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Nutrient Regeneration in an Aquatic Producer-Herbivore System

by

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Abstract

Aquatic organisms require nutrients for growth and reproduction. Within a lake, organisms rely on the regeneration of nutrients from sediments. Microbial communities provide this regeneration through decomposition of sediments. To examine the effect of nutrient regeneration on producer (algae) and herbivore (*Daphnia)* population equilibria and stability, high decomposition rates were simulated by artificially manipulating nutrient regeneration from sediments within mesocosm experiments. Mesocosms experiencing higher rates of regeneration demonstrated increased population stability, contrary to model and theory expectations, and higher *Daphnia* biomass. The experimental data were also used to test predictions of a producer-herbivore model that incorporates regeneration. Parameter estimates generated by model fits suggested that increased regeneration leads to higher per capita rates of sedimentation for algal biomass, contributing to the increased stability. The combination of experimental and modelling results suggest that bacteria and food quality may also have a role in determining the population dynamics of algae and *Daphnia*.

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Chapter One: Nutrient effects on population dynamics

1.1 Effects of disturbance on natural systems

The increasing spatial extent and intensity of interactions between humans and the natural environment has produced a greater need to understand how human disturbances affect ecosystems. Aquatic systems are especially susceptible to disturbances due to close proximity to urban areas and the requirement of large quantities of water, and the relatively quick transport of material throughout a system once in the water. A variety of human activities influence aquatic organisms. The harvesting of fish can translate to effects on trophic levels further down the food chain (Jeppesen et al. 1990a, Jeppesen et al. 1990b, Jeppesen et al. 1990c, Sondergaard et al. 1990, Tatrai et al. 2009), and similarly the stocking of fish can alter the composition of food webs (McNaught et al. 1999, Yang et al. 2005, Tatrai et al. 2009). By far the most studied disturbance on aquatic systems has been eutrophication (nutrient enrichment) through external inputs (Correll 1998, Khan and Ansari 2005, Withers and Jarvie 2008). External nutrient inputs can originate from sources such as agriculture, waste treatment facilities, and urban stormwater runoff (Bennett et al. 2001, Ulen et al. 2007, Tetzlaff et al. 2009). Regardless of the source of nutrient input it is important to understand internal processes such as nutrient uptake, competition, predation, growth, and death within aquatic systems, so that we can better predict how disturbances will affect the overall condition of a system.

Nutrient enrichment generally leads to large increases in the biomass of algae such as undesirable algal blooms in recreational lakes and even large blooms of toxic

cyanobacteria in sources of drinking water (Watson et al. 1997, Downing et al. 2001). Further studies of eutrophication have led to a better understanding of material cycling such as the movement of pelagic (water column) material to the benthic (water bottom/sediments) food chain (Darchambeau et al. 2005).

A better understanding of the effect of external inputs has coincided with the study of internal nutrient cycles in aquatic systems (Sterner et al. 1992, Elser and Urabe 1999, Essington and Carpenter 2000, Higgins et al. 2006). The major internal supply of nutrients to the water column of shallow aquatic systems is from accumulated dead organic material associated with sediments (Kilham and Kilham 1990, Caraco et al. 1992, Brett and Benjamin 2008). The release of sediment nutrients is commonly referred to as internal loading, but for the purposes of this thesis I will refer to it as regeneration given that this process returns material back to the water column where much of it originated. This form of nutrient regeneration is different from external enrichment because the availability of nutrients in the water due to regeneration is a result of biological processes (e.g. decomposition and competition). External enrichment is independent of the internal biology of an aquatic system. Changes in the regeneration rate can have strong effects on biological organisms by altering the availability of nutrients. These effects can produce a feedback that can, in turn, alter subsequent regeneration rates. External enrichment can have the same initial effect as regeneration, but the ability of organisms to modify either the presence or rate of external enrichment is absent. Nutrient cycles have been well established in aquatic systems (Wetzel 2001), but the direct effects of variable rates of sediment regeneration on population dynamics have not been well studied experimentally. Within aquatic systems the cycling of nutrients is determined by

complex biological feedbacks that continuously respond to and modify each other (DeAngelis 1992, Andersen 1997).

1.2 Theory and modelling of a *Daphnia*-algal system

Biological processes that drive population dynamics have been difficult to examine experimentally due to the many complex interactions that occur in natural systems. Population models have allowed ecologists to examine how these interactions can alter population dynamics, and so provide insight into the processes driving natural systems. One system that has allowed these theoretical models to be tested is that of interacting aquatic producers and herbivores (McCauley and Murdoch 1987, 1990, Sterner et al. 1992, Larsson and Miracle 1997, Elser et al. 2000, Yoshida 2005). Specifically, the interaction between the aquatic herbivore *Daphnia* and its algal prey can result in a wide range of complex dynamics (Murdoch and McCauley 1985, McCauley and Murdoch 1987, Kendall et al. 1999, McCauley et al. 1999, Grover et al. 2000) and this system has been used experimentally to both test and guide theoretical models (Gurney et al. 1990, McCauley et al. 1990, Murdoch et al. 1998, McCauley et al. 1999). *Daphnia* are aquatic filter feeders that generally feed on single-celled algae in the water column. A system composed of algae (prey) and *Daphnia* (predator) is very well characterized mathematically by density-dependent growth of the prey and a predator that exhibits a saturating feeding curve (Holling type II functional response).

The resulting population dynamics of *Daphnia*-algal systems can fall into three categories: 1) stable equilibrium densities; 2) oscillating densities that return to equilibrium; and 3) persistent cycles of oscillating prey and predator densities. Because

of the importance of nutrient enrichment in ecosystems, this type of model has also been used to explore the effect of enrichment on population dynamics (Rosenzweig 1971, McCauley et al. 1999, Persson et al. 2001, Diehl 2007). Enrichment has the effect of increasing the carrying capacity of a population, that is, the maximum density at which a population can be sustained for a given system. As a function of enrichment, the dynamics of this system can arise in the following ways (Figures in the appendices):

1) At low enrichment levels both predator and prey populations reach a stable equilibrium because prey growth is kept in check by the mortality from predator foraging;

2) As enrichment increases, population growth of the prey begins to exceed the foraging pressure exhibited by predators and the prey population increases towards carrying capacity. This "prey escape" is a result of the saturating functional response of the predator. When the prey reach sufficiently high density the predator feeding rate becomes constant (i.e. saturated). As prey continue to increase in density their per capita mortality by predation goes down, allowing them to further increase towards their carrying capacity. Eventually predator abundance increases, and so predator foraging then decreases prey abundance. When the prey population decreases to a low enough abundance the predator population then follows due to insufficient food. This pattern repeats, but is dampened to a stable equilibrium because enrichment is not high enough to produce sustained cycles;

3) At high enough enrichment the same pattern is exhibited as #2 above, but the increased carrying capacity of the system allows both prey and predators to increase to even greater abundances. Prey abundance declines to levels that cannot support a large

enough predator population for sustained pressure on the prey, and prey are able to escape the predator. The cycle of prey escape – herbivore growth – prey decline – herbivore decline is then sustained producing persistent cycles.

1.3 Incorporating sediment regeneration into models

Models and experiments using a *Daphnia*-algal system have highlighted the need to understand intrinsic biological interactions (e.g. competition, predation) in order to understand the effect of external drivers (e.g. nutrient inputs, temperature). (McCauley 1993, Gurney et al. 1996, De Roos and Persson 2001, McCauley et al. 2008). Theoretical models that attempt to qualitatively examine the dynamics of a producer-herbivore system often assume the presence of only two biotic compartments: a producer and the herbivore that feeds on it (McCauley et al. 1993, Sterner 1997, Andersen et al. 2004, Nelson et al. 2005). Nutrients can therefore only occur in the tissue of producer or herbivore and these theoretical models imply that organic nutrients in dead matter are mineralized instantaneously, back into producer biomass. The importance of nutrient cycles in aquatic systems has led to the development of population models that explore the effect of nutrient processing rates on population dynamics (Nisbet et al. 1991, DeAngelis 1992, Andersen 1997, Jang and Baglama 2005). The addition of a dead particulate organic matter pool (POM) with nutrient regeneration more closely resembles the food web of natural aquatic systems. These models have also shown a wide range of population dynamics and a result that directly links to this thesis: the models have been shown to introduce stability to a system experiencing fluctuating dynamics via changes in the regeneration rate of nutrients from the POM pool (Nisbet et al. 1991, Bischi 1992,

Norberg and DeAngelis 1997, Jang and Baglama 2005, Perhar and Arhonditsis 2009). Stability occurs as a result of a limiting nutrient being retained in POM, effectively lowering the carrying capacity of the system. The lower carrying capacity prevents the cycle of: prey escape – herbivore growth – prey decline – herbivore decline.

Although a number of population models have incorporated a sediment pool into the associated food web, experimental studies examining the direct effect of nutrient regeneration on population dynamics are currently lacking. If models are to be used to predict the effects of disturbances on natural populations, then experiments are needed to test the predictions of these models.

1.4 Thesis outline

In this thesis, I have combined the use of experimental data and a mathematical model to understand the role of phosphorus regeneration in an aquatic system. Two major questions are asked:

1) What is the effect of increased nutrient regeneration on the population dynamics of algae and *Daphnia*?

2) Can a simple mathematical model that incorporates a dead particulate organic matter pool successfully predict the dynamics, and subsequently provide realistic parameter estimates for the populations?

Each chapter is written in manuscript form with each major question being addressed by a separate chapter. Tables and figures for each chapter have been placed after each discussion.

Phosphorus regeneration was artificially manipulated in mesocosm experiments to observe the effect on the population dynamics of algae and *Daphnia*. This type of experiment allows a large number of replicate algae and *Daphnia* populations to be studied. The mesocosms were located within greenhouses that allowed environmental variables to be held relatively consistent across all mesocosms. Chapter 2 presents the experimental design and methods, and results pertaining to equilibria and stability. These results are some of the first that attempt to isolate the effect of regeneration on algae and *Daphnia* populations. Chapter 3 presents predictions from a simple producer-herbivore model, and uses the experimental data to produce estimates of per capita rates of production and loss in the system. The final chapter provides a summary of the major conclusions from the experiment and model, in the context of aquatic disturbance, and discusses future directions for research in this area.

Chapter Two: Effect of regeneration on Algae and *Daphnia* equilibrium biomass and stability

2.1 Introduction

The abundance of organisms in aquatic systems is tightly linked to the availability of phosphorus in the water column (Schindler 1977, 1978). Specifically, the abundance of algae and *Daphnia* show a clear increasing relationship with the concentration of phosphorus (Carpenter et al. 1999, DeMott and Gulati 1999, Elser et al. 2001, Xenopoulos et al. 2002). Phosphorus is an essential requirement for cellular constituents such as DNA, RNA, and ATP; however, in aquatic systems phosphorus is relatively low in abundance compared to other elements. This leads to frequent phosphorus limitation of organism growth. The effect of phosphorus on algal productivity has long been demonstrated by the increasing relationship between chlorophyll *a* (as a measure of algal biomass) and total phosphorus supply (Dillon and Rigler 1974, McCauley et al. 1989, Downing et al. 2001). In addition to directly increasing algal abundance, phosphorus enrichment also leads to increases in *Daphnia* biomass, whereby the increased production of algae is transferred through the food chain to *Daphnia*. However, increasing evidence suggests that it is not simply the abundance of phosphorus that determines the growth of *Daphnia*, but the elemental ratio of carbon and phosphorus (C:P) (Hessen 1992, Sterner and Hessen 1994, Hessen et al. 2002, Sterner and Elser 2002, Vrede et al. 2004, DeMott and Pape 2005). This ratio is important because an organism's growth requires a certain amount of carbon in conjunction with phosphorus to produce new biomass. The study of elemental ratios has fallen under the realm of ecological stoichiometry (Sterner and Elser

2002), which investigates the balance of elements in organisms and their food. Elemental needs are not the same for all organisms (several elements are required for growth and the ratios are different among organisms), which often introduces a mismatch between an organism's food and its own elemental composition and highlights the need to understand material cycling in ecosystems. Clearly not all algal and *Daphnia* biomass is composed of simply carbon and phosphorus, but in aquatic systems C:P is an important indicator of algal food quality for *Daphnia* (DeMott 2003). Lower C:P translates to increased phosphorus content and better food quality demonstrated by higher rates of growth and reproduction of *Daphnia* ingesting algae of this type (Sterner and Elser 2002). Variable growth and reproduction under variable C:P ratios occur because *Daphnia* have a narrow range of elemental composition in their body tissue (Hessen 1990, DeMott et al. 2004), and there algal prey typically displays very large ranges in elemental composition (Hecky et al. 1993, Hessen et al. 2003) producing the mismatch between consumer and food. Photoautotrophs (i.e. algae) are able to store carbon within their cells from photosynthesis, and this ability to produce large of amounts of stored energy (carbon) contributes to variable C:P ratios in algal cells. Although algae initially utilize light as an energy source, mathematical models typically account for the transfer of energy through a food web by tracking carbon flow (measured as carbon biomass). This thesis uses the same framework and investigates the material flow of carbon and phosphorus.

Simple food webs composed of algae and *Daphnia* display a wide range of population dynamics both in ponds and in laboratory populations (McCauley and Murdoch 1987, 1990, McCauley 1993, Grover et al. 2000, Nelson et al. 2001). In addition to the effect exhibited on equilibrium abundances, phosphorus can also play a

role in the population dynamics of aquatic systems. Increasing the supply of phosphorus not only increases population abundance, but can have implications for the qualitative type of dynamics exhibited by a population (Murdoch and McCauley 1985, Sterner et al. 1992, Nelson et al. 2001, Grover 2002). The range of dynamics produced includes: 1) stable equilibrium; a population reaches this level and returns to it even after a perturbation; 2) dampened oscillations towards a stable equilibrium; after a population is perturbed it fluctuates around the equilibrium before returning to the same abundance; 3) population cycles; produced from predator-prey limit cycles (Rosenzweig 1971). Large fluctuations associated with unstable dynamics (2 and 3 above) occur, because a high algal growth rate supported by a large supply of phosphorus allows algae to escape the control of *Daphnia* grazing. After edible biomass reaches its upper limit for growth (determined by the combination of light, temperature and nutrients), *Daphnia* are eventually able to graze down the edible biomass. However, edible biomass is then decreased by so much that it can no longer support the high *Daphnia* biomass and the *Daphnia* population then decreases rapidly as well. Once the *Daphnia* population is at a sufficiently low abundance, the cycle will start over again. A lower supply of phosphorus produces stability in this system because it does not allow large increases in algal growth followed by *Daphnia*, or the subsequent declines.

Within natural pond systems, the supply of phosphorus to algae and *Daphnia* is affected by processes such as water input/output, sedimentation and internal phosphorus loading/regeneration. Given the importance of these processes for natural systems, models (Nisbet et al. 1991, Norberg and DeAngelis 1997) have begun to be used to examine the role of decomposition and phosphorus regeneration from sediments in

determining the dynamics of algae and *Daphnia*. However, experiments that test the predictions from these types of models and the mechanisms they propose have been lacking. Thus I experimentally tested the effect of phosphorus regeneration on the population dynamics of algae and *Daphnia* to evaluate model predictions with experimental data (see Chapter 3 for closer examination of models of these systems).

The experiment artificially manipulates phosphorus regeneration from sediments and examines the equilibrium and dynamic responses of algae and *Daphnia*. The experimental system is closed to outside inputs of phosphorus, but is sufficiently enriched to produce unstable dynamics (McCauley et al. 1989, Nisbet et al. 1991, Watson et al. 1992, McCauley et al. 1999). Increased regeneration should result in increased availability of phosphorus in the water column for algae growth. Without regeneration, phosphorus is lost to the sediments and effectively lowers the carrying capacity of the system, increasing stability. Given the requirement of phosphorus for algae and *Daphnia* growth, an increase in phosphorus due to experimentally enhanced regeneration should increase algae and *Daphnia* equilibrium biomass. If the system is sufficiently enriched, models and theory predict large fluctuations in both algae and *Daphnia* biomass (decreasing system stability) with an increase in regeneration. Food quality for *Daphnia* is also predicted to be higher with increased regeneration as increased phosphorus availability for algal uptake should decrease the C:P of algae. Increased food quality should support higher *Daphnia* biomass. In addition to examining the direct effect of regeneration within *Daphnia*-absent or *Daphnia*-present treatments separately, comparisons between *Daphnia*-absent and *Daphnia*-present treatments should provide insight into the transfer of energy (carbon) and nutrients (phosphorus) within a food web.

For example, the biomass of algae should decrease with the presence of *Daphnia* under all regeneration conditions; however, the relative differences of these changes due to *Daphnia* between regeneration treatments can suggest differences in the flux of carbon and phosphorus within a food web. Based on the expectation that sediment regeneration increases the availability of phosphorus in the water column, I make the following predictions:

A) *Daphnia*-absent,

1) Increased regeneration should prevent an accumulation of sediments from occurring
2) Total phosphorus in the water column should be higher with increased regeneration
3) Increased regeneration should allow algal equilibrium biomass to increase

B) *Daphnia*-present,

1) Predictions 1) and 2) from above
2) *Daphnia* biomass should on average be higher with increased regeneration
3) Algae and *Daphnia* populations should exhibit large fluctuations with increased regeneration if system is sufficiently enriched
4) Food quality for *Daphnia* (algae C:P) should be better (lower C:P) with increased regeneration

2.2 Methods

2.2.1 Experimental setup

Experiments were carried out from May to September 2007 in greenhouses adjacent to ponds located on the University of Calgary campus. Communities of aquatic herbivores and producers were established in 800-litre polyethylene tanks with dimensions of 120cm x 60cm x 120cm. A total of 15 tanks were used consisting of 3 replicates for each of 5 treatments (Table 2.1). Tanks were filled with water from the Bow River, passed through a 1-µm polypropylene filter and ultraviolet filter to remove particulate matter and living organisms. Inorganic nutrients ($NaNO_3$ and K_2HPO_4) were added to the filtered water for all tanks to yield initial concentrations of 50 µg P L^{-1}) and 452 µg N L^{-1}) (a molar N:P ratio of 20:1 (Downing and McCauley 1992)). A 2-litre concentrated algae inoculum of *Chlamydomonas reinhardtii* (UTEX 90), *Scenedesmus denticulatus* (UTCC 153), *Ankistrodesmus convolutus* (UTCC 309), *Cryptomonas erosa* (UTCC 446), and *Oocystis polymorpha* (UTCC 9) was added to each tank, followed three days later by the addition of 300 individual *Daphnia pulex* (hereafter referred to as *Daphnia*). All algae species were obtained from the University of Toronto Culture Collection, except *Chlamydomonas reinhardtii* which was obtained from The Culture Collection of Algae at The University of Texas at Austin.

2.2.2 Sediment Removal and Regeneration

Particulate matter that settled to the bottom of tanks (i.e. sediment) in the regeneration treatments was removed using a sediment vacuum (Fig. 2.1). The “T”

suction-end was lowered to the bottom of a given tank, the vacuum pump was turned on, and then the suction-end was slowly moved across the bottom of the tank collecting sediments. Sediments were collected in a 4-L vacuum flask and transferred to separate sample containers in order for the sediments to settle to the bottom. Tank water and any *Daphnia* captured were removed from the top and put back into the tanks. The sediments were mixed and sub samples were taken to analyze for carbon and phosphorus (section 2.2.3 below). The estimated mass of phosphorus (method in section 2.2.3) removed was added back to the corresponding tanks as K_2HPO_4 along with $NaNO_3$ to yield a fixed molar N:P ratio of 20:1. This was done to prevent N from being the limiting nutrient (Downing and McCauley 1992) as phosphorus was repeatedly replenished and allow the analysis of population data to focus on growth effects of P.

Two different population treatments were established: 1) *Daphnia*-absent tanks; and 2) *Daphnia*-present tanks. Three regeneration treatments occurred in the experiment: 1) nutrients regenerated once per week (1x); 2) nutrients regenerated three times per week (3x); 3) absence of nutrient regeneration as a reference (0x). *Daphnia*-absent tanks only experienced 0x and 3x treatments due to logistical limitations; and *Daphnia*-present tanks experienced all 3 regeneration treatments. 0x tanks were used as a reference (and will be referred to as "reference tanks" in following sections) in order to observe dynamics without renewal of sediment phosphorus or nitrogen, while all water column, and biotic sampling procedures remained identical among treatments. Removal and regeneration of the sediments were scheduled as follows: all 1x tanks were vacuumed on Wednesdays and the inorganic nutrients returned on Fridays; all 3x tanks were vacuumed

on Mondays, Wednesdays, and Fridays with inorganic nutrients returned on Wednesdays, Fridays, and Mondays, respectively.

2.2.3 Chemical Analysis

Chemical analyses (excluding sediment phosphorus) were done on fractions < 35 µm, which is designated the edible fraction (particulate matter consumed by *Daphnia* (Gliwicz 1977, Porter et al. 1982, Lampert 1987)). It was not possible to distinguish the specific origin of phosphorus or carbon from within the water column (i.e. if it came from bacteria, nanoplankton, or algae), therefore reference to total phosphorus, particulate phosphorus, particulate carbon, and C:P of the < 35 µm fraction will be shown as "seston". Seston is commonly defined as the particulate material present in the open water (Wetzel 2001), and for the purpose of this thesis is restricted to particulate matter < 35 µm.

Carbon biomass of the edible fraction of algae was estimated through combustion of filtered samples. Samples were collected from tanks (see below) and passed through a 35-µm Nitex® filter. The filtrate was passed through a 1.2-µm (pore size) quartz filter (pre-combusted at 800°C) to collect the edible fraction of algae. Filters were combusted at 800°C in a Dohrmann DC-180 total organic C analyzer, or stored in a freezer if combustion was delayed. Sediment carbon content was estimated by the ash-free dry mass method. After sediments were removed from tanks they were passed through pre-weighed glass-fibre filters (type GF/C for particulate matter in water: 1.2-µm pore diameter) to collect particular matter which was combusted at 550°C.

Phosphorus content of the edible fraction of algae was estimated by the difference of total phosphorus (TP) and total dissolved phosphorus (TDP) using the ammonium molybdate method. Several samples (250 ml each) were taken from the water column and mixed together for each tank separately. A sub-sample was passed through a 35-µm Nitex® filter and the filtrate was analyzed for TP <35 µm. A separate sub-sample was passed through a GF/C filter (1.2-µm pore diameter) and the filtrate was analyzed for TDP. Sediment phosphorus was estimated using the ammonium molybdate method on the particulate matter of the sediments.

Seston C:P was calculated by the ratio of particulate carbon (moles C L^{-1}) to particulate phosphorus (moles P L^{-1}), and is a molar ratio.

2.2.4 Biotic Sampling

After thoroughly mixing the tanks, two 1-litre Nalgene®bottles were used to sample *Daphnia*. The samples were counted live and returned to the tanks after recording individual size (size-class: juvenile or adult), as well as the number of ovigerous females and eggs per adult female (fecundity). Biomass (mg C L^{-1}) of *Daphnia* was estimated by multiplying the observed density in each size class (0.7-1.0 mm, 1.0-1.4 mm, 1.4-2.0 mm, 2.0-2.5 mm, >2.5 mm) by the carbon weight for an individual in that size class using length to carbon-weight relationships (Downing and Rigler 1984), and summing these estimates over all size classes.

Two 1-L Nalgene® bottles were used to sample algae after mixing the tanks and these samples were kept in the dark until processing occurred in the lab. Edible (<35 µm

diameter) and inedible (>35 µm diameter) algae biomass was estimated from the measurement of chlorophyll *a*. These two fractions were separated using a 35-µm Nitex® filter, then filtered through a GF/C filter (1.2-µm pore diameter). Chlorophyll *a* retained on the filter was measured using acetone extraction and subsequent fluorescence on a Turner-Sequoia fluorometer. Algae samples were also preserved in Lugol's solution for species identification and enumeration if needed.

2.2.5 Statistical Analysis

Analyses were performed on the time-series data at the end of summer where a stable equilibrium for reference tanks is predicted to occur based on models with sediment regeneration. The designated equilibrium period for algae in tanks without *Daphnia* started 5 weeks after the large decline in algae biomass. In the presence of *Daphnia*, equilibrium started 5 weeks after *Daphnia* populations established (biomass > 0.1 mg C L^{-1}) in each of their respective tanks. Starting the equilibrium period at this time insured all *Daphnia* populations had gone through an initial peak in biomass and had decreased to average equilibrium levels.

A mean abundance at equilibrium was calculated by averaging values of a given variable over the equilibrium period. The Coefficient of Variation (standard deviation divided by the mean) calculated over the equilibrium period was used as a proxy to measure the stability of populations. More stable populations are able to remain near a given equilibrium abundance even after perturbations to that abundance (e.g. larger than normal mortality events). Low values of variation are indicative of relatively stable

populations that do not vary in abundance at equilibrium, and high values of variation indicate decreased stability where abundances fluctuate around equilibrium abundance. This yielded a single value of both the mean and coefficient of variation for each tank. The means and coefficients of variation were used to compare among treatments using a one-way analysis of variance (ANOVA) for each variable of the carbon and phosphorus fractions. A one-way analysis of covariance (ANCOVA) with seston C:P as the covariate was used to compare among treatments for algae and *Daphnia* biomass. The molar C:P was used as a covariate, because of its importance for the growth of algae, and in turn its value as an indicator of food quality for *Daphnia*. All statistical analyses were conducted in SAS version 9.1 (SAS Institute Inc. 2003). Statistical tables are included in the appendices showing detailed results of the tests.

2.3 Results

2.3.1 Regeneration

The effect of regeneration during the equilibrium period for both *Daphnia*-absent and *Daphnia*-present tanks was examined in three parts: (1) effect of both regeneration and seston C:P on algae equilibrium biomass; (2) the effect of both regeneration and seston C:P on *Daphnia* equilibrium biomass; (3) effect of regeneration on the C and P equilibrium concentrations. The main goal was to highlight the effect of regeneration on equilibrium biomass, while using possible differences in seston C and P to help explain the processes that lead to changes in equilibrium biomass.

Regeneration treatment differences, with respect to sediment production, were established as expected. Sediment accumulation at the end of the experiment was significantly greater in the reference tanks (0x) compared to tanks with artificial regeneration (1x, 3x) for both carbon (ANOVA, $P<0.05$) and phosphorus (ANOVA, $P<0.05$), in *Daphnia*-absent and *Daphnia*-present tanks (Fig. 2.2).

2.3.2 Algae biomass

2.3.2.1 *Daphnia*-absent

In the absence of *Daphnia*, regeneration and seston C:P did not show any significant effect on edible, inedible, or total algae equilibrium biomass (ANCOVA, $P>0.05$) (Fig. 2.3), nor on the stability exhibited by mean edible, inedible, and total algae biomass (ANCOVA, $P>0.05$) (Fig. 2.4). The proportions of edible and inedible algae biomass did not show a significant main effect of regeneration or seston C:P in *Daphnia*-absent tanks (ANCOVA, $P>0.05$).

2.3.2.2 *Daphnia*-present

In the presence of *Daphnia*, total algae and inedible algae equilibrium biomass were not affected by regeneration or seston C:P (ANCOVA, $P>0.05$) (Fig. 2.5); overall however, both total and inedible equilibrium biomass slightly increased with seston C:P. A significant effect of both treatment and seston C:P was shown regarding edible algae equilibrium biomass (ANCOVA, $P<0.05$). Regenerating sediment nutrients three times per week significantly reduced edible equilibrium biomass in D3x tanks by over a factor

of 4 when compared to D0x tanks (*a priori* contrast, $P<0.05$). However, regenerating sediment nutrients once per week did not affect edible equilibrium biomass when compared to D0x tanks (*a priori* contrast, $P>0.05$). Overall, edible equilibrium biomass showed a significant decreasing trend as seston C:P increased (partial regression coefficient, $P<0.05$). There was no significant difference in the stability of algae fractions among treatments as a function of seston C:P (ANCOVA, $P>0.05$), however D3x tanks did show a relative increase in stability compared to D0x tanks (Fig. 2.6). The proportions of edible and inedible equilibrium biomass did not show a significant main effect of regeneration or seston C:P in *Daphnia*-present tanks (ANCOVA, $P>0.05$). However, the proportion of edible algae was significantly lower in D3x tanks when compared to D0x tanks (*a priori contrast*, $P<0.05$), and thus the proportion of inedible algae was significantly higher in D3x tanks when compared to D0x tanks (*a-priori* contrast, $P<0.05$).

The addition of *Daphnia* significantly decreases the abundance of edible algae at equilibrium in both reference tanks (T-test, equal variance, df=4, t=5.09, $P<0.05$) and regenerated (3x) tanks (T-test, equal variance, df=4, t=8.71, $P<0.05$). Conversely, *Daphnia* significantly increase the abundance of inedible algae at equilibrium, in both reference tanks (T-test, unequal variance, df=2, t=3.86, $P<0.05$) and regenerated (3x) tanks (T-test, unequal variance, df=2, t=5.90, $P<0.05$) (Fig. 2.3, 2.5).

2.3.3 Daphnia biomass

Regeneration and seston C:P did not show a significant main effect on total, adult, or juvenile *Daphnia* equilibrium biomass (ANCOVA, $P>0.05$) (Fig. 2.7). However adult

biomass was significantly higher in D3x tanks; approximately double the biomass compared to D0x tanks (*a priori* contrast, $P<0.05$), and juvenile biomass showed a slight decrease with regeneration. Regeneration and seston C:P did not have a significant main effect on the stability of *Daphnia* equilibrium biomass (ANCOVA, $P>0.05$), however the stability of total *Daphnia* biomass was significantly greater in D3x tanks when compared to D0x tanks (*a priori* contrast, $P<0.05$), and stability appears to be greater in D3x tanks for both adult and juvenile biomass compared to D0x tanks (Fig. 2.8). The proportions of adult and juvenile biomass were significantly affected by regeneration; specifically, the proportion of adult biomass showed a significant increase in D3x tanks compared to D0x tanks (*a priori* contrast, $P<0.05$), and conversely the proportion of juvenile biomass was significantly lower in D3x tanks compared to D0x tanks (*a priori* contrast, $P<0.05$). No significant effect of regeneration or seston C:P was shown in *Daphnia* fecundity at equilibrium (ANCOVA, $P>0.05$), or on the variation (ANCOVA, $P>0.05$) (Fig. 2.9).

2.3.4 Carbon and phosphorus fractions

2.3.4.1 *Daphnia*-absent

Regeneration in the absence of *Daphnia* (A3x) did not produce significantly different equilibrium concentrations for seston P (Fig. 2.10), PC (Fig. 2.11), or C:P (Fig. 2.12) compared to reference tanks (A0x) (ANOVA, $P>0.05$), however A3x tanks had slightly lower equilibrium DP and higher equilibrium PP. Regeneration in the absence of *Daphnia* produced significantly less stability in seston PP (ANOVA, $P<0.05$) (Fig. 2.13),

and a similar trend of stability for TP, DP (Fig. 2.13), PC (Fig. 2.14), and C:P (Fig. 2.15) although not significant (ANOVA, P>0.05).

2.3.4.2 *Daphnia*-present

In the presence of *Daphnia*, the main effect of regeneration did not produce any significantly different equilibrium concentrations for seston P (ANOVA, P>0.05) (Fig. 2.16), however seston PC was significantly lower in regeneration tanks (D1x, D3x) when compared to reference tanks (D0x) (a priori contrast, P<0.05) (Fig. 2.17). Seston C:P did not show a significant difference among treatments (ANOVA, P>0.05), although equilibrium C:P of D0x tanks was almost double that of D3x tanks (Fig. 2.18). There was no significant effect of regeneration on the stability exhibited by seston P (AVOVA, P>0.05) (Fig. 2.19), PC (AVOVA, P>0.05) (Fig. 2.20), or C:P (AVOVA, P>0.05) (Fig. 2.21) in the presence of *Daphnia*; however the stability of P appears to increase with regeneration.

The addition of *Daphnia* dramatically lowers both the equilibrium concentration of seston P (Fig. 2.10, 2.16), and the concentration of seston PC (Fig. 2.11, 2.17). Seston C:P increases in D0x tanks from A0x tanks, while remaining about the same in D3x tanks compared to A3x tanks (Fig. 2.12, 2.18).

2.4 Discussion

2.4.1 Effect of regeneration on equilibrium biomass

2.4.1.1 *Daphnia*-absent

Algae were expected to reach a higher equilibrium biomass with increased regeneration due to increased availability of phosphorus; however, no differences were found in algae biomass between regeneration treatments in the absence of *Daphnia*. Since the increased availability of phosphorus should increase the growth rate of algae (McCauley et al. 1989, Watson et al. 1992), algae may also be experiencing increased loss rates (due to death, sinking or respiration) with regeneration resulting in similar biomass between treatments. It is possible for increases in algal growth to be accompanied by increased losses; for example the occurrence of self-shading (Agusti 1991, Carpenter et al. 1998, Huisman 1999, Huisman et al. 1999a, Huisman et al. 1999b). As algal abundance increases near the surface of the water utilizing light for photosynthesis, the increased biomass produced by regenerated phosphorus effectively blocks light from reaching lower in the water column. It is therefore possible that a smaller fraction of the algae population is able to use the increased phosphorus due to the emergence of light, rather than phosphorus, as a limiting factor. More algae biomass is then lost to sediments, and eventually removed by the experimental regeneration.

An alternate explanation for similar algae equilibrium biomass between treatments may be diversion of phosphorus from the algae in regeneration tanks into bacteria. After an initial decline in the algae population, a larger microbial population could be supported through the increased availability of phosphorus and increased

abundance of dissolved organic carbon (DOC) excreted by algae (Nalewajko et al. 1980, Laird et al. 1986) and even *Daphnia* (Darchambeau et al. 2003). Algae excrete DOC naturally, and bacteria can readily use this carbon source to produce more biomass (Olsen et al. 2002, Tittel and Kamjunke 2004, Docherty et al. 2006). With a readily available source of carbon, it is possible for bacteria to out-compete algae for P under limiting conditions (Currie and Kalff 1984a, 1984b, Danger et al. 2007), effectively lowering the carrying capacity of edible algae and the resulting equilibrium biomass.

Changes in the availability of phosphorus that may result in changes in algal per capita rates (e.g. sedimentation) will be further discussed in Chapter 3.

2.4.1.2 *Daphnia*-present

Regeneration significantly increased the *Daphnia* equilibrium for D3x tanks. Surprisingly, D1x tanks showed similar low *Daphnia* equilibrium biomass to the D0x tanks. The presence of *Daphnia* substantially reduces edible algae biomass through grazing, more so in D3x tanks while D1x edible algae biomass was similar to D0x biomass. With higher regeneration (D3x) increased phosphorus availability likely supports higher *Daphnia* biomass. However, it is possible that only regenerating sediments once per week does not maintain a high enough average phosphorus supply to support higher *Daphnia* biomass. Higher inedible algal biomass in D3x tanks is likely the result of increased grazing pressure on edible algae (McCauley and Briand 1979). Grazing allows inedible algae to take advantage of the increased availability of phosphorus by decreasing the competitive uptake of phosphorus by edible algae.

It is also likely that a larger bacterial population could be supported by increased availability of phosphorus, and an increase in the bacterial pool could actually help to maintain higher *Daphnia* biomass and lower edible algae biomass. As an alternate food source for *Daphnia* (Hessen and Andersen 1990, Kamjunke et al. 1999), bacteria are able to provide energy at times when a low edible algae population may be energy-limiting for *Daphnia*. The significantly higher adult *Daphnia* biomass in D3x tanks may be the combined result of an increase in phosphorus transfer to edible algae and bacteria from regeneration; as higher filtering rates by adults (Porter et al. 1982, Porter et al. 1983) would allow more efficient use of both food sources. Regenerating sediments only once per week may not be enough to stimulate a higher bacterial population, therefore *Daphnia* biomass does not have an alternate carbon source in times of low food availability.

Alternatively, the per capita rates of *Daphnia* may be affected by an increase in phosphorus availability and may be working through changes in food quality. An increase in regeneration inversely affects the C:P of seston in the experimental system, and a large body of evidence demonstrates, lower values of algae C:P translate to better food quality for *Daphnia* (Plath and Boersma 2001, DeMott 2003, DeMott et al. 2004). The possibility of changes occurring in the per capita rates of *Daphnia* as a function of food quality will be further examined in Chapter 3.

2.4.2 Effect of regeneration on stability

Daphnia and algae do not exhibit decreased stability with regeneration as expected. In fact, the stability in *Daphnia* biomass increases with regeneration. A likely explanation for the deviation from the theory is the importance of a branched food web in the algae-*Daphnia* system, which is not incorporated into many models. Diversion of phosphorus away from edible algae biomass causes phosphorus to be bound in a pool that is uncoupled from the producer-herbivore interaction. This food web shift has been shown to introduce more stability into the system (Kretzschmar and Adler 1993, Murdoch et al. 1998). Movement of phosphorus into inedible biomass effectively lowers the carrying capacity of edible algae, which prevents large fluctuations in both algae and *Daphnia* populations. With regeneration, higher bacterial biomass could be supported by the increased availability of phosphorus, and an increase in the bacterial pool could actually help to maintain higher *Daphnia* biomass while preventing large fluctuations in algal abundance. In a system experiencing unstable dynamics, the large decreases in *Daphnia* biomass following an initial growth phase could be buffered by the presence of an alternate food source for *Daphnia* (Genkai-Kato and Yamamura 2000, Perhar and Arhonditsis 2009). An alternate food source would prevent *Daphnia* biomass from decreasing below its ability to control edible algae, and further fluctuations would therefore be prevented.

2.4.3 Conclusions

Algal equilibrium biomass in the absence of *Daphnia* is the same under both regeneration scenarios, and may indicate a stable equilibrium abundance for this system at the given phosphorus level. In the presence of *Daphnia*, edible biomass is decreased due to grazing, and a diversion of phosphorus may lead to increased abundances of inedible algae and bacteria. Higher regeneration appears to support higher *Daphnia* biomass; however the presence of an increased time lag between D3x and D1x tanks appears to limit *Daphnia* equilibrium biomass in D1x tanks possibly as a result of phosphorus availability over time being lower on average.

Theoretical models predict producer-herbivore populations become destabilized at high nutrient levels. Here I experimentally manipulated nutrient regeneration rates to examine the effect of increased phosphorus availability on populations of algae and *Daphnia*. Interestingly, in the presence of regeneration, *Daphnia*-algae interactions are not destabilized, but rather become more stable. The increased availability of phosphorus maintains higher *Daphnia* biomass at equilibrium and subsequently exerts more grazing pressure on algae. Maintenance of higher *Daphnia* biomass and possible diversion of phosphorus to other compartments of the food web, appear to aid in the stability of the system by preventing large fluctuations in algal abundance and in turn *Daphnia* abundance.

Table 2.1: Treatment combinations of organisms and sediment regeneration.

Organisms	Treatment Label	Regeneration per week	Label
Algae only	*Daphnia*-absent	0	A0x
Algae only	*Daphnia*-absent	3	A3x
Daphnia + Algae	*Daphnia*-present	0	D0x
Daphnia + Algae	*Daphnia*-present	1	D1x
Daphnia + Algae	*Daphnia*-present	3	D3x

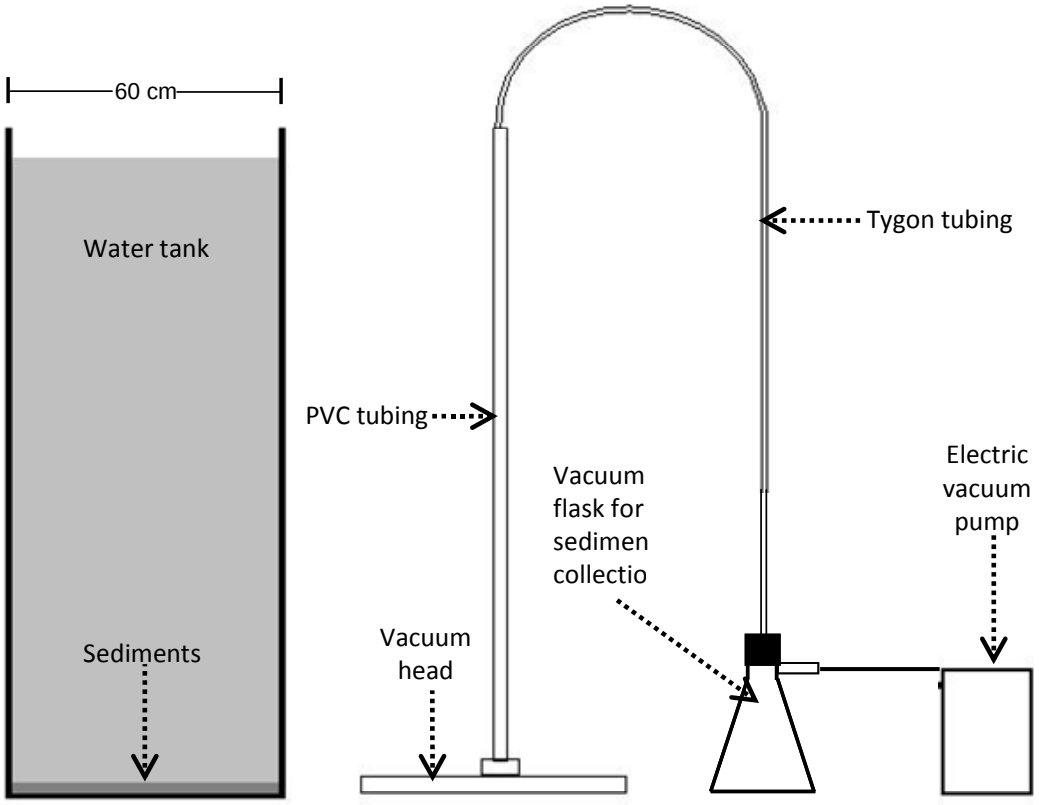

Figure 2.1: Sediment Vacuum

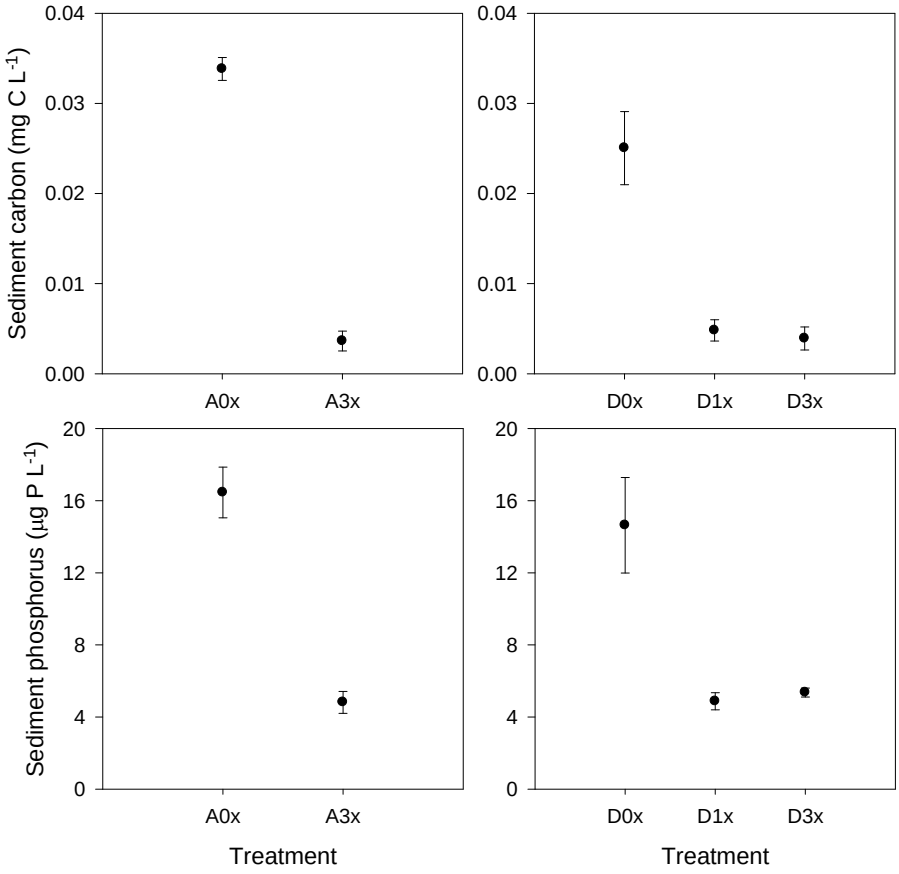

Figure 2.2: Mean abundance of sediment carbon (mg C L^{-1}) and phosphorus (µg P L^{-1}) accumulated at the end of the experiment in *Daphnia*-absent (left panels) and *Daphnia*-present (right panel) tanks. Abundance has been corrected for the volume of tank water to allow comparison of C and P from other variables. Error bars show standard error of means; n=3 for each treatment.

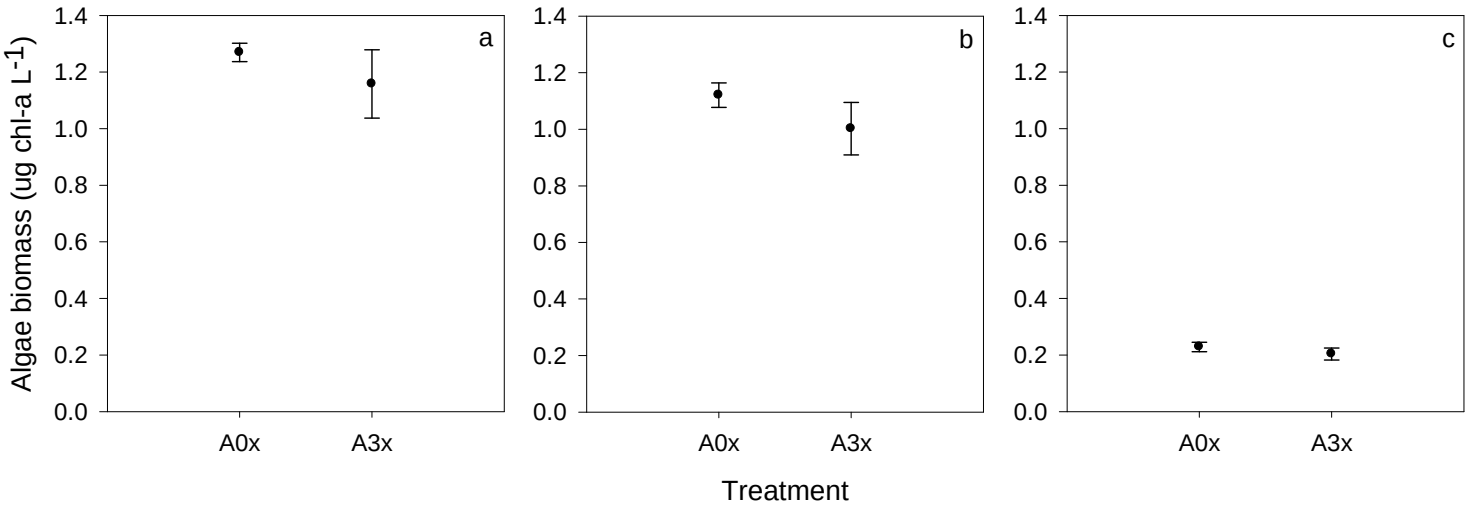

Figure 2.3: Equilibrium biomass (µg chlorophyll *a* L^{-1}) of total (a), edible (b), and inedible (c) algae compared between regeneration treatments (A0x, A3x) in *Daphnia*-absent tanks. Error bars show standard error of means; n=3 for each treatment.

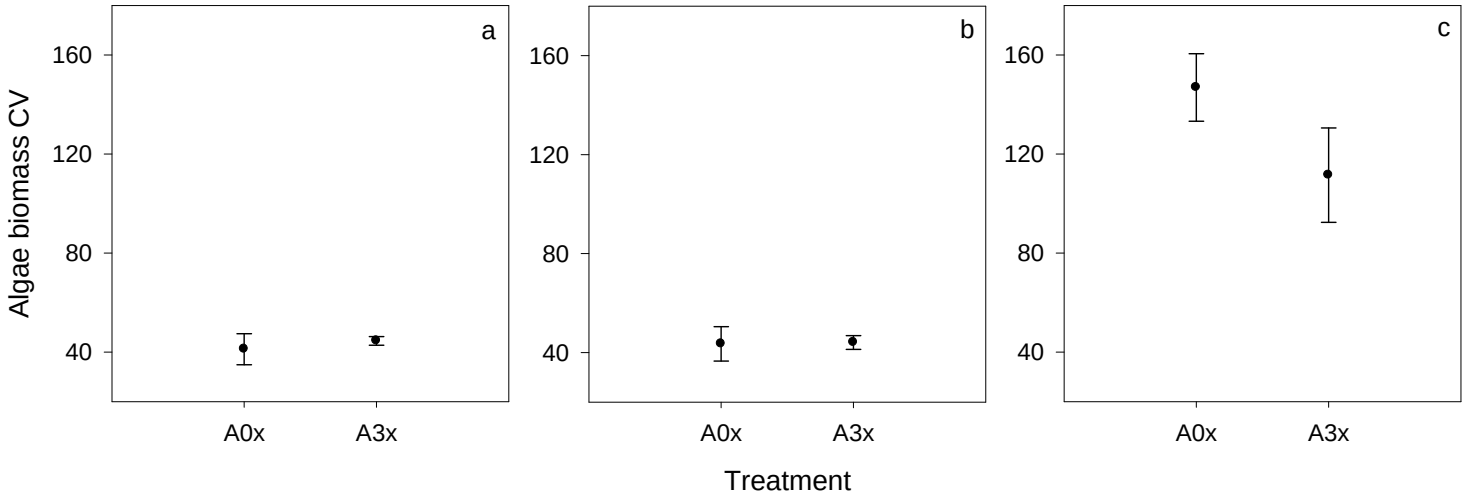

Figure 2.4: Mean coefficient of variation for total (a), edible (b), and inedible (c) algae biomass (µg chlorophyll *a* L^{-1}) at equilibrium; compared between regeneration treatments (A0x, A3x) in *Daphnia*-absent tanks. Error bars show standard error of means; n=3 for each treatment.

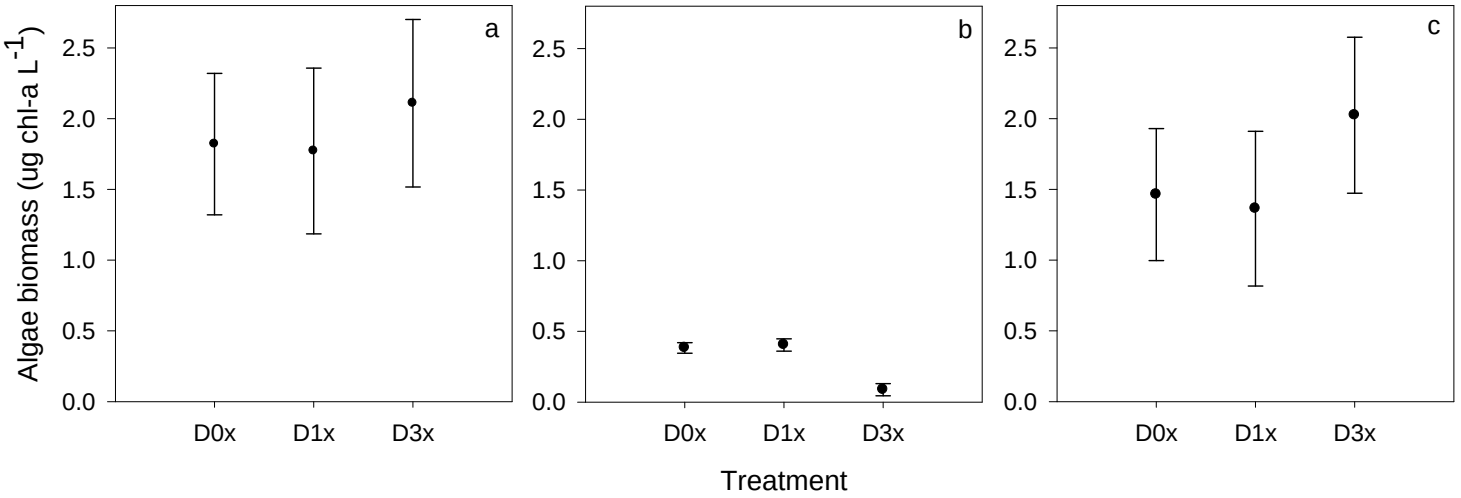

Figure 2.5: Equilibrium biomass (µg chlorophyll *a* L^{-1}) of total (a), edible (b), and inedible (c) algae compared among regeneration treatments (D0x, D1x, D3x) in *Daphnia*-present tanks. Error bars show standard error of means; n=3 for each treatment.

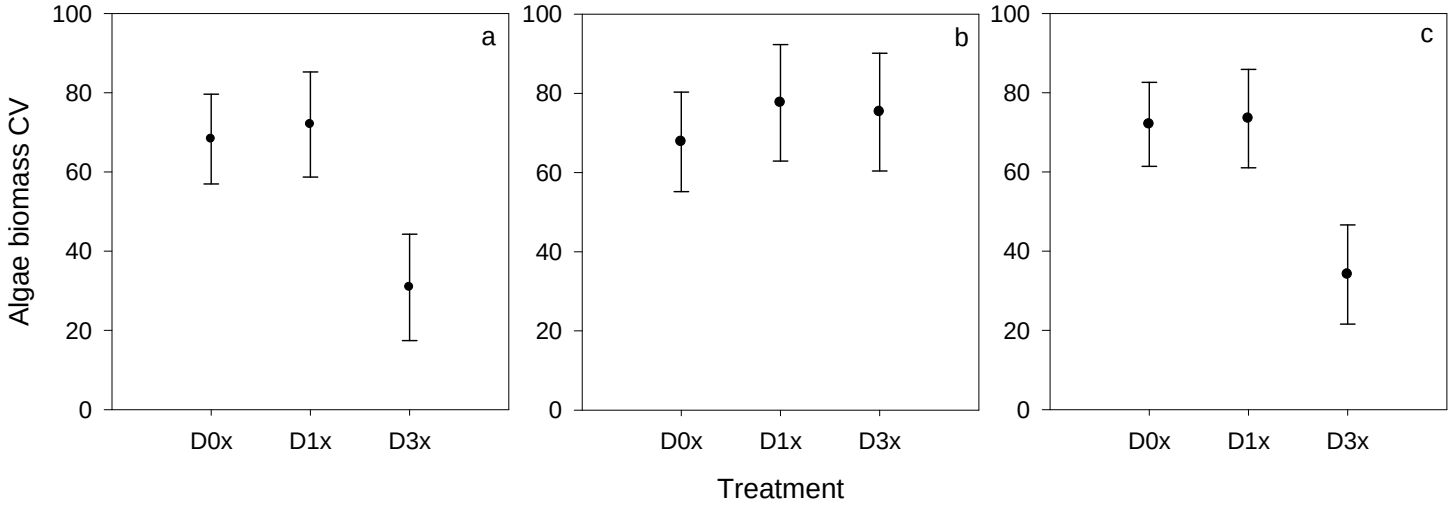

Figure 2.6: Mean coefficient of variation for total (a), edible (b), and inedible (c) algae biomass (µg chlorophyll *a* L^{-1}) at equilibrium; compared among regeneration treatments (D0x, D1x, D3x) in *Daphnia*-present tanks. Error bars show standard error of means; n=3 for each treatment.

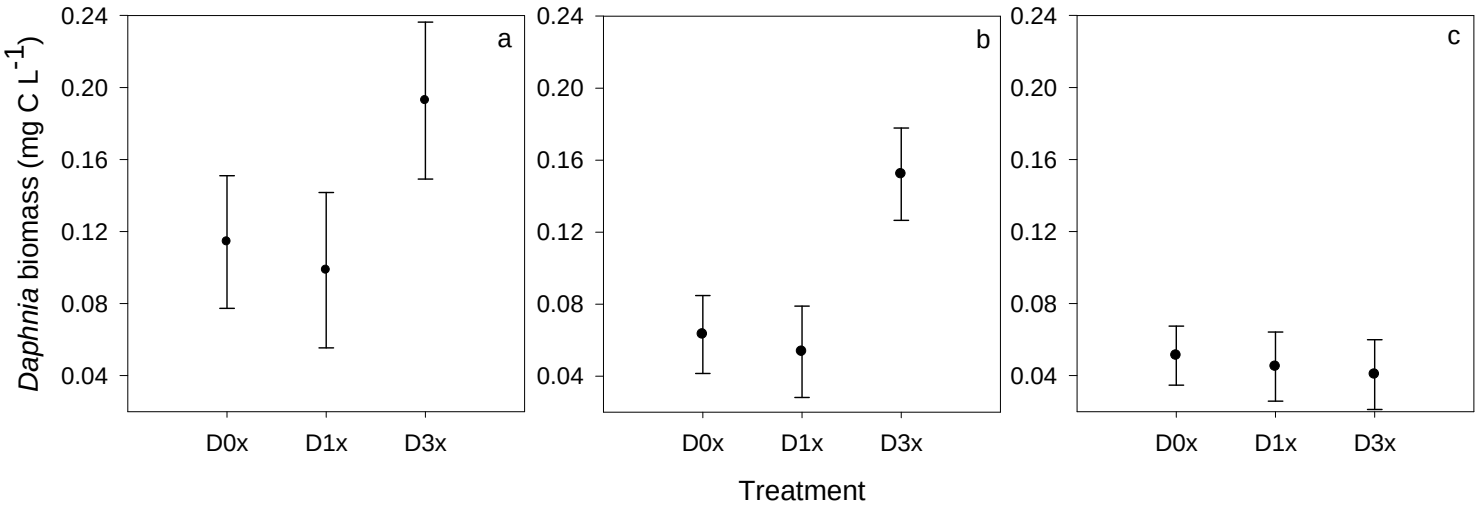

Figure 2.7: Equilibrium biomass (mg C L^{-1}) of total (a), adult (b), and juvenile (c) *Daphnia* compared among regeneration treatments (D0x, D1x, D3x). Error bars show standard error of means; n=3 for each treatment.

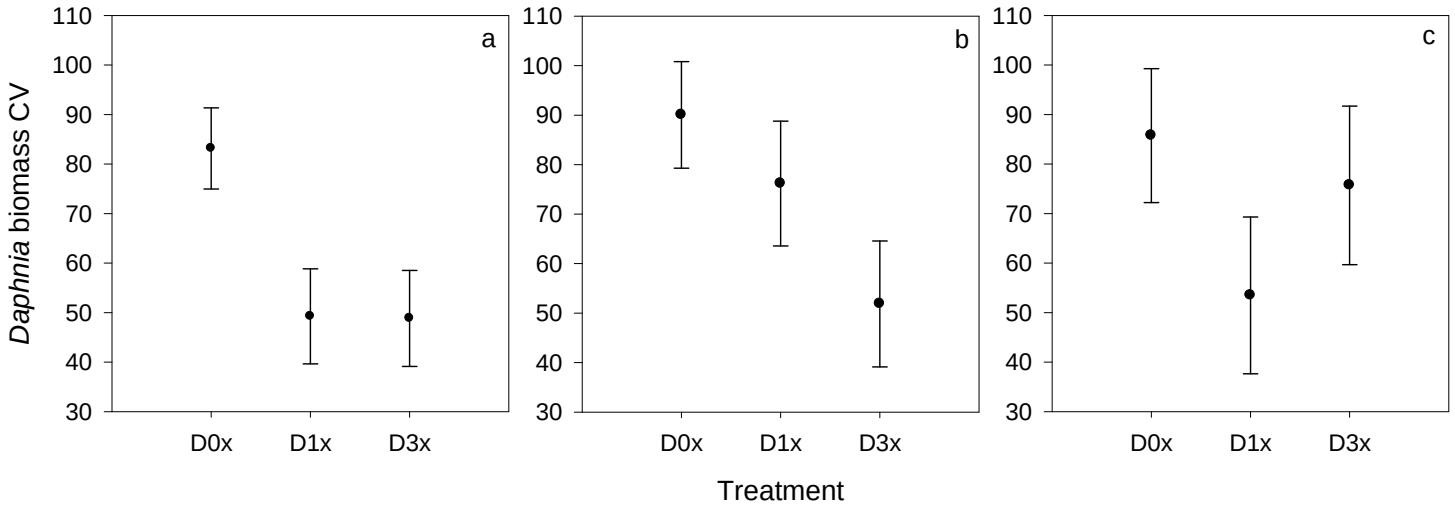

Figure 2.8: Mean coefficient of variation for total (a), adult (b), and juvenile (c) *Daphnia* biomass (mg C L^{-1}) compared among regeneration treatments (D0x, D1x, D3x). Error bars show standard error of means; n=3 for each treatment.

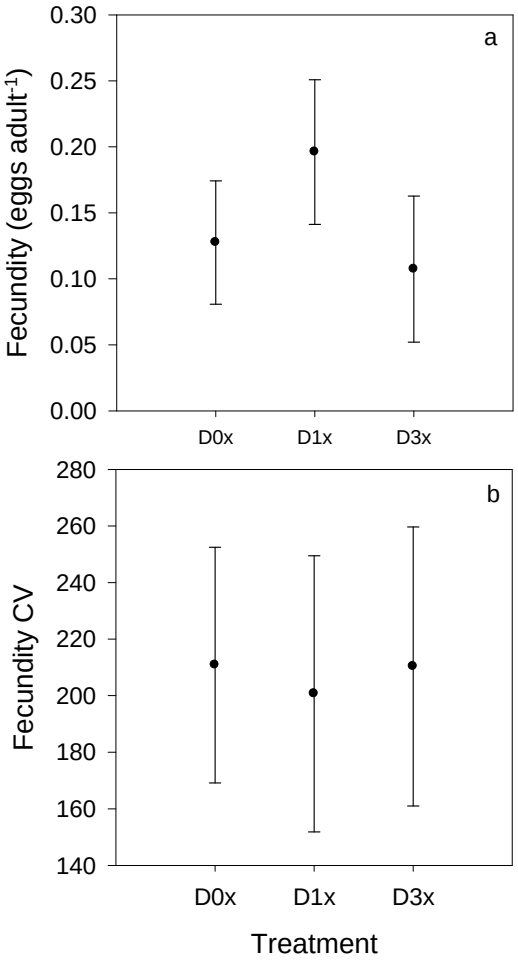

Figure 2.9: Equilibrium (a) and mean coefficient of variation (b) for number of eggs produced per adult (a) as a function of seston C:P at equilibrium; compared among regeneration treatments (D0x, D1x, D3x). Error bars show standard error of means; n=3 for each treatment.

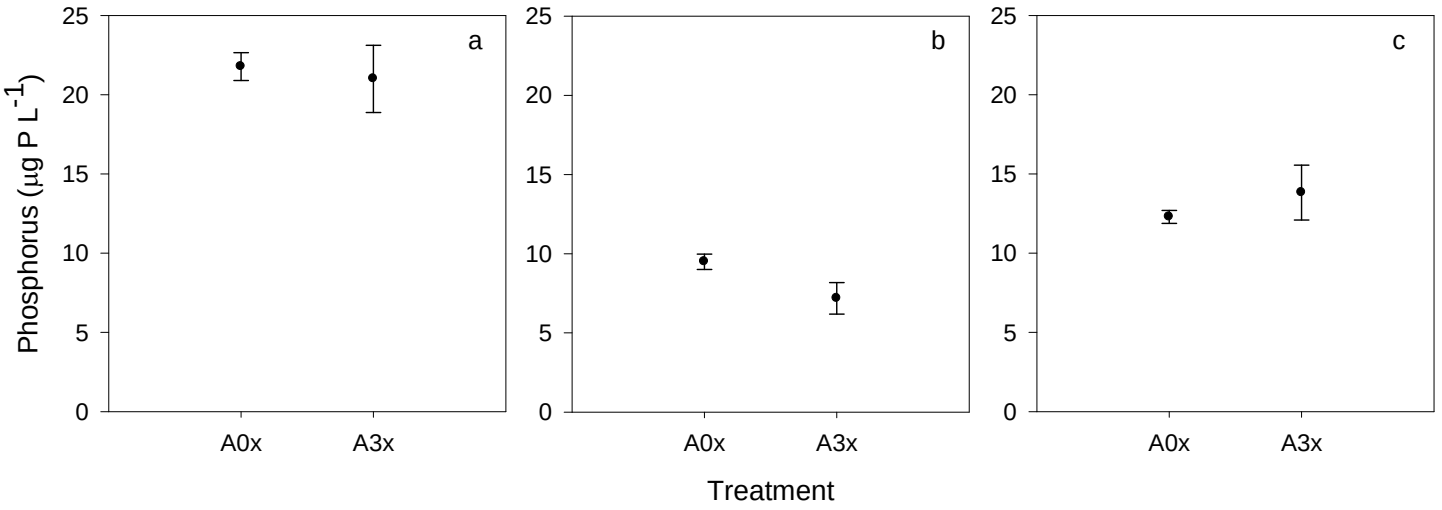

Figure 2.10: Equilibrium concentrations (µg P L^{-1}) of total (a), dissolved (b), and particulate (c) phosphorus; compared between regeneration treatments (A0x, A3x) in *Daphnia*-absent tanks. Error bars show standard error of means; n=3 for each treatment.

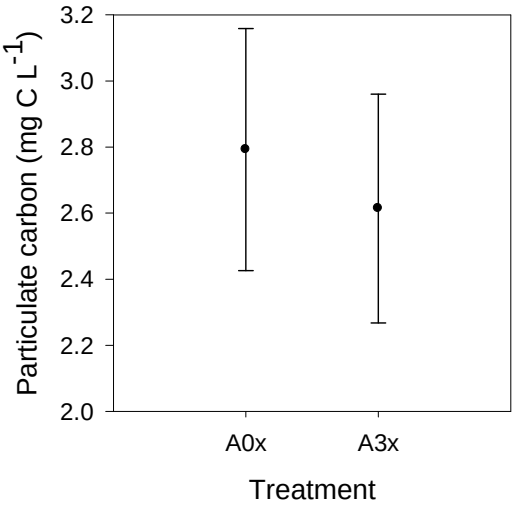

Figure 2.11: Equilibrium particulate carbon concentrations (mg C L^{-1}) compared between regeneration treatments (A0x, A3x) in *Daphnia*-absent tanks. Error bars show standard error of means; n=3 for each treatment.

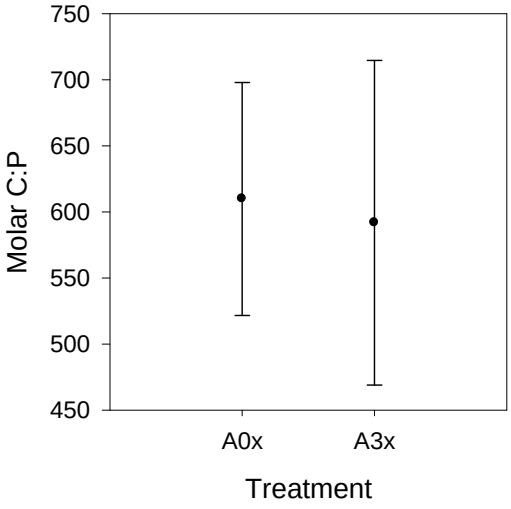

Figure 2.12: Equilibrium seston C:P compared between regeneration treatments (A0x, A3x) in *Daphnia*-absent tanks. Error bars show standard error of means; n=3 for each treatment.

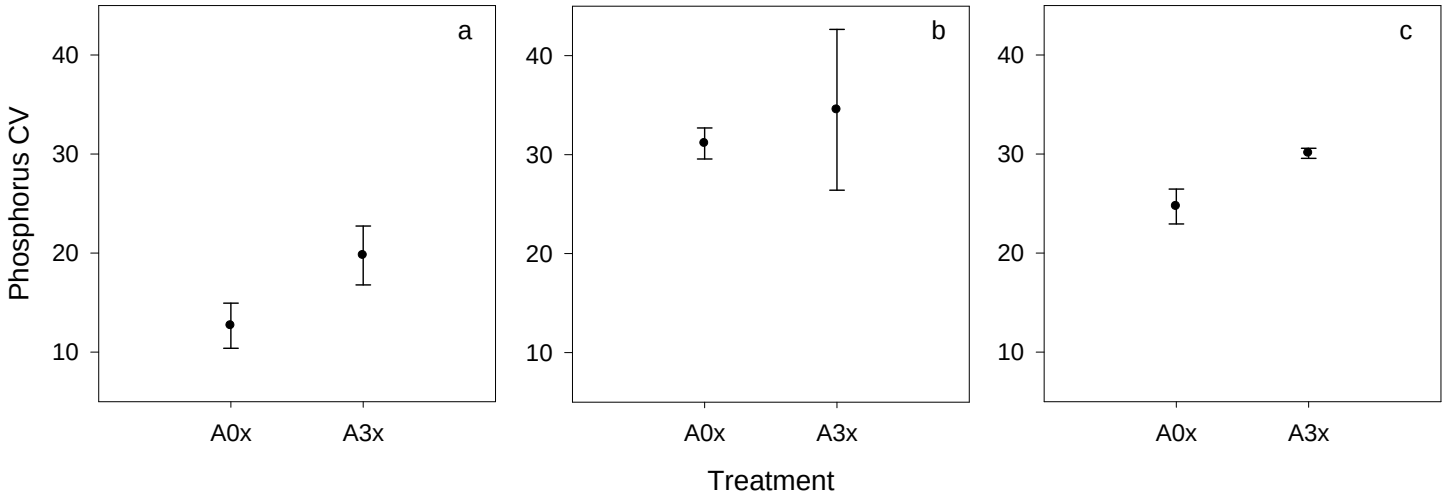

Figure 2.13: Mean coefficient of variation for total (a), dissolved (b), and particulate (c) phosphorus concentrations (µg P L^{-1}) at equilibrium; compared between regeneration treatments (A0x, A3x) in *Daphnia*-absent tanks. Error bars show standard error of means; n=3 for each treatment.

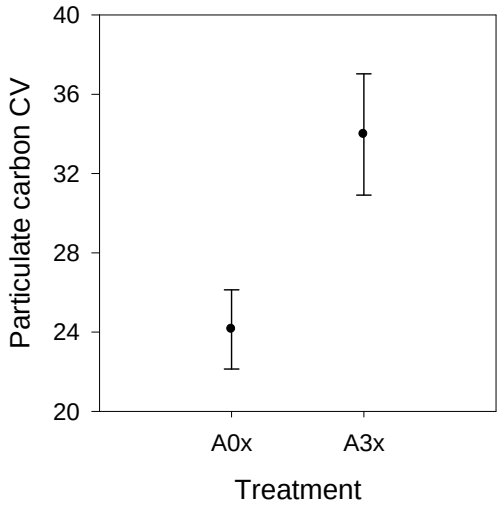

Figure 2.14: Mean coefficient of variation for particulate carbon concentrations (mg C L^{-1}) at equilibrium; compared between regeneration treatments (A0x, A3x) in *Daphnia*-absent tanks. Error bars show standard error of means; n=3 for each treatment.

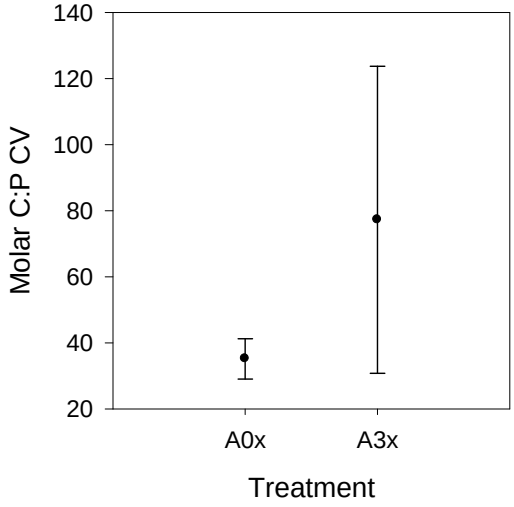

Figure 2.15: Mean coefficient of variation for seston C:P at equilibrium; compared between regeneration treatments (A0x, A3x) in *Daphnia*-absent tanks. Error bars show standard error of means; n=3 for each treatment.

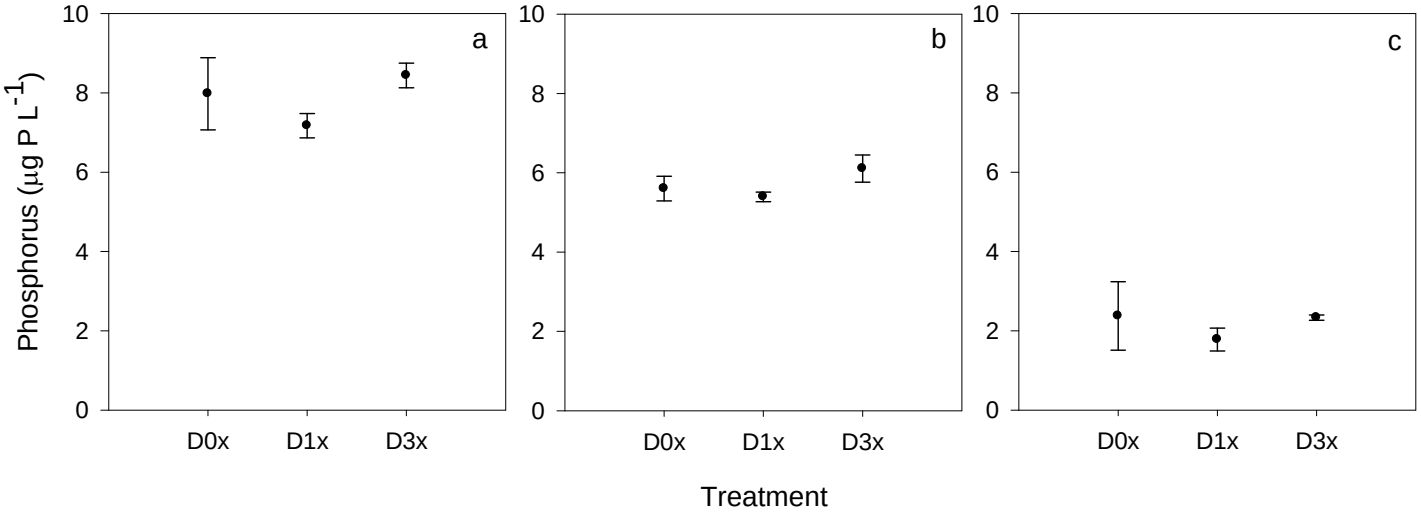

Figure 2.16: Equilibrium concentrations (µg P L^{-1}) of total (a), dissolved (b), and particulate (c) phosphorus; compared among regeneration treatments (D0x, D1x, D3x) in *Daphnia*-present tanks. Error bars show standard error of means; n=3 for each treatment.

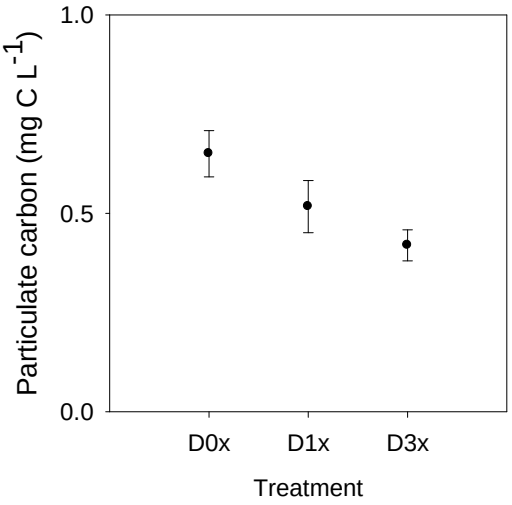

Figure 2.17: Equilibrium concentrations of particulate carbon (mg C L^{-1}) compared among regeneration treatments (D0x, D1x, D3x) in *Daphnia*-present tanks. Error bars show standard error of means; n=3 for each treatment.

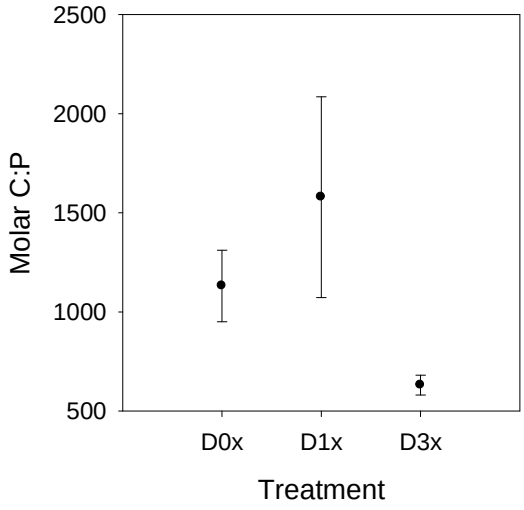

Figure 2.18: Equilibrium seston C:P compared among regeneration treatments (D0x, D1x, D3x) in *Daphnia*-present tanks. Error bars show standard error of means; n=3 for each treatment.

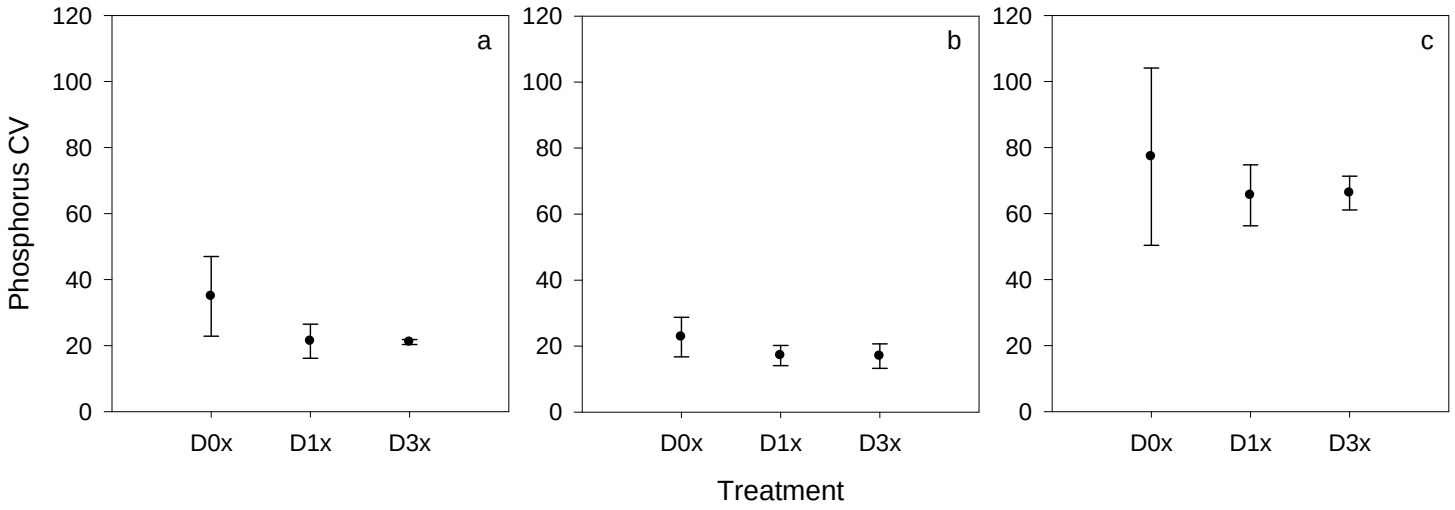

Figure 2.19: Mean coefficient of variation for total (a), dissolved (b), and particulate (c) phosphorus concentrations (µg P L^{-1}) at equilibrium; compared among regeneration treatments (D0x, D1x, D3x) in *Daphnia*-present tanks. Error bars show standard error of means; n=3 for each treatment.

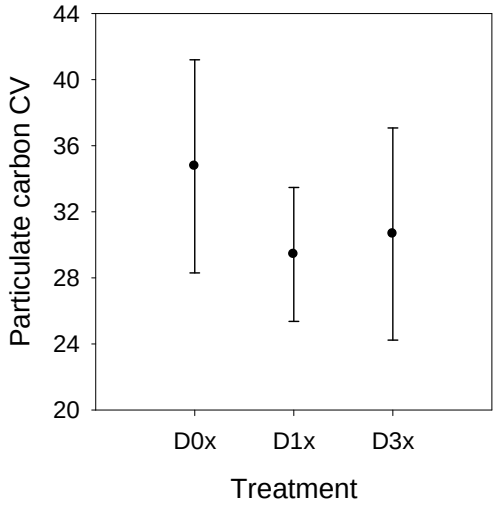

Figure 2.20: Mean coefficient of variation for particulate carbon concentrations (mg C L^{-1}) at equilibrium; compared among regeneration treatments (D0x, D1x, D3x) in *Daphnia*-present tanks. Error bars show standard error of means; n=3 for each treatment.

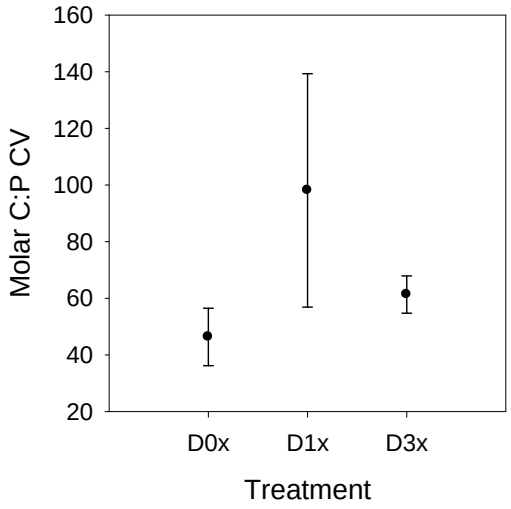

Figure 2.21: Mean coefficient of variation for seston C:P at equilibrium; compared among regeneration treatments (D0x, D1x, D3x) in *Daphnia*-present tanks. Error bars show standard error of means; n=3 for each treatment.

Chapter Three: Testing the predictions of a regeneration model using experimental data

3.1 Introduction

Population dynamics of *Daphnia* and their algal prey have been well studied through the use of experiments and theoretical models. Experiments show this producer-herbivore system can display a wide range of dynamics (Murdoch and McCauley 1985, Grover 1999, McCauley et al. 1999), and much of the theory has been devoted to explaining these dynamics through mathematical models (Gurney et al. 1990, McCauley et al. 1990, McCauley et al. 1996, Sterner 1997). The majority of modelling has focused on the flux of carbon (energy) within the food web, and more recent models that incorporate the flux of a limiting nutrient for growth (such as phosphorus) have been shown to describe the dynamics of natural populations quite well in certain cases (Andersen 1997, Muller et al. 2001, Andersen et al. 2004). However, even with the inclusion of a limiting nutrient many models cannot reconcile the dynamics that occur in natural populations. One explanation for the discrepancy is the omission of a particulate organic matter (POM) pool (consisting mainly of dead organisms) in the system. The microbial processes that occur within this pool (e.g. regeneration of phosphorus to the water column) can have a very pronounced effect on the dynamics of producers and consumers in both natural and model systems (Burns and Schallenberg 1998, Vadstein 2000, Cebrian and Lartigue 2004, Hessen 2006).

The absence of a POM pool in models is analogous to assuming an instantaneous rate of decomposition, which allows the phosphorus contained in dead matter to be

instantaneously available for algae growth. In systems such as this, the coupling between algae and *Daphnia* and the resulting dynamics are based only on per capita rates linked to those two pools. A POM pool adds a potential new dependency for *Daphnia*- algae dynamics. Given that decomposition of POM is the dominant path for regeneration of phosphorus back into the water column, algae growth is now limited by the rate of regeneration. It is possible for the sediments produced from dead organic matter to act as a nutrient "sink" within aquatic producer-herbivore systems (Darchambeau et al. 2005, Cymbola et al. 2008). In a system that is enriched with enough phosphorus to produce unstable dynamics, a low rate of decomposition of dead organic matter allows phosphorus to accumulate in the sediments and effectively lowers the carrying capacity of algae and *Daphnia*. This leads to more stable population dynamics of algae and *Daphnia* than would be expected simply considering the total nutrient mass of the system. In a system with a higher decomposition rate, the availability of phosphorus for algae and *Daphnia* remains higher and provides the potential for unstable dynamics.

The effects of decomposition/regeneration rates on population dynamics are not well known, and have not been well tested experimentally. Several parameters of algae and *Daphnia* growth and loss could potentially be affected by altered regeneration rates. To examine these possible effects, this chapter utilizes the dynamics from the experiment outlined in section 2.2 combined with a mathematical model that takes into account a particulate organic pool linked to the *Daphnia*-algal dynamics. The food web model (see Methods below) consists of two functional groups of algae: 1) edible (< 35µm in diameter; easily grazed by *Daphnia*); 2) inedible (> 35µm in diameter; unable to be grazed by *Daphnia*); the herbivore *Daphnia* pulex (hereafter referred to just as *Daphnia*),

a dead particulate organic pool (POM), and a dissolved nutrient (phosphorus) that is regenerated by microbial processing of the POM pool. Two functional groups of algae are included to match the food web that existed in this same experimental system (McCauley et al. 1988).

The model generated simulations of the population dynamics across four different scenarios: A0x) *Daphnia*-absent low regeneration; A3x) *Daphnia*-absent high regeneration; D0x) *Daphnia*-present low regeneration; D3x) *Daphnia*-present high regeneration. The model simulations yielded the following dynamic and equilibrium predictions, which are consistent with current theory (Nisbet et al. 1991, Norberg and DeAngelis 1997):

A) *Daphnia*-absent scenarios,
    1) Algae equilibrium biomass increases with an increase in P-regeneration;
    2) Edible algae maintains higher equilibrium biomass than inedible algae, provided smaller cells (edible algae) are better competitors for phosphorus;

B) *Daphnia*-present scenarios,
    1) Low regeneration rates produce stable population dynamics for algae and *Daphnia*;
    2) High regeneration rates produce unstable population dynamics (i.e. limit cycles and dampened oscillations) for algae and *Daphnia*.

The food web model was also used to fit the experimental data from Chapter 2 and estimate model parameters under the same four scenarios. Data were used from the 0x and 3x treatments from both *Daphnia*-absent and *Daphnia*–present scenarios from the experiment. The model fits focus on how dynamics from a low natural regeneration rate

(0x) are explained by model parameter values; as well as how the dynamics from a regeneration rate that approximates instantaneous feedback (3x) are explained by model parameter values. The model used continuous time differential equations, and the use of the D1x treatment would introduce a large discrete time component into the model that is not the focus of this analysis; therefore the D1x tanks are not used in the model fitting. The parameter estimates should provide insight into how decomposition rates affect algae and *Daphnia* growth and loss. In the absence of *Daphnia*, these parameters are per capita decomposition rate, and per capita sedimentation rate for both edible and inedible algae. In the presence of *Daphnia*, the same three parameters are fit in addition to the half saturation density for *Daphnia* grazing, assimilation efficiency of *Daphnia*, per capita loss of *Daphnia* biomass, and the interference coefficient exhibited by inedible algae on *Daphnia* grazing. The direct effect of variable decomposition rates on algae and *Daphnia* per capita rates has not been examined before and I attempt to gain insight into a possible mechanism that produces the population dynamics exhibited in both laboratory experiments and nature.

3.2 Methods

3.2.1 Model Description

The model I developed is a system of ordinary differential equations based on several previous models that examine population dynamics within an algae-*Daphnia* system (Nisbet et al. 1991, Norberg and DeAngelis 1997, Murdoch et al. 1998). The conceptual model and associated flow of carbon and phosphorus, is shown in Fig. 3.1.

My model contains four differential equations that describe edible algae biomass (A_E), inedible algae biomass (A_I), *Daphnia* biomass (D), and a detritus pool composed of dead particulate organic matter (*POM*). A dissolved nutrient pool (Q, phosphorus) is described by the difference between total phosphorus in the system and the phosphorus contained in each compartment.

The rate of change of edible algae is described by:

$$\frac{dA_E}{dt} = \left(\mu_E \cdot \frac{Q}{k_E + Q} \cdot A_E \right) - \left(sed_E \cdot A_E \right) - \left(\frac{\mathrm{I}_{\max} \cdot A_E}{A_E + A_{Eh0} + \left(\alpha \cdot \frac{Q_{total}}{q_E} \right)} \cdot D \right) \qquad (3.1)$$

where μ_E is the maximum growth rate of edible algae, k_E is the half saturation constant for phosphorus uptake by edible algae, sed_E is the per capita sedimentation rate of edible algae, I_{max} is the maximum ingestion rate of *Daphnia*, A_{Eh0} is the half saturation density for grazing in the absence of inedible algae , α is the inedible algae interference coefficient that decreases *Daphnia* grazing, Q_{total} is the total amount of phosphorus in the system, and q_E is the ratio of P (mg) to C (mg) for edible algae biomass.

The rate of loss of edible algae from the water column due to *Daphnia* grazing decreases in the presence of inedible algae, as the feeding mechanism of *Daphnia* is interfered with by inedible algae (Webster and Peters 1978, Holm et al. 1983, McCauley et al. 1988, Hawkins and Lampert 1989, Gilbert and Durand 1990). Inedible cells physically prevent individual *Daphnia* from forming a food bolus that is small enough to

be moved into the mandible and effectively increase the handling time of algae. The decreased feeding rate is expressed by an addition to the half saturation density,

$$A_{Eh0} + \left(\alpha \cdot \frac{Q_{total}}{q_E} \right)$$

that increases linearly with algae carrying capacity (Murdoch et al. 1998). The theoretical carrying capacity would occur when all phosphorus is tied up in edible algae biomass and corrected for edible algae P:C (A_E max = Q_{total} / q_E).

The rate of change of inedible algae is described by:

$$\frac{dA_I}{dt} = \left(\mu_I \cdot \frac{Q}{k_I + Q} \cdot A_I \right) - \left(sed_I \cdot A_I \right) \tag{3.2}$$

where μ_I is the maximum growth rate inedible algae, k_I is the half saturation constant for phosphorus uptake of inedible algae, and sed_I is the per capita sedimentation rate of inedible algae.

The rate of change of *Daphnia* biomass is described by:

$$\frac{dD}{dt} = \left(assim \cdot \frac{\mathrm{I}_{\max} \cdot A_E}{A_E + A_{Eh0} + \left(\alpha \cdot \frac{Q_{total}}{q_E} \right)} \cdot D \right) - \left(resp \cdot D \right) - \left(loss \cdot D \right) \tag{3.3}$$

where *assim* is the assimilation efficiency of *Daphnia*, *resp* is the per capita respiration rate of *Daphnia*, and *loss* is the natural per capita rate of mortality for *Daphnia*. *Daphnia* grazing follows a well established Holling type II functional response (DeMott 1982, Nisbet et al. 2004).

The rate of change of particulate organic matter is described by:

$$\frac{dPOM}{dt} = \left(sed_E \cdot A_E\right) + \left(sed_I \cdot A_I\right) + \left(\left(1 - assim\right) \cdot \frac{\mathrm{I}_{\max} \cdot A_E}{A_E + A_{Eh0} + \left(\alpha \cdot \frac{Q_{total}}{q_E} \right)} \cdot D \right) + \left(loss \cdot D\right) - \left(decomp \cdot POM\right) \tag{3.4}$$

where *decomp* is the per capita decomposition rate of *POM*. Faeces and food particles that are rejected by *Daphnia* sink through the water column and join the *POM* pool.

The system is closed to phosphorus and therefore Q_{total} is constant:

$$Q_{total} = (q_E \cdot A_E) + (q_I \cdot A_I) + (q_D \cdot D) + (q_{POM} \cdot POM) + Q \tag{3.5}$$

where q(*i*) is the ratio of P (mg) to C (mg) within inedible biomass (*I*), *Daphnia* biomass (*D*), and particulate organic matter (*POM*). Therefore at any given time the amount of dissolved phosphorus (*Q*) is:

$$Q = Q_{total} - (q_E \cdot A_E) + (q_I \cdot A_I) + (q_D \cdot D) + (q_{POM} \cdot POM) \tag{3.6}$$

The experimental results showed a decline in the total phosphorus available in the system over time, therefore a decreasing function for TP over time was included in the model to imitate the loss of phosphorus (Fig. 3.3):

$$Q_{total} = (0.6) \cdot Q_0 \cdot e^{-(0.05) \cdot t} + (0.4) \cdot Q_0 \cdot e^{-(0.001) \cdot t} \quad (3.7)$$

where Q_0 is the initial concentration of phosphorus in the system, and t is time. Figure 3.2 demonstrates the simulated loss of P from the system.

3.2.2 Predictive simulations

I used the model to simulate an algae and *Daphnia* system using two different decomposition rates: (1) a lower rate (0.05 day^{-1}) that is assumed to approximate the natural rate of decomposition in the experimental reference tanks (Norberg and DeAngelis 1997); (2) a higher decomposition rate (0.175 day^{-1}) that would resemble the effect of artificially increasing the rate of inorganic nutrient regeneration (Chapter 2) to test whether this manipulation decreases the stability of the system as would be expected from theory. The higher rate of 0.175 day^{-1} was calculated by using a 100% decomposition rate on regeneration days and integrating the decomposition rate over the previous days. Under these two different scenarios I expected the model to produce two qualitatively different results for the population dynamics of algae and *Daphnia* (outlined

in the Introduction). The model was used to generate simulations representing both the *Daphnia*-absent and *Daphnia*-present tanks (corresponding to the experimental design from Chapter 2) for a period of 500 days. The duration of the experiment lasted 100 days, but in order to determine if stable equilibrium densities occur over a longer time period 500 days was the duration used in the simulations. I then compared the four outcomes of the model predictions to the experimental dynamics (produced by the methods outlined in Chapter 2). Values for model parameters are listed in Table 3.1.

3.2.3 Fitting of experimental data

I fit the model to the experimental data (Chapter 2) and estimated population parameters using the DDEfit program developed by Wood (2001). My goal was to examine the effect of decomposition rate on several per capita rates within the model.

I first fit my experimental data from the *Daphnia*-absent tanks to estimate parameters from the model for algae. The parameters estimated from the model fitting were: 1) decomposition rate; 2) edible algae sedimentation rate; 3) inedible algae sedimentation rate. I did not fit algal growth parameters (maximum growth rate, and half saturation constant for uptake) because those parameters have been widely tested for this type of model and the values are robust (McCauley et al. 1990, Nisbet et al. 1991, Norberg and DeAngelis 1997). The three parameters were fit using A0x tanks to estimate the average rate of decomposition in reference tanks (where no sediment manipulation occurred). The decomposition rate was then increased to 0.175 to mimic the increased regeneration experienced by A3x tanks. This is a conservative estimate of the effect of regenerating 100% of the sediments accumulated, 3 out of 7 days during

each week. Using the higher decomposition rate, tanks from the A3x treatment were fit to estimate the sedimentation rate of edible and inedible algae.

The experimental data from *Daphnia*-present tanks were fit to estimate the following parameters: 1) decomposition rate; 2) edible algae sedimentation rate; 3) inedible algae sedimentation rate; 4) half saturation density for *Daphnia* grazing; 5) inedible algae grazing interference coefficient; 6) assimilation efficiency of *Daphnia*; 7) death/sedimentation losses for *Daphnia*. The *Daphnia* parameters were limited to these three (4, 6, 7 above) in part to limit the complexity of the fitting, and because the parameters left as constants have well documented values form laboratory tests (Smith and Kalff 1982, Bohrer and Lampert 1988). The parameters were first fit using the D0x tanks to estimate the average rate of decomposition in reference tanks. The D3x tanks were then fit using the average decomposition rate increased by 0.125 to estimate the remaining six parameters. Values for model parameters are listed in Table 3.1.

3.3 Results

3.3.1 Model predictions on the effect of increased regeneration

In the absence of *Daphnia* at a low decomposition rate, edible algae biomass dominates the system while inedible algae biomass decreases to zero (Fig. 3.3 top panel). When the decomposition rate is increased, edible algae exhibit greater biomass while inedible algae biomass decreases to zero (Fig. 3.3 bottom panel). However, with higher decomposition inedible algae maintain biomass greater than zero for a longer period.

In the presence of *Daphnia* at a low decomposition rate, edible algae still maintain a higher biomass than inedible algae, however inedible biomass persists. *Daphnia* maintain a relatively low biomass, and all three pools remain relatively stable over time (Fig. 3.4 top panel). With a higher decomposition rate all three pools become unstable, exhibiting large fluctuations that appear to dampen over time (Fig. 3.4 bottom panel). On average, inedible biomass is maintained at a greater level than edible biomass.

3.3.2 Comparison between predicted and experimental dynamics

In the absence of *Daphnia* at a low rate of decomposition, the pattern of edible and inedible algae biomass is consistent between the simulation and experimental results; edible biomass remains higher than inedible biomass over time (Fig. 3.3 top panel and Fig. 3.5 data points). Experimentally increasing the decomposition rate of POM did not increase the biomass of edible algae as predicted by the simulations (Fig. 3.3 bottom panel and Fig. 3.6 data points), however edible biomass was maintained a higher level than inedible biomass (Fig. 3.6 data points).

In the presence of *Daphnia* at a low rate of decomposition, the simulation predicts higher edible algae biomass compared to inedible biomass over the duration of the time series (Fig. 3.4 top panel). However, near the midpoint of the experiment inedible biomass quickly increases above edible biomass and remains higher until the end of the experiment (Fig. 3.7 data points). The simulation predicts a relatively low *Daphnia* biomass compared to edible algae biomass (Fig. 3.4 top panel), where as the experimental tanks show *Daphnia* biomass is maintained at a relatively high level compared to edible algae biomass (Fig. 3.7). Increasing the rate of decomposition in the simulation leads to

unstable dynamics for algae and *Daphnia* (Fig. 3.4 bottom panel). In contrast, experimentally increasing the rate of decomposition does not lead to relatively more unstable dynamics (Fig. 3.8 data points). Specifically, both edible and inedible biomass appears more stable.

3.3.3 Model fitting and parameter estimates

In the absence of *Daphnia*, the sedimentation rate for both edible and inedible algae increases with an increase in the decomposition rate (Table 3.2). At both rates of decomposition the average sedimentation rate of edible algae is higher than that of inedible algae. The decomposition rate estimated by the fits is about equal to the estimated rate used in the model simulations (Table 3.2 and Table 3.1 respectively).

Similarly in the presence of *Daphnia*, the sedimentation rate for both edible and inedible algae increases with an increase in the decomposition rate (Table 3.3). Again, at both rates of decomposition the average sedimentation rate of edible algae is higher than that of inedible algae. The presence of *Daphnia* also has the effect of decreasing sedimentation rates of algae when compared to the same treatment without *Daphnia*. Very little change is seen in parameters for *Daphnia* growth and loss (A_{Eh0}, *assim*, *loss*) (Table 3.3). Only one tank from either decomposition treatment showed any change in the half saturation density for grazing (A_{Eh0}) and the average is about the same (Table 3.3). One tank from the low decomposition treatment showed a decrease in assimilation efficiency (*assim*); however the averages between treatments are comparable in magnitude (Table 3.3). The loss rate of *Daphnia* biomass to the POM pool (*loss*) remained the same for all tanks between treatments (Table 3.3). The magnitude of

grazing interference from inedible algae (α) increased with an increase in the decomposition rate of POM (Table 3.3).

3.4 Discussion

3.4.1 Model simulations

Increasing the decomposition rate of POM in my model produces the same qualitative change in dynamics as existing models that incorporate a POM pool and decomposition (Nisbet et al. 1991, Norberg and DeAngelis 1997). At a higher decomposition rate, edible algae exhibit a higher equilibrium biomass in the absence of *Daphnia*. In the presence of *Daphnia*, a higher decomposition rate produces oscillations of both algae and *Daphnia* biomass around equilibrium, as opposed to stable abundances at a lower decomposition rate. In the absence of a POM, nutrients are instantaneously available from dead biomass and producers are able to quickly uptake the nutrients and produce biomass faster than herbivores can suppress the growth, commonly known as prey escape. In the presence of POM, higher decomposition rates can still provide dissolved nutrients fast enough to support prey escape. However, at lower decomposition rates, POM begins to act as a nutrient "sink" preventing the occurrence of prey escape as herbivores are able to suppress the producer population while maintaining a stable biomass.

3.4.2 Model fitting

The main effect of increasing the decomposition rate on the parameters in the system was an increase in the per capita sedimentation rate of both edible and inedible algae. The effect was consistent in both the absence and presence of *Daphnia*, yielding a higher average sedimentation rate for edible biomass compared to inedible biomass for all four scenarios. *Daphnia* model parameters estimated by fitting do not exhibit large differences between regeneration treatments. Both parameters for growth were estimated at values that contribute to a higher population growth rate for *Daphnia*. The half saturation density for *Daphnia* grazing (A_{Eh0}) remained low and the assimilation efficiency (*assim*) remained high. *Daphnia* death and sedimentation (*loss*) remained very low, which also allows higher population growth. The model assumes that maximum growth rate and nutrient uptake are higher for edible algae relative to inedible algae and those parameters remain constant in the model. This relative difference in per capita growth may contribute to the higher per capita sedimentation experienced by edible algae in all four scenarios. Higher per capita sedimentation of edible algae could be a result of the model compensating for higher per capita growth of edible algae. Increasing phosphorus regeneration should lead to higher production of edible biomass, but the model fits reveal a compensatory increase in the rate of loss of edible algae to balance the higher growth rate and results in the lower edible biomass. Several studies have described the increasing relationship of sedimentation with nutrient enrichment (Larocque et al. 1996, Flanagan et al. 2006), and also explain decreases in sedimentation in the presence of *Daphnia* (Larocque et al. 1996, Sarnelle 1999, Flanagan et al. 2006). It is thought that enrichment increases sedimentation through increases in algal size and

density, thereby increasing the sinking velocity of cells (Elser et al. 1995b, Larocque et al. 1996); and may also increase the death of cells by increasing the effects of self-shading through production of more biomass near the water surface (Huisman 1999, Huisman et al. 1999a, Huisman et al. 1999b). Additional results from the current experiment (not shown) indicate a higher weekly sedimentation rate (in terms of carbon and phosphorus) in the D3x tanks compared to the D1x tanks, demonstrating on average, a higher sedimentation rate with increased regeneration.

The model shows an increase in the grazing interference exhibited by inedible algae (α) in the presence of regeneration, which agrees with the observed increase in inedible biomass with regeneration. As *Daphnia* exert grazing pressure on edible algae, more phosphorus is diverted to inedible biomass (McCauley et al. 1988, Watson and McCauley 1988, Watson et al. 1992) and it increases the relative interference with *Daphnia* grazing (Hawkins and Lampert 1989, Gilbert and Durand 1990). Values for *Daphnia* feeding (A_{Eh0}), assimilation efficiency (*assim*), and death (*loss*) all contribute to higher net growth for *Daphnia*. These values are needed to compensate for very high sedimentation rates of edible algae that do not support high *Daphnia* biomass. However, the parameters are at quite extreme values compared to estimates provided by other studies (Paloheimo et al. 1982, Bohrer and Lampert 1988, Nisbet et al. 1989). It is possible that low algal biomass is not solely a result of high per capita sedimentation, and the biomass of *Daphnia* in the experiment is not simply a result of extreme parameter values. Two possible mechanisms can explain the low algal biomass experienced with regeneration, and the *Daphnia* biomass from the experiments: 1) bacterial growth

stimulated by the availability of phosphorus; and 2) food quality effects on the growth of *Daphnia*.

Stimulated bacterial growth may increase competition with algae and effectively lower algal biomass, which is manifested as increased per capita sedimentation in the model. Bacterial growth is in part fuelled by the release of dissolved organic carbon (DOC) by algae and it is possible that with an increase in phosphorus availability due to high regeneration rates, bacteria may out-compete algae for phosphorus. There is evidence that bacteria are better competitors for phosphorus than algae (Currie and Kalff 1984a, 1984b, Danger et al. 2007) and nutrient regeneration can stimulate bacterial growth given the available carbon source from algae (Chrzanowski et al. 1995, Olsen et al. 2002). Higher bacterial production could also support the higher *Daphnia* biomass exhibited under regeneration by providing an alternate food source for *Daphnia* (Hessen and Andersen 1990, Kamjunke et al. 1999). *Daphnia* are able to graze bacteria in both the water column and the sediments, which provide them with an alternate carbon source when algae are limiting. *Daphnia* populations in tanks without regeneration are also feeding on the bacteria and sediments, but the absence of regeneration likely lowers the food quality of this source.

Given that food quality is determined by C:P content, the lack of regeneration likely exhibits decreases in food quality (decreased C:P). Without regeneration, P becomes limiting and the C:P of algae increases. *Daphnia* are therefore food quality limited and under P-limitation tend to sequester P (Darchambeau et al. 2003, Darchambeau 2005). The sequestration of P causes a positive feedback through the food web whereby the C:P content of organisms remains low (Darchambeau et al. 2005).

Heterotrophic bacteria show a need for a low C:P of POM, which is due to the low C:P requirements for bacterial growth (Elser et al. 1995a). Therefore, the low availability of P in POM also causes bacteria to sequester P, but because of such a large presence of available carbon the C:P of bacteria likely increases. *Daphnia* are therefore limited by high C:P in both algae and bacteria in the absence of regeneration.

Conversely, food quality is likely higher in the presence of regeneration. Increased P-availability lowers the C:P of algae and allows higher *Daphnia* growth, but may also result in higher fluxes of P through the food web. Increases in algal food quality can result in increased P-excretion by *Daphnia* (Olsen et al. 1986). Increased excretion is a result of the limits by which *Daphnia* can utilize P to produce more biomass; i.e. if the biological machinery of *Daphnia* can only use so much P in a given time then the excess P is excreted or lost in feces. Lower algal C:P was recorded during the experiment for D3x tanks (section 2.3), and this difference could result in higher P-excretion and loss from feces compared to D0x tanks. The recycling of phosphorus from *Daphnia* then provides algae and bacteria with more P for growth. The availability of phosphorus above some threshold concentration in this system could maintain a positive feedback for high food quality, whereby the retention time of phosphorus in each compartment of the food web is relatively low and thus on average phosphorus is not limiting to any one compartment.

3.4.3 Conclusions

The model resulted in dynamics similar to those of existing theory. Increased decomposition/regeneration produced an increase in algal biomass in the absence of

Daphnia, and produced unstable dynamics in the presence of *Daphnia*. Interestingly, the dynamics of the experimental system show the opposite response. Stability of the *Daphnia*-algae system increases when regeneration is increased (also see Chapter 2). The increase in stability may be a result of regeneration not only increasing rates of growth of algae, but also stimulating an increase in the per capita sedimentation of algae. The model uses the availability of phosphorus to determine algal growth, but rates for *Daphnia* growth and POM decomposition are governed only by the availability of carbon in the model. Such extreme values produced by the model fits suggest that carbon limitation (food quantity) is not the only factor affecting *Daphnia* growth, and evidence suggests that food quality (C:P) plays a role. Modelling *Daphnia* growth and POM decomposition as a function of C:P would result in a more mechanistic dependence on phosphorus availability in the model.

Several models have used food quantity and quality to describe the population dynamics of producer-herbivore systems and yield consistent results with experiments and field observations (Muller et al. 2001, Andersen et al. 2004, Kooijman et al. 2004). However the inclusion of a microbial loop (POM and decomposition) that is also dependent on the ratio of carbon and phosphorus is currently lacking. A large body of evidence points to the dependence of microbial process on the nutrient content of POM and also shows that microbial processes are tightly linked to the aquatic food web in the water column. It should therefore be beneficial to examine the affects of material cycling through all of these compartments to better understand the dynamics of aquatic producers and herbivores.

Table 3.1: Model parameters and their values, used for the predictive simulation and empirical data fitting. A fitting value of "estimated" indicates a parameter that was estimated by the model fitting, other values are constants.

Parameter	Description	Units	Simulation Value	Fitting Value	Reference
μ_E	Edible algae maximum growth rate	day^{-1}	1.0	1.0	Smith and Kalff 1982
μ_I	Inedible algae maximum growth rate	day^{-1}	0.8	0.8	Smith and Kalff 1982
k_E	Edible algae half saturation density for phosphorus uptake	mg P L^{-1}	0.0068	0.0068	Smith and Kalff 1982
k_I	Inedible algae half saturation density for phosphorus uptake	mg P L^{-1}	0.0085	0.0085	Smith and Kalff 1982
sed_E	Edible algae per capita sedimentation rate	day^{-1}		estimated	No reference
sed_I	Inedible algae per capita sedimentation rate	day^{-1}		estimated	No reference
I_{max}	Maximum intake rate of edible algae by *Daphnia*	day^{-1}	1.0	1.0	Nisbet et al. 1991
A_{Eh0}	Half saturation density for *Daphnia* grazing	mg C L^{-1}	0.16	estimated	Nisbet et al. 1991
α	Inedible algae grazing interference coefficient	dimensionless 0.1 0.1	0.56	estimated	Murdoch et al. 1998
Q_{total}	Total phosphorus in the system	mg P L^{-1}	0.05	0.05	Experimental concentration
assim	Assimilation efficiency of *Daphnia*	dimensionless	0.8	estimated	Nisbet et al. 1991
resp	Per capita respiration losses for *Daphnia*	$^{-1}$	0.12	0.09	Nisbet et al. 1991
loss	Per capita death/sedimentation losses for *Daphnia*	$^{-1}$	0.03	estimated	Nisbet et al. 1991
decomp	Per capita decomposition rate of POM	day^{-1}	0.05, 0.175	estimated	Norberg and DeAngelis 1997
q_E, q_I, q_Z, q_{POM}	P:C of each pool	day day	mg P mg C^{-1}	0.015	0.015	Andersen and Hessen 1991

Table 3.2: Parameter estimates from the model fits of *Daphnia*-absent tanks.

Treatment	Tank	*decomp* (day^{-1})	sed_E (day^{-1})	sed_I (day^{-1})
Zero regeneration (reference tanks)	A0x1	0.056	0.360964	0.258018
	A0x2	0.0435	0.301289	0.215952
	A0x3	.0699	0.479103	0.33331
	Average	0.056467	0.380452	0.269093
Regenerated three times per week	A3x1	N/A:	0.69596	0.504464
	A3x2	fixed as	0.660924	0.506741
	A3x3	constant	0.63309	0.479522
	Average	(0.181467)	0.663325	0.496909

Table 3.3: Parameter estimates from the model fits of *Daphnia*-present tanks.

Treatment	Tank	*decomp* (day^{-1})	sed_E (day^{-1})	sed_I (day^{-1})	A_{Eh0} (mg C L^{-1})	*assim* (dimensionless)	*loss* (day^{-1})	*A* (dimensionless)
Zero regeneration (reference tanks)	D0x1	0.12269	0.387875	0.226021	0.168951	1	0.001	0.330642
	D0x2	0.147359	0.302566	0.362283	0.08	1	0.001	0.455624
	D0x3	0.280741	0.432873	0.350997	0.08	0.733181	0.001	0.0884
	Average	0.183597	0.374438	0.3131	0.10965	0.91106	0.001	0.291555
Regenerated three times per week	D3x1	N/A:	0.457954	0.429519	0.08	1	0.001	0.481026
	D3x2	fixed as	0.396043	0.4502	0.213225	1	0.001	0.358179
	D3x3	constant	0.596543	0.468429	0.08	1	0.001	0.506946
	Average	(0.308597)	0.483513	0.449383	0.124408	1	0.001	0.448717

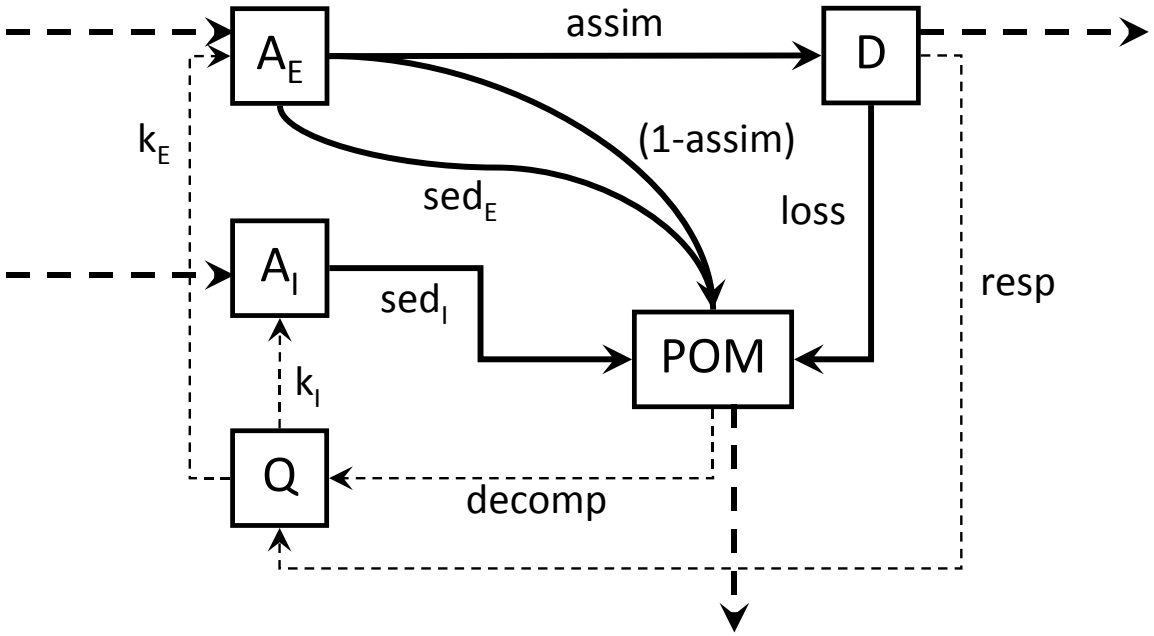

Figure 3.1: Conceptual schematic demonstrating the flow of carbon and phosphorus in the model. Where *Q* = dissolved phosphorus, A_E = edible algae, A_I=inedible algae, *D*=*Daphnia*, *POM*=particulate organic matter, k_E = half saturation constant for phosphorus uptake by edible algae, sed_E = per capita sedimentation rate of edible algae, k_I = half saturation constant for phosphorus uptake by inedible algae, sed_I = per capita sedimentation rate of inedible algae, *assim* = assimilation efficiency of *Daphnia*, (1-*assim*) = faeces from *Daphnia*, *resp* = respiration rate of *Daphnia*, *loss* = natural rate of mortality for *Daphnia*, *decomp* = per capita decomposition rate of POM. Solid bold lines indicate flow of both carbon and phosphorus, dashed bold lines indicate flow of carbon only, and small dashed lines indicated flow of phosphorus only.

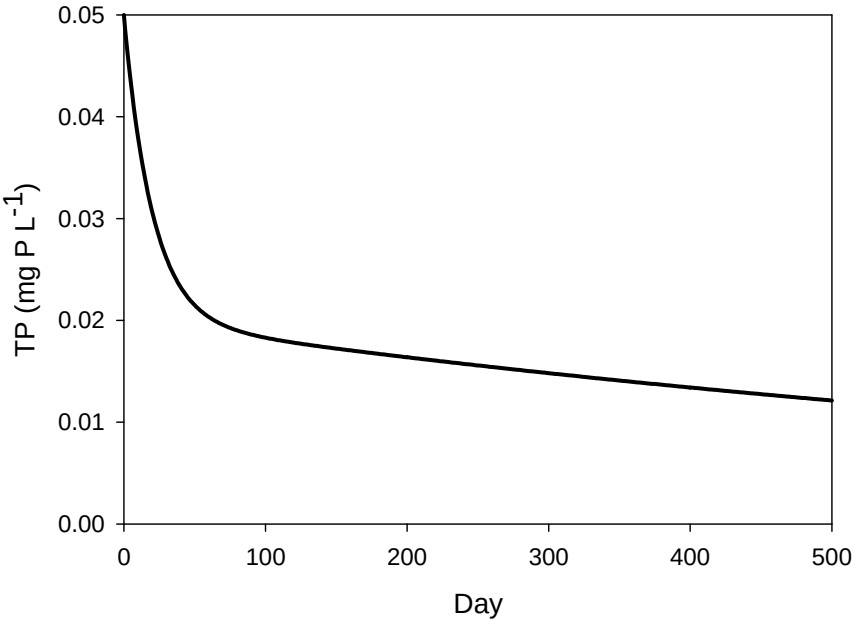

Figure 3.2: Simulated decrease in the total phosphorus (mg P L^{-1}) of the system over time.

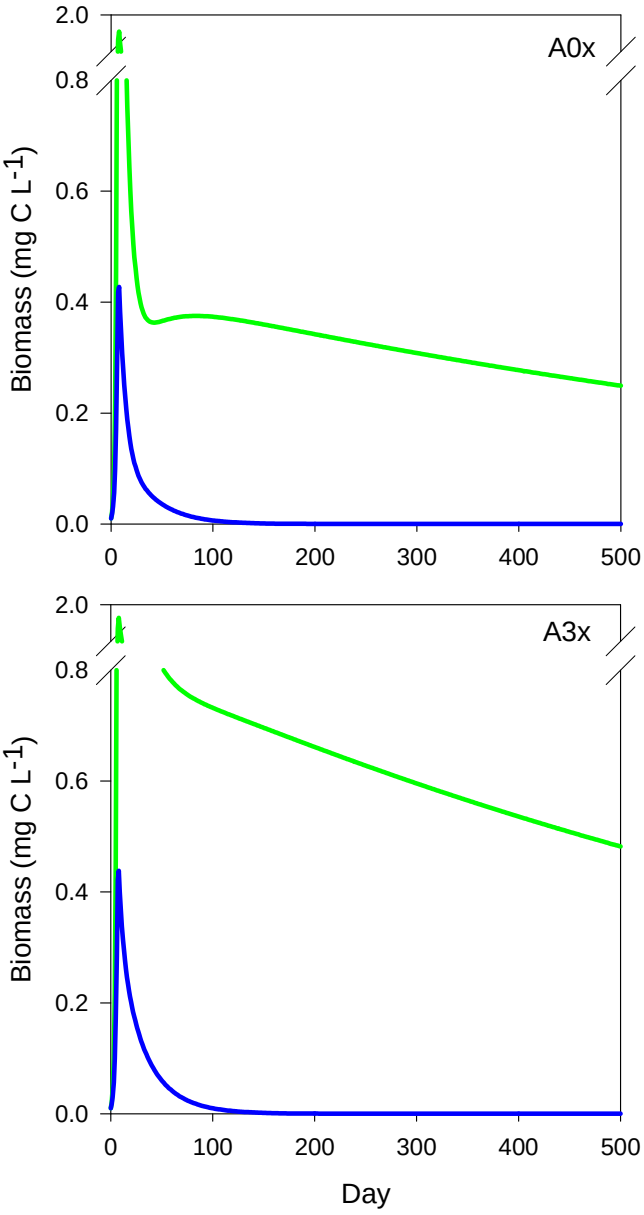

Figure 3.3: Model simulations of algae biomass (mg C L^{-1}) in *Daphnia*-absent tanks at low (0x, top panel) and high (3x, bottom panel) decomposition rates. Green line is edible biomass and blue line is inedible biomass.

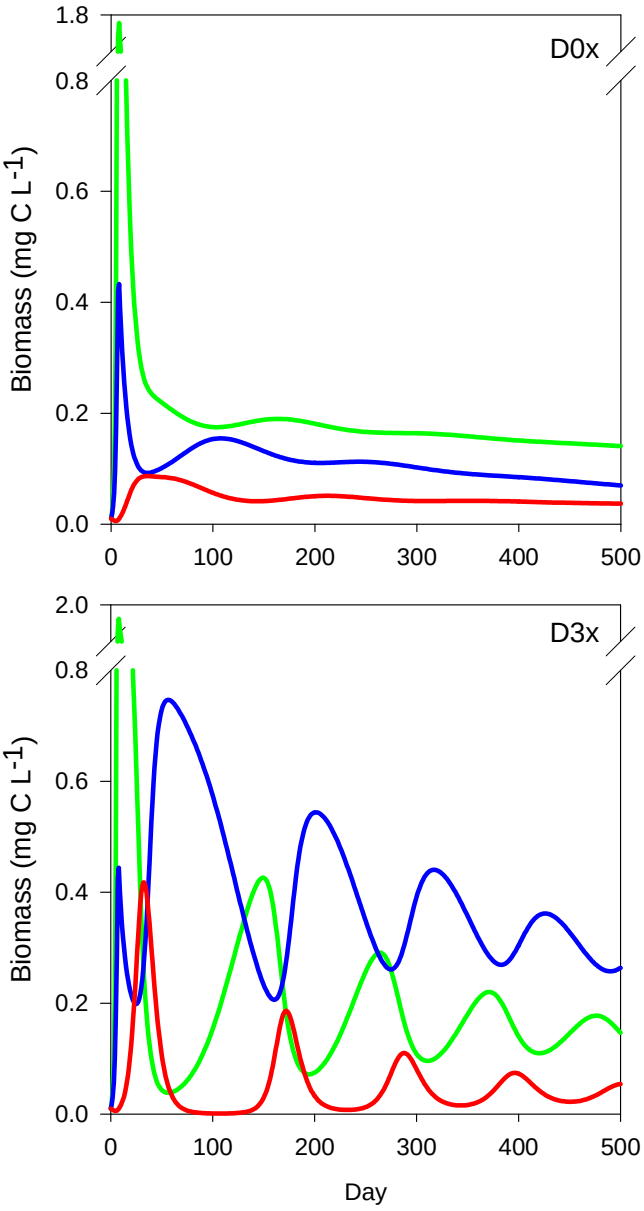

Figure 3.4: Model simulations of algae and *Daphnia* biomass (mg C L^{-1}) in *Daphnia*-present tanks at low (0x, top panel) and high (3x, bottom panel) decomposition rates. Green line is edible biomass, blue line is inedible biomass, and red line is *Daphnia* biomass.

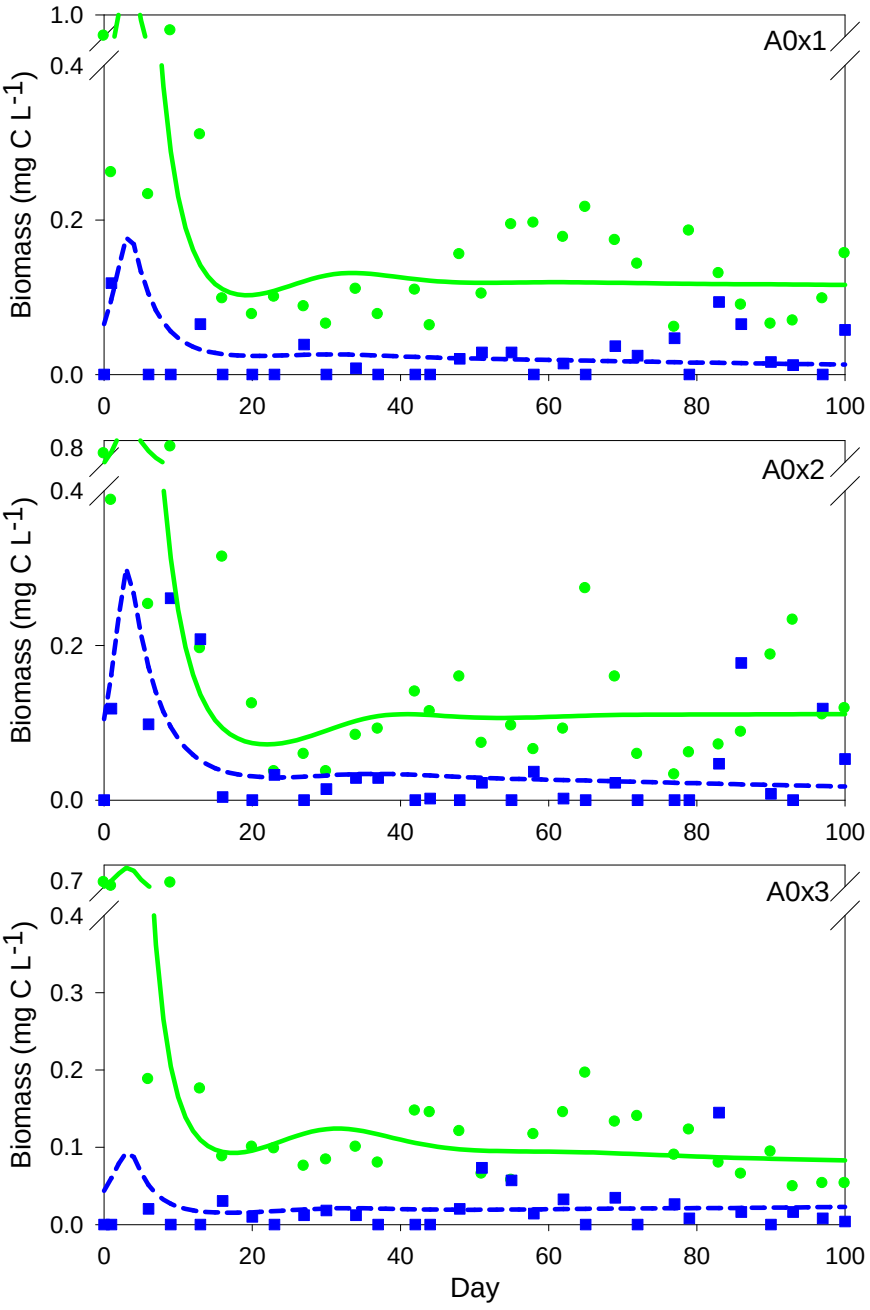

Figure 3.5: Experimental biomass (mg C L^{-1}) of edible (green circles) and inedible (blue squares) algae; and model fits of edible (green solid line) and inedible (blue dashed line) algae in *Daphnia*-absent low regeneration (A0x) tanks.

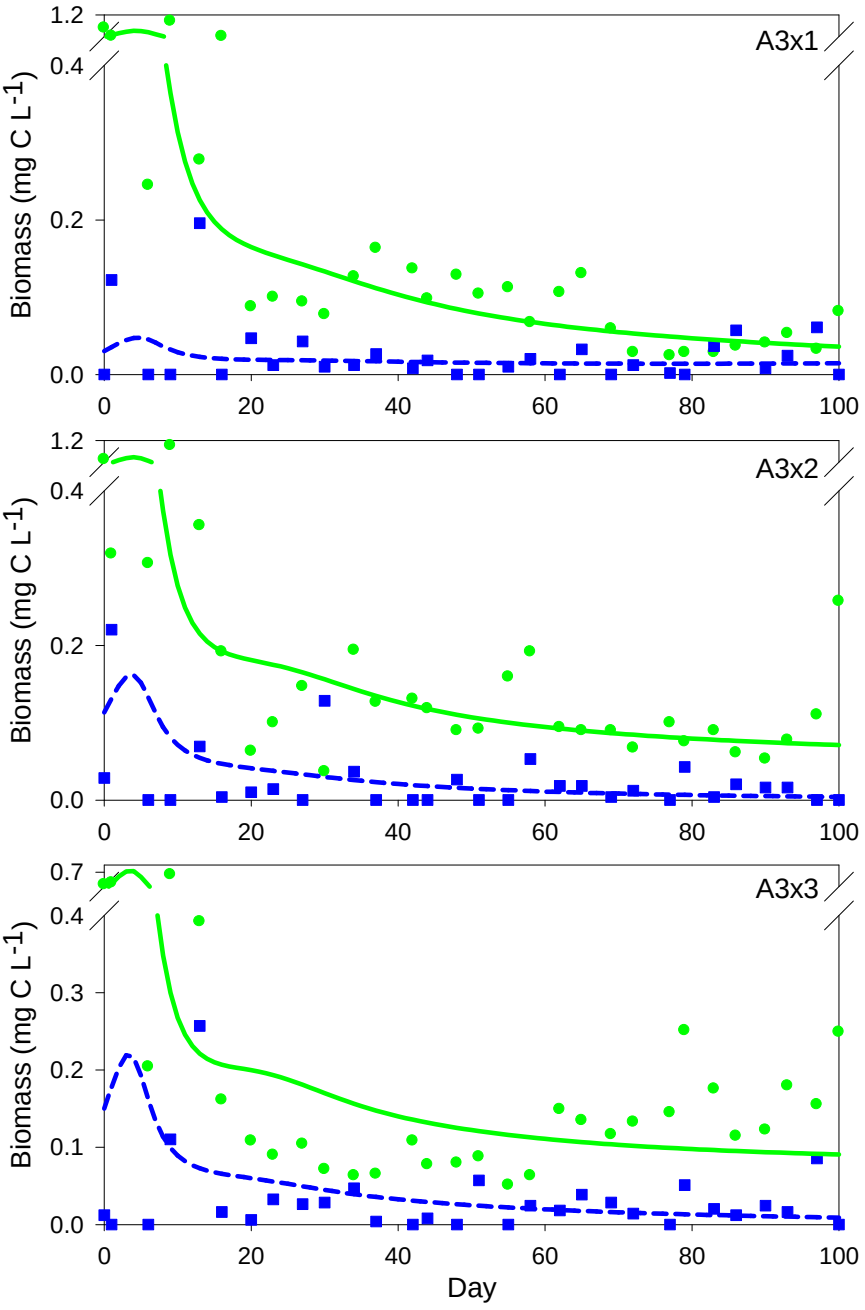

Figure 3.6: Experimental biomass (mg C L^{-1}) of edible (green circles) and inedible (blue squares) algae; and model fits of edible (green solid line) and inedible (blue dashed line) algae in *Daphnia*-absent high regeneration (A3x) tanks.

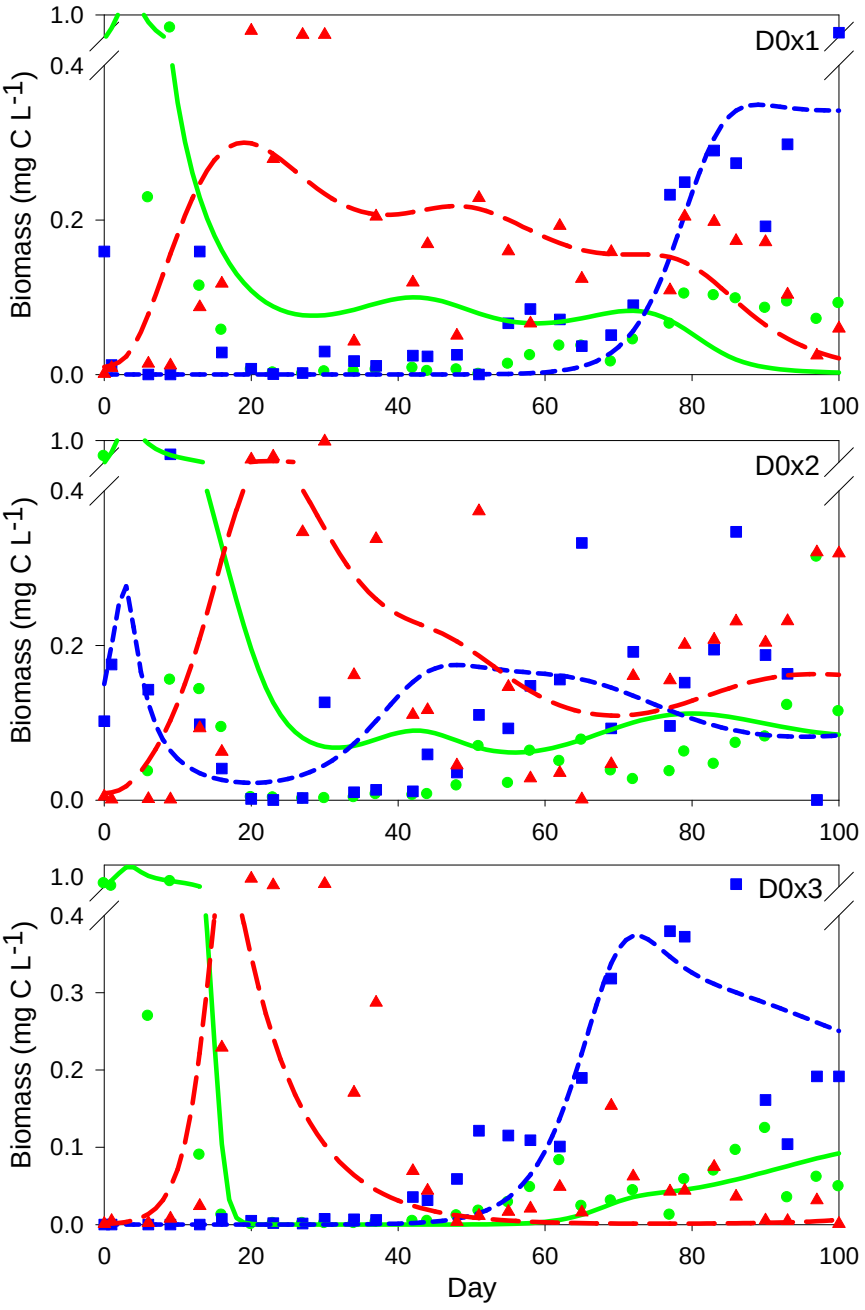

Figure 3.7: Experimental biomass (mg C L^{-1}) of edible (green circles) and inedible (blue squares) algae, and *Daphnia* (red triangles); and model fits of edible (green solid line) and inedible (blue medium dash line) algae, and *Daphnia* (red long dash line) in low regeneration (D0x) tanks.

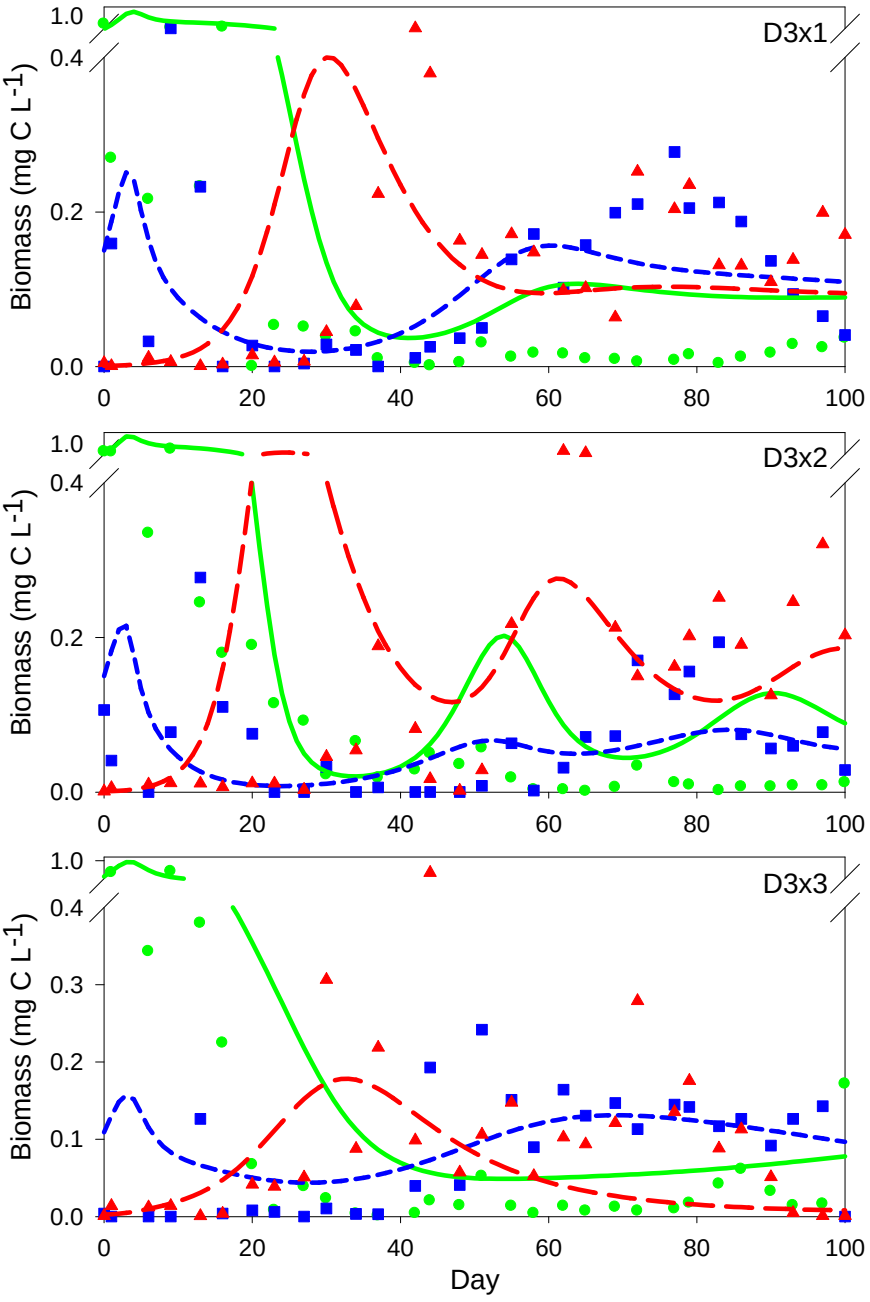

Figure 3.8: Experimental biomass (mg C L^{-1}) of edible (green circles) and inedible (blue squares) algae, and *Daphnia* (red triangles); and model fits of edible (green solid line) and inedible (blue medium dash line) algae, and *Daphnia* (red long dash line) in high regeneration (D3x) tanks.

Chapter Four: Conclusions

This thesis examines the link between phosphorus regeneration from sediments and the population dynamics of algae and *Daphnia*. It is one of the first experimental tests of this link and further extends our understanding of shallow aquatic systems using simple food webs that control for vertebrate and invertebrate predators and external nutrient loading. Although nutrient cycling has been well studied in freshwater systems (Wetzel 2001), the complex feedbacks that are modified by processes such as regeneration and the dynamic responses of organisms are not well understood. Theory and models that attempt to describe these systems have advanced in both complexity and understanding (McCauley et al. 1988, McCauley et al. 1996, Muller et al. 2001, Andersen et al. 2004, Kooijman et al. 2004), and have allowed for the formation of novel research questions. However, without testing new models with experimental data the direction of future research may not recognize important mechanisms.

The experimental results demonstrated that increased regeneration can produce higher *Daphnia* biomass, and the population dynamics were more stable. Possible mechanisms leading to this result include the diversion of phosphorus away from the edible algae-*Daphnia* interaction into inedible algae and bacteria, as well as food quality effects on *Daphnia* growth. Another mechanism could be a mismatch in parameter values for growth and loss processes between laboratory and mesocosm experiments. The constants used in the current model have been estimated by laboratory experiments under strict control of environmental variables such as temperature and light. However, in mesocosm experiments such as the one in this thesis, environmental variables fluctuate naturally (although fluctuations are consistent among mesocosms from all treatments).

These fluctuations could produce variations in the parameter values used in the model (e.g. uptake constants of phosphorus, maximum growth rates); and could lead to the absence of large amplitude cycles predicted by the model simulations. However, even if changes in parameter values move the system away from cycles, the relative increase in regeneration is still predicted to produce larger oscillations in biomass (decreased stability).

The grazing pressure of the *Daphnia* population on edible algae can produce a shift in the algae community to a higher proportion of inedible algae, due to a decrease in the competitive advantage of edible algae for nutrients (McCauley et al. 1988, Watson and McCauley 1988, Watson et al. 1992). Although this shift lowers the absolute amount of edible algae for *Daphnia*, the increased regeneration may promote increased bacterial growth. The presence of a larger bacterial pool can act as an alternate food source for *Daphnia* (Hessen and Andersen 1990, Kamjunke et al. 1999), buffering the population from large fluctuations during times of carbon limitation due to low biomass of edible algae.

A shift in food quality is another possible mechanism for the increase in stability observed with increased regeneration. High food quality arises when the C:P of edible algae and bacteria is low (Elser et al. 2000). This lower C:P of *Daphnia* food particles can contribute to increased per capita growth rates, which could produce higher *Daphnia* biomass in the presence of regeneration. As phosphorus availability increases, positive feedbacks can increase the flux of phosphorus through each compartment of the food web and maintain a lower C:P (Darchambeau et al. 2005). An alternate food source from

bacteria combined with possible changes in food quality for *Daphnia*, could contribute to increases in biomass and stability with increased regeneration.

A simple model that incorporated a particulate organic matter pool (POM) into a *Daphnia*-algal system was used to fit the experimental data in order to explain the effect of regeneration through differences in parameter estimates of the per capita rates. For both *Daphnia*-absent and *Daphnia*-present treatments, increases in regeneration were compensated by increases in the per capita sedimentation rate of both edible and inedible algae. This result follows similar patterns that arise from increases in nutrient enrichment leading to increases in sedimentation (Larocque et al. 1996, Sarnelle 1999). Increases in sedimentation arise from greater algal cell mass and can result in the emergence of light as the limiting factor for growth (as opposed to phosphorus). However, edible algae per capita sedimentation should be lower than inedible algae per capita sedimentation and estimates of parameter values appeared to be rather extreme for a *Daphnia*-algal system. Given that the model assumes only carbon (energy) limits *Daphnia* growth, those parameter values could be explained by factors other than carbon limitation. The mechanisms were raised in response to the experimental results, and also hold true in light of the modelling results. These mechanisms were the emergence of bacteria as an alternate food source for *Daphnia*, and the presence of food quality effects through the food web.

This thesis highlights the need to test model predictions with experimental data in order to guide the development of model structure. Discrepancies between empirical data and model predictions can often be explained by experimental evidence that already exists. For example, the incorporation of element ratios into population models has

produced interesting results that may explain some of the dynamics experienced by *Daphnia*-algal systems (Sterner 1997, Andersen et al. 2004). These results include an increase in stability at high levels of enrichment and conditions that result in the deterministic extinction of *Daphnia* populations. These effects are manifested through growth limitations on algae and food quality limitations on *Daphnia* as a function of element ratios. Recent models have also begun to look at the simultaneous limitation of multiple elements, such as carbon, phosphorus, and nitrogen, on producer-herbivore dynamics (Muller et al. 2001, Kooijman et al. 2004). These models provide a mechanistic framework based on physiology that contributes to the understanding of energy and nutrient process within biological systems. The combined effects of a POM pool and food quality have recently been investigated (Perhar and Arhonditsis 2009), and the results show that increased food quality allows higher *Daphnia* biomass which suppresses edible algae to lower levels. The stability of the system also changes whereby populations are more resistant to enrichment, and large fluctuations in abundances are avoided. This stability arises by incorporating food quality effects into the detritus pool (bacteria and POM), which is modelled as an alternate food source for *Daphnia*. We should be mindful however; that including the effects of such things as element ratios into model structure should not be for the sole reason of adding complexity to mimic complex systems, but to introduce physiological mechanisms that underpin growth and loss processes. It should be a goal of theoretical models to explain specific systems with physiological mechanisms, but retain the benefit of keeping models relatively general in order to be used to explain other systems as well.

When models accurately explain previous empirical data it presents an opportunity to first test the effects of a disturbance using the model, and subsequently utilize an experimental system to understand the effects of disturbance. This should continue to be a future direction taken by research in aquatic systems. In the case of a *Daphnia*-algal system the opportunity exists to conduct unique "perturbation experiments" whereby specific disturbances can be carried out on several replicate populations controlling for the effect of other variables. For example, populations of algae and *Daphnia* could be established and allowed to reach equilibrium densities. The response of the populations to several types of disturbances can then be carried out. This could include simulated increases in *Daphnia* mortality related to the introduction of planktivorous fish, the introduction of a variety of chemicals into the water column (pharmaceuticals, pesticides, elements required for growth), or the introduction of other zooplankton species that would compete with *Daphnia*. These types of experiments would allow the verification of model predictions, and would aid in the understanding of aquatic systems.

This thesis has outlined how regeneration can influence the population dynamics of a *Daphnia*-algal system. The results highlight how experimental data and theoretical models can be used together to understand some of the processes that occur in shallow aquatic systems. The increasing frequency of human disturbances on aquatic systems emphasizes the need to understand internal processes within the system so that long term effects can be predicted.

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APPENDIX A: *DAPHNIA*-ALGAL DYNAMICS

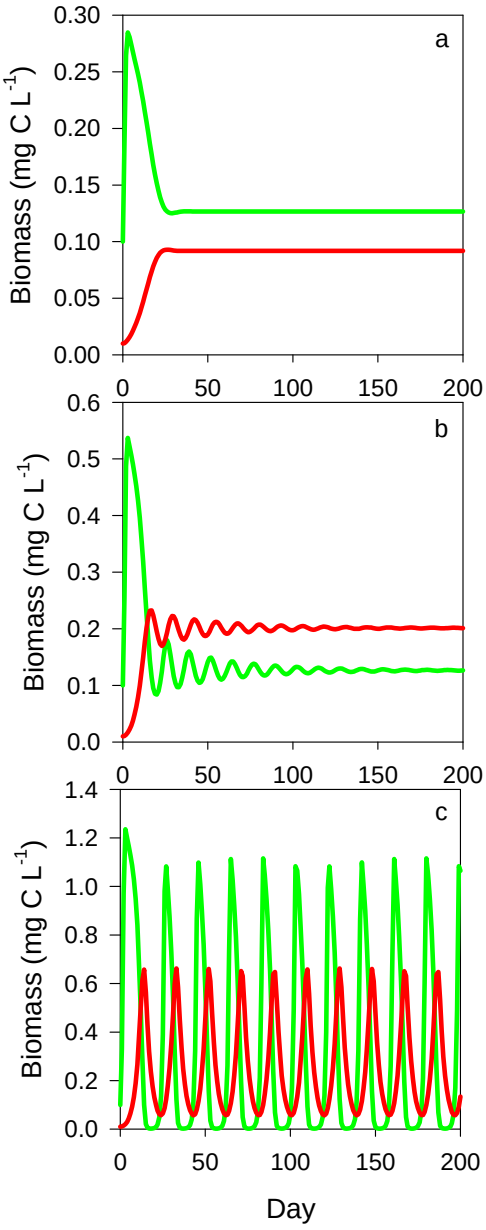

Figure A.1: *Daphnia*-algal dynamics as a function of nutrient enrichment. Population biomass (mg C L^{-1}) of algae (green line) and *Daphnia* (red line) over time (days) is stable at low enrichment (a); exhibits dampened oscillations at medium enrichment (b); and exhibits predator-prey cycles at high enrichment (c).

APPENDIX B: STATISTICAL TABLES

Table B.1: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among means for algae fractions in *Daphnia*-absent tanks.

Variable	Effect	DF	F value	P
Total biomass	treat	1	0.00	0.9834
	C:P	1	0.31	0.619
Edible biomass	treat	1	0.01	0.9416
	C:P	1	0.73	0.4546
Inedible biomass	treat	1	0.00	0.9685
	C:P	1	0.08	0.7984

Table B.2: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among coefficients of variation for algae fractions in *Daphnia*-absent tanks.

Variable	Effect	DF	F value	P
Total biomass	treat	1	0.44	0.5554
	C:P	1	0.04	0.8476
Edible biomass	treat	1	0.03	0.8648
	C:P	1	0.12	0.751
Inedible biomass	treat	1	0.40	0.5737
	C:P	1	2.31	0.2258

Table B.3: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among means for algae proportions in *Daphnia*-absent tanks.

Variable	Effect	DF	F value	P
Proportion of edible biomass	treat	1	0.44	0.5554
	C:P	1	0.04	0.8476
Proportion of inedible biomass	treat	1	0.40	0.5737
	C:P	1	2.31	0.2258

Table B.4: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among means for algae fractions in *Daphnia*-present tanks.

Variable	Effect	DF	F value	P
Total biomass	treat	2	0.08	0.9222
	C:P	1	4.42	0.0895
Edible biomass	treat	2	14.85	0.0079*
	C:P	1	7.45	0.0413*
Inedible biomass	treat	2	0.36	0.7151
	C:P	1	6.15	0.0559

*significant difference

Table B.5: A priori orthogonal contrasts comparing edible algae biomass (µg chl-*a* L^{-1}) among regeneration treatments in *Daphnia*-present tanks.

Contrast	DF	F value	P
D0x vs. D3x	1	26.57	0.0036*
D0x vs. D1x	1	0.14	0.7199
D0x vs. (D1x + D3x)	1	9.25	0.0287*

*significant difference

Table B.6: Estimate of intercept and partial regression coefficient for edible algae biomass (µg chl-*a* L^{-1}) as a function of seston C:P.

Parameter	Estimate	t value	P
intercept	0.43783767	7.61	0.0006*
coefficient	-0.0001311	-2.73	0.0413*

*significant difference

Table B.7: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among coefficients of variation for algae fractions in *Daphnia*-present tanks.

Variable	Effect	DF	F value	P
Total biomass	treat	2	2.55	0.1724
	C:P	1	0.40	0.5548
Edible biomass	treat	2	0.17	0.8517
	C:P	1	0.57	0.4832
Inedible biomass	treat	2	2.89	0.1468
	C:P	1	0.51	0.5077

Table B.8: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among means for algae proportions in *Daphnia*-present tanks.

Variable	Effect	DF	F value	P
Proportion of edible biomass	treat	2	5.65	0.0522
	C:P	1	5.91	0.0592
Proportion of inedible biomass	treat	2	5.65	0.0522
	C:P	1	5.91	0.0592

Table B.9: A priori orthogonal contrasts comparing the proportion of edible algae biomass (µg chl-*a* L^{-1}) among regeneration treatments in *Daphnia*-present tanks.

Contrast	DF	F value	P
D0x vs. D3x	1	9.09	0.0296*
D0x vs. D1x	1	0.43	0.5396
D0x vs. (D1x + D3x)	1	2.27	0.1923

*significant difference

Table B.10: A priori orthogonal contrasts comparing the proportion of inedible algae biomass (µg chl-*a* L^{-1}) among regeneration treatments in *Daphnia*-present tanks.

Contrast	DF	F value	P
D0x vs. D3x	1	9.09	0.0296*
D0x vs. D1x	1	0.43	0.5396
D0x vs. (D1x + D3x)	1	2.27	0.1923

*significant difference

Table B.11: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among means for *Daphnia* biomass.

Variable	Effect	DF	F value	P
Total biomass	treat	2	1.15	0.3891
	C:P	1	1.04	0.3546
Adult biomass	treat	2	3.99	0.0921
	C:P	1	3.09	0.1393
Juvenile biomass	treat	2	0.10	0.9104
	C:P	1	0.00	0.9794

Table B.12: A priori orthogonal contrasts comparing adult *Daphnia* biomass (mg C L^{-1}) among regeneration treatments.

Contrast	DF	F value	P
D0x vs. D3x	1	6.97	0.046*
D0x vs. D1x	1	0.08	0.7839
D0x vs. (D1x + D3x)	1	2.25	0.1942

*significant difference

Table B.13: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among coefficients of variation for *Daphnia* biomass.

Variable	Effect	DF	F value	P
Total biomass	treat	2	5.78	0.0502
	C:P	1	0.16	0.7082
Adult biomass	treat	2	2.63	0.1658
	C:P	1	0.63	0.4617
Juvenile biomass	treat	2	1.22	0.3711
	C:P	1	0.07	0.8035

Table B.14: A priori orthogonal contrasts comparing coefficients of variation for total *Daphnia* biomass (mg C L^{-1}) among regeneration treatments.

Contrast	DF	F value	P
D0x vs. D3x	1	7.22	0.0435*
D0x vs. D1x	1	7.31	0.0426*
D0x vs. (D1x + D3x)	1	11.55	0.0193*

*significant difference

Table B.15: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among means for *Daphnia* proportions.

Variable	Effect	DF	F value	P
Proportion of adult biomass	treat	2	6.67	0.0388*
	C:P	1	3.65	0.1142
Proportion of juvenile biomass	treat	2	6.67	0.0388*
	C:P	1	3.65	0.1142

*significant difference

Table B.16: A priori orthogonal contrasts comparing the proportion of adult *Daphnia* biomass (mg C L^{-1}) among regeneration treatments.

Contrast	DF	F value	P
D0x vs. D3x	1	11.9	0.0182*
D0x vs. D1x	1	0.07	0.7956
D0x vs. (D1x + D3x)	1	4.1	0.0989

*significant difference

Table B.17: A priori orthogonal contrasts comparing the proportion of juvenile *Daphnia* biomass (mg C L^{-1}) among regeneration treatments.

Contrast	DF	F value	P
D0x vs. D3x	1	11.9	0.0182*
D0x vs. D1x	1	0.07	0.7956
D0x vs. (D1x + D3x)	1	4.1	0.0989

*significant difference

Table B.18: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among means for *Daphnia* fecundity (number of eggs produced per adult).

Effect	DF	F value	P
treat	2	82.33	0.0024*
C:P	1	189.63	0.0008*
treat*C:P	1	90.86	0.0021*

*significant difference

Table B.19: Analysis of covariance comparing the main effect of regeneration (treat) and the covariate seston C:P among coefficients of variation for *Daphnia* fecundity (number of eggs produced per adult).

Effect	DF	F value	P
treat	2	0.01	0.9869
C:P	1	0.04	0.8415

Table B.20: Analysis of variance comparing the main effect of regeneration among means for the accumulation of sediment carbon and phosphorus at the end of the experiment; *Daphnia*-absent tanks.

Effect	DF	F value	P
carbon	1	325.08	< 0.0001
phosphorus	1	57.90	0.0016

Table B.21: Analysis of variance comparing the main effect of regeneration among means for the accumulation of sediment carbon and phosphorus at the end of the experiment; *Daphnia*-present tanks.

Effect	DF	F value	P
carbon	2	21.95	0.0017
phosphorus	2	12.44	0.0073

Table B.22: Analysis of variance comparing the main effect of regeneration among means for C and P fractions in *Daphnia*-absent tank.

Variable	DF	F value	P
TP	1	0.12	0.7514
DP	1	4.33	0.1059
PP	1	0.74	0.4392
PC	1	0.13	0.7414
C:P	1	0.01	0.911

Table B.23: Analysis of variance comparing the main effect of regeneration among coefficients of variation for C and P fractions in *Daphnia*-absent tanks.

Variable	DF	F value	P
TP	1	3.6	0.1306
DP	1	0.17	0.7023
PP	1	8.58	0.0429*
PC	1	7.23	0.0547
C:P	1	0.81	0.4199

*significant difference

Table B.24: Analysis of variance comparing the main effect of regeneration among means for C and P fractions in *Daphnia*-present tanks.

Variable	DF	F value	P
TP	2	1.21	0.3629
DP	2	1.75	0.2514
PP	2	0.40	0.6886
PC	2	4.35	0.0679
C:P	2	2.32	0.1794

Table B.25: A priori orthogonal contrasts comparing edible particulate carbon (mg C L^{-1}) among regeneration treatments in *Daphnia*-present tanks.

Contrast	DF	F value	P
D0x vs. D3x	1	8.64	0.026*
D0x vs. D1x	1	2.88	0.1404
D0x vs. (D1x + D3x)	1	7.17	0.0367*

*significant difference

Table B.26: Analysis of variance comparing the main effect of regeneration among coefficients of variation for C and P fractions in *Daphnia*-present tanks.

Variable	DF	F value	P
TP	2	1.08	0.3961
DP	2	0.54	0.6078
PP	2	0.16	0.859
PC	2	0.24	0.7968
C:P	2	1.15	0.3768