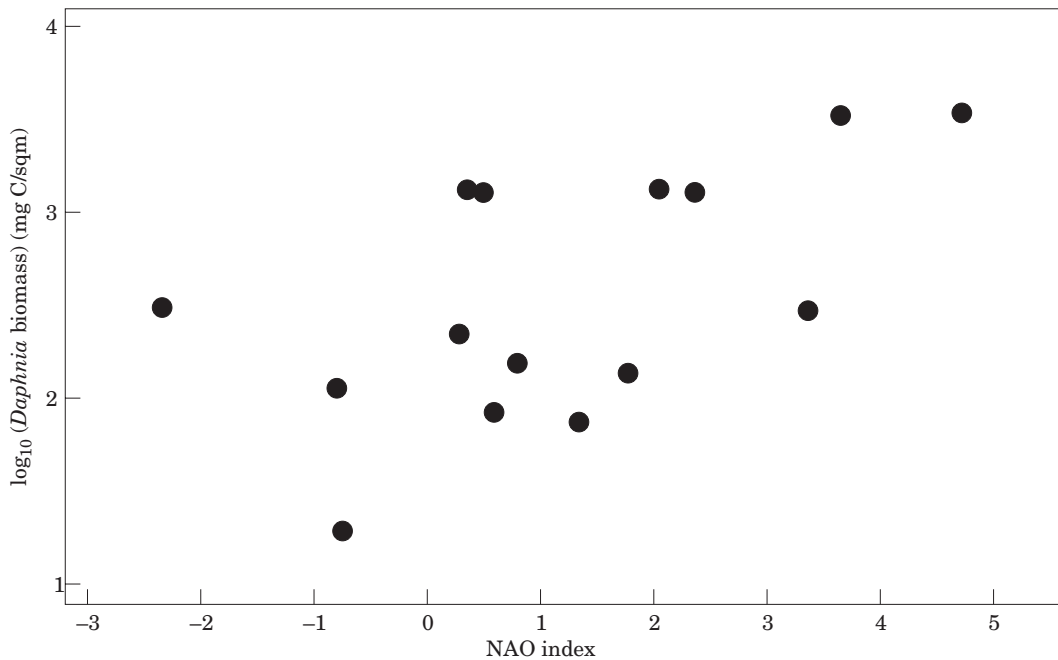

Figure 5. Relationship between average daphnid biomass in May and the NAO index (cf., Hurrell, 1995), 1979–1995.

in primary productivity has been small (Haese *et al.*, in press).

A number of studies have reported that global atmospheric changes, such as the El Niño Southern Oscillation (ENSO), strongly affect marine planktonic communities (Barber and Chavez, 1983; Karl *et al.*, 1995). Effects of ENSO are not restricted to marine communities; they also influence limnetic ones in North America (Goldman

et al., 1989). The NAO is an atmospheric signal that has a major effect on weather patterns in the Atlantic (Hurrell, 1995). Recently, Fromentin and Planque (1996) demonstrated the influence of the NAO on copepod abundances in the eastern North Atlantic. Our study is the first which reports a relationship between the NAO and the plankton of a continental European lake. Changes in the zooplankton community structure in mesotrophic Heiligensee in Berlin were found to be related to the recent occurrence of warm winters in central Europe (Adrian and Deneke, 1996). Further examples of a relationship between plankton dynamics in European lakes and large-scale weather patterns include the association between the position of the North wall of the Gulf Stream in the western Atlantic and various changes in lake ecosystems within the English Lake District (George and Taylor, 1995).

The effects of changing trophy and climate variability on daphnid biomass differ in their time scales and their seasonal setting. Compared with its oligotrophic state at the beginning of the century, biomass strongly increased throughout the annual cycle. Surprisingly, this holds even for late winter and early spring, when the growth of autotrophs is considered not nutrient but rather light limited. Phosphorus limitation of phytoplankton in Lake Constance is thought to be restricted to the period of stratification from late spring to autumn (Gaedke and Schweizer, 1993). Hence, increased nutrient loading is expected to show its largest effects during this period. This is supported by the patterns of daphnid increase observed from the 1950/60s to the 1980/90s: whereas biomass level had not changed during the first half of the year, markedly higher values were obtained during the latter period from July onwards.

In contrast to the response to changing trophy, climate variability correlates with daphnid biomass during spring. The onset of stratification and, hence, the start of the spring phytoplankton bloom in Lake Constance is sensitive to the weather regime during spring (Gaedke et al., in press). After the onset of stratification, downward mixing of heat and of algae is reduced and surface waters are heated more rapidly. Algae remain within the upper water column, which prevents them from being light limited and allows for rapid growth (Gaedke et al., in press). Hence, daphnids may benefit directly from stratification through increased water temperatures and/or indirectly via increased phytoplankton productivity. The former effect appears to be more important in Lake Constance (Gaedke et al., in press).

During summer, a direct effect of weather variability on daphnid biomass is less probable. Daphnia hyalina, the predominant species during summer, exhibits a pronounced diurnal vertical migration and stays during day time in the hypolimnion at low and relatively constant water temperatures (Geller, 1986). Furthermore, abundance during summer is controlled by a low food supply (Geller and Müller, 1985) and increased presence of invertebrate and vertebrate predators (Sommer et al., 1986).

For particular months, the short-term response to climate variability appears to be of a similar magnitude as the long-term response to eutrophication. Average daphnid biomass in May increased over the period of nutrient enrichment by a factor of 200, from 5 mg C m^{-2} (1920/24) to 1000 mg C m^{-2} (1979/95). Minimum (20 mg C m^{-2} in 1987) and maximum (3400 mg C m^{-2} in 1990) average biomass in May during 1979/1995 differed by almost the same factor. Despite this large variability in May, the annual average biomass remained fairly constant. Hence, a high seasonal resolution seems to be necessary if the influence of climate variability on daphnid population dynamics is to be detected in Lake Constance.

Although the annual average biomass appears not to be affected, the response to weather variability during spring might have important consequences for the entire food web. The daily ration of fish larvae in Lake Constance is at its maximum during May and June (Troschel and Rösch, 1991), suggesting that fish reproduction is adapted to exploit the mass occurrence of daphnids during this period. A shift in the timing of daphnid development by approximately 2 months may result in a temporal mismatch between the maximum demand of fish larvae and the maximum of daphnid biomass with negative effects on year-class strength of fish. Similar mechanisms have been discussed for marine ecosystems (Bollens et al., 1992; Gotceitas et al., 1996). Further investigations are required to explore whether the variability in the growth rate of daphnid populations has consequences for fish larvae and to obtain a mechanistic understanding of the relationship between the NAO and population growth.

To conclude, daphnid biomass in Lake Constance is strongly affected by changes in nutrient concentrations and weather patterns. The progressive response to 60 years of eutrophication is evident throughout the season. In contrast, the response to weather variability is more episodic and restricted to a particular time of the year. The lack of an unambiguous response of the zooplankton to the ongoing reduction of winter phosphorus concentrations by a factor of 3–4 within 15 years shows that effects of external forcing factors may be dampened within the plankton community and that only consequences of major environmental changes may be identified from field populations, even with frequent sampling. Natural populations are subject to a variability of several external factors which superimpose noise on individual trends. This is exemplified by the result that inter-annual fluctuations in weather conditions cause a short-term variability in daphnid

biomass of similar magnitude as the long-term variability attributed to pronounced eutrophication.

Acknowledgements

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