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Achieving Ecological Resilience Through Regime Shift Management

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Achieving Ecological Resilience Through Regime Shift Management

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ABSTRACT

Resilience has come to mean several things in the system sciences. The term is used to describe systems whose function is robust with respect to external disturbances. It is used to describe systems that tolerate faults in some internal component. It is also used to describe systems that have the capacity to recover after a complete collapse of system function. This monograph defines resilience in the last sense. This notion of resilience is often called *ecological resilience*. For a system to be ecologically resilient, one first accepts system collapse as being inevitable and then requires that the resources for subsequent system recovery be buried in the wreckage of that collapse.

The ecological concept of a *regime shift* plays an important role in describing abrupt shifts in ecosystem behavior. In particular, the collapse of system function may be seen as an instance of a regime shift. Restoring a collapsed ecosystem often involves walking the system through a sequence of alternative states before full recovery can be achieved. The transitions between these alternative states are also regime shifts. But in this case, these regime shifts are purposefully

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triggered to speed up the recovery process. Managing regime shifts that trigger system collapse provides a way to *conserve* existing system function. Managing regime shifts that systematically rebuild lost system function provides a way to *restore* lost system function. Regime shifts, therefore, play an important role in enhancing the ecological resilience of a dynamical system.

This monograph formalizes the ecologist's regime shift concept by identifying regimes with components (also known as basic sets) of a Morse decomposition of the system's chain recurrent set. This formalization allows the identification of two distinct regime shift mechanisms; one triggered by external shocks (shock-induced regime shift) and the other triggered by bifurcations of the system flow (bifurcation-induced regime shift). This allows one to define ecological resilience in terms of a discrete abstraction (called the *regime transition system*) that characterizes the sequences of shock-induced regime shifts that can be triggered in the system. This monograph shows how that transition system can be constructed from the system's differential equation model and demonstrates how it can be used to enhance the resilience of ecosystem foodwebs through the careful management of the system's regime shifts.

1

Introduction – What is a Resilient System?

Different scientific communities take different viewpoints of what it means for a dynamical system to be *resilient*. Engineers often use the term to describe systems that are *fault-tolerant* or *robust* to disturbances. Ecologists, on the other hand, use the term *ecological resilience* (Holling, 1996) to describe ecosystems that have the capacity to spring back after a catastrophic collapse. This monograph focuses on ecological resilience; where system collapse is taken as being inevitable, though the seeds for eventual system restoration are contained within the wreckage of that collapse. The dictionary states that resilience is the capacity to quickly recover from difficulties. This definition focuses on the ability to restore lost system function and seems to be in greater harmony with how ecologists use the term. This monograph, therefore, adopts the ecologist's view of system resilience.

Ecological resilience may be graphically illustrated by the bouncing ball in Figure 1.1. Hitting the floor is the collapse experienced by the falling ball. The rubber ball is resilient because it flies back into the air after hitting the floor. On the other hand, if the ball had been a wad of wet dough, it would have hit the floor and stuck there, thereby illustrating that a wet ball of dough is not resilient. The bouncing rubber

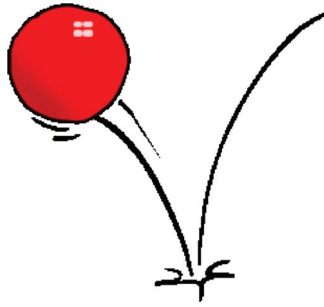


Figure 1.1: Bouncing ball.

ball can also be used to illustrate another aspect of resilient systems; namely that their behaviors are *recurrent*. After the rubber ball hits the ground, it bounces back into the air and then falls back to earth where it hits the ground again. This generates a sequence of bounces that continue for several cycles. In other words, resilient systems traverse a cycle of modes in which the system function (i.e., the ball's height above ground) declines until, upon hitting the floor, it redirects its kinetic energy and bounces back up. For the ball this decline is inevitable. What makes the ball resilient is that it can redirect or reorganize itself in a manner that allows recovery of some of its original height. This means that resilience refers not only to a system's ability to *withstand* collapse, it also refers to the ability of that system to *restore* lost system function.

Ecologically resilient systems therefore cycle back and forth between a *nominal* regime and an *alternative* regime. The transition between regimes is called a *regime shift*. Figure 1.2 illustrates these shifts graphically by plotting an energy (Lyapunov) function, $V(x)$, for a multi-stable system whose two stable equilibria are local minima of V . The region of attraction for one of the equilibria is the nominal regime and the region of attraction for the alternative equilibrium is the alternative regime. A regime shift occurs if an external disturbance causes the system state to jump from the nominal regime into the alternative regime. Once the system state enters the alternative regime, it remains in that regime until a future disturbance forces it back across the energy barrier separating the two regimes. We refer to this first shift as a *collapse*

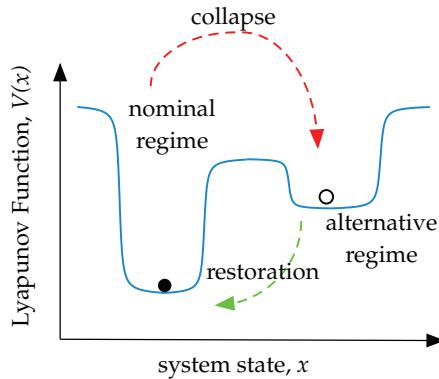


Figure 1.2: Regime shifts in a multi-stable system.

since the alternative regime is usually treated as being undesirable. System restoration occurs when the system state shifts back to the nominal regime. This restoration of system function will always occur in an ecologically resilient system, though it may take quite some time before the restoration is complete. For this reason, one may *intervene* by intentionally triggering regime shifts that force the system to jump back more quickly. Achieving ecological resilience for the system in Figure 1.2 therefore requires the *active management of regime shifts*. With regard to system collapse, regime shift management seeks to reduce the likelihood of an impending collapse. This management policy may also be called a *conservation* policy. For a collapsed system, regime shift management seeks to hasten the restoration of lost system function. This is done through a sequence of intentionally triggered regime shifts that form a restoration plan for the system.

This monograph introduces a mathematical framework for regime shift management that can be used to enhance a system's ecological resilience. There are at least three challenges to be overcome in the development of a framework for ecological resilience. The first challenge stems from the equilibrium-based view of regime shifts that was popularized in Scheffer *et al.* (2001). Real life ecosystems are non-equilibrium processes for which an equilibrium based notion of a regime is too restrictive. So our first problem involves finding a precise formalization of the regime shift concept that extends the equilibrium-based notion in

Scheffer *et al.* (2001) to non-equilibrium processes. In the second place we need to identify specific mechanisms driving a system state to jump into the alternative regime. A good understanding of the mechanisms triggering a regime shift will allow one to develop measures characterizing how close a system is to collapse. These measures play an important role in developing conservation policies seeking to forestall an impending shift. Finally, while system collapse is often sudden and catastrophic, restoration is often more complicated. It is usually impossible to jump back to the nominal regime with a single regime shift. In many cases, the system's resources need to be released and re-organized before a shift back to the nominal regime can be realized. This means that complex systems may need to follow a sequence of intermediate regimes (a.k.a. order of succession) before restoring full system function. So the third problem involves identifying a sequence of intermediate regimes leading back to full restoration of system function.

The following sections address these three challenges with regard to compartmental systems used in modeling ecosystem food webs. These system models are sometimes referred to as *consumer-resource systems* because their dynamics are governed by the flow of resources to consumers. In particular, we take the equilibrium-based notion of a regime and generalize it to define regimes in terms of the basic sets of a Morse decomposition for the system's chain recurrent set. A regime shift then occurs when the system state jumps between basic sets. This formalization allows us to identify two distinct regime shift mechanisms. There is a *bifurcation-induced* regime shift that is generated by local bifurcations of the system and there is a *shock-induced* regime shift that is triggered by impulsive shock like disturbances. For each of these regime shift mechanisms we show how semidefinite programming tools can be used to measure how close a system is to an impending regime shift. The monograph then turns to the problem of system restoration. In particular it uses a discrete abstraction of the system to characterize sequences of shock-induced regime shifts that the system can generate. This abstraction is then used to develop plans that realize the full restoration of a collapsed system through active management of its regime shifts.

The monograph draws on mathematical methods in systems/control theory as well as mathematical ecology. While its methods are demonstrated on models for ecosystem foodwebs, the approach can be used to describe the resilience of engineering infrastructure found in traffic networks, power distribution systems, and wastewater management. The results in this monograph, therefore, should be of interest to scientists and engineers interested in the mathematical foundations of resilient dynamical systems.

The remainder of the monograph is organized as follows. Section 2 defines regime shifts in terms of the system's basic sets. Section 3 introduces a measure of how close a system is to triggering a bifurcation-induced regime shifts, also called the D2B or distance-to-bifurcation. Section 4 uses a stochastic reachability problem to estimate the likelihood of a shock-induced regime shift. This likelihood provides a probabilistic measure of a system's susceptibility to shock-induced regime shifts. Section 5 uses algorithmic analysis of dynamical systems to construct a discrete abstraction of a system's regime shift sequences and then shows how this abstraction could be used to formulate restoration plans for a collapsed system. Section 6 closes with some comments on future directions for this work.

Further Readings: Control engineering approaches to resilience are frequently confined to fault detection and accommodation (Polycarpou and Helmicki, 1995) and fault tolerant control (Blanke *et al.*, 2006). This view of resilience has been important in reconfigurable flight control systems (Bodson and Groszkiewicz, 1997; Egbert and Halley, 2001). The ecological view of resilience, on the other hand, emphasizes renewal over an engineering desire for predictability. This perspective was raised in C.S. Holling's review essay (Holling, 1996) and was based on insights drawn from his earlier work concerning the resilience of terrestrial (forest) systems (Holling, 1973). This ecological viewpoint stresses the recurrent nature of resilient systems and later work sought to apply this notion to complex socio-ecological systems Holling (2001). A popularized extension of this recurrence idea was referred to as *panarchy* in Folke (2006) and Gunderson (2001) and has motivated the founding of international research organizations (*Resilience Alliance*

and *Stockholm Resilience Centre*) that study the ecological resilience of real-life socio-ecological systems.

Note on Mathematical Notation: The set of integers, real numbers, and complex numbers are denoted as $\mathbb{Z}$, $\mathbb{R}$, and $\mathbb{C}$, respectively. The vector space of n -dimensional real valued vectors (a.k.a. Euclidean n -space) is denoted as $\mathbb{R}^n$. The set of n by m real valued matrices is $\mathbb{R}^{n \times m}$. The set of non-negative n -dimensional real vectors is denoted as $\mathbb{R}_{\geq 0}^n$. A function $f: X \rightarrow Y$ is a rule that associates each element of the set X to at most one element of the set Y . The value that f takes at $x \in X$ is denoted as $f(x)$. A function with n continuous derivatives is said to be C^n .

2

Regime Shifts

Regime shifts (Folke *et al.*, 2004; Scheffer *et al.*, 2001) are large and sudden changes in the structure or function of an ecosystem due to external disturbances. The term originates with observed changes in an ecosystem that are seen as signaling a drastic shift in the quality of ecosystem services (Costanza *et al.*, 1997). Commonly cited examples of ecosystem regime shifts include the eutrophication of shallow lakes (Carpenter *et al.*, 1999; Scheffer *et al.*, 1993) due to increased nutrient loading, the collapse of fisheries due to overfishing (Daskalov, 2002; Daskalov *et al.*, 2007), degradation of coral reefs due to seasonal hurricanes (Hughes, 1994; Hughes *et al.*, 2007; Nyström *et al.*, 2000), and desertification due to climate change (Demenocal *et al.*, 2000; Foley *et al.*, 2003). Human communities rely on the services these ecosystems provide; especially with regard to food, fiber, and air/water purification. Regime shifts can disrupt the quality of these services to a degree that is catastrophic for those dependent communities. There is, therefore, tremendous interest in finding ways to more accurately forecast and manage impending ecosystem regime shifts.

Ecosystem scientists have proposed a number of statistical indices for detecting impending regime shifts. These indices include Fisher

information (Mayer *et al.*, 2006), increased variance (Scheffer *et al.*, 2009), critical slowing (Dakos *et al.*, 2008), and conditional heteroskedasticity (Seekell *et al.*, 2012). Experiments on food webs in whole lakes suggest these indices strengthen prior to the occurrence of a regime shift (Carpenter *et al.*, 2011), but these methods make little use of prior dynamical models and so it is unclear how to set detection thresholds for a meaningful false alarm rate. Moreover, these statistical indices provide little insight into the mechanisms driving a system towards a shift, and without such a mechanistic model it becomes unclear how one can develop policies that reliably forestall the occurrence of an impending regime shift. As a result, some have begun to question the practical value of the concept in adaptive resource management (Groffman *et al.*, 2006).

Ecologists often describe regime shifts in multi-stable systems as a transition between two stable equilibria. This viewpoint was popularized by Scheffer *et al.* in Scheffer *et al.* (2001). Figure 1.2 graphically illustrates an *equilibrium-based* regime shift in which the system state jumps between the Regions of Attraction (ROA) of alternative *stable* equilibria. While the principles in Figure 1.2 are easily grasped, there are several scenarios that do not easily fit into this picture. There are living systems (Fussmann *et al.*, 2000), for example, that shift from a stable equilibrium to a limit cycle associated with an *unstable* equilibrium. Other living systems (Rinzel, 1987) exhibit “bursting” where the system repeatedly cycles between an oscillatory burst and fixed point convergence. Do we view this as switching back and forth between two distinct regimes or simply a single complex regime? One may also find dynamical systems that have no stable equilibria and yet they appear to have a steady state limit cycle that asymptotically approaches a collection of heteroclinic orbits (Van Voorn *et al.*, 2007). Do the heteroclinic orbits represent distinct regimes or is the limit cycle a regime? The preceding scenarios suggest that the original equilibrium-based notion of a regime shift popularized by Scheffer *et al.* (2001) is not sufficiently general to describe the full range of behaviors seen in living systems.

This section uses a simple model for lake eutrophication (Carpenter *et al.*, 1999) to identify two regime shift mechanisms; *bifurcation-induced*

and *shock-induced* regime shifts. We then use more realistic compartmental models (Jacquez and Simon, 1993) of lake eutrophication to show that real-life systems exhibit behaviors that do not fit into the equilibrium-based notion of a regime shift. This observation provides the motivation for introducing the concept of a *non-equilibrium regime shift* in which regimes are defined with respect to the components (also known as *basic sets*) of a Morse decomposition of the system's chain recurrent set.

This section uses methods from dynamical systems theory to characterize the steady state behaviors of ecological food webs. Tutorial reviews of food web modeling and dynamical systems are provided in the section so it should be accessible to scientists and engineers with prior training in the mathematical modeling of dynamical systems similar to that found in Wiggins (2003).

2.1 Regime Shift Mechanisms for Shallow Lake Eutrophication

The equilibrium-based regime shift model for shallow lake eutrophication (Carpenter *et al.*, 1999) was tremendously influential because it provided ecologists with a concrete way to visualize the mechanisms triggering a regime shift. This subsection reviews that regime shift model for lake eutrophication and uses it to identify two regime shift mechanisms that we call a *bifurcation-induced* and *shock-induced* regime shift. These two mechanisms may be distinguished by the time scale of the external disturbances triggering the regime shift. Shock-induced shifts are triggered by an impulsive disturbance whose time scale is much shorter than the primary time scale of the original process. In general, these shifts are triggered by “shocks” to the system that cause the system state to “jump” into an alternative regime. Bifurcation-induced shifts, on the other hand, are triggered by a disturbance whose time scale is much longer than the primary time scale in the original process. These shifts are triggered when a slowly drifting system parameter causes a structural shift (a.k.a. bifurcation) in the system's flow field. This subsection describes these regime shift mechanisms with respect to eutrophication in shallow lakes.

Shallow lakes are bodies of fresh water that do not thermally stratify in the summer months (Scheffer, 2004). These lakes are most highly prized in a pristine state where the biota is diverse and the water is clean and clear. Nutrients such as nitrogen and phosphorus play an essential role in the health of such lakes, but excessive nutrient levels (also known as *nutrient loading*) significantly degrade lake health by triggering algae blooms. Nutrient loads triggering such blooms often occur when nutrient enriched runoff flows into the lake from farm fields and cities. The appearance of such algae blooms is called *eutrophication*. The water in a eutrophic lake shifts from a clear to a turbid state; turbidity being caused by the lake biota being dominated by a single organism, i.e., algae. The resulting loss in biodiversity has a significant negative impact on lake ecosystem services (food, fiber, and clean water).

Eutrophication of fresh water lakes may cascade into larger downstream bodies of water. In the midwestern United States, nutrients from small fresh water lakes are carried downstream to other receiving waters such as the Great Lakes, the Mississippi river, and finally to the Gulf of Mexico. The accumulation of excess nutrients in these downstream receiving waters will also trigger algae blooms that in turn create hypoxic dead zones where no fish can live. Such dead zones appear regularly in the Gulf of Mexico, Baltic sea, East China sea, the Kattegat, and along the Oregon coast (Diaz and Rosenberg, 2008). These dead zones disrupt the fisheries supported by these bodies of water and so there is tremendous interest in finding ways to restore eutrophic systems to their pristine state.

It is notoriously difficult to restore a eutrophic non-vegetated lake to its pristine state (Scheffer, 2004). Simply reducing lake nutrient levels will not trigger a shift back to the clear state due to the way nutrients (e.g., phosphorus) cycle through the system. Phosphorus is a critical nutrient for lake vegetation that is taken up by plants as soluble reactive phosphorus (SRP) and used to create plant biomass. This phosphorus rich biomass falls to the lake bottom as detritus when the plant dies. Subsequent decomposition of the detritus allows the phosphorus to adsorb to lake bottom sediments. In general this sediment bound phosphorus is not bio-available. But if the water column's nutrient concentration is low enough or if turbulence mixes lake sediments into

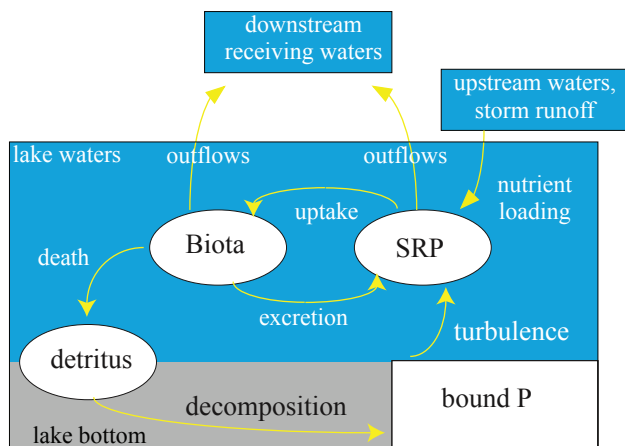


Figure 2.1: Phosphorus cycle in shallow lakes.

the water column, then the bound phosphorus desorbs back into the water column where it is again taken up by lake vegetation. The fate of phosphorus in the lake may be visualized by the *phosphorus cycle* shown in Figure 2.1. The key thing to note in Figure 2.1 is that the SRP concentration is governed multiple fluxes; an exchange with the biota, nutrient loading from external sources, outflows to downstream receiving waters, and finally a flux from the lake sediments. It is the interaction of these fluxes into the SRP compartment that give rise to regime shifts in eutrophic lakes.

One may mathematically model the mechanisms driving lake eutrophication as a compartmental system (Haddad *et al.*, 2010; Jacquez, 1972). Such systems consist of several *compartments* that are interconnected through fluxes of energy or mass. In particular, each compartment has a local state whose time rate of change is equal to the fluxes entering and exiting the compartment. The inter-compartmental flux is generally a function of the local states in the compartments. The phosphorus cycle in Figure 2.1 graphically portrays the compartmental system as a directed graph whose vertices are the compartments and whose edges are the inter-compartmental fluxes. In Figure 2.1, one sees four compartments within the lake; biota, SRP, detritus, and bound *P*. There are two external compartments (upstream and downstream waters)

representing sources and sinks for the system. The state of each lake compartment is taken as either nutrient concentration or biomass. The fluxes between compartments are shown by the yellow edges.

A number of compartmental models (DeAngelis, 1992) have been formulated for the cycle shown in Figure 2.1. But a particularly simple one was used in Carpenter *et al.* (1999) to explain lake eutrophication. This model had a single nutrient compartment whose local state, $P: \mathbb{R} \rightarrow \mathbb{R}_{\geq 0}$, represents an SRP trajectory that satisfies the following ordinary differential equation,

$$\dot{P}(t) = w(t) - \alpha P(t) + \frac{P^3(t)}{\theta^3 + P^3(t)} \quad (2.1)$$

where α, θ are positive constants. The first term on the right hand side (RHS) of Equation (2.1) is an input function, $w: \mathbb{R} \rightarrow \mathbb{R}_{\geq 0}$, representing the total influx of phosphorus from external sources. This is also called the *external loading* term. The second term on the RHS of the equation represents the outflows of water from the lake. The final term in the equation models the influx from sediment bound phosphorus back into the water column. This term is called the *internal loading* term.

The RHS of Equation (2.1) is plotted in Figure 2.2. The solid line in this plot is for a constant “nominal” external load, $w(t) = w_0$. The internal loading term has a sigmoidal nonlinearity that gives rise to two stable system equilibria shown by the shaded bullets. The left most equilibrium is associated with a pristine lake whose waters are clear (see picture on left side of figure). The right most equilibrium is associated with a eutrophic lake whose waters are clouded by algae (see picture on right side of figure). The region of attraction (ROA) for each stable equilibrium is shown by the shaded regions; with the green region representing the pristine regime and the red region representing the eutrophic regime. The graph in Figure 2.2 can be used to identify two distinct regime shift mechanisms; *shock-induced* and *bifurcation-induced* regime shifts.

Shock-induced regime shifts are triggered by impulsive shocks to the system. To illustrate this shock-induced shift on Figure 2.2, let us assume the initial lake state, $P(0)$, is in the pristine regime with a baseline external load of w_0 . A shock-induced shift occurs when a pulse

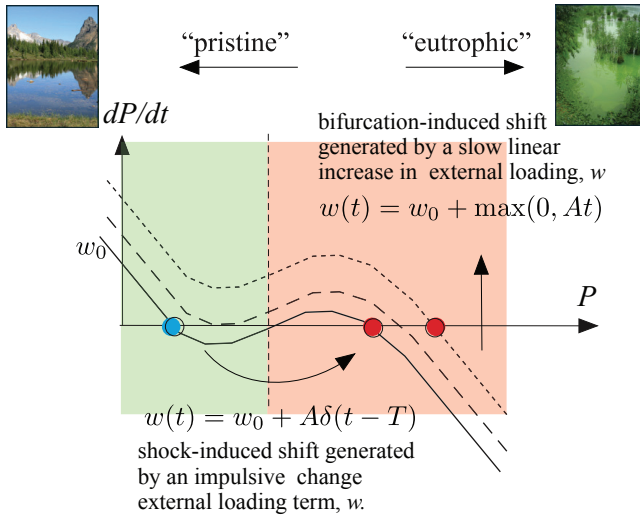


Figure 2.2: Eutrophication of shallow lake systems.

of nutrient is delivered to the lake. Such pulses may occur as a result of extreme rain events that increase runoff from agricultural fields for a short interval of time. We may model the nutrient pulse from a storm that hits at time T as

$$w(t) = w_0 + A\delta(t - T)$$

where $A > 0$ is the size of the pulse and δ is a Dirac impulse function. The delivery of this nutrient pulse at time instant T causes the system state, P , to jump by the amount A as shown in Figure 2.2. If that jump places the state in the ROA of the eutrophic equilibrium then the state remains in the eutrophic regime for all $t > T$ and we say a *shock-induced* regime shift has occurred. The minimum pulse amplitude, A , that drives the system into the eutrophic regime may be taken as a threshold whose size provides a measure of how vulnerable the system is to eutrophication caused by nutrient pulses.

Bifurcation-induced regime shifts are triggered by slow variations in the system parameters that cause a topological change in the trajectories satisfying the system's differential equation. Consider, for example, the following slow linear increase in the external loading term

of Equation (2.1)

$$w(t) = w_0 + \max\{0, At\}$$

where the linear increase begins at time $t = 0$ and proceeds at a slow rate, $A \ll 1$. Now consider the system trajectory over the two intervals $[t_0 - \delta, t_0]$ and $[t_0, t_0 + \delta]$ where $\delta > 0$. For most initial times, t_0 , there will be a smooth invertible map between the trajectory over $[t_0, t_0 + \delta]$ and the trajectory over $[t_0 - \delta, t_0]$. But there are certain initial times, say t_0^* , where no such invertible map exists. This time represents an abrupt change in the system's behavior that is the result of a *bifurcation* of the system trajectories. This abrupt change in qualitative behavior also represents a regime shift, but the mechanism triggering the shift is qualitatively different from the mechanism behind a shock-induced shift since it is caused by a change in the topology of the system trajectory, rather than a jump in the system state. We therefore refer to this particular regime shift as a bifurcation-induced regime shift.

Figure 2.2 can also be used to graphically illustrate the mechanism behind a bifurcation-induced regime shift. In particular, the slow linear increase in the external loading term, $w(t)$, causes the solid curve in the plot to slowly shift upward. For t close to zero, the pristine equilibrium remains stable, but at the threshold time t_0^* , the system trajectory changes abruptly because of a qualitative change in the system equilibria. In particular, when $t = t_0^*$, the RHS of the differential equation (dashed line) shows that the pristine equilibrium is now only marginally stable. Moreover for $t > t_0^*$ (dotted plot) the pristine equilibrium vanishes entirely and only the eutrophic equilibrium remains stable. This means that for $t > t_0^*$, the system state, P will asymptotically approach the eutrophic equilibrium and the lake will shift into a eutrophic state.

2.2 Regime Shifts in a Living System

The eutrophication model in Equation (2.1) is highly idealized and ignores the impact of the living compartments (what we call the biota) on the fate of phosphorus. A more complete model capturing the interactions between the nutrient and biotic compartments may be found in a predator-prey system studied in Fussmann *et al.* (2000)

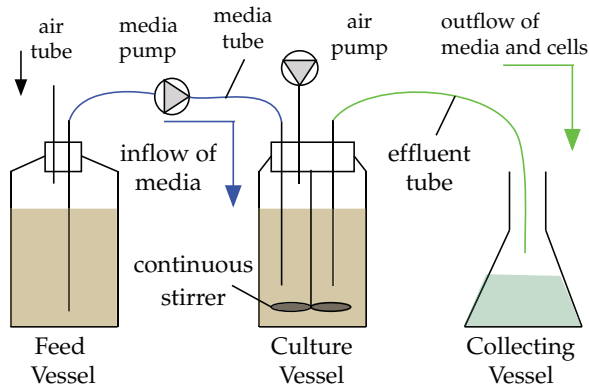


Figure 2.3: Biological chemostat.

and Tamba (2015). This system still exhibits eutrophication but its behaviors are no longer confined to fixed point convergence and it is a *living* system whose model has been experimentally validated through experiments with a biological chemostat. This subsection uses that living system to provide a concrete example of regime shifts involved in the collapse and restoration of the system's nominal regime.

A chemostat is a continuous culture device used to study the dynamics of nutrient limited micro-organisms (Smith and Waltman, 1995). The chemostat's physical set up, shown in Figure 2.3, consists of three interconnected vessels; a feed, culture, and collecting vessel. The feed vessel holds a liquid media containing all nutrients required for micro-organism growth. All nutrients are available in excess, except for one whose concentration in the feed vessel is denoted as N_{in} . By limiting this nutrient, one can study how variations in nutrient concentration affect the growth of the cultured organisms. In particular, one controls the nutrient's concentration in the culture vessel by adjusting the flow rate of media from the feed vessel into the culture vessel. The volume of the media in the culture vessel is kept constant by setting the outflow rate from the culture vessel into the collecting receptacle equal to the flow rate entering the culture vessel from the feed vessel. A continuous stirrer is used in the culture vessel to ensure the media is well mixed.

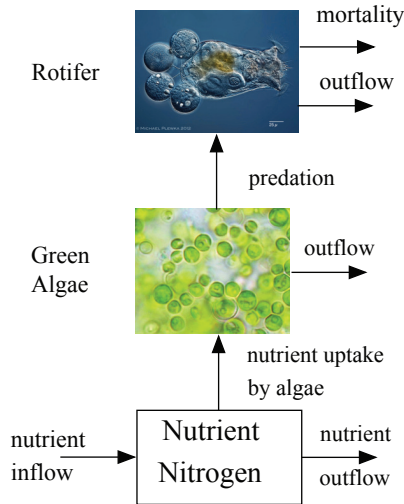


Figure 2.4: Predator-prey food web.

The *control variable* that the experimenter uses in the chemostat is the *dilution rate*. Let V denote the constant volume of the media in the culture vessel and let $F(t)$ denote the flow rate of media into and out of the culture vessel at time instant t . This flow rate is controlled by the media pump shown in Figure 2.3. The dilution rate, $\delta(t) = F(t)/V$, at time instant t is the ratio of the flow rate normalized by volume and represents the control input to this particular system.

The micro-organisms in the culture vessel consist of green algae and a planktonic consumer (predator) known as a rotifer. Together these organisms form a live predator prey system (Fussmann *et al.*, 2000) that can be modeled as a compartmental system consisting of three compartments; a producer (algae), consumer (rotifer), and nutrient (phosphorus) compartment as shown in Figure 2.4. *Producers* are micro-organisms, like green algae, that create biomass through photosynthesis. In this case, the growth rate in the producer compartment is limited by the availability of the limiting nutrient. *Consumers* are micro-organisms, like planktonic rotifers, that create biomass through the consumption of other organisms. In this case, the rotifers consume algae as prey and so the consumer's rate of growth is dependent on the algae concentration.

$$\begin{aligned}
\dot{N}(t) &= \text{flux in } N \text{ compartment} + \text{flux from feed vessel} \\
&\quad - \text{flux to collection vessel} \\
&= -\frac{b_c N(t)}{k_c + N(t)} P(t) + \delta N_{\text{in}} - \delta N(t) \\
\dot{P}(t) &= \text{flux due to reproduction} \\
&\quad - \text{flux due to predation} - \text{flux to collection receptacle} \\
&= \frac{b_c N(t)}{k_c + N(t)} P(t) - \eta \frac{b_b P(t)}{k_b + P(t)} C(t) - \delta P(t) \\
\dot{C}(t) &= \text{flux due to predation} \\
&\quad - \text{loss due to mortality} - \text{flux to collection vessel} \\
&= \frac{b_b P(t)}{k_b + P(t)} C(t) - m C(t) - \delta C(t)
\end{aligned}$$

Figure 2.5: State equations for Fussmann predator-prey system (Fussmann *et al.*, 2000).

Each compartment in this system has a local state. The nutrient compartment's local state, $N: \mathbb{R} \rightarrow \mathbb{R}_{\geq 0}$, is the nutrient's concentration in the culture vessel. The producer compartment's state, $P: \mathbb{R} \rightarrow \mathbb{R}_{\geq 0}$, is the algae concentration in the culture vessel. The consumer compartment's local state, $C: \mathbb{R} \rightarrow \mathbb{R}_{\geq 0}$, is the concentration of rotifers. Because of the way the chemostat was engineered, the time variations of these states are well modeled by the set of differential equations in Figure 2.5 where b_c , k_c , η , b_b , k_b and m are system parameters that are identified through maximum likelihood methods. The nutrient concentration in the feed vessel is a constant, N_{in} , and the dilution rate, $\delta: \mathbb{R} \rightarrow \mathbb{R}_{\geq 0}$, is the controlled input signal.

The differential equations in Figure 2.5 model mass balance relationships between the three compartments. In other words, the time rate of change of a compartment's local state is equal to the sum of the fluxes entering and exiting that compartment. The physical flux entering the nutrient compartment in the culture vessel is $\delta(t)N_{\text{in}}$ where $\delta(t)$ is the flow rate and N_{in} is the limiting nutrient's concentration in the feed vessel. The physical flux leaving each compartment of the feed vessel is that compartment's local state times the flow rate, $\delta(t)$. The flux entering the consumer compartment due to predation has a

Michaelis-Menten mass action kinetic,

$$\text{flux entering } C \text{ compartment due to predation} = \frac{b_c P(t)}{k_c + P(t)} C(t)$$

which models the fact that the consumer's functional response levels off for large producer concentrations. This flux entering the C compartment is balanced by a flux leaving the P compartment

$$\text{flux exiting } P \text{ compartment due to predation} = -\eta \frac{b_c P(t)}{k_c + P(t)} C(t)$$

where η models the feeding efficiency of the consumer. The fluxes connecting the N and P compartments model the fact that the producer's growth rate is dependent on the nutrient concentration and follows a similar mass balance kinetic. These particular dynamical relationships were empirically validated in Fussmann *et al.* (2000) to accurately predict the onset of Hopf bifurcations in live algae-rotifer systems implemented on a biological chemostat.

The differential equations in Figure 2.5 may be used to simulate what happens to the food web under various input flow rates, δ . Since this particular model has been experimentally validated, these simulation results should accurately predict what would be seen in the living system. The biotic parameters for the validated system (see Chapter 6 of Tamba, 2015) were $b_c = 3.3$, $k_c = 4.3$, $b_b = 2.25$, $k_b = 15$, $\eta = 4$, and $m = 0.1$. The nutrient concentration in the feed vessel was fixed at $N_{\text{in}} = 10$ and we treated the dilution rate, δ , as the “control” used to deliver a pulse of nutrient into the system. We initially set this dilution rate to

$$\delta(t) = \begin{cases} 0.1 & t < 100 \\ 2 & 100 < t < 120 \\ 0.1 & 120 < t \end{cases}$$

The objective is to see how the producer and consumer compartment states change in response to the nutrient pulse.

Figure 2.6 plots the simulated state trajectories for the nutrient, producer, and consumer compartments. There is an initial transient when the simulation starts. By day 25 the compartments have settled to the nominal equilibrium point. The nutrient pulse starts at $t = 100$

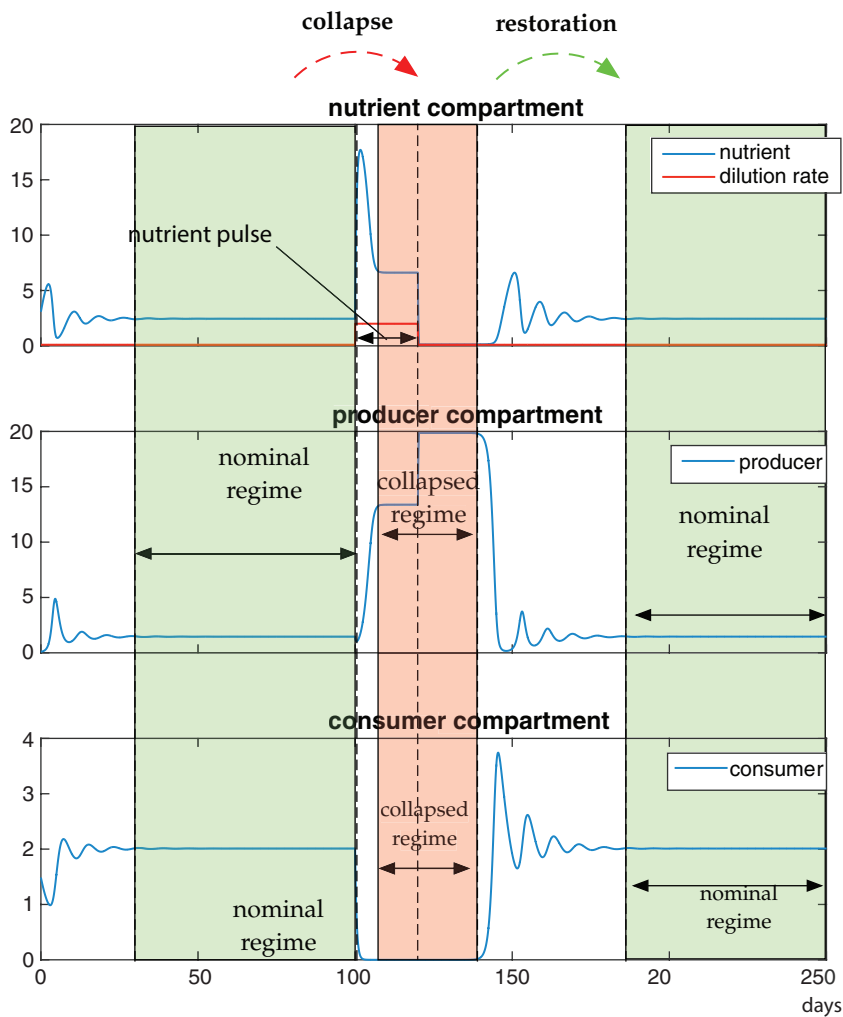


Figure 2.6: Simulated predator-prey system with nutrient pulse. Recovery after a nutrient pulse requires an intermediate phase over which the consumer compartment rebuilds itself.

days and causes an abrupt increase in the culture vessel’s nutrient concentration which quickly converges to a steady-state value once the producers begin consuming the excess nutrient. During this time interval the consumer concentration falls to nearly zero because the

dilution rate, δ , used to generate the nutrient pulse is large enough so that consumers are being flushed out of the system faster than they can reproduce. In terms of a real world scenario, this simulation may be said to represent lake eutrophication due to increased external nutrient loading. In particular, we see that the jump in external loading at $t = 100$ causes a shift in the system in which producer compartment saturates (i.e., an algae bloom).

Figure 2.6 also shows what happens when we try to reverse the algae bloom by reducing the nutrient inflows back to their original value. In particular, we return the dilution rate to its initial value for $t > 120$ days. We see, however, that the compartments do not immediately return to their original levels. In fact once the dilution rate is set back to 0.1, we see producer levels *rise* as a result of decreased flow through the culture vessel and the consumer compartment actually collapses to near zero until $t \approx 140$ days. It is only for time after 140 days that the consumer population grows to a level from which they can graze the producers back to their initial non-eutrophic level. What this time history suggests is that restoring a system back from its eutrophic state is not a reversible process. Full recovery of the pre-eutrophic regime requires the system to traverse a sequence of intermediate regimes that form what was referred to earlier as an *order of succession*.

2.3 Food Webs with Consumer-Resource Interactions

The predator-prey system in the preceding subsection was modeled as a compartmental system with *consumer-resource* interactions (Yodzis and Innes, 1992). Such models are commonly used by ecologists to build simulation models that study the impact of fisheries on lake ecosystems (Pauly *et al.*, 2000). They have also been validated against real-life lake systems (Boit *et al.*, 2012; Hamilton *et al.*, 2015). This subsection shows that these consumer-resource systems often exhibit non-equilibrium behaviors that do not fit easily within the equilibrium-based regime shifts of Scheffer *et al.* (2001).

Compartmental models for ecosystem food webs model each species in the web as a compartment. The species are also referred to as *guilds*. The local state of a compartment is the biomass of its associated guild.

A guild is classified as a *producer* if it does not consume other guilds to create biomass. A guild is classified as a *consumer* if it creates biomass by consuming other guilds. A consumer's consumption rate is a nonlinear sigmoidal function of the resources in its *resource pool*; i.e., the set of all guilds it consumes.

Let $N = \{1, 2, \dots, n\}$ denote a set of n guilds and let $N_p \cup N_c = N$ denote a partition of these guilds into *producers*, N_p , and *consumers*, N_c . For any guild $i \in N$, we define its *resource pool*, $\mathcal{R}_i \subset N$, as those guilds that are consumed by guild i . The resource pool, $\mathcal{R}_i$, will be empty if i is a producer and is non-empty if i is a consumer. In a similar way, it will be convenient to define a *consumer pool*, $\mathcal{C}_i \subset N_c$, as those guilds consuming guild i .

Each guild has a local state. The i th guild's state trajectory, $x_i: \mathbb{R} \rightarrow \mathbb{R}_{\geq 0}$, takes values $x_i(t)$ representing how much "biomass" is in that guild at time t . For producer guilds ($i \in N_p$), the local state's trajectory satisfies the following ordinary differential equation

$$\dot{x}_i(t) = r_i \left(1 - \frac{x_i}{K_i}\right) - \sum_{k \in \mathcal{C}_i} r_k x_k \frac{x_i}{1 + \sum_{\ell \in \mathcal{R}_k} x_\ell} \quad (2.2)$$

where r_i is the i th guild's *growth rate* and K_i is a parameter representing the producer's *carrying capacity*. For consumer guilds ($i \in N_c$) the local state trajectory satisfies the differential equation

$$\begin{aligned} \dot{x}_i = & -m_i x_i + \sum_{k \in \mathcal{R}_i} \eta r_i x_i \frac{x_k}{1 + \sum_{\ell \in \mathcal{R}_k} x_\ell} \\ & - \sum_{k \in \mathcal{C}_i} r_k x_i \frac{x_k}{1 + \sum_{\ell \in \mathcal{R}_k} x_\ell} \end{aligned} \quad (2.3)$$

where m_i is the guild's *mortality rate*, η is the consumer's *feeding efficiency*, and the other constants and functions are as defined above for the producer equation.

Not all systems satisfying Equations (2.2) and (2.3) are biologically plausible. To be biologically plausible the trophic relationships (i.e., who eats whom) and the value of the system parameters must conform to what is observed in real life. Ecologists ensure the biological plausibility of the model by forming trophic relationships in accordance with a niche model (Williams and Martinez, 2000) and by allometric scaling of

system parameters such as growth rate, carrying capacity, and mortality rate (Brown *et al.*, 2004; Sibly *et al.*, 2012). The niche model randomly assigns a *niche value* to each guild that may be taken as the average body mass of the guild. For each guild, the model randomly generates an interval of niche values that can be consumed by that guild. This model has been shown to be consistent with several real-life food webs (Williams and Martinez, 2000).

The predator-prey model in Figure 2.5 is a specific example of a consumer-resource system. The procedure used by the niche model, however, can also be used to randomly generate arbitrarily large model food webs that may be seen as biologically plausible (Williams and Martinez, 2000). The state equations for one such randomly generated food web are

$$\begin{aligned}
 \dot{x}_1 &= x_1 \left(1 - x_1 - 0.68 \frac{x_2}{1 + x_1} - 0.40 \frac{x_5}{1 + \sum_{i=1}^4 x_i} \right) \\
 \dot{x}_2 &= x_2 \left(-0.012 + 0.41 \frac{x_1}{1 + x_1} - 0.59 \frac{x_3}{1 + x_2} - 0.57 \frac{x_4}{1 + x_2} \right. \\
 &\quad \left. - 0.40 \frac{x_5}{1 + \sum_{i=1}^4 x_i} \right) \\
 \dot{x}_3 &= x_3 \left(-0.012 + 0.35 \frac{x_2}{1 + x_2} - 0.40 \frac{x_5}{1 + \sum_{i=1}^4 x_i} - 0.39 \frac{x_6}{1 + \sum_{i=3}^5 x_i} \right) \\
 \dot{x}_4 &= x_4 \left(-0.012 + 0.34 \frac{x_2}{1 + x_2} - 0.40 \frac{x_5}{1 + \sum_{i=1}^4 x_i} - 0.39 \frac{x_6}{1 + \sum_{i=3}^5 x_i} \right) \\
 \dot{x}_5 &= x_5 \left(-0.012 + 0.24 \sum_{j=1}^4 \frac{x_j}{1 + \sum_{i=1}^4 x_i} - 0.39 \frac{x_6}{1 + \sum_{i=3}^5 x_i} \right) \\
 \dot{x}_6 &= x_6 \left(-0.012 + 0.235 \sum_{j=3}^5 \frac{x_j}{1 + \sum_{i=3}^5 x_i} \right)
 \end{aligned}$$

This randomly generated consumer-resource system is a 6 guild food web with a single producer and five consumer guilds. A directed graph showing the trophic relationships between the guilds is shown in Figure 2.7(a). In this graph, the lowest level is for the producer (guild 1), the primary consumers (guild 2 and 5) are in the middle, and there are three secondary consumers (guild 3, 4, and 6). An edge in the graph indicates

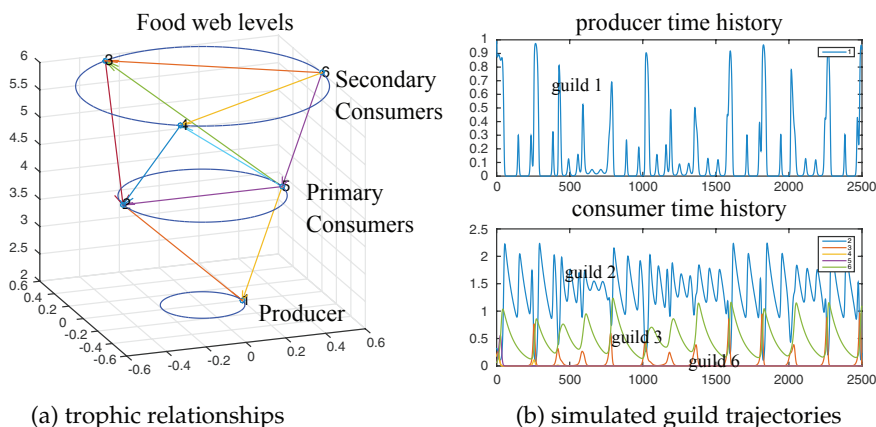


Figure 2.7: Randomly generated consumer-resource networks with 6 guilds.

that one guild feeds on the other. Simulated trajectories for this food web are shown in Figure 2.7(b). The top plot shows the producer’s trajectory and the bottom plot shows the trajectories of the consumer guilds. There are two things to note here. First, only three of the guilds (2, 3, and 6) maintain positive biomass. Second the behavior of these active guilds is dominated by interacting recurrent orbits that are consistent with a *non-equilibrium* dynamical system. In other words, this type of “complex” behavior is what one would expect to see in real-life food webs and it is for this reason that the equilibrium viewpoint of regime shifts is too simplistic to be of use in managing real-life regime shifts. The next subsection introduces a more sophisticated view of regime shifts based on the Morse decomposition of the dynamical system’s steady-state behaviors.

2.4 Non-Equilibrium Regime Shifts

The equilibrium-based regime shifts depicted in Figure 1.2 are too restrictive to describe the behavior of food webs that have periodic or chaotic orbits. The simulated trajectories shown in Figure 2.7 exhibit distinct non-equilibrium behaviors for which it is unclear how one might associate a “stable” equilibrium with a given regime. This observation suggests we need a more general way of characterizing system regimes.

This subsection addresses that issue by defining regimes with respect to strongly connected components of the system's positive limit set, what is sometimes called a *Morse decomposition* of the limit set. This monograph refers to shifts between these components as *non-equilibrium regime shifts*.

A dynamical system's limit sets consists of those states that the system's orbits return to over and over again. Introductory textbooks such as Wiggins (2003) provide formal definitions, but we will need a more sophisticated set of results that were originally established in Conley (1978). The following Subsection 2.4.1 reviews the results and concepts from Conley (1978) that are needed for the generalized definition of a "non-equilibrium" regime shift that is given in Subsection 2.4.2.

2.4.1 Morse Decompositions and Basic Sets

To define precisely what is meant by a Morse decomposition, we first assume that the system equations,

$$\dot{x}(t) = f(x(t))$$

generate unique compact and continuous trajectories. This means that the dynamical system may be characterized by an ordered pair, (X, ϕ) , where $X \subset \mathbb{R}^n$ is called the *state space* and $\phi: \mathbb{R} \times X \rightarrow X$ is a continuous map such that for any $p \in X$ and all $s, t \in \mathbb{R}$, we know $\phi(s + t, p) = \phi(s, \phi(t, p))$ and $\phi(0, p) = p$. It will be convenient to introduce two partial maps of ϕ . The first partial map, $\Phi_t: X \rightarrow X$, is called the system's *flow*. This map takes value $\Phi_t(p) = \phi(t, p)$ for some fixed $t \in \mathbb{R}$ and any $p \in X$. The second partial map, $x(\cdot, p): \mathbb{R} \rightarrow \mathbb{R}^n$, is called the *trajectory* through a point $p \in X$ at $t = 0$ and takes values $x(t, p) = \phi(t, p)$ for any $t \in \mathbb{R}$. The *complete orbit* through point $p \in X$ is defined as

$$\gamma_p = \{q \in \mathbb{R}^n: q = \phi(t, p), t \in \mathbb{R}\}$$

In other words a complete orbit is the set of points that lie on the trajectory through p . Orbits that are restricted to $t \geq 0$ are called *forward orbits* and those restricted to $t \leq 0$ are called *backward orbits*.

A subset $S \subset X$ of the state space is said to be *invariant* if for any $p \in S$, we also have $\phi(t, p) \in S$ for all $t \in \mathbb{R}$. If for any $p \in S$, we

know $\phi(t; p) \in S$ for all $t \geq 0$, then S is *positively invariant*. In a similar way, the restriction that backward orbits starting at $p \in S$ remain in S implies S is *negatively invariant*. We will assume throughout that the orbits of the system are compact (closed and bounded sets in $\mathbb{R}^n$). For our applications, this is not an unreasonable requirement since the local state (population size) of all compartments in a living system must remain bounded. If all orbits of (X, ϕ) are compact then there must exist an invariant set, S , such that the restriction of the flow to S is an automorphism; i.e., $\Phi_t: S \rightarrow S$ for all $t \in \mathbb{R}$. Given a system, (X, ϕ) , with compact orbits, we are interested in characterizing the set of all *chain recurrent states* (i.e., states that are returned to infinitely often) (Conley, 1978; Easton, 1998) since we will use this set to define the system's regimes.

An ϵ -chain from $p \in X$ to $q \in X$ is a finite sequence $\{(x_k, \tau_k)\}_{k=1}^N$ of points in $X \times \mathbb{R}$ such that $N \geq 2$, $x_1 = p$, $x_N = q$ and

$$|x_{k+1} - \phi(\tau_k, x_k)| < \epsilon$$

The ϵ -chain is a sequence of points that more closely tracks an orbit of a dynamical system as ϵ goes to zero. A point $p \in S$ is said to be *ϵ -chain recurrent* if there is an ϵ -chain from p back to itself. We say an infinite length chain, $\{x_k, \tau_k\}_{k=1}^\infty$, is a *periodic ϵ -chain* if there exists an ϵ -chain recurrent point, p , and an increasing sequence of integers $\{N_j\}_{j=1}^\infty$ with $N_1 = 1$ such that $\{x_k, \tau_k\}_{k=N_j}^{N_{j+1}}$ is an ϵ chain from p back to itself for all $j = 1, 2, \dots, \infty$.

Let $S \subset X$ be a compact positively invariant set of the system and consider two sets $A, B \subset S$. We define $\text{ch}_\epsilon(A, B; S)$ as the union of all ϵ -chains in S that start in A and end in B . We say a state $p \in S$ is *ϵ -chain recurrent* if $\text{ch}_\epsilon(p, p; S)$ is nonempty and we let

$$R_\epsilon(S) = \{p \in S: \text{ch}_\epsilon(p, p; S) \text{ is nonempty}\}$$

denote the *ϵ -chain recurrent set* with respect to compact set $S \subset X$. The system's *chain recurrent set*, $R(S)$, with respect to compact $S \subset X$ is then defined as the intersection of all its ϵ -chain recurrent sets

$$R(S) = \bigcap_{\epsilon > 0} R_\epsilon(S)$$

Long term steady state behaviors are contained in the system's "positive limit set". Given any point $p \in S$, one says q is a *positive limit point* of p if there is an infinite sequence $\{\tau_k\}_{k=1}^{\infty}$ such that $\tau_k \rightarrow \infty$ as $k \rightarrow \infty$ and $\lim_{\tau_k \rightarrow \infty} \phi(\tau_k; p) = q$. The *positive limit set* of the set S , $\Omega(S)$, is defined (Bhatia and Szego, 1970) as the set of all points, p , for which there exist a sequence of pairs $\{p_k, t_k\}_{k=1}^{\infty}$ such that $p_k \in S$ and $\lim_{k \rightarrow \infty} t_k = \infty$ such that $\lim_{k \rightarrow \infty} x(t_k; p_k) = p$ where $x(t; q)$ is the forward trajectory from initial state q for $t \geq 0$. As noted in Isidori and Byrnes (2008), the positive limit set, $\Omega(S)$, contains the *steady state behaviors* of the system which are also contained within the system's chain recurrent set, $R(S)$.

Given any two points, p and q , in the chain recurrent set, $R(S)$, we can introduce a binary relation that says $p \sim q$ if and only if for all $\epsilon > 0$ there exists a periodic ϵ -chain containing p and q . One can easily show that this binary relation is an equivalence relation which means the chain recurrent set can be decomposed as the union of mutually exclusive equivalence classes. In particular, we denote the equivalence class that a point $p \in R(S)$ lies in as $[R(S)]_p$. These equivalence classes are called *basic sets*. Note that because the system's positive limit set $\Omega(S)$ is contained within $R(S)$, this means that the positive limit set of the system can also be decomposed with respect to the basic sets of $R(S)$ by simply taking the intersection of $\Omega(S)$ with each of the basic sets $\{[R]_p(S)\}$. We will denote these "basic" sets for the positive limit set as $[\Omega]_p(S)$ where p is some state in $\Omega(S)$. One can use a result known as Conley's decomposition theorem (Conley, 1978) to place a partial order on these basic sets. Ordered decompositions of invariant sets are sometimes called *Morse decompositions* and so the basic sets of $\Omega(S)$ can also be referred to as a Morse decomposition of the positive limit set.

What one intuitively thinks of as a *steady-state* behavior was discussed in Isidori and Byrnes (2008) and related back to the classical notion of a positive limit set given in Bhatia and Szego (1970). The introduction of ϵ -chain recurrence in Conley (1978) provided a way to characterize the topology of $\Omega(S)$ in terms of isolated components (basic sets) that could then be globally related through the partial order discussed in Conley's fundamental decomposition theorem. This

last point is important for the study of regime shifts, because it not only defines a “regime” in terms of basic sets, but more importantly it provides a way to *globally* relate different regimes; that relationship being defined in the next subsection as the existence of a shock-induced regime shift between two distinct regimes.

2.4.2 Generalized Regime Shift Concept

Let us consider a dynamical system, (X, ϕ) , where S is the largest compact invariant set in X . Since we know the system’s positive limit set, $\Omega(S)$, can be decomposed into a collection of basic sets $[\Omega]_p(S)$, we will define a system *regime* as one of these basic limit sets. A *regime shift* occurs when the system state switches between these basic sets as a result of an external disturbance (i.e., a shock-induced regime shift) or a change in the topology of these basic sets (i.e., a bifurcation-induced regime shift). Note that the regime shift mechanisms are essentially the same as we defined before for the lake eutrophication example, but now the regimes are no longer defined with respect to stable system equilibria. They are defined with respect to a Morse decomposition of the system’s positive limit set and this characterization means that the regime shift concept can now be extended to non-equilibrium systems.

Let us now consider a realistic example of a food web whose regimes are defined in terms of the positive limit set’s basic sets. We consider a tritrophic extension of the Rosenzweig–MacArthur predator prey system (Rosenzweig and MacArthur, 1963). The original Rosenzweig–MacArthur system consists of a producer and a “primary” consumer. This model can be extended to a three guild system by adding a “secondary” consumer that only feeds on the primary consumer. The resulting tritrophic food web shown in Figure 2.8 assumes the producer is algae, the primary consumer is a planktonic crustacean such as *Daphnia*, and the secondary consumer is a lake fish such as a black crappie. This simple food web is well known to exhibit a range of complex behaviors that include chaotic orbits (Hastings and Powell, 1991).

We model this food web as a non-negative compartmental system with the consumer-resource interactions introduced in the preceding subsection. The model has three compartments for the producer (x_1),

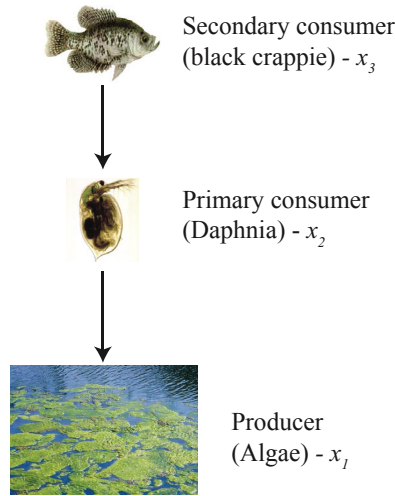


Figure 2.8: Tritrophic food web.

the primary consumer (x_2), and the secondary consumer (x_3). The compartmental states satisfy the following set of differential equations

$$\dot{x}_1 = r_1 x_1 \left(1 - \frac{x_1}{K}\right) - r_2 \frac{x_1 x_2}{\theta_1 + x_1} \quad (2.4)$$

$$\dot{x}_2 = \eta_2 r_2 \frac{x_1 x_2}{\theta_1 + x_1} - r_3 \frac{x_2 x_3}{\theta_2 + x_2} - m_2 x_2 \quad (2.5)$$

$$\dot{x}_3 = \eta_3 r_3 \frac{x_2 x_3}{\theta_2 + x_2} - m_3 x_3 \quad (2.6)$$

where K is the producer's carrying capacity. The parameters r_i , η_i , and m_i denote the growth rate, feeding efficiency and mortality rate of guild i , respectively. The RHS of these equations model fluxes entering and exiting the compartment. The producer Equation (2.4) has two terms; the first term models growth due to photosynthesis and the second term models predation by the primary consumer. The primary consumer Equation (2.5) has three terms; the first term models growth due to predation on the producer, the second term models losses due to predation by the secondary consumer, and the third term models losses due to mortality. The secondary consumer's Equation (2.6) is similar to that of the primary consumer and has only two fluxes; one