

# Multiple states in river and lake ecosystems

**C. Lisa Dent<sup>\*</sup>, Graeme S. Cumming and Stephen R. Carpenter**

*Center for Limnology, University of Wisconsin, Madison, WI 53706, USA*

Nonlinear models of ecosystem dynamics that incorporate positive feedbacks and multiple, internally reinforced states have considerable explanatory power. However, linear models may be adequate, particularly if ecosystem behaviour is primarily controlled by external processes. In lake ecosystems, internal (mainly biotic) processes are thought to have major impacts on system behaviour, whereas in rivers, external (mainly physical) factors have traditionally been emphasized. We consider the hypothesis that models that exhibit multiple states are useful for understanding the behaviour of lake ecosystems, but not as useful for understanding stream ecosystems. Some of the best-known examples of multiple states come from lake ecosystems. We review some of these examples, and we also describe examples of multiple states in rivers. We conclude that the hypothesis is an oversimplification; the importance of physical forcing in rivers does not eliminate the possibility of internal feedbacks that create multiple states, although in rivers these feedbacks are likely to include physical as well as biotic processes. Nonlinear behaviour in aquatic ecosystems may be more common than current theory indicates.

**Keywords:** multiple states; threshold; river; lake; ecosystem

## 1. INTRODUCTION

Freshwater ecology has a rich tradition of evolutionary and ecological models, both linear and nonlinear. Occam's razor has led freshwater ecologists to favour simpler linear models. Nonlinear models often require the estimation of many parameters, and the uncertainty associated with these estimates diminishes the usefulness of the models (Ludwig & Walters 1985). In addition, nonlinear models often perform more poorly than linear ones in confrontations with data (Ludwig & Walters 1985; Carpenter 2001). Conversely, linear models of ecosystem dynamics are not always satisfactory. Some well-known biotic mechanisms are best understood by nonlinear models. For example, small perturbations do not always result in proportionally small responses (Ricker 1963). Behavioural or population changes in keystone species can produce abrupt changes in ecosystem processes (Mangel & Clark 1988). Aquatic ecosystems may appear to exist in multiple states, each of which is robust to certain types of perturbations (Scheffer 1997). Freshwater restoration ecology offers many examples of altered states that have proved refractory to management (National Research Council 1992). The ability of nonlinear models to represent behaviour, such as thresholds, multiple stable states and hysteresis, warrants careful consideration.

Nonlinear models that include multiple stable states are often illustrated by a 'ball and cup' metaphor in which the ecosystem (the ball) can move among locally stable attractors (the cups) on a stability landscape controlled by slowly changing factors, such as geomorphology or long-

lived organisms (DeAngelis & Waterhouse 1987) (figure 1). Internal feedback mechanisms act to keep the system in a particular state, or cup. The strength of these internal feedbacks is represented by the depth of the cup. An incremental change in an external driver, such as climate, can cause a sudden change in system state when internal stabilizing mechanisms are overcome and the system shifts to a new state. If feedbacks also exist that reinforce the new state, recovery to the original state may be hysteretic, that is, a reversal in the driver may not restore the original state. Thus, a persistent change in ecosystem state may be explained by a persistent change in an external driver (for example, a dam on a river), or it may be due to an incremental or transient change in a driver combined with feedbacks that are endogenous to the ecosystem (for example, a pulse of phosphorus input that shifts a lake into a eutrophic condition maintained by high nutrient recycling). We are particularly interested in cases in which multiple states are under endogenous control; i.e. in which the presence of certain processes reinforces their continued presence. Note that the concept of multiple states is a mathematical construct of nonlinear systems. In reality, it is not easy to define the possible states or to detect when a system moves from one basin to another. Nonetheless, given sufficient data it may be possible to model ecosystem behaviour with equations that exhibit multiple states.

Rivers and lakes differ in the relative importance of exogenous (often abiotic) versus endogenous (often biotic) control (Ryder & Pesendorfer 1989; Grimm 1993; but see also Naiman *et al.* 2000*b*). Rivers are generally considered to be open ecosystems, highly influenced by their surroundings and by abiotic disturbance, particularly hydrologic regime. In contrast, lakes are more stable, more isolated and more biotically controlled. In the ball and cup framework, systems dominated by endogenous feedbacks

<sup>\*</sup> Author for correspondence (ldent@facstaff.wisc.edu).

One contribution of 11 to a special Theme Issue 'The biosphere as a complex adaptive system'.

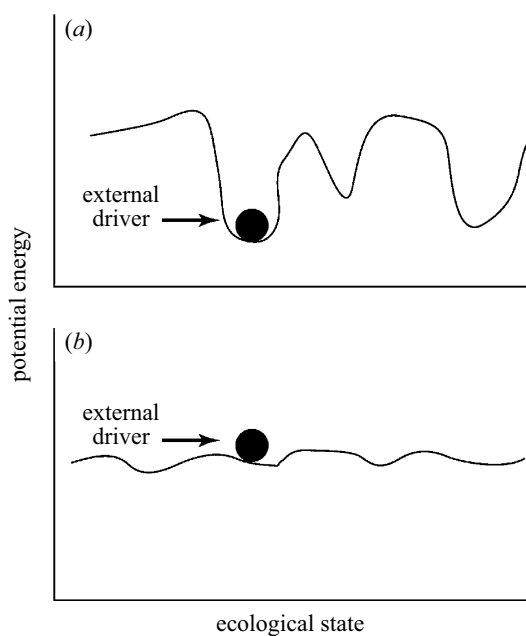


Figure 1. Hypothetical stability landscapes of a system with strong internal feedbacks (a) and weak internal feedbacks (b). The ball represents an ecosystem, which rolls into valleys or cups that represent different states. Internal feedbacks in the ecosystem act to keep it in a particular state by increasing the energy needed to push it out of a cup. Continued incremental change in the external driver can overcome internal feedbacks and rapidly move the ecosystem into a neighbouring cup. In the flat stability landscape (b), the ecosystem moves easily between different states, which may not even be detectable.

are represented by stability landscapes with well-developed cups representing persistent states where the ball comes to rest (figure 1a), while systems dominated by external forcing are represented by flat stability landscapes with shallow pits (figure 1b). Note that the stability landscape itself is not fixed; it changes over time due to variation in slow variables, including human activities that may alter the vulnerability of the system to external shocks. Freshwater systems appear to exhibit the full range of stability landscapes, ranging from desert streams regulated largely by flood regime (Grimm 1993) to lakes dominated by internal feedbacks (Scheffer 1997). In the former case, the concept of multiple states may be of little use for explaining ecosystem dynamics, while in the latter case, multiple states may have considerable explanatory value.

Are multiple states a useful concept for understanding biotically driven lakes but not physically forced streams? One goal of this paper is to show that this hypothesis is an oversimplification. To do so, we review three examples of nonlinearities in lake ecosystems that can be modelled by multiple states. The mechanisms range from physical-chemical to entirely biotic, illustrating that multiple states are not exclusively generated by biological feedbacks. We then consider river ecosystems and review examples of possible multiple states, again driven by diverse processes including physical and biotic mechanisms. Based on this review, we conclude that multiple-state models can be useful in studies of both lakes and rivers. In addition, the spatial and temporal scale of interest may determine the utility of multiple states as an explanation of system

dynamics. Finally, we discuss trade-offs between linear and nonlinear models and the implications for management strategies.

## 2. MULTIPLE STATES IN LAKES

### (a) *Eutrophication by non-point pollution*

Eutrophication is a process of over-enrichment with nutrients that leads to blooms of toxic algae, deoxygenation, fish kills and other problems of aquatic ecosystems (Smith 1998). Lakes appear to exhibit two alternate states with respect to nutrient load. In the oligotrophic, or clear-water state, the water has a low biomass of phytoplankton and low recycling rates of nutrients from sediment to water. In the eutrophic, or turbid-water state, phytoplankton biomass is high, often forming noxious blooms, and recycling of nutrients from sediment to water is rapid.

Eutrophication is usually caused by anthropogenic discharge of wastewater or by non-point pollution: nutrient-rich run-off from land to streams, lakes or coastal oceans (Carpenter *et al.* 1998a). Both phosphorus and nitrogen are involved (Guildford & Hecky 2000) although concern often focuses on phosphorus (Carpenter *et al.* 1998a). Increased run-off of phosphorus from land to freshwaters is associated with a build-up of phosphorus concentrations in agricultural soils (Bennett *et al.* 2001).

Phosphorus input to lakes can sink directly to the sediments, or be taken up by primary producers. Phosphorus assimilated by biota is eventually added to sediments. Sediment phosphorus is recycled to the overlying water, and this recycling can be slow or fast depending on the chemical conditions (Nürnberg 1984). If the water is oxygenated, recycling tends to be slow because phosphorus is immobilized by insoluble iron complexes. If the water is anoxic, iron is reduced to a soluble form and the phosphorus is recycled rapidly. High production of organic matter increases respiration near the sediment surface, thereby decreasing oxygen concentration, accelerating phosphorus release and establishing a feedback that sustains eutrophication.

A model based on the shift from slow to fast recycling leads to alternate states of the phosphorus cycle in lakes (Carpenter *et al.* 1999b). In the model (details in Appendix A), algal biomass exhibits two stable states separated by a sharp transition (figure 2). Phosphorus inputs to the lake are determined by the proportion of farms that are intensively fertilized versus those that are conservatively tilled. Phosphorus is also recycled from sediments at a rate determined by organic matter production. Figure 2 shows the effects of the proportion of intensive farms (which controls input of phosphorus to the lake) and the flushing rate (which controls efflux of phosphorus from the lake). As the proportion of intensive farms is increased, a threshold is crossed that shifts the system abruptly from the low-P to the high-P state. The reverse transition to a low-P state occurs at a different threshold at a lower proportion of intensive farms. Thus, the threshold level of intensive farming needed to restore the system is substantially lower than the level of intensive farming that caused eutrophication. The difference between the threshold levels of intensive farming is greater at lower flushing rates. That is, for slowly flushing lakes, relatively severe reductions of intensive farming are required to reverse eutrophication.

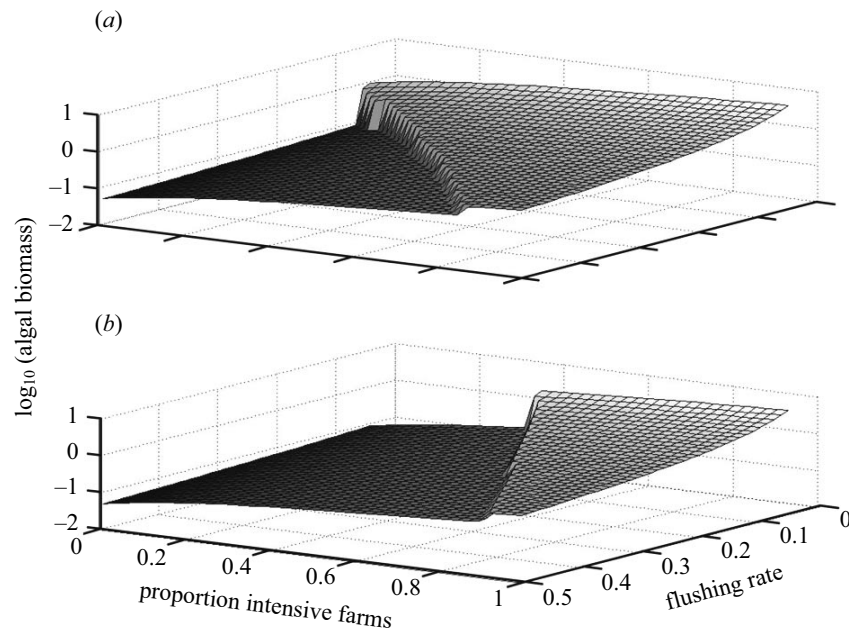


Figure 2. Surfaces of algal biomass (log scale) as a function of the proportion of intensive farms and the flushing rate of the lake in the eutrophication model. (a) Illustration of algal biomass during recovery from eutrophication, as the proportion of intensive farms is slowly decreased for a fixed flushing rate. (b) Illustration of algal biomass during the onset of eutrophication, as the proportion of intensive farms is slowly increased for a fixed flushing rate.

The recognition of alternate feedback regimes in oligotrophic versus eutrophic lakes integrates a substantial body of limnological research. The model explains all of the major mechanisms for controlling eutrophication (Carpenter *et al.* 1999b). It also explains divergent case studies in which eutrophication proved reversible, hysteretic (reversible by extreme intervention after some delay), or irreversible (Carpenter *et al.* 1999a). The implications of the model for policy choice and incentive design are discussed by Carpenter *et al.* (1999b) and Scheffer *et al.* (2000), respectively.

#### (b) Water clarity in shallow lakes

In shallow lakes, a different set of feedbacks between macrophytes, plankton and nutrients controls lake clarity. Lakes colonized by macrophytes tend to be clear, while those dominated by plankton are turbid. In each case, feedbacks between nutrients, turbidity and the biota stabilize conditions over a range of external perturbations, but abrupt transitions occur when these stabilizing factors are overcome (Scheffer 1997).

The clear-water state in shallow lakes is accompanied by well-established macrophyte populations. Submerged macrophytes have been shown to increase water clarity through a variety of mechanisms, including reducing resuspension of bottom material, reducing nutrients available for phytoplankton and providing a refuge for zooplankton (that graze on phytoplankton) from predation (figure 3) (Canfield *et al.* 1984; Carpenter & Lodge 1986; Faafeng & Mjelde 1998; Scheffer & Jeppesen 1998). In most lakes, the main factor that limits colonization by macrophytes is light (Scheffer & Jeppesen 1998), so a macrophyte-induced increase in water clarity creates a positive feedback, in which increased abundance of submerged macrophytes leads to increasingly clearer water and the further establishment of macrophytes. However,

under turbid conditions, it is difficult for macrophytes to become established due to low light conditions. Phytoplankton experience less competition for nutrients and less grazing pressure, and the water is likely to remain turbid.

The transition from a clear, macrophyte-dominated shallow lake to a turbid, unvegetated lake may be caused by increased nutrient loading or by direct damage to the macrophytes as a result of overwintering bird populations, herbicides or violent storms (Scheffer & Jeppesen 1998). A clear, vegetated state is unlikely to occur when the total phosphorus level of the lake exceeds 0.05–0.15 mg l<sup>-1</sup>, unless the nitrogen input is low (Hosper & Jagtman 1990; Jeppesen *et al.* 1990). The size and depth of the lake are also important; extremely shallow lakes are more vulnerable to stochastic episodes that may cause a shift from one state to another (Scheffer 1997), and the relative proportion of water affected by macrophytes in the littoral zone is higher. The potential for sudden switches between alternate states is reduced by both very high and very low nutrient levels due to high algal growth and low macrophyte growth, respectively (Carpenter *et al.* 1998b). Rapid transitions are most likely at intermediate nutrient levels.

Humans typically prefer clear-water lakes to turbid ones, raising the issue of whether shallow lakes can be deliberately manipulated to produce a clear-water state (Hosper & Jagtman 1990; Scheffer 1997). The nonlinear view of the dynamics of shallow lakes predicts several consequences of remediation that are not expected under a linear model. For example, reduction of nutrient inputs to turbid shallow lakes may result in widely different lake responses (some remain turbid whereas others become clear), depending on conditions prior to the treatment. The nonlinear model also explains why a sudden, rapid transition from clear to turbid may occur as a consequence of apparently minor environmental fluctuations. Hosper (1998) suggests a set of management actions aimed

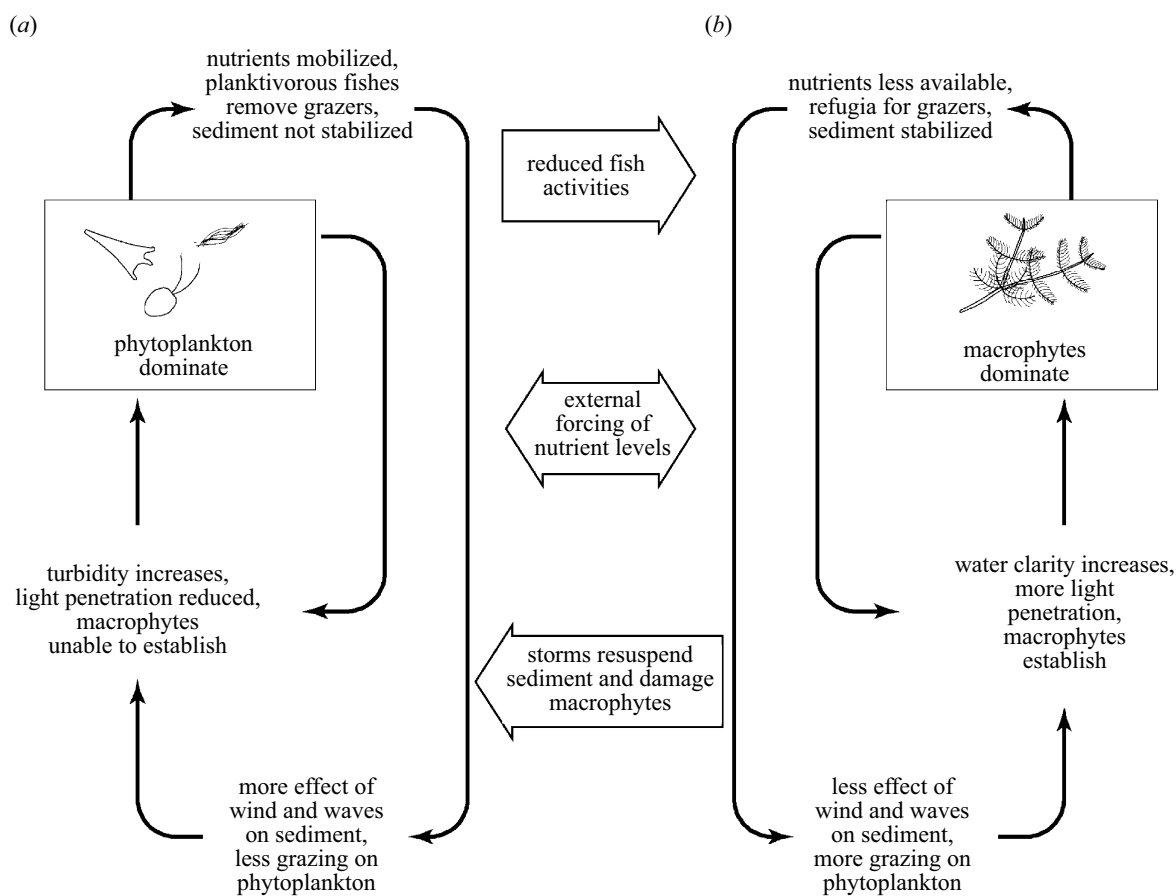


Figure 3. Conceptual model for multiple states of water clarity in shallow lakes. (a) Feedbacks associated with the turbid state, and (b) feedbacks associated with the clear-water state. Processes that can move the system from one state to the other are shown between (a) and (b).

specifically at moving systems out of a stable turbid state, including flushing the lake with low-nutrient water during winter, and reducing planktivorous fishes, thereby increasing grazer pressure on phytoplankton.

### (c) *Trophic cascades and phytoplankton biomass*

Nutrients establish the potential primary production of lakes, but variation around this potential is affected by the structure of the food web. The concept of trophic cascades was introduced to explain this variation (Carpenter *et al.* 1985). Piscivorous fishes, at the top of the food web, can regulate the abundance of planktivorous fishes. Planktivorous fishes in turn feed size selectively on zooplankton, producing a sharp distinction between small-bodied and large-bodied zooplankton assemblages in the presence or absence of planktivorous fishes, respectively (Brooks & Dodson 1965). Phytoplankton losses to zooplankton grazing depend on the density and body size of zooplankton; large *Daphnia* (waterfleas) are particularly effective grazers. Thus, high densities of piscivores can cause low densities of planktivores, allowing large-bodied *Daphnia* to flourish and graze phytoplankton to low concentrations. Conversely, in the absence of piscivores, planktivores can become abundant, selectively removing large-bodied zooplankton and thereby allowing phytoplankton to reach high concentrations.

Thus, trophic cascades can lead to lakes with either small *Daphnia* populations dominated by small individuals

and high algal biomass, or large abundant *Daphnia* and relatively low algal biomass, and with abrupt transitions from one state to another.

A model of food-web interactions producing multiple states predicts that interactions between trophic levels can significantly affect the threshold at which a state change occurs (Scheffer *et al.* 1997). Consider two of the trophic links: (i) *Daphnia* feeding on phytoplankton; and (ii) planktivorous fishes feeding on *Daphnia*. The dynamics of these coupled populations are very different despite their common predator-prey relationship. In the *Daphnia*-algae case, classic predator-prey cycles are common. Increasing numbers of *Daphnia* reduce algal biomass, leading to a reduction of *Daphnia* due to food limitation, which allows the algal population to rebound, leading to an increase in the *Daphnia* population, etc. (figure 4). In the case of *Daphnia* consumption by fishes, the situation is different because fishes have alternative sources of food (i.e. a type III functional response). Fish density does not react directly to *Daphnia* density, leading to the possibility of over-exploitation and the collapse of the *Daphnia* population (figure 4). The sigmoidal line in figure 4 is analogous to the fold in figure 2. As the planktivorous fish population increases (comparable to increasing the proportion of intensively fertilized farms), the population of *Daphnia* decreases slowly (comparable to the slowly increasing algal biomass in figure 2). If fishes and *Daphnia* were the only populations in the model, *Daphnia* would collapse at the

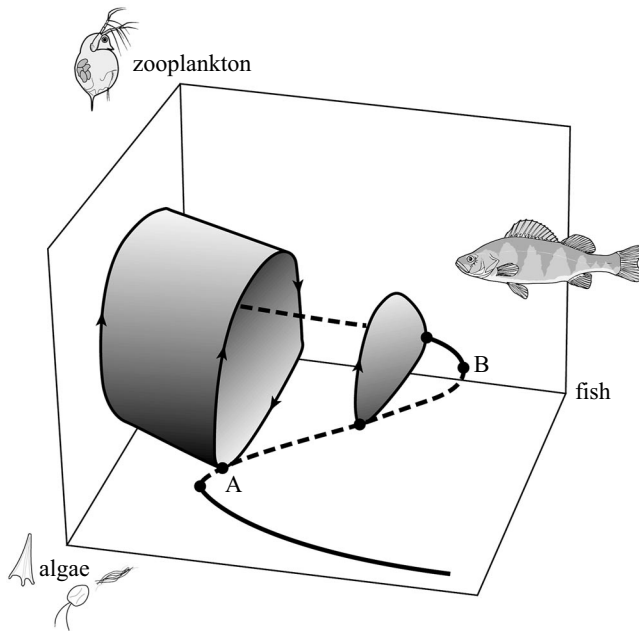


Figure 4. Schematic representation of the predicted effect of planktivorous fishes on the dynamics of zooplankton and algae. The presence of zooplankton–algae cycles causes the zooplankton to collapse to a lower fish density (B) than would be expected (A), leading to uncontrolled blooms of algae. (Adapted from Scheffer *et al.* (1997).)

bend (B in figure 4) in the sigmoidal curve. However, the presence of *Daphnia*–algae cycles changes the point at which *Daphnia* collapse such that it occurs at a much lower fish density (A in figure 4). Here, the cycles hit the middle section of the sigmoidal curve that marks the critical border of the attraction valley, and the system collapses into a state with almost no *Daphnia* and a dense population of phytoplankton.

Two mechanisms are involved in this state change. First, *Daphnia* numbers crash, due largely to depletion of their food and, subsequently, the population is trapped at this low level by fish predation. The population oscillations make *Daphnia* more vulnerable to over-exploitation by planktivorous fishes. In a sense, the oscillations have the same effect as external perturbations: they increase the probability that the system will shift from one state to another. As lakes become progressively enriched, temporal variability of plankton tends to increase. The model by Scheffer *et al.* (1997) suggests how such cycles, in the presence of planktivorous fishes, can lead to a collapse of zooplankton populations and uncontrolled blooms of phytoplankton.

#### (d) Summary

The behaviour of lake ecosystems can often be explained by nonlinear models that include multiple states. These states are maintained by local, endogenous processes that may temporarily mask a response to external perturbation. The concept of multiple states has advanced both the theory and the management of lake ecosystems. We now turn to river ecosystems and ask whether nonlinear models with multiple, endogenously maintained states are also useful in understanding these systems.

### 3. NONLINEAR DYNAMICS IN RIVERS

#### (a) River channel change

Geomorphologists have long acknowledged the existence of nonlinearities and multiple states in the behaviour of river channels (e.g. Schumm 1973). A classic example involves the formation of arroyos in the American Southwest (Dodge 1902; Cooke & Reeves 1976). An arroyo is a steep-sided, narrow stream channel in valley-floor alluvium that persists for many decades. Between 1850 and 1910, many streams in the Southwest made an abrupt transition from wide, vegetated valleys to barren, entrenched arroyos. Although the ultimate causes of the transition are debatable (Cooke & Reeves 1976), the causal feedbacks between vegetation and hydrology are well understood (figure 5) (Bull 1997). Plant communities influence run-off patterns from hill slopes, increasing hydraulic roughness and resistance to erosion. By reducing water velocity, plants increase deposition of sand and deep infiltration of water that produces a clay soil favouring further plant growth. Reduction of plant cover, whether by grazing, climate change or other factors, increases local scour, causing stream flow convergence and reducing infiltration, which further weakens the remaining plants. This positive feedback mechanism promotes the development of increasingly entrenched and barren channels. Eventually aggradation commences and the channels fill in, but this may take many centuries, whereas arroyo cutting may take only a few years.

Other work has also shown that changes in river-channel form may be nonlinear (Murray & Paola 1994; Lane & Richards 1997). In a model of river meandering by Stolum (1996), the river exhibited two contrasting domains of high and low sinuosity. During high sinuosity periods, positive feedback among cut-off events (e.g. the formation of ox-bow lakes) straightened the river and accelerated local change, causing more cut-offs. Eventually, this led to a low sinuosity condition in which cut-offs, when they occurred, did not cascade. Sinuosity then increased gradually via the enlargement of bends caused by bank erosion. Stolum showed that the distribution of cut-off events followed a power law over nearly two orders of magnitude, suggesting that the river was in a dynamic state of self-organized criticality.

Much of the geomorphological evidence suggesting that fluvial systems exhibit internally generated nonlinear behaviour is based on theoretical modelling exercises. Identification of bifurcations in real systems requires continual observation over long time-periods (Lane & Richards 1997) and, in general, such bifurcations could result from either internal or external processes (Huggett 1988). The difficulties of detecting nonlinear behaviour in channel form, from the time-series data of four rivers, are discussed by Montgomery (1993). Nonetheless, an understanding of the nonlinear nature of river-channel change is essential to the prediction of the impact of human alterations of rivers and their catchments. In the case of arroyo cutting, the nonlinear perspective emphasizes the fragile nature of these systems and the difficulty of restoration. Once cut, deep arroyos may take hundreds of years to backfill. Large sums of money spent on reclamation are unlikely to restore the high water table needed to maintain riparian plant communities. In contrast, reaches that are

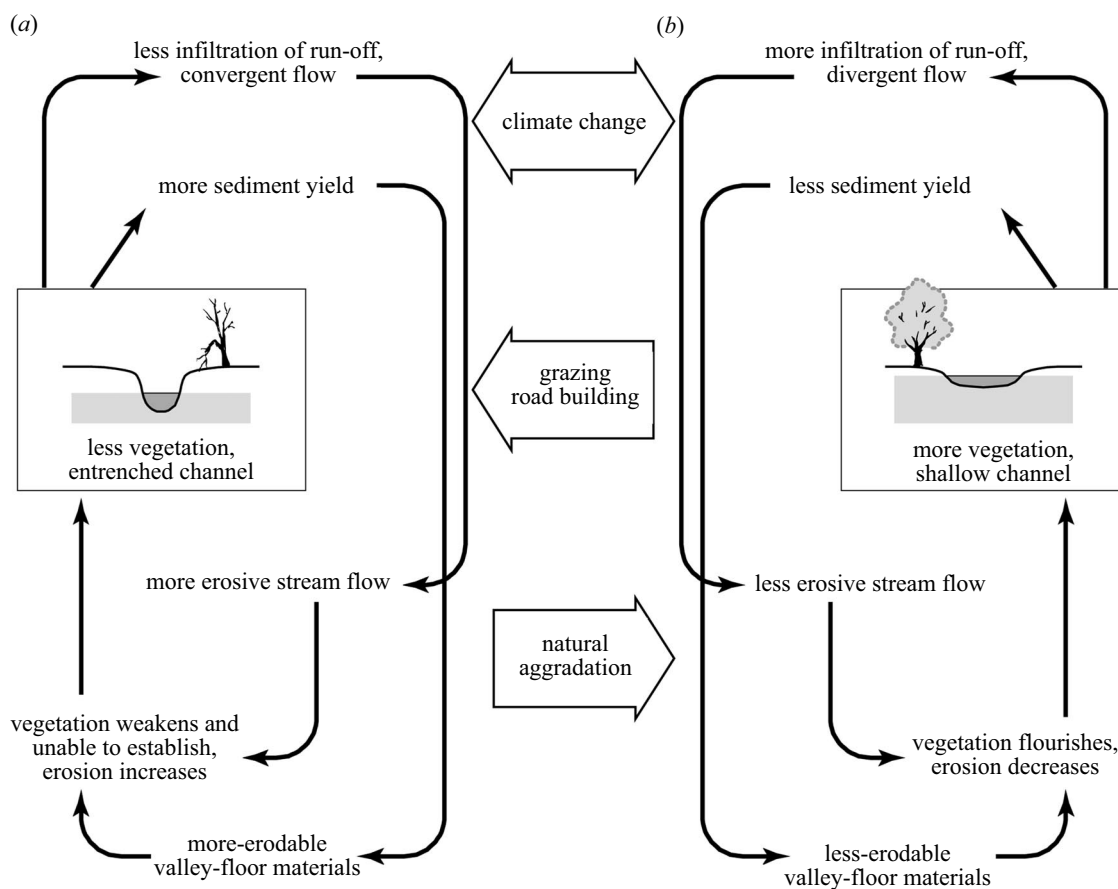


Figure 5. Conceptual model for multiple states of river-channel form. (a) Feedbacks associated with the entrenched channel (arroyo), and (b) feedbacks associated with the shallow channel. Processes that can move the system from one state to the other are shown between (a) and (b).

still unentrenched may be relatively easy to stabilize through soil-conservation measures.

#### (b) *Competition in riparian communities*

Interactions between riparian vegetation, hydrology and river morphology affect the community composition of riparian forests. Riparian zones hold a central place in the hydrological cycle due to their location at the interface between groundwater and surface water (Naiman & Decamps 1997; Tabacchi *et al.* 2000). The composition of riparian vegetation, in turn, is strongly influenced by hydrology; particularly flood regime and groundwater levels. Changes in flood regime affect seedling establishment, channel incision, sediment transport and depth to water table (Shafroth *et al.* 1998; Bendix & Hupp 2000; Scott *et al.* 2000). Although these interactions are not typically cast in terms of nonlinear dynamics, positive feedbacks and biological thresholds are likely to exist.

A specific example is provided by the invasion of riparian zones by the exotic tree species *Tamarix ramosissima*, the saltcedar (Busch & Smith 1995) (figure 6). Saltcedar is a drought-tolerant, salinity-tolerant species that has successfully invaded thousands of hectares of floodplain habitat in regulated rivers of the southwestern United States. River regulation has facilitated the invasion of saltcedar in several ways. Upstream dams often cause a narrowing of braided stream channels that is associated with increased recruitment of both native and exotic species on the former riverbed (Friedman *et al.* 1998).

Changes in flooding due to regulation reduce seedling establishment of native tree species that are adapted to the natural flow regime (Stromberg 1993; Johnson 2000). Lowering of the water table due to reduced flows has also detrimentally affected native riparian trees (Stromberg *et al.* 1996; Horton & Clark 2001) to the advantage of saltcedar.

Once established, saltcedar can change local water conditions and flood regime. In arid regions, woody riparian vegetation is heavily dependent on alluvial groundwater (Patten 1998). Local reductions in the groundwater level may be caused by species that effectively exploit groundwater. Saltcedar can reach a lower water table and use more water per unit sapwood than several native species (Sala *et al.* 1996; Cleverly *et al.* 1997; Horton & Clark 2001). Shafroth *et al.* (2000) found that saltcedar saplings were significantly less vulnerable than indigenous species to groundwater depletion. This competitive advantage could lead to increased establishment of saltcedar, lowering the water table further and causing the loss of more native trees (Cleverly *et al.* 1997). Saltcedar is also salt tolerant and excretes salts that may reduce the germination of salt-sensitive species (Busch & Smith 1995). In addition, large stands of saltcedar may change the flood regime of a river. Saltcedar stands are dense and extensively rooted, leading to trapping of sediment and bank stabilization. The ensuing enlargement of stream banks and islands may narrow river channels and impede downstream flow, altering flood intensity and extent (Graf

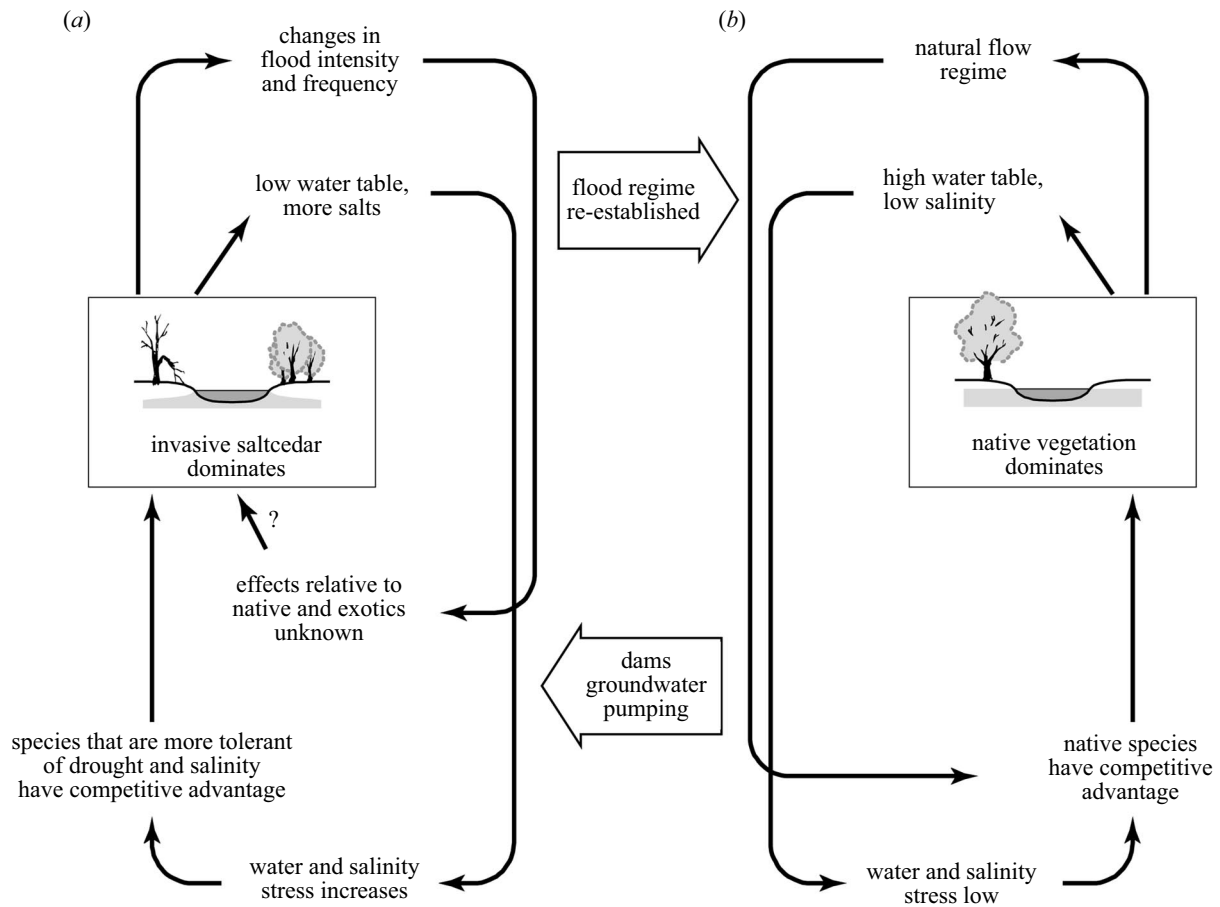


Figure 6. Conceptual model for multiple states of riparian vegetation. (a) Feedbacks associated with dominance by the invasive saltcedar, and (b) feedbacks associated with native riparian vegetation. Processes that can move the system from one state to the other are shown between (a) and (b).

1978; Blackburn *et al.* 1982; Zavalati 2000). Such changes could affect the competitive relationship between native riparian trees and the invasive saltcedar.

Multiple effects of river regulation could thus initiate an invasion by saltcedar that is difficult to reverse and potentially quite costly (Zavalati 2000). Reintroduction of flooding has been suggested to re-establish native tree species in the Southwest, but this will only succeed if native species can outcompete saltcedar (Sher *et al.* 2000). An understanding of the differing responses to flood regime and the competitive relationships between saltcedar and native riparian trees will be essential to establishing a successful restoration. In general, the effect of riparian vegetation on hydrological processes is underestimated (Tabacchi *et al.* 2000). Consideration of riparian systems in terms of thresholds and nonlinearities could prove key to managing rivers appropriately for the multiple, potentially conflicting demands that are made of them.

### (c) *Biotic control of nutrients*

A unique feature of streams is their directionality. Upstream events almost always have downstream effects. If downstream events also influence those upstream, a positive feedback may be created. An example of this type of phenomenon is provided by salmon. Many species of salmon undergo massive, periodic spawning migrations from the ocean into freshwater systems where the adults

lay eggs and die; the salmon then hatch and grow in the environment that has been enriched by the bodies of their parents, creating a situation in which larger numbers of adult salmon will both lay more eggs and more effectively facilitate the survival of their offspring.

The potentially large number of salmon carcasses that is retained in stream and lake ecosystems contributes nutrients and organic matter to the local biota. Stable isotope studies indicate that periphyton, aquatic invertebrates, riparian vegetation and rearing salmonids become enriched with marine-derived nitrogen in systems with anadromous salmon (Bilby *et al.* 1996; Fujiwara & Highsmith-Raymond 1997; Larkin & Slaney 1997; Wold & Hershey 1999). In productive streams, in which light is more limiting than nutrients, salmon migrations are unlikely to increase substantially rates of production (Rand *et al.* 1992). In less-productive streams and lakes, however, the influx of salmon may significantly affect the local environment, increasing production during the important high-mortality, post-hatching phase of the juvenile salmon.

The discovery that carcass-derived nitrogen from returning spawners can have a significant impact on the success of the next generation of salmon suggests that there could be a critical number of returning salmon necessary to maximize juvenile production. Schmidt *et al.* (1998) analysed a time-series of limnological data and salmon productivity for Karluk Lake, Alaska, and found that

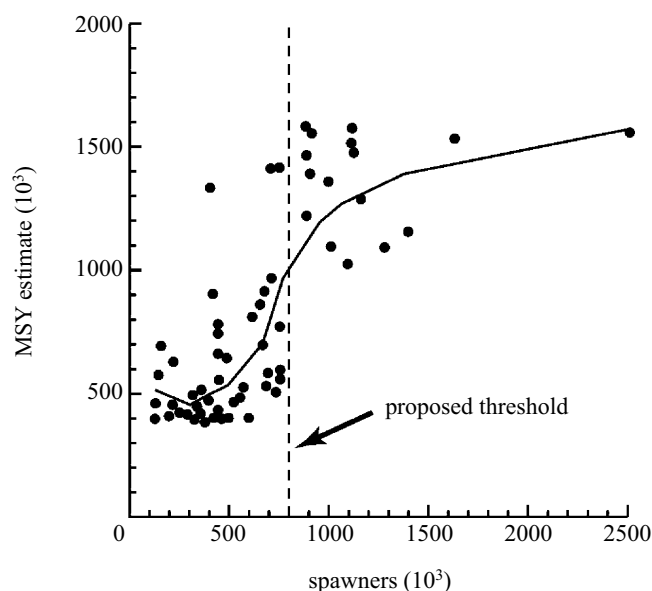


Figure 7. Relationship between predicted salmon recruits (MSY) and spawner abundance of sockeye salmon in Karluk Lake (adapted from Schmidt *et al.* 1998).

sockeye salmon accounted for 40% or more of the total phosphorus in the lake. A graphical assessment of actual spawner abundance versus predicted MSY indicated a production threshold at about 0.8 million spawners, suggesting that this level of spawners is needed to avoid a negative effect on the population (figure 7). The productivity of the system is also linked to the timing of the salmon runs and the proportion of early-run and late-run spawners. Bilby *et al.* (2001) found that the nitrogen stable isotope ratio of one-year-old coho salmon increased with the number of spawners the previous autumn, up to a saturating level. A better understanding of the positive feedbacks between spawning salmon and stream productivity could improve estimates of the number of spawners required to maintain salmon production and could uncover more interactions between fishes and their habitat.

In general, spatially subsidized consumers, such as salmon, can affect local resources in rivers via trophic cascades (Polis *et al.* 1997). Downstream–upstream linkages may be an important source of positive feedbacks that are often not recognized due to time-lags between downstream alterations and visible upstream responses (Pringle 1997).

#### 4. DISCUSSION

These examples demonstrate that nonlinear models can be useful in explaining ecological phenomena in both lakes and rivers. The importance of physical forcing in rivers does not eliminate the possibility of local feedbacks within the system. However, it is our impression that in rivers these feedbacks probably involve geomorphology and hydrology, whereas in lakes, purely biotic feedbacks can have major impacts. For both lakes and rivers, detection of nonlinearities is scale dependent. Over small areas and short periods of time, it is difficult to detect internally maintained alternative states. For example, at the scale of a river reach for a few years, community and ecosystem

changes may be explained by physical forcing by flood regime. Similarly, at the scale of a lake for a few years, one is likely to perceive a single trophic state reinforced by local feedbacks. At broader spatial scales, a collection of lakes or rivers may appear to exhibit different states, which could be externally or internally maintained. Techniques for analysing systems with slow and fast variables in the context of multiple states are described by Rinaldi & Scheffer (2000). Observations over long time-periods are necessary to detect changes in feedbacks in a single lake or river ecosystem (Lane & Richards 1997). Attempts to test experimentally the conditions under which multiple stable states occur must pay particular attention to scale (Petraitis & Latham 1999).

It has been suggested that most physical, chemical and biological phenomena in rivers are spatially organized, whereas lakes may be better understood through their temporal organization (Ryder & Pesendorfer 1989). In general, the importance of directional flow and horizontal connections has led to an emphasis on spatial complexity rather than temporal complexity in river ecology (e.g. Fisher *et al.* 1998; Ward 1998; Lewis *et al.* 2000; Naiman *et al.* 2000a). However, temporal variation in stream flow has also been identified as an essential driver of river biodiversity, production and sustainability (Poff *et al.* 1997; Ward 1998). The quantity, timing and variability of a flow regime create a mosaic of habitats to which river organisms have adapted. Within this framework, the possibility of internal feedback should not be overlooked. The traditional view of streams as hierarchically, physically controlled systems is challenged by increasing numbers of cases of strong biotic control (Naiman *et al.* 2000b). For example, coarse woody debris from riparian trees determines channel morphology and habitat in many rivers, and large mammals, such as riparian browsers or beavers, profoundly change the physical structure of rivers. Given the many interactions between biotic and physical environments in rivers, models including multiple states and threshold responses could be useful. The potential for nonlinear behaviour also implies that changes in state may be abrupt and difficult to reverse, particularly when hydrology and geomorphology are involved.

We propose that nonlinear responses in aquatic systems may be more general than current theory indicates. If so, the precautionary principle advises that nonlinear models should be considered. In general, it is more costly to assume that multiple states are absent when in fact they are present, than to falsely conclude that they are present (Carpenter 2001). Decision analyses are very sensitive to assumptions about the reversibility of the response to a change in the variable being managed (such as pollutant loading rate or resource harvest rate). The assumption of smooth, reversible ecosystem dynamics made by linear models leads to relatively high pollutant loads or harvest rates, because if a mistake is made, recovery is easy. In contrast, the assumption of multiple states will lead to more cautious loading or harvest rates to account for the possibility of a costly period of recovery. In the absence of substantial evidence, it is dangerous to assume that this possibility is negligible.

There are also strong arguments for choosing simple models over more complex ones, however, particularly when data are limited. The central thread of the simple

versus complex model debate follows the same form as arguments for Akaike's information criterion (Burnham & Anderson 1998). Increasing the number of parameters in a model may allow the model to fit more closely the scatter of data but, at the same time, it increases estimation error and the chances of overfitting to match the individual idiosyncrasies of a particular dataset. Evaluation of the relationship between fitting error and estimation error makes it possible to identify an optimal point at which both kinds of error are minimized. Although nonlinear models are conceptually more complex than linear ones, they do not necessarily use more parameters. Nonlinear models that use relatively few parameters may be more accurate, and hence result in greater predictability than linear models. Conversely, nonlinear models that rely on too many parameters may prove worse than linear models. The best strategy may be to build many models, including a few simple nonlinear ones in the mix; the performance of each can then be tested to find the best model or set of models. However, this assumes that data are available to discern between models, which is often not the case (Carpenter & Pace 1997).

One approach to this dilemma is to develop a better catalogue of situations and circumstances when nonlinear responses may contribute to our understanding of ecosystem function. We have attempted to contribute to such a catalogue with our examples. One factor to consider is the relative stability of the ecosystem at the scale of interest. If we consider lakes and streams along a continuous axis of stability, lakes are generally more stable than streams, but some lakes are relatively unstable, such as temporary ponds, and some rivers are relatively stable, such as spring-fed streams. More stable systems are likely to have strong internal feedbacks and to exhibit multiple-state behaviour. We stress that the scale of the question will determine the perceived stability of the system. In addition, there are several features that apply to most of the examples we have described, and may provide guidance on when to expect nonlinear responses. These features include a capacity within the system for resource accumulation followed by release of these resources (such as nutrients retained by macrophytes or salmon), a mix of slow- and fast-acting variables (such as fish and zooplankton population dynamics, or soil development and erosion by flooding), and shifts of control between multiple drivers. The coupling of slowly and rapidly changing variables, together with the possibility of a shift in control, seems to be a common element of many cases in which nonlinear models have been useful.

Our findings indicate that managers should always consider the potential for transitions between multiple states, as systems that appear to be changing slowly may nonetheless be on a trajectory to a sudden shift. The most problematic threshold responses are those that result in irreversible negative changes. Management efforts should focus on prevention of such events. Given that it is impossible to control all the stressors on an ecosystem, Crowder *et al.* (1996) recommend that managers focus on ameliorating those stressors that either have compound effects or have the potential to exceed an ecosystem threshold and produce a collapse. For example, in the Kingston Basin of Lake Ontario, species that are particularly important in maintaining internal feedbacks (e.g.

macrophytes) have been identified and targeted for monitoring (Crowder *et al.* 1996). Even when unforeseen thresholds are crossed and the system enters an undesirable state, an understanding of the feedbacks involved may result in successful remediation. Extensive experience with shallow Dutch lakes has led to the development of management actions designed to overcome internal feedbacks and allow turbid lakes to become clear again (Hosper 1998). In general, an understanding of multiple-state behaviour can assist in both prevention and recovery from undesirable states.

We thank Garry Peterson, Emily Stanley, Bea Beisner and an anonymous reviewer for their helpful comments on the paper. This research was supported by the National Science Foundation and by the Andrew W. Mellon Foundation. Graeme Cumming was funded by a David H. Smith Fellowship from the Nature Conservancy. This is publication DHS2001-2 of the David H. Smith Conservation Research Fellowship Program.

## APPENDIX A

A mass-balance model that represents the essential dynamics of the soil-sediment-water-phosphorus system (Carpenter *et al.* 1999b) is

$$S_{t+1} = S_t + a_1FT - a_2(1 - F)TS_t - L_2S_t, \quad (\text{A1})$$

$$M_{t+1} = M_t + sP_t - bM_t - rM_t f(P_t), \quad (\text{A2})$$

$$P_{t+1} = P_t + I(S_t) - (s + h)P_t + rM_t f(P_t), \quad (\text{A3})$$

where  $I(S_t) = L_1FT + L_2S_t$  and  $f(P_t) = P^Q/(m^Q + P^Q)$ . Here, we ignore the stochastic terms included by the soil-water-phosphorous system at time  $t$  (Carpenter *et al.* 1999b). There are three state variables: mass of phosphorus in soil ( $S$ ), in sediment ( $M$ ) and in water ( $P$ ). A total area of farmland  $T$  is divided into intensively fertilized land (proportion  $0 < F < 1$ ) and conservatively tilled land (proportion  $1 - F$ ). Soil dynamics are controlled by the rate of soil enrichment by intensive fertilization ( $a_1$ ), the rate of soil depuration by conservative tillage ( $a_2$ ) and the transport rate of soil to the aquatic system ( $L_2$ ). In addition, the input function  $I(S)$  includes a term for direct discharge of phosphorus from intensive agriculture ( $L_1$ ). Sediment dynamics include input from sedimentation ( $s$ ), permanent burial of phosphorus that cannot be recycled ( $b$ ) and maximum recycling rate ( $r$ ). The function  $f(P)$  represents the shift in feedback from slow recycling to fast recycling (Carpenter *et al.* 1999a). The exponent  $Q$  controls the steepness of the recycling curve, and the  $P$  level at which the recycling rate is half maximal is  $m$ . Water phosphorus dynamics include inputs from the watershed  $I(S)$ , sedimentation ( $s$ ) and hydraulic flushing rate ( $h$ ), and recycling. Results of the model are shown in figure 2 for the following set of parameter values:  $a_1 = 0.1$ ,  $a_2 = 0.001$ ,  $L_2 = 0.002$ ,  $L_1 = 0.2$ ,  $s = 0.5$ ,  $b = 0.001$ ,  $r = 1$ ,  $m = 1$ ,  $Q = 8$ .

## REFERENCES

- Bendix, J. & Hupp, C. R. 2000 Hydrological and geomorphological impacts on riparian plant communities. *Hydrol. Process.* **14**, 2977-2990.  
 Bennett, E., Carpenter, S. & Caraco, N. 2001 Human impact

- on erodible phosphorus and eutrophication: a global perspective. *BioScience* **51**, 227–234.
- Bilby, R. E., Fransen, B. R. & Bisson, P. A. 1996 Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can. J. Fish. Aquat. Sci.* **53**, 164–173.
- Bilby, R. E., Fransen, B. R., Walter, J. K. & Scarlett, W. J. 2001 Preliminary evidence of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. *Fisheries* **26**, 6–14.
- Blackburn, W. H., Knight, R. W. & Schuster, J. L. 1982 Saltcedar influence on sedimentation in the Brazos river. *J. Soil Water Conserv.* **37**, 298–301.
- Brooks, J. L. & Dodson, S. I. 1965 Predation, body size, and composition of plankton. *Science* **150**, 28–35.
- Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference*. New York: Springer.
- Bull, W. B. 1997 Discontinuous ephemeral streams. *Geomorphology* **19**, 227–276.
- Busch, D. E. & Smith, S. D. 1995 Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecol. Monogr.* **65**, 347–370.
- Canfield, D. E. J., Shireman, J. V., Colle, D. E. & Haller, W. T. 1984 Prediction of chlorophyll a concentration in Florida lakes; importance of aquatic macrophytes. *Can. J. Fish. Aquat. Sci.* **41**, 497–501.
- Carpenter, S. R. 2001 Alternate states of ecosystems: evidence and some implications. In *Ecology: achievement and challenge* (ed. M. C. Press, N. J. Huntly & S. Levin), pp. 357–383. Oxford, UK: Blackwell Science.
- Carpenter, S. R. & Lodge, D. M. 1986 Effects of submersed macrophytes on ecosystem processes. *Aquat. Bot.* **26**, 341–370.
- Carpenter, S. R. & Pace, M. L. 1997 Dystrophy and eutrophy in lake ecosystems: implications of fluctuating inputs. *Oikos* **78**, 3–14.
- Carpenter, S. R., Kitchell, J. F. & Hodgson, J. R. 1985 Cascading trophic interactions and lake productivity. *BioScience* **35**, 634–639.
- Carpenter, S. R., Caraco, N. F., Correll, D. L., Howarth, R. W., Sharpley, A. N. & Smith, V. H. 1998a Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Applic.* **8**, 559–568.
- Carpenter, S. R., Van Donk, E. & Wetzel, R. G. 1998b Nutrient-loading gradient in shallow lakes. In *The structuring role of submerged macrophytes in lakes* (ed. E. Jeppesen, M. Sondergaard, M. Sondergaard & K. Christoffersen), pp. 393–396. Ecological Studies, vol. 131. New York, Springer.
- Carpenter, S. R., Ludwig, D. & Brock, W. A. 1999a Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Applic.* **9**, 751–771.
- Carpenter, S. R., Brock, W. A. & Hanson, P. C. 1999b Ecological and social dynamics in simple models of ecosystem management. *Conserv. Ecol.* **3**, 4. See <http://www.consecol.org/vol3/iss2/art4>.
- Cleverly, J. R., Smith, S. D., Sala, A. & Devitt, D. A. 1997 Invasive capacity of *Tamarix remosissima* in a Mojave desert floodplain: the role of drought. *Oecologia* **111**, 12–18.
- Cooke, R. U. & Reeves, R. W. 1976 *Arroyos and environmental change in the American south-west*. Oxford, UK: Clarendon.
- Crowder, A. A., Smol, J. P., Dalrymple, R., Gilbert, R., Mathers, A. & Price, J. 1996 Rates of natural and anthropogenic change in shoreline habitats in Kingston basin, Lake Ontario. *Can. J. Fish. Aquat. Sci.* **53**(Suppl.), 121–135.
- DeAngelis, D. L. & Waterhouse, J. C. 1987 Equilibrium and non equilibrium concepts in ecological models. *Ecol. Monogr.* **57**, 1–21.
- Dodge, R. E. 1902 Arroyo formation. *Science* **15**, 746.
- Faafeng, B. A. & Mjelde, M. 1998 Clear and turbid water in shallow Norwegian lakes related to submerged vegetation. In *The structuring role of submerged macrophytes in lakes* (ed. E. Jeppesen, M. Sondergaard, M. Sondergaard & K. Christoffersen), pp. 361–368. Ecological Studies, vol. 131. New York: Springer.
- Fisher, S. G., Grimm, N. B., Martí, E., Holmes, R. M. & Jones, J. B. 1998 Material spiraling in stream corridors: a telescoping ecosystem model. *Ecosystems* **1**, 19–34.
- Friedman, J. M., Osterkamp, W. R., Scott, M. L. & Auble, G. T. 1998 Downstream effects of dams on channel geometry and bottomland vegetation: regional patterns in the Great Plains. *Wetlands* **18**, 619–633.
- Fujiwara, M. & Highsmith-Raymond, C. 1997 Harpacticoid copepods: potential link between inbound adult salmon and outbound juvenile salmon. *Mar. Ecol. Progr. Ser.* **158**, 205–216.
- Graf, W. L. 1978 Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. *Geol. Soc. Am. Bull.* **89**, 1491–1501.
- Grimm, N. B. 1993 Implications of climate change for stream communities. In *Biotic interactions and global change* (ed. P. M. Kareiva, J. G. Kingsolver & R. B. Huey), pp. 293–314. Sunderland, MA: Sinauer.
- Guildford, S. J. & Hecky, R. E. 2000 Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: is there a common relationship? *Limnol. Oceanogr.* **45**, 1213–1223.
- Horton, J. L. & Clark, J. L. 2001 Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. *Forest Ecol. Mngmt* **140**, 239–247.
- Hosper, S. H. 1998 Stables states, buffers and switches: an ecosystem approach to the restoration and management of shallow lakes in the Netherlands. *Water Sci. Technol.* **37**, 151–164.
- Hosper, S. H. & Jagtman, E. 1990 Biomanipulation additional to nutrient control for restoration of shallow lakes in the Netherlands. *Hydrobiologia* **200–201**, 523–534.
- Huggett, R. J. 1988 Dissipative systems: implications for geomorphology. *Earth Syst. Process. Landforms* **13**, 45–49.
- Jeppesen, E., Jensen, J. P., Kristensen, P., Sondergaard, M., Mortensen, E., Sortkjaer, O. & Olrik, K. 1990 Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes. 2. Thresholds, long-term stability and conclusions. *Hydrobiologia* **200–201**, 219–228.
- Johnson, W. C. 2000 Tree recruitment and survival in rivers: influence of hydrological processes. *Hydrol. Process.* **14**, 3051–3074.
- Lane, S. N. & Richards, K. S. 1997 Linking river channel form and process: time, space and causality revisited. *Earth Surf. Process. Landforms* **22**, 249–260.
- Larkin, G. S. & Slaney, P. A. 1997 Implications of trends in marine-derived nutrient influx to south central British Columbia salmonid production. *Fisheries* **22**, 16–24.
- Lewis, W. M., Hamilton, S. K., Lasi, M. A., Rodriguez, M. & Saunders III, J. F. 2000 Ecological determinism on the Orinoco floodplain. *BioScience* **50**, 681–692.
- Ludwig, D. & Walters, C. J. 1985 Are age-structured models appropriate for catch-effort data? *Can. J. Fish. Aquat. Sci.* **42**, 1066–1072.
- Mangel, M. & Clark, C. W. 1988 *Dynamic modeling in behavioral ecology*. Princeton University Press.
- Montgomery, K. 1993 Nonlinear dynamics and river meandering. *Area* **25**, 97–108.
- Murray, A. B. & Paola, C. 1994 A cellular model of braided rivers. *Nature* **371**, 54–57.
- Naiman, R. J. & Decamps, H. 1997 The ecology of interfaces: riparian zones. *A. Rev. Ecol. Syst.* **28**, 621–658.
- Naiman, R. J., Bilby, R. E. & Bisson, P. A. 2000a Riparian

- ecology and management in the Pacific coastal rain forest. *BioScience* **50**, 996–1011.
- Naiman, R. J., Elliot, S. R., Helfield, J. R. & O'Keefe, T. C. 2000b Biophysical interactions and the structure and dynamics of riverine ecosystems: the importance of biotic feedbacks. *Hydrobiologia* **410**, 79–86.
- National Research Council 1992 *Restoration of aquatic ecosystems: science, technology and public policy*. Washington, DC: National Academy Press.
- Nürnberg, G. 1984 Prediction of internal phosphorus load in lakes with anoxic hypolimnia. *Limnol. Oceanogr.* **29**, 135–145.
- Patten, D. T. 1998 Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* **18**, 498–512.
- Petraitis, P. S. & Latham, R. E. 1999 The importance of scale in testing the origins of alternative community states. *Ecology* **80**, 429–442.
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., Sparks, R. E. & Stromberg, J. C. 1997 The natural flow regime. *BioScience* **47**, 769–784.
- Polis, G. A., Anderson, W. B. & Holt, R. D. 1997 Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *A. Rev. Ecol. Syst.* **28**, 289–316.
- Pringle, C. M. 1997 Exploring how disturbance is transmitted upstream: going against the flow. *J. N. Am. Bent. Soc.* **16**, 425–438.
- Rand, P. S., Hall, C. A. S., McDowell, W. H., Ringler, N. H. & Kennen, J. G. 1992 Factors limiting primary productivity in Lake Ontario tributaries receiving salmon migrations. *Can. J. Fish. Aquat. Sci.* **49**, 2377–2385.
- Ricker, W. F. 1963 Big effects from small causes: two examples from fish population dynamics. *J. Fish. Res. Bd Can.* **20**, 257–264.
- Rinaldi, S. & Scheffer, M. 2000 Geometric analysis of ecological models with slow and fast processes. *Ecosystems* **3**, 507–521.
- Ryder, R. A. & Pesendorfer, J. 1989 Large rivers are more than flowing lakes: a comparative review. In *Proc. Intl Large River Symp.* (ed. D. P. Dodge), pp. 65–85. *Can. Fish. Aquat. Sci.* special publication 106.
- Sala, A., Smith, S. D. & Devitt, D. A. 1996 Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave desert floodplain. *Ecol. Appl.* **6**, 888–898.
- Scheffer, M. 1997 *Ecology of shallow lakes*. London: Chapman & Hall.
- Scheffer, M. & Jeppesen, E. 1998 Alternative stable states. In *The structuring role of submerged macrophytes in lakes* (ed. E. Jeppesen, M. Sondergaard, M. Sondergaard & K. Christoffersen), pp. 397–406. *Ecological Studies*, vol. 131. New York: Springer.
- Scheffer, M., Rinaldi, S., Kuznetsov, Y. A. & Van Nes, E. H. 1997 Seasonal dynamics of *Daphnia* and algae explained as a periodically forced predator–prey system. *Oikos* **80**, 519–532.
- Scheffer, M., Brock, W. A. & Westley, F. 2000 Socioeconomic mechanisms preventing optimum use of ecosystem services: an interdisciplinary theoretical analysis. *Ecosystems* **3**, 451–471.
- Schmidt, D. C., Carlson, S. R., Kyle, G. B. & Finney, B. P. 1998 Influence of carcass-derived nutrients on sockeye salmon productivity of Karluk Lake, Alaska: importance in the assessment of an escapement goal. *N. Am. J. Fish. Mngmt* **18**, 743–763.
- Schumm, S. A. 1973 Geomorphic thresholds and complex response of drainage systems. In *Fluvial geomorphology* (ed. M. Morisawa), pp. 299–310. Binghamton, NY: State University of New York.
- Scott, M. L., Lines, G. C. & Auble, G. T. 2000 Channel incision and patterns of cottonwood stress and mortality along the Mojave river, California. *J. Arid Environ.* **44**, 399–414.
- Shafroth, P. B., Auble, G. T., Stromberg, J. C. & Patten, D. T. 1998 Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams river, Arizona. *Wetlands* **18**, 577–590.
- Shafroth, P. B., Stromberg, J. C. & Patten, D. T. 2000 Woody riparian vegetation responses to different alluvial water table regimes. *West. N. Am. Nat.* **60**, 66–76.
- Sher, A. A., Marshall, D. L. & Gilbert, S. A. 2000 Competition between native *Populus deltoids* and invasive *Tamarix ramosissima* and the implications for re-establishing floodplain disturbance. *Conserv. Biol.* **14**, 1744–1754.
- Smith, V. 1998 Cultural eutrophication of inland estuarine and coastal waters. In *Successes, limitations and frontiers in ecosystem science* (ed. M. Pace & P. Groffman), pp. 7–49. New York: Springer.
- Stolum, H. 1996 River meandering as a self-organizing process. *Science* **271**, 1710–1713.
- Stromberg, J. C. 1993 Fremont cottonwood–gooding willow riparian forests: a review of their ecology, threats and recovery potential. *J. Arizona–Nevada Acad. Sci.* **26**, 97–109.
- Stromberg, J. C., Tiller, R. & Richter, B. 1996 Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecol. Appl.* **6**, 113–131.
- Tabacchi, E., Lambs, L., Guillo, H., Planty-Tabacchi, A. M., Muler, E. & Decamps, H. 2000 Impacts of riparian vegetation on hydrological processes. *Hydrol. Process.* **14**, 2959–2976.
- Ward, J. V. 1998 Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biol. Conserv.* **83**, 269–278.
- Wold, A. K. F. & Hershey, A. E. 1999 Effects of salmon decomposition on biofilm growth and wood decomposition. *Can. J. Fish. Aquat. Sci.* **56**, 767–773.
- Zavalati, E. 2000 The economic value of controlling an invasive shrub. *Ambio* **29**, 462–467.

## GLOSSARY

MSY: maximum sustainable yield