Predictive Limnology: Inductive or Deductive Ecological Models?

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Abstract: The paper presumes that not the inductive or deductive nature of models decides on their benefit for limnology but the aim of prediction and whether a model does meet it. It is distinguished between short-term and long-term predictions as common in limnology. Short-term predictions are necessary for tactical control of sudden escalating impacts on freshwater systems such as harmful algal blooms or toxic contamination. Long-term predictions are needed for strategic management of gradual escalating impacts on freshwater systems such as eutrophication or acidification. Two ecological models are used to demonstrate that: (1) deductive deterministic models are invaluable for strategic management to assess alternative control options before implementation, and (2) inductive neural network models prove to become invaluable for tactical control to predict timing, magnitudes and succession of harmful impacts.

1. INTRODUCTION

There is a dispute in the literature about the role that models play for ecology , and especially for limnology. Despite a broad consensus that models are needed for hypotheses testing and predictions about properties of lakes and rivers, the question arises which types of models are most useful for which aim.
Scheffer and Beets (1994) distinguish between simple generic and complex simulation models arguing that only simple models have potential for unravelling the functioning of ecosystems, supposing that complex models are uncontrollable. Regarding a third type of models they renew the question brought up by Levins (1968) and Simberloff (1983), whether abstract models of theoretical ecologists contribute at all to understanding of nature.
Livingstone and Imboden (1996) distinguish between inductive statistical and deductive deterministic models concluding that only deterministic predictions based on all available information , including knowledge of relevant processes obtained in other context, are likely to be of most value. As a compromise, they propose a combination of a deductive, process-oriented basis with a minimum of inductive elements describing processes that are not yet well enough understood to be modelled otherwise.
Peters (1986) refers to Popper (1972) concluding that the only objective test for understanding is predictive success and therefore any dispute between the inductive and deductive approach must be based on their respective predictive power. Consequently, Rigler and Peters (1995) plead for the inductive approach arguing that only empirical, holistic models can produce useful predictions in limnology. Hakanson and Peters (1995) back up this view stating that mainly simple statistical models have proven predictive power and applicability, establishing the sub-discipline predictive limnology.

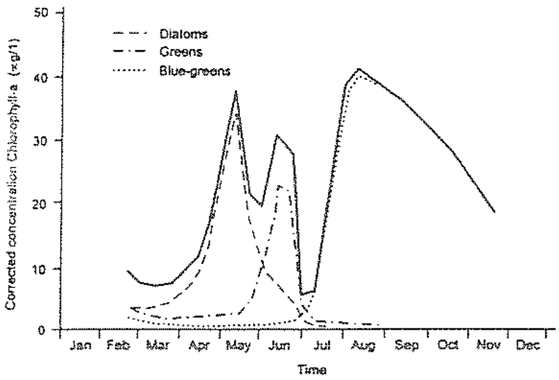
The aim of this paper is to discuss achievements by the inductive neural network model ANNA and the deductive deterministic model SALMOSED in the context of this dispute. Results show that both models are explanatory and predictive but achieve different resolution in time and species. Following Popper (1972) that the only objective test for understanding is predictive success, it is concluded that different types of models are needed in limnology depending on aims of predictions. From our experience deductive models have proven to be predictive tools in limnology for strategic planning to assess a variety of management scenarios in a medium- and long-term context (see Chapra and Canale, 1991; Recknagel 1989; Recknagel et al., 1995). Artificial neural network models emerged as an inductive model in limnology only recently proving already its predictive capacity for tactical control in a short-term context (Recknagel et al., 1997a, b; Recknagel, 1997; Wilson and Recknagel, 1997).

2. PREDICTION OF PHYTOPLANKTON ABUNDANCE IN LAKES

Modelling emerges as an useful method to improve the explanation, prediction and control of harmful algal blooms, where both modelling approaches, the inductive and the deductive, are intensively explored with varying success.
In Fig. 1 three deductive models for phytoplankton abundance are documented. Each of them represents a prototype model for different views on algal dynamics. Bierman (1976) gave an excellent example for using the ecosystem level for deterministic simulations of the succession of algal groups. This approach was widely used in the seventies and eighties representing phytoplankton in pelagic food-web models by so-called functional groups. The differentiation of phytoplankton according to size and/or physiology was a first step towards referring the simulated dominance of an algae group to specific impairments of water quality. Okada and Aiba (1983) have chosen the population level to simulate the vertical distribution of *Microcystis* in a calm water column over time. They determined vertical and temporal rates of photosynthesis and buoyancy to simulate emergence and disappearance of *Microcystis* blooms at the surface of eutrophic waters. No interactions with competing phytoplankton species and the remaining food-web were considered. In an attempt to explain qualitatively species succession of algae in a specific lake, Reynolds (1984) constructed a nomogram for species assemblages related to seasons and trophic states of lakes.

Reynolds (1984) synthesised in this heuristic model knowledge on 49 algae species using data of twelve mainly temperate lakes.

In Fig. 2 three prototypes of inductive models for phytoplankton are documented. Sakamoto (1966), and later Dillon and Rigler (1974) developed the first empirical models for steady-state predictions of chlorophyll-a in lakes depending on the total phosphorus concentration. Vollenweider (1967) generalised this model type by predicting chlorophyll-a depending on total phosphorus input and hydraulic retention time, that is widely used for trophic status classification of lakes. Whitehead and Hornberger (1984) applied the time series approach to model chlorophyll-a dynamics in the River Thames. Hypothetical growth, death and transport rates for a phytoplankton mass-balance were updated by recursive estimation techniques using measured reference data. Recknagel et al. (1997a, b) used artificial neural networks for modelling and prediction of timing and magnitudes of blue-green algae species in freshwater lakes and a river. They utilised historical time series of limnological data to extract patterns responsible for abundance and succession of blue-green algae species.



(a)

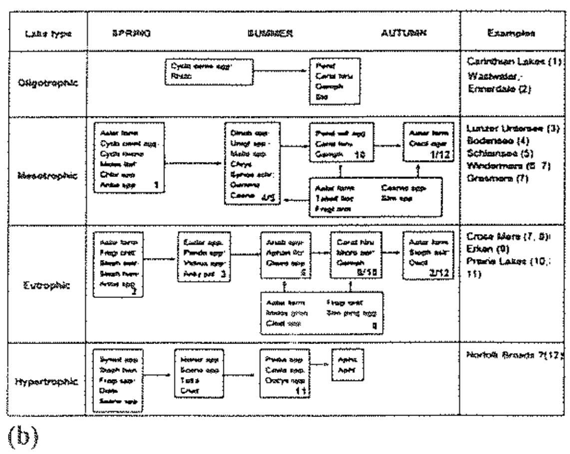


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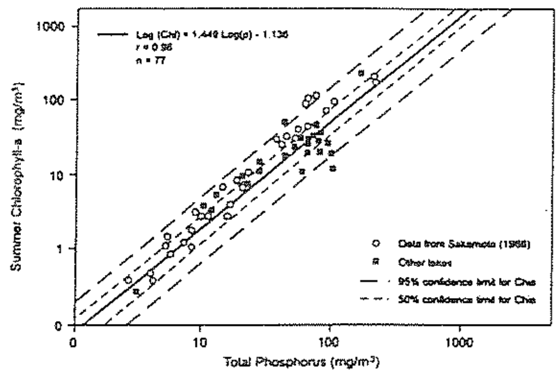
Fig. 1: Deductive Modelling of phytoplankton: (a) Food web dynamics (Bierman, 1976); (b) Species succession (Reynolds, 1984)



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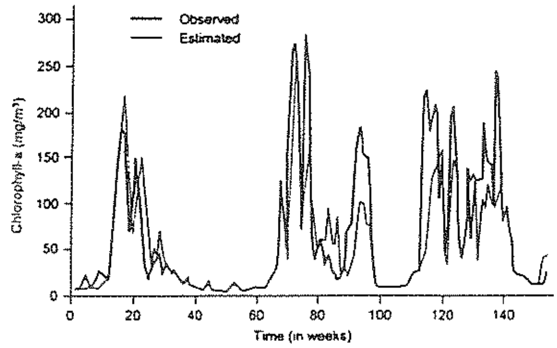

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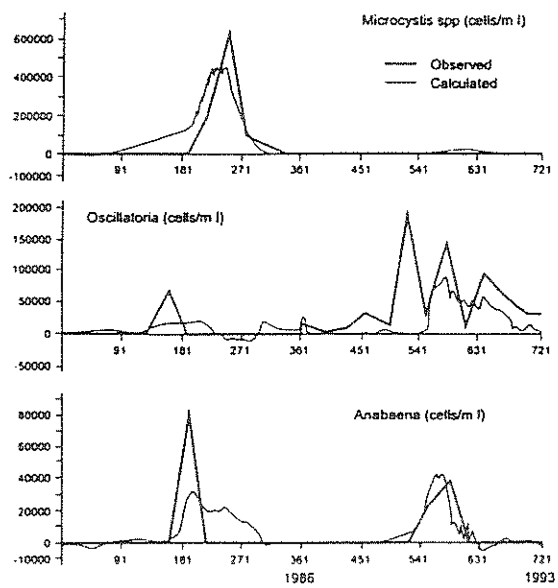


(c)

Fig. 2: Inductive modelling of phytoplankton: (a) Chlorophyll-a steady state (Dillon and Rigler, 1974); (b) Chlorophyll-a dynamics (Whitehead and Hornberger, 1984); (c) Species dynamics (Recknagel et al., 1997a, b)

2.1. Deductive model SALMOSED

The model SALMOSED (Benndorf and Recknagel 1982; Recknagel et al. 1995) is a deterministic lake ecosystem model representing three functional algal groups (colonial blue-green algae, microplankton diatoms and green algae / nanoplankton diatoms) and interactions with the pelagic food web and nutrient cycles. It has been validated for a variety of lakes with different trophic states, morphometry and climate conditions (Recknagel 1989). In Figs.3 and 4 strategic predictions by the model SALMOSED are documented regarding assessment of alternative management options. The scenario analysis in Fig. 3 assesses medium-term effects of management options on algal growth in the humic Barossa Reservoir, South Australia. It shows that artificial destratification of the Barossa Reservoir in summer may decline algal biomass by up to 50%. But it would no longer be a sustainable control option for algal growth, as soon as current water discolouration by allochthonous organic carbon is stopped. The scenario analysis in Fig. 4 assesses long-term effects of management options on algal growth in Lake Yunoko, Japan. It shows that a significant decrease of algal biomass by up to 60 % in summer can be achieved over a period of ten years by the combination of a 50% reduction of external phosphorus loading and artificial destratification. Single sediment dredging in the first year as an alternative option for destratification would not be advisable, as eutrophication processes in Lake Yunoko are driven mainly by external phosphorus loadings.

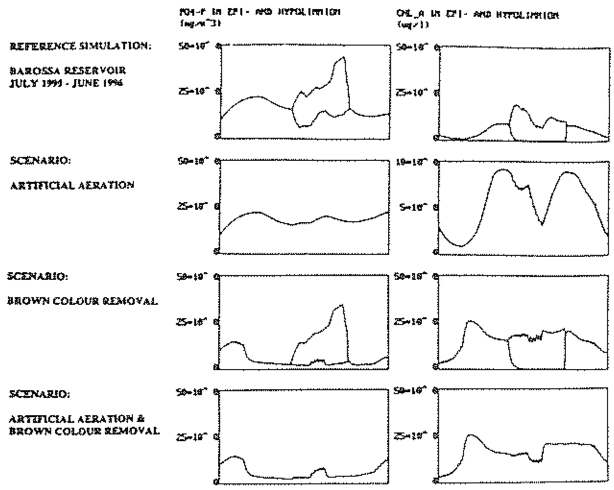


Fig. 3: Scenario analysis on eutrophication control of the humic Barossa Reservoir by artificial destratification

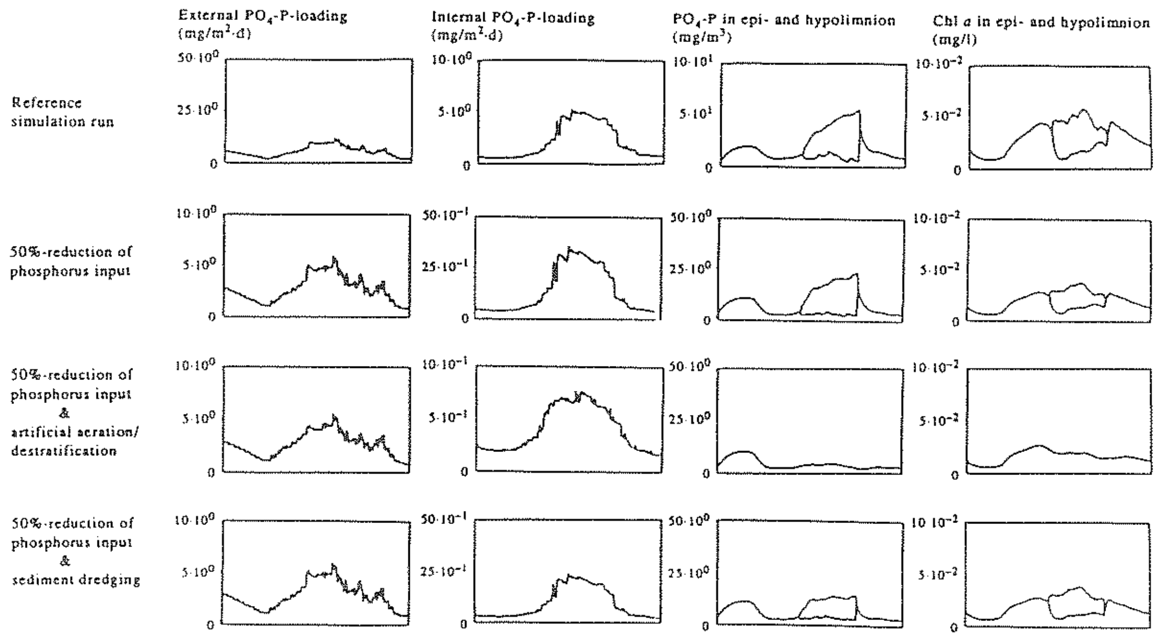


Fig. 4: Scenario analysis on long-term effects of eutrophication control of Lake Yunoko by reduction of phosphorus input, artificial destratification and a single sediment dredging 10 years after introduction in 1980

2.2. Inductive model ANNA

ANNA is an artificial neural network model for predicting species abundance and succession of blue-green algae in freshwater lakes (Recknagel et al. 1997a; Recknagel et al. 1997b; Recknagel 1997c; Wilson and Recknagel 1997). ANNA is characterised by a feedforward architecture with backpropagation for training and a hyperbolic transfer function to calculate activation levels of neurons. It has been validated for three lakes under different climate conditions and proved to be predictive for up to five abundant algal species. The most comprehensive case study with ANNA was conducted for the shallow hypertrophic Lake Kasumigaura (Japan) recurring abundant in blue green algae species. Limnological time-series for ten years from Lake Kasumigaura were used for training and validation. Measurements of controlling factors for algal growth and mortality such as water transparency, nutrient concentrations and zooplankton densities were represented in the input layer. Measurements of the 5 dominating blue-green algae species *Microcystis, Oscillatoria, Phormidium, Gomphospheria* and *Anabaena* were represented in the output layer. In Fig. 5 results of split-plot validation of the model ANNA are represented. Independent phytoplankton data of the years 1986 and 1993 are compared with data predicted by the neural network after training with data sets of the eight remaining years. Results show that the model predicts the major peak events of the five blue-green algae species well in timing and magnitudes. Wilson and Recknagel (1997) show that further improvements are possible using optimised configuration and cross-validation.

In an attempt to prove explanatory potential of the model ANNA a scenario analysis was carried out to test hypotheses on algal succession in Lake Kasumigaura. A succession of *Microcystis* by *Oscillatoria* was observed in Lake Kasumigaura from the years before 1987 to the years from 1987 afterwards by Takamura et al. (1992). As they measured a significant increase in the TN (total nitrogen)/TP (total phosphorus) ratio from 10 to approx. 20 corresponding with the timing of species succession, they proposed to consider the changed nutrient conditions as the possible reason for the species succession.

In the framework of a scenario analysis alternative explanations for the species succession in Lake Kasumigaura were tested with ANNA. Following four scenarios have been defined and tested: (1) swap phosphorus and nitrogen data between 1986 and 1993, (2) swap zooplankton data between 1986 and 1993, (3) swap light, temperature and Secchi depth data between 1986 and 1993, (4) swap chlorophyll-a data between 1986 and 1993. Fig. 5 shows the results of the scenario analysis. While the swap of the nutrient conditions between 1986 and 1993 did not influence the behaviour of *Microcystis, Oscillatoria* experienced a shift of its maximum peak from 1993 to 1986. The same behaviour of the two species resulted in the swap of zooplankton data as studied in scenario 2. The only case where the maximum peak of *Microcystis* was shifted from 1986 to 1993 was in scenario 3, where light, temperature and Secchi depth data were swapped between 1986 and 1993. But this conditions in scenario 3 caused significant decreases of peaks of *Oscillatoria* in both years. Finally, scenario 4 shows that chlorophyll-a is obviously the most sensitive forcing function of the model for *Oscillatoria* by strengthening maximum peaks in 1993, while chlorophyll-a did not affect significantly the behaviour of *Microcystis*.

The scenario analysis allows to conclude that *Microcystis* seems less to be affected by the change in nutrient conditions between 1986 and 1993 but by the change in light, transparency and temperature conditions. In contrast, *Oscillatoria* seems to be not only sensitive to changes in nutrient conditions but to changes in zooplankton conditions too.

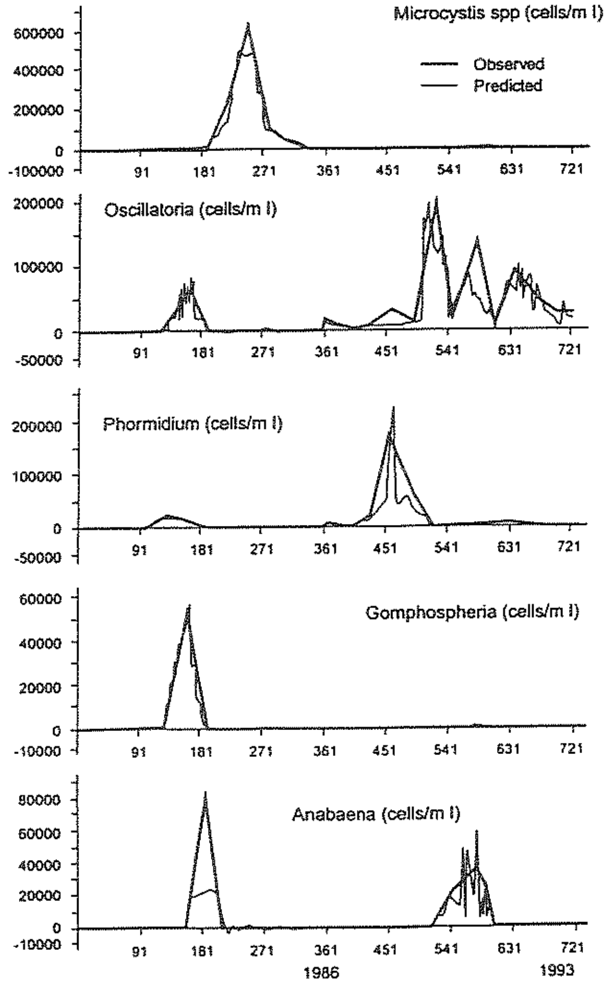
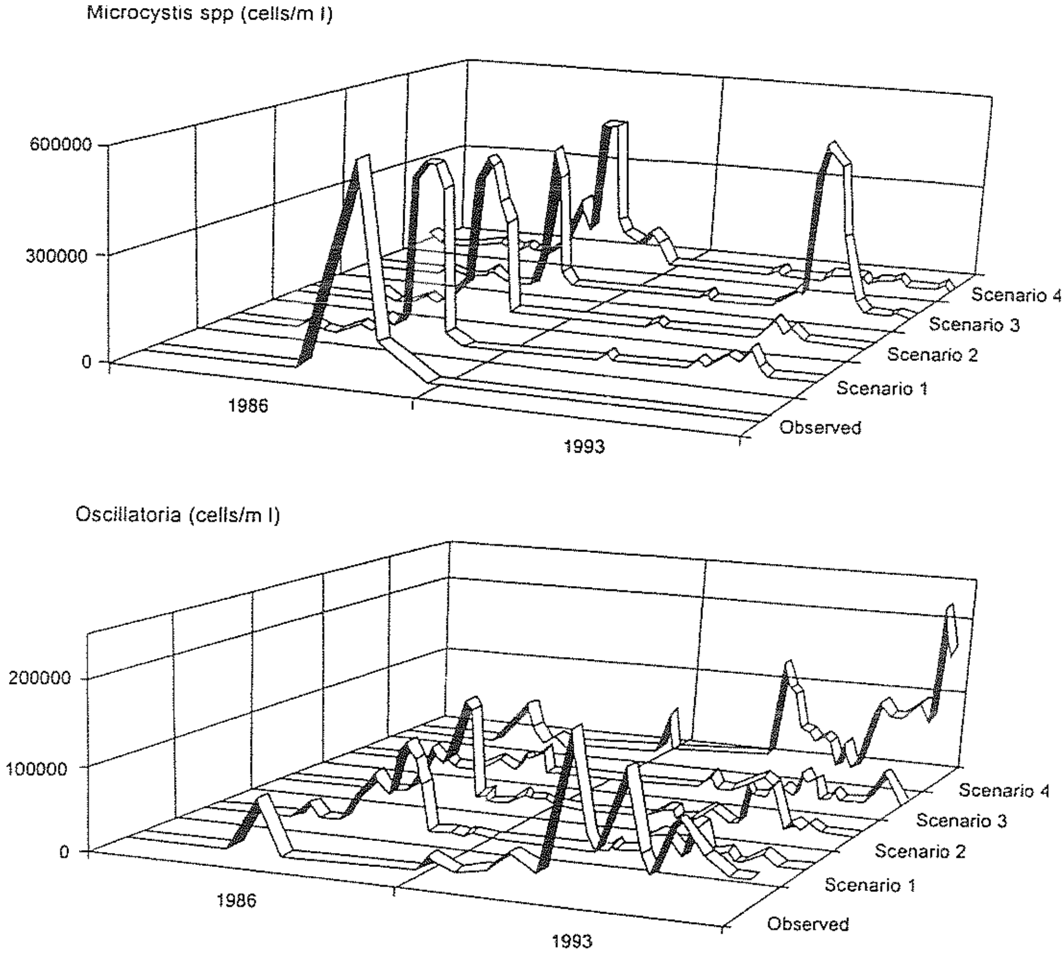


Fig. 5: Validation of the phytoplankton model ANNA trained by data sets for eight single years choosing the best predicting day for the years 1986 and 1993



Scenario 1: Swap phosphorus and nitrogen data between 1986 and 1993
Scenario 2: Swap zooplankton data between 1986 and 1993
Scenario 3: Swap light, temperature and Secchi depth data between 1986 and 1993
Scenario 4: Swap chlorophyll-a data between 1986 and 1993

Fig. 5: Scenario analysis on succession of *Microcystis* by *Oscillatoria*

3. CONCLUSIONS

(1) Predictive limnology as synonym for models with predictive validity and practical applicability for characteristics of freshwater systems requires a variety of models to meet aims of predictions regarding resolution in time and species.
(2) Steady-state predictions by statistical inductive models have reached a high degree of validity and practical applicability in limnology but give no explanation and lack in resolution of time and species.
(3) Artificial neural networks promise a new quality of inductive modelling in limnology. They prove to be predictive and explanatory for sudden escalating limnological problems such as algal blooms due to high resolution in time and species.
(4) Deterministic deductive models prove to be predictive and explanatory for gradually escalating limnological problems such as eutrophication or acidification. They are invaluable for long-term predictions of strategic management despite restrictions in resolution of time and species.

4. ACKNOWLEDGEMENTS

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