# COMMENT

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# Climatic warming and regime shifts in lake food webs—some comments

In a recent issue of *Limnology and Oceanography*, Scheffer et al. (2001) argued that ''the probability of clear water phases increases with increasing lake water temperature in shallow lakes and that small decreases in temperature may create a shift to a turbid state and an increase to a clearwater state.'' They based their evidence on a correlation between a defined clearwater state and the winter North Atlantic Oscillation (NAO) index in Dutch lakes and a simple minimal pelagic fish-zooplankton-phytoplankton-temperature model. Our perception of the role of temperature for lake water clarity is quite different, and in the present Comment we argue that the analysis by Scheffer et al. (2001) does not warrant these conclusions. We do agree, however, with several of the statements made by Scheffer et al. (2001)—for instance, that lake temperature is correlated with the winter NAO index, as was also demonstrated by, for example, Straile and Adrian (2000). We also agree that fish may influence both seasonal variations in zooplankton grazing pressure on phytoplankton (Jeppesen et al. 1997*a*) and the time of the appearance or absence of clearwater phases.

First we examine the empirical analysis. Scheffer et al. (2001) analyzed 257 seasonal chlorophyll *a* patterns in 71 shallow Dutch lakes and found that the probability of a clearwater phase is positively related to the NAO index. Although the regression is significant, the variance explained is very low ($r^2 = 0.10$). Furthermore, the data sources used in the analysis are debatable, because the average length is <4 yr per lake, and the number of the lakes and specific lakes included varied from year to year. Furthermore, the authors did not, in our opinion, make sufficient corrections for the effects of the changes in nutrient loading and other management schemes that have occurred in Dutch lakes (Hosper 1997) during the 16 yr (1975–1991) encompassed by the analysis. The authors sought somehow to correct for this by including average Chl *a* as an independent variable, but fish manipulation and total phosphorus (TP)–loading reduction have different impacts on the seasonal dynamics of Chl *a* and thus the chances of obtaining a predefined threshold for the shift to a clearwater state.

To test the empirical findings of Scheffer et al. (2001), we analyzed data from 29 shallow Danish lakes sampled fortnightly during summer over the past 8–12 yr (Table 1). The lakes were mesotrophic to hypertrophic and included turbid and clearwater lakes ranging in size from small to large. Like Scheffer et al. (2001), we also found annual temperatures to be correlated with winter NAO (Table 2). Multiple logistic regression on the full data set revealed that the probability of a clearwater state (defined as in Scheffer et al. 2001: when Chl *a* declines to $<5$ $\mu$g L$^{-1}$ at least once during May–August) increased significantly with decreasing summer (May 1–Oct 1) or annual mean Chl *a*. However, contrary to the finding by Scheffer et al., this probability was not significantly related to NAO (Table 3). This is also true if alternative thresholds of 10, 25, 50, or 100 $\mu$g L$^{-1}$ or a dip >25% below summer average was used (Table 2). If we instead used the logistic regression methods suggested by Van Donk et al. (2003) in their comments to Scheffer et al. (2001), in which the NAO index is nested within the categorical variable ''lake'' (excluding the main effect of the lakes), then 6 of the 29 lakes showed a significant ($\chi^2 = 5.1$–$6.4$, $p < 0.02$–$0.05$, without correction for multiple comparisons) positive relationship to NAO at the 5 $\mu$g L$^{-1}$ threshold. However, these were all clearwater lakes (i.e., they were in a clearwater state for 85%–100% of the year) and the relationship to NAO therefore most likely reflects that the NAO index was mainly positive from 1989 to 2000. Thus, when analyzing the lakes separately, we found no significant relationships for any of the lakes, irrespective of which of the above threshold criteria for clearwater lakes was used ($p > 0.2$–$0.9$). Yet, in the majority of the lakes, TP and, with it, Chl *a*, has declined since 1989 because of external loading reduction (Fig. 1; Jeppesen et al. 2002). For these lakes, our analyses may be confounded, because the effect of loading reduction (higher chances of a clearwater state with time) may counterbalance the effect of changes in NAO, given that the latter declined significantly overall during the study period (Table 2). However, we did not find any relationship ($p > 0.4$–$0.9$) with NAO for the five study lakes that are used as reference lakes in our monitoring program (Fig. 1). For these lakes, external loading has not changed systematically during the study period, because they are situated in catchments with very little human activity (Jensen et al. 1997). In fact, for both data sets, Chl *a* tended to be lower in years with the lowest NAO than in the adjacent years (Fig. 1). This indicates that lakes tend to be more clear after low than high winter NAO, which contradicts the view of Scheffer et al. (2001).

We next consider the model of Scheffer et al. (2001). It was, as clearly recognized by the authors, very crude, including only fish, zooplankton, phytoplankton, and temperature, with fish being regulated solely by temperature and various predetermined biomass values. This simple model omits important factors. First, it does not account for the fact that the internal loading of shallow lakes increases with temperature (Jensen and Andersen 1992; Søndergaard et al. 2001). Algal growth will therefore be higher than predicted by the model. Higher temperatures also favor cyanobacteria, which may negatively influence the grazers (Wetzel 2001).

Table 1. Selected morphometric and annual mean (1 Mar–1 Dec) physicochemical variables for the 29 lakes included in the analyses.

| Variable | Mean | SD | Min. | Max. |
|---|---|---|---|---|
| Area (km$^2$) | 1.9 | 6.8 | 0.05 | 40 |
| Mean depth (m) | 2.2 | 1.2 | 0.8 | 5.6 |
| Total phosphorus (mg L$^{-1}$) | 0.18 | 0.18 | 0.011 | 1.51 |
| Total nitrogen (mg L$^{-1}$) | 2.3 | 1.4 | 0.33 | 6.6 |
| Chlorophyll *a* (mg L$^{-1}$) | 74 | 77 | 16 | 541 |

Second, fish abundance is altered by temperature. In Danish lakes, a warm early summer often leads to higher abundance of planktivorous young-of-the-year (YOY) fish (Fiskeøkologisk Laboratorium 2000) and thereby expectedly a higher predation pressure on large-bodied zooplankton and, thus, higher Chl *a*. Moreover, a shorter period of ice cover due to global warming may reduce winter mortality of fish, which in turbid lakes dominated by planktibenthivorous fish, may lead to a higher predation pressure on zooplankton in spring and early summer before the YOY fish add extra predation pressure on the zooplankton in mid- to late summer. Thus, in several Danish lakes, high zooplankton : phytoplankton ratios and high Secchi depths occurred in the spring and early summer, after the only winter with long-lasting ice cover in the 1990s (1995/1996) (Jensen et al. 1997). Lower abundance in cold years has also been seen for pelagic smelt (*Osmerus eperlanus*) in Swedish lakes (Nyberg et al. 2001) and for a number of warm-water species in Finnish lakes (Lehtonen and Lappalainen 1995). All the factors mentioned point toward a greater probability of lakes in a turbid state in our region remaining turbid when the temperature increases rather than shifting to a clearwater state at a certain temperature threshold, as predicted by Scheffer et al. (2001). Moreover, we know today that the dominant zooplanktivorous fish in shallow lakes are omnivorous and prey extensively on benthic organisms (Vander Zanden and Vadeboncoeur 2002). It is therefore doubtful whether predictions from a model focusing only on pelagic interactions are reliable.

Another weak point of the model is the lack of focus on long-term changes. Both the monitoring data from the Dutch and Danish lakes and the model employed by Scheffer et al. (2001) only cover effects of short-term changes in climate—that is, structural shifts expected to result from more persistent climatic changes were not included. If we look solely at the interactions between fish and plankton, as done by Scheffer et al. (2001), there are several reasons to expect that, over a longer time, the probability for a shift to the clearwater state in nutrient-rich, shallow lakes would decline when temperature increases because of greater predation pressure on zooplankton. First, the number of fish species, and not least the potentially zooplanktivorous ones, increases from cold to warm lakes (Fernando 1994); this most likely would increase the predation pressure on zooplankton. A second reason is that the degree of omnivory increases in European lakes from Denmark to Spain (European Union projects BIOMAN and ECOFRAME unpubl. data), which implies that fish become less dependent on zooplankton but more capable of controlling them if they exceed a certain density or size threshold where zooplankton predation becomes worthwhile. Another effect of sustained temperature increase is that the spawning period will be prolonged and several species may have more than one cohort per year (Fernando 1994); this would most likely result in greater and more prolonged predation on zooplankton in warmer climates and may be why the zooplankton community tends to be dominated by small species in the subtropical and tropical regions (Dumont 1994). Finally, reduced winter fish kill resulting from warmer winters and increased recruitment of YOY fish during warm summers, as mentioned above, will increase the predation on the zooplankton. There will of course be exceptions—for instance, if the lake is exposed to periodic desiccation or salinization due to higher temperatures, resulting in fish kill or a reduction in species number. Also, high-altitude lakes with naturally low species numbers may show a different pattern (Dumont 1994). However, even keeping such exceptions in mind, we reach the opposite conclusion of Scheffer et al. (2001)—the zooplankton grazing control of phytoplankton in nutrient-rich shallow lakes without macrophytes generally decreases with increasing temperature and not the other way round.

The picture becomes much more unpredictable if additional factors regulating the dynamics of shallow lakes are included, especially the response of submerged macrophytes to changes in temperature (or associated changes in, e.g., water level) and the derived effects hereof (Jeppesen et al. 1997*b*). New investigations undertaken in the United Kingdom have indicated that macrophyte-dominated lakes with relatively low nutrient levels remain macrophyte-dominated when temperature rises a few degrees (McKee et al. 2002), but the development in lakes with intermediate nutrient lev-

Table 2. Pearson correlation coefficient ($n = 315$) from 29 shallow Danish lakes sampled fortnightly during summer and otherwise monthly during 8–12 years. *** $P<0.0001$, ** $P<0.001$, * $P<0.5$. Only $P<0.005$ can be accepted as significant because of repeated measures.

| | Year | Annual mean chlorophyll *a* ($\mu$g L$^{-1}$) | Summer mean chlorophyll *a* ($\mu$g L$^{-1}$) | Summer mean temperature (°C) | Annual mean temperature (°C) |
|---|---|---|---|---|---|
| Winter NAO | −0.46*** | 0.10 | 0.07 | 0.18** | 0.30*** |
| Year | | −0.17** | −0.17** | 0.11* | 0.05 |
| Annual mean chlorophyll *a* ($\mu$g L$^{-1}$) | | | 0.89*** | 0.04 | −0.05 |
| Summer mean chlorophyll *a* ($\mu$g L$^{-1}$) | | | | 0.04 | −0.07 |
| Summer mean temperature (°C) | | | | | 0.68*** |

Table 3. Logistic regression of the probability of obtaining a clearwater phase with NAO (left) and NAO as well as annual mean chlorophyll *a* (CHLA) using various cut points for defining clearwater lakes (see text for definition).

| | NAO only | | | NAO and CHLA | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Cut point | Slope-NAO | $\chi^2$ | $P>$ | Slope-NAO | $\chi^2$ | $P>$ | Slope-CHLA | $\chi^2$ | $P<$ |
| 5 $\mu$g L$^{-1}$ | −0.03 ± 0.05 | 0.40 | 0.52 | 0.007 ± 0.08 | 0.01 | 0.92 | −0.06 ± 0.008 | 61.7 | 0.0001 |
| 10 $\mu$g L$^{-1}$ | −0.06 ± 0.04 | 1.31 | 0.25 | −0.08 ± 0.08 | 0.9 | 0.34 | −0.08 ± 0.001 | 73.2 | 0.0001 |
| 25 $\mu$g L$^{-1}$ | −0.002 ± 0.05 | 0.002 | 0.96 | 0.07 ± 0.08 | 0.7 | 0.41 | −0.07 ± 0.009 | 75.8 | 0.0001 |
| 50 $\mu$g L$^{-1}$ | −0.002 ± 0.06 | 0.001 | 0.97 | 0.08 ± 0.08 | 1.3 | 0.25 | −0.04 ± 0.005 | 63.1 | 0.0001 |
| 100 $\mu$g L$^{-1}$ | −0.09 ± 0.11 | 0.76 | 0.38 | −0.01 ± 0.11 | 0.011 | 0.91 | −0.01 ± 0.002 | 31.6 | 0.0001 |
| 25% dip | 0.05 ± 0.05 | 1.0 | 0.32 | 0.05 ± 0.04 | 1.18 | 0.27 | −0.002 ± 0.002 | 1.2 | >0.27 |

els (where regime shifts may occur) has yet to be studied. Increasing temperatures may cause the water table to fall; this often enhances the chances for macrophytes to become established, which may shift some lakes from turbid to clear (Blindow et al. 1997). Yet the global circulation models (IPCC 1996) also predict increasing precipitation to mid- and north European coastal lakes due to global warming, which enhances the risk of a turbid state rather than a shift to a clearwater state.

Minimal models have been frequently employed in recent studies of shallow lake ecology, not least in the discussion of regime shifts (Scheffer 1998). The advantage of these models is that it is easy to understand their cause-effect relationships and the numerical methods behind them. How-

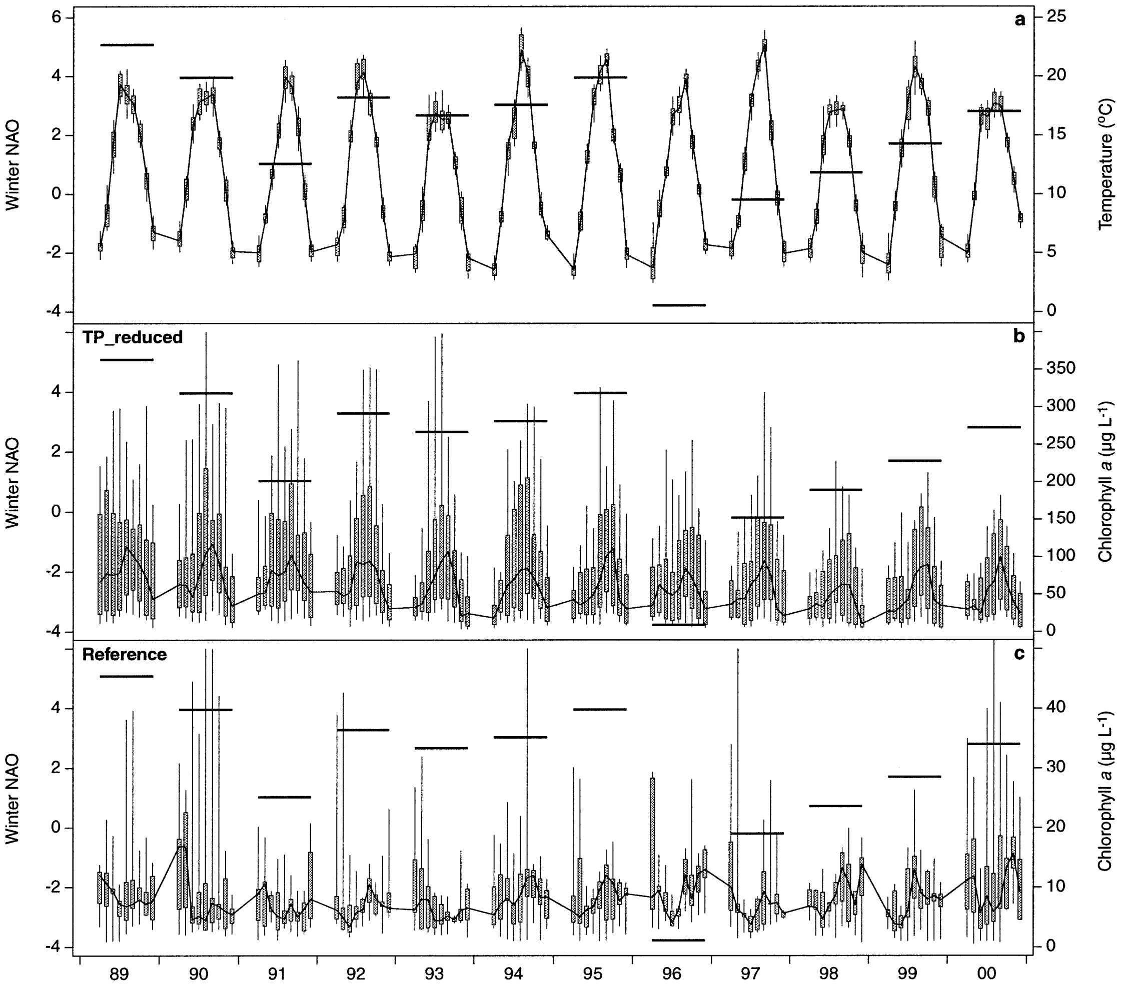

Fig. 1. Boxplot of (a) lake water temperatures in 24 Danish lakes followed fortnightly during summer and otherwise monthly 1989–2000, (b) Chl *a* in 19 of the lakes subjected to reduced TP loading during the study period, and (c) for five reference lakes situated in areas with no systematic changes in external loading during the 12 yr. Five of the 29 lakes were excluded because they were not studied for all 12 yr. Data from January and February are omitted because of scarcity of data. Thick bars represent 25–75 percentiles, and thin lines represent 10–90 percentiles; means are shown by a thick, connected line. Horizontal bars indicate the NOA winter index.

ever, their simplicity is also their weakness. In our opinion, minimal models should be used with special caution for forecasting, because this involves extrapolations. Admittedly, Scheffer et al. (2001) only argued that their minimal model results may give a plausible explanation of the observed increased probability of a clearwater phase at higher temperature. Yet, in our opinion, they use the results to draw too firm and most likely wrong conclusions about probable regime shifts in shallow north temperate coastal lakes following climate warming.

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