

The response of the pelagic food web to re-oligotrophication of a large and deep lake (L. Constance): Evidence for scale-dependent hierarchical patterns?

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with 2 figures and 2 tables

Abstract: Large (472 km²) and deep ($z_{\text{mean}}=101$ m) Lake Constance is undergoing re-oligotrophication. Total phosphorus during winter mixing (TP_{mix}) decreased by from exceeding 80 µg/l during 1975–1981 to 22 µg/l in 1996. Average summer values of Secchi and euphotic depth rose significantly from 4.5 to 6.5 m and from 10.5 to 13 m, respectively. The algal species composition changed and, during summer, total algal biomass declined by 50% and primary production by 25%. Standing stocks of well-edible algae, rotifers, and herbivorous and carnivorous crustaceans did not exhibit a trend with TP_{mix} , whereas their species compositions or egg-ratios were partially altered. The age-at-capture of planktivorous whitefish increased slightly. We tested the hypotheses that (1) changes should above all be observed at the level of individuals or within species (altering, e.g., C:P- or egg-ratios) prior to shifts within communities (affecting, e.g., the taxonomical composition) and at the community level (influencing, e.g., total biomass or production). This would imply that it is more appropriate to conceptualize step-wise responses along a hierarchical gradient of advancing aggregation as suggested by hierarchy theory rather than simultaneous changes at all hierarchical levels. (2) Responses become dampened along the food chain and with increasing body size, i.e., bottom-up control is most important for autotrophs. All communities studied (phytoplankton, crustaceans, fish) reacted at the individual level (e.g., by changes of (re)production rates) and/or within the community (e.g., by modified taxonomical composition), whereas alterations of bulk parameters of the entire community were restricted to phytoplankton. Hence, the first hypothesis is partially supported by the observed reactions and demands further testing. The second is clearly supported by our data when comparing autotrophs and consumers, but not when comparing crustaceans and fish. The testing of these hypotheses is complicated by the large differences in size and, consequently, in reaction times of pelagic organisms on the one hand and the rather fixed time scale of limnological research on the other hand. The different time scales imply a selective perception of the various potential responses of the differently sized organisms as the time scales of the responses depend on body size and the level of aggregation. For example, we are more likely to establish physiological or behavioral changes of fish and taxonomical or biomass variations of phytoplankton. Acknowledging the scale dependence and level of aggregation is also crucial for cross-system comparisons.

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Introduction and objectives

Changes in trophic conditions of surface waters are one of the major anthropogenic impacts on these ecosystems. On the one hand, numerous case studies and analyses have been undertaken in order to improve our understanding and predictive power of the response of aquatic ecosystems and especially of phytoplankton to altering nutrient concentrations (e.g., PERSSON et al. 1988, SAS 1989, REYNOLDS 1992, SCHEFFER et al. 1993, CHORUS 1995, JEPPESEN et al. 1997). On the other hand, eutrophication and re-oligotrophication studies may be close to whole-lake experiments providing valuable insight into the regulation of food webs which is difficult to obtain otherwise (OKSANEN et al. 1981, CARPENTER et al. 1985, 1987, MCQUEEN et al. 1989, DUARTE 1995). The objectives of the present paper are

- to add to this effort from a food web perspective,
- to summarize and compare the responses of various groups of pelagic organisms of different body size and trophic position (mostly phytoplankton, crustacean zooplankton, and fish) to changes in nutrient concentrations which occurred in large and deep Lake Constance during the last 15 years of re-oligotrophication, and
- to try to identify general regularities from this case study by formulating two hypotheses and comparing their predictions to the comprehensive long-term observations from Lake Constance.

It is evaluated whether it is more appropriate to conceptualize a step-wise response along a gradient of increasing aggregation as suggested by hierarchy theory such as a successive response of the physiology of individuals followed by variations of the species composition and then by the community biomass, or a more or less simultaneous reaction at all hierarchical levels. Such analyses are complicated by the scale dependence of the persistence of communities (FROST et al. 1988, RAHEL 1990). Furthermore, the different kinds of responses may be diversely recorded for distinct groups of organisms owing to our specific scale of observations. Results are related to findings from other lakes undergoing re-oligotrophication (SAS 1989).

Trophic history of Lake Constance and spatio-temporal window of nutrient depletion

Upper Lake Constance (in German: Bodensee-Obersee) is a large (472 km²) and deep ($z_{\max} = 253$ m, $z_{\text{mean}} = 101$ m), perialpine lake of warm-monomictic character on the northern fringe of the Alps (47°50'N). Its trophic conditions have changed throughout its history. Palaeolimnological investigations indicate the impact of man on the lake's chemistry since the Roman period two thousand years ago (WESSELS 1998). More recent sediment records analysed with respect to pigment concentrations and taxonomic composition of diatoms revealed that the lake underwent pronounced eutrophication from the beginning of this century until the late seventies. Regular, direct measurements of nutrient concentrations in the open water body started in 1951 and concentrated on phosphorus (P) which was identified as the most limiting nutrient in Lake Constance (ELSTER 1979, SOMMER 1987). A strong, continuous increase of the total phosphorus concentrations during winter mixing (TP_{mix}) from 7 to more than 80 $\mu\text{gP l}^{-1}$ (i.e., by a factor of about 11) was observed from 1951 to about 1980 (GÜDE et al. 1998). Intensive measures to reduce the P-inflow to the lake began during the late sixties, dampened the increase of P-concentrations in the mid-seventies, and prevented a further

enhancement of TP_{mix} by 1980. A period of re-oligotrophication followed with a steady decrease of TP_{mix} from exceeding 80 (1975-1981) to around 30 $\mu\text{g/l}$ in 1993 and 18 $\mu\text{g l}^{-1}$ in 1997, that is TP_{mix} lessened by a factor of 3-4 during the past 15-18 years. Despite the fairly high maximum values of TP_{mix} suggesting eutrophic conditions, chlorophyll concentrations and algal species composition indicated a mesotrophic or meso-eutrophic state (OECD 1982, KÜMMERLIN 1998). The entire water column remained constantly oxygenated which reduced the internal loading from the sediment. This may be attributable to the large depth of the lake ($z_{mean}=101$ m, $z_{max}=253$ m) (JEPPSEN et al. 1997) which prevents recycling of P from the deep layer into the euphotic zone during stratification (GÜDE et al. 1998, GÜDE & GRIES 1998). Furthermore, in deep lakes, the ratio between euphotic and mixing depth drops below the level of sustainable growth at lower chlorophyll concentrations compared to shallow lakes which have smaller mixing depths (REYNOLDS 1992).

The decline of TP_{mix} implies that the seasonal and vertical extension of P-depletion, which presumably is relevant for algal growth, changed greatly (GAEDKE & SCHWEIZER 1993, GAEDKE 1998, her Fig. 1, GÜDE et al. 1998). At maximum eutrophication, concentrations of soluble reactive phosphorus (SRP) were consistently below 3 $\mu\text{g l}^{-1}$ (i.e., at a level presumably limiting growth of numerous algal species (SOMMER 1987, SAS 1989, REYNOLDS 1992)) only during summer (July to September/October) and in the uppermost 10-20 m. During recent years, SRP fell below the level of detection (1 $\mu\text{gP l}^{-1}$) from around April to October/November and down to depths between 20-40 m. Maximum seston C:P-ratios increased continuously during re-oligotrophication and phytoplankton C:P-ratios were above 200:1 (weight by weight) from July to September 1995 (HOCHSTÄDTER 1997). From about November to March/April, algal growth is light-limited owing to a large mixing depth (up to 100 m) relative to the euphotic depth (up to about 20 m) (TILZER & BEESE 1988). As a result, the re-oligotrophication process started in a system with moderate nutrient limitation during a part of the season (SOMMER 1987 and literature cited therein). Consequently, responses are to be expected without a prolonged time lag as no nutrient reduction is required to impose nutrient limitation (CHORUS 1995), and the first and most pronounced responses are expected in summer, followed by (late) spring and (early) autumn. In winter, no direct impact of nutrient concentrations on the pelagic community should occur.

If not indicated otherwise, TP_{mix} is used as a reference value for the P-concentrations available during the subsequent growing period. Processes influencing the TP-concentrations such as P-loading, -sedimentation, -recycling, and -release from the sediment are not considered in this analysis. Minimum concentrations of nitrate remained at all sampling dates and depths above 400 $\mu\text{gN/l}$ (GAEDKE 1998, GÜDE et al. 1998), i.e., well above the threshold commonly assumed for nitrogen limitation (ca. 150-300 $\mu\text{g/l}$; SAS 1989).

Summary of changes observed during re-oligotrophication

In Lake Constance, the long-term dynamics of water chemistry and of the phytoplankton, crustacean, and fish communities during changing nutrient conditions are well-documented, especially during re-oligotrophication (e.g., ELSTER 1979, WALZ et al. 1987, EINSLE 1988, KÜMMERLIN & BÜRGI 1989, TILZER et al. 1991, GAEDKE & SCHWEIZER 1993, SOMMER et al. 1993, ROSSKNECHT 1998, ECKMANN & RÖSCH 1998, GAEDKE 1998, GAEDKE & WEISSE 1998, GÜDE & GRIES 1998, GÜDE et al. 1998, HÄSE et al. 1998, HOFMANN 1998, KÜMMERLIN

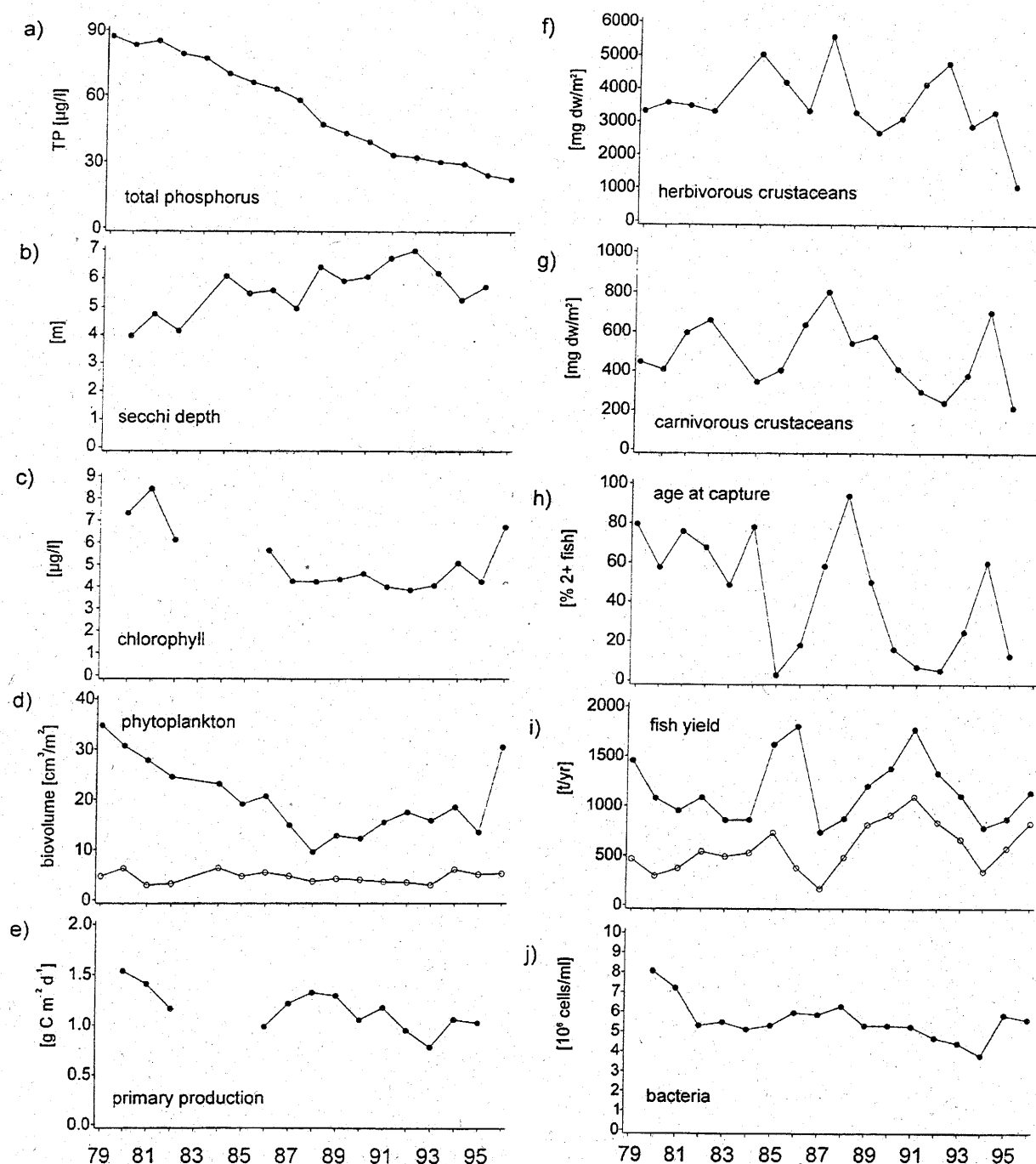


Fig. 1. Long-term development (about 1979-1996) of different parameters indicating the trophic state of Lake Constance. a) Total phosphorus concentrations during winter mixing (from IGKB, for details see GÜDE et al. 1998), b) Average Secchi depth during summer (HÄSE et al. 1998), c) Average chlorophyll concentration in the uppermost 20 m during summer (HÄSE et al. 1998), d) Full dots: average algal biovolume in the uppermost 20 m during summer (cells larger than about 4 µm in length); open circles: average biovolume of "well-edible" phytoplankton in summer (for details see text and GAEDKE 1998), e) Average depth-integrated primary production in summer (HÄSE et al. 1998), f) Average biomass of predominantly herbivorous crustaceans (daphnids, *Eudiaptomus*, *Bosmina*) in summer (STRAILE & GELLER 1998), g) Average biomass of mainly carnivorous crustaceans (*Cyclops*, *Leptodora*, *Bythotrephes*) in summer (STRAILE & GELLER 1998), h) Percentage of 2+ fish in the catch. A linear regression line decreases significantly at the 5-% level which points to a slight increase of the age-at-capture (full time series and data set in ECKMANN & RÖSCH 1998, their Fig. 3), i) Full dots: annual fish

Table 1. Summary of responses to re-oligotrophication of standing stocks and turn-over rates of major functional groups of the pelagic food web of Lake Constance (ca. 1979-1993) (cf. Fig. 1).

P-concentration during homothermy	reduction to ca. 33%
Secchi depth and euphotic depth in summer	increasing
total algal biomass in summer	reduction to ca. 50%
chlorophyll concentration in summer	reduction to ca. 50%
biomass of well-edible algae in summer	unchanged
primary production in summer	reduction to ca. 75%
biomass of rotifers	unchanged (1984-96)
biomass of herbivorous crustaceans in all seasons	unchanged
biomass of carnivorous crustaceans in all seasons	unchanged
reproduction rate of <i>Daphnia galeata</i>	decreasing ?!
age-at-capture of planktivorous whitefish	increasing
habitat and diet composition of fish	some changes
planktivorous fish yield	unchanged
bacterial abundance in summer	declining?
bacterial production	unchanged?

1998, SIMON et al. 1998, STRAILE & GELLER 1998, and literature cited therein, respectively). The present evaluations are based upon the experience gathered during re-oligotrophication which cannot be repeated here in detail, but the reader is referred to the literature cited above. Chemical and plankton measurements were performed weekly (in winter approximately biweekly) at a sampling station ($z_{\max}=147$ m) in the north-western, fjord-like arm (Überlinger See) of the main basin of Upper Lake Constance.

The phytoplankton, crustacean, and fish communities have reacted, at least slightly, to the changes of P-concentrations during re-oligotrophication (Fig. 1, Tables 1, 2). The effect of decreasing nutrient concentrations is non-linear, buffered within the phytoplankton community, and dampened along the food chain as judged by bulk parameters such as biomass and total primary production (Table 1). Total algal biovolume and chlorophyll concentrations declined by ca. 50% (GAEDKE 1998) and primary production by about 25% during summer (HÄSE et al. 1998). The decline of algal biovolume is mostly restricted to large, less-edible species (e.g., pennate diatoms, Chlorophyta, and Cyanophyta; the latter were always of minor importance), whereas standing stocks of well-edible algae, such as small unicellular phytoflagellates, small centric diatoms (e.g., *Stephanodiscus parvus*), and *Chlorella*, remained constant (Fig. 1; GAEDKE 1998). Secchi and euphotic depths provide additional indications for the trophic state of the lake as water transparency is highly dependent on chlorophyll concentrations in Lake Constance (TILZER & BEESE 1983). Average summer values of Secchi and euphotic depths augmented significantly from 4.5 to 6.5 m and from 10.5 to 13 m, respectively (Fig. 1, Table 1), as did minimum values (HÄSE et al. 1998). Total biomass of herbivorous and carnivorous crustaceans (Fig. 1; STRAILE & GELLER 1998) and of rotifers (STRAILE, pers. comm.) remained

yield of Upper Lake Constance; open circles: contribution of coregones to total fish yield (full time series in ECKMANN & RÖSCH 1998, their Figs. 1, 2), j) Bacterial abundance in 0-10 m averaged from June-September (GÜDE, unpubl.). Otherwise, summer is defined as the period after the clear-water phase until the end of the algal summer development (for details see GAEDKE & SCHWEIZER 1993).

Table 2. Hierarchy of responses of phytoplankton, crustacean zooplankton, and planktivorous fish to decreasing P-concentrations observed during the period of re-oligotrophication (1979-around 1993, depending on the group of organisms)

1. Responses at the level of individuals or within species:

- presumably phytoplankton from late spring to early autumn (e.g., maximum C:P-ratios may have increased (HOCHSTÄDTER 1997); in general, weak evidence owing to a lack of suitable measurements).
- zooplankton in summer (e.g., reduction of egg-ratios, STRAILE, unpubl.). The genetic structure of the *Daphnia galeata-hyalina* complex shifted in parallel with the trophic state (WEIDER et al. 1997).
- fish in summer (e.g., slower growth rates inferred from higher age-at-capture, fewer excursions of perch and cyprinids to the pelagic realm in summer, perch switched at smaller sizes from zooplanktivory to piscivory and piscivory of adults became more important (ECKMANN & RÖSCH 1998 and pers. comm.)).

2. Changes in the temporal organisation and taxonomical composition within the communities:

- phytoplankton in spring and especially in summer (pronounced changes of the taxonomical composition which also affect functional attributes such as cell size, vulnerability to grazing, and degree of mixotrophy, and changes in the temporal occurrence of species and their mass abundance (GAEDKE 1998).
- abundances of some rotifer species exhibit significant trends (STRAILE, pers. comm.).
- *Daphnia galeata* appears later in spring and vanishes earlier in autumn under more oligotrophic conditions, consistent (?) decline of *Bosmina* sp. (STRAILE & GELLER 1998).
- The ratio between coregones and perch in the catch increased in recent years, but causal links to re-oligotrophication are uncertain (ECKMANN & RÖSCH 1998 and pers. comm.).

3. Changes in cumulative properties at the level of entire communities:

- Autotrophic biomass and to a lesser extent production decreased in summer (GAEDKE 1998, HÄSE et al. 1998).
 - Changes of the species inventory occur within the phytoplankton community (KÜMMERLIN 1998) to which they are restricted so far.
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unchanged. In contrast to the crustacean community, abundances of some rotifer species exhibited trends related to phosphorus concentrations (STRAILE, pers. comm.). The annual fish yield varied greatly without a distinct trend so far (Fig. 1).

Unaltered standing stocks at consecutive trophic levels despite decreasing nutrient concentrations may result from modified turn-over rates (OKSANEN et al. 1981, PERSSON et al. 1988). The higher reduction in summer algal biomass than in primary production (inferred from ^{14}C -fixation, i.e., not necessarily implying biosynthesis!) points to an increase in weight-specific production rates. They are likely to buffer, but probably do not compensate, the consequences of reduced algal biomass for herbivores. The higher chlorophyll-specific production rates are caused at least partially by the integration over depth. The latter buffers shifts of algal biomass which strongly influence primary production since light-dependent primary production extends to greater depths at lower chlorophyll concentrations and vice versa. The relevance of these mechanisms during re-oligotrophication was demonstrated for Lake Constance (HÄSE et al. 1998). First evaluations of egg-ratios suggest a lower production rate of *Daphnia galeata* (but not *D. hyalina*) in recent years (STRAILE, pers. comm.) (Tab. 1). *D. galeata* is adapted to

more eutrophic conditions and dominates in early summer. Lower egg-ratios of crustaceans would fit with the observed higher age-at-capture of planktivorous whitefish (*Coregones lavaretus*) (Fig. 1) indicating lower growth rates during recent years (ECKMANN & RÖSCH 1998). The fat content of whitefish diminished (RÖSCH, pers. comm.). Habitat preferences and diet composition of perch (*Perca fluviatilis*) changed towards the pattern known from previous more oligotrophic conditions (HARTMANN & NÜMANN 1977, HARTMANN & LÖFFLER 1978). Perch and cyprinids (e.g. *Rutilus*) have been less frequently encountered in the pelagic zone in summer since about 1992-93. In autumn, piscivory of perch became recently more important at smaller-size (IBKF 1997, RÖSCH, pers. comm.). Thus, one may speculate that the buffering of the response of standing stocks along the food chain is enhanced by higher weight-specific turn-over rates at the first trophic level and lower ones at the following trophic levels.

In the main basin of Upper Lake Constance, bacterial abundances (i.e. DAPI-stained particles) in the depth of 0-10 m tend to decrease in summer (e.g., averaged from mid June to September) (Fig. 1), but not on an annual average (monitoring data from IGKB, GÜDE, pers. comm., 1990). However, the interannual variability found in this time series is not reflected in observations performed in the north-western arm of Upper Lake Constance (Überlinger See) from 1990 onwards (SIMON et al. 1998, their Fig. 4). At this site, annual bacterial production did not show any trend (measurements from the more eutrophic period are restricted to one year). The long-term patterns of the plankton community described above are largely confirmed by investigations performed weekly to monthly by the International Commission for the Protection of Lake Constance (IGKB) at a central station in Upper Lake Constance (MÜLLER 1998).

Working hypotheses

To learn general lessons from a case study, the manifold and often interrelated responses have to be classified by means of abstractions. The implicit reduction of complexity must be performed with great care as it may have far-reaching consequences for the results. Two hypotheses are formulated and tested. They are embedded into the mutually supplementing frameworks of (I) hierarchy theory and of (II) general concepts regarding the structure and functioning of (pelagic) ecosystems (e.g., OKSANEN et al. 1981, CARPENTER et al. 1985, PERSSON et al. 1988, MCQUEEN et al. 1989).

Hierarchy of step-wise responses

This hypothesis assumes that the food web organization may be approximated by a nested hierarchical structure (MÜLLER 1992) and that different levels, which exhibit specific dynamic properties, can be defined. Each level incorporates all inferior subsystems and, in turn, is part of higher levels itself. The higher levels determine the overall envelope in which the lower ones may (re)act. The latter represent the biological potential of the entire system. Central ideas of hierarchy theory are that variations at higher levels are smaller than the sums of the variations of the parts, and that higher levels vary and respond on larger spatio-temporal scales than do lower ones. The latter idea was confirmed for different plankton groups of Lake Constance (GAEDKE et al. 1996a). This capacity to filter signals from lower levels is thought to be partially attributed to the potential of self-organization and not merely to the law of great

numbers (for details see e.g. MÜLLER 1992). Studies of aquatic and terrestrial communities revealed that stability at higher levels of aggregation does not demand stability at the level of individual species (FROST et al. 1988, RAHEL 1990 and lit. cited therein). Community stability was found to depend on the spatial and temporal scale, the level of (taxonomical) resolution, and the numerical resolution, i.e., whether the absolute abundance, abundance rankings, or the presence or absence (species inventory) is considered.

As in most abstraction procedures, the allocation of features of the real world to distinct conceptual units remains arbitrary to some extent. In the present study, three hierarchical levels are distinguished at which responses to trophic changes may occur:

1. The level of processes occurring within species including physiological characteristics, elementary composition (e.g. C:P-ratio), individual growth or turn-over rates, behaviour, genetic shifts, and clonal composition.
2. The level of processes occurring within communities consisting of numerous species which exhibit some functional similarities (e.g., phytoplankton, crustacean zooplankton, and fish). This level includes the taxonomical composition of the community, the relative importance of various functional sub-groups (e.g., well- and less-edible algae, raptorial and filter feeders), and the temporal organisation. The latter may be derived from, e.g., the species succession and the timing of mass development of individual species.
3. The level of cumulative properties (or collective attributes) of the entire communities such as the total biomass, production, or species inventory or diversity. The distinction between changes in the taxonomical composition (i.e., the relative importance of individual species) and in the species inventory (i.e., the presence or absence of species) is not absolute, but a gradual transition from the first to the second is to be expected.

Variations at higher levels may exert feed-back effects on lower ones. For example, improved light and oxygen conditions owing to reduced algal biomass or changes in zooplankton biomass and grazing pressure (level III) may alter the taxonomical composition (level II). As most attributes mentioned above may equally well be modified by other factors than nutrient changes, independent evidence is required to establish causal mechanisms (see below).

It is hypothesized that responses to external forcing occur subsequently at the three different hierarchical levels and at different time scales, i.e., the level at which responses to external variations are observed is taken as a measure of the reaction strength. This leads to the following expectations:

- (1) In the beginning of the oligotrophication process, resources are utilized more efficiently by the organisms. Physiological or behavioral adaptations, such as migration to the littoral zone implying changes in the diet composition, may happen at the level of individual organisms or a shift among different clones. Seasonal patterns and properties of the entire community remain largely unaffected.
- (2) If a more severe resource depletion entails that minimum demands of individual species are not met for prolonged periods of time, systematic changes in the taxonomic composition take place, and they may concern functional properties of the entire community as well. For example, the share of species with low resource demands or species that exploit alternative nutrient sources such as mixotrophs may increase. The temporal organization of the community may vary, for example, through a shift of the mass occurrence of individual species from summer to spring. Such processes depend on the response time of the organisms relative to the variability of the environmental factor. The species inventory and community biomass remain largely unaltered at this stage.

- (3) Finally, total community biomass and process rates such as production initially decrease during the most resource-depleted periods if the internal capacity of the system to buffer the external variations at the first and second level is exhausted. The species inventory may change owing to local extinction or immigration of species.

Dependence on trophic positions and intrinsic scales (body size)

Based on common knowledge of the functioning of pelagic ecosystems, the various groups of pelagic organisms are supposed to respond differently to alterations in the seasonal nutrient regime. First, it is to be expected that the impact of such a bottom-up effect is most important for primary producers and becomes buffered along the food chain, i.e., organisms with higher trophic positions are presumably less affected by nutrient changes, but are equally well or more strongly under top-down control (e.g., CARPENTER et al. 1985, PERSSON et al. 1988, MCQUEEN et al. 1986, 1989). Primary production (and often production of heterotrophic bacteria) depends directly on the uptake of inorganic nutrients. Provided that the main food web structure remains similar, growth of herbivores (including juveniles of many carnivorous species) may be influenced by variations in the quantity and quality (e.g. C:P-ratio, edibility) of autotrophic production, whereas carnivores are mostly affected by the quantity of herbivores because the elementary composition of prey and predator is similar.

Secondly, trophic positions and individual body weights of organisms are related to each other in pelagic food webs as there is roughly a succession of autotrophs, herbivores, and carnivores along the size gradient (e.g. GAEDKE et al. 1996b). The larger body sizes of organisms at higher trophic levels imply, in turn, that they have longer generation times, higher spatial mobility, and respond more slowly to environmental changes than the small primary producers. Thus, strength and time scale of potential reactions are supposed to be linked together via body size, and the most pronounced and fastest reactions are expected for phytoplankton.

A further complication arises from the restricted time scale perceived by human investigators. Given that limnological research is usually conducted at a fixed time scale of days to months or at most a few years (but see below), we are more likely to record taxonomical changes in phytoplankton communities and physiological responses of fish (cf. SCHINDLER 1990). Hence, the differences in intrinsic time scales of organisms varying greatly in body size have to be accounted for when measuring and comparing the reactions at diverse hierarchical levels.

Comparison between observations and hypotheses

The reactions of the various communities observed so far are largely in accordance with predictions derived from the two working hypotheses formulated above (Table 2), but interesting deviations do occur. Considering the postulated step-wise response along a gradient of increasing aggregation, the following statements can be made:

- First vs. second level: For each group of organisms, there is evidence that individual level changes took place prior to or simultaneously with reactions at the next higher hierarchical level (Table 2, Fig. 2). Alterations at the individual level are better established for fish than for smaller-sized organisms which may at least partially be an artefact of our scale of per-

- HARTMANN, J. & LÖFFLER, H. (1978): Saisonale bodennahe Verteilung von Fischen im eutrophierten Bodensee. – Arch. Hydrobiol. **83**: 69-79.
- HARTMANN, J. & NÜMANN, W. (1977): Percids of Lake Constance, a lake undergoing eutrophication. – J. Fish. Res. Board Can. **34**: 1670-1677.
- HARTMANN, J. & PROBST, L. (1995): Divergent distributions of prey and predator, a fishing effect? – Aquat. Sci. **57**: 106-118.
- HÄSE, C., GAEDKE, U., SEIFRIED, A., BEESE, B. & TILZER, M.M. (1998): Phytoplankton response to re-oligotrophication in large and deep Lake Constance: Photosynthetic rates and chlorophyll concentrations. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **53**: 159-178.
- HOCHSTÄDTER, S. (1997): Erstellung und Analyse von Phosphornahrungsnetzen im pelagischen Kreislauf des Bodensees. – Dissertation, Universität Konstanz, Hartung-Gorre Verlag, Konstanz, Germany, 158 pp.
- HOFMANN, W. (1998): The response of *Bosmina* (*Eubosmina*) to eutrophication of Lake Constance (Obersee): the subfossil record. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **53**: 275-283.
- IBKF (1997): Die Fischerei im Bodensee-Obersee im Jahre 1996. – Gesamtbericht zur IBKF 1997, 8 pp.
- JEPPSEN, E., JENSEN, J.P., SØNDERGAARD, M., LAURIDSEN, T., PEDERSEN, L.J. & JENSEN, L. (1997): Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. – Hydrobiologia **342/343**: 151-164.
- KÜMMERLIN, R. (1998): Taxonomical response of the phytoplankton community of Upper Lake Constance (Bodensee-Obersee) to eutrophication and re-oligotrophication. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **53**: 109-117.
- KÜMMERLIN, R. & BÜRGI, H.-R. (1989): Die langjährige Entwicklung des Phytoplanktons im Bodensee (1961-1986). – Ber. IGKB **39**: 1-175 (ISSN 1011-1263).
- MCQUEEN, D.J., JOHANNES, M.R. S., POST, J.R., STEWART, T.J. & LEAN, D.R.S. (1989): Bottom-up and top-down impacts on freshwater pelagic community structure. – Ecol. Monogr. **59**: 289-309.
- MCQUEEN, D.J., POST, J.R. & MILLS, E.L. (1986): Trophic relationships in freshwater pelagic ecosystems. – Can. J. Fish. Aquat. Sci. **43**: 1571-1581.
- MÜLLER, F. (1992): Hierarchical approaches in ecosystem theory. – Ecol. Modelling **63**: 215-242.
- MÜLLER, H. (1998): Limnologischer Zustand des Bodensees 1997. – Ber. IGKB **25**.
- OECD (1982): Eutrophication of waters, monitoring, assessment and control. – OECD, Paris, 154 pp.
- OKSANEN, L., FRETWELL, S.D., ARRUDA, J. & NIEMALA, P. (1981): Exploitation ecosystems in gradients of primary productivity. – Am. Nat. **118**: 240-261.
- PERSSON, L., ANDERSSON, G., HAMRIN, S.F. & JOHANSSON, L. (1988): Predator regulating and primary production along the productivity gradient of temperate lake ecosystems. – In: CARPENTER, S.R. (ed.): Complex interactions in Lake Communities. – Springer, New York, pp. 45-65.
- RAHEL, F. (1990): The hierarchical nature of community persistence: a problem of scale. – Am. Nat. **136**: 328-344.
- REYNOLDS, C.S. (1992): Eutrophication and the management of planktonic algae: What Vollenweider couldn't tell us. – In: SUTCLIFFE, D.W. & JONES, J.G. (eds.): Eutrophication: Research and application to water supply. – Freshwat. Biol. Ass., pp. 4-29.
- ROSSKNECHT, H. (1998): Langjährige Untersuchungen chemischer Parameter im Bodensee-Obersee. – Ber. IGKB **48**.
- SAS, H. (1989): P48 – Lake restoration by reduction of nutrient loading. – Academia Verlag, Sankt Augustin, Germany, 497 pp.
- SCHEFFER, M., HOSPER, S.H., MEIJER, M.-L., MOSS, B. & JEPPSEN, E. (1993): Alternative equilibria in shallow lakes. – TREE **8**: 275-279.
- SCHINDLER, D.W. (1990): Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem function and structure. – OIKOS **57**: 25-41.
- SCHMIEDER, K. (1997): Littoral zone – GIS of Lake Constance: A useful tool in lake monitoring and autecological studies with submersed makrophytes. – Aquatic Botany. **58**: 333-346.

- SIMON, M., BUNTE, C., SCHULZ, M., WEISS, M. & WÜNSCH, C. (1998): Bacterioplankton dynamics in Lake Constance (Bodensee): Substrate utilization, growth control, and long-term trends. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **53**: 195-221.
- SOMMER, U. (1987): Factors controlling the seasonal variation in phytoplankton species composition – a case study for a nutrient rich, deep lake. – Prog. Phycol. Res. **5**: 123-178.
- (1993): The scientific basis of eutrophication management: Reconciling basic physiology and empirical biomass models. – Mem. Ist. Ital. Idrobiol. **52**: 89-111.
- SOMMER, U., GAEDKE, U. & SCHWEIZER, A. (1993): The first decade of oligotrophication of Lake Constance. II. The response of phytoplankton taxonomic composition. – Oecologia **93**: 276-284.
- STABEL, H.-H. & KLEINER, J. (1995): Folgen der Phosphatabnahme für die Entwicklung im Bodensee. – gwf **136**: 601-607.
- STRAILE, D. (1995): Die saisonale Entwicklung des Kohlenstoffkreislaufes im pelagischen Nahrungsnetz des Bodensees – Eine Analyse von massenbilanzierten Flußdiagrammen mit Hilfe der Netzwerktheorie. – Dissertation, Universität Konstanz, Hartung-Gorre Verlag, Konstanz, Germany, 157 pp.
- STRAILE, D. & GELLER, W. (1998): Crustacean zooplankton in Lake Constance from 1920 to 1995: Response to eutrophication and re-oligotrophication. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **53**: 255-274.
- TILZER, M.M. & BEESE, B. (1988): The seasonal productivity cycle and controlling factors in Lake Constance. – Schweiz. Z. Hydrol. **50**: 1-39.
- TILZER, M.M., GAEDKE, U., SCHWEIZER, A., BEESE, B. & WIESER, T. (1991): Interannual variability of phytoplankton productivity and related parameters in Lake Constance: No response to decreased phosphorus loading? – J. Plankton Res. **13**: 755-777.
- WALZ, N., ELSTER, H.-J. & MEZGER, M. (1987): The development of the rotifer community structure in Lake Constance during its eutrophication. – Arch. Hydrobiol. Suppl. **74**: 452-487.
- WANG, N. & ECKMANN, R. (1994): Distribution of perch (*Perca fluviatilis* L.) during the first year of life in Lake Constance. – Hydrobiologia **277**: 135-143.
- WEIDER, L.J., LAMPERT, W., WESSELS, M., COLBOURNE, J.K. & LIMBURG, P. (1997): Long-term genetic shifts in a microcrustacean egg bank associated with anthropogenic changes in the Lake Constance ecosystem. – Proc. R. Soc. Lond. B **264**: 1613-1618.
- WESSELS, M. (1998): Late-Glacial and postglacial sediments in Lake Constance (Germany) and their palaeolimnological implications. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **53**: 411-449.
- WINFIELD, I.J., RÖSCH, R., APPELBERG, M., KINNERBÄCK, A. & RASK, M. (1998): Recent introductions of the ruffe (*Gymnocephalus cernuus*) to *Coregonus* and *Perca* lakes in Europe and an analysis of their natural distributions in Sweden and Finland. – J. Great Lake Research **24**: 235-248.

