II REGIME SHIFTS IN LAKES

Introduction

Lakes are an exceptionally promising type of ecosystem for research on regime shifts.

All lakes are similar in fundamental ways, so it is possible to observe regime shifts over

and over, compare case studies to test ideas about underlying causes, or even create

regime shifts experimentally. The possibilities for comparison and experimentation

make it easier to understand the processes that lead to regime shifts, or those that

maintain the resilience of particular regimes. This modular feature of lakes is a great

advantage for studying regime shifts. Similar opportunities are offered by only a few

other types of ecosystems, such as small watersheds and oceanic islands.

This book will focus on three types of regime shifts that have been observed

repeatedly in lakes: eutrophication, large changes in fish populations or communities,

and coordinated shifts in food web structure (trophic cascades). These types of regime

shifts emphasize pelagic phenomena, and in this respect connect to previous

Excellence in Ecology volumes by Cushing (1996) and Reynolds (1997). My selection

of examples is necessarily arbitrary and incomplete.   For example, benthos of lakes,

and benthic-pelagic interactions, will likely prove to be a rich arena for regime shifts

(Paine 1994) building upon the excellent examples provided by Scheffer (1997) and

Jeppesen et al. (1998). Ecological stoichiometry provides several cases of multiple

stable states (Sterner and Elser 2002) and growth of that field seems likely to yield more examples in the future.

The primary goal of this chapter is to review observations of regime shifts in whole lake ecosystems. The study of regime shifts starts with patterns observed in the dynamics of whole lakes, as well as experimental and comparative studies aimed at understanding the processes that produce the patterns. In addition, the chapter introduces some models addressed in later chapters. The models are introduced graphically and conceptually. Mathematical versions of the models are presented in later chapters.

This chapter contains three main sections, corresponding to the three types of regime shifts that will be addressed by the book. Each section describes a phenomenon in a general way, discusses processes for the regime shifts, reviews examples, and presents a model graphically.

Phosphorus and Eutrophication

Definition and causes

Lake phosphorus cycles exhibit two different regimes, as seen in the history of Lake Mendota (Chapter I). Each regime tends to be stabilized by a distinct set of feedbacks. In one regime, phosphorus inputs, phytoplankton biomass, and phosphorus

regeneration from sediments are relatively low. The water is relatively clear. Such lakes are called oligotrophic. Lakes in the contrasting regime are called eutrophic (Smith 1998). Eutrophic lakes have high phosphorus inputs, high phytoplankton biomass, turbid water, and high return rates of phosphorus from sediments. Eutrophication is a syndrome caused by over-enrichment with phosphorus (Smith 1998). Eutrophication leads to excessive plant production, blooms of toxic cyanobacteria (also called blue-green algae), increased frequency of anoxic events, and fish kills. Species of macrophytes, invertebrates, and fishes may be extirpated. Eutrophication also occurs in flowing waters and oceans (Smith 1998). The oceanic phosphorus cycle appears to have alternate states caused by biogeochemical mechanisms similar to those described below for deep, thermally stratified lakes (Van Cappellen and Ingall 1994).

Excess inputs of phosphorus are the most common cause of lake eutrophication (Schindler 1977). In this respect, lakes differ from many other ecosystems in which nitrogen is the most limiting mineral nutrient. Nitrogen can also be an important nutrient in lakes, but, unlike phosphorus, nitrogen can be fixed from the atmosphere. Thus if phosphorus is abundant, nitrogen rarely remains a limiting factor for long. There are exceptions, such as lakes in which nitrogen fixation or assimilation is limited by trace metals (Vitousek and Howarth 1991). Increasingly, ecosystems are enriched by nitrogen applied as fertilizers or derived from atmospheric pollutants (Vitousek et al. 1997a, Howarth et al. 2002). Increased availability of fixed nitrogen could promote phosphorus limitation in some circumstances.

Excess phosphorus inputs to lakes usually come from sewage, industrial discharges, and agriculture. In North America and Western Europe, nutrient runoff from agricultural and urban lands has become the most important phosphorus source as municipal and industrial sources have been curtailed (Carpenter et al. 1998a). Agriculture is particularly important as a source of phosphorus pollution. Excessive fertilizer use causes phosphorus to accumulate in soils (Bennett et al. 2001). During runoff events, phosphorus-enriched soils are washed into lakes, where some of the phosphorus dissolves and is taken up by algae. In some cases, soil particles become saturated with phosphorus and dissolved phosphate ions are carried to lakes in surface- or groundwater (Carpenter et al. 1998a, Bennett et al. 2001). Although phosphorus may be rapidly stripped from the water by sinking particles, it can also be recycled rapidly from sediments or by animals.

Once it enters the lake, phosphorus stimulates algal growth, including blooms of toxic cyanobacteria. Decay of algae consumes oxygen, and can thereby create anoxic episodes which suffocate living organisms. Rooted aquatic plants may be lost due to shading by algae suspended in the water. Fish species may be lost due to anoxic events. Loss of rooted plants also reduces food supply and habitat for fishes (Olson et al. 1998). The vegetation provides substrate for invertebrates which are consumed by fishes. Vegetation also shelters fishes from predators.

Recycling of phosphorus is critical for maintaining plant production of lakes. In many lakes, primary producers obtain more of their phosphorus from recycling than from inputs. Phosphorus is recycled by several mechanisms in lakes. Recycling by animals (excretion or egestion) can supply a significant fraction of the phosphorus demand for phytoplankton growth during summer. Both herbivorous zooplankton and fishes are potentially important sources of phosphorus to phytoplankton (Carpenter et al. 1992, Schindler and Eby 1997, Elser et al. 1988). Recycling from sediments stabilizes eutrophication, especially in deep lakes (see below). In shallow water, wind-mixed waters can resuspend sediments and thereby move phosphorus from sediments into the water. However, P may also be removed as it sorbs to sediment particles which re-settle to the bottom of the lake.

Shallow lakes: a special case

Shallow lakes are not thermally stratified. They can mix to the bottom at any time of the year. Also, shallow lakes may support beds of rooted aquatic plants (macrophytes) that cover most of the area of the lake. Consequently, in shallow lakes, a unique set of processes affects the transition between clear and turbid water (Scheffer 1997, Jeppesen et al. 1998). These processes are different from those described in the previous section, which can occur in any lake. Because of these unique mechanisms of transition between regimes, shallow lakes can be considered as a special case.

Transitions between clear-water and turbid states of shallow or non-stratified lakes are the most thoroughly studied regime shifts in limnology (Scheffer 1997, Jeppesen et al. 1998). In the turbid state, phytoplankton are the dominant primary producers. Rooted aquatic plants are sparse, because of shading by phytoplankton. Also, bottom-feeding fishes uproot the macrophytes, and some waterfowl eat macrophytes. Phosphorus release from sediments may be rapid, because the sediments are exposed to waves and are easily resuspended. In the clear-water state, macrophytes, periphyton, and their epiphytes are the dominant primary producers and phytoplankton concentrations are low. Recycling of phosphorus to phytoplankton is slow, because the rooted plants stabilize sediments and monopolize nutrients during the growing season. In addition, phytoplankton may be grazed heavily by zooplankton. The macrophytes provide the zooplankton with a refuge from fish predation. Regime shifts between turbid and clear water in shallow lakes have been the subject of a rich diversity of limnological studies and an influential body of models and theory.

Deep lakes: biogeochemical basis of alternate states

In most temperate lakes, temperature gradients create two layers during the growing season: an upper, well-mixed layer of warm water called the epilimnion, which floats on a lower, colder more isolated layer or hypolimnion (Fig. 4). Mixing of water, energy, and solutes between the epilimnion and hypolimnion is limited. One of the largest material fluxes between the layers is the downward flux of sedimenting particles.

The layering of deep lakes creates a process for alternate states that is completely different from the one seen in shallow lakes. During summer stratification, waters of the hypolimnion cannot be reoxygenated by contact with the atmosphere. Thus the oxygen content of the hypolimnion depends on the initial endowment of oxygen at the onset of stratification, and the rate that oxygen is depleted by organic matter decay. If the hypolimnetic water remains oxygenated, phosphorus is bound by insoluble complexes with iron and is therefore not available for recycling to primary producers (Mortimer 1941, 1942). If the hypolimnetic water becomes anoxic, however, the iron is chemically reduced to a soluble form and phosphate is released into the water (Mortimer 1941, 1942). Turbulence at the upper edge of the hypolimnion, or mixing episodes that entrain hypolimnetic water into surface waters, make this dissolved phosphate available to phytoplankton in the epilimnion (Soranno et al. 1997).

This process requires a sufficient iron to bind phosphate when the hypolimnion is oxygenated. In many lakes, there is sufficient iron available. Under some conditions, for example lakes that have received high inputs of sulfate from atmospheric pollution, low availability of iron may limit this mechanism (Caraco et al. 1991). In such lakes, phosphate recycling may be high even while the hypolimnion is oxygenated, because there is insufficient iron to bind the phosphate in sediments.

In most lakes, therefore, oxygen concentration of the hypolimnion acts as a regulator of phosphorus release from sediments. The oxygen concentration of the hypolimnion is affected by the production of phytoplankton in the upper waters of the

lake. As the phytoplankton die, they sink, and the greater the production of phytoplankton the greater the flux of sinking organic matter to the hypolimnion. If the flux of decomposing material into the hypolimnion is low, then the rate of oxygen consumption in the hypolimnion is also low and the hypolimnion may remain oxygenated through the summer. If the hypolimnion remains oxygenated, recycling of phosphorus is low. In contrast, if the flux of decomposing material is sufficiently large, then oxygen depletion will be fast enough to deoxygenate the hypolimnion during the summer. Once the hypolimnion is anoxic, phosphate recycling can be rapid.

This process creates the possibility of alternate states. When phosphorus inputs are low, phytoplankton production is low, the hypolimnion remains oxygenated, phosphorus recycling is low, and the clear-water state of the lake is reinforced. When phosphorus inputs are high, the feedbacks shift. Phytoplankton production is high, the hypolimnion is deoxygenated, phosphorus recycling is high, and the turbid-water state of the lake is reinforced. As phosphorus inputs increase from low to high rates, there is an increase in the frequency of anoxia, from essentially zero at low rates of phosphorus input to nearly 100% of the summer at high rates of phosphorus input (Reckhow 1979). Thus the recycling flux rises from near zero to a maximal rate over the gradient of phosphorus inputs (Carpenter et al. 1999b).

To predict the annual recycling of phosphorus in a lake, one needs to know the daily rate of phosphorus release from sediments (Nürnberg 1984) and the duration of anoxia during summer stratification. Rates of P release from sediments have been

reviewed by Nürnberg (1984) and are reasonably predictable (see Chapter III). What controls the duration of anoxia in stratified lakes? The rate of hypolimnetic oxygen depletion increases with phosphorus and algal biomass of the lake, and with hypolimnetic water temperature, and decreases with thickness of the hypolimnion (Cornett and Rigler 1980, Charlton 1980). According to these empirical models, the number of days per summer that a hypolimnion is anoxic should increase with phosphorus concentration and temperature, and decrease with thickness of the hypolimnion (Carpenter et al. 1999b). Other analyses reach similar conclusions (Nürnberg 1995). The probability of anoxia is a sigmoid function of phosphorus concentration (Reckhow 1979). This probability is directly related to the amount of time that sediments are overlain by anoxic water. Thus, the mass of phosphorus recycled each year in a lake should be a sigmoid function of the phosphorus concentration, increase directly with hypolimnetic water temperature, and decrease with thickness of the hypolimnion. This relationship is developed quantitatively later in this Excellence in Ecology book.

Recovery from eutrophication: delays and irreversibility

We now have decades of experience with managing eutrophication in hundreds of lakes around the world (Cooke et al. 1993). Case studies of projects to reverse eutrophication reveal a mix of successes and failures. These studies illuminate the processes that stabilize eutrophication, as well as strategies for breaking down the resilience of the eutrophic condition and restoring clear water.

In some cases, eutrophication has been halted or reversed by reducing phosphorus inputs (Edmondson 1991). Success is most common in lakes that are deep, with cold, oxygen-rich deep waters. In other cases, successfully-managed lakes have rapid flushing rates. Whether deep or rapidly flushed, these lakes have great capacity to dilute phosphorus and maintain oxygenated conditions. Also, some lakes which recovered rapidly from eutrophication were eutrophic for only a few years. Such lakes may not accumulate a large mass of phosphorus in the sediments.

Lake Washington (Washington, USA) is a well-known example of eutrophication that responded directly and rapidly to decreased inputs of phosphorus (Edmondson 1991). Eutrophication symptoms were recognized during the 1950s, and the problem was traced to sewage discharges. Diversion of effluent began in 1963, and by 1967 almost all (99%) of the sewage effluent had been diverted from the lake. Notable improvements in water quality occurred within a year of completing the diversion. By 1971, Secchi disk transparency exceeded that of the 1950s. By 1975, Secchi transparency had increased from 1.0 m to 4.0 m, total phosphorus decreased from 70 to 16 mg m^{-3}, and chlorophyll decreased from 35 to 4 mg m^{-3} (Edmondson 1979).

In many cases, however, the degree of eutrophication has not responded to reductions of phosphorus input (Sas 1989, UN National Research Council 1992). Instead, rapid, efficient recycling of phosphorus within the lake has maintained eutrophication despite reductions of inputs. In some of these cases, eutrophication has

eventually been reversed by removing phosphorus from the lake (e.g. by dredging) or immobilizing phosphorus (e.g. by adding aluminum sulfate to sediments). In other cases, eutrophication could not be reversed.

Shagawa Lake (Minnesota, USA) is an example of a lake that did not respond to reductions of phosphorus input. Like Lake Washington, Shagawa Lake suffered eutrophication due to sewage inputs. Poor water quality prompted limited sewage treatment in 1911, but water quality continued to deteriorate. Treatment improvements in 1952 failed to improve water quality. Finally, in 1973, a new treatment plant was built which decreased phosphorus inputs by more than 80% (Larsen et al. 1979, 1981). Phosphorus loading models predicted that annual average total phosphorus concentration should drop from 51 to 12 mg m^{-3}, but the concentration dropped only to 29 mg m^{-3}. More importantly, summer concentrations of total phosphorus and chlorophyll remained unchanged, and severe blooms of blue-green algae continued to occur. The cause was efficient release of phosphorus from lake sediments during periods of anoxia (Larsen et al. 1981). Over a long period of time, it is possible that sediment phosphorus will be depleted and summer algal blooms will decline, as occurred in other lakes with delayed responses to reduced phosphorus input (Welch et al. 1986). However, by 1991 --18 years or 24 complete hydrologic flushings after the reduction of phosphorus input-- the lake had not yet recovered (US National Research Council 1992).

Model for eutrophication

The literature reviewed so far suggests that lake water quality can be likened to an old-fashioned pan balance (Fig. 5). The two pans of the balance represent clear water or turbid water with high concentrations of algae. The ecosystem (black ball in Fig. 5) can lie in either pan. Disturbances to the ecosystem, such as runoff events triggered by big rainstorms, may affect the ecosystem but only a rather large disturbance will move the ecosystem between pans. If excess phosphorus is added to a clear lake, it will slowly build up in the sediments. Eventually, phosphorus accumulates to the point where the lake is highly vulnerable to any disturbance that increases phosphorus in the water. After such a disturbance, algae concentrations will increase and the decay of these algae will trigger phosphorus recycling that grows more algae. The resulting feedback tips the lake into a self-sustaining eutrophic state with turbid water due to growth of algae. Once the lake is eutrophic, it is necessary to reduce phosphorus inputs and perhaps also disturb the lake by some management intervention to tip the balance back toward clear water.

One can also construct a graphical model that captures the features of eutrophication represented by the physical model of the pan balance. The graphical model is consistent with, but simpler than, other models for lake eutrophication (Reckhow and Chapra 1983; Chapra and Reckhow 1983; Scavia and Robertson 1979). The model presented here is designed to capture the essential patterns and processes of eutrophication with minimal complexity. This chapter will explain the model using

graphs. Mathematical versions of the model will be presented in Chapters III and V.

More detailed expositions of this model are presented by Carpenter et al. (1999b), Dent

et al. (2002), and Ludwig et al. (2003).

The model incorporates mass balance for phosphorus (P) in a watershed-lake

system (Fig. 6). Land use and land cover affect P content of watershed soils. In many

watersheds, agricultural fertilizers and manures are the most important source of P to

the soil (Bennett et al. 2001). Phosphorus input, or loading, from the watershed to the

lake is carried in runoff driven by precipitation events and snowmelt (Soranno et al.

1996). For a given watershed, the parameters that link soil P concentration, climate,

and loading depend on local topography and hydrologic flow paths (Soranno et al.

1996).

The amount of P in the water is affected by the watershed or release from lake

sediments, and loss due to hydraulic outflow or sedimentation (Fig. 6). P in sediment

may be released to the overlying water, or may be buried in layers of sediment that are

too deep to be recycled. P concentrations in lake water are highly correlated with

phytoplankton biomass (Schindler et al. 1978, Canfield and Bachmann 1981), and for

the purposes of this model lake water P and algal biomass are assumed to be

interchangeable. The model does not calculate phytoplankton biomass, but instead

assumes that it is directly related to P mass or concentration in the water.

Stability of the model depends on processing of P by outflow and sedimentation (straight line), and inputs plus recycling (curved lines) (Fig. 7). Equilibria occur where source curves (inputs plus recycling) intersect loss lines (outflow plus sedimentation). At stable equilibria, or attractors, the P declines to the equilibrium after a small increase in P, because losses exceed sources. Also, the system increases to the equilibrium after a small decrease in P, because sources then exceed losses. At unstable equilibria, or repellers, the P increases to a higher equilibrium point after a small increase in P, or decreases to a lower equilibrium point after a small decrease in P.

Two hypothetical lakes are shown in Fig. 7A. Lake 2 has higher average input from the soil (intercepts of curved lines) and a higher maximum rate of recycling (height of curved lines). Both lakes have identical outflow and sedimentation. Both lakes have three equilibria. The middle one is an unstable repeller, and the upper and lower ones are locally stable attractors. The steady state at low P concentration is the clear-water state, and the steady-state at high P concentration is the turbid or eutrophic state.

Resilience of a state is measured by the distance (in P units) from a stable steady-state to the unstable steady state. The resilience of the clear-water state is greater for Lake 1 than for Lake 2. Resilience is related to the size of a stochastic shock that the system can absorb without changing states. A shock which moves the system from one stable state past the unstable steady state will shift the system to the other stable state. For example, a P input event that is larger than the resilience of the

clear-water state will push the lake past the unstable steady state, and recycling will then drive the P level to the eutrophic steady state.

Soil P affects the probability distribution of input events to the lake (Fig. 7B). These input events are driven by variable and unpredictable storms and snowmelt, so we model them as a random variable. The logarithm of input event magnitude can often be described by a Student-t or gamma distribution (Carpenter et al. 1999b, Reed-Anderson and Carpenter 2002). The logarithm of annual inputs often fits a Student-t distribution (Reckhow 1979, Lathrop et al. 1998, Carpenter et al. 1999b). The watershed of Lake 2 has high-P soils causing a higher mean input rate and broader distribution of stochastic shocks. Because the resilience of the clear-water state is low for Lake 2, there is a relatively high probability of a shock large enough to move Lake 2 out of the clear-water state. In contrast, the watershed of Lake 1 has low-P soils causing a relatively low mean input rate. The probability distribution has low variance, so large input events are rare. Because the resilience of the clear-water state for Lake 1 is rather large, there is a low probability that a random input event will shift Lake 1 to the turbid state.

In summary, the eutrophication model describes clear- and turbid-water states of lakes, as well as the probability distribution of P inputs. The shift from clear to turbid water usually involves shrinkage of the resilience of the clear-water state (e.g. Lake 1 to Lake 2 in Fig. 7A) as well as a large P input event. The shrinkage of resilience can be caused by P buildup in sediments, increased P inputs, or both. The reverse shift – from

turbid to clear water – requires expansion of the resilience of the clear-water state (e.g. Lake 2 to Lake 1 in Fig. 7A). The increase in resilience involves a reduction in P inputs. Reducing the mean P input rate usually decreases the variance as well, so large P input events are less frequent. In addition, some lakes have been manipulated to increase the P outflow rate or decrease P recycling (Cooke et al. 1993), both of which increase resilience of the clear-water state.

According to the model, measures of susceptibility to eutrophication are related to resilience. For example, the P recycling rate or the P input distribution are better measures of eutrophication than the P concentration in the water (Beisner et al. 2003a). P recycling rate is related to resilience, and the P input distribution is related to the probability of shocks that exceed resilience. P concentration in the water, in contrast, is a rapidly-changing variable that may not accurately indicate resilience.

This model can represent the behavior of most case studies of lake eutrophication, and all current methods for managing P in lakes (Carpenter et al. 1999b). For example, P management methods may decrease inputs, reduce recycling by dredging sediments or treating them with aluminum sulfate to precipitate the P, reduce recycling by oxygenating the hypolimnion, or remove P by increasing the hydraulic flushing rate (Cooke et al. 1993). All of these can be represented by manipulating or fitting the appropriate parameters of the model. Riparian buffers (shoreline vegetation that can intercept nutrient inputs before they reach the lake) affect the mean and variance of P inputs (Weller et al. 1998, Reed-Anderson and Carpenter

2002). Effects of these parameters can be represented in the model by modifying the distribution of P inputs. Biomanipulation, a management method based on trophic cascades (see below), can also be represented in the model, by increasing the rate of removal of P from the lake water or decreasing the rate of recycling. In terms of the P cycle, biomanipulation works by decreasing P availability to phytoplankton. This occurs by increasing flux to sediments, sequestering P in bodies of animals, or decreasing flux of P from littoral sediments to pelagic water (Carpenter et al. 1992, Schindler et al. 1996, Jeppesen et al. 1998). The role of trophic cascades in the P cycle of lakes leads us to consider regime shifts connected to fish population dynamics and food webs.

Depensatory Dynamics in Aquatic Food Webs

Pelagic Regime Shifts

Since Ricker's (1963) famous paper about "big effects from small causes", many of the case studies of big changes in pelagic ecosystems have come from studies of fish and fishing. Long-term observations of fish stocks sometimes exhibit sharp changes that suggest regime shifts (Steele 1996, 1998). Even in the absence of direct scientific observation, changes in fish resources may be recorded, perhaps in harvest records or archeological information. A change in a fish stock may have notable human consequences without large ecological impacts (Steele 1998). However, many changes due to fishing have significantly altered marine food webs (Steele 1996, Jackson et al. 2001). Similar changes have occurred in freshwater ecosystems subject

to sport fishing (Post et al. 2002), although interactions of fishing with other factors such as species invasion and eutrophication must also be considered when interpreting long-term changes in lake food webs (Kitchell and Carpenter 1993).

Sizeable changes in fish stocks have occurred ever since there were fisheries (Jackson et al. 2001). Even in prehistoric times large marine vertebrates such as whales, manatees, seals, crocodiles, jewfish, swordfish, sharks, and rays have been extirpated from coastal ecosystems, or driven to functionally trivial populations, by overfishing (Jackson et al. 2001). Over time scales of decades to centuries, these changes in top predators cascaded through near-shore marine communities. Often, unfished species became abundant, and later were fished by humans. In some cases, population expansions of unfished species led to overcrowding and epidemic disease. Climatic changes at decadal to millennial scales may trigger or enhance regime shifts in marine food webs. Furthermore, coastal eutrophication may interact with food web shifts to intensify ecosystem changes (Jackson et al. 2001, Scheffer et al. 2001a). For example, eutrophication may create turbid or anoxic water which causes die-offs of benthic organisms or fish kills. Massive and ongoing changes in marine ecosystems over thousands of years suggest that it is impossible to define a baseline equilibrial state (Steele 1998).

Changes driven by fishing can cascade through an entire food web (see later section on trophic cascades). In the Black Sea, industrial fishing began about 1970 and depleted stocks of top predators such as dolphins, bluefish, bonito and mackerel

(Daskalov 2002). Stocks of planktivorous fishes (such as anchovy and sprat) increased during the 1970s, and became a target for the fishery in the 1980s. At the same time, the Black Sea was subject to species invasions, as well as eutrophication by anthropogenic nutrient input (Zaitsev and Mamaev 1997). Jellyfish biomass, especially that of the exotics *Mnemiopsis* and *Beroe*, increased as fish biomass declined. Biomass of herbivorous zooplankton decreased, in part due to predation by jellyfish. Phytoplankton biomass increased, and dense blooms became frequent. The decline in water transparency caused a decrease in benthic algae, especially the formerly dominant red alga *Phyllophora*. Oxygen content declined, leading to hypoxia and loss of benthic animals and plants. The post-1970 regime differed from the pre-1970 regime at every level of the trophic system. After 1970, large pelagic predators were rare, pelagic planktivorous fishes and blooms of jellyfish were common, herbivorous zooplankton biomass was low, phytoplankton biomass and bloom frequency increased, and benthic communities were degraded. These shifts had at least three drivers: overfishing, species invasions, and eutrophication.

In lakes, species invasions are an increasingly important factor in ecosystem change (Kolar and Lodge 2000). Ecosystem impacts of invasion may interact with those of fishing, eutrophication, and climate change. In the Laurentian Great Lakes, extensive food web changes were attributed to fishing and invasion (Christie 1974). Following invasion of the sea lamprey, stocks of lake trout and burbot declined. This decline was followed by increases in the prey species of these top predators, such as deepwater cisco and the exotics rainbow smelt and alewife. Lake herring declined,

apparently due to predation of juveniles by rainbow smelt. Thus the major changes in

Great Lakes ecosystems prior to the 1950s were driven by overfishing and lamprey

invasion. Resilience of Great Lakes ecosystems to subsequent invasions was reduced

by loss of the top predators, lake trout and burbot.

Species invasions also cause significant changes in smaller lakes (Kolar and

Lodge 2000, Lodge 2001). Sparkling Lake (Wisconsin, USA) was invaded by rainbow

smelt (*Osmerus mordax*) in 1982 (Hrabik et al. 1998). The native planktivore, cisco

(*Coregonus artedii*), did not recruit successfully after the smelt introduction, and was

functionally eliminated from the food web by 1987. Predation by smelt on young-of-the-

year cisco was an important factor in the cisco decline. Piscivorous fishes in Sparkling

Lake also declined in abundance after the smelt introduction (unpublished data, North

Temperate Lakes LTER site, http://lter.limnology.wisc.edu). A second invader, rusty

crayfish (*Orconectes rusticus*) which entered the lake in 1985, may have contributed to

piscivore declines by eliminating macrophyte beds that provided crucial habitat for

juvenile fishes (Lodge et al. 2000, Wilson 2002). However, smelt invasions have

caused stocks of walleye (*Stizostedion vitreum*) to collapse in other lakes (Gilbert 2002).

Although walleye feed on smelt, walleye fail to recruit within four to six years of smelt

invasion in some lakes, and eventually the population of walleye disappears from the

lake. These patterns suggest that the predation impact of smelt on juvenile walleye is

less than that of adult walleye on smelt. Case histories of smelt invasion suggest an

important role for size-specific predation in regime shifts of lake fish communities.

Rusty crayfish also appear to play an important role, perhaps by degrading fish habitat and also by consuming fish eggs (Lodge et al. 2000).

Processes and Models

Regime shifts in lake or marine ecosystems appear to have multiple causes, including fishing, eutrophication, habitat alteration, and climate change. In fisheries stock analysis, much attention has focused on the possibility that overfishing may increase the vulnerability of a population to other factors, or directly trigger the collapse of a population to a low level. Many simple population models, such as the logistic equation, predict higher per-capita population growth rates at low population densities. This phenomenon is called compensation. But what if per-capita population growth rates decrease when the population falls below some critical level? This phenomenon is called depensation or the Allee effect (Asmussen 1979, Hilborn and Walters 1992, Frank and Brickman 2000). Predictions of food web dynamics can be quite different for compensatory and depensatory models.

Detection of depensation in time series of single populations has proven difficult (Myers et al. 1995). Statistical problems are numerous, including short time series, lack of data at extremely low and high population densities, and large observation errors (Hilborn and Walters 1992). Liermann and Hilborn (1997) devised a test statistic for depensation and calculated its probability distribution for 115 fish stocks, each of which was studied for 15 or more years. Results spanned a wide range, from strong

depensation to hypercompensation (i.e. extreme increase in per-capita population growth at low densities). However, most of the mass of the probability distributions lay on the depensatory side, indicating significant probability of depensation. Thus it is inappropriate to assume that depensation will not occur. These authors conclude that fish stock analyses should use models that include the possibility of both depensation and hypercompensation. At low population sizes, both collapse and explosive growth are possible.

What might cause depensation in fish populations? Suggested mechanisms include reduced reproductive success, inbreeding, impaired aggregation, inefficiency of food location, or predator-prey interactions with multiple domains of attraction (Asmussen 1979, Emlen 1984, Hilborn and Walters 1992). De Roos and Persson (2002) presented a general model of size-structured predation for two species that prey on each other in a size-dependent manner. Larger individuals of each species eat smaller individuals of the other species. If larger individuals of one species become rare for some reason, that species' recruitment can be eliminated by predation from the other species, leading to a depensatory collapse.

Walters and Kitchell (2001) proposed a mechanism that follows from the strong size-selectivity of aquatic trophic interactions. According to this "cultivation-depensation" process, high adult densities of a particular fish species suppress predation on juveniles of that species, by either consuming predators directly or by changing predator behavior (Fig. 8). Low adult densities, however, fail to suppress

predators, leading to heavy predation on juveniles and negative population growth. They argued that certain regime shifts in marine food webs, such as the collapse of North Atlantic cod stocks, could be explained by cultivation-depensation. Other examples are discussed by Post et al. (2002) and de Roos and Persson (2002).

Figures 8 and 9 present results from a simple model for a food-web process of depensation that is similar to that of Walters and Kitchell (Carpenter 2001, 2002). For certain combinations of parameters, the fish population has two steady states (Fig.9A). The upper steady state is stable. The lower steady state is not stable. If the population is perturbed below the lower steady state, it will collapse to zero. Three different stability outcomes are possible, depending on the parameters that control rate of harvest of the adult fishes, and the rate of predation on juvenile fishes (Fig. 9B). If the harvest rate of adults is sufficiently high, there is no stable steady state and the fish population collapses to zero. If both harvest rate of adults and predation on juveniles are sufficiently small, there is no unstable steady state, there is no depensation, and the population has only a positive stable steady state. There is an intermediate range of parameters that yields two steady states, one stable and the other unstable, as depicted in Fig. 9B.

Habitat changes, such as loss of rooted aquatic plants, may affect rates of interspecific predation in ways that cause depensation (Carpenter and Gunderson 2001, Carpenter 2002). An example of how habitat change might affect the predation rate on juvenile fishes is shown in Fig. 8B. If the mortality curve for juveniles responds to

habitat as in Fig. 8B, the system can gradually change from one stability domain to another, with potentially catastrophic consequences for the fish population (Carpenter 2002). If this mechanism is embedded in a more complex food web model, changes that resemble regime shifts can occur (Walters and Kitchell 2001). If such changes occur in a model for stock assessment and management decisions that affect harvest rates, very complex dynamics can occur (Carpenter and Gunderson 2001). A relatively simple version of this model will be studied in more detail in Chapter VI. In the remainder of this chapter, we will turn to the implications of shifts in fish populations for lower trophic levels in lakes.

Trophic Cascades

Annual phosphorus input is a reliable predictor of mean pelagic chlorophyll during the growing season. Chlorophyll is a commonly-used measure of phytoplankton biomass, and a correlate of primary production rate. Concentration of phosphorus during spring mixing is frequently used as an index of P input rate. Fig. 10 shows one of many published relationships between this indicator of P input and chlorophyll. Generally, such plots show significant correlations, yet a substantial proportion of the variance in chlorophyll cannot be explained by nutrients. Trophic cascades can explain a significant amount of the missing variance (Carpenter and Kitchell 1993, Carpenter et al. 2001b).

Trophic cascades connect fishes to phosphorus and phytoplankton, as follows. In the absence of piscivorous fishes, planktivorous fishes may be abundant. These fishes feed size-selectively on zooplankton, eliminating the larger-bodied herbivores. In contrast, lakes with abundant piscivorous fishes have few planktivorous fishes. Large-bodied zooplankton can thrive, and are often the dominant pelagic herbivores when planktivorous fishes are rare (but see Elser et al. 1998). The effect of fishes on total zooplankton biomass may be small, but the shift in body size has significant implications for chlorophyll (Fig. 10B). Larger-bodied herbivores tend to have higher per-capita grazing rates, broader diets, and lower recycling rates of P than smaller-bodied ones (Gliwicz 1980, Peters and Downing 1984, Elser et al. 1988). Often, the largest herbivores in lake plankton are species of *Daphnia*, which have rapid numerical response, broad diets, and high physiological requirements for P (Gliwicz 1980, Elser et al. 1996). The latter characteristic of *Daphnia* causes their excreta to be P-deficient, and thereby promotes P-limitation which contributes to the inverse relationship between *Daphnia* biomass and chlorophyll (Sterner et al. 1992, Sterner and Elser 2002). In general, a trophic cascade is a series of reciprocal predator-prey linkages that alters biomass or productivity across more than one link of a food web (Pace et al. 1999). The term was introduced to ecology by Paine (1980) and applied to lakes by Carpenter et al. (1985).

Comparisons and Experiments

The discovery and demonstration of trophic cascades and their effects on phytoplankton biomass took a long time. Hrbacek et al. (1961) showed that differences in algal biomass among fishponds could be attributed to the effects of fishes on the food web. The impact of size-selective predation by fishes was described by Brooks and Dodson (1965), who noted the implications for phytoplankton. Shapiro et al. (1975) introduced the idea of biomanipulation – a management tool to mitigate nuisance algae blooms by reconfiguring the food chain. In whole-lake experiments, the fish components of two nearby lakes were exchanged. Piscivorous bass were moved from Peter Lake to Tuesday Lake (Michigan, USA), and an equal biomass of planktivorous minnows was moved from Tuesday Lake to Peter Lake. This reciprocal transplant of fish biomass caused large and opposite shifts in the zooplankton community, chlorophyll, and primary production (Carpenter et al. 1987, Carpenter and Kitchell 1993). These experiments manipulated only the food web, and employed an unmanipulated reference lake to screen for possible confounding effects of weather or other factors. They showed that food web manipulations alone could create approximately three-fold changes in primary producer biomass and production, as well as changes in nutrient cycling and plankton community structure.

At the whole-lake scale, manipulation strength is a critical factor in the experimental outcome. Manipulation strengths of several successful whole-lake experiments were shown to be within the range of typical variation of predator populations (Carpenter et al. 1991). A number of whole-lake manipulations have produced significant food web effects from manipulations within the range of natural

variability of predator populations (Carpenter et al. 1987, McQueen et al. 1989, Hansson et al. 1998, Carpenter et al. 2001b). Manipulations must be strong enough to create a detectable change in noisy data (Carpenter 1988a,b, 1989; Hansson et al. 1998). Weak manipulations are uninformative, because lack of effect could be explained by either absence of a cascade, or a high level of noise in the data. Thus, manipulations that approximate the range of natural range of fish community composition are most likely to provide informative yet reasonably realistic results.

Biomanipulations are changes in food web structure to improve water clarity through trophic cascades (Shapiro et al. 1975, Carpenter et al. 1985). Some biomanipulations were combined with other types of interventions to improve water quality, so interpretation of food web effects is not straightforward, but nevertheless some conclusions may be drawn. In a broad review of case studies, Hansson et al. (1998) concluded that biomanipulation was most useful as a trigger for secondary processes that reduced recycling of nutrients. In other words, biomanipulation may cause a regime shift, but the shift may be unstable unless other ecosystem changes such as reduced P loading are implemented as well. Hansson et al. (1998) stressed the importance of rapid, massive manipulation of fishes, which may be difficult in large lakes. Kitchell (1992) and Lathrop et al. (2002) described the even greater challenges of biomanipulating an eutrophic lake when an additional trophic level – human anglers – is prominent. Despite the complications of coping with an additional human trophic level, they found significant effects of food web change on the ecosystem of Lake Mendota.

The interaction of trophic cascades with nutrient enrichment has been debated.

Some authors have argued that cascade effects are weak in highly enriched lakes

(Benndorf 1995, Reynolds 1994). Comparative studies suggest that both nutrients and

trophic cascades have powerful impacts (Fig. 10), but impacts of changing these factors

cannot be inferred from comparative studies alone (Carpenter et al. 1991). Simple

stoichiometric models of grazer-algae-nutrient systems in chemostats demonstrate

multiple stable states consistent with trophic cascades (Sterner and Elser 2002). While

nutrients and food web structure can be manipulated independently in enclosures or

small containers, it may be difficult to extrapolate results of container experiments to

whole ecosystems in the field (Carpenter 1996, Schindler 1998, Pace 2000). The

keystone grazer *Daphnia* has a high physiological requirement for phosphorus,

suggesting that at least moderate levels of this nutrient are required for trophic

cascades to occur (Elser et al. 1998, Sterner and Elser 2002). Collectively, these

patterns suggest that effects of nutrients and cascades on lake productivity may interact

in complex ways.

The combined effects of nutrient enrichment and trophic cascades on primary

producers were studied by manipulating nutrients and food web structure independently

in whole-lake experiments. These experiments showed that trophic cascades had

strong impacts on primary producers across a range of nutrient loading rates (Carpenter

et al. 2001b). Both inorganic N and P were added in a ratio designed to maintain P

limitation of phytoplankton. At the highest P input rates, inorganic P accumulated in the

surface waters of the lakes, indicating that some other factor (perhaps light transmission) was limiting algal growth. Thus, the experiments spanned a range of situations from unenriched P-limited conditions, through enriched but still P-limited conditions, to conditions under which P was saturating.

Algal biomasses of a planktivore-dominated lake and a piscivore-dominated lake were compared over the full range of nutrient input rates (Fig. 11). Results for an unenriched reference lake are also presented. Each data point is the mean for an annual growing season. Over the range of experimental nutrient loadings, the planktivore-dominated lake had about three times more chlorophyll than the piscivore-dominated lake (Fig. 11). Primary production was about six-fold greater in the planktivore-dominated lake than in the piscivore dominated lake (Carpenter et al. 2001b). Similar differences were seen if the phytoplankton responses were calculated per unit volume instead of per unit area (Carpenter et al. 2001b).

This brief summary has stressed the whole-lake studies of trophic cascades that used comparative and experimental approaches. Most of the discussion about ecosystem impact of cascades has centered on studies using one of these two approaches.   However, long-term data sets also offer important insights, and are especially pertinent to considerations of models for trophic cascades.   Models of cascades should be consistent with data from long-term studies.

Long-Term Observations of Trophic Cascades

Long-term observations of fisheries are more abundant in the literature than long-term

data for entire pelagic food webs. Here I define "long-term" as spanning more than one

lifespan of the longest-lived species in the food web. In pelagic ecosystems, this

longest-lived species is usually the top carnivore, a fish species. A few selected

examples are reviewed here. I have chosen lakes which were not manipulated

experimentally during the time period of study. One lake (Lake Mendota) was subjected

to a management intervention near the end of the period of study, but this intervention

only intensified the natural event described below (Lathrop et al. 2002).

Winterkill eliminated the top carnivore, largemouth bass (*Micropterus salmoides*),

from Wintergreen Lake (Michigan, USA) in 1978 (Mittelbach et al. 1995). Following

extirpation of the bass, planktivorous fish abundance increased and large-bodied

herbivorous zooplankton declined. The ecosystem remained in this state until

largemouth bass were reintroduced in 1986. As the bass population grew, planktivore

abundance decreased about 100-fold, zooplankton biomass increased about ten-fold,

large-bodied *Daphnia* returned to a prominent role in the food web, and water clarity

increased substantially. These limnological changes are similar to those in European

lakes from which fishes were removed (Scheffer 1997, Jeppesen et al. 1998). In

Wintergreen Lake, however, the changes were caused by a cascade driven by a top

carnivore. In another case study of partial winterkill, part of the populations of both

piscivores and planktivores were killed (McQueen et al. 1989). The partial kill of both

trophic levels led to responses that were weaker and more short-lived than those

observed by Mittelbach et al. (1995), but there were qualitatively similar responses in the zooplankton (McQueen et al. 1989).

The impacts of a dominant planktivore, cisco (*Coregonus artedii*), were documented for Lake Mendota using time series data (Rudstam et al. 1993). In years of low cisco biomass, zooplankton were dominated by large-bodied *Daphnia pulicaria*. Biomass of this zooplankton increased earlier in the spring, and lasted longer into the summer, than biomass of the zooplankton that dominated when cisco were abundant. Low levels of cisco were associated with a longer period of clear water during spring and early summer, apparently a consequence of heavy grazing by *D. pulicaria*. In years of high cisco abundance, spring and summer zooplankton were dominated by the smaller-bodied *D. galeata mendotae*. During spring, *D. galeata* biomass develops at warmer water temperatures than those required by *D. pulicaria*. Consequently, when cisco are abundant, grazer biomass develops later in the spring. *D. galeata* can escape control by cisco, overgraze their resources, and cause a clear water phase. However, *D. galeata* are more susceptible to starvation than *D. pulicaria*, and their biomass consequently drops to low levels after the clear water phase. This causes grazing pressure on phytoplankton to be low through most of the summer when cisco are abundant.

Some long-term analyses of trophic cascades demonstrate cyclic changes in lake food webs. Yellow perch (*Perca flavescens*) in Crystal Lake (Wisconsin, USA) oscillated, with individual age classes dominating the population for periods of about

five years (Sanderson et al. 1999). These authors considered diverse possible causes

for the cycles, and concluded that inter-cohort predation was a key factor. When

juvenile perch are present in the lake, they cannibalize young-of-the-year (YOY) perch

and prevent recruitment. This process tends to form a single age class of juvenile

perch. By the time the cohort reaches reproductive maturity, its reproductive impact on

YOY outweighs any impact of predation. Adult perch may be less abundant than

juveniles, and benthic prey may partially replace YOY prey in adult perch diets. Thus, in

the absence of juvenile perch, a new year class of perch can survive.

The yellow perch cycles have complex effects on plankton (Sanderson 1998). In

years when juvenile perch were absent, *Daphnia* dominated the zooplankton and

chlorophyll concentrations were lower than in years when juvenile perch were abundant.

Similar cycles, and similar ecosystem consequences, are known from population

dynamics of other fishes such as vendace (Hamrin and Persson 1986) and pink salmon

(Shiomoto et al. 1997).

Similar processes of age-class interaction were noted in a study of Paul Lake

(Michigan, USA), an undisturbed reference lake for whole-lake experiments on trophic

cascades (Post et al. 1997). Cannibalism by largemouth bass suppressed recruitment.

As bass densities declined due to gradual mortality of adults, a window of opportunity

opened for recruitment in which YOY bass were abundant enough to survive predation

by the adult bass remaining in the lake. Zooplankton are a major diet item for YOY

bass in their first summer. The large cohort of zooplanktivorous YOY bass had predictable effects on lower trophic levels (Post et al. 1997).

Annually-resolved pigment concentrations from laminated lake sediments exhibited cycles with periods of three to five years (Carpenter and Leavitt 1991). The cycles were pronounced for fossil pigments that tend to be deposited in zooplankton feces, but no cycles were evident for pigments that have multiple sources or mainly terrestrial sources. The pattern in the sediment record is consistent with a trophic cascade triggered by periodic year classes lasting 3 to 5 years. This period corresponds with the lifespans of the top carnivores of this lake's food web (Carpenter and Leavitt 1991).

These case studies suggest that cyclic trophic cascades in lakes tend to be synchronized with the lifespans of the top predators.. Pink salmon and vendace have lifespans of two years, corresponding with the food web cycles (Hamrin and Persson 1986, Shiomoto et al. 1997). The mix of species in the lake studied by paleolimnological methods had lifespans of three to five years, corresponding with the cycles found in the sediment archive (Carpenter and Leavitt 1991). Yellow perch lifespans are variable and may be somewhat longer than the five-year cycle described by Sanderson et al. (1999). Other studies are not long enough to assess the existence of cycles, but do demonstrate food web regimes that correspond to the duration of a predator cohort.

Models

Numerous mathematical models have been used for describing trophic cascades. Two
of these will be discussed here. The first uses simple equations, most linear, to
represent the year-to-year dynamics of food webs over a long period of time (Carpenter
1988a, 1989). The second uses more complicated nonlinear mathematics, and is
intended to represent dynamics of plankton within an ice-free season (Scheffer et al.
1997, Scheffer et al. 2000b, 2001b).

A pelagic food chain model with four dynamic variables (Fig. 12) includes
piscivorous fishes, planktivorous fishes, zooplankton, and phytoplankton (Carpenter
1988a,1989). There are two external factors: littoral zone resources (e.g. benthic
invertebrates) consumed by fishes, and stochastic physical-chemical drivers (e.g.
climate effects on nutrient loading or fish recruitment). Food resources from the littoral
zone can sustain fish stocks through fluctuations in pelagic resource levels, and thereby
maintain fish predation with significant implications for pelagic communities (Schindler
and Scheuerell 2002). Exogenous stochastic forcing is assumed to be independent for
fish recruitment and phytoplankton. The planktivore component implicitly includes two
species, an obligately planktivorous fish and juvenile piscivores. Recruitment of juvenile
piscivores is proportional to adult piscivore biomass, but cannibalism of juvenile
piscivores also increases with adult piscivore biomass. When adult piscivores are
abundant, they can consume all of their progeny. When adult piscivores are at low
abundance, some juveniles can escape cannibalism and survive to adulthood. In

consequence, a large year class of piscivores can occur only when the abundance of the previous year class has declined by natural mortality or fishing. This phenomenon creates cycles in the time series of phytoplankton and zooplankton, driven by the life cycle of the top carnivore in the food chain. The period of the cycle is about the same length as the top carnivore life history (Carpenter 1988a). In the year that the large year class is created, high planktivory leads to high phytoplankton biomass. Once the juvenile planktivores recruit to the piscivore compartment, planktivory is low, so zooplankton biomass increases and phytoplankton biomass decreases. This situation will persist until the adult piscivore biomass has declined to the point where a new year class can form. Model results include cycles with periods about equal to the life history length of the top carnivore.

A model of trophic cascades with just two dynamic variables, phytoplankton and zooplankton, exhibits multiple attractors (Scheffer 1997, Scheffer et al. 1997, 2000b, 2001b). Some of these attractors are stable points and others are stable cycles. The model's attractors are shown in a three-dimensional space of algal biomass, planktivorous fish biomass and zooplankton biomass (Fig. 13). These results were obtained for a rather high level of phosphorus input. They show complex effects of changes in planktivorous fish biomass. At low levels of planktivorous fish biomass, phytoplankton and zooplankton oscillate in a predator-prey cycle (grey surface at low fish biomass). When planktivorous fish biomass grows to the level of point O_1, the predator-prey cycle intersects a repeller (denoted by the dashed line). The ecosystem moves to a stable attractor on the solid line between points F_0 and F_1. Along this line,

phytoplankton biomass is high and zooplankton biomass is low. At relatively high fish biomass, a strong decrease in phytoplankton biomass could shift the system to a stable attractor between points F_2 and H. Such a perturbation of phytoplankton biomass could occur after a heavy rain that flushed the lake, for example. If fish biomass remains between F_2 and H (solid line), the system is stable, with low phytoplankton and zooplankton biomass. If the fish biomass is between points H and O_2, there is a stable predator-prey oscillation of phytoplankton and zooplankton (grey surface). If fish biomass is at point O_2, the predator-prey oscillation again intersects a repeller on the dashed line, and the system moves to a stable point on the solid line between F_0 and F_1, with high phytoplankton biomass and low zooplankton biomass.

The crash to a low zooplankton – high algae state when oscillations cross the dashed line in the region between O_1 and O_2 has important implications for seasonal plankton changes in eutrophic lakes. This model behavior resembles a pattern that occurs in many eutrophic lakes, in which a springtime phase of heavy grazing and clear water gives way to a summer phase of low grazing and high biomass of algae. The ecological explanation for the zooplankton crash involves two different mechanisms. First, the zooplankton numbers decline, due largely to depletion of their food, and second, the zooplankton population is trapped at this low level by fish predation. Eventually, population oscillations make the zooplankton more vulnerable to overexploitation by planktivorous fish. In this 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, and to some extent this increase may be related to predator-prey cycles. This model suggests how such cycles, in the presence of planktivorous fish, can lead to collapse of zooplankton populations and to blooms of phytoplankton unrestrained by grazing.

Summary

Even though regime shifts are not common, many have been observed in limnology. This chapter describes three types of regime shifts known from many examples in lakes: eutrophication, depensatory shifts in fish populations or fish community composition, and the shift in food webs between dominance by piscivores and large-bodied grazers versus planktivores and small-bodied grazers (trophic cascades). Anthropogenic drivers such as phosphorus input, habitat alteration, species invasions and overfishing are often factors in regime shifts.

Scientific analysis to understand regime shifts is difficult, because the events are not common and causes are usually multiple. Lakes may be an especially good study system for regime shifts, because there are many lakes in the world, and therefore many opportunities to observe regime shifts. Long-term study is necessary, but not sufficient, to understand regime shifts. Cross-system comparisons and whole-ecosystem experiments also play important roles. All three of these approaches – long-term study, comparative study, and whole-ecosystem experiments – have been important in understanding regime shifts in lakes. Because multiple scientific

approaches are necessary to understand regime shifts, synthesis of many studies is required. In this respect, the study of regime shifts is similar to many other problems in ecology (Pickett 1999, Ford and Ishii 2001).

The examples described in this chapter show that it is difficult to generalize about regime shifts. The cases do have a few features in common. All seem to involve more than one spatial or temporal scale (watershed and lake in eutrophication; slow-turnover adult fish and rapid-turnover juvenile fish in fishery regimes; two to four trophic levels with a wide range in turnover rate for trophic cascades). All seem to involve the interaction of slowly-changing and rapidly-changing variables. In eutrophication, the turnover time of phosphorus ranges from about a century in watershed soil, to decades in sediment, to much less than a year in lake water. Both fishery regimes and trophic cascades involve food web components with very different turnover times. All of the cases involve stochastic factors: climate-driven runoff pulses and mixing events in eutrophication, and stochastic recruitment events in fishery regimes and trophic cascades.

Simple mathematical models have been useful for understanding regime shifts in lakes and many other types of ecosystems (Carpenter 2001, Scheffer et al. 2001a). Selected examples of useful models are summarized in this chapter. A comprehensive review would require a much longer document. Nevertheless, the few examples presented here illustrate some of the diversity of models that have been used to describe lake regime shifts. Using the models we can understand which dynamics can

be explained by our abstractions, and which cannot. We can also attempt to explain observations in a post-hoc way. But to what extent are such models useful for anticipating the future? Can regime shifts be predicted? The next four chapters will address the use of models for description, prediction and management of regime shifts.

Figures

Figure 5. Pan balance model of eutrophication. The left and right sides of the pan

balance represent clear and turbid water, respectively. The ball represents the

ecosystem, which can lie in either pan. External shocks such as weather events will not

shift the ball between pans, if the shocks are sufficiently small. As phosphorus is added

to the lake and builds up in the sediments, the lake becomes more vulnerable to shocks

that may shift it to the turbid, eutrophic side of the balance. (Original)
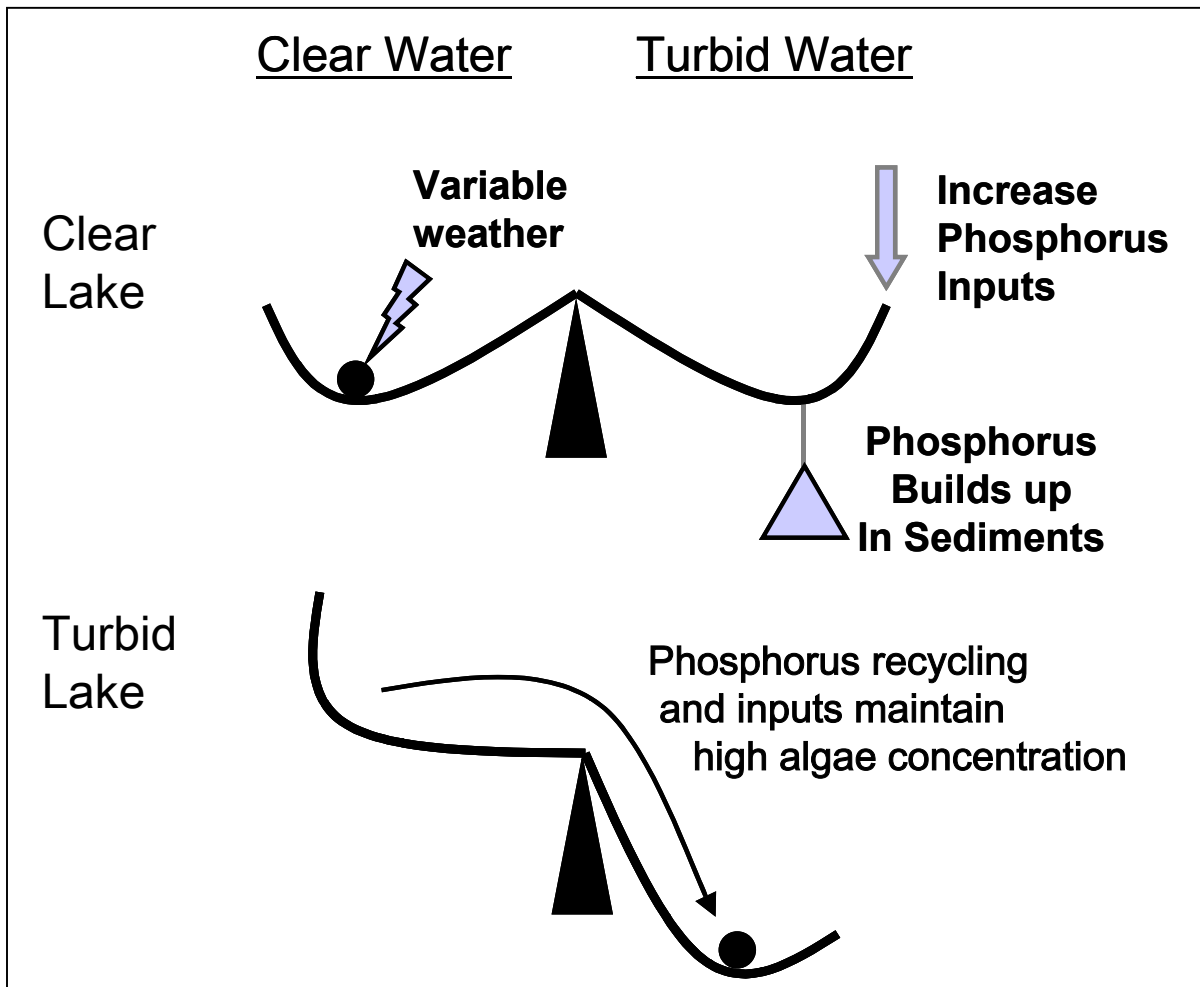
Figure 6. Major pools and flows of phosphorus in lake eutrophication (boxes and black arrows). Gray arrows show effects of major drivers, climate and land use and cover. (Original)
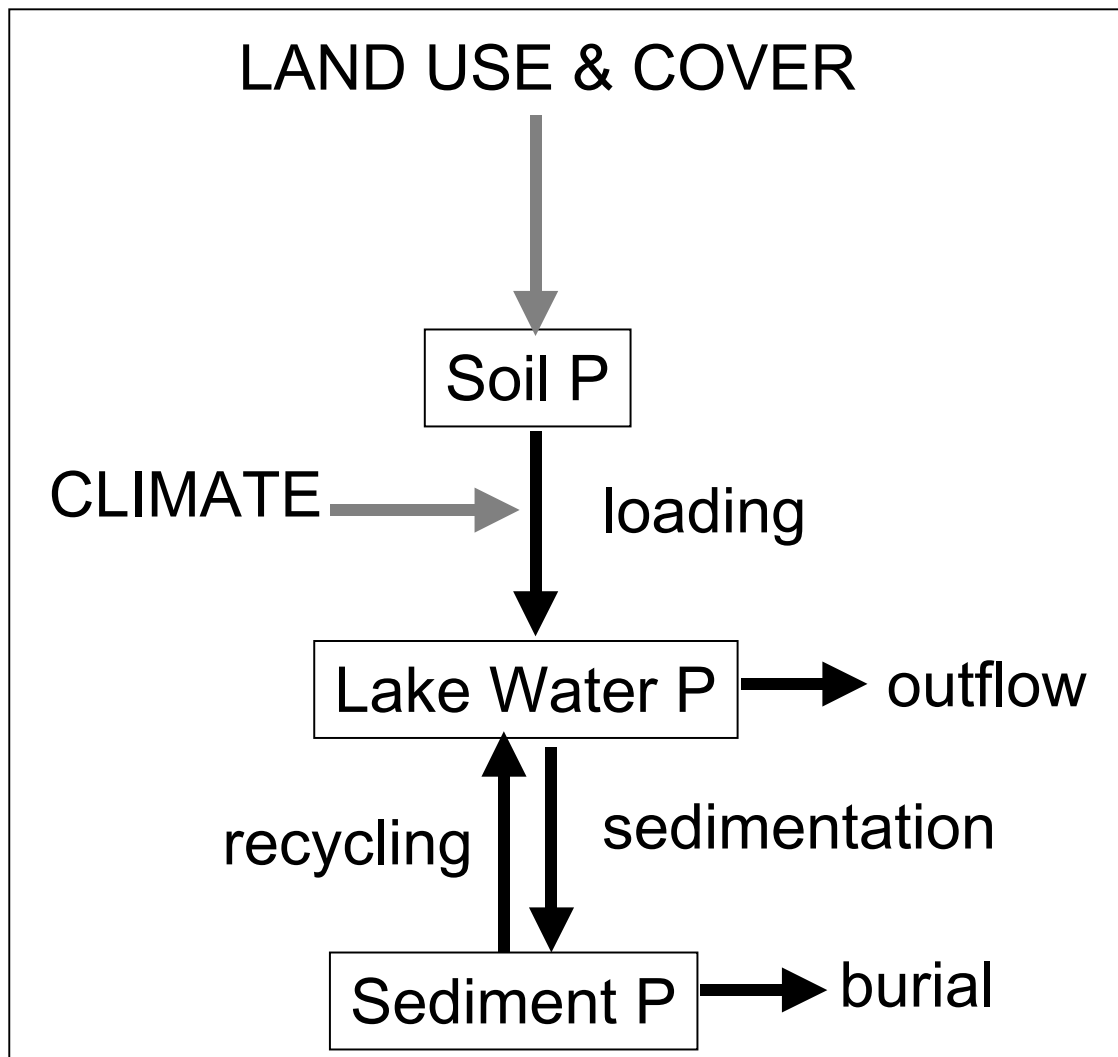
Figure 7. (A) Phosphorus flux rates versus water phosphorus concentration. Straight line shows outflow plus sedimentation fluxes. Curved lines show P loading from watershed (intercept) plus recycling from sediments for 2 hypothetical lakes. Steady-states occur where inputs balance outputs, i.e. where the lines intersect. At the stable steady states, a slight increase in P causes outputs to exceed inputs, and a slight decrease in P causes inputs to exceed outputs. In either case, the lake returns to the stable steady state. At the unstable steady states, a slight change in P tips the P level toward either the higher or lower steady state. (B) Probability distributions of phosphorus input (or loading) for the 2 hypothetical lakes. In each curve, likelihood of a given input rate is plotted against input rate. The area under both curves is the same (one). (Original)

Figure 8. Size-selective predation leading to depensation in the model of Carpenter (2001). A. Food web relating adults and juveniles of a piscivorous fish population to a second species (forage fish) which is consumed by adult piscivores but consumes juvenile piscivores. B. Mortality rates of juvenile piscivores versus population density of adult piscivores. Juvenile mortality has two components, intraspecific (density-dependent) mortality and predation by the forage fish. Dashed line shows predation mortality of juvenile piscivores caused by an increase in the amount of habitat usable for refuge from predation by the juvenile piscivore. (Original)
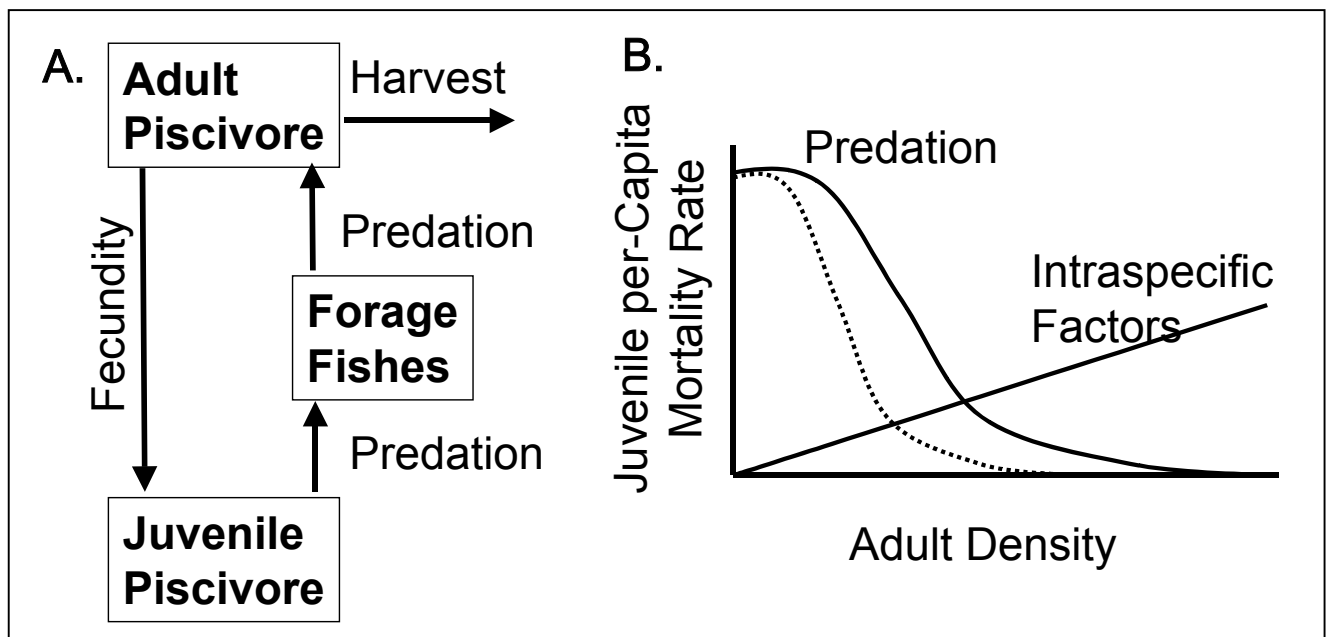
Figure 9. Alternate stable states in the model presented in Figure 5 (Carpenter 2001).

A. Rates of fecundity and mortality versus adult density. B. Bifurcation diagram

showing rates of predation on juveniles and harvest of adults that lead to the three

possible stability conditions – stable persistence; alternate states (critical depensation);

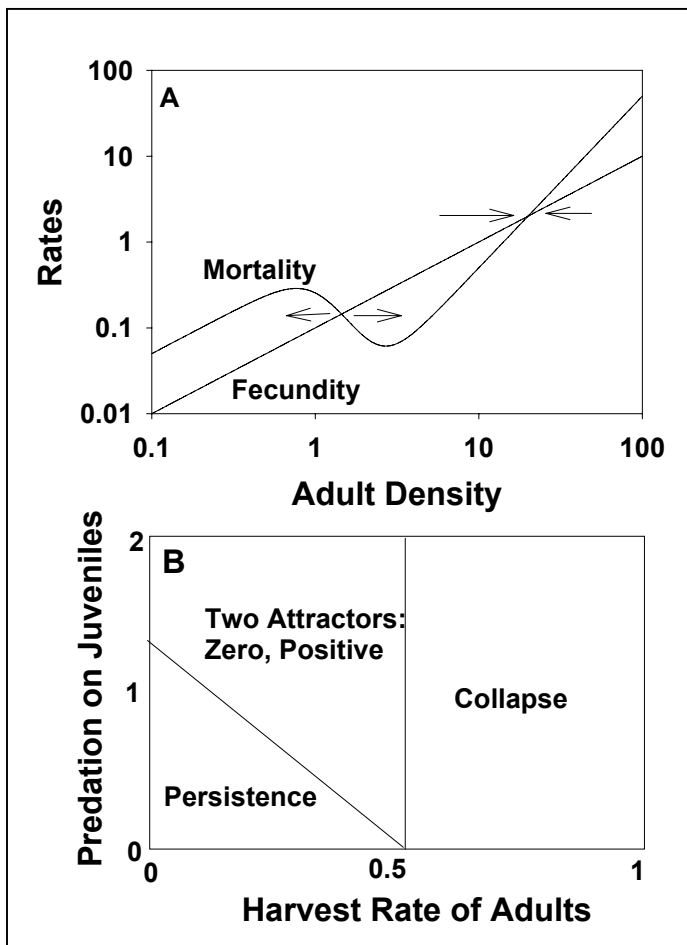or collapse of the fish population. Reproduced by permission of © Blackwell Publishing

Company.

Figure 10. Chlorophyll concentration (photic zone mean, mg m^{-3}) versus (A) total phosphorus concentration (mg m^{-3}) at spring overturn and (B) mean length of all zooplankton (mm) for Wisconsin and Ontario lakes studied by Carpenter et al. (1991). Each point is the mean of two to six years of data for one lake. Total phosphorus and zooplankton mean length are not significantly correlated (r = 0.14). Reproduced by permission of © Springer-Verlag, New York.
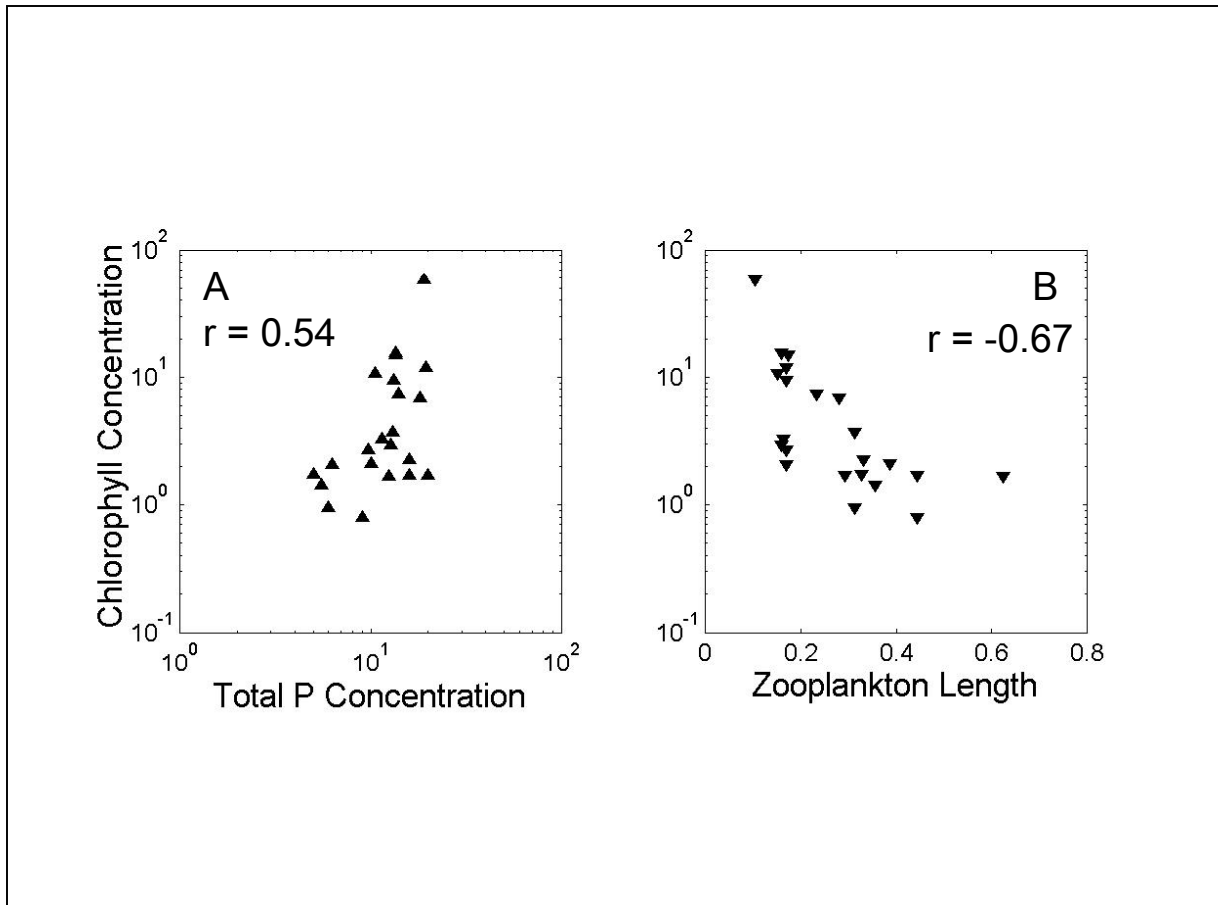
Figure 11. Chlorophyll density (integrated vertically through the photic zone, mg m^{-2}) versus phosphorus input rate (mg m^{-2} d^{-1}) for an unmanipulated reference lake (X) and lakes with food webs dominated by planktivores (open circles) and piscivores (closed circles) (Carpenter et al. 2001b). Error bars show $\pm$ standard error. Reproduced by permission of © Ecological Society of America.
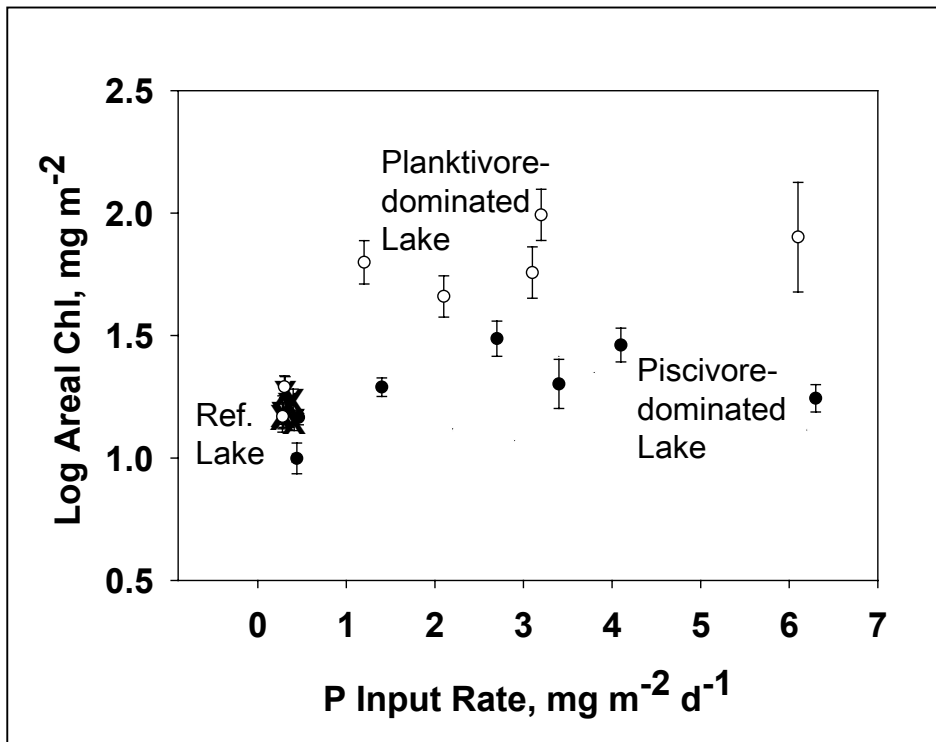
Figure 12. Flow chart of the trophic cascade model of Carpenter (1988a). Open boxes denote state variables, shaded boxes denote external influences. Black straight arrows indicate consumption, gray straight arrows indicate recruitment processes, dashed line indicates non-predatory mortality of piscivores (including fishing and natural mortality), and curved black arrows indicate stochastic effects. (Original)
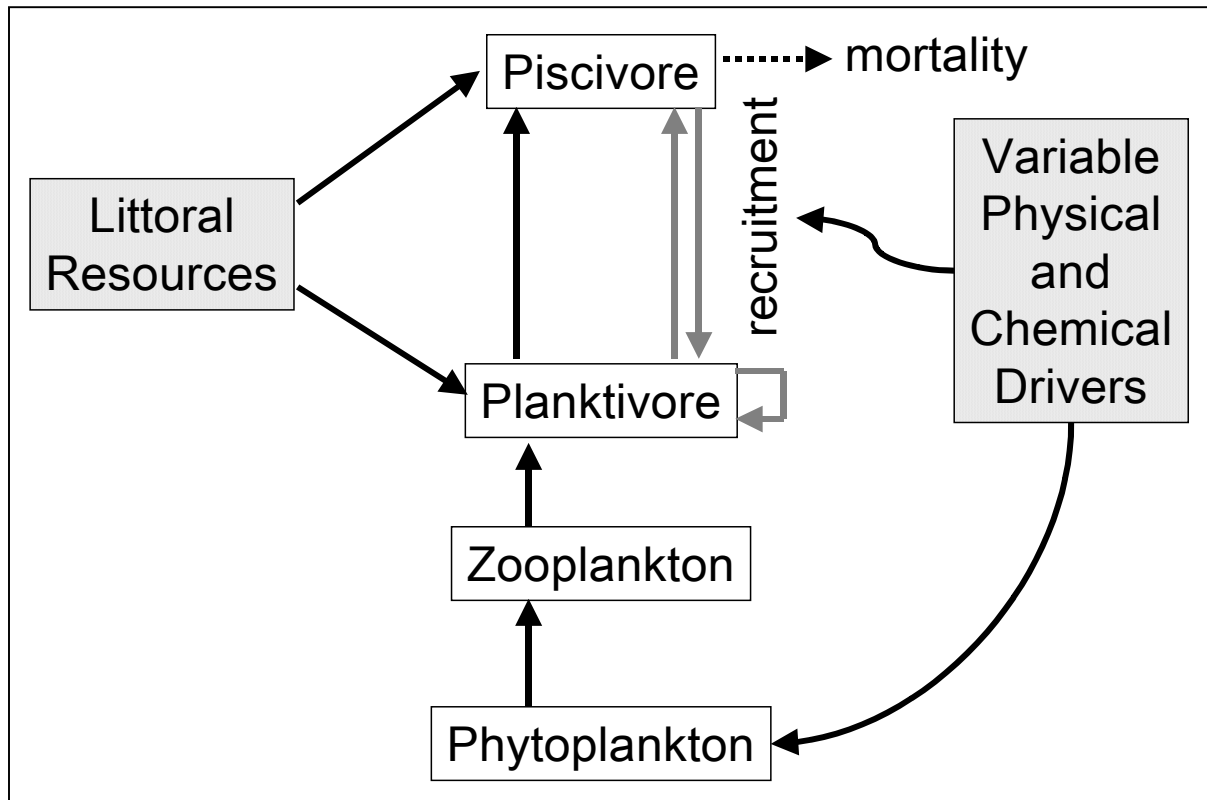
Figure 13. Stability manifolds for the trophic cascade model of Scheffer et al. (2000b).

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