

Alternative Equilibria in Shallow Lakes

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The turbidity of lakes is generally considered to be a smooth function of their nutrient status. However, recent results suggest that over a range of nutrient concentrations, shallow lakes can have two alternative equilibria: a clear state dominated by aquatic vegetation, and a turbid state characterized by high algal biomass. This bi-stability has important implications for the possibilities of restoring eutrophied shallow lakes. Nutrient reduction alone may have little impact on water clarity, but an ecosystem disturbance like foodweb manipulation can bring the lake back to a stable clear state. We discuss the reasons why alternative equilibria are theoretically expected in shallow lakes, review evidence from the field and evaluate recent applications of this insight in lake management.

The theoretical possibility of ecosystems having more than one equilibrium has long been recognized^{1,2}. Support from field data is less easily obtained. However, recent observations in shallow lakes have led aquatic ecologists to suspect that these ecosystems may indeed possess two alternative stable states, a turbid and a clear one³⁻⁷. Many ecological mechanisms are probably involved, but the whole feedback system is thought to center around the interaction between submerged vegetation and turbidity (Fig. 1). Vegetation tends to enhance water clarity, while a high turbidity, on the other hand, prevents the growth of submerged plants. The adverse impact of turbidity on vegetation growth is simply a matter of light limitation. Submerged plants can only grow down to a certain turbidity-dependent depth (Fig. 2) beyond which the light availability becomes too low⁹. The positive effect of vegetation on water clarity is the result of a number of different mechanisms: resuspension of bottom material is reduced by vegetation¹⁰; aquatic plants provide a refuge against planktivorous fish for phytoplankton-grazing zooplankton³; veg-

etation suppresses algal growth due to a reduction of nutrient availability¹¹; and plants release allelopathic substances that are toxic to algae¹².

Although the quantitative importance of each of these submechanisms is often hard to assess and may vary between lakes, analysis of comprehensive data sets supports the view that there is an overall positive effect of vegetation on water transparency in freshwater lakes. Lakes with a high cover of submerged macrophytes tend to have a higher transparency than lakes with the same nutrient status in which vegetation is sparse or absent (Fig. 3).

Theory of alternative lake equilibria

Whether these ecological mechanisms may indeed be expected to cause alternative stable states has been explored extensively by means of minimal models^{5,6}. The

basic idea, however, can already be clarified by a simple graphical approach (Fig. 4). Vegetation can stabilize a clear-water state in shallow lakes up to relatively high nutrient loadings, but once the system has switched to a turbid state, it takes a strong nutrient reduction to enable recolonization by plants. This graphical analysis is based on some rather crude simplifications like the assumption that submerged vegetation disappears abruptly at a critical turbidity, but models employing more realistic assumptions⁶ produce similar results (an example is given in Box 1).

The stability properties of such systems can be visualized by means of 'marble-in-cup' pictures (Fig. 5). The equilibrium line with 'catastrophe fold' shown at the bottom of the figure is computed from the vegetation-algae model explained in Box 1. The valleys in the stability landscapes correspond to stable

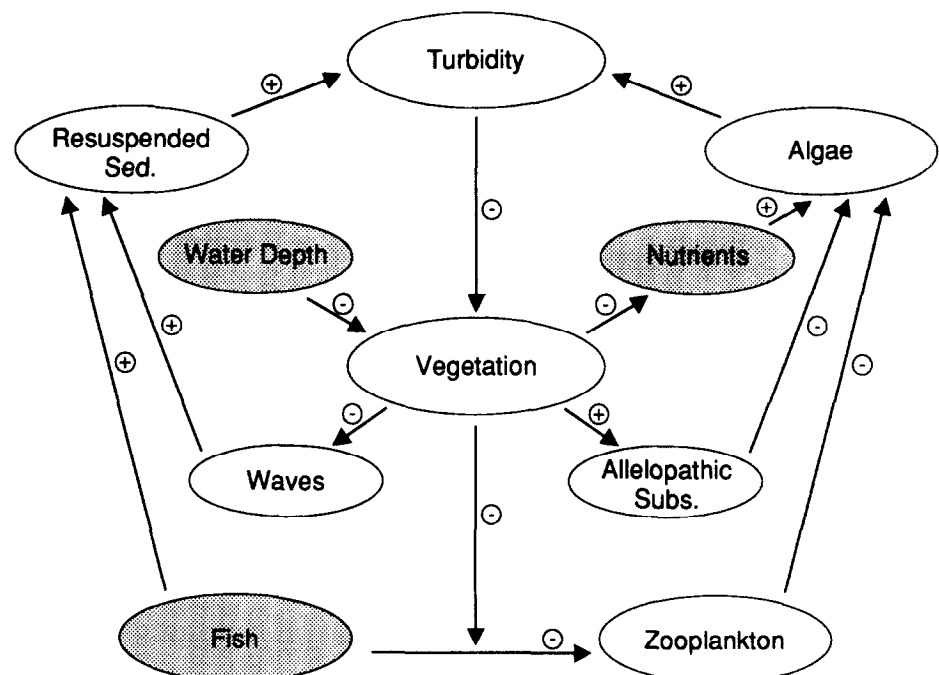


Fig. 1. Main feed-back loops thought to be responsible for the existence of alternative equilibria in shallow lake ecosystems. The qualitative effect of each route in the diagram can be determined by multiplying the signs along the way. In this way it can be seen that both the vegetated and the turbid state are self-reinforcing. The qualitative effect of management measures discussed in this review can be checked in the same way if a 'manager' box with positive or negative arrows pointing to either of the shaded parts of the system is added.

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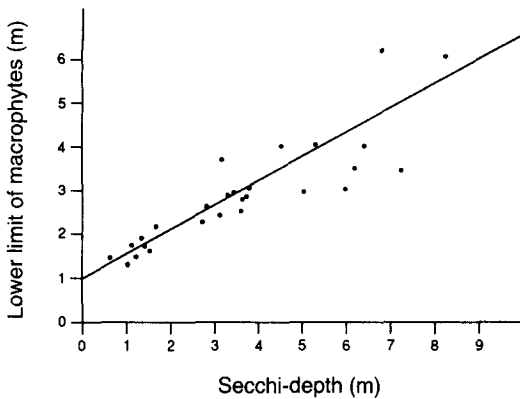


Fig. 2. Relation between transparency ('secchi-depth') and the lower limit of vegetation in 27 Finnish lakes⁸.

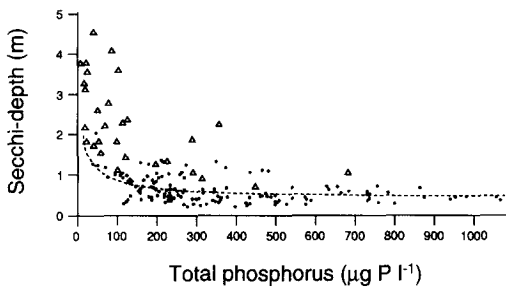


Fig. 3. Summer mean transparency ('secchi-depth') in relation to lake water total phosphorus for shallow Danish lakes with (triangles) and without (dots) high cover of submerged vegetation⁷.

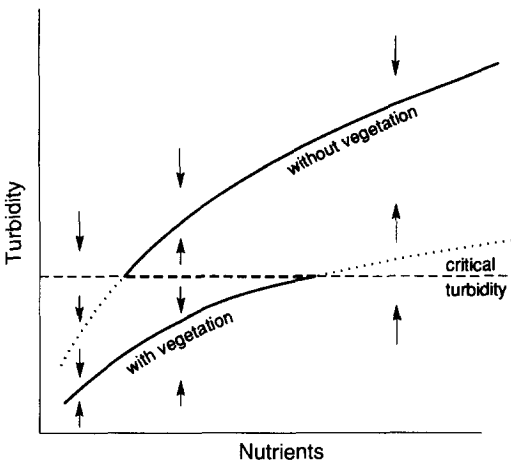


Fig. 4. Alternative equilibrium turbidities related to the presence and absence of aquatic vegetation⁶. Equilibrium turbidity increases with rising nutrient level, but as vegetation reduces turbidity, two different relations apply depending on the presence or absence of vegetation. Vegetation presence itself, however, also depends on turbidity. Light limitation prevents growth below a (turbidity-dependent) depth, and since shallow lakes are often rather homogeneous in depth, the response of the vegetated area to turbidity tends to be discontinuous. To construct this figure we assume the extreme case of total disappearance of vegetation from the lake when the turbidity exceeds a threshold value at which the critical light level for vegetation growth at this depth is reached. Consequently, the 'with vegetation' line applies below the critical turbidity and the 'without vegetation' line above this level. Hence, the dashed parts of the two equilibrium lines do not represent stable states. The emerging picture shows that at low nutrient levels only the vegetated clear equilibrium exists and at high nutrient levels only the turbid vegetationless one. However, over a range of intermediate nutrient concentrations two alternative stable states are possible. Here, the critical turbidity represents the breakpoint of the system separating the attraction areas of these alternative states. Arrows indicate the direction of change in turbidity when the system is out of equilibrium.

parts of the fold curve, and the hill tops to the dashed breakpoint part marking the separation between the basins of attraction. Each picture in the series shows the stability properties at a different nutrient status. The front landscape represents a hypertrophic situation in which just one, turbid, equilibrium exists. The rear picture represents the pristine state of a lake, a low-nutrient situation in which a clear-water equilibrium is the only possible stable state. Between these two extremes there is a range of nutrient levels over which two alternative equilibria exist.

The response of a lake with these stability properties to eutrophication and subsequent restoration efforts can be derived from this representation. Starting at the pristine state, a moderate increase in nutrient level gives rise to an alternative turbid equilibrium, but if no large perturbations occur, the system will remain in the clear state. Continuing enrichment, however, gradually causes the stability of the clear state to shrink to nil, making it more and more vulnerable to perturbations that may bring it within the basin of attraction around the turbid equilibrium. Even in the absence of perturbations the hysteresis period in which the lake hardly responds to nutrient loading will finally end with a catastrophic transition into a turbid state at the inflection point of the catastrophe fold where the clear-water equilibrium disappears.

Obviously, restoration of such a lake by reducing the nutrient level may often have little effect, since the system can show hysteresis again, staying in its current turbid state. However, in this situation a change to the alternative clear-water equilibrium can be achieved in other ways. One way to force a switch is by 'pushing the ball over the hill top', bringing it within the attraction basin of the clear state. More specifically this requires a temporary reduction in the turbidity of the lake, sufficiently large to allow recolonization by submerged vegetation. The other obvious possibility from the theoretical point of view is to 'move the hill top temporarily to the other side of the ball'. The hill top is situated at the critical turbidity for recolonization

by submerged vegetation (Fig. 5). Since it is water depth in combination with turbidity that determines whether the underwater light level for vegetation development is met, the hill top can be moved by changing the water level. Lowering the water level causes an increase in critical turbidity and it can be seen from Fig. 5 that this may bring a system from a formerly stable turbid state on the upper equilibrium line into the attraction area of the vegetated state.

A high potential impact of vegetation on the system and a sigmoidal decrease of vegetation with turbidity are important in the proposed mechanisms (Fig. 4 and Box 1). Therefore, the phenomenon of alternative clear and turbid stable states is expected to be restricted to shallow lakes of homogeneous depth, where a major part of the water body can be occupied by plants and small changes in turbidity or water level can have a relatively high impact on vegetation when the light climate is just critical for plant growth at the average lake depth.

Evidence from the field

The theoretical results supply a search image of the symptoms to look for in the real world. For instance, one would expect some sets of shallow lakes to show a bimodality of states, being clear or turbid depending on history rather than physical and chemical conditions. Also, relatively swift transitions from a vegetated clear state to a turbid vegetationless situation and vice versa should occur as a response to disturbances or changes in external factors other than nutrients. The current literature on shallow lakes does indeed provide several observations of these phenomena.

A good example of a set of shallow lakes showing bimodality of state is the Great Linford sand and gravel pit complex in England. The site has 14 lakes excavated over the past 40 years. Some were dry-dug, others wet-dug. The digging method appears to have a pronounced effect on turbidity. Dry digging results in clear lakes, while wet digging results in turbid ones because of a high loading of fine silt. Remarkably, after some decades

the wet-dug lakes are still turbid and devoid of vegetation, whereas the dry-dug ones remained clear and richly vegetated¹³. In 1987, part of the fish stock was removed from one of the turbid lakes. This led to a reduction of turbidity, and large weed beds quickly developed in the 25 year old lake, which had no such growth previously^{14,15}. The lake has, so far, remained in this state, supporting the view that clear and turbid states are indeed alternative stable equilibria.

Another way to trace bimodality of states is to analyse the history of one lake rather than the current situation in a set of lakes. Some lakes are known to have switched back and forth between a clear vegetated state and a distinct turbid situation repeatedly in the past. Although the information about such switches is often anecdotal, there are some relatively well-documented cases also.

A good example of a switching lake is the shallow Tomahawk Lagoon in New Zealand^{16,17}, in which phytoplankton and aquatic vegetation have predominated in turn for periods of 1–5 years since 1963. In the clear, vegetation-dominated years phytoplankton production can be reduced by as much as two orders of magnitude. The mechanism inducing the switches has not been explained yet, but the strong contrast between the two states suggests that they are separate equilibria.

A similar situation is found in Lake Takern and Lake Krankesjön, two shallow lakes in the south of Sweden¹⁸. Periods with clear water and abundant submerged vegetation have alternated with periods of turbid water and sparse submerged vegetation over the past 40–50 years without considerable change in the external nutrient loading. Although the mechanism of change is difficult to reconstruct, there are indications that changes in the water level affecting the performance of submerged macrophytes may have been an important trigger of the switches in these lakes. The best available information comes from Lake Krankesjön^{18,19} which showed a marked change from clear to turbid in the early 1970s after an increase in water level. A low water period during 1985 and 1986 seems to have been

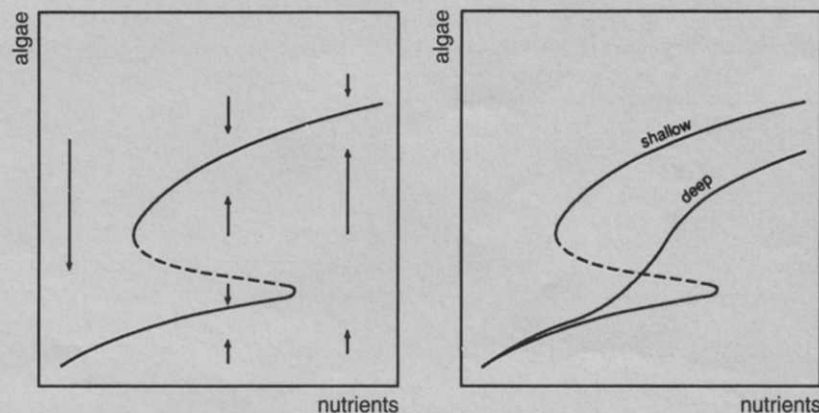
Box 1. A vegetation–algae model

A simple model⁶ of the interaction between the growth of planktonic algae (A) and the abundance of vegetation (V) illustrates the potential for alternative equilibria in shallow lakes:

$$\frac{dA}{dt} = rA \left(\frac{N}{N+h_N} \right) \left(\frac{h_V}{V+h_V} \right) - cA^2$$

$$V = \frac{h_A^p}{A^p + h_A^p}$$

Algal growth is basically logistic with a maximum intrinsic growth rate (r) and a competition coefficient (c) as parameters. In addition, growth increases in a monod fashion with the nutrient level and decreases in a similar way with vegetation abundance (h_N and h_V being the half-saturation constants). Vegetation abundance is a negative sigmoidal function of algal biomass (h_A being a half-saturation constant again). The value of the power (p) shapes this relation. A high value of p causes it to approach a step function representing the disappearance of vegetation from a shallow lake of homogeneous depth around a critical algal biomass where turbidity makes the average depth of the lake unsuitable for plant growth. If the equilibrium density of phytoplankton ($dA/dt = 0$) is plotted against the nutrient level for the shallow lake case, a catastrophe fold arises which is a smooth edged version of the representation derived graphically in Fig. 4.



The response of vegetation to increased turbidity will be less discontinuous in deeper lakes with gradually declining slopes⁶. When we mimic this by decreasing p , the range of nutrient values over which alternative equilibria exist becomes smaller until the alternative equilibria disappear and the response of phytoplankton equilibrium density to nutrient level becomes continuous. Obviously, each depth profile will have its own vegetation–turbidity response, but the result suggests that alternative equilibria arising from the modelled interaction are limited to shallow lakes. Another reason to expect this is that the effect of vegetation on turbidity will be strongest in shallow water where the vegetation structure can fill the whole water column. High vegetation impact can be represented in the model by decreasing the h_V . It appears that such an increase of vegetation impact does indeed increase the tendency of the model to generate alternative stable states.

the onset for a pronounced switch back to a clear state with abundant vegetation growth and waterfowl.

Obviously, the fact that these observations fit the theory is by no means a proof of its validity. Alternative explanations may exist in any specific case, and it is questionable whether experimental determination of the unique responsible mechanism is feasible at all in ecosystems^{20–22}. Nevertheless, the case for the alternative stable state idea appears strong enough to persuade lake managers to aim at forcing turbid shallow lakes into a clear equilibrium with a single perturbation²³.

Application to the management of shallow lakes

The restoration of eutrophied turbid shallow lakes is notoriously difficult. Reduction of the nutrient loading rarely leads to a satisfactory recovery of the clear state in shallow lakes. This can in part be explained from the release of buffered phosphorus from the sediment delaying the response of the actual nutrient level of the water to the reduced external loading^{24–27}. However, the current theory of bi-stability suggests an additional explanation. Even if the nutrient level is considerably reduced, this will often be insufficient to restore the clear-water

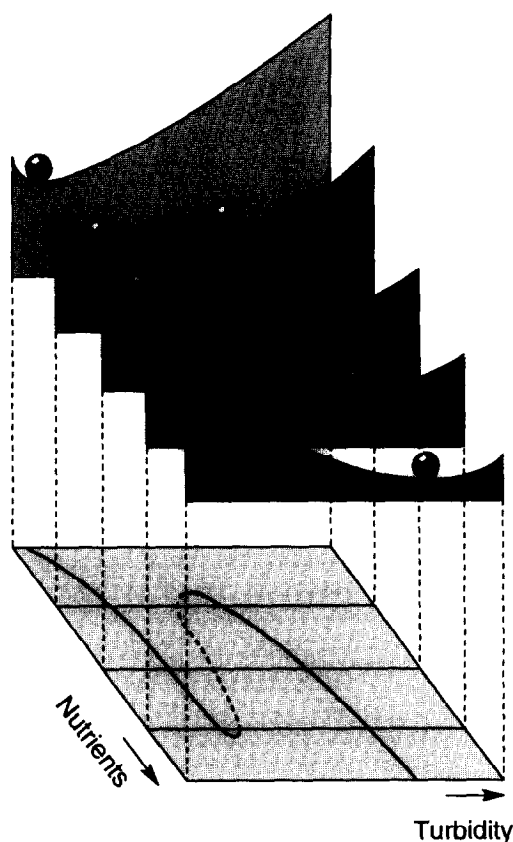


Fig. 5. Stability properties of a shallow lake system at different nutrient levels, as derived from model analyses⁶.

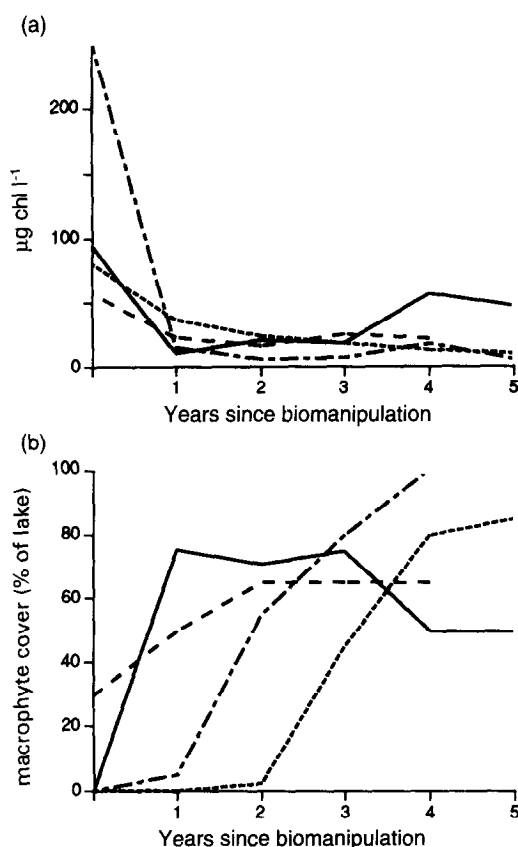


Fig. 6. Sustained effects of biomanipulation on (a) chlorophyll and (b) macrophytes in four shallow lakes³⁴.

state in bi-stable shallow lakes, as the turbid equilibrium can be (locally) stable down to low nutrient levels (Figs 4,5). In such cases restoration requires an additional 'shock

therapy' to bring the ecosystem within the basin of attraction of the alternative clear-water equilibrium.

Recently, reduction of the fish stock ('biomanipulation'²⁸) has been successfully applied to several turbid shallow lakes to enforce such a switch^{11,29,30}. Two mechanisms seem to be predominantly responsible for the initial increase of clarity after fish stock reduction in shallow lakes (Fig. 1). In the first place, the strongly debated^{31,32} trophic cascade effect is observed^{11,30}. Reduction of the predation pressure by planktivorous fish allows populations of large-bodied zooplankters to peak and graze down the algal biomass causing clear water in spring^{33,34}. At least as important as the trophic cascade, however, is the effect of reduced sediment resuspension in many shallow lakes^{29,35}. When the fish community is dominated by species that feed at the bottom like carp (*Cyprinus carpio*) or bream (*Abramis brama*), resuspended bottom material is often the main cause of turbidity, and consequently removal of fish leads to an almost instantaneous increase of transparency.

In shallow lakes, the increase of transparency after biomanipulation is typically followed by a strong development of submerged vegetation in the following years^{11,29,30}. Recruitment of the remaining fish is generally good under the new conditions, giving rise to large numbers of young fish in the subsequent years. Such small fish are mainly planktivorous and can potentially exert a huge predation pressure on zooplankton. Nonetheless, the lakes stay clear, presumably because of the manifold stabilizing effect of vegetation on the clear-water situation³⁶. An analysis of the long-term response of four particularly well-studied cases³⁶ shows that these lakes have remained in the obtained clear-water state for at least 4–5 years (Fig. 6). Although changes are still occurring and it is uncertain whether they will all stay clear in the future, the current results support the alternative stable state hypothesis.

As argued, lowering the water level should be another possibility for inducing the switch to a vegetated clear state – an idea that is supported by the likelihood that

the pronounced changes in the Swedish lakes Krankesjön and Takern^{18,19} are induced by natural water level fluctuations. We are not aware of cases where the water level has been manipulated with the explicit purpose of changing the ecosystem state, but it is known that the effect of such manipulation on the community of shallow lakes can be dramatic. A well documented example is the case of the Swedish Lake Tännaren³⁷. The construction of a dam increased the water level in this shallow (< 2 m) lake by 0.5 m, causing a decrease in vegetated area from 80% to 14% of the lake bed. The large numbers of birds that used to forage in the vegetated lake disappeared, and the water that had been sufficiently clear to see the bottom through the vegetation became turbid because of wind resuspension of the unconsolidated sediment and increased algal growth. A subsequent lowering of the water level would be necessary to check whether the clear and the turbid state are indeed alternative equilibria in this specific case, but the response of the lake illustrates the potential of water level manipulation as a tool for managing the ecosystem state of shallow eutrophic lakes.

Obviously, many of the mechanisms governing the dynamics of shallow lake communities are still poorly understood, and it remains difficult to determine whether an alternative clear equilibrium may be expected in any specific case. Nonetheless, the current experiences are encouraging from a management point of view, since they suggest that shallow lakes which stay turbid despite reduced nutrient loading may be permanently restored by a single perturbation.

References

- 1 Noy-Meir, I. (1975) *J. Ecol.* 63, 459–483
- 2 May, R.M. (1977) *Nature* 269, 471–477
- 3 Hosper, S.H. (1989) *Hydrobiol. Bull.* 23, 5–11
- 4 Timms, R.M. and Moss, B. (1984) *Limnol. Oceanogr.* 29, 472–486
- 5 Scheffer, M. (1989) *Hydrobiol. Bull.* 23, 73–85
- 6 Scheffer, M. (1990) *Hydrobiologia* 200/201, 475–486
- 7 Jeppesen, E. et al. (1990) *Hydrobiologia* 200/201, 219–227
- 8 Wetzel, R.G. (1975) *Limnology*, Saunders
- 9 Spence, D.H.N. (1982) *Adv. Ecol. Res.* 12, 37–125

- 10 James, W.F. and Barko, J.W. (1990) *Arch. Hydrobiol.* 120, 129–142
- 11 Van Donk, E., Grimm, M.P., Gulati, R.D. and Klein Breteler, J.P.G. (1990) *Hydrobiologia* 200/201, 275–290
- 12 Wiium-Andersen, S. (1987) *Arch. Hydrobiol. Beih.* 27, 167–172
- 13 Giles, N. (1986) *Game Conservancy Ann. Rev.* 18, 130–133
- 14 Giles, N. (1988) *Game Conservancy Ann. Rev.* 20, 136–137
- 15 Wright, R.M. and Phillips, V.E. (1992) *Aquatic Botany* 43, 43–49
- 16 Mitchell, S.F. *et al.* (1988) *Int. Revue Ges. Hydrobiol.* 73, 145–170
- 17 Mitchell, S.F. (1989) *Aquat. Bot.* 33, 101–110
- 18 Blindow, I. (1992) *Freshwater Biology* 28, 15–27
- 19 Andersson, G., Blindow, I., Hargeby, A. and Johansson, S. (1990) *Anser* 29, 53–62
- 20 Quinn, J.F. and Dunham, A.E. (1983) *Am. Nat.* 122, 602–617
- 21 Roughgarden, J. (1983) *Am. Nat.* 122, 583–601
- 22 Scheffer, M. and Beets, J. *Hydrobiologia* (in press)
- 23 Hosper, S.H. and Jagtman, E. (1990) *Hydrobiologia* 200/201, 523–534
- 24 Cullen, P. and Forstberg, C. (1988) *Hydrobiologia* 170, 321–336
- 25 Sas, H. (1989) *Lake Restoration by Reduction of Nutrient Loading: Expectations, Experiences, Extrapolations*, Academia Verlag
- 26 Jeppesen, E. *et al.* (1991) *Mem. Ist. Ital. Idrobiol.* 48, 127–148
- 27 Van Der Molen, D.T. and Boers, P.C.M. *Hydrobiologia* (in press)
- 28 Gulati, R.D., Lammens, E.H.R.R., Meijer, M-L. and Van Donk, E., eds (1990) *Bio-manipulation, Tool for Water Management*, Kluwer
- 29 Meijer, M-L., de Haan, M.W., Breukelaar, A.W. and Buiteveld, H. (1990) *Hydrobiologia* 200/201, 303–316
- 30 Søndergaard, M. *et al.* (1990) *Hydrobiologia* 200/201, 229–240
- 31 DeMelo, R., France, R. and McQueen, D.J. (1992) *Limnol. Oceanogr.* 37, 192–207
- 32 Carpenter, S.R. and Kitchell, J.F. (1992) *Limnol. Oceanogr.* 37, 208–213
- 33 Carpenter, S.R. (1988) *Complex Interactions in Lake Communities*, Springer-Verlag
- 34 Scheffer, M. (1992) *Oikos* 62, 271–282
- 35 Breukelaar, A.W., Lammens, E.H.R.R., Klein Breteler, J.P.G. and Tatrai, I. *Verh. Internat. Verein. Limnol.* (in press)
- 36 Meijer, M-L. *et al.* *Hydrobiologia* (in press)
- 37 Wallstein, M. and Forsgren, P-O. (1989) *J. Aquat. Plant Manage.* 27, 32–37

Phylogenetic Relationships and Evolutionary Processes in East African Cichlid Fishes

Axel Meyer

Since their discovery almost one hundred years ago, the adaptive radiations of cichlid fishes in the largest East African lakes have fascinated biologists. They are a prime example of explosive speciation. Among vertebrates, these species assemblages are the most species rich and the most diverse, morphologically, ecologically and behaviorally. Recent phylogenetic analyses of molecular data and refined knowledge about the geological history of the East African lakes are throwing new light on the evolutionary history of these extraordinary fish faunas.

The cichlid fish faunas of the three largest East African lakes, Victoria, Tanganyika and Malawi, are enormously diverse. Each of these lakes (Fig. 1) contains a radiation of several hundred species¹, almost all of which are endemic to their particular lake. These radiations make the Cichlidae one of the most species-rich vertebrate families (Fig. 2). Their special history is highlighted by the coexistence of other families of fish that have not undergone this kind of spectacular evolution. The origin and maintenance of the cichlid species assemblages have been the subject of much research and debate^{1–5}. Yet, the phylogenetic relationships among the endemic faunas have remained largely unresolved, since no morphological feature could be found to be characteristic of a particular radiation^{6,7}.

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The species flocks of the three lakes each contain a wide array of morphologically and behaviorally highly specialized cichlids¹. Part of the reason for this diversification might be a morphological feature peculiar to cichlids⁸: a second set of jaws in back of the buccal cavity, the modified pharyngeal jaws, which are functionally decoupled from the oral jaws. This is believed to allow cichlids to become highly specialized on particular types of prey and might give them a competitive advantage over other fish that lack these modified jaws⁸. Some of these specializations are paralleled in cichlid species endemic to different lakes. For example, the Victoria endemic *Macropodus bicolor* and the Malawi endemic *Chilotilapia rhoadesi* both have highly derived dentition, jaw structures and feeding behaviors; and both prey on gastropods by crushing their shells with their oral jaws^{1,7}.

Until recently, it was not known whether each of the assemblages is a monophyletic flock that can be traced back to a single ancestral species and consequently whether

the morphological similarities between members of different flocks evolved as convergences. Alternatively, specializations could have arisen only once and could indicate polyphyletic origins for the species flocks with each of several lineages having a geographic distribution that extends beyond the boundaries of a single lake^{6,7}. This interpretation would indicate that relationships of recent common ancestry exist among many of the members of the three species flocks^{1,7}. Molecular approaches, especially the study of the mitochondrial genome by restriction enzyme analysis and, more recently, by DNA sequencing are providing many new insights and some surprising results^{9–11}.

Monophyly of the Lake Victoria superflock

Lake Victoria is the youngest of the three large lakes. It started to form about 250 000 to 750 000 years ago¹, yet it contained (see epitaph below) a species flock of >300 endemic haplochromine cichlids. The lake had its origin from two westward flowing rivers,