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Assessing the effects of native freshwater mussels on aquatic nitrogen dynamics

Jeremy Scott Brill
University of Iowa

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ASSESSING THE EFFECTS OF NATIVE FRESHWATER MUSSELS ON AQUATIC
NITROGEN DYNAMICS

by

Jeremy Scott Brill

An Abstract

Of a thesis submitted in partial fulfillment of the
requirements for the Doctor of Philosophy degree
in Civil and Environmental Engineering
in the Graduate College of
The University of Iowa

December 2012

Thesis Supervisor: Assistant Professor Craig L. Just

ABSTRACT

Management of the nitrogen cycle has been identified as one of fourteen grand challenges for engineering and is an especially important issue for agricultural watersheds of the Upper Midwest. In large river systems, it has become increasingly important to understand the interactions between abiotic and biotic processes that influence nitrogen cycling. Native freshwater mussels are one of the most influential organisms in aquatic ecosystems due to their ability to transfer nutrients from the overlying water to the sediments and stimulate production across multiple trophic levels. The goal of this study was to utilize flow-through laboratory mesocosms, highly time resolved water chemistry data, and a mass balance model to assess the effects of native freshwater mussels on aquatic nitrogen dynamics. The effects of mussels on concentrations of nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton in the overlying water of the mesocosms were analyzed using untreated Iowa River water.

Concentration changes for nitrate, ammonium, and phytoplankton were determined to be significantly different (ANCOVA, $p < 0.05$) between mesocosms containing mussels and mesocosms without mussels (control). Results from this study indicated that mussels increased ammonium via mussel excretion, indirectly increased nitrate via nitrification of the excreted ammonium, and decreased phytoplankton via mussel filtration. Results also indicated that mussels increased nitrite and total nitrogen concentrations and demonstrated minimal impacts on organic nitrogen. The majority of nitrogen mass delivered to the overlying water by mussels was in the form of ammonium and nitrate (nitrate mass was added via nitrification of the excreted ammonium).

The deterministic mass balance model developed to better understand the effects of mussels on nitrogen dynamics was calibrated with literature values and highly time resolved data and grab samples obtained from laboratory mesocosm experiments.

Sensitivity analyses identified hydraulic retention time, temperature, denitrification rate, and mussel ammonium excretion rate as the most influential variables in mesocosms containing mussels. The sensitivity analyses also demonstrated the difficulty in modeling the dynamic nature of the mesocosms and emphasized the need to constrain the model variables with observed experimental measurements. Application of the model predicted that increases in phytoplankton concentrations significantly influenced the effect of mussels on nitrogen dynamics in the overlying water of the mesocosms.

The results of this study will aid the scalability of mussel effects to larger systems and will help to predict how changes in environmental conditions influence the interactions of biotic and abiotic processes. These findings will help determine to what extent the effects of mussels should be included in strategies for nitrogen management.

Abstract Approved: _____
Thesis Supervisor

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CERTIFICATE OF APPROVAL

PH.D. THESIS

This is to certify that the Ph.D. thesis of

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has been approved by the Examining Committee
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For my Mom and Dad

Unless someone like you cares a whole awful lot, nothing's going to get better. It's not.

- Dr. Seuss, *The Lorax*

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Management of the nitrogen cycle has been identified as one of fourteen grand challenges for engineering and is an especially important issue for agricultural watersheds of the Upper Midwest. In large river systems, it has become increasingly important to understand the interactions between abiotic and biotic processes that influence nitrogen cycling. Native freshwater mussels are one of the most influential organisms in aquatic ecosystems due to their ability to transfer nutrients from the overlying water to the sediments and stimulate production across multiple trophic levels. The goal of this study was to utilize flow-through laboratory mesocosms, highly time resolved water chemistry data, and a mass balance model to assess the effects of native freshwater mussels on aquatic nitrogen dynamics. The effects of mussels on concentrations of nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton in the overlying water of the mesocosms were analyzed using untreated Iowa River water.

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The results of this study will aid the scalability of mussel effects to larger systems and will help to predict how changes in environmental conditions influence the interactions of biotic and abiotic processes. These findings will help determine to what extent the effects of mussels should be included in strategies for nitrogen management.

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LIST OF ABBREVIATIONS

CV	Coefficient of Variation
d	Days
DI	Deionized
g	Grams
h	Hours
km	Kilometers
km ²	Square Kilometers
L	Liters
m	Meters
m h ⁻¹	Meters per Hour
mg L ⁻¹	Milligrams per Liter
mg-N L ⁻¹	Milligrams per Liter as Nitrogen
mg-P L ⁻¹	Milligrams per Liter as Phosphorus
min	Minutes
mm	Millimeters
mmol	Millimole
R ²	Coefficient of Determination
Tg	Teragrams (10 ¹² grams)
UMR	Upper Mississippi River
µg L ⁻¹	Micrograms per Liter
µmol	Micromole
y	Years

CHAPTER 1

INTRODUCTION

Perspective

River restoration projects have become increasingly important in maintaining the abundance of healthy, self-sustaining river systems. River managers have been pursuing ecologically based restoration strategies to improve degraded waterways instead of the historically “hard” engineering solutions (Palmer et al. 2005). This transition has led to the development of new fields of study, such as ecohydraulics, which focuses on the interface between hydraulics and the ecology of rivers, estuaries, and wetlands over a wide range of temporal and spatial scales. Unfortunately, the interactions of these biotic and abiotic processes are poorly understood in large river systems (Newton et al. 2011).

Improving the understanding of large river ecohydraulics is especially important for the Upper Mississippi River (UMR), where reducing nitrogen loading to the Gulf of Mexico is a persistent ecological problem. Anthropogenic processes, primarily fertilizer manufactured for food production and cultivation of leguminous crops, convert more nitrogen gas from the atmosphere into reactive forms than the combined effects of all Earth’s terrestrial processes (Rockstrom et al. 2009). These reactive forms of nitrogen (primarily ammonium and nitrate) often end up in the environment in areas such as estuarine and coastal waters, where nitrogen is the macronutrient that most often limits primary production (Day et al. 1989). Extensive mismanagement of nitrogen in the UMR has led to severe hypoxia (the presence of low levels of dissolved oxygen in bottom waters) on the continental shelf of the northern Gulf of Mexico (Raymond et al. 2008). While investigating possible solutions to the hypoxia problem, researchers have begun to move beyond being concerned about nitrogen in the regions where it is discharged to investigating how nitrogen moves through large watersheds and over long distances (Mitsch et al. 2001).

Concentrations of inorganic nitrogen vary temporally and spatially especially in small systems where considerable differences occur even at the diurnal time scale (Mulholland et al. 2006; Pellerin et al. 2009; Scholefield et al. 2005). Recent studies suggest that diurnal variations in nitrogen concentrations are also present in large rivers such as the UMR (Bark 2010; Bril 2010). A clear explanation for the variations in nitrogen concentrations is difficult to determine and likely reflects a combination of riverine biological processes and variations in the physical transport of nitrogen (Pellerin et al. 2009). Thus, to better understand the variability of nitrogen concentrations in riverine ecosystems, the organisms that influence these processes need to be understood.

Native freshwater mussels (Unionioida, herein referred to as mussels) are a guild of benthic, burrowing, suspension-feeding bivalves. Mussels are large (25 to 200+ mm in length), long-lived (usually >25 y) invertebrates that transfer nutrients and energy from the overlying water to sediments through their filtering activity and stimulate production across trophic levels (Christian et al. 2005; Vaughn et al. 2008). The biomass of healthy mussel beds can exceed the biomass of all other benthic organisms by an order of magnitude (Layzer et al. 1993; Negus 1966), and production by mussels can equal that of all other macrobenthos in many rivers (Strayer et al. 1994; Vaughn et al. 2004).

In large productive rivers, mussels influence the nitrogen cycle by removing phytoplankton (Thorp et al. 1998) and other nitrogen-containing particulate organic matter from the overlying water and converting it to forms of reactive nitrogen that can be further transformed and/or assimilated by bacteria and other organisms (Vaughn et al. 2004). Specifically, native mussels provide nitrogen to the benthic zone through excretion of ammonium and through biodeposition of feces and pseudofeces (Vaughn and Hakenkamp 2001).

The important functional roles mussels perform in aquatic ecosystem processes, such as the nitrogen cycle, are threatened by drastic declines in mussel populations. Historically, mussels dominated the benthic biomass in North American rivers (Strayer et

al. 1994), but many of the mussel populations have declined in recent years due primarily to habitat alteration (Bogan 1993). More than 200 of the known 300 species of mussels are listed as extinct, threatened, or vulnerable (Master et al. 2000); as such, mussels are the most imperiled faunal group in North America. Because many of the ecological processes performed by mussels scale linearly with biomass (Vaughn et al. 2008), it is becoming increasingly important to understand how potential losses in mussel populations will affect river function (Vaughn et al. 2004).

In the UMR, efforts to assess the effects of river restoration strategies on native mussels (e.g. island construction, water level drawdown) are underway (Newton et al. 2011). However, the full effects of ecological disturbances on native mussels may not be expressed for decades as some ecosystem processes have slow response times (Newton et al. 2008). Modeling ecosystems to understand and predict the behavior of complex systems via computer simulations has become a widely utilized tool (Jamu and Piedrahita 2002a; Odum and Odum 2000; Schreuders et al. 2004). Furthermore, the collection of highly timed resolved data have been shown to enable accurate modeling of the effects of nutrient dynamics on surface water biology (Hanrahan et al. 2001) and is essential for enhancing our understanding of aquatic nitrogen biogeochemical cycling (Sandford et al. 2007).

Thus, the goal of this study was to couple the continuous input of untreated river water in flow-through mesocosms and highly time resolved data with a dynamic ecosystem model to assess the effects of native mussels on aquatic nitrogen dynamics. Given the known ecosystem functions of mussels, we hypothesized that mussels would influence nitrogen cycling in the overlying water by increasing concentrations of ammonium and nitrate due to ammonium excretion and subsequent nitrification to nitrate, and by decreasing concentrations of nitrogen-containing phytoplankton. It was also assumed that in large, agricultural river systems, the effect of mussels on aquatic nitrogen dynamics would be most sensitive to changes in flow, temperature, and light.

Research Hypotheses

The overall objective of this study was to better understand the effects of native freshwater mussels on aquatic nitrogen dynamics in the overlying water of the Iowa River. To accomplish this, a flow-through laboratory mussel habitat (mesocosm) with a continuous input of untreated Iowa River water was constructed to measure highly time resolved water chemistry data. A mass balance model was then developed to simulate the nitrogen dynamics of the mesocosms under different experimental conditions. To complete the primary research objective, the following hypotheses were tested:

Hypothesis #1: Laboratory-based mesocosms containing native freshwater mussels exhibit increased concentrations of ammonium and nitrate and decreased concentrations of phytoplankton in the overlying water compared to mesocosms with no mussels.

Hypothesis #2: In laboratory-based mesocosms, the effect of native freshwater mussels on aquatic nitrogen dynamics is most sensitive to changes in flow, temperature, and light.

Thesis Organization

This thesis contains six chapters to address the previously described research hypotheses. Chapter 2 contains a literature review discussing the nitrogen cycle, nitrogen dynamics in river ecosystems, native freshwater mussels and their impact on nitrogen dynamics, and dynamic ecosystem models including STELLA.

Chapter 3 investigates the effects of mussels on nitrate, ammonium, and phytoplankton in the overlying water using flow-through mesocosms. Highly time resolved (30 min) water chemistry data were collected in mesocosms containing mussels and mesocosms without mussels. The highly time resolved data were used to evaluate if concentration changes for nitrate, ammonium, and phytoplankton were significantly different between the mussel treatments and control treatments. The purpose of Chapter 3 is to address Hypothesis 1.

Chapter 4 replicates the experiment completed in Chapter 3 with a more extensive grab sample data set but a shorter experimental time period. More nitrogen species were analyzed in the overlying water (nitrite, organic nitrogen, and total nitrogen) and nitrate and ammonium measurements were obtained from the pore water of the mesocosms. The purpose of Chapter 4 is to address Hypothesis 1.

Chapter 5 describes and investigates the development, calibration, and evaluation of a dynamic mass balance model created using STELLA. Flow-through mesocosms and highly time resolved data were again used to assess the effects of mussels on nitrogen dynamics. Measurements from the mesocosm experiments were used to calibrate the model. Single and multiple variable sensitivity analyses determined the most influential model variables and what other combinations of model variables demonstrated a similar result to the calibrated model outputs. A model application exercise was completed to evaluate how nitrogen dynamics were influenced by increasing phytoplankton concentrations and mussel biomass. The purpose of Chapter 5 is to address Hypothesis 1 and Hypothesis 2.

Chapter 6 summarizes the research findings and the implications for managing nitrogen in large river systems. This chapter also describes suggested areas for future research. The Appendix includes sensor specifications, water chemistry data, STELLA model inputs, and model variables for the sensitivity runs that met the criteria established by the multiple variable sensitivity analysis.

CHAPTER 2

LITERATURE REVIEW

The Nitrogen Cycle

Nitrogen is one of the most abundant elements on earth. However, less than 2% is available to organisms (Galloway 1998). Nitrogen that organisms can utilize is known as reactive nitrogen (defined as N bonded to C, O, or H, as in NO_x , NH_x , organic N) and is created largely by biological nitrogen fixation of unreactive nitrogen (triple-bonded N_2) (Figure 2.1). This biological fixation provides about 90-130 Tg of reactive nitrogen per year on the continents (Wetzel 2001). Reactive nitrogen is also created from lightning strikes, but this process accounts for less than 1% of total reactive nitrogen.

The Nitrogen Cycle Challenge

The natural nitrogen cycle has been drastically altered by human activities (Canfield et al. 2010; Rockstrom et al. 2009). Energy production, fertilizer production, and cultivation of crops that utilize symbiotic microbes (e.g. legumes and rice) has resulted in the fixation of an additional 150 Tg of reactive nitrogen per year (Wetzel 2001). Given that nitrogen is an integral part of expanding food production for increasing populations, it is expected that anthropogenic conversion of unreactive to reactive nitrogen will continue to rise. Much of this reactive nitrogen will enter surface and groundwater ecosystems causing persistent ecological problems such as hypoxia.

Hypoxia occurs when dissolved oxygen concentrations are below 2 mg L^{-1} (Rabalais et al. 2001). Hypoxia is caused by stratification of the overlying water and by excess nutrient delivery to the Gulf of Mexico from the extensively row-cropped Midwest via the Mississippi River (Figure 2.2) (Rabalais et al. 2002). The overload of nutrients enters the Gulf and stimulates the excess growth of phytoplankton. The higher levels of the food web cannot consume all of the phytoplankton and it sinks to the seabed where bacteria decompose the remains. This increase in microbial oxygen consumption

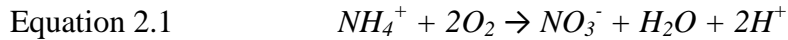
decreases the dissolved oxygen concentrations to levels below which aquatic life can survive, thus creating a “dead zone.” Furthermore, the less dense freshwater from the Mississippi River is warmer and less saline than the ocean water below which causes stratification. This stratification can create hypoxic conditions that last for months. From 1993 to 2000, the Gulf of Mexico dead zone ranged in size from 16,000 to 20,000 km² annually (Rabalais et al. 2001). In 2011, the dead zone was determined to be over 17,520 km² (Figure 2.3).

Nitrogen Dynamics in River Ecosystems

Nitrogen occurs in freshwater systems in a variety of forms including: dissolved molecular N₂, ammonium (NH₄⁺), ammonia (NH₃), nitrite (NO₂⁻), nitrate (NO₃⁻), and organic compounds (e.g. amino acids, amines, proteins) (Figure 2.4). Sources of nitrogen to river ecosystems are dominated by inputs from surface and groundwater drainage, especially in large rivers where human activities in the drainage basins are high (Wetzel 2001). Other nitrogen sources include nitrogen fixation that occurs in the water and the sediments or atmospheric sources such as precipitation. Nitrogen losses from a river ecosystem are dominated by effluent outflow but also include sedimentation loss and volatilization from the water surface (e.g. ammonium at high pH, N₂ formed in bacterial denitrification). The nitrogen species analyzed in this study were nitrate, ammonium, organic nitrogen, nitrite, and total nitrogen.

Nitrate

Nitrate that occurs in freshwater systems is generated as a product of nitrification. Nitrification, which occurs under aerobic conditions, is generally defined as the biological conversion of organic and inorganic nitrogenous compounds from a reduced state to a more oxidized state (Alexander 1965). In well-oxygenated systems, nitrate may diffuse to the overlying water following nitrification (Wetzel 2001). The overall reaction for nitrification is as follows:



Nitrate is reduced to nitrogen gas (N₂) through microbial denitrification. Denitrification is the biochemical reduction of oxidized nitrogen anions (nitrate and nitrite) affiliated with the oxidation of organic matter (Wetzel 2001). The denitrification reactions occur in anaerobic environments and in anoxic sediments where oxidizable organic substances are abundant (Wetzel 2001). The general reaction sequence is as follows:



Nitrate can also be reduced to ammonium through assimilation by algae and larger hydrophytes (Wetzel 2001). Uptake by photoautotrophs is believed to be an important retentive process as diurnal daytime reductions of nitrate have been observed under base flow conditions (Burns 1998).

The rates of nitrification and denitrification are largely dependent on the redox conditions present in the interstitial waters of the river sediments. In organic-rich sediments, the zone of nitrification is typically limited to the upper 2-3 mm of the sediment and denitrification occurs below the stratum of nitrifier activity (Cooke and White 1987a; Cooke and White 1987b). Rates of denitrification have also been shown to increase rapidly under shaded conditions or darkness as bacterial respiration depletes oxygen in the microzones (Wetzel 2001).

Nitrate concentrations vary regionally, seasonally, and spatially. Nitrate concentrations tend to be highest in rivers that are influenced by agricultural runoff (e.g. UMR) (Wetzel 2001). Furthermore, the loadings of both nitrate and ammonium to river ecosystems are influenced by the activity of terrestrial vegetation of the riparian zones; nitrogen concentrations tend to be higher during periods of vegetation dormancy or following the losses from harvesting or fire (McClain et al. 1994; Spencer and Hauer 1991).

Ammonium

Ammonium found in freshwater is generated as a primary end product of the decomposition of organic matter by heterotrophic bacteria or to a lesser extent by the biological dissimilation of nitrate (Wetzel 2001). Sediment-bound ammonium can also be released into the overlying water under certain conditions and the rates of this diffusion transport can be increased substantially by the activities of benthic invertebrates (e.g. freshwater mussels, chironomid larvae) (Wetzel 2001). Furthermore, ammonium is an excretory product of higher aquatic animals (e.g. freshwater mussels), but this source is typically thought to be insignificant when compared to that generated by bacterial decomposition.

Similar to nitrate, ammonium concentrations vary regionally, seasonally, and spatially within river ecosystems based on the level of productivity and the extent of pollution from organic matter. Generally, ammonium concentrations are low in well-oxygenated waters (Wetzel 2001). This is especially true in large eutrophic river systems (e.g. UMR) where much of the ammonium is rapidly nitrified and exported downstream as nitrate (Lipschultz et al. 1986).

Organic Nitrogen

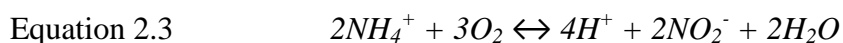
Organic nitrogen exists in river ecosystems as both a particulate and dissolved form. Particulate nitrogen consists of particulate organic nitrogen (PON), adsorbed ammonium, and organic nitrogen that is adsorbed to particles (Wetzel 2001). In unpolluted rivers, the weight ratio of particulate organic carbon (POC) to PON is relatively constant at 8-10 (Malcolm and Durum 1976; Meybeck 1982).

Dissolved organic nitrogen (DON) is measured less frequently in natural river waters, but almost always constitutes a major part of the total dissolved nitrogen (world average $\approx 40\%$) (Meybeck 1982; Wetzel et al. 1977). The concentration of DON has been found to frequently exceed that of dissolved inorganic nitrogen (DIN), including ammonium, nitrate, and nitrite (Berman and Bronk 2003). DON typically enters a river

system from terrestrial leaching or runoff and can also form within the river system through excretion by phytoplankton, macrophytes, and bacteria (Berman and Bronk 2003). DON is removed from a river system by bacterial and phytoplankton uptake, photochemical decomposition, or abiotic adsorption (Berman and Bronk 2003). While DIN concentrations and discharge often vary diurnally and seasonally within a river system, DON and dissolved organic carbon (DOC) are relatively constant (Manny and Wetzel 1973).

Nitrite

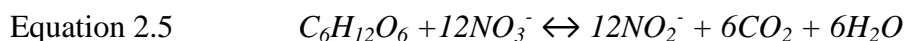
Nitrite in river ecosystems is primarily generated as an intermediate product of nitrification and denitrification. Ammonium is converted to nitrite through the initial nitrification process completed by bacteria, fungi, and autotrophic organisms:



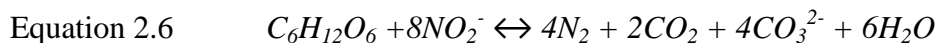
Nitrite is then oxidized to nitrate by:



Nitrite is generated by denitrification through the oxidation of a carbon source (e.g. glucose) and the reduction of nitrate:



Nitrite is then reduced to molecular nitrogen:



Nitrite has been shown to accumulate in conditions of low temperature and high pH, but concentrations are typically very low in well-oxygenated conditions (Wetzel 2001).

Total Nitrogen

Total nitrogen is defined as the sum of nitrate, ammonium, nitrite, and organic nitrogen. Total nitrogen should not be confused with Total Kjeldahl Nitrogen (TKN), which is defined as the sum of ammonium and organic nitrogen (not nitrate or nitrite). In well-oxygenated and productive river systems, total nitrogen tends to consist primarily of nitrate and organic nitrogen. This has been demonstrated in the UMR, where the average total nitrogen flux from the UMR to the Gulf of Mexico was found to be primarily nitrate ($\approx 60\%$) followed by organic nitrogen ($\approx 38\%$) and ammonium ($\approx 2\%$) (Goolsby and Battaglin 2001; Goolsby et al. 2000).

Phytoplankton in River Ecosystems

Phytoplankton is defined as the algae of the open water of lakes and large streams. Phytoplankton in river ecosystems are usually dominated by a small number of taxa but diversity can increase in large rivers (Wetzel 2001). As rivers become more disturbed or polluted, phytoplankton diversity is often reduced or lost (Patrick 1988).

Growth characteristics of phytoplankton are often difficult to evaluate due to the changes that occur in the physiological properties of each algal species as well as changes in environmental factors. The important factors that regulate growth and succession are: (a) light and temperature, (b) buoyancy regulation (i.e. means of remaining within the photic zone by altering settling rates), (c) inorganic nutrient factors, (d) organic micronutrient factors and interactions of organic compounds with inorganic nutrient availability, and (e) biological factors of competition and predation (Wetzel 2001). Phytoplankton growth is counterbalanced by losses of sedimentation out of the photic zone, viral and fungal parasitism, and predation (e.g. zooplankton, mussels). These mortality losses couple with the growth factors to determine succession and rates of productivity (Wetzel 2001).

Phytoplankton and Nitrogen Dynamics

In general, there is a positive correlation between high-sustained productivity of phytoplankton populations and average concentrations of inorganic and organic nitrogen (Wetzel 2001). In large river systems, especially those that have been disturbed by agriculture, nutrient limitations to primary production are minimal as adequate nutrients such as nitrogen are typically available to support maximum rates of photosynthesis (Welker and Walz 1998; Wetzel 2001). Thus, light availability is the dominant factor regulating phytoplankton growth as much of the control of photosynthetic productivity in large river systems is attributed to the availability of solar insolation reaching the water and its attenuation within the water (Bott 1983; Minshall 1978; Wetzel and Ward 1992).

Nitrogen Dynamics in the Iowa River

The Iowa River Basin is located in east-central Iowa (Figure 2.5), which is one of many areas with water quality concerns attributed to high nitrogen loads from agricultural lands (Alexander et al. 2008). The major tributary to the Iowa River is the Cedar River and together the two rivers drain a watershed area of $\sim 32,740 \text{ km}^2$. The Iowa River flows in a southeasterly direction and discharges to Navigation Pool 18 of the UMR.

Like many rivers in the Midwest, the Iowa River Basin's main nitrogen management issue is due to high loadings of nitrate. The annual export of nitrate from Iowa's rivers is estimated to contribute 11.3% of the nitrate that the Mississippi River delivers to the Gulf of Mexico, despite Iowa occupying $<5\%$ of the total drainage area (Alexander et al. 2008). The main nonpoint source of nitrate in Iowa is agriculture, primarily the widespread use of nitrogen fertilizer (Schilling and Lutz 2004). In certain Iowa rivers, average nitrate loads were shown to be equivalent to $\approx 20\%$ of the nitrogen fertilizer applied (Heffernan et al. 2010). Other nonpoint nitrate sources related to agriculture include the application of livestock manure, legume fixation, and mineralization of soil nitrogen (Burkart and James 1999; Goolsby et al. 1999; Hallberg 1987).

The mean annual nitrate concentrations in Iowa rivers has been shown to have a direct linear correlation to the amount of land in a watershed that contains row crops (Schilling and Libra 2000). Nitrate typically enters streams and rivers by leaching from row-cropped fields and moving as shallow groundwater. This groundwater discharge and discharge of groundwater by tile drainage provide the main pathway for nitrate to enter Iowa's streams and rivers (Hallberg 1987).

Native Freshwater Mussels

Native freshwater mussels (herein referred to as mussels) are benthic, burrowing, filter-feeding bivalves that are often considered ecosystem engineers due to the important functions they perform in rivers, streams, and lakes (Strayer et al. 2004; Vaughn and Hakenkamp 2001). There are over 1,000 species worldwide of these large (25 to 200+ mm in length), long-lived (typically >25 y) invertebrates with 300 species present in North America (Master et al. 2000). However, due to drastic declines in mussel populations, mussels have been classified as the most imperiled faunal group in North America; over 200 of the 300 species are listed as extinct, imperiled, or vulnerable (Master et al. 2000). Because many of the functional roles mussels perform in aquatic ecosystems increase with biomass (Strayer et al. 1999), decreases in mussel populations are likely to affect ecosystem function (Vaughn et al. 2008).

Ecosystem Impacts

Mussels stimulate production across multiple trophic levels by transferring nutrients and energy from the overlying water to the sediments through their filtering activity (Spooner and Vaughn 2006; Vaughn et al. 2007). Water temperature, particle size and concentration, flow regime, and bivalve size and gill morphology all have been found to influence mussel filtration rate (Vaughn and Hakenkamp 2001). In large productive rivers, mussels have been shown to feed almost exclusively on phytoplankton (Thorp et al. 1998).

Mussels are also able to influence food availability for other aquatic organisms directly and indirectly through nutrient excretion and biodeposition of organic matter (Vaughn et al. 2008). Mussel biodeposition is the sum of pseudofeces (material filtered but not ingested) and feces (material ingested but not assimilated) production (Nalepa et al. 1991). The effects of mussels on nutrient translocation and cycling are dependent on mussel biomass, species composition, and environmental conditions (Vaughn et al. 2008). Lake studies have shown that freshwater mussels open their valves more frequently under decreased light intensity (Englund and Heino 1994; Englund and Heino 1996). This diurnal phenomenon in mussel valve behavior has also been observed in laboratory studies (Bril 2010).

Mussels and their spent shells (from dead mussels) also provide or improve habitat for other aquatic organisms by providing physical structure and stabilizing and bioturbating sediments (Vaughn et al. 2008). Macroinvertebrate densities have been found to be higher in mussel beds (aggregations of mussels) than outside beds (Vaughn and Spooner 2006) and macroinvertebrates tend to aggregate on sediments that contain mussel biodeposits (Howard and Cuffey 2006; Spooner and Vaughn 2006).

Impacts on Nitrogen Dynamics

Most of the research examining the effects of mussels on aquatic nitrogen dynamics focuses primarily on the invasive zebra mussels (Bruesewitz et al. 2008; Bruesewitz et al. 2006; Gardner et al. 1995; Lavrentyev et al. 2000). The research that has been completed on mussels (native species) indicate they primarily influence nitrogen dynamics in large river systems by filtering particulate organic nitrogen (i.e. phytoplankton) from the overlying water and releasing reduced forms of soluble nitrogen near the sediment-water interface (Figure 2.6). Mussels provide these reduced forms of nitrogen to the benthic zone through the excretion of ammonium and through biodeposition of feces and pseudofeces. Nitrifying bacteria then readily convert the

ammonium to nitrite, which can be oxidized to nitrate depending on redox conditions. The nitrate is then reduced to nitrite, which can be converted to nitrogen gas by denitrifying bacteria with the aid of mussel-derived organic carbon (feces and pseudofeces).

Ammonium

Ammonium concentrations in the overlying water have been shown to be higher in systems containing mussels (Vaughn et al. 2008) and ammonium has been shown to increase with increasing mussel biomass (Vaughn et al. 2004; Vaughn and Hakenkamp 2001; Vaughn et al. 2008). Increases in ammonium concentrations in the overlying water are likely attributable to mussel excretion of ammonium. Excretion rates of ammonium vary with species, size, reproductive stage, food availability, and environmental conditions (Spooner and Vaughn 2008; Vaughn et al. 2008). Mussels may also increase ammonium concentrations in the overlying water as diffusion rates of sediment-bound ammonium can be increased several fold by the bioturbation activities of benthic invertebrates (Henriksen et al. 1983).

Nitrate

The effects of mussels on nitrate concentrations in the overlying water are not well established. Nitrate concentrations in the overlying water are expected to be higher in mussel-containing systems as nitrate has been shown to increase with increasing mussel biomass (Vaughn et al. 2004). The increase in ammonium concentrations in the overlying water (caused by mussel excretion) combined with well-oxygenated conditions likely leads to more ammonium being nitrified to nitrate, thus increasing nitrate concentrations. Mussels may also indirectly increase nitrate concentrations in the overlying water by increasing the amount of dissolved oxygen present at the sediment-water interface through the bioturbation of sediments during burrowing activities (Vaughn et al. 2008). This bioturbation indirectly increases nitrate concentrations by

creating conditions where the ammonium released by the mussels is more readily oxidized to nitrite/nitrate.

Conversely, mussels may indirectly decrease nitrate concentrations in the overlying water by indirectly increasing denitrification rates at the sediment-water interface. Under anaerobic conditions, and in the presence of a rich source of carbohydrates, nitrate can be converted to molecular nitrogen gas by denitrifying bacteria, sequentially via nitrite, nitric oxide, and nitrous oxide. Zebra mussels have been shown to indirectly hasten the conversion of nitrate to nitrogen gas in anaerobic sediments by supplying readily available organic carbon (feces) (Bruesewitz et al. 2008) and carbohydrates in the form of glycoproteins that are the primary component of the mucus that mussels excrete when packaging and rejecting undesirable filtered particles (pseudofeces).

Phytoplankton

Research has shown that chlorophyll *a* (phytoplankton) concentrations in the overlying water decrease in the presence of mussels (Boltovskoy et al. 2009; Vaughn et al. 2004). However, studies have also shown that under certain conditions, high densities of mussels can increase chlorophyll *a* concentrations in the overlying water through an ammonium fertilization effect (Vaughn et al. 2008). A mesocosm study on marine mussels indicated that phytoplankton concentrations were significantly reduced in systems containing mussels, but phytoplankton growth rates increased with high mussel density (Prins et al. 1995). This was explained as the result of a shift towards faster growing phytoplankton (diatoms) present in the mussel systems and increased nutrient availability caused by mussel excretion.

Organic Nitrogen

There is minimal research evaluating the effects of mussels on organic nitrogen in the overlying water. Mussels are known to provide nutrients to the benthic zone through

biodeposition of feces and pseudofeces (Vaughn and Hakenkamp 2001). This deposited material is known to contain organic nitrogen (Christian et al. 2008) and the rates of biodeposition have been shown to increase with increasing food supply (Vaughn et al. 2004). However, the relationship between organic nitrogen deposited at the sediment-water interface and organic nitrogen present in the overlying water is not well established.

Mussels in the Iowa River

The Iowa River is an important resource for mussels in Iowa and has historically been defined as one of the State's best mussel habitats (Frest 1987). However, data collected in mussel surveys from 1984-1985 and 1988-1999 showed a >50% decline in species richness (Arbuckle and Downing 2000). This sharp decline in species richness has caused many segments of the Iowa River to be listed on the Iowa Department of Natural Resource's Section 303 (d) list of impaired waters since 2002 (Figure 2.7) (IDNR 2011).

Despite the decline in mussel populations, the Iowa River still supports a diverse mussel community as 25 species have been collected live within the last 8 y (ESI 2012). Some of the collected species were the federally endangered Higgins' eye mussel (*Lampsilis higginsii*) and the Iowa state endangered species Pistolgrip (*Tritogonia verrucosa*) and Yellow Sand Shell (*Lampsilis teres*). The most common mussel species found in recent surveys of the Iowa River include Pimpleback (*Quadrula pustulosa*), Plain Pocketbook (*Lampsilis cardium*), and Threeridge (*Amblema plicata*) (ESI 2012).

Dynamic Ecosystem Modeling

Simulation models are useful tools in analyzing and understanding complex ecological systems and biogeochemical cycling of nutrients (Anderson 1992). Several commercially-available, systems-based, software tools have been introduced to support the development of dynamic ecological systems models (Rizzo et al. 2006). Modeling

tools such as STELLA, Madonna, GoldSim, and Simulink are becoming increasingly popular due to their easy-to-use, graphical icon-based interface than can be understood by novice modelers (Costanza and Voinov 2001).

STELLA (isee systems, inc., Lebanon, New Hampshire) is a modeling software package with an object-oriented programming language that uses an iconographic to facilitate the construction of dynamic system structures (Costanza and Gottlieb 1998). The differential equations are defined by the user as stocks and flows. Stocks are defined as a balance unit that changes with each time step and flows represent a positive or negative change of flux. Converters are used to represent input variables and arrows represent mathematical relationships between the modeled elements. The numerical integration methods available for use in STELLA are the Euler method, the 2nd-Order Runge Kutta method, and the 4th-Order Runge Kutta method. Output values can be easily checked through graphing or table features and model outputs or equations can be quickly exported as text files to be used in other software programs. STELLA also has a built-in sensitivity analysis function that is useful for analyzing model results.

The dynamic systems software package Berkeley Madonna (Macey and Oster, Berkeley, California) is a modeling tool that was developed under sponsorship from the National Science Foundation (NSF) and the National Institute for Health (NIH) (Rizzo et al. 2006). Equations used in Madonna can be formulated manually in the equation editor or drawn graphically using the available flowchart editor. Differential equations in Madonna are solved using the Euler method, the 2nd-Order Runge-Kutta method, the 4th-Order Runge Kutta method, or the Rosenbrock method. Users can also design a custom time integration method within the software. Madonna allows users to quickly input and output data by using text files loading as vectors or matrices. Sensitivity analyses and optimization functions are built-in options in the Madonna software. Although it can be applied to a variety of ecological problems, Madonna is best suited for mechanical engineering and chemistry applications (Rizzo et al. 2006).

The software package GoldSim (GoldSim Technology Group, Redmond, Washington) is a flexible modeling tool that can be applied to simple static and deterministic systems or to complex systems with high degrees of uncertainty (Rizzo et al. 2006). The increase in applicability is a result of the programming capabilities of GoldSim being more flexible and advanced than STELLA or Madonna. Models in GoldSim are created by constructing an influence diagram using built-in elements that are represented by graphical icons or programming equations. In complex models, GoldSim is used to arrange the system in a hierarchical, modular manner. GoldSim is also 'dimensionally aware' and is able to convert outputs to user-specified inputs (e.g. unit conversions). This feature, along with many other built-in features that address uncertainty, allow GoldSim to minimize error in model outputs. Differential equations in GoldSim are solved using the Euler method of integration.

The dynamic systems software package Simulink (Mathworks Inc., Natick, Massachusetts) is an add-on package to MATLAB and is run as a block diagram visual modeling tool (Rizzo et al. 2006). Although Simulink uses the same MATLAB language and functions, it does not require lines of code to be written. Instead, models are developed in an icon-based interface that enables a conceptual diagram of the system being analyzed. Different groups of variables and operations can be added as sub-modules and used to transform an overly complex model into a more comprehensible diagram. Differential equations defined in Simulink are solved using the Euler method, Runge-Kutta, Gear, and Rosenbrock. Similar to Madonna, users can also design a custom time integration method within the software. Simulink also possesses the ability to interpolate a value for missing time steps if data are not available.

The dynamic systems software package chosen for this research was STELLA. Several studies have used STELLA to examine nutrient cycling in aquatic ecosystems (Jamu and Piedrahita 2002a; Jamu and Piedrahita 2002b; Mayo and Bigambo 2005; Schreuders et al. 2004). Stock and flow-based models such as STELLA are known for

providing an improved conceptual understanding of an ecological system (Rizzo et al. 2006). The current available version is STELLA 9.1.4.

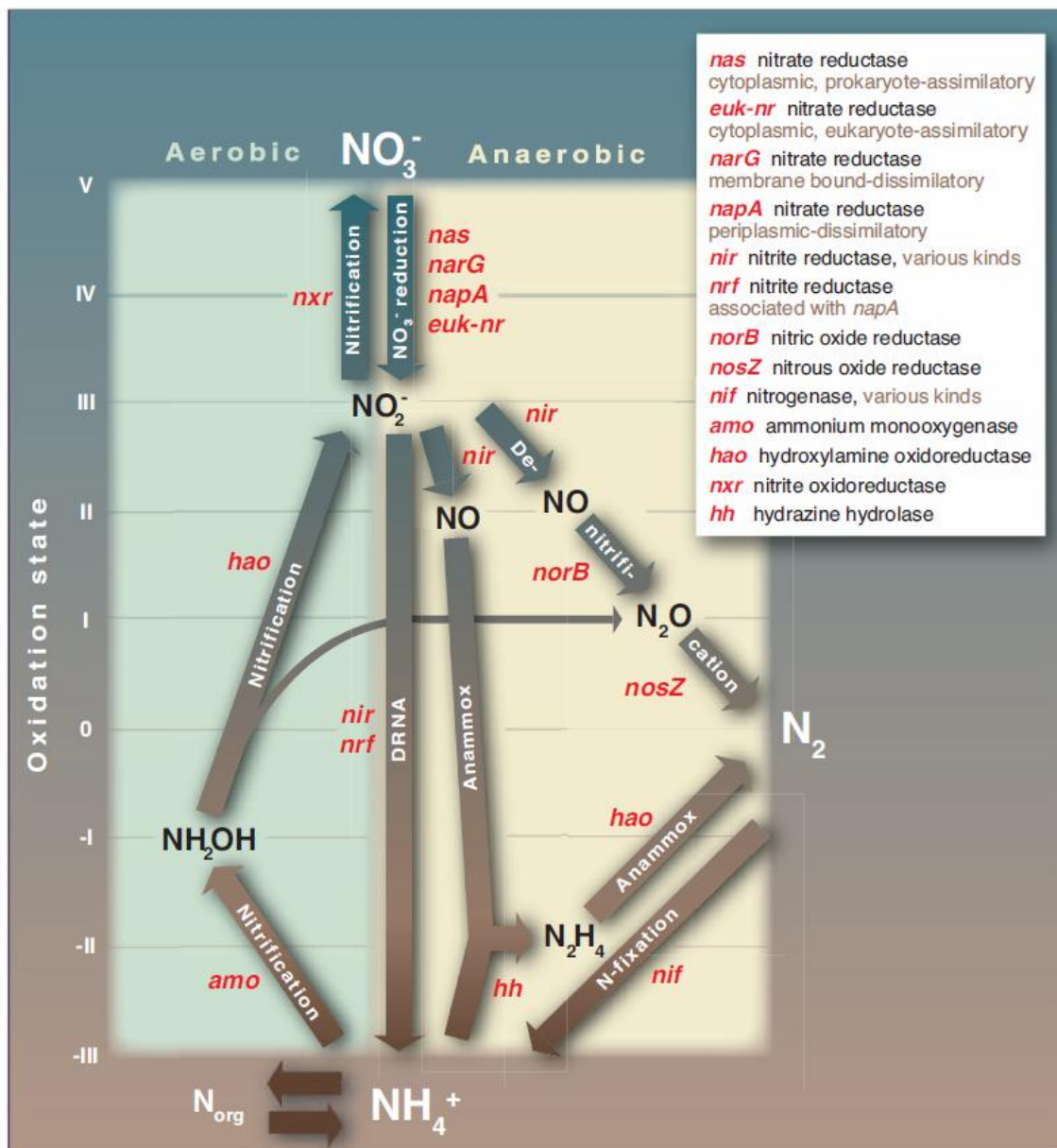


Figure 2.1: The major biological transformation pathways of the nitrogen cycle in the natural environment and their associated enzymes.

Source: Canfield et al. 2010

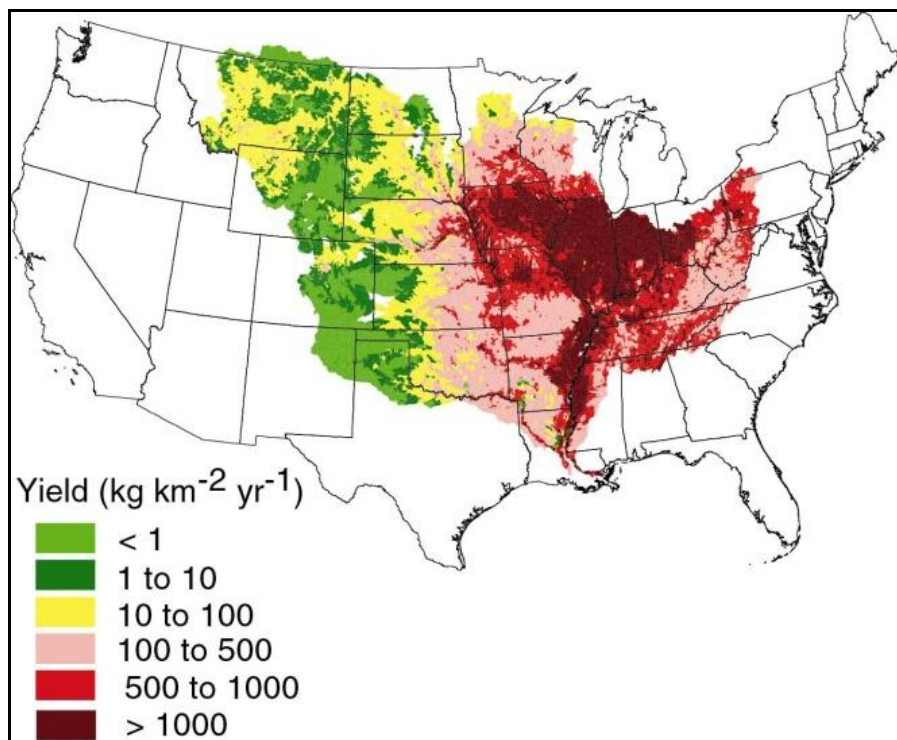


Figure 2.2: Total nitrogen yield delivered to the Gulf of Mexico from the incremental drainage reaches within the basin of the Mississippi and Atchafalaya Rivers.

Source: Alexander et al. 2008

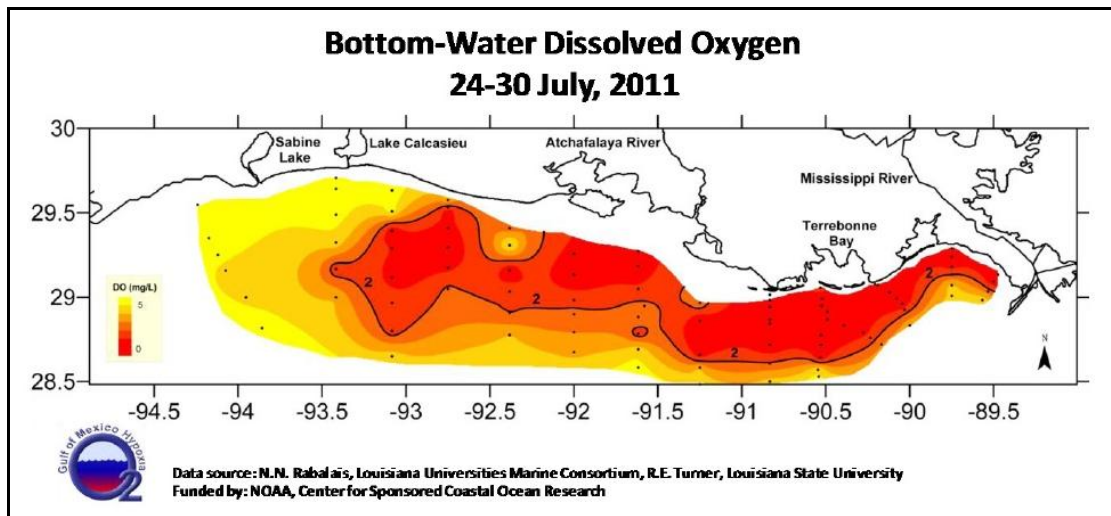


Figure 2.3: Bottom dissolved oxygen (DO) measurements (mg L^{-1}) for the Gulf of Mexico dead zone July 24-30, 2011.

Source: LUMCON 2011

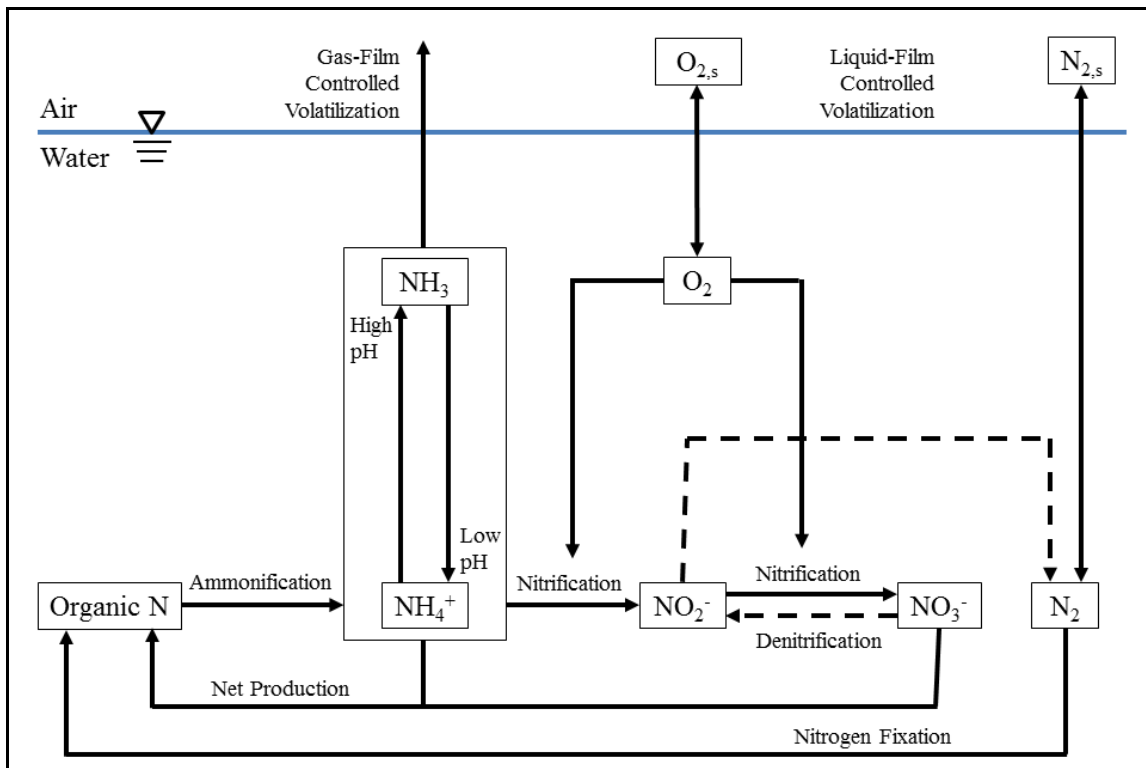


Figure 2.4: The nitrogen cycle in natural waters.

Source: Chapra 1997

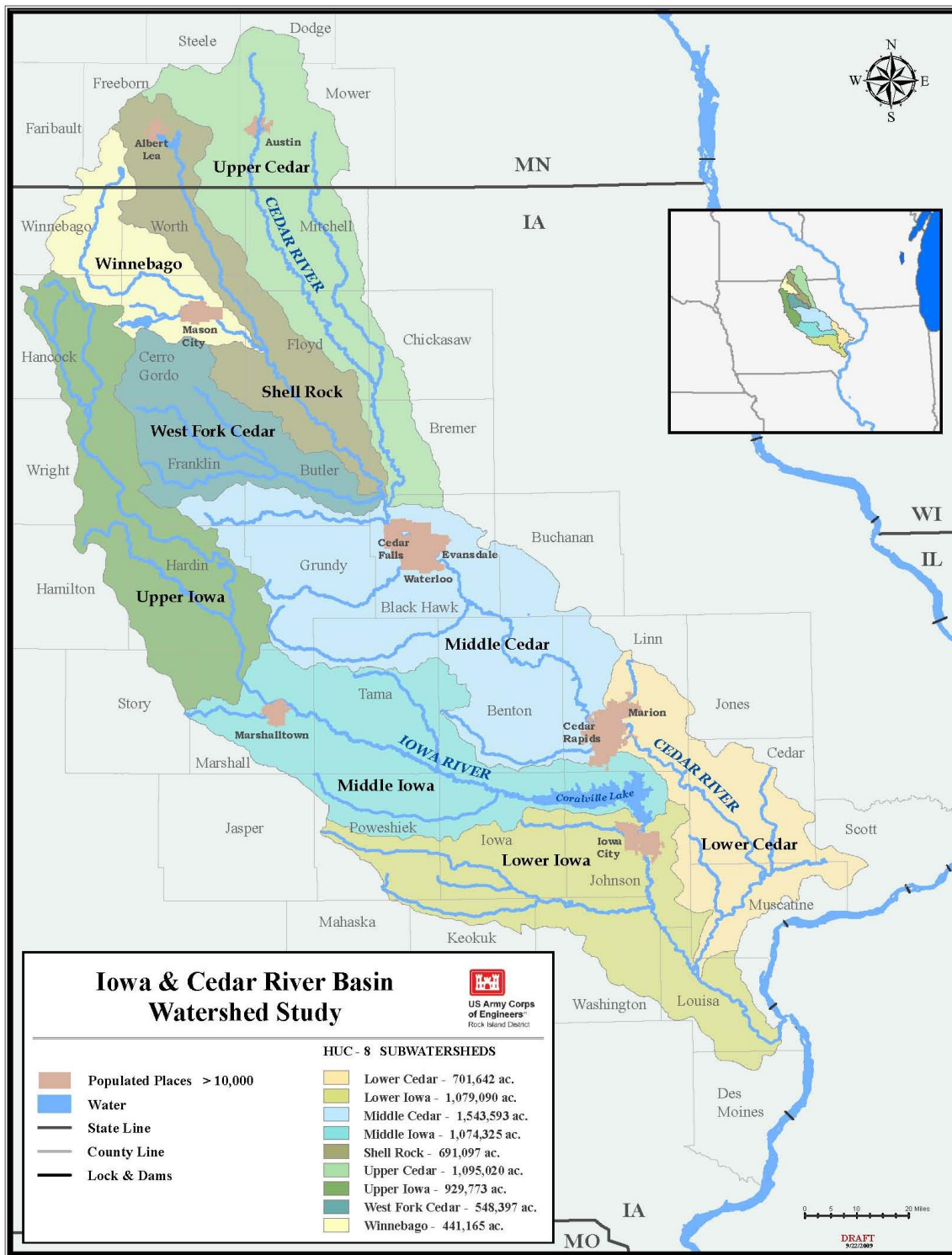


Figure 2.5: The Iowa River Basin (which includes the Cedar River Basin) drains approximately 32,740 km² in east-central Iowa and southeast Minnesota.

Source: U.S. Army Corps of Engineers 2012

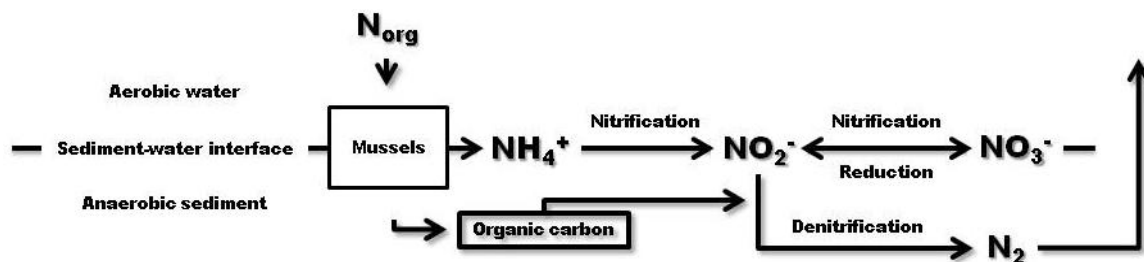


Figure 2.6: In large productive rivers, mussels influence the nitrogen cycle by removing nitrogen-containing particulate organic matter (i.e. phytoplankton) from the overlying water and converting it to forms of reactive nitrogen that can be further transformed and/or assimilated by bacteria and other organisms.

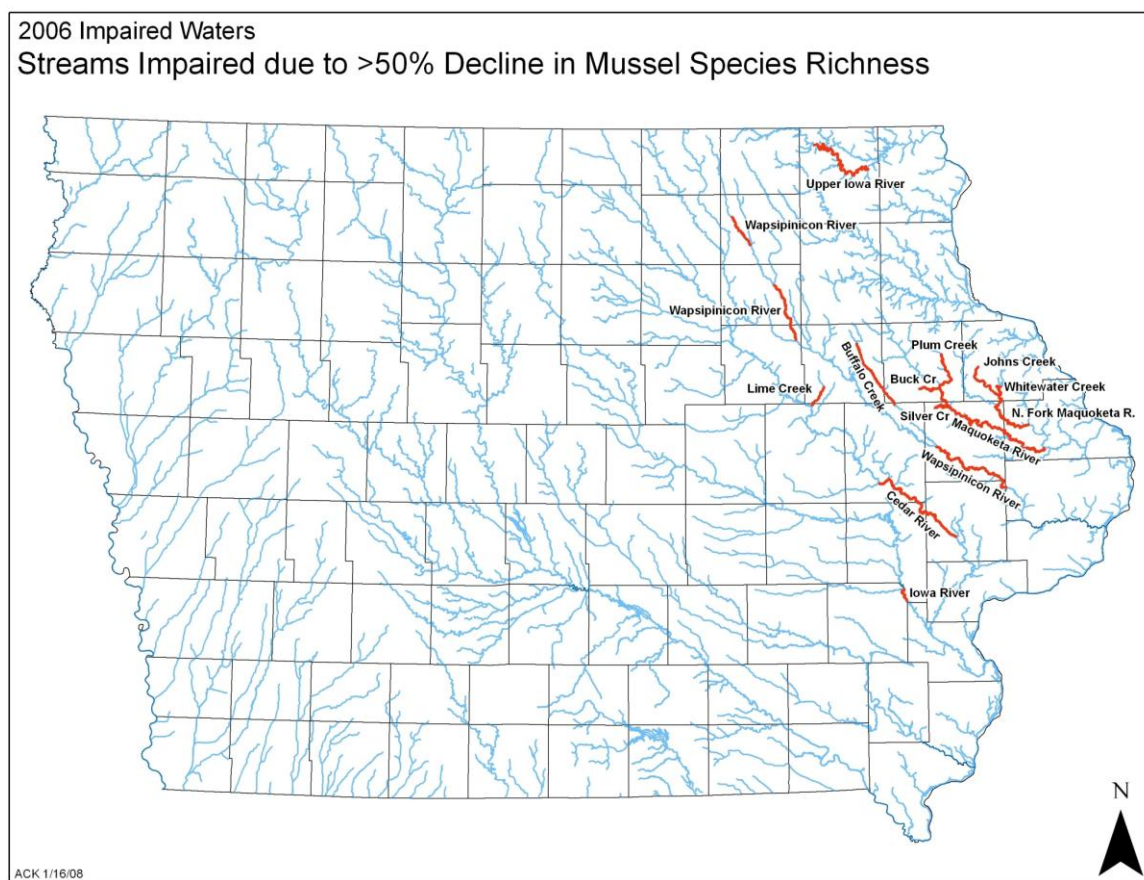


Figure 2.7: The Iowa River is one of many rivers in Iowa listed on the Iowa Department of Natural Resource's Section 303 (d) list of impaired waters due to declines in mussel populations.

Source: IDNR 2006

CHAPTER 3
THE EFFECT OF NATIVE FRESHWATER MUSSELS
ON NITROGEN DYNAMICS IN FLOW-THROUGH
MESOCOSMS: PART I

Purpose

The objective of this chapter was to test Hypothesis 1 by utilizing highly time resolved data to evaluate the effects of mussels on nitrogen dynamics in laboratory-based, flow-through mesocosms. We investigated the variations in nitrate, ammonium, and phytoplankton concentrations in mesocosms that were fed with a continuous supply of untreated river water. We then quantified a first-order “mussel effect rate” for nitrate, ammonium, and phytoplankton as a means to predict the effect of mussels in streams and rivers.

Abstract

The effects of mussels on nitrate, ammonium, and phytoplankton in the overlying water were investigated using flow-through mesocosms. Highly time resolved (30 min) water chemistry data were collected for 40 d in mesocosms ($n = 4$) containing mussels and mesocosms ($n = 2$) without mussels (control). The flow-through mesocosms design was determined to sufficiently mimic natural conditions for temperature, photosynthetically active radiation, and phytoplankton composition and biomass. Concentration changes for nitrate, ammonium, and phytoplankton were determined to be significantly different (ANCOVA, $p < 0.05$) between the mussel treatments and control treatments. This study highlighted the calibration challenges associated with relatively new commercial sensors. The less than accurate calibrations achieved when comparing sensor measurements to grab samples provided little confidence in the determined mussel effects and calculated mussel effect rates.

Introduction

The development of successful nitrogen management plans for large river systems is dependent on understanding how aquatic systems naturally process nitrogen. Highly time resolved data provide a means to capture variations in nitrogen concentrations that are known to fluctuate temporally and spatially in both small and large scale systems (Bark 2010; Mulholland et al. 2006; Pellerin et al. 2009; Scholefield et al. 2005). These variations in nitrogen concentrations are often influenced by the interactions between river hydrology and river ecology. However, the interactions of these biotic and abiotic processes are not well understood in large river systems (Newton et al. 2011). Thus, it is important to understand the organisms that influence these processes and how they affect the ability of the river to naturally process nitrogen.

Mussels are expected to influence the nitrogen cycle by removing phytoplankton (their primary food source in large rivers) from the overlying water and depositing reduced forms of nitrogen near the sediment-water interface. This mussel-facilitated deposition of reduced nitrogen near the sediment-water interface occurs through excretion of ammonium and through biodeposition of feces and pseudofeces (Vaughn and Hakenkamp 2001). Excretion rates vary with species, size, age, food availability, and environmental conditions (Vaughn et al. 2008). It is expected that the mussel excretion of ammonium will increase ammonium concentrations in the overlying water. Under aerobic conditions, ammonium can be converted to nitrite and further oxidized to nitrate by nitrifying bacteria that are ubiquitous in bulk river water and in oxic sediments. Therefore, it is also expected that the ammonium excreted by mussels will be nitrified to nitrate, causing an increase in nitrate concentrations in the overlying water.

River managers are especially concerned with nitrogen concentrations in the overlying water that can be easily transported downstream. However, the effects of mussels on nitrogen dynamics in the overlying water of large river systems are not well understood. Highly time resolved data have been shown to reveal unique biogeochemical

cycles influenced by aquatic organisms in a small agricultural watershed (Loperfido et al. 2010). Thus, the objective of this study was to utilize highly time resolved data to quantify the effect of mussel populations on nitrogen processing in laboratory-based, flow-through mesocosms.

Materials and Methods

Study Area and Organisms

The UMR drains ~480,000 km² and consists of 14 major tributaries. One such tributary is the Iowa River, a ~520 km long tributary in eastern Iowa that drains a watershed area of ~32,740 km². Similar to most of the tributaries in the UMR, predominant land cover in the Iowa River Basin is agricultural (>90%) with principal crops being corn, soybeans, hay, and oats. The extensively row-cropped landscape is one of many Iowa rivers with significant nitrogen management issues. The annual export of nitrate from Iowa surface waters is estimated to contribute 11.3% of the nitrate that the Mississippi River delivers to the Gulf of Mexico, despite Iowa occupying <5% of the total drainage area (Alexander et al. 2008).

The Iowa River has historically been defined as one of the State's best mussel habitats (Frest 1987) and is not yet infested with zebra mussels (USACE 2002). However, data collected in mussel surveys from 1984-1985 and 1988-1999 show >50% decline in species richness (Arbuckle and Downing 2000). This sharp decline in species richness has caused many segments of the Iowa River to be listed on the Iowa Department of Natural Resource's Section 303 (d) list of impaired waters since 2002 (IDNR 2011). Despite the recent decline in mussel populations, the Iowa River contains a moderate diversity of mussels with 25 species found in recent surveys (ESI 2012). *Amblema plicata* and *Lampsilis cardium* were selected for this study due to their abundance in the Iowa River (Zohrer 2006) and throughout the UMR (Newton et al. 2011).

Mesocosm Experiment

A 40 d mesocosm experiment was conducted from February 2012 to March 2012 using flow-through mesocosms (61 x 61 x 61 cm) fed with a continuous supply of untreated Iowa River water (Figure 3.1). Treatments ($n = 6$) included 4 mesocosms containing mussels and 2 mesocosms without mussels (control). Mesocosms were lined with clean, dry sand and filled with 140 L of Iowa River water. Continuous flow of Iowa River water was provided via a 415-L head tank. The gravity-fed system provided an average flow rate of $\approx 16 \text{ L h}^{-1}$, which resulted in an average hydraulic retention time of $\approx 9 \text{ h}$ in each mesocosm. Complete mixing in each mesocosm was provided by 1500 L h^{-1} submersible pumps. Mesocosms were illuminated with two 1000-watt solar simulators on a 12:12 h light-dark cycle.

Twenty-five adult *A. plicata* (mean, 95 mm) and 25 adult *L. cardium* (mean, 120 mm) were obtained from the Iowa River in November 2011 (Figure 3.2). Between November 2011 and February 2012, flow rate, light intensity, circulation rate, and sensor sampling rate were optimized in preparation for the full-scale experiment. The 40 d experiment began 1 February 2012. We placed 13 mussels per mesocosm ($40 \text{ mussels m}^{-2}$); this density approximates that found in mussel beds in the UMR (Newton, unpublished data). Mussel beds are defined as aggregations of mussels where many or all of the species found co-occur at densities 10 to 100 times higher than those outside the bed.

Water Chemistry Sensing

Hydrolab multi-probe sondes ($n = 4$, model DS5, Hach Chemical Company, Loveland, Colorado) were used to measure highly time resolved (30 min) water chemistry data in the overlying water of each mesocosm and for the head tank (river water influent). One Hydrolab was shared between duplicate mesocosms as enabled by valve-actuated mesocosm outlets that automatically rinsed, filled, and drained the Hydrolab sample cup (Figure 3.3). The Hydrolabs measured chlorophyll *a* (compact

fluorometer), ammonium (ion selective electrode), nitrate (ion selective electrode), dissolved oxygen (luminescent dissolved oxygen), temperature (variable resistance thermistor), pH (KCl impregnated glass bulb), and conductivity (fixed potential electrodes). Measurements were taken in the overlying water 10 cm above the substrate.

Custom-made tipping buckets with magnetic reed switches were used to measure influent flow and an unrestricted overflow was used to control outflow.

Photosynthetically active radiation (PAR) sensors were used to measure light intensity at the substrate (model SQ-120, Apogee Instruments, Logan, Utah) and water surface (model LI190SB-L, Campbell Scientific, Logan, Utah) of each mesocosm. All Hydrolab-measured water chemistry data were collected and stored using 2 dataloggers (model CR1000, Campbell Scientific, Logan, Utah). Specifications for each of the sensors used can be found in the Appendix (Table A.1).

Grab Samples

Grab samples ($n = 15$) were collected periodically from the overlying water of each mesocosm and from the head tank for comparison to Hydrolab measurements. Nitrate was determined using the LaMotte Nitrate Test Kit Method and a Trilogy Nitrate/Nitrite Module (Turner Designs, Sunnyvale, California). Additional grab samples ($n = 4$) were analyzed by the State Hygienic Laboratory at the University of Iowa (Coralville, Iowa). Nitrate was determined by cadmium reduction using EPA Method 353.2. Ammonium was determined by the alkaline phenol-based method using Lachat Method 10-107-06-1-J. Chlorophyll *a* was determined by fluorescence using EPA Method 445.0 Rev. 1.2. Phytoplankton biomass was determined by microscopic examination and counting using Standard Methods 10200 (APHA 1996). Results from simultaneously collected chlorophyll *a* and phytoplankton samples were used to create a response factor to calibrate the chlorophyll *a* sensor on the Hydrolabs.

Measured chlorophyll *a* concentrations ($\mu\text{g L}^{-1}$) were converted to phytoplankton biomass (mg L^{-1}) based on a linear relationship established using the phytoplankton biomass concentrations determined by the State Hygienic Laboratory. The mass of nitrogen in total phytoplankton biomass was calculated by using the empirical formula $\text{C}_{106}\text{H}_{263}\text{O}_{110}\text{N}_{16}\text{P}$ to represent phytoplankton (Chapra 1997). Phytoplankton biomass (mg L^{-1}) was converted to phytoplankton biomass as nitrogen (herein referred to as phytoplankton, mg-N L^{-1}) by using the following equation:

$$\text{Equation 3.1} \quad (X \text{ mg L}^{-1} \text{ Phyto}) * (1 \text{ mole Phyto} / 3550 \text{ g}) * (15 \text{ mole N} / 1 \text{ mole Phyto}) * \dots \\ \dots (14 \text{ g N} / 1 \text{ mole N}) = X(0.063) \text{ mg-N L}^{-1}$$

Data Analysis

The raw Hydrolab measurements for nitrate, ammonium, and phytoplankton revealed diurnal features and trends in nitrogen dynamics, but also highlighted the calibration challenges associated with relatively new commercial sensors. These challenges were addressed through point-by-point comparisons to grab sample data and the development of calibration factors that were applied to each Hydrolab sensor data series. This technique is analogous to the widely used internal standards method for the most accurate quantification of chemical species by gas or liquid chromatography. The calibration factors were derived by dividing the reported Hydrolab concentrations by the respective grab sample concentrations. The individual calibration factors were then averaged to obtain a single calibration factor that was applied to the raw Hydrolab data for nitrate, ammonium, and phytoplankton.

Analysis of covariance (ANCOVA) was used to determine the statistical significance between the mussel and control treatments using the General Linear Model with flow, temperature, time, and PAR as covariates. Statistical significance was defined by the Tukey Method 95% simultaneous confidence intervals. ANCOVA analyses were completed using Minitab (version 16; Minitab Inc., State College, Pennsylvania).

To quantify the effect of mussels on nitrate, ammonium, and phytoplankton, concentrations measured at each time step in the head tank were subtracted from the concentrations measured in each mesocosm as a means to normalize the data. This was done to offset for rapid changes in water chemistry attributable to the Iowa River. Linear regressions were performed on the average treatment concentrations to determine the rate of removal/production of nitrate, ammonium, and phytoplankton for each treatment.

The rate attributable to mussels was determined by subtracting the rate in the control treatments from the rate in the mussel treatments. This “mussel effect rate” was standardized to tissue dry mass to correct for size differences between the two mussel species. Dry tissue mass (M , g) was predicted for each mussel based on measured shell length (L , mm) and using the allometric function $M = aL^b$. The values for the parameters a and b were obtained from data on mussels in Navigation Pool 10 of the UMR (Newton et al. 2011).

The percent difference and coefficient of determination (R^2) were calculated for nitrate, ammonium, and phytoplankton as an additional means to evaluate the difference between mussel and control treatments. The percent difference was calculated at each time step and then averaged over the entire experimental time period to obtain an average percent difference.

Results

System Characterization

The highly time resolved water chemistry data were used to quantify characteristics of the overall laboratory mesocosm (Figure 3.4). Water temperature remained relatively constant throughout the experiment with an average value of $\approx 15^\circ\text{C}$. During the 12 h light cycle of the solar simulator, PAR at the water surface was $\approx 750 \mu\text{mol m}^{-2} \text{s}^{-1}$ and PAR at the substrate was $\approx 100 \mu\text{mol m}^{-2} \text{s}^{-1}$. Diatoms were the most dominant taxa present in the mesocosms (82%), followed by protozoa (8%) and

chlorophyta (5%) (Figure 3.5). Total phytoplankton biomass in the mesocosms (11.5 mg L⁻¹) was within the range observed in the Iowa River (4.5 to 22.4 mg L⁻¹).

The Effect of Mussels

Analysis of the nitrogen dynamics in the overlying water indicated that nitrate was the most dominant species in the mesocosms. The raw Hydrolab data for nitrate revealed a less than accurate calibration when compared with the grab sample measurements (Figure 3.6). Therefore, the calibration factors (Table 3.1) derived from grab sample comparison were used to recalibrate all Hydrolab data. The calibration factors for Mesocosm 1 and Mesocosm 2 (control treatments) were 1.03 and 1.54, respectively. The calibration factors for Mesocosm 3, Mesocosm 4, Mesocosm 5, and Mesocosm 6 (mussel treatments) were 1.47, 1.00, 1.05, and 1.38, respectively. The calibration factors for the two Hydrolabs measuring the head tank (river influent) were 1.80 and 1.08, respectively.

The calibrated Hydrolab data (Figure 3.7) indicated lower nitrate concentrations present in the mussel treatments compared to the control treatments (percent difference = -12.8%, $R^2 = 0.88$) (Table 3.2). Conversely, the grab sample measurements indicated that nitrate concentrations were higher in the mussel treatments (28.9%, $R^2 = 0.29$). The results of the ANCOVA analysis revealed that nitrate concentrations measured in the mussel treatments were significantly different from those observed in the control treatments ($p < 0.05$).

The raw Hydrolab data for ammonium also revealed a less than accurate calibration when compared with the grab sample measurements (Figure 3.8). Therefore, the calibration factors (Table 3.3) derived from grab sample comparison were used to recalibrate all Hydrolab data. The calibration factors for Mesocosm 1 and Mesocosm 2 (control treatments) were 3.00 and 3.80, respectively. The calibration factors for Mesocosm 3, Mesocosm 4, Mesocosm 5, and Mesocosm 6 (mussel treatments) were

5.80, 3.20, 4.80 and 6.20, respectively. The calibration factors for the two Hydrolabs measuring the head tank (river influent) were 3.20 and 4.20, respectively.

The calibrated Hydrolab data (Figure 3.9) indicated ammonium concentrations were lower in the mussel treatments compared to the control treatments (-11.0%, $R^2 = 0.43$) (Table 3.2). The grab sample measurements were all below detection limits so the difference between the control and mussel treatments could not be determined. The results of the ANCOVA analysis revealed that ammonium concentrations measured in the mussel treatments were significantly different from those observed in the control treatments ($p < 0.05$).

Similar to nitrate and ammonium, the raw Hydrolab data for phytoplankton revealed a less than accurate calibration when compared with the grab sample measurements (Figure 3.10). Therefore, the calibration factors (Table 3.4) derived from grab sample comparison were used to recalibrate all Hydrolab data. The calibration factors for Mesocosm 1 and Mesocosm 2 (control treatments) were 1.00 and 0.51, respectively. The calibration factors for Mesocosm 4 and Mesocosm 5 (mussel treatments) were 0.67 and 1.00, respectively. The calibration factors for the two Hydrolabs measuring the head tank (river influent) were 1.16 and 1.33, respectively. The chlorophyll *a* sensor on the Hydrolab measuring Mesocosm 3 and Mesocosm 6 was inoperable so these mesocosms were not included in the phytoplankton analysis.

The calibrated Hydrolab data (Figure 3.11) revealed decreased concentrations of phytoplankton in the mussel treatments as compared to the control treatments (-22.9%, $R^2 = 0.12$) (Table 3.2). The grab sample measurements also indicated lower concentrations of phytoplankton in the mussel treatments (-23.5%). The results of the ANCOVA analysis revealed that phytoplankton concentrations measured in the mussel treatments were significantly different from those observed in the control treatments ($p < 0.05$).

Quantifying the Mussel Effect

The calibrated and normalized Hydrolab nitrate data (Figure 3.12) indicated that nitrate was decreasing in both treatments relative to the river influent (head tank). The linear regressions performed on the normalized Hydrolab data indicated that the rate of removal in the mussel treatments ($-0.016 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.56$) was greater than the rate of removal in the control treatments ($-0.012 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.70$) (Table 3.5). This resulted in a nitrate mussel effect rate of $-0.004 \text{ mg-N L}^{-1} \text{ d}^{-1}$, which demonstrated that the amount of nitrate in the mussel treatments was decreasing over time relative to the amount of nitrate in the control treatments.

The calibrated and normalized Hydrolab ammonium data (Figure 3.13) indicated that ammonium was increasing in the control treatments and decreasing in the mussel treatments relative to the river influent. Thus, the linear regressions performed on the normalized Hydrolab data indicated ammonium was being produced in the control treatments ($0.0004 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.29$) and being removed in the mussel treatments ($-0.0001 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.08$) (Table 3.5). This resulted in an ammonium mussel effect rate of $-0.001 \text{ mg-N L}^{-1} \text{ d}^{-1}$, which demonstrated that the amount of ammonium in the mussel treatments was decreasing over time relative to the amount of ammonium in the control treatments.

The calibrated and normalized Hydrolab phytoplankton data (Figure 3.14) indicated that phytoplankton was increasing in both treatments relative to the river influent. The linear regressions performed on the normalized Hydrolab data indicated that the rate of production in the mussel treatments ($0.0009 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.003$) was higher than the rate of production in the control treatments ($0.0007 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.001$) (Table 3.5). This resulted in a phytoplankton mussel effect rate of $0.0002 \text{ mg-N L}^{-1} \text{ d}^{-1}$, which demonstrated that the amount of phytoplankton in the mussel treatments was increasing over time relative to the amount of phytoplankton in the control treatments.

Discussion

System Characterization

The experimental setup for this study allowed us to meet our goal of replicating the natural river environment as closely as possible in our laboratory-based mesocosm system. The average water temperature in the mesocosms ($\approx 15^{\circ}\text{C}$) was similar to the average water temperature in the Iowa River from March-May and September-November (Espinosa-Villegas et al. 2004). The PAR at the water surface of the mesocosms ($\approx 750 \mu\text{mol m}^{-2} \text{s}^{-1}$) was comparable to the PAR observed on a typical day under natural conditions ($\approx 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Alados et al. 2000). The flow rates in the mesocosms were kept significantly lower than typical flow rates in the Iowa River (Espinosa-Villegas et al. 2004) so the effects of mussels could be more easily quantified. The mesocosms were also able to maintain similar phytoplankton composition and biomass to those observed in the Iowa River. The Iowa River phytoplankton communities contained an increased distribution of taxa but diatoms were still the most dominant taxa present in both systems. This difference in taxa distribution is likely attributable to river productivity conditions based on when the Iowa River samples were collected (September 2011) compared to when the mesocosm samples were collected (March 2012).

The Effect of Mussels

The highly time resolved data collected in this study revealed diurnal features and trends in nitrogen dynamics, but also highlighted the calibration challenges associated with relatively new commercial sensors. We partially addressed these challenges by using calibration factors calculated from grab sample measurements. As expected, the grab sample measurements indicated nitrate concentrations were higher in the mussel treatments compared to the control treatments. However, the calibrated Hydrolab measurements for nitrate indicated concentrations were lower in the mussel treatments.

This was not expected given that nitrate concentrations have been shown to increase with increasing mussel biomass (Vaughn et al. 2004). Furthermore, it was expected that the well-oxygenated conditions of the mesocosms would facilitate the conversion of ammonium excreted by mussels into nitrate; thus increasing nitrate concentrations in the overlying water.

The calibrated Hydrolab data also revealed ammonium concentrations were lower in mussel treatments, which was not expected as the literature indicates ammonium concentrations increase in the presence of mussels (Vaughn et al. 2004; Vaughn and Hakenkamp 2001; Vaughn et al. 2008). This observation could not be confirmed, as grab sample measurements for the mussel and control treatments were below the method detection limit. This highlighted the need for a more sensitive ammonium measurement procedure.

The calibrated Hydrolab data and grab sample measurements both indicated that phytoplankton concentrations were lower in the mussel treatments. This was expected due to phytoplankton being the primary food source of mussels in large river systems (Thorp et al. 1998). Furthermore, studies have shown that chlorophyll *a* concentrations tend to decrease in systems containing mussels (Boltovskoy et al. 2009; Prins et al. 1995; Vaughn et al. 2004).

Due to the differences observed between the grab samples and Hydrolab data for ammonium and nitrate, we have little confidence in any of the nitrate, ammonium, or phytoplankton results derived from the calibrated Hydrolab data, including the calculated mussel effect rates. We expect that the less than adequate results obtained from the calibrated Hydrolabs are due to an insufficient number of grab samples used to develop the calibration factors. This demonstrates that a more extensive set of grab sample measurements is essential, especially if sensors measuring highly time resolved data are to be used to assess the effect of mussel populations on nitrogen processing in our mesocosms.

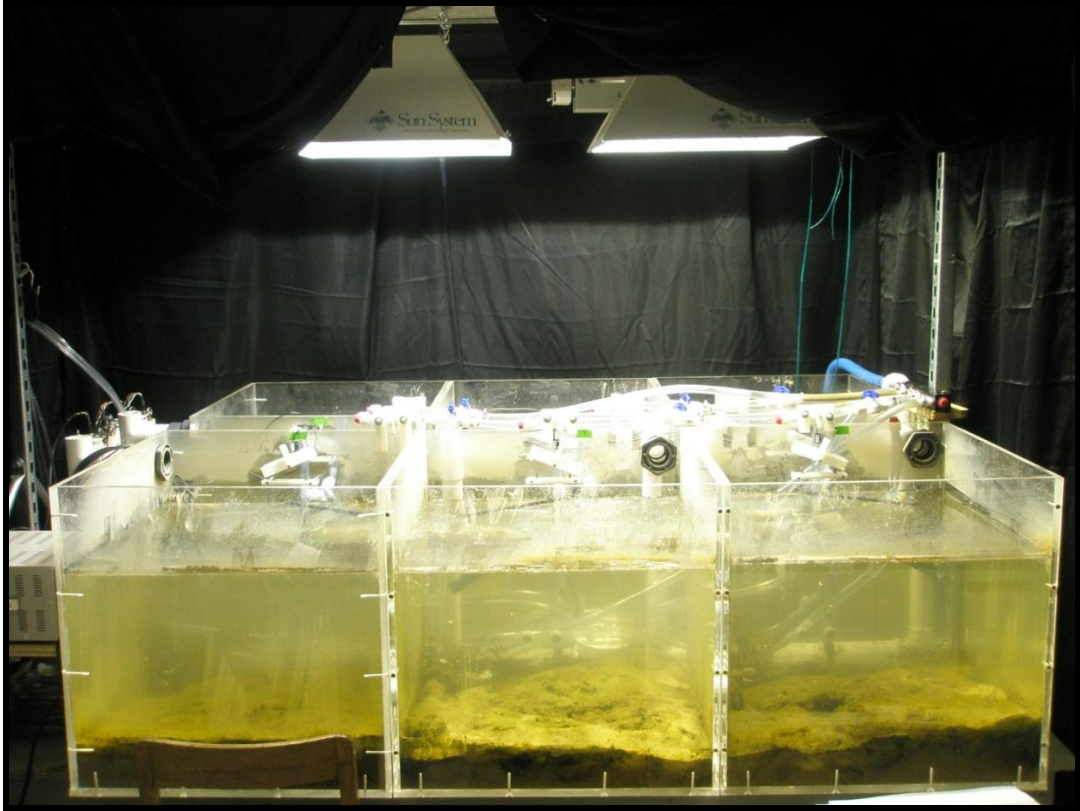


Figure 3.1: Full mussel laboratory mesocosm setup (head tank containing continuous supply of Iowa River water not shown).

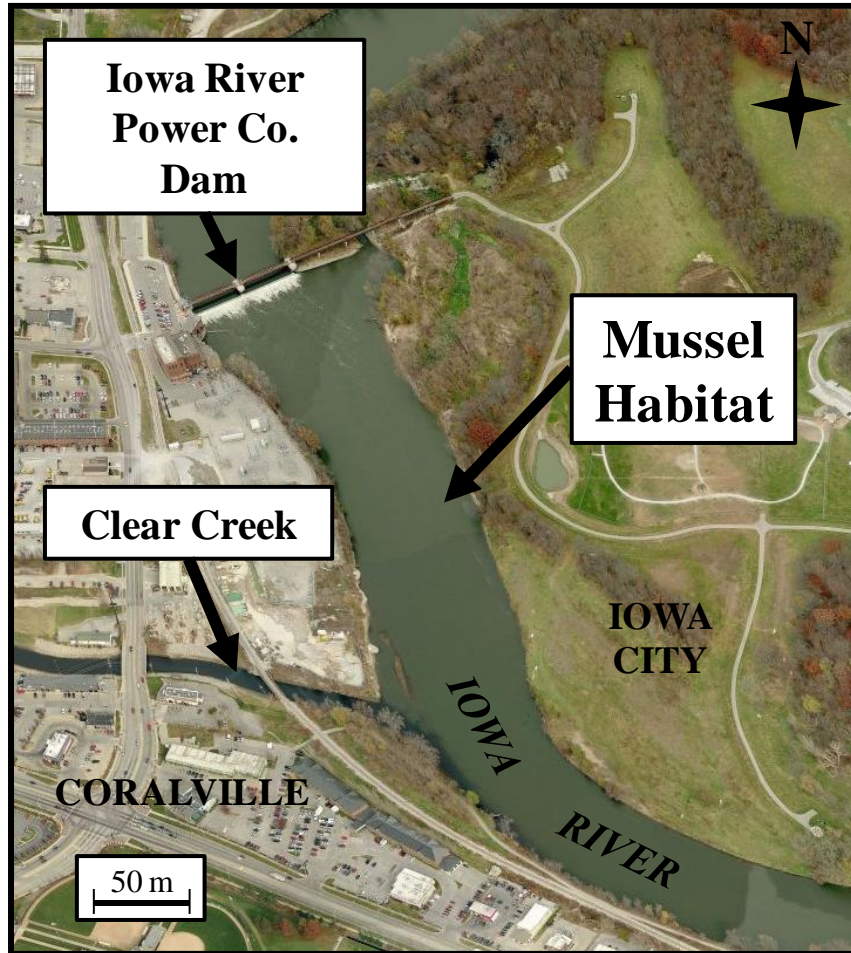


Figure 3.2: All mussels included in the study were obtained from a mussel habitat in the Iowa River located in Iowa City, Iowa near the mouth of Clear Creek.

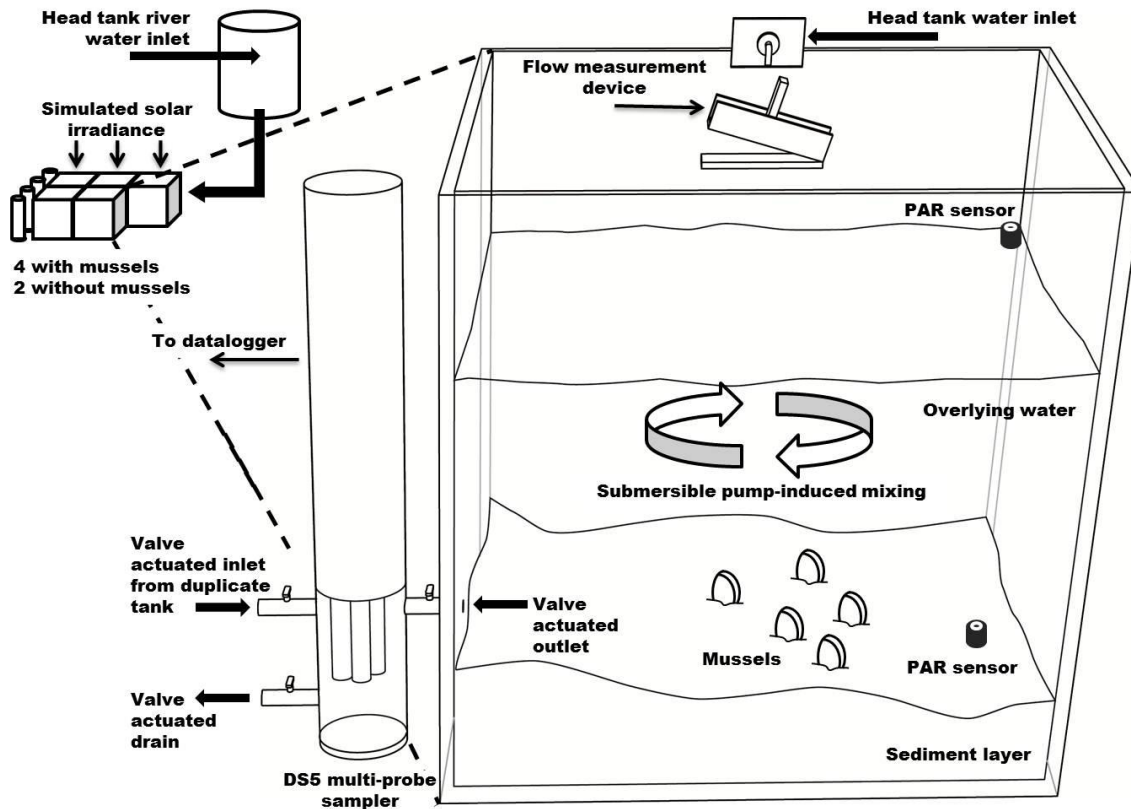


Figure 3.3: Detailed schematic of laboratory-based, flow-through mesocosm irradiated with simulated sunlight and equipped with multi-probe Hydrolab, PAR sensors, a flow measurement device, and a re-circulating pump.

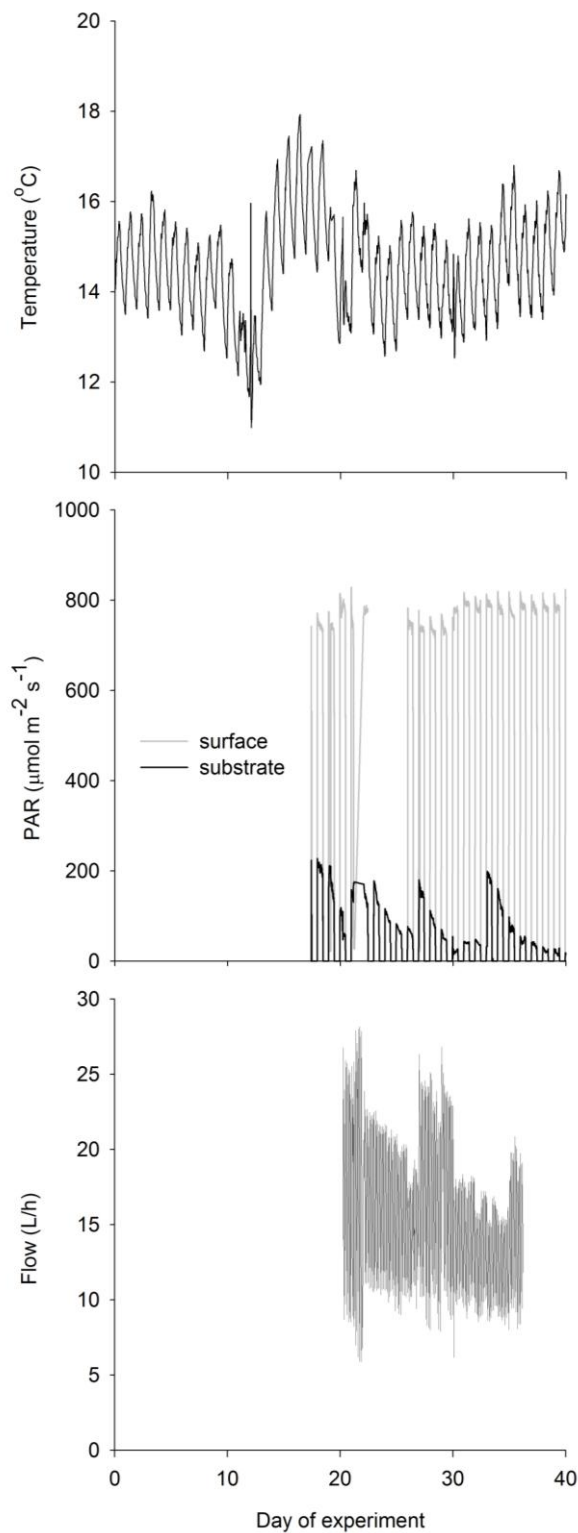


Figure 3.4: The influent river water temperature was measured for the entire 40 d experiment. PAR sensors were added after 18 d to enable the measurement of simulated solar irradiance. Flow was measured after 20 d following the installation of custom flow sensors on each mesocosm.

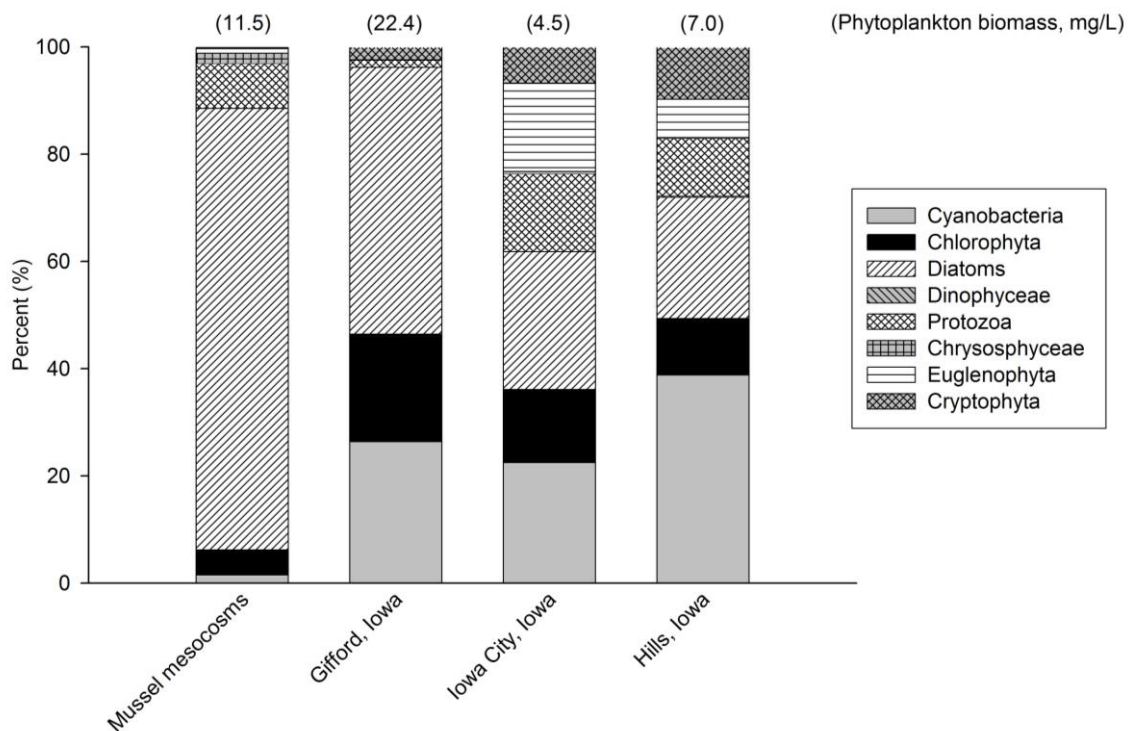


Figure 3.5: The phytoplankton taxa distribution in the mussel mesocosms was more abundant in diatoms and less abundant in cyanobacteria as compared to 3 locations along the Iowa River. Phytoplankton biomass (shown parenthetically) was 11.5 mg L^{-1} in the mussel mesocosms at the time of sampling which was within the range (4.5 to 22.4 mg L^{-1}) measured in the river. These data provide evidence that the primary mussel food sources in the mesocosms is similar to that found in the natural environment.

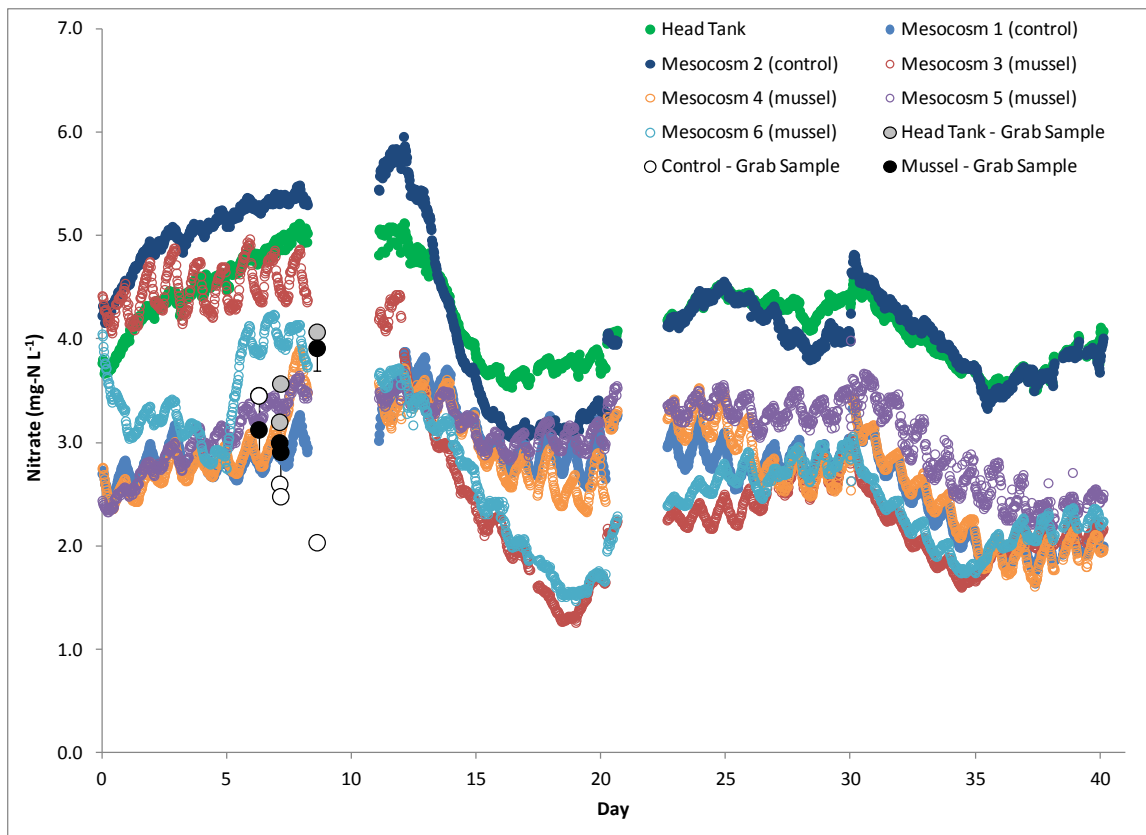


Figure 3.6: Grab sample measurements and raw Hydrolab data for nitrate (mg-N L^{-1}). Hydrolab measurements are shown for each of the mesocosms and grab samples were averaged for each treatment. Error bars on grab sample measurements represent ± 1 SD. Gaps in data are attributable to Hydrolab error.

Table 3.1: Nitrate Hydrolab measurements (mg-N L^{-1}) and corresponding grab sample measurements (mg-N L^{-1}) used to calculate calibration factors.

	Day	Mesocosm 1 (3) ^a	Mesocosm 2 (4)	Mesocosm 3 (2)	Mesocosm 4 (3)	Mesocosm 5 (1)	Mesocosm 6 (2)	Head Tank (4) ^b	Head Tank (1)
Hydrolab (mg-N L^{-1})	6.27	2.78	5.30	4.41	2.82	3.21	3.88	6.03	3.58
	7.10	2.90	5.31	4.45	2.96	3.36	3.97	6.18	3.74
	7.15	2.91	5.40	4.49	3.08	3.34	3.99	6.20	3.74
	8.60	---	---	---	---	---	---	---	---
Grab Sample (mg-N L^{-1})	6.27	3.46	3.45	3.50	2.83	3.35	2.82		3.46
	7.10	2.60	---	3.00	---	3.00	---		3.20
	7.15	2.48	---	2.69	---	3.13	---		3.57
	8.60	2.04	---	4.07	---	3.76	---		4.07
Calibration Factor	6.27	0.80	1.54	1.26	1.00	0.96	1.38	1.74	1.04
	7.10	1.12	---	1.48	---	1.12	---	1.93	1.17
	7.15	1.17	---	1.67	---	1.07	---	1.74	1.05
	8.60	---	---	---	---	---	---	---	---
Average		1.03	1.54	1.47	1.00	1.05	1.38	1.80	1.08
Standard Deviation		0.20	---	0.20	---	0.08	---	0.11	0.07
Coefficient of Variation		19.4%	---	13.9%	---	7.9%	---	6.1%	6.8%

^a The number of the Hydrolab used to measure the water chemistry in each mesocosm is given in parentheses

^b The mesocosm system was set up so that the head tank was measured by two different Hydrolabs

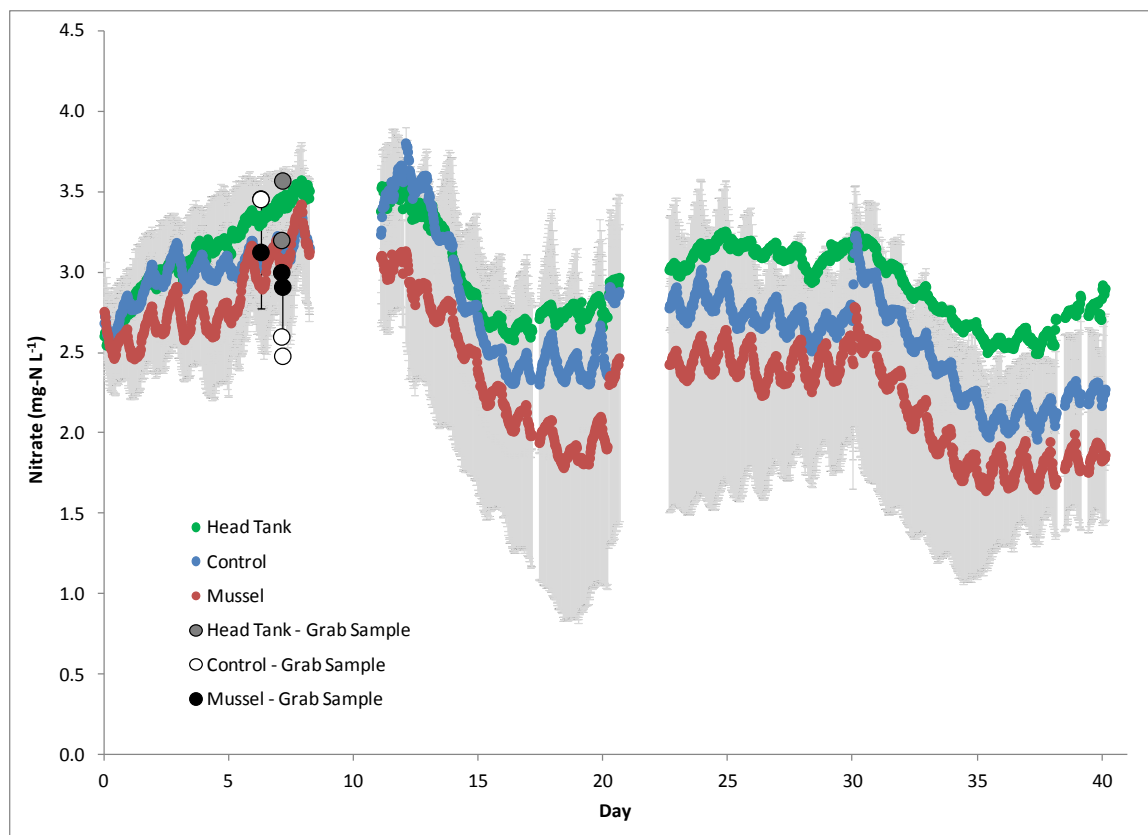


Figure 3.7: Average grab sample measurements and calibrated Hydrolab measurements for nitrate (mg-N L^{-1}). Error bars represent ± 1 SD. Gaps in data are attributable to Hydrolab error.

Table 3.2: Average percent difference and coefficient of determination (R^2) values between control and mussel treatments for grab samples and calibrated Hydrolab measurements.

Parameter	Percent Difference		Coefficient of Determination (R^2)	
	Grab Sample	Hydrolab	Grab Sample	Hydrolab
Nitrate	7.7%	-12.8%	0.90	0.88
Ammonium	0.0%	-11.0%	---	0.43
Phytoplankton	-23.5%	-22.9%	---	0.12

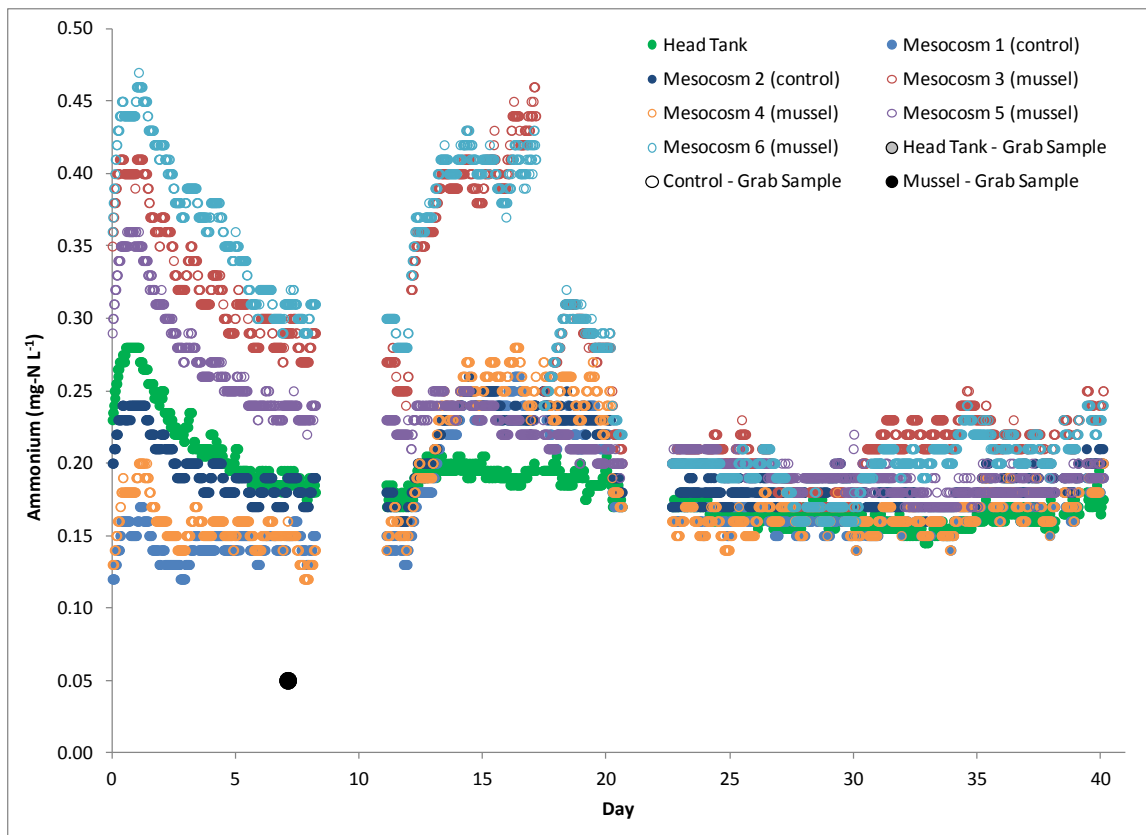


Figure 3.8: Grab sample measurements and raw Hydrolab data for ammonium (mg-N L⁻¹). Hydrolab measurements are shown for each of the mesocosms and grab samples were averaged for each treatment. Gaps in data are attributable to Hydrolab error.

Table 3.3: Ammonium Hydrolab measurements (mg-N L^{-1}) and corresponding grab sample measurements (mg-N L^{-1}) used to calculate calibration factors.

	Day	Mesocosm 1 (3) ^a	Mesocosm 2 (4)	Mesocosm 3 (2)	Mesocosm 4 (3)	Mesocosm 5 (1)	Mesocosm 6 (2)	Head Tank (4) ^b	Head Tank (1)
Hydrolab (mg-N L^{-1})	7.10	0.15	0.19	0.29	0.16	0.24	0.31	0.16	0.21
Grab Sample (mg-N L^{-1})	7.10	0.05	0.05	0.05	0.05	0.05	0.05		0.05
Calibration Factor	7.10	3.00	3.80	5.80	3.20	4.80	6.20	3.20	4.20
Average		3.00	3.80	5.80	3.20	4.80	6.20	3.20	4.20
Standard Deviation		---	---	---	---	---	---	---	---
Coefficient of Variation		---	---	---	---	---	---	---	---

^a The number of the Hydrolab used to measure the water chemistry in each mesocosm is given in parentheses

^b The mesocosm system was set up so that the head tank was measured by two different Hydrolabs

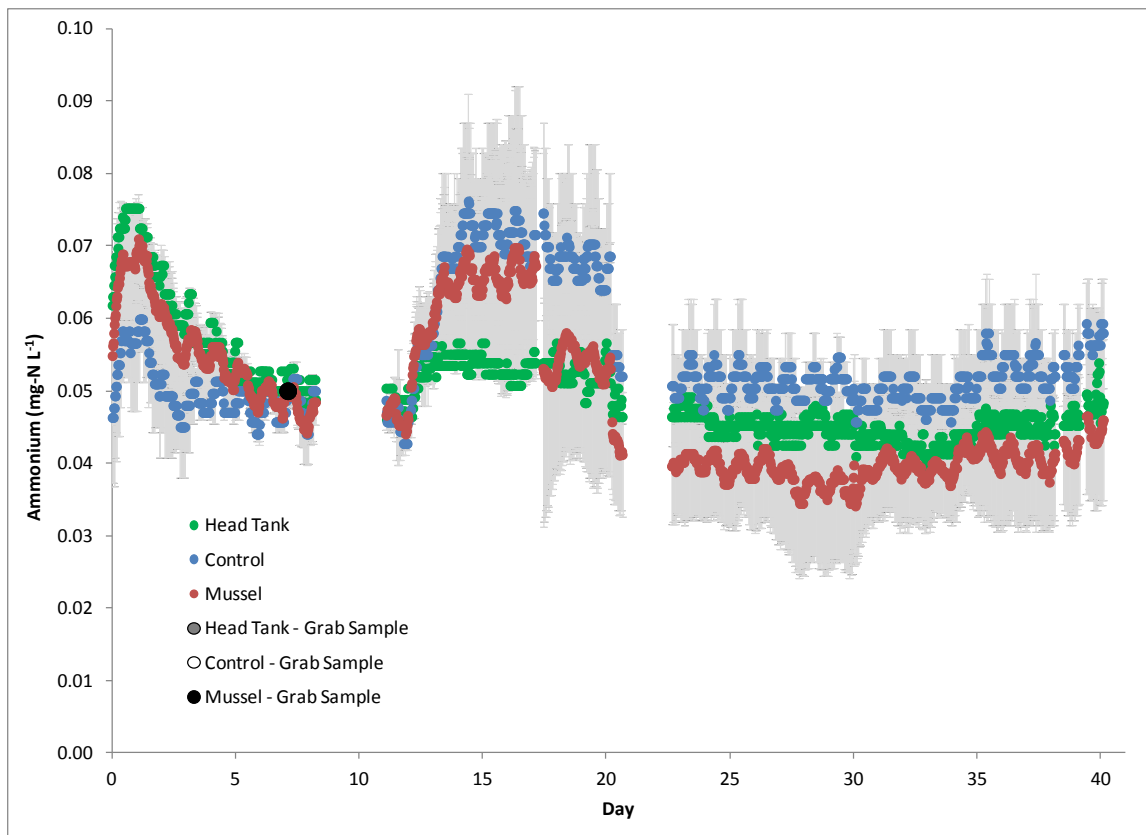


Figure 3.9: Average grab sample measurements and calibrated Hydrolab measurements for ammonium (mg-N L^{-1}). Error bars represent ± 1 SD. Gaps in data are attributable to Hydrolab error.

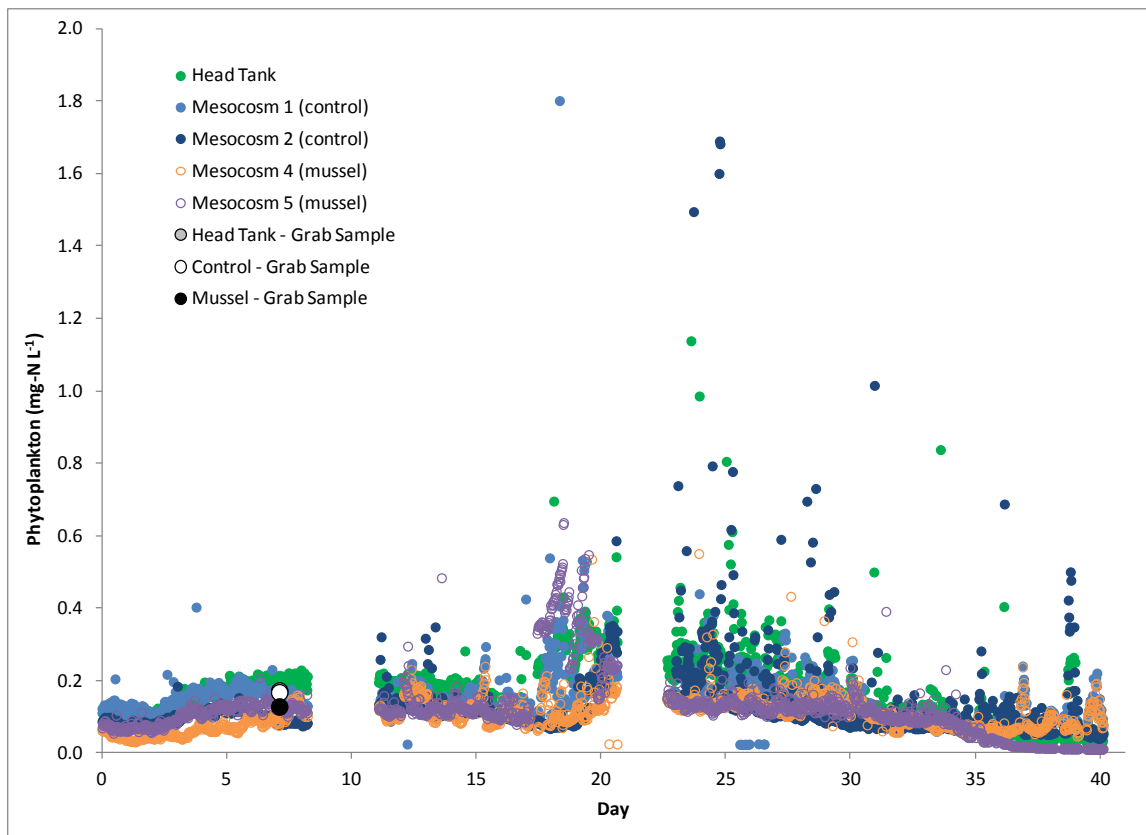


Figure 3.10: Grab sample measurements and raw Hydrolab data for phytoplankton (mg-N L⁻¹). Hydrolab measurements are shown for each of the mesocosms and grab samples were averaged for each treatment. Gaps in data are attributable to Hydrolab error.

Table 3.4: Phytoplankton Hydrolab measurements (mg-N L^{-1}) and corresponding grab sample measurements (mg-N L^{-1}) used to calculate calibration factors.

	Day	Mesocosm 1 (3) ^a	Mesocosm 2 (4)	Mesocosm 3 (2) ^b	Mesocosm 4 (3)	Mesocosm 5 (1)	Mesocosm 6 (2) ^b	Head Tank (4) ^c	Head Tank (1)
Hydrolab (mg-N L^{-1})	7.10	0.17	0.09	---	0.08	0.12	---	0.20	0.23
Grab Sample (mg-N L^{-1})	7.10	0.17	---	0.13	---	0.12	---	0.17	
Calibration Factor ^d	7.10	1.00	0.51	---	0.67	1.00	---	1.16	1.33
Average		1.00	0.51	---	0.67	1.00	---	1.16	1.33
Standard Deviation		---	---	---	---	---	---	---	---
Coefficient of Variation		---	---	---	---	---	---	---	---

^a The number of the Hydrolab used to measure the water chemistry in each mesocosm is given in parentheses

^b The chlorophyll *a* sensor on Hydrolab 2 was inoperable

^c The mesocosm system was set up so that the head tank was measured by two different Hydrolabs

^d The Hydrolab values for Mesocosm 1 and 5 (calibration factor = 1) were used to calculate the calibration factors for Mesocosm 2 and 4, respectively

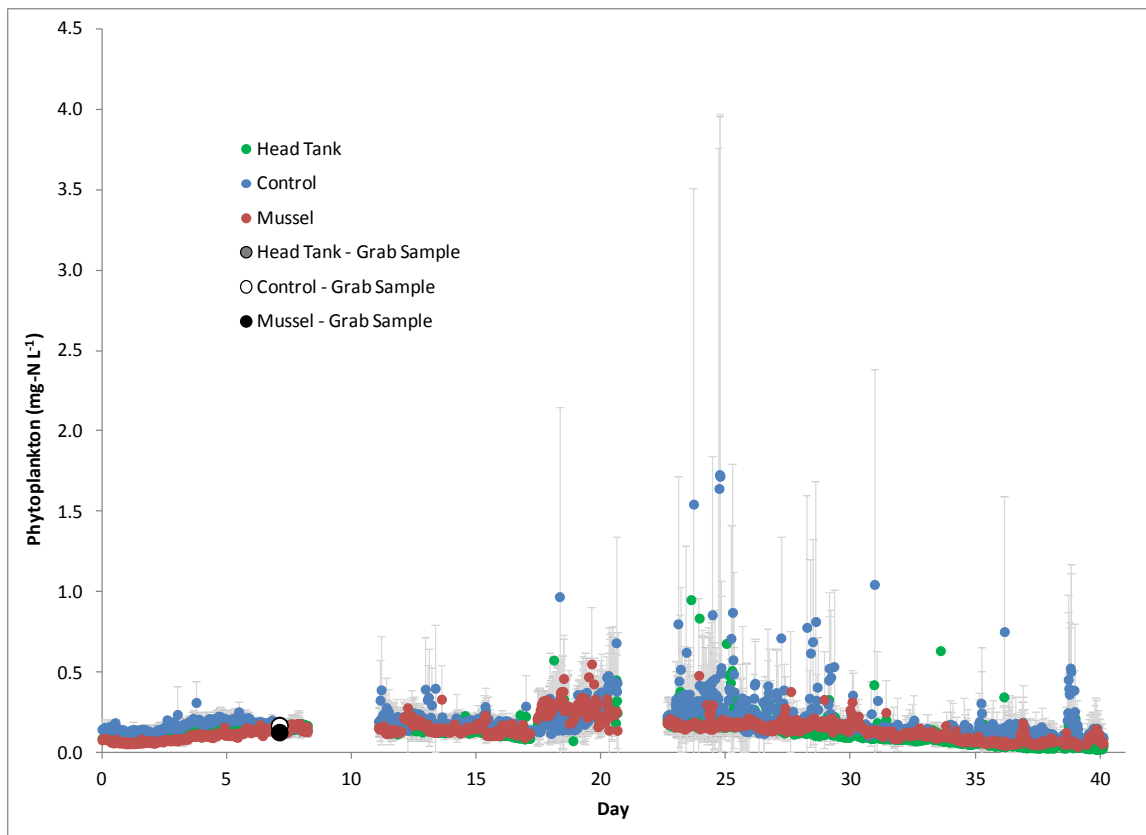


Figure 3.11: Average grab sample measurements and calibrated Hydrolab measurements for phytoplankton (mg-N L^{-1}). Error bars represent ± 1 SD. Gaps in data are attributable to Hydrolab error.

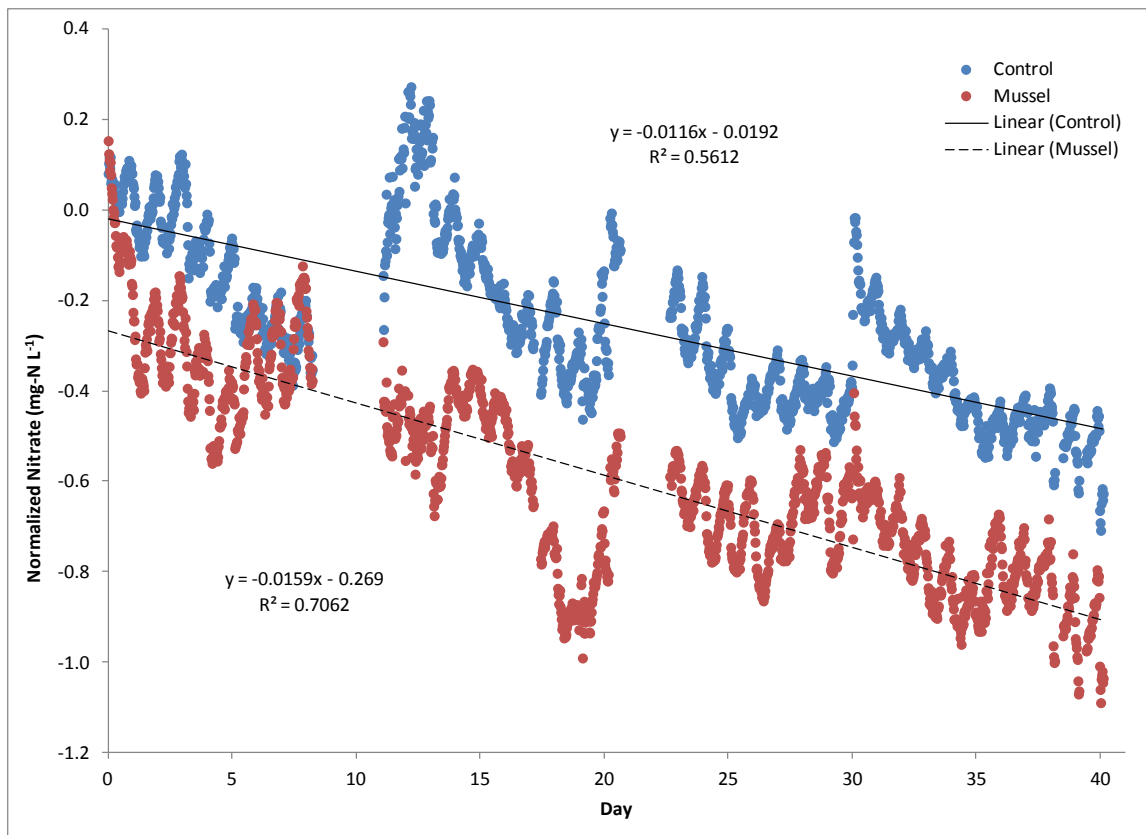


Figure 3.12: The average calibrated Hydrolab nitrate concentrations (mg-N L^{-1}) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

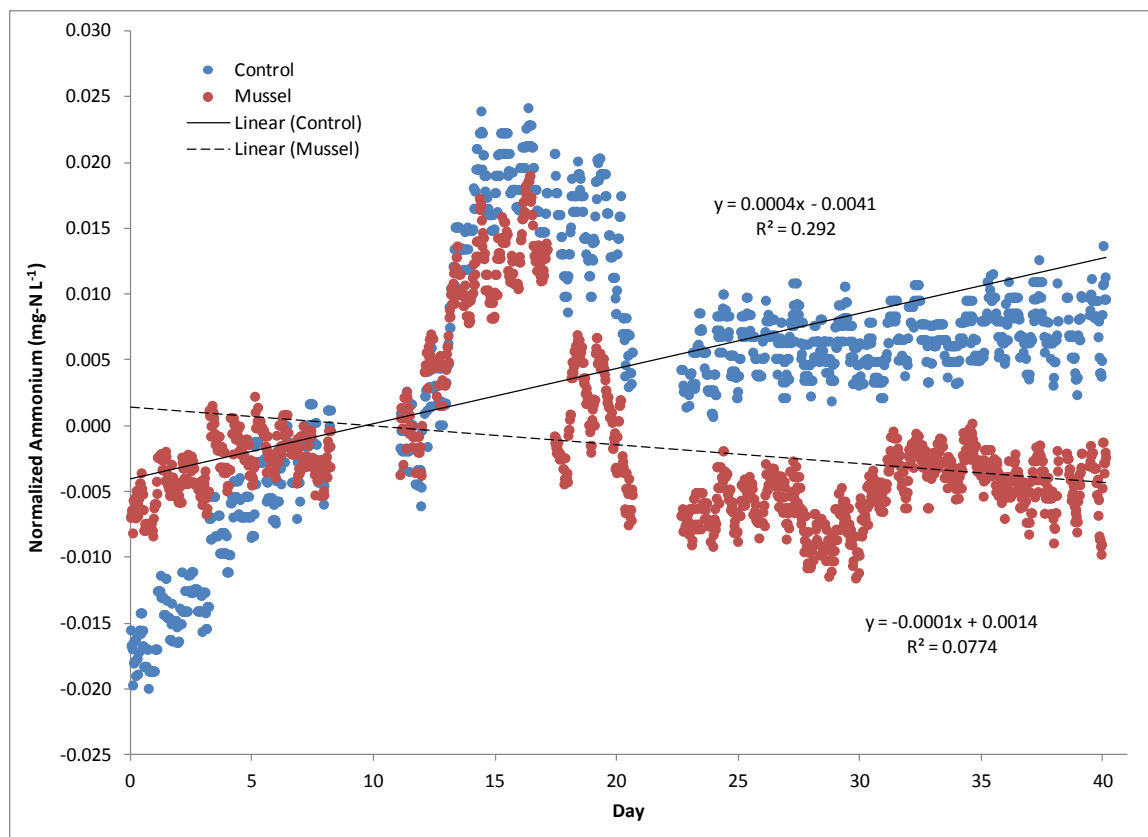


Figure 3.13: The average calibrated Hydrolab ammonium concentrations (mg-N L⁻¹) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

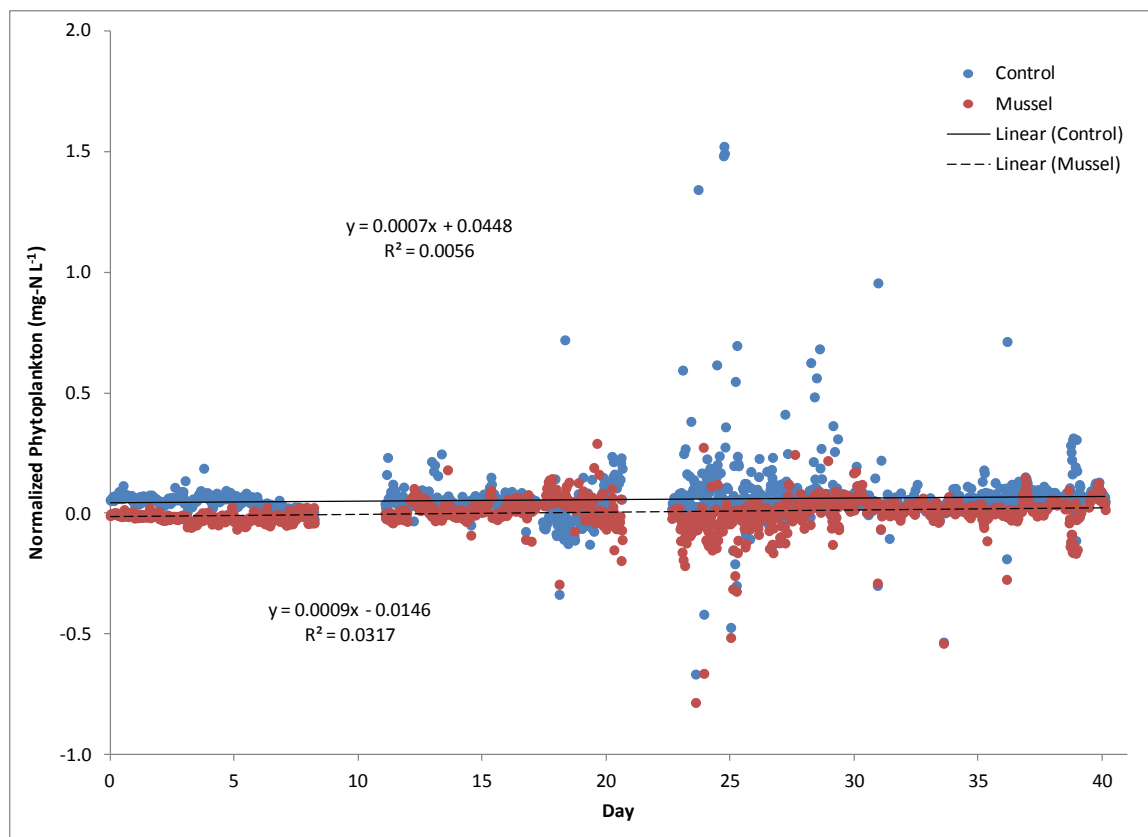


Figure 3.14: The average calibrated Hydrolab phytoplankton concentrations (mg-N L^{-1}) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

Table 3.5: The change in nitrogen species concentrations over time for the normalized data from the mussel and control treatments as measured in the overlying water.

Parameter	Treatment	Rate in Overlying Water ^a		Mussel Effect Rate ^b	
		($\text{mg-N L}^{-1} \text{ d}^{-1}$)	($\text{mg-N L}^{-1} \text{ d}^{-1}$)	(mg-N d^{-1})	($\text{mg-N d}^{-1} \text{ g}^{-1} \text{ dry mass}$)
Nitrate	Control	-0.012 (0.56)	-0.004	-0.56	-0.005
	Mussel	-0.016 (0.70)			
Ammonium	Control	0.0004 (0.29)	-0.001	-0.07	-0.001
	Mussel	-0.0001 (0.08)			
Phytoplankton Biomass	Control	0.0007 (0.001)	0.0002	0.03	0.0003
	Mussel	0.0009 (0.003)			

^a R^2 values for linear regressions are shown in parentheses

^b The mussel effect rate was determined by subtracting the rate in the control treatments from the rate in the mussel treatments

CHAPTER 4
THE EFFECT OF NATIVE FRESHWATER MUSSELS
ON NITROGEN DYNAMICS IN FLOW-THROUGH
MESOCOSMS: PART II

Purpose

Similar to Chapter 3, the objective of this chapter was to test Hypothesis 1 by utilizing highly time resolved data to evaluate the effects of mussels on nitrogen dynamics in laboratory-based, flow-through mesocosms. We improved upon the experiment in Chapter 3 by obtaining more frequent grab samples to better calibrate the Hydrolab sensors. We decreased the length of the experiment but increased the number of nitrogen species analyzed by investigating the variations in nitrate, ammonium, phytoplankton, nitrite, organic nitrogen, and total nitrogen concentrations in the mesocosms. The concentrations of nitrate and ammonium were also analyzed in the pore water of each mesocosm. We also quantified a normalized “mussel effect rate” for nitrate, ammonium, and phytoplankton as a means to predict the effect of mussels in streams and rivers. Lastly, we quantified the amount of nitrogen mass added or removed from the overlying water by mussels throughout the length of the experiment.

Abstract

The effects of mussels on nitrate, ammonium, and phytoplankton in the overlying water were investigated using flow-through mesocosms. Highly time resolved (30 min) water chemistry data were collected for 7 d in mesocosms containing mussels ($n = 2$) and mesocosms without mussels (control, $n = 2$). The flow-through mesocosms design was determined to sufficiently mimic natural conditions for temperature, photosynthetically active radiation, and phytoplankton composition and biomass. Concentration changes for nitrate, ammonium, and phytoplankton were determined to be significantly different (ANCOVA, $p < 0.05$) between the mussel treatments and control treatments. Calibrated

Hydrolab data and grab sample measurements indicated that ammonium and nitrate concentrations increased in mussel treatments and phytoplankton concentrations decreased. Grab samples also demonstrated that nitrite and total nitrogen increased in mussel treatments but minimal differences were observed for organic nitrogen. The changes in concentrations attributable to mussels were found to add more nitrogen mass to the overlying water than they removed. Poor linear correlations were obtained from the changes in concentrations for nitrate and phytoplankton, which provided little confidence in the calculated mussel effect rates.

Introduction

Given the similarity between this chapter and Chapter 3, the same introduction was used for both (see Chapter 3).

Materials and Methods

Mesocosm Experiment

A 7 d mesocosm experiment was conducted in July 2012 using flow-through mesocosms (61 x 61 x 61 cm) fed with a continuous supply of untreated Iowa River water. Treatments ($n = 4$) included 2 mesocosms containing mussels and 2 mesocosms without mussels (control). Mesocosms were lined with clean, dry sand and filled with 140 L of Iowa River water. Continuous flow of Iowa River water was provided via a 415-L head tank. The gravity-fed system provided an average flow rate of $\approx 55 \text{ L h}^{-1}$, which resulted in an average hydraulic retention time of $\approx 2.5 \text{ h}$ in each mesocosm. Complete mixing in each mesocosm was provided by 1500 L h^{-1} submersible pumps. Mesocosms were also illuminated with two 1000-watt solar simulators on a 12:12 h light-dark cycle.

Study Organisms

Fifty adult *A. plicata* (mean, 95 mm) and 25 adult *L. cardium* (mean, 120 mm) were obtained from the Iowa River in May 2012 (Figure 3.2). Between May 2012 and July 2012, flow rate, light intensity, sensor configurations, and grab sample frequency were optimized in preparation for the full-scale experiments. The 7 d experiment began 13 July 2012. We placed 25 mussels per mesocosm (70 mussels m⁻²); this density represents the high range of those found in mussel beds in the UMR (Newton, unpublished data). Mussel beds are defined as aggregations of mussels where many or all of the species found co-occur at densities 10 to 100 times higher than those outside the bed.

Water Chemistry Sensing

Hydrolab multi-probe sondes ($n = 5$, model DS5, Hach Chemical Company, Loveland, Colorado) were used to measure highly time resolved (30 min) water chemistry data in the overlying water of each mesocosm and for the head tank. One Hydrolab was placed in each of the mesocosms and the head tank. The Hydrolabs measured chlorophyll *a* (compact fluorometer), ammonium (ion selective electrode), nitrate (ion selective electrode), dissolved oxygen (luminescent dissolved oxygen), temperature (variable resistance thermistor), pH (KCl impregnated glass bulb), and conductivity (fixed potential electrodes). All Hydrolab measurements were taken in the overlying water 10 cm above the substrate.

Custom-made tipping buckets with magnetic reed switches were used to measure influent flow and an unrestricted standpipe was used to control outflow.

Photosynthetically active radiation (PAR) sensors were used to measure light intensity at the substrate (model SQ-120, Apogee Instruments, Logan, Utah) and water surface (model LI190SB-L, Campbell Scientific, Logan, Utah) of each mesocosm. All Hydrolab-measured water chemistry data were collected and stored using 2 dataloggers

(model CR1000, Campbell Scientific, Logan, Utah). Specifications for each of the sensors used can be found in the Appendix (Table A.1).

Grab Samples

Grab samples were collected from the overlying water of each mesocosm and from the head tank for comparison to Hydrolab measurements and to provide additional water chemistry data. Grab samples were collected daily at 8:00, 10:00, and 16:00 for the entire 7 d experiment. All samples were taken in the overlying water 10 cm above the substrate.

The grab samples were analyzed for nitrate, ammonium, nitrite, total nitrogen, and chlorophyll *a*. Nitrate was determined using the Dimethylphenol Method (Reference Method: 40 CFR 141) and ammonium was determined using the Salicylate Method (Reference Method: EPA 350.1). Nitrite was measured using the Diazotization Method (Reference Method: EPA 353.2) and total nitrogen was measured using the Persulfate Digestion Method (Reference Method: Standard Methods 4500-N C). Chlorophyll *a* was measured by fluorescence (Reference Method: EPA 445.0 Rev. 1.2) and results were used to create a response factor to calibrate the chlorophyll *a* sensor on the Hydrolabs. Grab sample measurements for organic nitrogen were estimated by subtracting the sum of nitrate, ammonium, and nitrite from the total nitrogen measurements. Grab samples were also obtained in the pore water of the mesocosms for nitrate and ammonium. Samples were taken \approx 3-5 cm below the sediment-water interface and were analyzed using the techniques listed above.

Additional grab samples ($n = 2$) were analyzed by the State Hygienic Laboratory at the University of Iowa (Coralville, Iowa) to determine phytoplankton biomass and community composition. Phytoplankton biomass and the distribution of phytoplankton taxa was determined by microscopic examination and counting (Reference Method: Standard Methods 10200).

Measured chlorophyll *a* concentrations ($\mu\text{g L}^{-1}$) were converted to phytoplankton biomass (mg L^{-1}) based on literature values that established linear relationships for the proportion of chlorophyll *a* in phytoplankton wet weight. The average conversion factor obtained from the literature was used (Kasprzak et al. 2008). The mass of nitrogen in total phytoplankton biomass was calculated by using the empirical formula $\text{C}_{106}\text{H}_{263}\text{O}_{110}\text{N}_{16}\text{P}$ to represent phytoplankton (Chapra 1997). Phytoplankton biomass (mg L^{-1}) was converted to phytoplankton biomass as nitrogen (herein referred to as phytoplankton, mg-N L^{-1}) by using Equation 3.1.

Data Analysis

The raw Hydrolab measurements for nitrate, ammonium, and phytoplankton revealed diurnal features and trends in nitrogen dynamics, but again highlighted the calibration challenges associated with relatively new commercial sensors. These challenges were addressed through point-by-point comparisons to an extensive grab sample data set and the development of statistically evaluated calibration factors that were applied to each Hydrolab sensor data series. This technique is analogous to the widely used internal standards method for the most accurate quantification of chemical species by gas or liquid chromatography. The calibration factors were derived by dividing the reported Hydrolab concentrations by the respective grab sample concentrations. The individual calibration factors were then averaged to obtain a single calibration factor that was applied to the raw Hydrolab data for nitrate, ammonium, and phytoplankton.

Analysis of covariance (ANCOVA) was used to determine the statistical significance between the mussel and control treatments using the General Linear Model with flow, temperature, time, and PAR as covariates. Statistical significance was defined by the Tukey Method 95% simultaneous confidence intervals. ANCOVA analyses were completed using Minitab (version 16; Minitab Inc., State College, Pennsylvania).

To quantify the effect of mussels on nitrate, ammonium, and phytoplankton, concentrations measured at each time step in the head tank were subtracted from the concentrations measured in each mesocosm as a means to normalize the data. This was done to offset for rapid changes in water chemistry attributable to the Iowa River. Linear regressions were performed on the average treatment concentrations to determine the rate of removal/production of nitrate, ammonium, and phytoplankton for each treatment. Grab sample measurements were also normalized to head tank concentrations and linear regressions were performed to determine processing rates.

The rate attributable to mussels was determined by subtracting the rate in the control treatments from the rate in the mussel treatments. This normalized “mussel effect rate” was standardized to tissue dry mass to correct for size differences between the two mussel species. Dry tissue mass (M , g) was predicted for each mussel based on measured shell length (L , mm) and using the allometric function $M = aL^b$. The values for the parameters a and b were obtained from data on mussels in Navigation Pool 10 of the UMR (Newton et al. 2011).

As another means to quantify the effect of mussels on nitrogen dynamics in the mesocosms, the amount of nitrogen mass added to or removed from the overlying water was calculated. This mussel effect on nitrogen mass was determined by subtracting the mass flux at each time step in the control treatments from the respective mass flux in the mussel treatments. Mass fluxes were calculated using the average flow rate (55 L h^{-1}) and concentrations measured by the grab samples and Hydrolabs (concentrations were not normalized to the head tank). The Right Riemann Sum Method was then applied by multiplying the calculated differences between the mussel and control concentrations by the increment of each respective time step (e.g. 30 min) to obtain nitrogen mass. The mussel effect on nitrogen mass was determined for nitrate, ammonium, and phytoplankton using the calibrated Hydrolab data and the grab sample measurements.

The mussel effect on nitrogen mass was also determined for organic nitrogen, nitrite, and total nitrogen using the grab sample measurements.

The percent difference and coefficient of determination (R^2) were calculated for nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton as an additional means to evaluate the difference between mussel and control treatments. The percent difference was calculated at each time step and then averaged over the entire experimental time period to obtain an average percent difference.

Results

System Characterization

The highly time resolved water chemistry data were used to quantify characteristics of the overall laboratory mesocosm. Dissolved oxygen in the control treatments (6.8 mg L^{-1}) was higher than the mussel treatments (5.9 mg L^{-1}). Water temperature remained relatively constant throughout the experiment with an average value of $\approx 25^\circ\text{C}$. During the 12 h light cycle of the solar simulator, PAR at the water surface was $\approx 730 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and PAR at the substrate was $\approx 40 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Diatoms were the most dominant taxa present in the mesocosms (50%), followed by cyanobacteria (19%), chlorophyta (18%), and protozoa (11%) (Figure 4.1). Total phytoplankton biomass in the mesocosms (2.5 mg L^{-1}) was below the range observed in the Iowa River (4.5 to 22.4 mg L^{-1}). The Reynolds Number estimated for the mesocosms was 420,500.

The Effect of Mussels

Analysis of the nitrogen dynamics in the overlying water indicated that nitrate ($\approx 50\%$) and organic nitrogen ($\approx 41\%$) were the most dominant species in the mesocosms. The raw Hydrolab data for nitrate revealed a less than accurate calibration when compared with the grab sample measurements (Figure 4.2). Therefore, the calibration factors (Table 4.1) derived from grab sample comparison were used to recalibrate all

Hydrolab data. The calibration factors for Mesocosm 1 and Mesocosm 2 (control treatments) were 1.59 and 2.10, respectively. The calibration factors for Mesocosm 3 and Mesocosm 4 (mussel treatments) were 1.59 and 1.24, respectively. The calibration factor for the head tank (river influent) was 1.36. The calibrated Hydrolab data (Figure 4.3) indicated higher nitrate concentrations present in the mussel treatments compared to the control treatments (percent difference = 5.9%, $R^2 = 0.96$) (Table 4.2). Grab sample measurements also indicated nitrate concentrations were higher in the mussel treatments (6.4%, $R^2 = 0.96$). The results of the ANCOVA analysis revealed that nitrate concentrations measured in the mussel treatments were significantly different from those observed in the control treatments ($p < 0.05$). Grab samples for nitrate in the pore water indicated nitrate concentrations were higher in the mussel treatments (44.3%, $R^2 = 0.03$) (Figure 4.4, Table B.1), but significant variability in the measurements was observed.

The raw Hydrolab data for ammonium also revealed a less than accurate calibration when compared with the grab sample measurements (Figure 4.5). Therefore, the calibration factors (Table 4.3) derived from grab sample comparison were used to recalibrate all Hydrolab data. The calibration factors for Mesocosm 1 and Mesocosm 2 (control treatments) were 4.77 and 3.99, respectively. The calibration factors for Mesocosm 3 and Mesocosm 4 (mussel treatments) were 4.33 and 4.72, respectively. The calibration factor for the head tank (river influent) was 3.34. The calibrated Hydrolab data (Figure 4.6) demonstrated similar results to the grab samples as both indicated significantly higher ammonium concentrations present in the mussel treatments compared to the control treatments (Hydrolab = 98.3%, $R^2 = 0.08$; Grab Samples = 111.7%, $R^2 = 0.002$) (Table 4.2). The results of the ANCOVA analysis revealed that ammonium concentrations measured in the mussel treatments were significantly different from those observed in the control treatments ($p < 0.05$). Grab sample measurements for the pore water also indicated significantly higher ammonium concentrations present in the mussel treatments (162.3%, $R^2 = 0.02$) (Figure 4.7).

Similar to nitrate and ammonium, the raw Hydrolab data for phytoplankton revealed a less than accurate calibration when compared with the grab sample measurements (Figure 4.8). Therefore, the calibration factors (Table 4.4) derived from grab sample comparison were used to recalibrate all Hydrolab data. The calibration factors for Mesocosm 1 and Mesocosm 2 (control treatments) were 0.65 and 0.69, respectively. The calibration factors for Mesocosm 3 and Mesocosm 4 (mussel treatments) were 0.35 and 0.62, respectively. The calibration factor for the head tank (river influent) was 0.49. The calibrated Hydrolab data (Figure 4.9) exhibited decreased concentrations of phytoplankton in the mussel treatments as compared to the control treatments (-46.0%, $R^2 = 0.28$) (Table 4.2). The grab sample measurements also indicated lower concentrations of phytoplankton in the mussel treatments (-45.6%, $R^2 = 0.90$). The results of the ANCOVA analysis revealed that phytoplankton concentrations measured in the mussel treatments were significantly different from those observed in the control treatments ($p < 0.05$).

Grab sample measurements for organic nitrogen indicated minimal changes between the control and mussel treatments (1.9%, $R^2 = 0.44$) (Figure 4.10). Nitrite concentrations were determined to increase substantially in the mussel treatments (71.7%, $R^2 = 0.01$) (Figure 4.11). Total nitrogen concentrations also increased in the mussel treatments as compared to the control treatments (9.5%, $R^2 = 0.63$) (Figure 4.12).

Quantifying the Mussel Effect

Mussel Effect Rate

The calibrated and normalized Hydrolab (Figure 4.13) and grab sample (Figure 4.14) nitrate data indicated that nitrate was decreasing in both treatments relative to the river influent (head tank). The linear regressions performed on the normalized Hydrolab data indicated that the rate of removal in the control treatments ($-0.008 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.18$) was greater than the rate of removal in the mussel treatments ($-0.005 \text{ mg-N L}^{-1} \text{ d}^{-1}$,

$R^2 = 0.09$) (Table 4.5). This resulted in a nitrate mussel effect rate of $0.003 \text{ mg-N L}^{-1} \text{ d}^{-1}$, which demonstrated that the amount of nitrate in the mussel treatments was increasing over time relative to the amount of nitrate in the control treatments. Conversely, the linear regressions performed on the normalized grab sample data indicated that the rate of removal in the control treatments ($-0.004 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.07$) was less than the rate of removal in the mussel treatments ($-0.009 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.29$). This resulted in a nitrate mussel effect rate of $-0.005 \text{ mg-N L}^{-1} \text{ d}^{-1}$, which demonstrated that the amount of nitrate in the mussel treatments was decreasing over time relative to the amount of nitrate in the control treatments.

The calibrated and normalized Hydrolab (Figure 4.15) and grab sample (Figure 4.16) ammonium data indicated that ammonium was decreasing in both treatments relative to the river influent. The linear regressions performed on the normalized Hydrolab data indicated the rate of removal in the control treatments ($-0.003 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.68$) was less than the rate of removal in the mussel treatments ($-0.005 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.70$) (Table 4.5). The linear regressions performed on the normalized grab sample data also indicated the rate of removal in the control treatments ($-0.005 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.22$) was less than the rate of removal in the mussel treatments ($-0.017 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.70$). The Hydrolab and grab sample data resulted in ammonium mussel effect rates of $-0.002 \text{ mg-N L}^{-1} \text{ d}^{-1}$ and $-0.012 \text{ mg-N L}^{-1} \text{ d}^{-1}$, respectively, which indicated the amount of ammonium in the mussel treatments was decreasing over time relative to the amount of ammonium in the control treatments.

The calibrated and normalized Hydrolab (Figure 4.17) and grab sample (Figure 4.18) phytoplankton data indicated that phytoplankton was increasing in both treatments relative to the river influent. The linear regressions performed on the normalized Hydrolab data indicated that the rate of production in the control treatments ($0.031 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.40$) was higher than the rate of production in the mussel treatments ($0.030 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.09$) (Table 4.5). This resulted in a phytoplankton mussel effect rate

of $-0.001 \text{ mg-N L}^{-1} \text{ d}^{-1}$, which demonstrated that the amount of phytoplankton in the mussel treatments was decreasing over time relative to the amount of phytoplankton in the control treatments. Conversely, the linear regressions performed on the normalized grab sample data indicated that the rate of production in the control treatments ($0.007 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.23$) was less than the rate of production in the mussel treatments ($0.014 \text{ mg-N L}^{-1} \text{ d}^{-1}$, $R^2 = 0.33$). This resulted in a phytoplankton mussel effect rate of $0.007 \text{ mg-N L}^{-1} \text{ d}^{-1}$, which demonstrated that the amount of phytoplankton in the mussel treatments was increasing over time relative to the amount of phytoplankton in the control treatments.

Mussel Effect on Nitrogen Mass

The calibrated Hydrolab data for nitrate indicated that the increases in nitrate concentrations in mussel treatments added 299.8 mg-N to the overlying water over the experimental length (7 d) (Table 4.6). The nitrate grab sample measurements demonstrated a similar result by indicating that the mussel effect on nitrate added 286.6 mg-N to the overlying water. The calibrated Hydrolab data for ammonium indicated that increases in ammonium concentrations caused by mussels added 399.1 mg-N to the overlying water. The grab sample measurements estimated that the mussel effect on ammonium added 352.4 mg-N to the overlying water. The calibrated Hydrolab data for phytoplankton indicated that decreases in phytoplankton caused by mussels removed 540.9 mg-N from the overlying water. The phytoplankton grab sample measurements demonstrated a similar result by indicating mussels removed 568.2 mg-N to the overlying water. The grab sample measurements for organic nitrogen, nitrite, and total nitrogen indicated changes in concentrations attributable to mussels added 109.6 mg-N, 156.6 mg-N, and 959.8 mg-N to the overlying water, respectively.

Discussion

System Characterization

The experimental setup for this study was designed to replicate the natural river environment as closely as possible and to simulate the environmental conditions that would maximize the mussel effect on nitrogen dynamics. The Reynolds Number estimated for the mesocosms (420,500) was lower than the range of Reynolds Numbers that have been observed in the Mississippi River (4,000,000 to 80,000,000) (Molinas and Wu 2001). The lower turbulence was expected to be favorable to mussels as studies have shown that mussels prefer main channel border areas and small side channels as opposed to the main channel (Zigler et al. 2008). The flow rates in the mesocosms were kept significantly lower than typical flow rates in the Iowa River (Espinosa-Villegas et al. 2004) so the effects of mussels could be more easily quantified.

The average water temperature in the mesocosms ($\approx 25^{\circ}\text{C}$) was similar to the average water temperature in the Iowa River in June through August (Espinosa-Villegas et al. 2004). This represents the time of year when mussels are expected to demonstrate the most significant influence on nutrient processing (Spooner and Vaughn 2008; Vaughn et al. 2008). Dissolved oxygen concentrations in the control (6.8 mg L^{-1}) and mussel (5.9 mg L^{-1}) treatments were lower than typical values observed in the Iowa River (8 mg L^{-1}) (Espinosa-Villegas et al. 2003). However, the lower oxygen levels were not expected to influence the mussels' ability to process nitrogen as they were still above the concentrations needed by mussels (McMahon 1996; Yu and Culver 1999). The PAR at the water surface of the mesocosms ($\approx 730 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) was comparable to the PAR observed on a typical day under natural conditions ($\approx 1000 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) (Alados et al. 2000).

The mesocosms were also able to maintain similar phytoplankton biomass and composition to that observed in the Iowa River, which provides evidence that the primary mussel food sources in the mesocosms were similar to that found in the natural

environment. Phytoplankton biomass in the mesocosms was below typical levels in the Iowa River, but this was expected given the lack of precipitation and lack of nutrient runoff that was experienced throughout the summer of 2012.

The Effect of Mussels

Many studies evaluating the functional roles of mussels have been conducted in small systems with high hydraulic retention times (Christian et al. 2008; Howard and Cuffey 2006; Vaughn et al. 2004). Re-circulating mesocosms have been used to obtain more precise estimates of mussel effects at shorter time scales (Vaughn et al. 2004; Vaughn et al. 2008). To our knowledge, this is the first study to couple the continuous input of untreated river water in flow-through mesocosms with highly time resolved water chemistry data to assess the effects of mussels on nitrogen dynamics. We acknowledge that the chemical fluxes in the influent river water dominate the diurnal and longer-term variations in nitrate, ammonium, phytoplankton, nitrite, organic nitrogen, and total nitrogen measured in the mesocosms. But, the highly time resolved data and substantial grab sample data set enabled us to show statistically significant difference in nitrogen processing attributable to mussels.

As expected, the results of this experiment indicated that mussels affected the nitrogen cycle in the overlying water of the mesocosms by increasing nitrate and ammonium concentrations and decreasing phytoplankton concentrations. We expect that the observed increases in ammonium concentrations were attributable to mussel excretion. Although direct excretion rates were not measured as part of this study, re-circulating mesocosm studies have demonstrated increased ammonium concentrations in systems containing mussels (Vaughn et al. 2008) and ammonium has been shown to increase with increasing mussel biomass (Vaughn et al. 2004; Vaughn and Hakenkamp 2001; Vaughn et al. 2008).

Nitrate concentrations in the overlying water were expected to be indirectly increased by mussels via nitrification of the excreted ammonium. The increased ammonium concentrations in the overlying water (due to mussel excretion) and the well-oxygenated conditions of the mesocosms allowed for ammonium to be oxidized to nitrate by nitrifying bacteria that are ubiquitous in bulk river water. The increases in nitrate concentrations in the mussel treatments compares to a re-circulating mesocosm study that indicated nitrate concentrations increased with increasing mussel biomass (Vaughn et al. 2004). We would also expect mussels to indirectly increase nitrate concentrations in the overlying water by increasing the amount of dissolved oxygen present at the sediment-water interface through the bioturbation of sediments during burrowing activities (Vaughn et al. 2008). This bioturbation creates conditions at the sediment-water interface where the ammonium released by the mussels is more readily oxidized to nitrite/nitrate.

The decrease in phytoplankton concentrations in mussel treatments was also expected given that phytoplankton is the primary food source of mussels in large river systems (Thorp et al. 1998). Furthermore, re-circulating mesocosm studies have shown that chlorophyll *a* concentrations tend to decrease in systems containing mussels (Boltovskoy et al. 2009; Prins et al. 1995; Vaughn et al. 2004).

Mussels also increased nitrite concentrations, which was expected given the increase in ammonium and nitrate, and their impact on nitrite through nitrification and denitrification, respectively. The amount of phytoplankton removed by mussels was too low to influence organic nitrogen concentrations. Total nitrogen, which was composed primarily of nitrate and organic nitrogen (>91%), demonstrated minimal increases in mussel treatments compared to control treatments ($\approx 10\%$). We assumed this difference was statistically significant because no change in organic nitrogen was observed, and the changes in nitrate ($\approx 5\%$) were determined to be significantly different between the treatments (ANCOVA, $p < 0.05$).

The increase in total nitrogen in the mussel treatments compared to the control treatments indicated mussels were adding more nitrogen (ammonium, nitrate, and nitrite) to the overlying water than they were removing (phytoplankton). It is expected that this difference was caused by increases in ammonium at the sediment-water interface and the subsequent nitrification of this ammonium to nitrate. Average concentrations of ammonium in the pore water were much higher in mussel treatments ($\approx 3 \text{ mg-N L}^{-1}$) than control treatments ($\approx 0.7 \text{ mg-N L}^{-1}$). This increase in pore water ammonium was attributable to mussel excretion. However, it could also have been caused by the increased organic matter present in mussel treatments (see Chapter 3), and the decomposition of this organic matter to ammonium by heterotrophic bacteria (hydrolysis). The ammonium in the pore water and any sediment-bound ammonium could also have been released into the overlying water by mussels, as the rates of diffusion transport have been shown to increase substantially due to mussel bioturbation (Henriksen et al. 1983).

Furthermore, when mussels are stressed, they have been shown to increase ammonium excretion rates by catabolizing biochemical reserves to compensate for reduced consumption and energy (Spooner and Vaughn 2008). Given that the mussels were not in their natural habitat and that their food source (phytoplankton) was below typical river levels (Espinosa-Villegas et al. 2003), it is reasonable to assume they were experiencing stress and exhibiting increased ammonium excretion rates. Mussels were able to maintain these increased ammonium excretion rates due to their ability to store nitrogen. A stable isotope study on 12 species of mussels (including *L. cardium*) demonstrated that every species reached a level of nitrogen enrichment greater than the bulk suspended organic matter (Raikow and Hamilton 2001). This indicates that mussels in the mesocosms were able to consistently add more nitrogen to the overlying water than they were able to remove, causing an increase in total nitrogen concentrations.

Quantifying the Mussel Effect

Mussel Effect on Nitrogen Mass

The calibrated Hydrolab data and grab sample measurements resulted in similar changes in nitrogen mass added/removed by mussels for nitrate, ammonium, and phytoplankton. The method used for calculating the mussel effect on nitrogen mass (Riemann Sum Method) was assumed to be more accurate with an increased number of data points. This emphasizes the importance of a highly time resolved data set when estimating the amount of mass mussels add or remove from the mesocosms.

The results indicated that the effect of mussels on ammonium resulted in more nitrogen being delivered to the overlying water (352.4 to 399.1 mg-N) than the effect of mussels on any of the other nitrogen species. Standardizing this addition of nitrogen to dry tissue mass of mussels (0.266 to 0.301 mg-N d⁻¹ g⁻¹) resulted in a mussel ammonium excretion rate slightly lower than the range of literature values (0.336 to 2.8 mg-N d⁻¹ g⁻¹) (Baker and Hornbach 2000; Baker and Hornbach 2001; Christian et al. 2008; Spooner and Vaughn 2008). The total amount of nitrogen mussels delivered to the overlying water (by increasing nitrate, ammonium, and nitrite) was greater (965.1 mg-N L⁻¹ d⁻¹) than the amount they removed (via phytoplankton clearance, 540.9 mg-N L⁻¹ d⁻¹). This provided further evidence that mussels produced an increase in total nitrogen concentrations, as discussed in the above section.

Mussel Effect Rate

The linear regressions performed on the changes in concentrations for nitrate, ammonium, and phytoplankton were less than adequate. These poor linear correlations provided little confidence in the calculated mussel effect rates. The highly time resolved data demonstrated the complexity and nonlinearity of the mesocosm system, which revealed significant limitations in utilizing first-order rates to predict the effect of mussels on nitrogen dynamics.

Implications for River Ecosystems

The results of this study indicate that the most important effect of mussels on nitrogen dynamics in the overlying water is the direct excretion of ammonium. In many freshwater systems, ammonium uptake rates are comparable to or exceed ammonium regeneration rates (Gardner et al. 1995). However, the increase in ammonium concentrations attributable to mussel excretion observed in our study indicates the regeneration rates in mussel treatments are higher than uptake rates. This has also been observed for zebra mussels and illustrates the importance of mussels as an additional heterotrophic component of the ecosystem (Gardner et al. 1995).

Depending on the rate of mixing, the mineralized nitrogen in the sediments of river ecosystems may not be immediately available for phytoplankton and other aquatic organisms (Kaspar et al. 1985). The ammonium and subsequent nitrate added to the overlying water by mussels provides a readily available nitrogen source. This increase in readily available nitrogen is expected to facilitate local algal growth and increase the range of nutritional resources for other grazers (Spooner et al. 2012). In marine systems, the increase in nutrient resources has been shown to result in more palatable algae which can be better controlled by grazers (Duffy et al. 2007). It is also expected that the increases in readily available nitrogen will increase microbial activity (Spooner et al. 2012), which is important given the influence of bacteria in the aquatic nitrogen cycle.

The net nitrogen increase in treatments containing mussels is also expected to stimulate the detritus-based food chain (Kaspar et al. 1985) and influence the density and richness of benthic organisms (Christian et al. 2008). Although not measured as a part of this study, the densities of macroinvertebrates, periphyton (attached algae), and vascular plants have been shown to increase in the presence of mussels (Vaughn et al. 2008; Vaughn and Spooner 2006; Vaughn et al. 2002).

The ability of mussels to remove organic matter and phytoplankton from the overlying water and provide nutrients to the sediment-water interface is also expected to

influence the diversity of benthic organisms by increasing sedimentation rates. Mussels have been described as large filters that form fast-sedimenting pellets from planktonic particles which contributes to sediment with a finer texture and a higher moisture content (Kaspar et al. 1985). In marine systems, the diversity of benthic organisms has been shown to decrease in mussel treatments (Kaspar et al. 1985; Tenore et al. 1982), as the increase in sedimentation is expected select for species that are more adaptable to low oxygen levels or the instability of finer-textured, high-organic sediments.

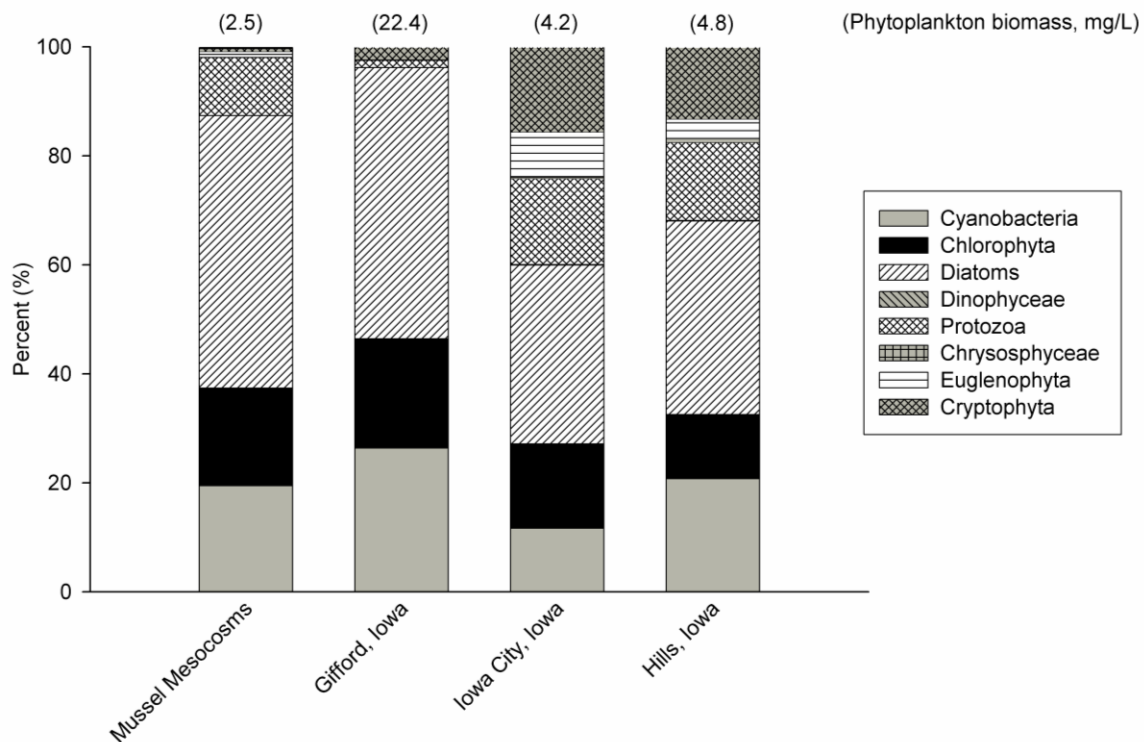


Figure 4.1: The average phytoplankton taxa distribution in the mesocosms was comparable to average taxa distributions observed at 3 locations in the Iowa River. Phytoplankton biomass (shown parenthetically) was 2.5 mg L^{-1} in the mussel mesocosms at the time of sampling which was below the range (4.5 to 22.4 mg L^{-1}) measured in the river.

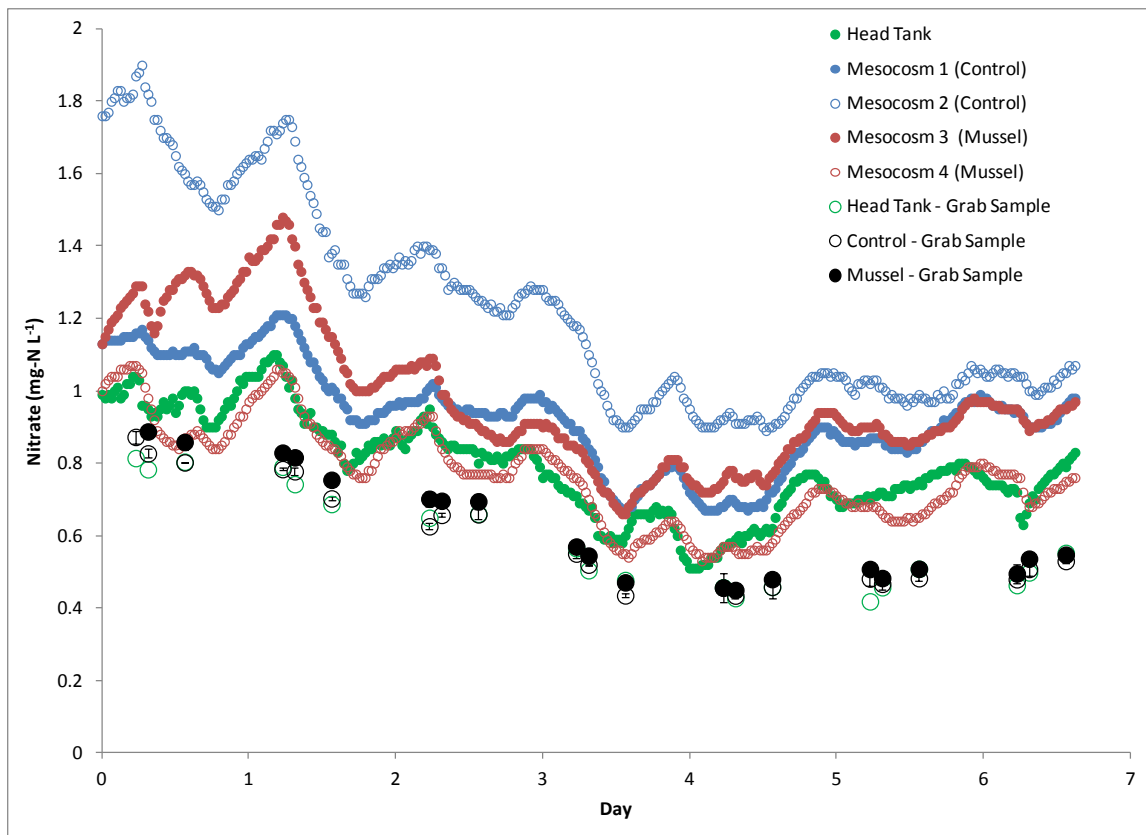


Figure 4.2: Grab sample measurements and raw Hydrolab data for nitrate (mg-N L⁻¹). Hydrolab measurements are shown for each of the mesocosms and grab samples were averaged for each treatment. Error bars on grab sample measurements represent ± 1 SD.

Table 4.1: Nitrate Hydrolab measurements (mg-N L^{-1}) and corresponding grab sample measurements (mg-N L^{-1}) used to calculate calibration factors.

Day	Hydrolab Measurements (mg-N L^{-1})					Grab Sample Measurements (mg-N L^{-1})					Calibration Factor				
	Control		Mussel		Head	Control		Mussel		Head	Control		Mussel		Head
	Mesocosm 1	Mesocosm 2	Mesocosm 3	Mesocosm 4	Tank	Mesocosm 1	Mesocosm 2	Mesocosm 3	Mesocosm 4	Tank	Mesocosm 1	Mesocosm 2	Mesocosm 3	Mesocosm 4	Tank
0.23	1.16	1.87	1.29	1.07	1.04	0.86	0.89	1.16	1.04	0.81	1.35	2.11	1.11	1.03	1.28
0.31	1.14	1.82	1.22	0.98	0.95	0.82	0.84	0.89	0.88	0.78	1.39	2.18	1.37	1.11	1.21
0.56	1.21	1.60	1.32	0.87	1.00	0.80	0.80	0.84	0.87	0.80	1.51	2.00	1.56	1.00	1.24
1.23	1.11	1.74	1.48	1.05	1.07	0.78	0.79	0.83	0.83	0.79	1.42	2.21	1.78	1.27	1.35
1.31	1.18	1.69	1.40	1.01	0.98	0.77	0.79	0.82	0.81	0.74	1.53	2.15	1.70	1.25	1.32
1.56	1.01	1.38	1.15	0.84	0.88	0.70	0.71	0.76	0.75	0.69	1.45	1.95	1.52	1.12	1.28
2.23	1.01	1.39	1.09	0.93	0.95	0.63	0.62	0.69	0.72	0.65	1.60	2.25	1.59	1.30	1.46
2.31	0.98	1.34	0.99	0.84	0.86	0.66	0.65	0.70	0.70	---	1.48	2.05	1.42	1.21	---
2.56	0.94	1.25	0.90	0.77	0.80	0.67	0.65	0.68	0.71	0.66	1.41	1.93	1.32	1.09	1.21
3.23	0.89	1.18	0.84	0.76	0.71	0.56	0.54	0.58	0.56	0.57	1.59	2.19	1.46	1.35	1.26
3.31	0.84	1.10	0.80	0.70	0.67	0.52	0.52	0.54	0.55	0.50	1.61	2.12	1.47	1.28	1.33
3.56	0.67	0.90	0.66	0.55	0.60	0.44	0.43	0.48	0.46	0.48	1.53	2.09	1.38	1.19	1.26
4.23	0.68	0.92	0.75	0.57	0.57	0.48	0.43	0.45	0.46	0.46	1.40	2.15	1.66	1.24	1.25
4.31	0.69	0.91	0.76	0.56	0.59	0.43	0.44	0.45	0.45	0.43	1.61	2.07	1.71	1.23	1.38
4.56	0.72	0.90	0.77	0.58	0.62	0.48	0.44	0.48	0.48	0.46	1.50	2.06	1.60	1.21	1.35
5.23	0.87	1.02	0.90	0.69	0.70	0.49	0.47	0.51	0.51	0.42	1.76	2.18	1.78	1.36	1.67
5.31	0.87	1.01	0.88	0.66	0.72	0.48	0.46	0.48	0.49	0.46	1.82	2.21	1.85	1.35	1.58
5.56	0.86	0.99	0.86	0.65	0.75	0.49	0.48	0.51	0.51	0.51	1.77	2.07	1.69	1.28	1.48
6.23	0.95	1.04	0.95	0.76	0.72	0.48	0.48	0.48	0.51	0.46	1.98	2.18	1.99	1.48	1.56
6.31	0.90	1.00	0.89	0.68	0.69	0.50	0.52	0.54	0.54	0.50	1.82	1.92	1.66	1.27	1.39
6.56	0.96	1.05	0.95	0.75	0.79	0.53	0.53	0.55	0.55	0.55	1.80	2.00	1.74	1.37	1.43
										Average	1.59	2.10	1.59	1.24	1.36
										Standard Deviation	0.17	0.10	0.20	0.12	0.13
										Coefficient of Variation	11.0%	4.6%	12.8%	9.6%	9.5%

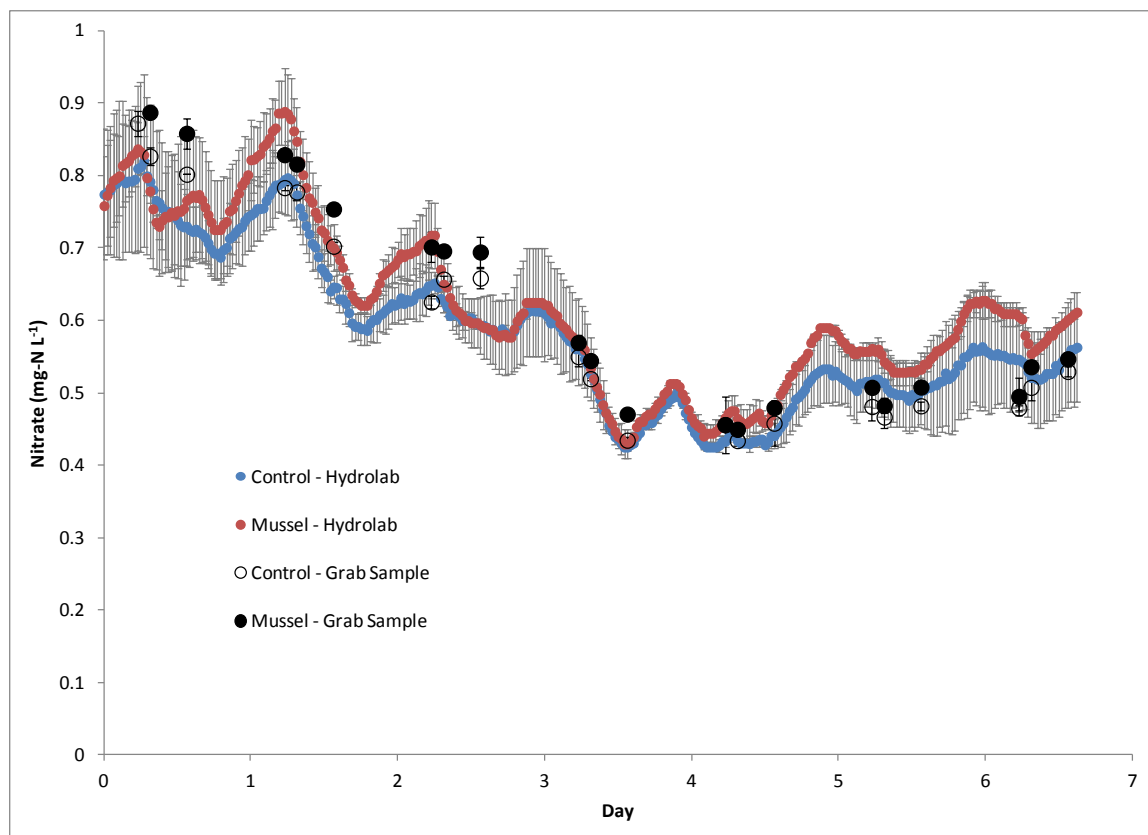


Figure 4.3: Average grab sample measurements and calibrated Hydrolab measurements for nitrate (mg-N L^{-1}). Error bars represent ± 1 SD.

Table 4.2: Average percent difference and coefficient of determination (R^2) values between control and mussel treatments for grab samples and calibrated Hydrolab measurements.

Parameter	Percent Difference		Coefficient of Determination (R^2)	
	Grab Sample	Hydrolab	Grab Sample	Hydrolab
Nitrate	5.4%	5.9%	0.99	0.96
Ammonium	111.7%	98.3%	0.002	0.08
Phytoplankton	-45.6%	-46.0%	0.90	0.28
Organic Nitrogen	1.9%	---	0.44	---
Nitrite	71.7%	---	0.01	---
Total Nitrogen	9.5%	---	0.63	---
Nitrate (Pore Water)	44.3%	---	0.03	---
Ammonium (Pore Water)	162.3%	---	0.02	---

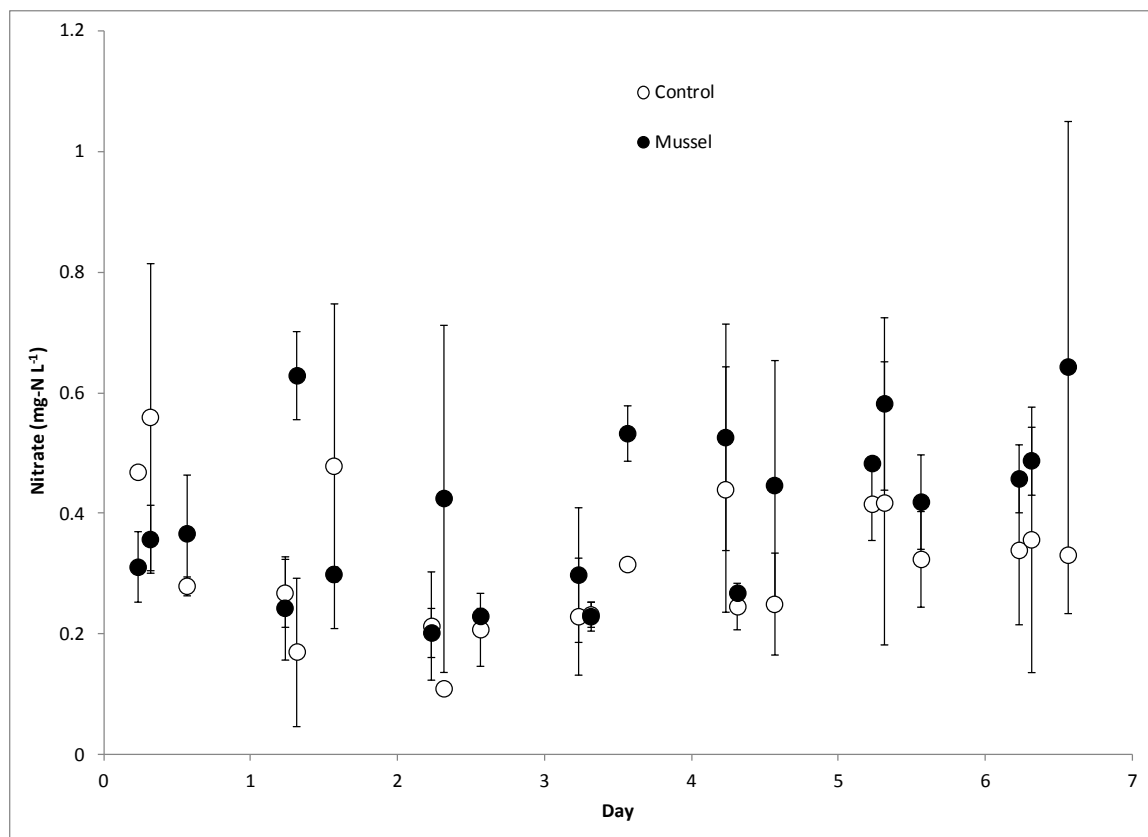


Figure 4.4: Average grab sample measurements for nitrate in the pore water of the control and mussel treatments (mg-N L⁻¹). Error bars represent ± 1 SD.

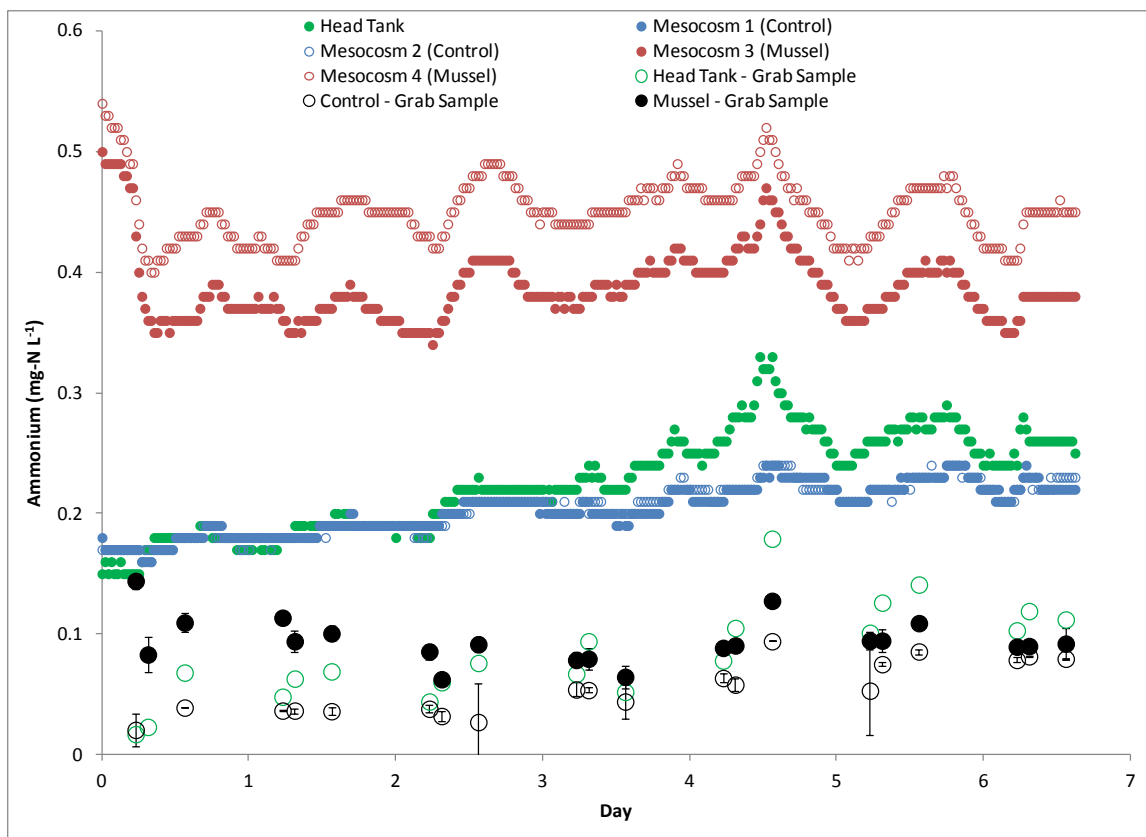


Figure 4.5: Grab sample measurements and raw Hydrolab data for ammonium (mg-N L⁻¹). Hydrolab measurements are shown for each of the mesocosms and grab samples were averaged for each treatment. Error bars on grab sample measurements represent ± 1 SD.

Table 4.3: Ammonium Hydrolab measurements (mg-N L^{-1}) and corresponding grab sample measurements (mg-N L^{-1}) used to calculate calibration factors.

Day	Hydrolab Measurements (mg-N L^{-1})					Grab Sample Measurements (mg-N L^{-1})					Calibration Factor							
	Control		Mussel			Head Tank	Control		Mussel			Head Tank	Control		Mussel			Head Tank
	Mesocosm 1	Mesocosm 2	Mesocosm 3	Mesocosm 4	Mesocosm 1		Mesocosm 2	Mesocosm 3	Mesocosm 4	Mesocosm 1	Mesocosm 2		Mesocosm 3	Mesocosm 4				
0.23	0.17	0.17	0.43	0.46	0.15	0.01	0.03	0.15	0.14	0.02	15.45	5.67	2.89	3.31	8.82			
0.31	0.16	0.17	0.36	0.41	0.17	---	---	0.09	0.07	0.02	---	---	3.87	5.62	7.39			
0.56	0.18	0.18	0.36	0.43	0.18	0.04	0.04	0.10	0.12	0.07	4.62	4.62	3.46	3.74	2.65			
1.23	0.18	0.18	0.36	0.41	0.18	0.04	0.04	0.12	0.11	0.05	4.86	5.00	3.08	3.73	3.75			
1.31	0.18	0.18	0.35	0.41	0.19	0.04	0.04	0.09	0.10	0.06	4.74	5.14	3.98	4.10	3.02			
1.56	0.19	0.19	0.37	0.45	0.19	0.03	0.04	0.10	0.11	0.07	5.59	5.00	3.85	4.29	2.75			
2.23	0.19	0.19	0.35	0.43	0.18	0.04	0.04	0.08	0.09	0.04	4.75	5.28	4.32	4.78	4.09			
2.31	0.20	0.19	0.36	0.43	0.20	0.03	0.04	0.06	0.06	0.06	6.90	5.43	5.90	6.72	3.33			
2.56	0.21	0.21	0.41	0.48	0.23	---	0.05	0.09	0.10	0.08	---	4.20	4.71	5.00	3.03			
3.23	0.20	0.20	0.37	0.44	0.22	0.05	0.06	0.07	0.08	0.07	4.00	3.45	5.00	5.30	3.28			
3.31	0.21	0.20	0.38	0.44	0.24	0.05	0.06	0.07	0.09	0.09	4.04	3.64	5.21	5.12	2.55			
3.56	0.19	0.20	0.39	0.45	0.22	0.05	0.03	0.06	0.07	0.05	3.52	5.88	6.72	6.34	4.23			
4.23	0.21	0.22	0.40	0.46	0.26	0.07	0.06	0.09	0.09	0.08	3.18	3.61	4.65	5.05	3.33			
4.31	0.22	0.22	0.42	0.47	0.28	0.05	0.06	0.09	0.09	0.11	4.07	3.55	4.67	5.16	2.67			
4.56	0.24	0.24	0.46	0.51	0.33	0.09	0.09	0.12	0.13	0.18	2.55	2.55	3.71	3.89	1.84			
5.23	0.22	0.22	0.37	0.43	0.26	0.03	0.08	0.09	0.10	0.10	8.15	2.78	4.16	4.30	2.57			
5.31	0.22	0.22	0.37	0.44	0.26	0.07	0.08	0.09	0.10	0.13	2.97	2.89	4.20	4.36	2.06			
5.56	0.23	0.23	0.40	0.47	0.28	0.08	0.09	0.11	0.11	0.14	2.74	2.64	3.74	4.23	1.99			
6.23	0.22	0.22	0.36	0.41	0.24	0.08	0.08	0.09	0.09	0.10	2.86	2.75	3.96	4.66	2.33			
6.31	0.23	0.23	0.38	0.45	0.26	0.08	0.08	0.09	0.09	0.12	2.84	2.80	4.27	4.95	2.18			
6.56	0.22	0.23	0.38	0.45	0.26	0.08	0.08	0.08	0.10	0.11	2.78	2.88	4.58	4.46	2.32			
Average											4.77	3.99	4.33	4.72	3.34			
Standard Deviation											2.98	1.16	0.89	0.84	1.73			
Coefficient of Variation											62.5%	29.0%	20.5%	17.8%	51.7%			

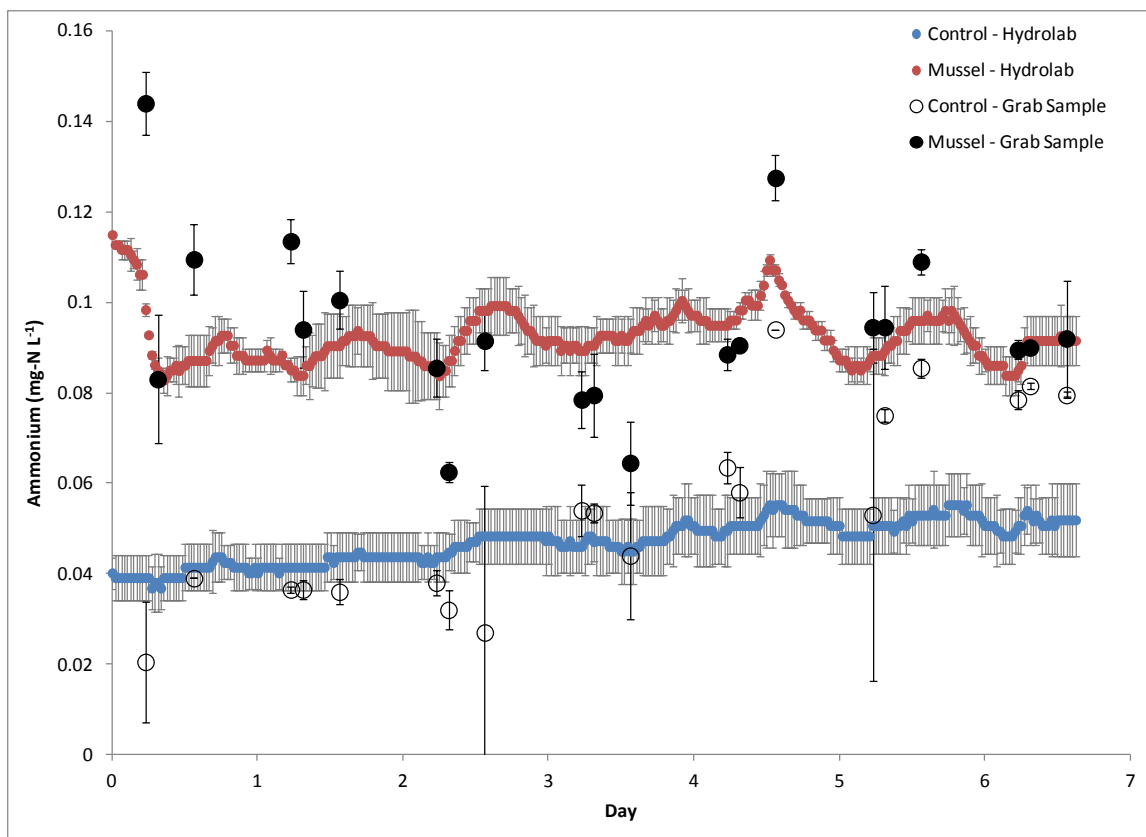


Figure 4.6: Average grab sample measurements and calibrated Hydrolab measurements for ammonium (mg-N L^{-1}). Error bars represent ± 1 SD.

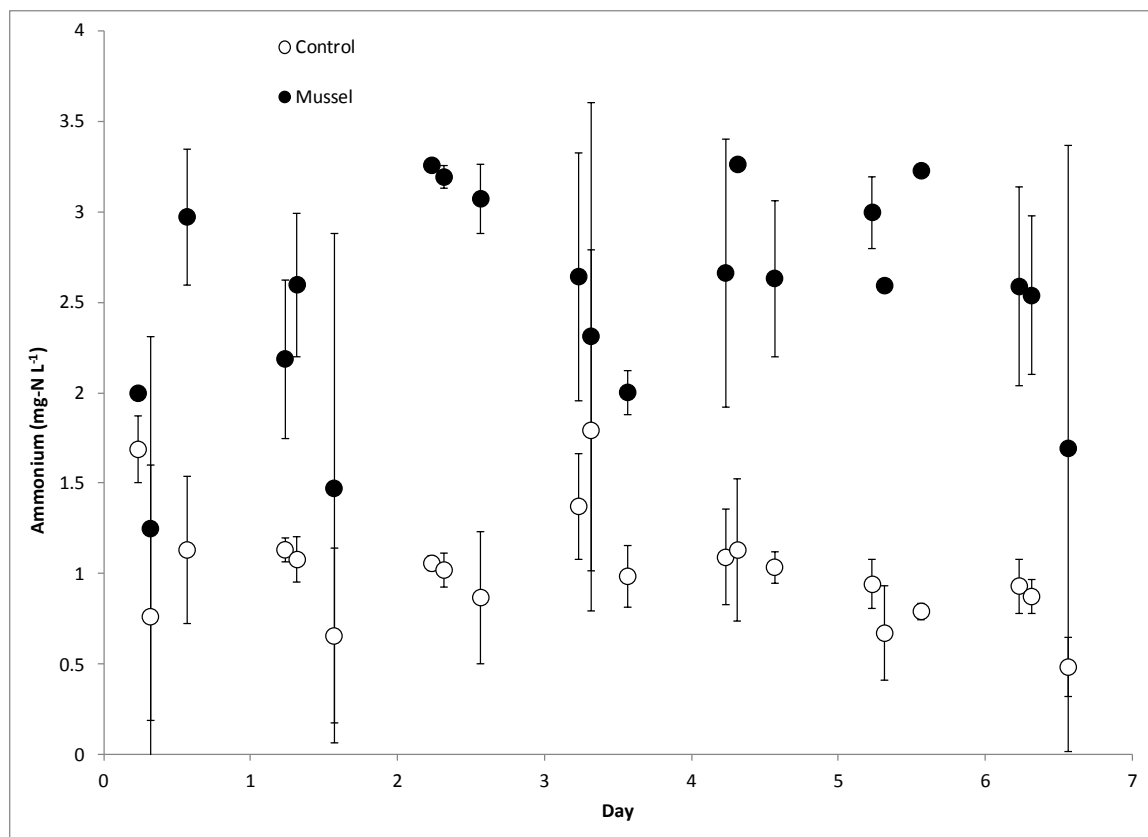


Figure 4.7: Average grab sample measurements for ammonium in the pore water of the control and mussel treatments (mg-N L⁻¹). Error bars represent ± 1 SD.

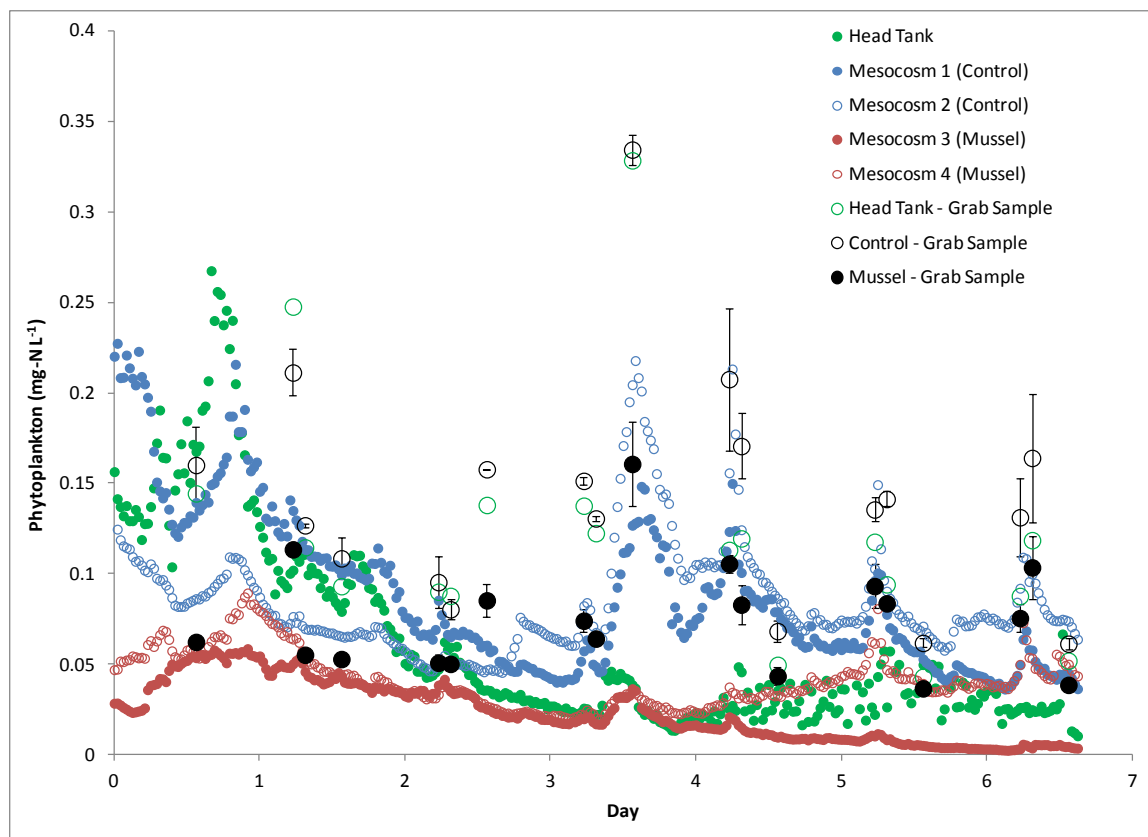


Figure 4.8: Grab sample measurements and raw Hydrolab data for phytoplankton (mg-N L^{-1}). Hydrolab measurements are shown for each of the mesocosms and grab samples were averaged for each treatment. Error bars on grab sample measurements represent ± 1 SD.

Table 4.4: Phytoplankton Hydrolab measurements (mg-N L^{-1}) and corresponding grab sample measurements (mg-N L^{-1}) used to calculate calibration factors.

Day	Hydrolab Measurements (mg-N L^{-1})					Grab Sample Measurements (mg-N L^{-1})					Calibration Factor							
	Control		Mussel			Head	Control		Mussel			Head	Control		Mussel			Head
	Mesocosm 1	Mesocosm 2	Mesocosm 3	Mesocosm 4	Tank	Mesocosm 1	Mesocosm 2	Mesocosm 3	Mesocosm 4	Tank	Mesocosm 1	Mesocosm 2	Mesocosm 3	Mesocosm 4	Tank			
0.23	0.20	0.10	0.04	0.06	0.13	---	---	---	---	---	---	---	---	---	---			
0.31	0.15	0.10	0.04	0.07	0.19	---	---	---	---	---	---	---	---	---	---			
0.56	0.14	0.09	0.05	0.06	0.17	0.14	0.18	0.06	0.06	0.14	0.96	0.49	0.86	0.90	1.16			
1.23	0.13	0.08	0.05	0.06	0.10	0.22	0.20	0.11	0.11	0.25	0.61	0.38	0.44	0.57	0.41			
1.31	0.11	0.07	0.05	0.05	0.11	0.13	0.13	0.06	0.05	0.11	0.90	0.55	0.82	0.98	0.97			
1.56	0.10	0.07	0.04	0.04	0.08	0.12	0.10	0.05	0.05	0.09	0.85	0.65	0.80	0.84	0.85			
2.23	0.09	0.05	0.04	0.03	0.05	0.11	0.09	0.05	0.05	0.09	0.81	0.61	0.71	0.70	0.53			
2.31	0.07	0.05	0.04	0.04	0.06	0.08	0.08	0.05	0.05	0.09	0.86	0.59	0.73	0.68	0.68			
2.56	0.06	0.05	0.03	0.03	0.04	0.16	0.16	0.08	0.09	0.14	0.38	0.30	0.32	0.29	0.26			
3.23	0.06	0.08	0.02	0.02	0.03	0.15	0.15	0.08	0.07	0.14	0.38	0.55	0.25	0.32	0.19			
3.31	0.05	0.07	0.02	0.02	0.02	0.13	0.13	0.06	0.06	0.12	0.38	0.51	0.27	0.32	0.18			
3.56	0.13	0.20	0.04	0.03	0.04	0.33	0.34	0.18	0.14	0.33	0.39	0.60	0.21	0.24	0.12			
4.23	0.12	0.16	0.02	0.04	0.03	0.18	0.24	0.11	0.10	0.11	0.69	0.66	0.19	0.37	0.22			
4.31	0.10	0.12	0.02	0.03	0.05	0.18	0.16	0.09	0.08	0.12	0.55	0.79	0.17	0.44	0.38			
4.56	0.08	0.09	0.01	0.03	0.04	0.07	0.06	0.04	0.05	0.05	1.09	1.35	0.24	0.70	0.72			
5.23	0.10	0.10	0.01	0.06	0.02	0.14	0.13	0.08	0.10	0.12	0.69	0.79	0.12	0.60	0.19			
5.31	0.08	0.09	0.01	0.05	0.03	0.14	0.14	0.09	0.08	0.09	0.54	0.65	0.10	0.57	0.28			
5.56	0.05	0.07	0.01	0.04	0.05	0.06	0.06	0.03	0.04	0.04	0.88	1.12	0.15	1.00	1.16			
6.23	0.05	0.09	0.00	0.05	0.03	0.15	0.12	0.07	0.08	0.09	0.34	0.79	0.05	0.62	0.30			
6.31	0.06	0.10	0.00	0.05	0.02	0.14	0.19	0.09	0.12	0.12	0.42	0.53	0.04	0.46	0.21			
6.56	0.05	0.07	0.00	0.05	---	0.06	0.06	0.04	0.04	0.05	0.71	1.25	0.12	1.24	---			
Average											0.65	0.69	0.35	0.62	0.49			
Standard Deviation											0.23	0.28	0.29	0.28	0.35			
Coefficient of Variation											35.9%	40.0%	82.5%	44.2%	71.2%			

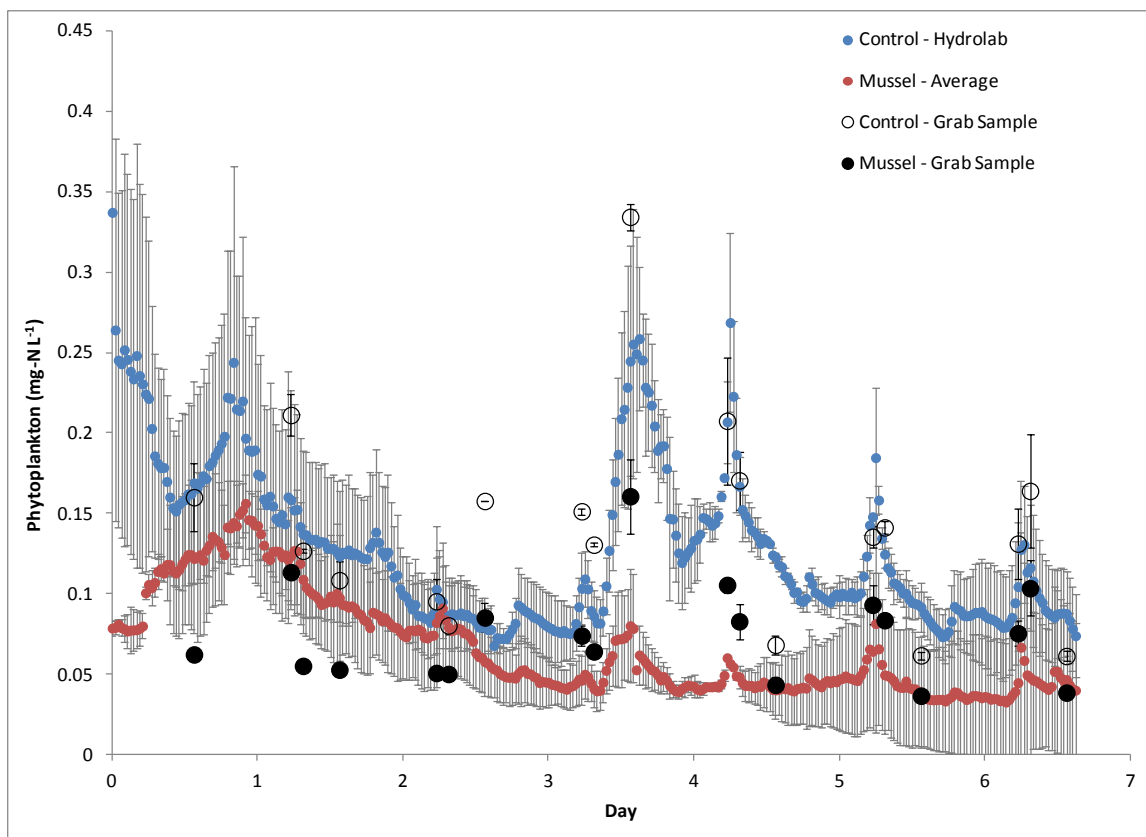


Figure 4.9: Average grab sample measurements and calibrated Hydrolab measurements for phytoplankton (mg-N L^{-1}). Error bars represent ± 1 SD.

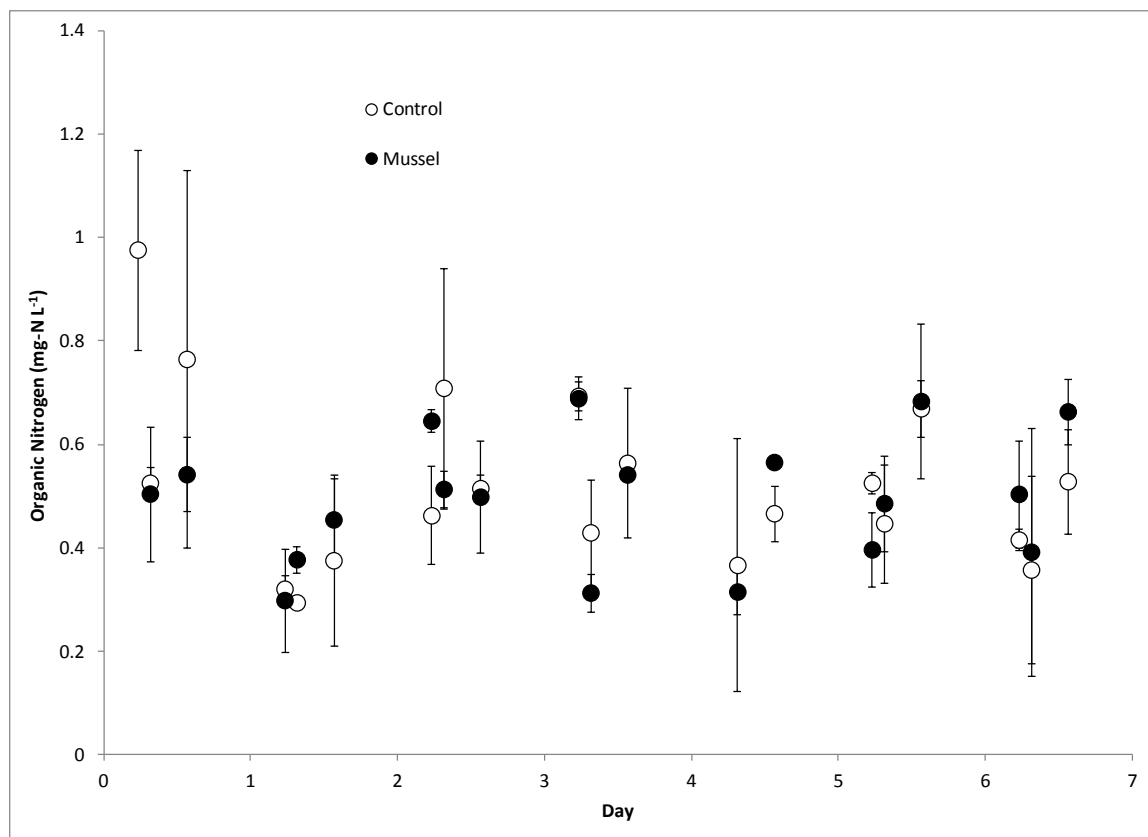


Figure 4.10: Average grab sample measurements for organic nitrogen in the overlying water of the control and mussel treatments (mg-N L⁻¹). Error bars represent ± 1 SD.

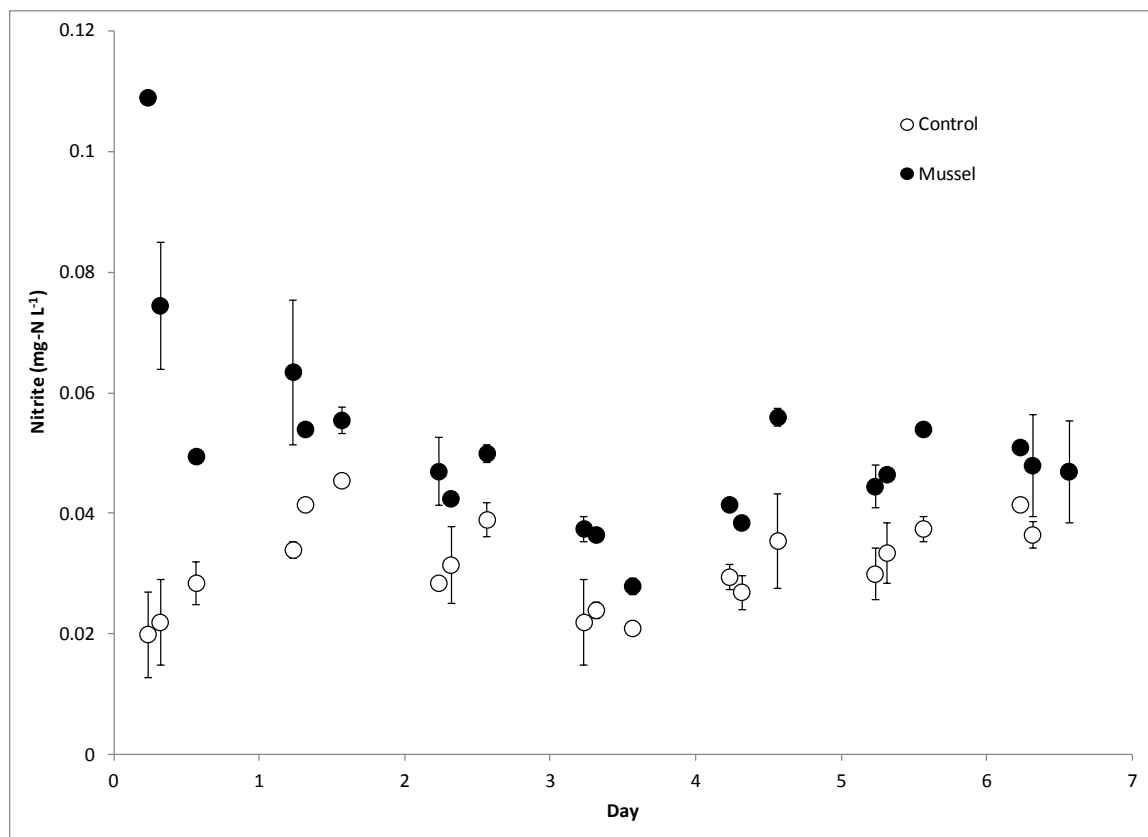


Figure 4.11: Average grab sample measurements for nitrite in the overlying water of the control and mussel treatments (mg-N L⁻¹). Error bars represent ± 1 SD.

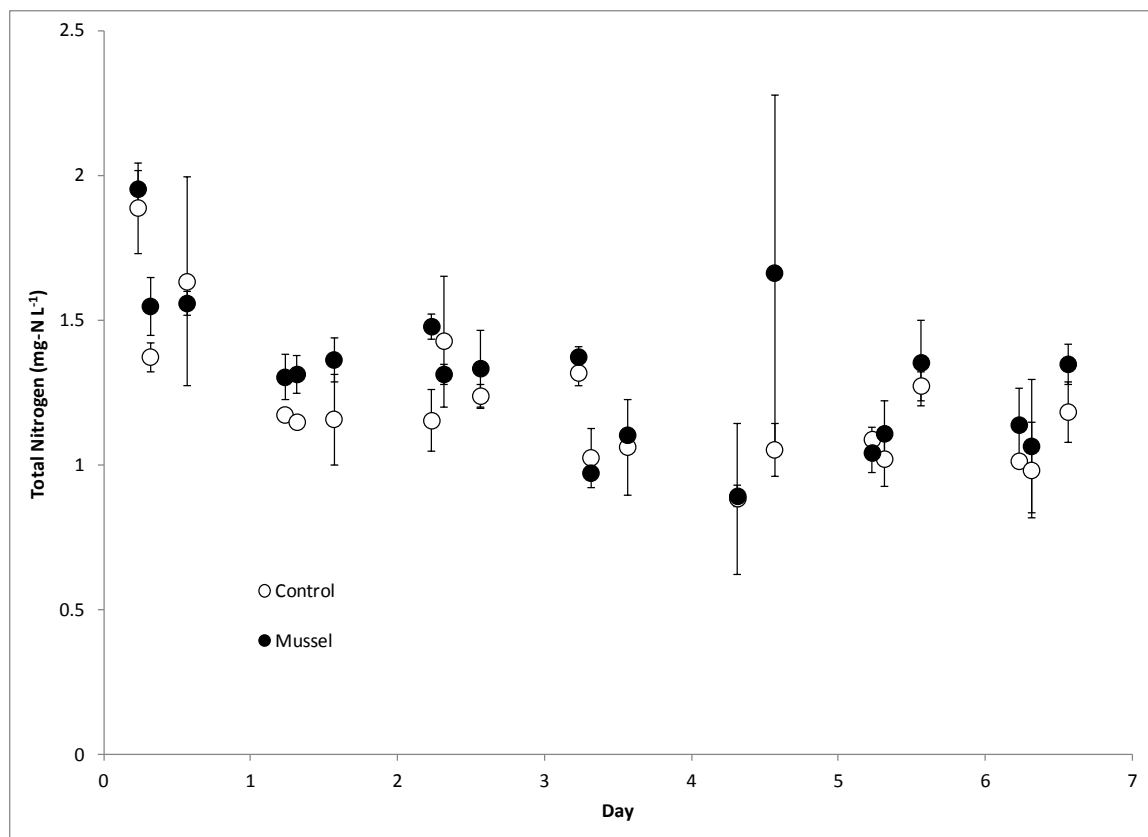


Figure 4.12: Average grab sample measurements for total nitrogen in the overlying water of the control and mussel treatments (mg-N L⁻¹). Error bars represent ± 1 SD.

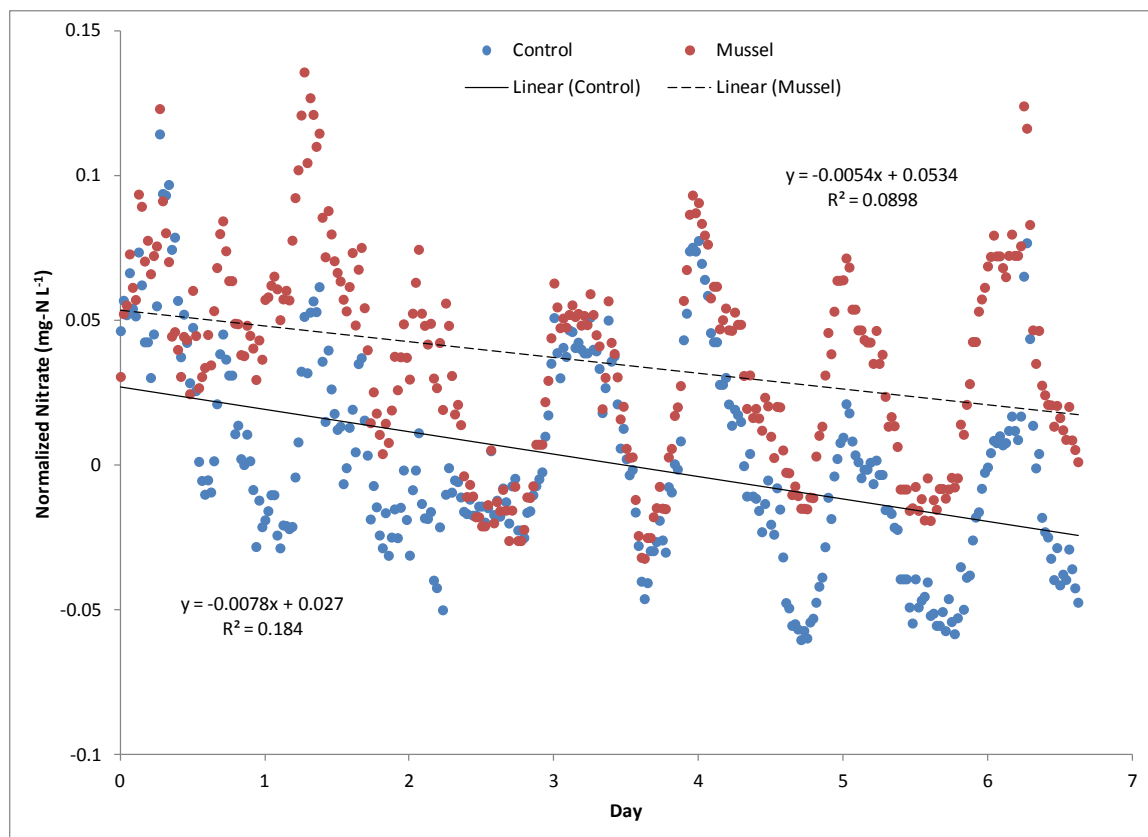


Figure 4.13: The average calibrated Hydrolab nitrate concentrations (mg-N L⁻¹) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

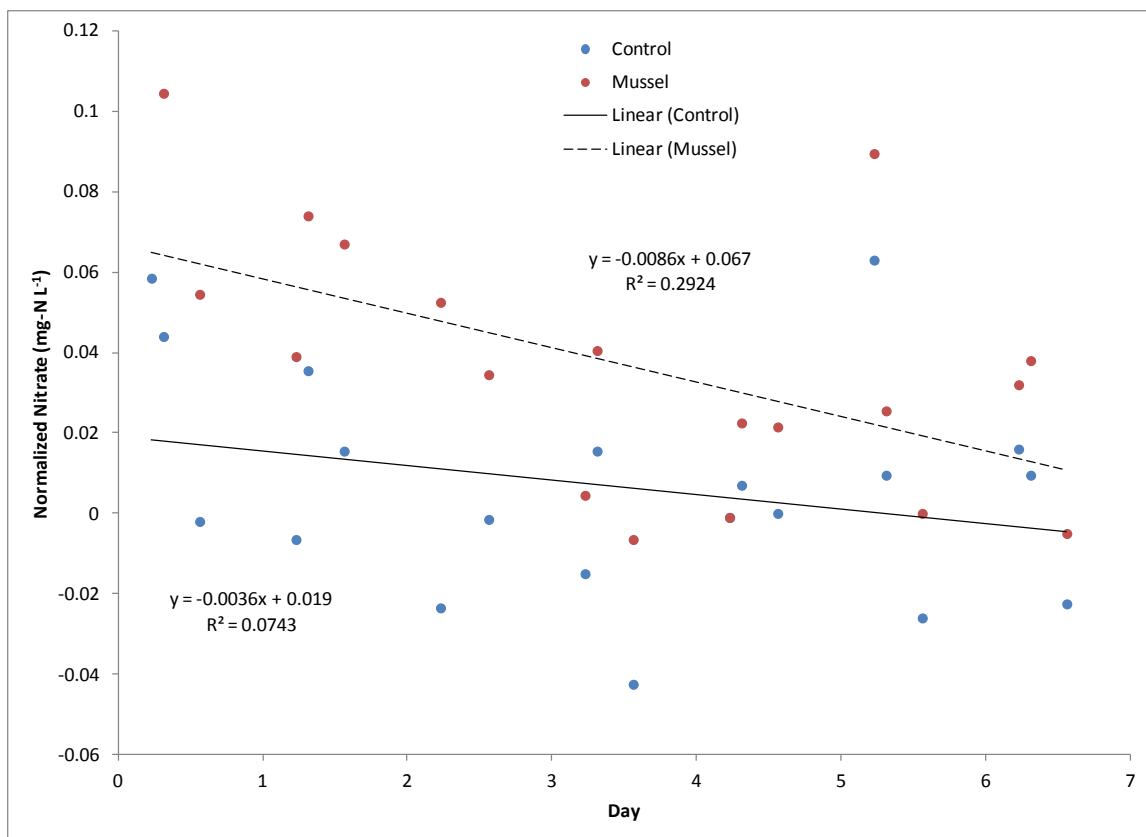


Figure 4.14: The nitrate grab sample nitrate measurements (mg-N L⁻¹) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

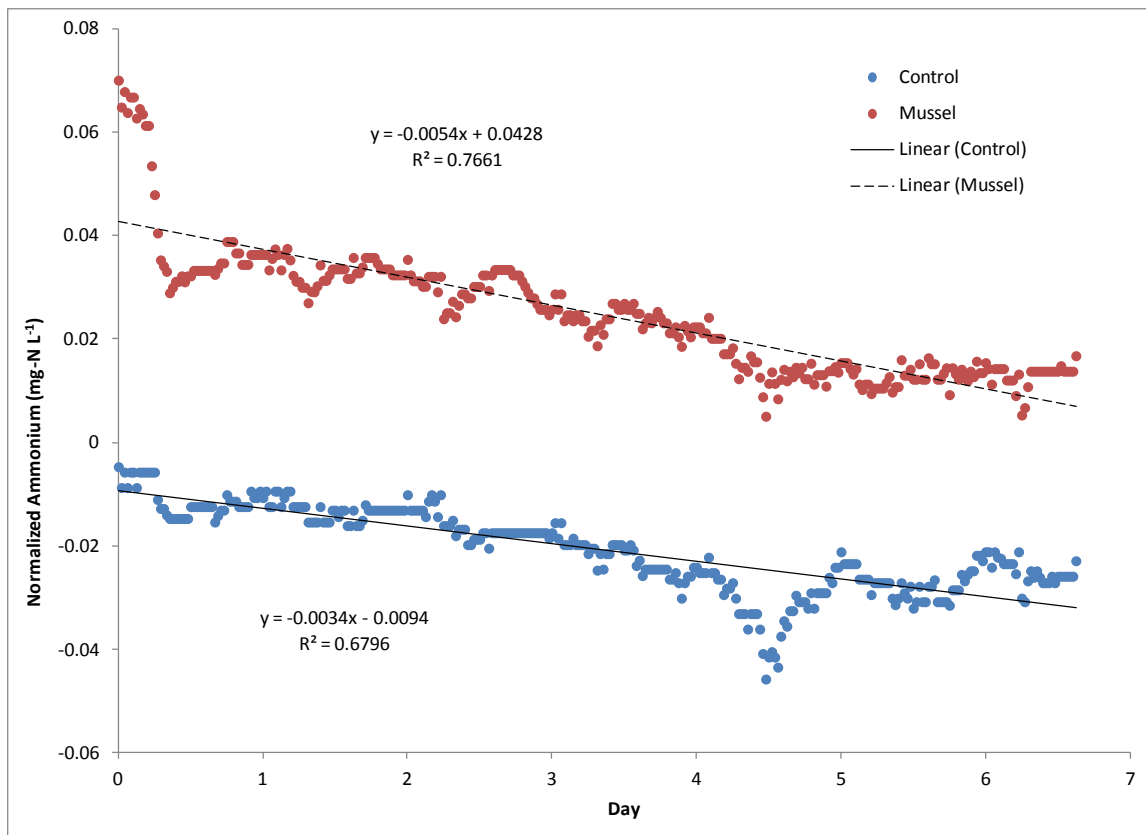


Figure 4.15: The average calibrated Hydrolab ammonium concentrations (mg-N L⁻¹) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

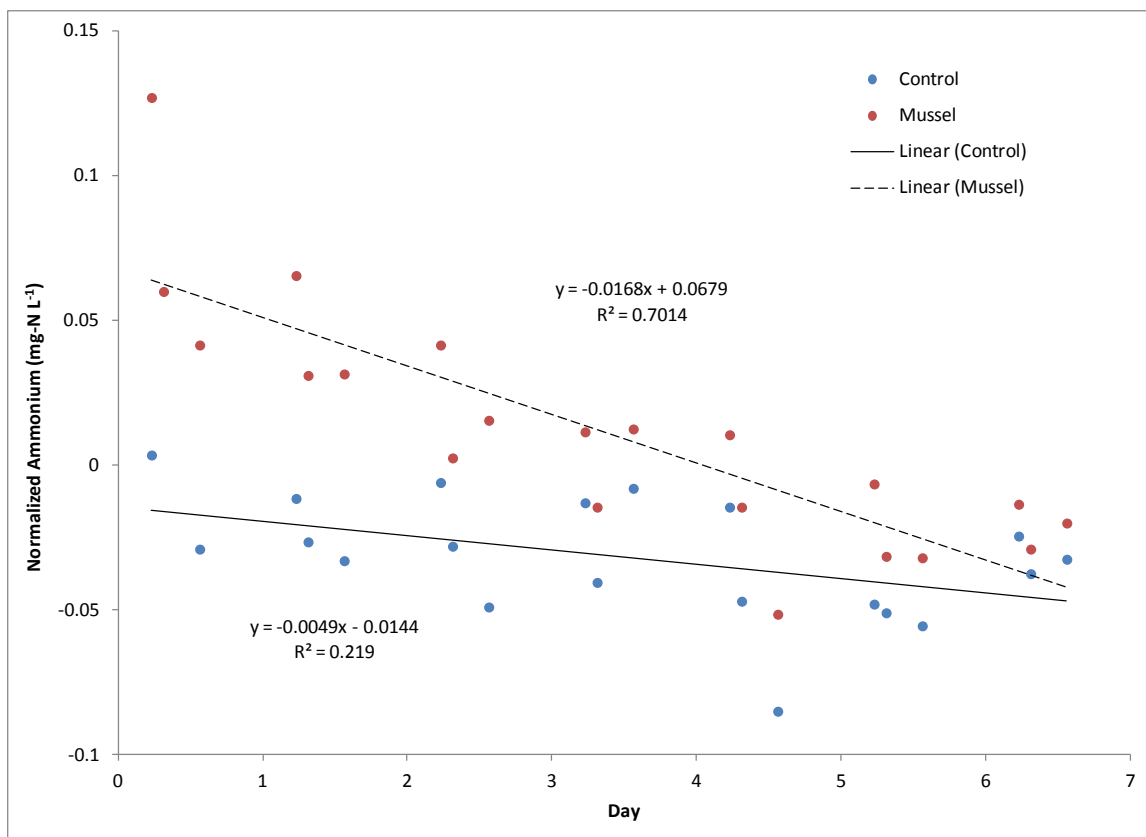


Figure 4.16: The ammonium grab sample measurements (mg-N L^{-1}) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

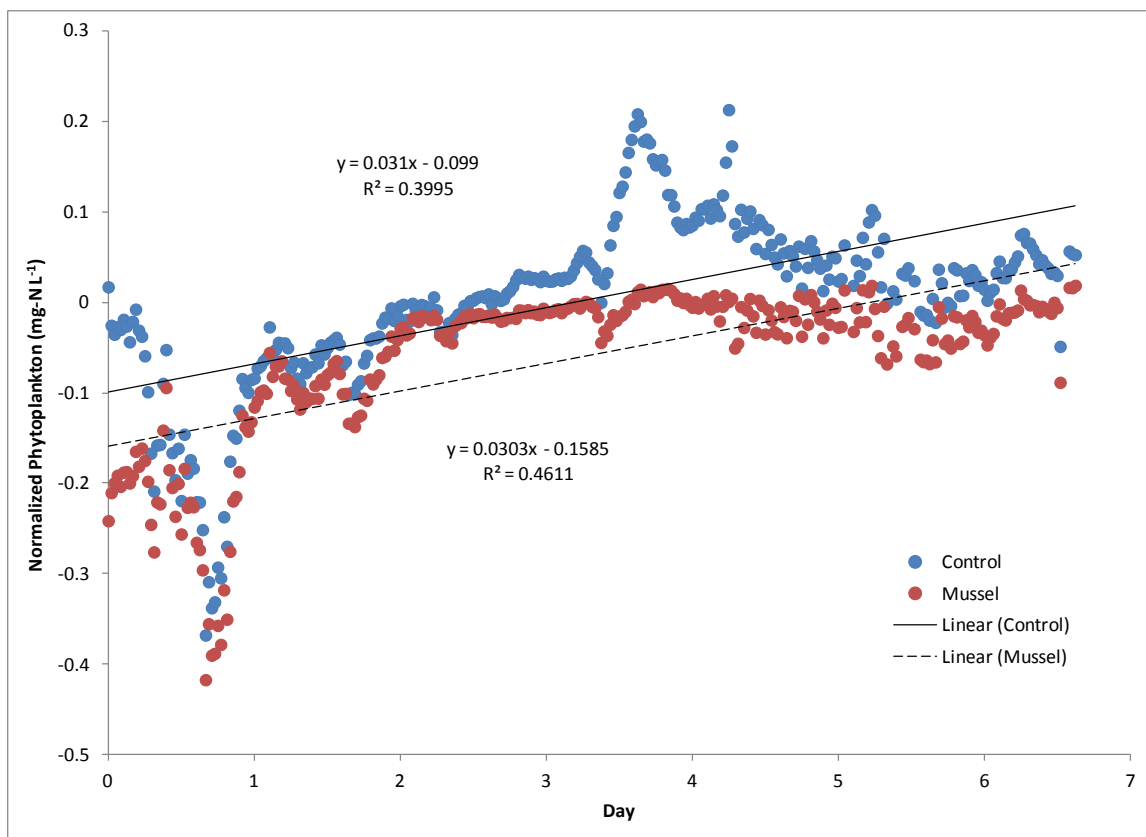


Figure 4.17: The average calibrated Hydrolab phytoplankton concentrations (mg-N L⁻¹) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

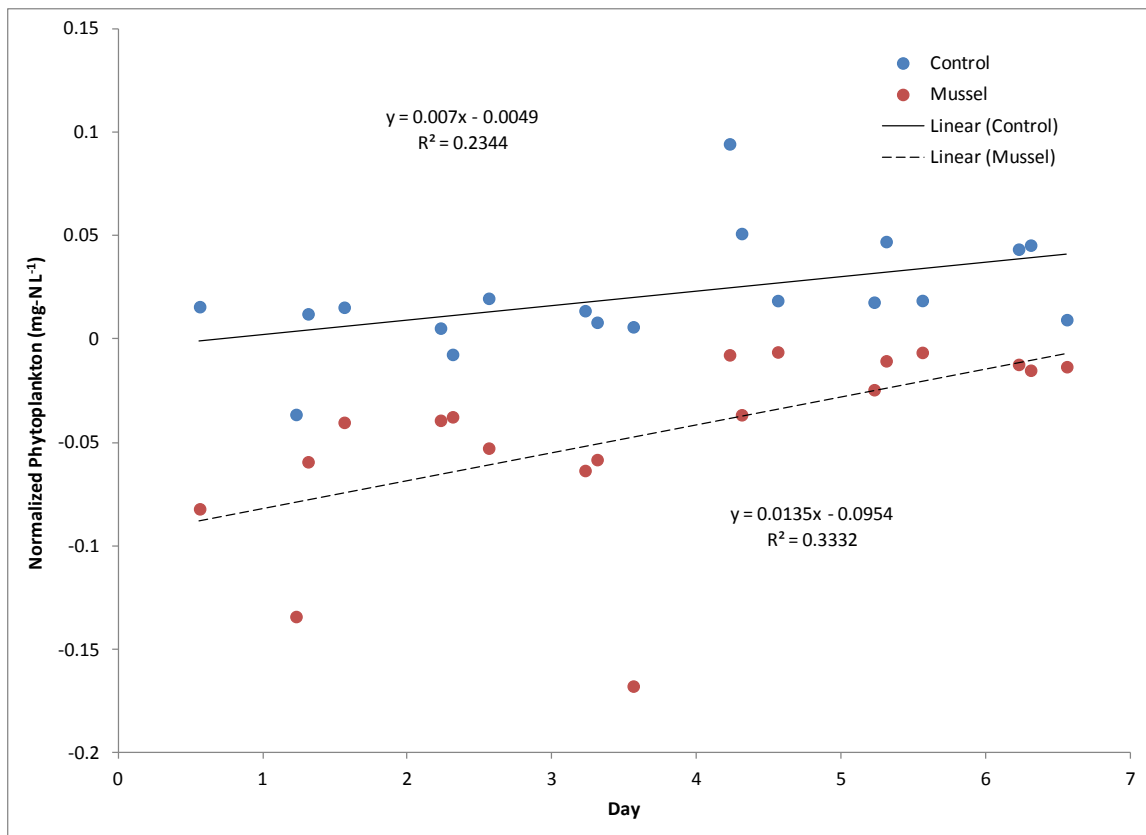


Figure 4.18: The phytoplankton grab sample measurements (mg-N L^{-1}) were normalized to the river water influent (head tank) to determine processing rates for each treatment.

Table 4.5: The change in nitrogen species concentrations over time for the normalized data from the mussel and control treatments as measured in the overlying water.

Parameter	Treatment	Rate in Overlying Water ^a	Normalized Mussel Effect Rate ^b		
		(mg-N L ⁻¹ d ⁻¹)	(mg-N L ⁻¹ d ⁻¹)	(mg-N d ⁻¹)	(mg-N d ⁻¹ g ⁻¹ dry mass)
Nitrate (Hydrolab)	Control	-0.008 (0.18)	0.003	0.42	0.002
	Mussel	-0.005 (0.09)			
Nitrate (Grab Sample)	Control	-0.004 (0.07)	-0.005	-0.70	-0.004
	Mussel	-0.009 (0.29)			
Ammonium (Hydrolab)	Control	-0.003 (0.68)	-0.002	-0.28	-0.001
	Mussel	-0.005 (0.70)			
Ammonium (Grab Sample)	Control	-0.005 (0.22)	-0.012	-1.68	-0.008
	Mussel	-0.017 (0.70)			
Phytoplankton Biomass (Hydrolab)	Control	0.031 (0.40)	-0.001	-0.14	-0.001
	Mussel	0.030 (0.46)			
Phytoplankton Biomass (Grab Sample)	Control	0.007 (0.23)	0.007	0.98	0.005
	Mussel	0.014 (0.33)			

^a R² values for linear regressions are shown in parentheses

^b The linear mussel effect rate was determined by subtracting the rate in the control treatments from the rate in the mussel treatments

Table 4.6: The amount of mass mussels added or removed from the overlying water of the mesocosms was calculated for nitrate, ammonium, phytoplankton, organic nitrogen, nitrite, and total nitrogen.

Parameter	Measurement	Mussel Effect on Mass of Nitrogen		
		(mg-N)	(mg-N d ⁻¹)	(mg-N d ⁻¹ g ⁻¹ dry mass)
Nitrate	Hydrolab	299.8	45.3	0.226
	Grab Sample	286.6	43.3	0.216
Ammonium	Hydrolab	399.1	60.3	0.301
	Grab Sample	352.4	53.2	0.266
Phytoplankton	Hydrolab	-540.9	-81.7	-0.408
	Grab Sample	-568.2	-85.8	-0.429
Organic Nitrogen	Hydrolab	---	---	---
	Grab Sample	109.6	16.5	0.083
Nitrite	Hydrolab	---	---	---
	Grab Sample	156.6	23.6	0.118
Total Nitrogen	Hydrolab	---	---	---
	Grab Sample	959.8	144.9	0.724

CHAPTER 5

A MUSSEL NITROGEN DYNAMICS MODEL FOR LABORATORY MESOCOSMS

Purpose

This chapter builds upon Chapter 4 by developing an improved strategy for quantifying the effects of mussels on nitrogen dynamics in the laboratory mesocosms. We demonstrated in Chapter 4 that even with a highly calibrated data set, a mussel effect rate could not be captured through linear regression. Thus, the objective of this study was to develop, calibrate, and evaluate a deterministic mass balance model that could be used to simulate the effect of mussels in the mesocosms. The model was calibrated with highly time resolved data and grab samples obtained from laboratory mesocosm experiments evaluated under different environmental conditions (flow and no flow) and treatments (mussel and no mussel). We utilized the model to identify the processing rates and environmental conditions that would most influence the scalability of the mussel effects. Hypothesis 1 and Hypothesis 2 were tested with the results from this study.

Abstract

A deterministic mass balance model was developed to better understand the effects of mussels on nitrogen dynamics in the overlying water of laboratory mesocosms. The model was developed using STELLA modeling software and calibrated using literature and observed parameter values from mesocosm experiments. The model simulated nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton concentrations in the overlying water of the mesocosms. The model correlated well with the experimental measurements and predicted that changes in nitrate and total nitrogen concentrations attributable to mussels were small relative to the concentrations present in the mesocosms. The model also predicted that mussels increased ammonium and nitrite, decreased phytoplankton, and did not significantly affect organic nitrogen. Sensitivity

analysis results demonstrated that the most sensitive model variables in the mussel treatments were hydraulic retention time, temperature, denitrification rate, and mussel ammonium excretion rate. The sensitivity analysis also demonstrated the difficulty in modeling the dynamic nature of the mesocosms and revealed the need to constrain the model with observed experimental measurements. Application of the model predicted that increases in phytoplankton concentrations significantly influenced the effect of mussels on nitrogen dynamics in the overlying water.

Introduction

Using computer simulations to model ecosystem dynamics has become a widely studied and important tool for understanding and predicting the behavior of complex systems (Odum and Odum 2000). One of the best dynamic systems software packages for developing a better conceptual understanding of ecological systems is STELLA (Rizzo et al. 2006). STELLA is a user-friendly software package that has been shown to be very effective in simulating nitrogen dynamics in complex systems (Jamu and Piedrahita 2002b; Mayo and Bigambo 2005).

One of the most important stages in the model building process is model evaluation (Jamu and Piedrahita 2002b). Typically, model evaluation consists of model verification, sensitivity analysis, and validation (Swartzman and Kaluzny 1987). Model verification is the process of reviewing general model behavior and the accuracy of assumptions incorporated into the model. Sensitivity analyses are often used to highlight the most important processes in a system, determine the model variables that would require high accuracy in estimation, and identify areas for future research (Jamu and Piedrahita 2002b). The process of testing the behavior of the model by comparing its output to observed data is model validation (Swartzman and Kaluzny 1987).

The collection of highly time resolved data allows for modeling processes to be calibrated and evaluated like never before. Highly time resolved data have been shown

to accurately simulate the effects of nutrient dynamics (Hanrahan et al. 2001) and dissolved oxygen (Loperfido et al. 2009) on surface water biology. Coupling highly time resolved data with a dynamic STELLA model provides a means to better understand the effects of mussels on aquatic nitrogen dynamics. Thus, the goal of this study was to develop, calibrate, and evaluate a dynamic mass balance model to identify the processes that are most influenced by mussels in the aquatic nitrogen cycle.

Materials and Methods

Model Development

The models in this study were developed using the commercial modeling software STELLA (isee systems, inc., Lebanon, New Hampshire). A STELLA model was developed to simulate the overlying water of the laboratory mesocosms under flow (Figure 5.1) and no flow conditions (Figure 5.2). Both models were equipped to simulate the laboratory mesocosms with mussel and no mussel (control) treatment conditions.

The models in this study were dynamic, deterministic, and mechanistic models that simulated nitrate, ammonium, organic nitrogen, nitrite, and phytoplankton in the overlying water of a laboratory mesocosm system. The STELLA models were based on mass balance equations used in water quality modeling. The simulation time step of each model was 30 min and the model differential equations were solved numerically using Euler's method. The model results for nitrate, ammonium, nitrite, and organic nitrogen were added together to simulate total nitrogen concentration. The variables used in the STELLA models are defined in Table 5.1.

Nitrate

Nitrate was modeled to include inputs of nitrification and nitrate inflow and outputs of plant uptake, denitrification, and nitrate outflow:

Equation 5.1
$$dn_{n,t} / dt = k_n(T)n_{a,t} + n_{n,t-1} / \tau - (1 - F_{am})k_g(T, N, I)a_t \dots$$

$$\dots - k_{dn}(T)n_{n,t} - n_{n,t} / \tau$$

where,

$n_{n,t}$ = nitrate concentration at time t (mg-N L⁻¹)

$k_n(T)$ = temperature-dependent nitrification rate (h⁻¹)

$n_{a,t}$ = ammonium concentration at time t (mg-N L⁻¹)

$n_{n,t-1}$ = nitrate concentration at time t-1 (mg-N L⁻¹)

τ = hydraulic retention time (h)

F_{am} = preference for ammonium as a nitrogen source for phytoplankton
(dimensionless)

$k_g(T, N, I)$ = phytoplankton growth rate (h⁻¹)

a_t = phytoplankton concentration at time t (mg-N L⁻¹)

$k_{dn}(T)$ = temperature-dependent denitrification rate (h⁻¹)

The mass balance equation used to represent nitrate was based on the assumption that mussels would not directly influence nitrate in the overlying water. For the no flow STELLA model, the inflow and outflow terms were removed from the mass balance equation. The adjusted mass balance equation was written as follows:

$$\text{Equation 5.2} \quad dn_{n,t} / dt = k_n(T)n_{a,t} - (1 - F_{am})k_g(T, N, I)a_t - k_{dn}(T)n_{n,t}$$

The theta equation was used to represent the effect of temperature for all first-order reactions used in the models. A value of $\theta = 1.08$ was used (Chapra 1997) and the corresponding equation for temperature effect was as follows:

$$\text{Equation 5.3} \quad k_{g,T} = k(20)\theta^{T-20}$$

where,

$k(20)$ = first-order reaction rate at 20 °C (h⁻¹)

θ = temperature correction coefficient

T = temperature (°C)

Ammonium

Ammonium was modeled to include inputs of organic nitrogen hydrolysis, phytoplankton respiration/excretion, mussel ammonium excretion, and ammonium inflow. Losses were modeled as plant uptake, nitrification, and ammonium outflow:

Equation 5.4

$$dn_{a,t}/dt = k_{hn}(T)n_{o,t} + k_{ra}(T)a_t + n_{a,t-1}/\tau + \dots$$

$$\dots(M_{ex}M_b)(M_{cl}M_b a_t) - F_{am}k_g(T, N, I)a_t - k_n(T)n_{a,t} - n_{a,t}/\tau$$

where,

$n_{a,t}$ = ammonium concentration at time t (mg-N L⁻¹)

$k_{hn}(T)$ = temperature-dependent organic nitrogen hydrolysis rate (h⁻¹)

$n_{o,t}$ = organic nitrogen concentration at time t (mg-N L⁻¹)

$k_{ra}(T)$ = temperature-dependent phytoplankton respiration and excretion rate (h⁻¹)

a_t = phytoplankton concentration at time t (mg-N L⁻¹)

$n_{a,t-1}$ = ammonium concentration at time t-1 (mg-N L⁻¹)

τ = hydraulic retention time (h)

M_{ex} = mussel excretion rate of ammonium (h⁻¹ g⁻¹ dry mass)

M_b = total mussel biomass as dry weight (g)

M_{cl} = mussel clearance rate (h⁻¹ g⁻¹ mussel dry weight)

F_{am} = preference for ammonium as a nitrogen source for phytoplankton
(dimensionless)

$k_g(T, N, I)$ = phytoplankton growth rate (h⁻¹)

$k_n(T)$ = temperature-dependent nitrification rate (h⁻¹)

The amount of ammonium excreted by mussels was a function of mussel biomass and amount of phytoplankton removed by mussels (mussel clearance).

Plant uptake was assumed to consist solely of ammonium uptake by phytoplankton. The preference for ammonium as a nitrogen source for phytoplankton (referred to as fraction of inorganic nitrogen uptake) was computed as:

Equation 5.5
$$F_{am} = (n_{a,t}n_{n,t}) / ((k_{am} + n_{a,t})(k_{am} + n_{n,t})) + \dots$$

$$\dots(n_{a,t}k_{am}) / ((n_{a,t} + n_{n,t})(k_{am} + n_{n,t}))$$

where,

$n_{n,t}$ = nitrate concentration at time t (mg-N L⁻¹)

k_{am} = the half-saturation constant for ammonium preference (mg-N L⁻¹)

For the no flow STELLA model, the inflow and outflow terms were removed from the respective mass balance equations. The adjusted mass balance equation was written as follows:

Equation 5.6
$$dn_{a,t}/dt = k_{hn}(T)n_{o,t} + k_{ra}(T)a_t + (M_{ex}M_b)(M_{cl}M_b a_t) - \dots$$

$$\dots F_{am}k_g(T, N, I)a_t - k_n(T)n_{a,t}$$

Organic Nitrogen

Organic nitrogen was modeled to include inputs of phytoplankton death and organic nitrogen inflow and outputs of hydrolysis, settling, and organic nitrogen outflow:

Equation 5.7
$$dn_{o,t}/dt = k_d(T)a_t + n_{o,t-1}/\tau - k_{hn}(T)n_{o,t} - (V_{s,o}/H)n_{o,t} - n_{o,t}/\tau$$

where,

$n_{o,t}$ = organic nitrogen concentration at time t (mg-N L⁻¹)

$k_d(T)$ = temperature-dependent phytoplankton death rate (h⁻¹)

a_t = phytoplankton concentration at time t (mg-N L⁻¹)

$n_{o,t-1}$ = organic nitrogen concentration at time t - 1 (mg-N L⁻¹)

τ = hydraulic retention time (h)

$k_{hn}(T)$ = temperature-dependent organic nitrogen hydrolysis rate (h⁻¹)

$V_{s,o}$ = organic nitrogen settling velocity (m h⁻¹)

H = water depth (m)

The mass balance equation used to represent organic nitrogen was based on the assumption that mussels would not directly influence organic nitrogen in the overlying water. For the no flow STELLA model, the inflow and outflow terms were removed from the mass balance equation. The adjusted mass balance equation was written as follows:

$$\text{Equation 5.8} \quad \frac{dn_{o,t}}{dt} = k_d(T)a_t - k_{hm}(T)n_{o,t} - (V_{s,o}/H)n_{o,t}$$

Nitrite

Nitrite was modeled to include inputs of nitrification (ammonium to nitrite), denitrification (nitrate to nitrite), and inflow and outputs of nitrification (nitrite to nitrate), denitrification (nitrite to N₂ gas), and outflow:

$$\text{Equation 5.9} \quad \frac{dn_{i,t}}{dt} = k_{ai}(T)n_{a,t} + k_{ni}(T)n_{n,t} + n_{i,t-1}/\tau - k_{in}(T)n_{i,t} \dots \\ \dots - k_{ig}(T)n_{i,t} - n_{i,t}/\tau$$

where,

$n_{i,t}$ = nitrite concentration at time t (mg-N L⁻¹)

$k_{ai}(T)$ = temperature-dependent conversion rate of ammonium to nitrite (h⁻¹)

$n_{a,t}$ = ammonium concentration at time t (mg-N L⁻¹)

$k_{ni}(T)$ = temperature-dependent conversion rate of nitrate to nitrite (h⁻¹)

$n_{n,t}$ = nitrate concentration at time t (mg-N L⁻¹)

$n_{i,t-1}$ = nitrite concentration at time t-1 (mg-N L⁻¹)

τ = hydraulic retention time (h)

$k_{in}(T)$ = temperature-dependent conversion rate of nitrite to nitrate (h⁻¹)

$k_{ig}(T)$ = temperature-dependent conversion rate of nitrite to nitrogen gas (h⁻¹)

The mass balance equation used to represent nitrite was based on the assumption that mussels would not directly influence nitrite in the overlying water. For the no flow STELLA model, the inflow and outflow terms were removed from the respective mass

balance equations. The mass balance equation for the scenarios without flow was written as follows:

$$\text{Equation 5.10} \quad \frac{dn_{i,t}}{dt} = k_{ai}(T)n_{a,t} + k_{ni}(T)n_{n,t} - k_{in}(T)n_{i,t} - k_{ig}(T)n_{i,t}$$

Phytoplankton

Phytoplankton was modeled to include inputs of photosynthesis and inflow and outputs of death, settling, respiration/excretion, mussel clearance, and outflow. The mass balance equation for phytoplankton was written as follows:

$$\text{Equation 5.11} \quad \frac{da_t}{dt} = k_g(T, N, I)a_t + a_{t-1}/\tau - k_d(T)a_t - (V_{s,a}/H)a_t - k_{ra}(T)a_t - \dots$$

$$\dots (M_{cl}M_b)a_t - a_t/\tau$$

where,

a_t = phytoplankton concentration at time t (mg-N L⁻¹)

$k_g(T, N, I)$ = first-order growth rate as a function of temperature, nutrients, and light (h⁻¹)

a_{t-1} = phytoplankton concentration at time t – 1 (mg-N L⁻¹)

τ = hydraulic retention time (h)

$k_d(T)$ = temperature-dependent phytoplankton death rate (h⁻¹)

$V_{s,a}$ = phytoplankton settling rate (m h⁻¹)

H = water depth (m)

$k_{ra}(T)$ = temperature-dependent phytoplankton respiration/excretion rate (h⁻¹)

M_{cl} = mussel clearance rate (h⁻¹ g⁻¹ mussel dry weight)

M_b = total mussel biomass as dry weight (g)

The mussel clearance rate was defined as the volume of water from which a mussel has filtered all algal particles in a given time (Spooner and Vaughn 2008). This volume was divided by the total mesocosm volume to estimate the fraction of

phytoplankton removed by mussels over time. The amount of phytoplankton removed by mussels was a function of mussel biomass.

For the no flow STELLA model, the inflow and outflow terms were removed from the mass balance equation. The adjusted mass balance equation was written as follows:

$$\text{Equation 5.12} \quad da_t/dt = k_g(T, N, I)a_t - k_d(T)a_t - (V_{s,a}/H)a_t - k_{ra}(T)a_t - (M_c/M_b)a_t$$

Phytoplankton Photosynthesis

Phytoplankton photosynthesis was computed as:

$$\text{Equation 5.13} \quad \text{PhytoPhoto} = k_g(T, N, I)a_t$$

where,

$k_g(T, N, I)$ = phytoplankton photosynthesis rate as a function of temperature, nutrients, and light (h^{-1}):

$$\text{Equation 5.14} \quad k_g(T, N, I) = k_{g,T}\varphi_N\varphi_L$$

where,

$k_{g,T}$ = maximum phytoplankton growth rate at temperature T (h^{-1})

φ_N = phytoplankton nutrient attenuation factor (dimensionless)

φ_L = phytoplankton light attenuation coefficient (dimensionless)

Temperature

The theta equation was used to represent the effect of temperature on phytoplankton photosynthesis. A value of $\theta = 1.066$ (Eppley 1972) was used in the model for this study. The equation for temperature effect was as follows:

$$\text{Equation 5.15} \quad k_{g,T} = k_{g,20}\theta^{T-20}$$

where,

$k_{g,20}$ = phytoplankton growth rate at the reference temperature 20 °C (h^{-1})

θ = temperature correction coefficient

T = temperature (°C)

Nutrients

The phytoplankton nutrient attenuation factor was determined using the Michaelis-Menten equation. It was assumed that the nutrient in shortest supply would control growth:

Equation 5.16
$$\varphi_N = \min\{\varphi_n, \varphi_p\}$$

where,

φ_N = phytoplankton nutrient attenuation factor (dimensionless)

φ_n = nitrogen attenuation factor (dimensionless)

φ_p = phosphorus attenuation factor (dimensionless)

The nitrogen attenuation factor was calculated as follows:

Equation 5.17
$$\varphi_n = n / (k_{sn} + n)$$

where,

φ_n = nitrogen attenuation factor (dimensionless)

n = available nitrogen concentration (mg-N L⁻¹)

k_{sn} = nitrogen half-saturation constant (mg-N L⁻¹)

The phosphorus attenuation factor was calculated as follows:

Equation 5.18
$$\varphi_p = p / (k_{sp} + p)$$

where,

φ_p = phosphorus attenuation factor (dimensionless)

p = available phosphorus concentration (mg-P L⁻¹)

k_{sp} = phosphorus half-saturation constant (mg-P L⁻¹)

Light

The light attenuation factor for phytoplankton growth (ϕ_L) was estimated by measurements obtained from the photosynthetically active radiation (PAR) sensors. The PAR measurement at the substrate and the PAR measurement at the water surface were averaged to determine a representative PAR measurement for the middle of each mesocosm. The average PAR measurement (Langley d^{-1}) was then converted to a light attenuation factor using estimates from Steele's Equation, Smith's Function, and Half-Saturation Model for phytoplankton light dependence (Figure 5.3). The light attenuation factor was determined based on the assumption that phytoplankton growth is inhibited at high light levels (Steele 1965).

Conversion of Chlorophyll *a* to Phytoplankton

For this study, measured chlorophyll *a* concentrations ($\mu\text{g L}^{-1}$) were converted to phytoplankton biomass (mg L^{-1}) based on literature values that established linear relationships for the proportion of chlorophyll *a* in phytoplankton wet weight. The average conversion factor obtained from the literature was used (Kasprzak et al. 2008).

The impact of phytoplankton on nitrogen dynamics was evaluated by determining the nitrogen content of the phytoplankton biomass. The mass of nitrogen in total phytoplankton biomass was calculated by using the empirical formula $\text{C}_{106}\text{H}_{263}\text{O}_{110}\text{N}_{16}\text{P}$ to represent phytoplankton (Chapra 1997). Phytoplankton biomass (mg L^{-1}) was converted to phytoplankton biomass as nitrogen (herein referred to as phytoplankton, mg-N L^{-1}) by using Equation 3.1.

Total Nitrogen

As previously discussed, the model results for nitrate, ammonium, nitrite, and organic nitrogen were added together to simulate total nitrogen concentration:

Equation 5.19
$$n_{total,t} = n_{n,t} + n_{a,t} + n_{i,t} + n_{o,t}$$

where,

$n_{total,t}$ = total nitrogen concentration at time t (mg-N L⁻¹)

$n_{n,t}$ = nitrate concentration at time t (mg-N L⁻¹)

$n_{a,t}$ = ammonium concentration at time t (mg-N L⁻¹)

$n_{i,t}$ = nitrite concentration at time t (mg-N L⁻¹)

$n_{o,t}$ = organic nitrogen concentration at time t (mg-N L⁻¹)

Model Calibration

The calibration procedure involved running the models using inputs from observed data, comparing model outputs against observations, and making appropriate adjustments to model variables until a general fit between model outputs and measured values was achieved. The dataset chosen for calibrating the flow and no flow STELLA models consisted of observations collected during two laboratory mesocosm experiments. Experiment 1 was completed with flow conditions and Experiment 2 was completed without flow conditions. Each experiment contained control (no mussel) and mussel treatments. The calibration process was designed to choose model variables that favored the flow model as the flow-through mesocosms were assumed to provide the best representation of a “near natural” large river system.

Mesocosm Experiments

Experiment 1 was a 10 d mesocosm experiment that was conducted in August 2012 using flow-through mesocosms (61 x 61 x 61 cm) fed with a continuous supply of untreated Iowa River water. Treatments ($n = 4$) included 2 mesocosms containing mussels and 2 mesocosms without mussels (control). Mesocosms were lined with clean, dry sand and filled with 140 L of Iowa River water. Continuous flow of Iowa River water was provided via a 415-L head tank. The gravity-fed system provided a constant flow rate of 8.5 L h⁻¹, which resulted in a hydraulic retention time of 16 h in each mesocosm. To maintain nitrate concentrations within the optimal measurement range of

the water quality sensors being used, the head tank was continuously dosed with an artificial nitrate source (sodium nitrate). The head tank was spiked with additional sodium nitrate on Day 2, 4, and 7.

Upon completion of Experiment 1, inflow and outflow was stopped and the overlying water was drained from each mesocosm. After the mesocosms were refilled with 140 L of untreated Iowa River water and each mesocosm was spiked with sodium nitrate, Experiment 2 began. Experiment 2 was a 21 d mesocosm experiment that was conducted from August 2012 to September 2012 using completely mixed mesocosms (61 x 61 x 61 cm). Treatments ($n = 4$) included 2 mesocosms containing mussels and 2 mesocosms without mussels (control). Each mesocosm was spiked with additional sodium nitrate on Day 9. Due to evaporative losses, 4-8 L of deionized (DI) water was added to each mesocosm on Day 3, 7, 9, 14, and 18 to maintain a constant mesocosm volume.

For both Experiment 1 and Experiment 2, complete mixing in each mesocosm was provided by 1500 L h⁻¹ submersible pumps. Mesocosms were also illuminated with two 1000-watt solar simulators on a 12:12 h light-dark cycle.

Study Organisms

Fifty adult *A. plicata* (mean, 95 mm) and 25 adult *L. cardium* (mean, 120 mm) were obtained from the Iowa River in May 2012 (Figure 3.2). Between the completion of the experiment completed in Chapter 3 (July 2012) and August 2012, flow rate, sensor configurations, and grab sample frequency were optimized in preparation for Experiment 1 and Experiment 2. We placed 25 mussels per mesocosm (70 mussels m⁻²); this density represents the high range of those found in mussel beds in the UMR (Newton, unpublished data). Dry tissue mass (M , g) was predicted for each mussel based on measured shell length (L , mm) and using the allometric function $M = aL^b$. The values for the parameters a and b were obtained from data on mussels in Navigation Pool 10 of the

UMR (Newton et al. 2011). The same mussels were used in both Experiment 1 and Experiment 2.

Water Chemistry Sensing

Hydrolab multi-probe sondes ($n = 5$, model DS5, Hach Chemical Company, Loveland, Colorado) were used to measure highly time resolved (30 min) water chemistry data in the overlying water of each mesocosm and for the head tank (river water influent, Experiment 1 only). One Hydrolab was placed in each of the mesocosms and the head tank. The Hydrolabs measured chlorophyll *a* (compact fluorometer), ammonium (ion selective electrode), nitrate (ion selective electrode), dissolved oxygen (luminescent dissolved oxygen), temperature (variable resistance thermistor), pH (KCl impregnated glass bulb), and conductivity (fixed potential electrodes). A reagent-free ultraviolet absorption nitrate sensor ($n = 2$, model Nitratax sc, Hach Chemical Company, Loveland, Colorado) was placed in one mussel mesocosm and one control mesocosm to provide an additional source of highly time resolved (30 min) nitrate data. All Hydrolab and Nitratax measurements were taken in the overlying water 10 cm above the substrate.

Custom-made tipping buckets with magnetic reed switches were used to measure influent flow and an unrestricted standpipe was used to control outflow (Experiment 1 only). Photosynthetically active radiation (PAR) sensors were used to measure light intensity at the substrate (model SQ-120, Apogee Instruments, Logan, Utah) and water surface (model LI190SB-L, Campbell Scientific, Logan, Utah) of each mesocosm. All Hydrolab-measured water chemistry data were collected and stored using 2 dataloggers (model CR1000, Campbell Scientific, Logan, Utah). Specifications for each of the sensors used in the study can be found in the Appendix (Table A.1).

Grab Samples

Grab samples were collected periodically from the overlying water of each mesocosm and from the head tank (Experiment 1 only) for comparison to

Hydrolab/Nitratax measurements and to provide additional water chemistry data required for model calibration. Grab samples were collected on Day 0, 2, 4, 8, and 10 for Experiment 1 and on Day 0, 3, 8, 14, and 18 for Experiment 2. All samples were taken in the overlying water 10 cm above the substrate.

The grab samples were analyzed for nitrate, ammonium, nitrite, total nitrogen, and chlorophyll *a*. Nitrate was determined using the Dimethylphenol Method (Reference Method: 40 CFR 141) and ammonium was determined using the Salicylate Method (Reference Method: EPA 350.1). Nitrite was measured using the Diazotization Method (Reference Method: EPA 353.2) and total nitrogen was measured using the Persulfate Digestion Method (Reference Method: Standard Methods 4500-N C). Chlorophyll *a* was measured by fluorescence (Reference Method: EPA 445.0 Rev. 1.2) and results were used to create a response factor to calibrate the chlorophyll *a* sensor on the Hydrolabs. Grab sample measurements for organic nitrogen were estimated by subtracting the sum of nitrate, ammonium, and nitrite from the total nitrogen measurements. Experimental measurements were also obtained in the pore water of the mesocosms for nitrate and ammonium. Samples were taken \approx 3-5 cm below the sediment-water interface and were analyzed using the techniques listed above.

Model Inputs

Measurements from Experiment 1 and Experiment 2 were used to provide model input values for the flow and no flow STELLA models, respectively. All first-order model variables (denitrification rate, nitrification rate, mussel excretion rate, etc.) were obtained from the literature (Baker and Hornbach 2000; Baker and Hornbach 2001; Chapra 1997; Christian et al. 2008; Espinosa-Villegas et al. 2003; Richardson et al. 2004; Schnoor 1996; Spooner and Vaughn 2008; Strauss et al. 2004). Henceforth, “model variables” will refer to the first-order rates (denitrification, nitrification, phytoplankton settling, etc.) and measured environmental conditions (light, temperature, flow) used in

the models. “Model parameters” will refer to nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton.

STELLA Model with Flow

For the STELLA model with flow, continuous inputs obtained from the head tank measurements in Experiment 1 were used at every time step (30 min) to represent river influent. Necessary input parameters included nitrate, ammonium, organic nitrogen, nitrite, and phytoplankton. Model inputs for nitrate and phytoplankton were obtained from the head tank Hydrolab. Ammonium concentrations in the head tank were below the Hydrolab detection limits so the model inputs were obtained through linear interpolation of the head tank grab samples. Model inputs for organic nitrogen and nitrite were also obtained through linear interpolation of head tank grab samples.

Measurements of water temperature and light attenuation factor were obtained from the Hydrolabs and PAR sensors located in the mesocosms, respectively. Mesocosm measurements were used as continuous model inputs for water temperature and light attenuation factor to better simulate the mesocosm systems.

The initial value for nitrate in each treatment was obtained from the initial mesocosm value measured by each respective Nitratax sensor. The initial value for ammonium, organic nitrogen, and nitrite in each treatment was obtained from the respective grab sample measured on Day 0. The initial value for phytoplankton in each treatment was obtained from the initial mesocosm value measured by each respective Hydrolab. The model input values for each time step of the STELLA model with flow are available in the Appendix (Table C.1).

STELLA Model without Flow

For the STELLA model without flow, measurements from Experiment 2 were used as initial values for nitrate, ammonium, organic nitrogen, nitrite, and phytoplankton. The initial value for nitrate in each treatment was obtained from the initial mesocosm

value measured by each respective Nitratax sensor. The initial value for ammonium, organic nitrogen, and nitrite in each treatment was obtained from the respective grab sample measured on Day 0. The initial value for phytoplankton in each treatment was obtained from the initial mesocosm value measured by each respective Hydrolab.

Given that the STELLA model without flow did not contain any continuous river influents, the only continuous model inputs used were water temperature and light attenuation factor. Measurements of water temperature and light attenuation factor were obtained from the Hydrolabs and PAR sensors located in the mesocosms, respectively.

The STELLA model without flow also contained model inputs from the sodium nitrate spike and the addition of DI water to the mesocosms. The nitrate spike was added as a one-time model input on Day 9 and the DI water was added as a model input on Day 3, 7, 9, 14, and 18. The model input values for each time step of the STELLA model without flow are available in the Appendix (Table C.2).

Model Performance

The percent difference and coefficient of determination (R^2) was calculated between the model outputs and grab samples to evaluate model performance. The percent difference was calculated at each time step and then averaged over the entire experimental time period to obtain an average percent difference. The average percent difference and R^2 was also calculated between model outputs and Nitratax measurements for nitrate and between model outputs and Hydrolab measurements for phytoplankton. The average percent difference and R^2 value was not determined between model outputs and grab sample measurements for phytoplankton due to error in grab sample analysis.

The effects of mussels on mesocosm nitrogen dynamics predicted by the models were determined by calculating the average percent difference and R^2 between the control and mussel treatment model outputs. These values were then compared to the effects of mussels determined by the corresponding experimental measurements (grab samples,

Nitratax, Hydrolab) to evaluate how well the models predicted the mussel effects in the mesocosms.

The effects of mussels on nitrogen mass were also compared between the model outputs and experimental measurements. The mussel effect on nitrogen mass was determined by subtracting the mass flux at each time step in the control treatments from the respective mass flux in the mussel treatments. Mass fluxes were calculated using the average flow rate (8.5 L h^{-1}). The Right Riemann Sum Method was then applied by multiplying the calculated differences between the mussel and control concentrations by the increment of each respective time step (e.g. 30 min) to obtain nitrogen mass.

Sensitivity Analyses

A single variable and multiple variable sensitivity analysis was performed on the calibrated models. The sensitivity analyses were run for both the flow and no flow STELLA models under control and mussel treatment conditions. All sensitivity analyses were completed using the Sensi Specs function in STELLA.

Single Variable Analysis

The single variable analysis was completed by adjusting a single model variable (e.g. denitrification rate, mussel biomass) and evaluating how the change in model input affected model outputs for nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton. The single variable sensitivity analysis was completed for the following model variables: nitrification rate, denitrification rate, light, temperature, hydraulic retention time (flow model only), maximum phytoplankton growth rate, phytoplankton death rate, phytoplankton settling rate, phytoplankton respiration/excretion rate, organic nitrogen hydrolysis rate, organic nitrogen settling rate, mussel biomass (mussel scenarios only), mussel phytoplankton clearance rate (mussel scenarios only), and mussel ammonium excretion rate (mussel scenarios only).

The value of the model variable for each sensitivity run was determined by dividing the range of literature values (Table 5.2) into equal increments so that a minimum of four sensitivity runs could be completed for each of the variables listed above. The results of the sensitivity analysis were analyzed by calculating a normalized sensitivity coefficient (NSC), the coefficient of determination (R^2), and the percent difference. The normalized sensitivity coefficient was defined as (Fasham et al. 1990):

$$\text{Equation 5.20} \quad NSC = (|\Phi - \Phi_o| / |P - P_o|) * (|P_o| / |\Phi_o|)$$

where,

Φ = average value of a parameter (e.g. nitrate, ammonium) over the simulation period for the sensitivity run

Φ_o = average value of a parameter (e.g. nitrate, ammonium) over the simulation period for the calibrated model

P = value of model variable used in sensitivity run

P_o = value of model variable used in the calibrated model

The model variables with the highest normalized sensitivity coefficients were determined to be the most sensitive.

The coefficient of determination (R^2) was calculated between each sensitivity run and the calibrated model outputs. The coefficient of determination for each sensitivity run was averaged together to obtain a compiled coefficient of determination for each of the analyzed model variables. The variables with the lowest coefficient of determination were determined to be the most sensitive.

The percent difference between the sensitivity run model outputs and the calibrated model outputs was also calculated. The percent difference was determined as follows:

$$\text{Equation 5.21} \quad \% \text{ Difference} = (SV_t - MV_t) / MV_t$$

where,

SV_t = sensitivity analysis value at time t (mg-N L⁻¹)

MV_t = calibrated model value at time t (mg-N L⁻¹)

The percent difference was calculated at each time step and then averaged over the entire simulation time to obtain an average percent difference for each sensitivity run. The percent difference for each sensitivity run was then averaged together to obtain a compiled percent difference value for each of the analyzed model variables. The compiled percent difference values were used to determine if the sensitivity runs resulted in higher (+ %) or lower (- %) model results than the calibrated model outputs.

Multiple Variable Analysis

The multiple variable sensitivity analysis was completed by simultaneously adjusting all of the model variables and evaluating how the changes in model inputs affected model outputs for nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton. The multiple variable sensitivity analysis was completed for the same model variables as the single variable sensitivity analysis.

The values for the model variable were adjusted at random using the sensitivity analysis tool in STELLA (Sensi Specs). The selection of the model variables was based on a Gaussian distribution derived from the range of literature values (Table 5.2). STELLA randomly selected a value from each respective model variable distribution to complete a sensitivity run. Any of the model variables that were assigned a negative value by STELLA were assumed to be zero. A total of 2,000 combinations of model variables were run for the sensitivity analysis of each of the model scenarios (flow mussel, flow control, no flow mussel, no flow control).

A pivot table in Microsoft Excel was used to evaluate the large number of model runs to determine how the changes in model inputs affected the model outputs. The average, coefficient of determination (R^2), and normalized sensitivity coefficient was calculated for each sensitivity run and compared to the respective calibrated model

outputs to determine which model variables were most influential. The results from the multiple variable sensitivity analysis were also used to determine what other combinations of model variables predicted a model output similar to those obtained in the calibrated model.

The two criteria used to determine which combinations of model variables would predict a similar result to the calibrated model were as follows: 1) the average concentration of the sensitivity run had to be within 5% of the calibrated model average concentration, and 2) the R^2 value between sensitivity run and calibrated model had to be greater than 0.95. The sensitivity runs that met both of these conditions were then evaluated by their respective NSC values to determine which model variables were most influential.

Model Application

The STELLA models were used to examine how increases in phytoplankton concentrations would affect the nitrogen dynamics in the laboratory mesocosms. Given that the amount of phytoplankton present in the mesocosms during Experiment 1 and Experiment 2 was well below typical levels for the Iowa River (Espinosa-Villegas et al. 2003), two model applications were run with increased phytoplankton. Model Application 1 was run using the average chlorophyll *a* concentration measured in the Iowa River in 2003 ($60 \mu\text{g L}^{-1}$, Espinosa-Villegas et al. 2003). The chlorophyll *a* concentration was converted to phytoplankton concentration using the method previously described in this chapter. Model Application 2 was run using the maximum chlorophyll *a* concentration measured in the Iowa River in 2003 ($415 \mu\text{g L}^{-1}$, Espinosa-Villegas et al. 2003). Model Application 1 and Model Application 2 were run for both the flow and no flow STELLA models under control and mussel treatment conditions. The results were compared to the calibrated model outputs to examine how increases in phytoplankton affected mesocosm nitrogen dynamics.

In the STELLA models (both with and without flow), the initial phytoplankton value was adjusted to 0.65 mg-N L^{-1} ($60 \text{ } \mu\text{g L}^{-1}$ chlorophyll *a*) for Model Application 1 and 4.5 mg-N L^{-1} ($415 \text{ } \mu\text{g L}^{-1}$ chlorophyll *a*) for Model Application 2. In the STELLA model with flow, the phytoplankton influent (river phytoplankton) was changed from a variable input (obtained via the head tank Hydrolab) to a constant value that was assumed to be the same as the initial phytoplankton concentration.

Model Application 1 and Model Application 2 were also run using two different mussel densities. Density 1 was representative of the number of mussels present in the mesocosm experiments ($70 \text{ mussels m}^{-2}$). Density 2 was representative of the number of mussels found at a pool-wide scale in the UMR (2.9 to $4.5 \text{ mussels m}^{-2}$, Newton et al. 2011). It was assumed that Density 2 would provide an approximation for the number of mussels that exist throughout any given reach of the Iowa River.

The results for Model Application 1 and Model Application 2 were compared to the calibrated model outputs by determining the average percent difference and the coefficient of determination (R^2). The mussel Density 2 Model Application results were compared to the control Model Application results and mussel Density 1 Model Application results to evaluate the influence of decreasing mussel density. The Density 2 results were compared to the control and Density 1 results for each Model Application using the average percent difference and R^2 values.

Results

Model Calibration

The STELLA models were calibrated under the assumption that the majority of the model variables would remain the same between the flow and no flow scenarios (Table 5.3). This was determined to be a reasonable assumption given that the experimental conditions between the flow and no flow experiments were nearly identical

and that no direct measurements for the model variables were obtained as part of this study (other than temperature, light and flow).

The only model variables that differed between the flow and no flow models were mussel phytoplankton clearance rate and mussel ammonium excretion rate. The mussel phytoplankton clearance rate was higher in the calibrated flow model ($0.00002 \text{ h}^{-1} \text{ g}^{-1}$) than the calibrated no flow model ($0.000015 \text{ h}^{-1} \text{ g}^{-1}$). Conversely, the mussel ammonium excretion rate was lower in the flow model ($0.15 \text{ h}^{-1} \text{ g}^{-1}$) than the no flow model ($1.15 \text{ h}^{-1} \text{ g}^{-1}$). These rates were adjusted to reflect changes in mussel behavior attributable to an assumed increase in stress due to a lack of continuous river water influent. When stressed, certain species of mussels have been shown to decrease filtration rates (Spooner and Vaughn 2008) which indicates clearance rates of phytoplankton would decrease. Mussels under stress have also been shown to increase ammonium excretion rates by catabolizing biochemical reserves to compensate for reduced consumption and energy (Spooner and Vaughn 2008).

The only other difference in the model variables was the denitrification rate between the control and mussel treatments. A higher denitrification rate was used in the mussel models (0.006 h^{-1}) than the control models (0.004 h^{-1}) based on the assumption that mussel deposition of organic matter at the sediment-water interface increased overall denitrification (Bruesewitz et al. 2008).

Model Performance

The average percent difference and coefficient of determination (R^2) values (Table 5.5) were used to determine how well the model outputs correlated to experimental observations (Table 5.6). The effect of mussels predicted by the models was determined by calculating the average percent difference and R^2 between the control and mussel model outputs (Table 5.4).

STELLA Model with Flow

The nitrate outputs for the STELLA model with flow correlated very well with grab samples for both the control (average percent difference = -0.5%, $R^2 = 0.962$) and mussel (average percent difference = -8.5%, $R^2 = 0.979$) treatments (Figure 5.4). The control (22.2%, $R^2 = 0.963$) and mussel (7.5%, $R^2 = 0.916$) model outputs also correlated well with Nitratax measurements. Nitrate model outputs demonstrated minimal differences between nitrate concentrations in the control and mussel treatments (-1.8%, $R^2 = 0.996$). Grab samples (10.2%, $R^2 = 0.973$) and Nitratax measurements (11.1%, $R^2 = 0.992$) demonstrated a similar result but indicated nitrate concentrations were slightly higher in the mussel treatments. Model outputs and experimental measurements from both treatments demonstrated differences from head tank measurements. The grab samples indicated that nitrate concentrations in the pore water were higher in the mussel treatments (8.5%) (Figure 5.5). The pore water results for nitrate and ammonium are given in the Appendix (Table B.2).

The ammonium model outputs also correlated well with grab samples for the control (-13.0%, $R^2 = 0.759$) and mussel (-13.4%, $R^2 = 0.569$) treatments (Figure 5.6). The model outputs demonstrated differences between the control and mussel treatments with higher concentrations observed in the mussel treatments (101.4%, $R^2 = 0.525$). Grab samples also indicated ammonium concentrations were higher in the mussel treatments than the control treatments (123.7%, $R^2 = 0.469$). Model outputs and grab samples from both treatments again demonstrated differences between ammonium concentrations in the head tank and mesocosms. The grab samples indicated that ammonium concentrations in the pore water were much higher in the mussel treatments (294.8%) (Figure 5.5).

The organic nitrogen model outputs for the control (-4.5%, $R^2 = 0.417$) and mussel (-6.7%, $R^2 = 0.669$) treatments correlated relatively well with grab samples (Figure 5.7). Model outputs indicated minimal differences between control and mussel

treatments (0.0%, $R^2 = 1$) and grab samples exhibited similar results (1.8%, $R^2 = 0.914$). Model outputs and grab samples for both treatments demonstrated differences from head tank measurements.

The nitrite model outputs demonstrated a reasonable correlation to the grab samples for the control (-0.7%, $R^2 = 0.398$) and mussel (19.4%, $R^2 = 0.652$) treatments (Figure 5.8). Nitrite concentrations were found to be higher in the mussel treatments for both the model outputs (56.4%, $R^2 = 0.655$) and grab samples (36.1%, $R^2 = 0.862$). Model outputs and grab samples from both treatments again indicated differences between nitrite concentrations in the head tank and mesocosms.

The total nitrogen model outputs correlated well with the grab samples for the control (-1.4%, $R^2 = 0.919$) and mussel (-8.6%, $R^2 = 0.962$) treatments (Figure 5.9). Given that nitrate was the predominant nitrogen species in this study, the total nitrogen model outputs were similar to the nitrate model results in that minimal differences were observed between the control and mussel treatments (-0.8%, $R^2 = 0.995$). Grab sample measurements demonstrated a similar result but indicated nitrate concentrations were slightly higher in the mussel treatments (9.4%, $R^2 = 0.968$). Model outputs and experimental measurements from both treatments demonstrated differences from head tank measurements.

Model outputs for phytoplankton did not correlate well with Hydrolab measurements for either the control (-44.0%, $R^2 = 0.383$) or mussel (82.7%, $R^2 = 0.076$) treatments (Figure 5.10). The phytoplankton model outputs demonstrated minimal differences between the control and mussel treatments (-7.7%, $R^2 = 0.884$). However, the Hydrolab measurements indicated that phytoplankton was significantly higher in the control treatments than the mussel treatments (-67.4%, $R^2 = 0.067$). Model outputs for both treatments did not demonstrate significant differences from the head tank measurements. However, Hydrolab measurements from both treatments did demonstrate differences from head tank measurements.

Mussel Effect on Nitrogen Mass

The model outputs for nitrate indicated that the slight decreases in nitrate concentrations in mussel treatments removed 126.7 mg-N from the overlying water over the experimental length (10 d) (Table 5.7). However, the grab sample and Nitratax measurements indicated that mussel treatments added 694.7 mg-N and 687.1 mg-N to the overlying water, respectively. The model outputs for ammonium indicated that increases in ammonium concentrations added 31.9 mg-N to the overlying water, and the grab samples indicated a similar addition of 30.3 mg-N. The minimal changes in organic nitrogen concentrations demonstrated that mussels added 0.5 mg-N to the overlying water. The grab samples demonstrated that minimal changes in organic nitrogen concentrations removed 10.7 mg-N. Increases in nitrite concentrations in mussel treatments indicated mussels added 24.9 mg-N, and the grab samples demonstrated a similar result of 14.8 mg-N. Decreases in total nitrogen concentrations predicted in the mussel treatments demonstrated that mussels removed 39.4 mg-N. However, the grab samples indicated that the slight changes in total nitrogen concentrations added 716.7 mg-N. The model outputs revealed that changes in phytoplankton concentrations removed 12.9 mg-N from the overlying water. The grab samples indicated a higher removal of 139.8 mg-N. The dynamic equilibrium simulated by the STELLA model indicated the mussels contained the greatest store of nitrogen mass (Figure 5.11).

STELLA Model without Flow

The nitrate outputs for the STELLA model without flow indicated an adequate correlation with the grab samples for the control (25.1%, $R^2 = 0.965$) and mussel (-35.7%, $R^2 = 0.874$) treatments (Figure 5.12). The control (9.7%, $R^2 = 0.943$) and mussel (-23.5%, $R^2 = 0.832$) model outputs demonstrated an improved correlation with the Nitratax measurements. The model outputs indicated differences between the control and mussel treatments with lower nitrate concentrations in the mussel treatments (-7.0%. $R^2 =$

0.416). However, the grab samples (160.4%, $R^2 = 0.241$) and Nitratax measurements (77.5%, $R^2 = 0.089$) indicated nitrate concentrations were higher in the mussel treatments. The treatments were greatly influenced by the nitrate spike on Day 9 as model outputs, grab samples, and Nitratax measurements illustrated that nitrate concentrations were higher in the mussel treatments before the nitrate spike and lower in the mussel treatments after the spike. The grab samples also indicated that nitrate concentrations in the pore water were higher in the mussel treatments (74.3%) (Figure 5.13). The pore water results for nitrate and ammonium are given in the Appendix (Table B.2).

The ammonium model outputs demonstrated a mediocre correlation with grab samples for the control (44.0%, $R^2 = 0.804$) and mussel (-63.8%, $R^2 = 0.976$) treatments (Figure 5.14). Higher concentrations of ammonium were predicted in the mussel treatments (241.8%, $R^2 = 0.943$) but both treatments indicated ammonium was removed from the system. The grab samples also demonstrated ammonium concentrations were higher in the mussel treatments (2,768.9%, $R^2 = 0.857$). The grab samples also indicated that ammonium concentrations in the pore water were much higher in the mussel treatments (399.0%) (Figure 5.13).

The correlation between organic nitrogen model outputs and grab samples was poor for the control (-14.4%, $R^2 = 0.023$) and mussel (-49.3%, $R^2 = 0.148$) treatments (Figure 5.15). Model outputs indicated that organic nitrogen was removed in both the control and mussel treatments but that there were lower concentrations in the mussel treatments (-33.6%, $R^2 = 0.997$). Grab samples indicated that organic nitrogen concentrations were higher in the mussel treatments (18.9%) but the R^2 value between the two treatments was very poor ($R^2 = 0.000$).

The nitrite model outputs did not correlate well with the grab samples for the control (-13.3%, $R^2 = 0.021$) or mussel (-28.0%, $R^2 = 0.083$) treatments (Figure 5.16). Model outputs indicated that nitrite was removed in both the control and mussel

treatments with higher concentrations in the mussel treatments (208.1%, $R^2 = 0.922$). The grab samples also indicated that nitrite concentrations were higher in the mussel treatments (623.4%, $R^2 = 0.539$).

The total nitrogen control model outputs correlated very well with grab samples (1.9%, $R^2 = 0.909$) but the correlation between the mussel model outputs and grab samples was mediocre (-39.8%, $R^2 = 0.881$) (Figure 5.17). The model outputs indicated that overall total nitrogen concentrations were lower in the mussel treatments than the control treatments (-14.5%, $R^2 = 0.505$). However, the grab sample results demonstrated total nitrogen was higher in the mussel treatments (76.7%), although the correlation between the two treatments was low ($R^2 = 0.251$). Model outputs indicated that total nitrogen was removed in both treatments but that total nitrogen was higher in the mussel treatments before the nitrate spike and lower after the nitrate spike.

The phytoplankton model outputs for the mussel treatments correlated well with the Hydrolab measurements (3.2%, $R^2 = 0.217$) but the model outputs indicated a poor correlation with the Hydrolabs for the control treatments (-48.4%, $R^2 = 0.037$) (Figure 5.18). The model outputs demonstrated that phytoplankton was removed in both treatments but higher concentrations were present in the control treatments (-85.5%, $R^2 = 0.982$). The Hydrolab results also indicated that phytoplankton was higher in the control treatments (-86.9%, $R^2 = 0.012$) but the high variability of the Hydrolab measurements resulted in poor correlation between the two treatments.

Single Variable Sensitivity Analysis

The normalized sensitivity coefficient (NSC) and coefficient of determination (R^2) were both used to determine the most sensitive model variables for each model run. The two coefficients complement each other well as the NSC is calculated as a function of the average model output and the individual model variable used for each simulation. Alternatively, the R^2 values are computed by taking the model outputs from individual

time steps into account and are used to determine the level of variability that exists between the model output and sensitivity run output.

STELLA Model with Flow

The single variable sensitivity analysis for the STELLA model with flow indicated that the most sensitive model variables for the control treatments were hydraulic retention time, temperature, denitrification, and nitrification rate. The most sensitive model variables in the mussel treatments were hydraulic retention time, temperature, denitrification, and mussel ammonium excretion.

Nitrate

Nitrate model outputs were most sensitive to changes in hydraulic retention time, temperature, denitrification rate, and mussel ammonium excretion rate (Table 5.8). For the control treatments, hydraulic retention time resulted in the lowest R^2 value (0.708) followed by denitrification rate (0.860) and temperature (0.998). The lowest R^2 values in the mussel treatments were hydraulic retention time (0.724), denitrification rate (0.873), and mussel ammonium excretion rate (0.965). The highest NSC value for the control treatments was temperature (0.105) followed by hydraulic retention time (0.082) and denitrification rate (0.051). The highest NSC values for the mussel treatments were also temperature (0.141), hydraulic retention time (0.093), and denitrification rate (0.077).

On average, the sensitivity runs resulted in higher nitrate concentrations (positive percent difference) for hydraulic retention time (0.6% control, 1.0% mussel), mussel ammonium excretion rate (14.8%), and temperature (0.1% control, 7.0% mussel), and lower nitrate concentrations (negative percent difference) for denitrification rate (-39.2% control, -36.8% mussel).

Ammonium

The sensitivity analysis results for ammonium indicated that the model outputs were most sensitive to changes in mussel phytoplankton clearance rate, hydraulic retention time, mussel ammonium excretion rate, mussel biomass, temperature, and nitrification rate (Table 5.9). For the control treatments, temperature resulted in the lowest R^2 value (0.851) followed by hydraulic retention time (0.900) and nitrification rate (0.903). The lowest R^2 values for the mussel treatments were mussel phytoplankton clearance rate (0.597), hydraulic retention time (0.726), and mussel ammonium excretion rate (0.735). The highest NSC values for the control treatments were nitrification rate (1.743), hydraulic retention time (1.404), and temperature (1.073). For the mussel treatments, the highest NSC values were nitrification rate (1.843), temperature (1.304), and mussel biomass (0.633).

On average, the sensitivity runs resulted in higher ammonium concentrations for mussel phytoplankton clearance rate (324.0%), hydraulic retention time (98.8% control, 39.4% mussel), mussel ammonium excretion rate (408.3%), temperature (33.5% control, 66.9% mussel), and nitrification rate (124.2% control, 133.8% mussel), and lower ammonium concentrations for mussel biomass (-20.4%).

Organic Nitrogen

The sensitivity analysis results for organic nitrogen indicated that the model outputs were most sensitive to changes in organic nitrogen settling rate, hydraulic retention time, organic nitrogen hydrolysis rate, and phytoplankton death rate (Table 5.10). For the control treatments, organic nitrogen settling rate resulted in the lowest R^2 value (0.687) followed by hydraulic retention time (0.953) and organic nitrogen hydrolysis rate (0.993). The lowest R^2 values for the mussel treatments were also organic nitrogen settling rate (0.687), hydraulic retention time (0.953), and organic nitrogen hydrolysis rate (0.994). The highest NSC values for the control treatments were organic

nitrogen settling rate (0.020), phytoplankton death rate (0.008), and hydraulic retention time (0.007). Similarly, the highest NSC values for the mussel treatments were organic nitrogen settling rate (0.020), phytoplankton death rate (0.007), and hydraulic retention time (0.007).

On average, the sensitivity runs resulted in higher organic nitrogen concentrations for hydraulic retention time (0.5% control, 0.4% mussel), and lower organic nitrogen concentrations for organic nitrogen settling rate (-47.5% control and mussel), organic nitrogen hydrolysis rate (-7.9% control, -8.0% mussel), and phytoplankton death rate (-0.2% control and mussel).

Nitrite

The sensitivity analysis results for nitrite indicated that the model outputs were most sensitive to changes in mussel phytoplankton clearance rate, mussel ammonium excretion rate, hydraulic retention time, mussel biomass, temperature, and nitrification rate (Table 5.11). For the control treatments, temperature resulted in the lowest R^2 value (0.869) followed by nitrification rate (0.901) and hydraulic retention time (0.940). The lowest R^2 values for the mussel treatments were mussel phytoplankton clearance rate (0.568), mussel ammonium excretion rate (0.713), and hydraulic retention time (0.834). The highest NSC values for the control treatments were nitrification rate (0.997), temperature (0.895), and hydraulic retention time (0.810). For the mussel treatments, the highest NSC values were temperature (0.918), nitrification rate (0.740), and mussel biomass (0.471).

On average, the sensitivity runs resulted in higher nitrite concentrations for mussel phytoplankton clearance rate (241.9%), mussel ammonium excretion rate (304.0%), hydraulic retention time (46.5% control, 17.1% mussel), temperature (23.4% control, 44.0% mussel), and nitrification rate (58.3% control, 36.2% mussel), and lower nitrite concentrations for mussel biomass (-15.2%).

Total Nitrogen

The sensitivity analysis results for total nitrogen indicated that model outputs were most sensitive to changes in hydraulic retention time, denitrification rate, mussel ammonium excretion rate, organic nitrogen settling rate, and temperature (Table 5.12). For the control treatments, hydraulic retention time resulted in the lowest R^2 value (0.709) followed by denitrification rate (0.842) and organic nitrogen settling rate (0.994). The lowest R^2 values in the mussel treatments were hydraulic retention time (0.724), denitrification rate (0.857), and mussel ammonium excretion rate (0.947). The highest NSC value for the control treatments was temperature (0.094) followed by hydraulic retention time (0.077) and denitrification rate (0.041). The highest NSC values for the mussel treatments were also temperature (0.131), hydraulic retention time (0.083), and denitrification rate (0.062).

On average, the sensitivity runs resulted in higher total nitrogen concentrations for hydraulic retention time (1.1% control, 1.2% mussel), mussel ammonium excretion rate (16.8%), and temperature (0.4% control, 6.3% mussel), and lower total nitrogen concentrations for denitrification rate (-30.4% control, -28.2% mussel) and organic nitrogen settling rate (-10.1% control).

Phytoplankton

The sensitivity analysis results for phytoplankton indicated that the model outputs were most sensitive to changes in phytoplankton settling rate, hydraulic retention time, mussel phytoplankton clearance rate, phytoplankton respiration/excretion rate, light, and maximum phytoplankton growth rate (Table 5.13). For the control treatments, phytoplankton settling rate resulted in the lowest R^2 value (0.821) followed by hydraulic retention time (0.941) and phytoplankton respiration/excretion rate (0.967). The lowest R^2 values for the mussel treatments were phytoplankton settling rate (0.861), hydraulic retention time (0.889), and mussel phytoplankton clearance rate (0.904). The highest

NSC values for the control treatments were phytoplankton respiration/excretion rate (0.525), maximum phytoplankton growth rate (0.511), and light (0.403). For the mussel treatments, the highest NSC values were maximum phytoplankton growth rate (0.515), light (0.507), and phytoplankton respiration/excretion rate (0.503).

On average, the sensitivity runs resulted in higher phytoplankton concentrations for hydraulic retention time (1.6% control, 3.6% mussel), phytoplankton respiration/excretion rate (33.0% control, 30.6% mussel), and maximum phytoplankton growth rate (5.2% control and mussel), and lower phytoplankton concentrations for phytoplankton settling rate (-47.5% control, -46.4% mussel), mussel phytoplankton clearance rate (-39.1%), and light (-14.3% control, -15.4% mussel).

STELLA Model without Flow

The single variable sensitivity analysis for the STELLA model without flow indicated that the most sensitive model variables for the control treatments were phytoplankton respiration/excretion, phytoplankton maximum growth rate, temperature, and denitrification rate. The most sensitive model variables in the mussel treatments were phytoplankton respiration/excretion, phytoplankton maximum growth rate, and temperature.

Nitrate

The nitrate model outputs were most sensitive to changes in denitrification rate, phytoplankton respiration/excretion rate, temperature, and maximum phytoplankton growth rate (Table 5.8). For the control treatments, denitrification rate resulted in the lowest R^2 value (0.695) followed by temperature (0.956) and phytoplankton respiration/excretion rate (0.998). The lowest R^2 values in the mussel treatments were denitrification rate (0.299), phytoplankton respiration/excretion rate (0.661), and temperature (0.669). The highest NSC value for the control treatments was temperature (1.096) followed by denitrification rate (0.397) and maximum phytoplankton growth rate

(0.338). The highest NSC values for the mussel treatments were phytoplankton respiration/excretion rate (352.7), maximum phytoplankton growth rate (2.601), and temperature (1.690).

On average, the sensitivity runs resulted in higher nitrate concentrations for denitrification rate (83.7% control, 55.9% mussel) and temperature (39.6% control, 103.8% mussel). The sensitivity runs resulted in lower nitrate concentrations in the control treatments and higher nitrate concentrations in the mussel treatments for phytoplankton respiration/excretion rate (-12.9% control, 165,000% mussel) and maximum phytoplankton growth rate (-11.5% control, 220.2% mussel).

Ammonium

The sensitivity analysis results for ammonium indicated that the model outputs were most sensitive to changes in mussel phytoplankton clearance rate, phytoplankton settling rate, phytoplankton respiration/excretion rate, organic nitrogen hydrolysis rate, maximum phytoplankton growth rate, and nitrification rate (Table 5.9). For the control treatments, phytoplankton respiration/excretion rate resulted in the lowest R^2 value (0.518) followed by phytoplankton settling rate (0.530) and organic nitrogen hydrolysis rate (0.630). The lowest R^2 values for the mussel treatments were mussel phytoplankton clearance rate (0.388), phytoplankton settling rate (0.493), and phytoplankton respiration/excretion rate (0.509). The highest NSC values for the control treatments were maximum phytoplankton growth rate (12.41), nitrification rate (8.973), and phytoplankton respiration/excretion rate (3.642). For the mussel treatments, the highest NSC values were phytoplankton respiration/excretion rate (3,706.0), nitrification rate (24.55), and maximum phytoplankton growth rate (11.95).

On average, the sensitivity runs resulted in higher ammonium concentrations for phytoplankton respiration/excretion rate (313.3% control, 8,224,000% mussel), organic nitrogen hydrolysis rate (59.3% control, 9.2% mussel), maximum phytoplankton growth

rate (830.2% control, 4,400.9% mussel), and nitrification rate (1,800.8% control, 17,343.3% mussel), and lower ammonium concentrations for mussel phytoplankton clearance rate (-44.4%) and phytoplankton settling rate (-46.8% control, -47.9% mussel).

Organic Nitrogen

The sensitivity analysis results for organic nitrogen indicated that the model outputs were most sensitive to changes in organic nitrogen settling rate, phytoplankton respiration/excretion rate, organic nitrogen hydrolysis rate, maximum phytoplankton growth rate, and light (Table 5.10). For the control treatments, organic nitrogen settling rate resulted in the lowest R^2 value (0.470) followed by phytoplankton respiration/excretion rate (0.688) and organic nitrogen hydrolysis rate (0.988). The lowest R^2 values for the mussel treatments were also organic nitrogen settling rate (0.329), phytoplankton respiration/excretion rate (0.711), and organic nitrogen hydrolysis rate (0.867). The highest NSC values for the control treatments were maximum phytoplankton growth rate (1.291), phytoplankton respiration/excretion (0.873), and light (0.339). The highest NSC values for the mussel treatments were phytoplankton respiration/excretion rate (35.77), maximum phytoplankton growth rate (0.332), and organic nitrogen settling rate (0.191).

On average, the sensitivity runs resulted in higher organic nitrogen concentrations for phytoplankton respiration/excretion rate (27.3% control, 6,775.8% mussel) and maximum phytoplankton growth rate (44.3% control, 15.1% mussel), and lower organic nitrogen concentrations for organic nitrogen settling rate (-51.0% control, -49.6% mussel), organic nitrogen hydrolysis rate (-51.9% control, -54.1% mussel), and light (-4.2% control).

Nitrite

The sensitivity analysis results for nitrite indicated that the model outputs were most sensitive to changes in mussel phytoplankton clearance rate, organic nitrogen

hydrolysis rate, phytoplankton settling rate, phytoplankton respiration/excretion rate, maximum phytoplankton growth rate, and nitrification rate (Table 5.11). For the control treatments, organic nitrogen hydrolysis rate resulted in the lowest R^2 value (0.443) followed by phytoplankton respiration/excretion rate (0.589) and maximum phytoplankton growth rate (0.741). The lowest R^2 values for the mussel treatments were mussel phytoplankton clearance rate (0.412), phytoplankton settling rate (0.500), and phytoplankton respiration/excretion rate (0.509). The highest NSC values for the control treatments were maximum phytoplankton growth rate (10.46), nitrification rate (3.546), and phytoplankton respiration/excretion (3.025). For the mussel treatments, the highest NSC values were phytoplankton respiration/excretion (3,346.8), maximum phytoplankton growth rate (11.436), and nitrification rate (2.659).

On average, the sensitivity runs resulted in higher nitrite concentrations for organic nitrogen hydrolysis rate (51.1% control), phytoplankton respiration/excretion rate (222.7% control, 6,680,800% mussel), maximum phytoplankton growth rate (613.0% control, 3,808% mussel), and nitrification rate (572.1% control, 1,139% mussel), and lower nitrite concentrations for mussel phytoplankton clearance rate (-37.5%) and phytoplankton settling rate (-46.4% mussel).

Total Nitrogen

The sensitivity analysis results for total nitrogen indicated that model outputs were most sensitive to changes in denitrification rate, phytoplankton respiration/excretion rate, temperature, organic nitrogen settling rate, and maximum phytoplankton growth rate (Table 5.12). For the control treatments, denitrification rate resulted in the lowest R^2 value (0.709) followed by organic nitrogen settling rate (0.951) and temperature (0.955). The lowest R^2 values in the mussel treatments were denitrification rate (0.447), phytoplankton respiration/excretion rate (0.681), and temperature (0.745). The highest NSC value for the control treatments was temperature (0.887) followed by denitrification

rate (0.314) and phytoplankton respiration/excretion rate (0.051). The highest NSC values for the mussel treatments were phytoplankton respiration/excretion rate (358.2), maximum phytoplankton growth rate (2.414), and temperature (1.453).

On average, the sensitivity runs resulted in higher total nitrogen concentrations for denitrification rate (66.7% control, 38.0% mussel), temperature (30.8% control, 79.0% mussel), and maximum phytoplankton growth rate (178.7% mussel) and lower total nitrogen concentrations for organic nitrogen settling rate (-11.5% control). The sensitivity runs resulted in lower total nitrogen concentrations in the control treatments and higher nitrate concentrations in the mussel treatments for phytoplankton respiration/excretion rate (-4.0% control, 137,900% mussel).

Phytoplankton

The sensitivity analysis results for phytoplankton indicated that the model outputs were most sensitive to changes in phytoplankton respiration/excretion rate, phytoplankton settling rate, mussel phytoplankton clearance rate, maximum phytoplankton growth rate, and light (Table 5.13). For the control treatments, phytoplankton settling rate resulted in the lowest R^2 value (0.464) followed by phytoplankton respiration/excretion rate (0.586) and maximum phytoplankton growth rate (0.671). The lowest R^2 values for the mussel treatments were phytoplankton respiration/excretion rate (0.453), phytoplankton settling rate (0.454), and mussel phytoplankton clearance rate (0.522). The highest NSC values for the control treatments were maximum phytoplankton growth rate (20.92), phytoplankton respiration/excretion rate (12.90), and light (3.301). For the mussel treatments, the highest NSC values were phytoplankton respiration/excretion rate (4,565), maximum phytoplankton growth rate (13.53), and light (2.683).

On average, the sensitivity runs resulted in higher phytoplankton concentrations for phytoplankton respiration/excretion rate (911.7% control, 11,180,000% mussel), maximum phytoplankton growth rate (1,877.1% control, 5,347.0% mussel), and light

(13.0% control, 68.9% mussel), and lower phytoplankton concentrations for phytoplankton settling rate (-49.1% control, -49.0% mussel) and mussel phytoplankton clearance rate (-39.4%).

Multiple Variable Sensitivity Analysis

The multiple variable sensitivity analysis resulted in a total of 48,000 model outputs. Each of the four model scenarios (control flow, mussel flow, control no flow, mussel no flow) contained 2,000 model outputs for each of the six parameters (nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton). Of the 48,000 total runs, only 1.15% (554) predicted a result comparable to the calibrated model outputs (average within $\pm 5\%$, $R^2 \geq 0.95$) for one of the six parameters. The analysis did not return any sensitivity run that met the criteria for all six parameters. The most parameters that met the criteria for a single sensitivity run was three. The model variables for each of the sensitivity runs that met the established criteria for the flow (Table D.1, Table D.2) and no flow (Table D.3, Table D.4) models are given in the Appendix.

STELLA Model with Flow

The results from the STELLA model with flow contained 472 of the 554 sensitivity runs (85.2%) that met the criteria for the entire multiple variable sensitivity analysis. The control treatments indicated the most sensitive variables for these runs were hydraulic retention time, light, maximum phytoplankton growth rate, and phytoplankton respiration/excretion. The mussel treatments indicated the most sensitive variables were hydraulic retention time, nitrification rate, phytoplankton respiration/excretion rate, light, and maximum phytoplankton growth rate.

Control Treatment

The multiple variable sensitivity analysis for the control treatment of the STELLA model with flow resulted in the highest number of sensitivity runs that met the

established criteria. There were 263 out of the 12,000 sensitivity runs (2.19%) that predicted a result similar to the calibrated model outputs for at least one of the analyzed parameters. Fifty-one of the sensitivity runs met the criteria for nitrate, 0 met the criteria for ammonium, 135 met the criteria for organic nitrogen, 14 met the criteria for nitrite, 50 met the criteria for total nitrogen, and 13 met the criteria for phytoplankton.

None of the sensitivity runs met the criteria for all six of the analyzed parameters. The highest number of parameters that met the criteria within a single sensitivity run was three. There were 4 different sensitivity runs that met the criteria for three of the analyzed parameters. Each of these 4 runs met the criteria for nitrate, organic nitrogen, and total nitrogen. There were 18 sensitivity runs that met the criteria for two parameters and the remaining sensitivity runs (215) met the criteria for only one parameter.

An average NSC value for each model variable was calculated for the 263 sensitivity runs that met the criteria for at least one parameter, the 22 sensitivity runs that met the criteria for at least two parameters, and the 4 sensitivity runs that met the criteria for three parameters (Table 5.14). The NSC value determined which model variables were most sensitive within each group. The NSC values for the 4 sensitivity runs that met the criteria for three parameters indicated the most sensitive model variables were maximum phytoplankton growth rate (0.294), light (0.191), and hydraulic retention time (0.113). The NSC values for the 22 runs that met the criteria for at least two parameters demonstrated the most sensitive variables were phytoplankton respiration/excretion rate (0.798), light (0.500), and hydraulic retention time (0.322). The NSC values for the 263 runs that met the criteria for at least one parameter indicated the most sensitive variables were maximum phytoplankton growth rate (1.711), light (0.353), and hydraulic retention time (0.177).

The average value of each model variable was also calculated for the 263 sensitivity runs that met the criteria for at least one parameter, the 22 sensitivity runs that met the criteria for at least two parameters, and the 4 sensitivity runs that met the criteria

for three parameters (Table 5.15). The sensitivity run model variables were calculated for comparison to the model variables used in the calibrated model (Table 5.3). The nitrification rates defined for the sensitivity runs that met the criteria ($0.069\text{-}0.104\text{ h}^{-1}$) were lower than the rate used in the calibrated model (0.2 h^{-1}). The sensitivity run denitrification rates ($0.022\text{-}0.044\text{ h}^{-1}$) were higher than the rate used in the model (0.004 h^{-1}). The average light attenuation factor also tended to be higher in the sensitivity runs ($0.46\text{-}0.71$) than the model (0.42). The average temperature was much lower in the sensitivity runs ($-0.92\text{-}14.96\text{ }^{\circ}\text{C}$) than the model ($24\text{ }^{\circ}\text{C}$) but the hydraulic retention time was similar (sensitivity runs = $15.95\text{-}17.32\text{ h}$; model = 16.72 h). Maximum phytoplankton growth rate was also similar (sensitivity runs = $-0.060\text{-}0.063\text{ h}^{-1}$; model = 0.059 h^{-1}) and phytoplankton death rate was lower in the sensitivity runs ($0.0063\text{-}0.0066\text{ h}^{-1}$) than the model (0.008 h^{-1}). Phytoplankton settling rate was much higher in the sensitivity runs ($0.029\text{-}0.057\text{ m h}^{-1}$) than the model (0.001 m h^{-1}). Phytoplankton respiration/excretion rate was lower in the sensitivity runs ($0.01\text{-}0.012\text{ h}^{-1}$) than the model (0.02 h^{-1}) but the organic nitrogen hydrolysis rate was higher (sensitivity runs = $0.003\text{-}0.0046\text{ h}^{-1}$; model = 0.0001 h^{-1}). The organic nitrogen settling rate for the model (0.001 m h^{-1}) fit within the range of rates used in the sensitivity runs ($0\text{-}0.009\text{ m h}^{-1}$).

Mussel Treatment

The multiple variable sensitivity analysis for the mussel treatment of the STELLA model with flow resulted in the second highest number of sensitivity runs that met the established criteria. There were 209 out of the 12,000 sensitivity runs (1.74%) that predicted a result similar to the calibrated model outputs for at least one of the analyzed parameters. Fifty of the sensitivity runs met the criteria for nitrate, 0 met the criteria for ammonium, 112 met the criteria for organic nitrogen, 0 met the criteria for nitrite, 47 met the criteria for total nitrogen, and 0 met the criteria for phytoplankton.

Similar to the control model, none of the sensitivity runs met the criteria for all six of the analyzed parameters. The highest number of parameters that met the criteria within a single sensitivity run was two. There were 11 different sensitivity runs that met the criteria for two of the analyzed parameters. The remaining sensitivity runs (187) met the criteria for only one parameter.

An average NSC value for each model variable was calculated for the 209 sensitivity runs that met the criteria for at least one parameter and the 22 sensitivity runs that met the criteria for two parameters (Table 5.14). The NSC values for the 22 sensitivity runs that met the criteria for two parameters indicated the most sensitive model variables were phytoplankton respiration/excretion rate (1.084), maximum phytoplankton growth rate (0.279), and hydraulic retention time (0.117). The NSC values for the 209 runs that met the criteria for at least one parameter indicated the most sensitive variables were nitrification rate (1.374), light (0.550), and hydraulic retention time (0.423).

The average value of each model variable was also calculated for the 209 sensitivity runs that met the criteria for at least one parameter and the 22 sensitivity runs that met the criteria for two parameters (Table 5.15). The nitrification rates defined for the sensitivity runs (0.036 and 0.099 h^{-1}) were lower than the rate used in the calibrated model (0.2 h^{-1}). The sensitivity run denitrification rates (0.031 and 0.038 h^{-1}) were higher than the rate used in the model (0.006 h^{-1}). The average light attenuation factor also tended to be higher in the sensitivity runs (0.47 and 0.51) than the model (0.42). The average temperature was much lower in the sensitivity runs (2.12 and 11.97 °C) than the model (24 °C) but the hydraulic retention time was similar (sensitivity runs = 16.46 and 17.68 h; model = 16.72 h). Maximum phytoplankton growth rate was also similar (sensitivity runs = -0.061 and 0.063 h^{-1} ; model = 0.059 h^{-1}) and phytoplankton death rate was lower in the sensitivity runs (0.0063 and 0.0064 h^{-1}) than the model (0.008 h^{-1}). Phytoplankton settling rate was much higher in the sensitivity runs (0.046 and 0.062 m h^{-1}).

¹) than the model (0.001 m h^{-1}). Phytoplankton respiration/excretion rate was lower in the sensitivity runs (0.008 and 0.01 h^{-1}) than the model (0.02 h^{-1}) but the organic nitrogen hydrolysis rate was higher (sensitivity runs = 0.0032 and 0.0033 h^{-1} ; model = 0.0001 h^{-1}). The organic nitrogen settling was much higher in the sensitivity runs (0.011 and 0.019 m h^{-1}) than the model (0.001 m h^{-1}). The average mussel biomass defined for the sensitivity runs (91.0 and 115.4 g) was lower than the model (200 g). However, the mussel phytoplankton clearance rate (sensitivity runs = 0.00033 and $0.00038 \text{ h}^{-1} \text{ g}^{-1}$; model = $0.00002 \text{ h}^{-1} \text{ g}^{-1}$) and mussel ammonium excretion rate (sensitivity runs = 1.15 and $1.22 \text{ h}^{-1} \text{ g}^{-1}$; model = $0.15 \text{ h}^{-1} \text{ g}^{-1}$) were both higher in the sensitivity runs.

STELLA Model without Flow

The results from the STELLA model without flow contained 82 of the 554 sensitivity runs (14.8%) that met the criteria for the entire multiple variable sensitivity analysis. The control treatments indicated the most sensitive variables for these runs were phytoplankton death rate, maximum phytoplankton growth rate, and temperature. The mussel treatments indicated the most sensitive variables were maximum phytoplankton growth rate, light, and phytoplankton death rate.

Control Treatment

The multiple variable sensitivity analysis for the control treatment of the STELLA model without flow resulted in 46 out of the 12,000 sensitivity runs (0.38%) that predicted a result similar to the calibrated model outputs for at least one of the analyzed parameters. Twenty of the sensitivity runs met the criteria for nitrate, 0 met the criteria for ammonium, 17 met the criteria for organic nitrogen, 1 met the criteria for nitrite, 4 met the criteria for total nitrogen, and 4 met the criteria for phytoplankton. None of the sensitivity runs met the criteria for all six of the analyzed parameters. All of the 46 sensitivity runs met the criteria for only one parameter.

The average NSC value for each model variable was calculated for the 46 sensitivity runs that met the criteria (Table 5.14). The average NSC values indicated the most sensitive variables were phytoplankton death rate (5.793), maximum phytoplankton growth rate (0.488), and temperature (0.167).

The average value of each model variable was also calculated for the 46 sensitivity runs (Table 5.15). The nitrification rate defined for the sensitivity runs that met the criteria (0.084 h^{-1}) was lower than the rate used in the calibrated model (0.2 h^{-1}). The sensitivity run denitrification rate (0.027 h^{-1}) was higher than the rate used in the model (0.004 h^{-1}). The average light attenuation factor was very similar between the sensitivity runs (0.47) and the model (0.42). The average temperature was much lower in the sensitivity runs ($11.3 \text{ }^{\circ}\text{C}$) than the model ($24 \text{ }^{\circ}\text{C}$) but the maximum phytoplankton growth rate was similar (sensitivity runs = -0.064 h^{-1} ; model = 0.059 h^{-1}). Phytoplankton death rate was lower in the sensitivity runs (0.0067 h^{-1}) than the model (0.008 h^{-1}). The average phytoplankton settling rate was much higher in the sensitivity runs (0.053 m h^{-1}) than the model (0.001 m h^{-1}). Phytoplankton respiration/excretion rate was lower in the sensitivity runs (0.012 h^{-1}) than the model (0.02 h^{-1}) but the organic nitrogen hydrolysis rate was higher (sensitivity runs = 0.0033 h^{-1} ; model = 0.0001 h^{-1}). The organic nitrogen settling rate defined for the sensitivity runs (0.017 m h^{-1}) was higher than the rate used in the model (0.001 m h^{-1}).

Mussel Treatment

The multiple variable sensitivity analysis for mussel treatment of the STELLA model without flow resulted in the lowest number of sensitivity runs that met the established criteria. There were 36 out of the 12,000 sensitivity runs (0.3%) that predicted a result similar to the calibrated model outputs for at least one of the analyzed parameters. Nine of the sensitivity runs met the criteria for nitrate, 3 met the criteria for ammonium, 14 met the criteria for organic nitrogen, 0 met the criteria for nitrite, 5 met

the criteria for total nitrogen, and 5 met the criteria for phytoplankton. Similar to the control model, none of the sensitivity runs met the criteria for all six of the analyzed parameters and all of the 36 sensitivity runs met the criteria for only one parameter.

The average NSC value for each model variable was calculated for the 36 sensitivity runs that met the criteria (Table 5.14). The average NSC values indicated the most sensitive variables were maximum phytoplankton growth rate (0.197), light (0.185), and phytoplankton death rate (0.167).

The average value of each model variable was calculated for the 36 sensitivity runs that met the criteria (Table 5.15). The nitrification rate defined for the sensitivity runs (0.13 h^{-1}) was lower than the rate used in the calibrated model (0.2 h^{-1}). The sensitivity run denitrification rate (0.04 h^{-1}) was higher than the rate used in the model (0.006 h^{-1}). The average light attenuation factor was higher in the sensitivity runs (0.62) than the model (0.42). The average temperature was much lower in the sensitivity runs ($10.04 \text{ }^{\circ}\text{C}$) than the model ($24 \text{ }^{\circ}\text{C}$) but maximum phytoplankton growth rate was similar (sensitivity runs = -0.067 ; model = 0.059 h^{-1}). Phytoplankton death rate was lower in the sensitivity runs (0.0063 h^{-1}) than the model (0.008 h^{-1}). Phytoplankton settling rate was much higher in the sensitivity runs (0.041 m h^{-1}) than the model (0.001 m h^{-1}). Phytoplankton respiration/excretion rate was lower in the sensitivity runs (0.011 h^{-1}) than the model (0.02 h^{-1}) but the organic nitrogen hydrolysis rate was higher (sensitivity runs = 0.0038 h^{-1} ; model = 0.0001 h^{-1}). The organic nitrogen settling was much higher in the sensitivity runs (0.021 m h^{-1}) than the model (0.001 m h^{-1}). The average mussel biomass defined for the sensitivity runs (109.1 g) was lower than the model (200 g). However, the mussel phytoplankton clearance rate (sensitivity runs = $0.00031 \text{ h}^{-1} \text{ g}^{-1}$; model = $0.000015 \text{ h}^{-1} \text{ g}^{-1}$) and mussel ammonium excretion rate (sensitivity runs = $1.44 \text{ h}^{-1} \text{ g}^{-1}$; model = $1.15 \text{ h}^{-1} \text{ g}^{-1}$) were both higher in the sensitivity runs.

Model Application

Previous analyses of the phytoplankton community composition in the mesocosms indicated that phytoplankton taxa distribution in the laboratory mesocosms was comparable to the average taxa distribution observed in the Iowa River (Figure 3.5, Figure 4.1). Using the Model Applications to increase phytoplankton concentrations to Iowa River levels greatly influenced the mussel effects on nitrogen dynamics predicted by the flow and no flow STELLA models.

STELLA Model with Flow

Increasing phytoplankton concentrations in Model Application 1 and Model Application 2 was most influential on ammonium, nitrite, and phytoplankton in the STELLA models with flow (Table 5.16). The Density 2 mussel model results were determined to be more comparable to the control Model Applications than the Density 1 mussel Model Applications (Table 5.17).

Nitrate

The nitrate results for Model Application 1 indicated an increase in nitrate concentrations in the mussel treatments for Density 1 (20.9%, $R^2 = 0.993$) and a decrease in nitrate concentrations for Density 2 (-5.2%, $R^2 = 0.993$) as compared to the calibrated model outputs (Figure 5.19). For the control treatments, minimal differences were observed between the Model Application 1 results and the calibrated model outputs (-3.0%, $R^2 = 0.999$). The results from mussel Density 2 correlated better with the control Model Application 1 results (-4.1%, $R^2 = 0.996$) than the mussel Model Application 1 results for Density 1 (-20.4%, $R^2 = 0.993$).

The nitrate results for Model Application 2 indicated a substantial increase in nitrate concentrations for Density 1 (157.5%, $R^2 = 0.748$) and a decrease in nitrate concentrations for Density 2 (-24.0%, $R^2 = 0.748$) and the control treatments (-19.9%, $R^2 = 0.952$) (Figure 5.20). Similar to Model Application 1, the results from mussel Density

2 correlated better with the control Model Application 2 results (-8.5%, $R^2 = 0.996$) than the mussel Density 1 Model Application 2 results (-64.9%, $R^2 = 0.761$).

Ammonium

The ammonium results for Model Application 1 indicated a substantial increase in ammonium concentrations for Density 2 (54.4%, $R^2 = 0.062$) and the control (187.0%, $R^2 = 0.153$) and an even larger increase in Density 1 (670.2%, $R^2 = 0.093$) (Figure 5.21).

The results from mussel Density 2 still correlated better with the control Model Application 1 results (3.1%, $R^2 = 0.991$) than the mussel Model Application 1 results for Density 1 (-80.2%, $R^2 = 0.891$).

The ammonium results for Model Application 2 indicated a substantial increase in ammonium concentrations for the control (1,111.3%, $R^2 = 0.028$) and Density 2 (556.1%, $R^2 = 0.019$) and an even larger increase for Density 1 (4,702.2%, $R^2 = 0.057$) (Figure 5.22). The results from mussel Density 2 again correlated better with the control Model Application 2 results (2.2%, $R^2 = 0.999$) than the mussel Density 1 Model Application 2 results (-87.7%, $R^2 = 0.904$).

Organic Nitrogen

The organic nitrogen results for Model Application 1 indicated higher organic nitrogen concentrations in the control (9.3%, $R^2 = 0.996$), Density 1 (9.1%, $R^2 = 0.997$), and Density 2 (9.6%, $R^2 = 0.996$) treatments (Figure 5.23). The results from mussel Density 2 correlated equally well with the control Model Application 1 results (0.3%, $R^2 = 1$) and the mussel Model Application 1 results for Density 1 (0.5%, $R^2 = 1$).

The organic nitrogen results for Model Application 2 indicated a substantial increase in organic nitrogen concentrations in the control (69.1%, $R^2 = 0.829$), Density 1 (67.1%, $R^2 = 0.846$), and Density 2 (70.7%, $R^2 = 0.822$) treatments (Figure 5.24). The results from mussel Density 2 again correlated equally well with the control Model

Application 2 results (1.0%, $R^2 = 1$) and the Density 1 Model Application 2 results (2.0%, $R^2 = 0.999$).

Nitrite

The nitrite results for Model Application 1 indicated an increase in ammonium concentrations for Density 2 (38.6%, $R^2 = 0.146$) and the control (108.8%, $R^2 = 0.266$) and a substantial increase in nitrite concentrations for Density 1 (483.5%, $R^2 = 0.092$) (Figure 5.25). The results from mussel Density 2 correlated better with the control Model Application 1 results (1.0%, $R^2 = 0.984$) than the mussel Model Application 1 results for Density 1 (-75.7%, $R^2 = 0.739$).

The nitrite results for Model Application 2 indicated a substantial increase in nitrite concentrations for the control (656.2%, $R^2 = 0.013$) and Density 2 (407.3%, $R^2 = 0.010$) and an even larger increase for Density 1 (3,399.9%, $R^2 = 0.033$) (Figure 5.26). The results from mussel Density 2 again correlated better with the control Model Application 2 results (1.2%, $R^2 = 0.998$) than the mussel Density 1 Model Application 2 results (-86.1%, $R^2 = 0.824$).

Total Nitrogen

The total nitrogen results for Model Application 1 indicated an increase in total nitrogen concentrations in the mussel treatments for Density 1 (26.1%, $R^2 = 0.986$) and minimal differences in total nitrogen concentrations for the control (1.0%, $R^2 = 0.998$) and Density 2 (-1.2%, $R^2 = 0.997$) treatments (Figure 5.27). The results from mussel Density 2 correlated better with the control Model Application 1 results (-2.9%, $R^2 = 0.996$) than the mussel Model Application 1 results for Density 1 (-20.8%, $R^2 = 0.990$).

The total nitrogen results for Model Application 2 indicated a substantial increase in total nitrogen concentrations for Density 1 (191.8%, $R^2 = 0.618$) and slight increases in total nitrogen concentrations for Density 2 (4.5%, $R^2 = 0.892$) and the control (7.1%, $R^2 = 0.912$) treatments (Figure 5.28). Similar to Model Application 1, the results from

mussel Density 2 correlated better with the control Model Application 2 results (-3.4%, $R^2 = 0.996$) than the mussel Density 1 Model Application 2 results (-61.4%, $R^2 = 0.748$).

Phytoplankton

As expected, the phytoplankton results for Model Application 1 indicated a substantial increase in phytoplankton concentrations for the control (1,438.1%, $R^2 = 0.140$), Density 1 (1,487.8%, $R^2 = 0.095$), and Density 2 (1,573.3%, 0.087) treatments (Figure 5.29). The results from mussel Density 2 correlated better with the control Model Application 1 results (2.1%, $R^2 = 0.998$) than the mussel Model Application 1 results for Density 1 (5.3%, $R^2 = 0.994$).

The phytoplankton results for Model Application 2 indicated an even larger increase in phytoplankton concentrations for the control (10,500.5%, $R^2 = 0.140$), Density 1 (10,843.5%, $R^2 = 0.095$), and Density 2 (11,432.4%, $R^2 = 0.087$) treatments (Figure 5.30). The results from mussel Density 2 again correlated better with the control Model Application 2 results (2.1%, $R^2 = 0.998$) than the mussel Density 1 Model Application 2 results (5.3%, $R^2 = 0.994$).

STELLA Model without Flow

Increasing phytoplankton concentrations in Model Application 1 and Model Application 2 was influential on all the parameters in the STELLA model without flow (Table 5.16). The Density 2 mussel model results were determined to be more comparable to the control Model Applications than the Density 1 mussel Model Applications (Table 5.17).

Nitrate

The nitrate results for Model Application 1 in the STELLA model without flow indicated a large increase in nitrate concentrations in the Density 1 (551.3%, $R^2 = 0.410$) treatments and a decrease in nitrate concentrations for the control (-6.9%, $R^2 = 0.997$) and

Density 2 (-29.3%, $R^2 = 0.918$) treatments as compared to the model outputs (Figure 5.31). The results from mussel Density 2 correlated better with the control Model Application 1 results (-32.3%, $R^2 = 0.732$) than the mussel Model Application 1 results for Density 1 (-86.0%, $R^2 = 0.150$).

The nitrate results for Model Application 2 again indicated an extremely large increase in nitrate concentrations for Density 1 (3,981.5%, $R^2 = 0.292$) and a decrease in nitrate concentrations for the control (-45.0%, $R^2 = 0.828$) and Density 2 (-20.8%, $R^2 = 0.757$) treatments (Figure 5.32). The results from mussel Density 2 did not correlated well with either the control Model Application 2 results (511.4%, $R^2 = 0.489$) or the mussel Density 1 Model Application 2 results (-96.6%, $R^2 = 0.081$).

Ammonium

The ammonium results for Model Application 1 indicated a substantial increase in ammonium concentrations for the control (340.1%, $R^2 = 0.809$) and Density 2 (81.0%, $R^2 = 0.760$) and an even larger increase in ammonium concentrations for Density 1 (1,667.4%, $R^2 = 0.925$) (Figure 5.33). The results from mussel Density 2 correlated better with the control Model Application 1 results (2.2%, $R^2 = 0.930$) than the mussel Model Application 1 results for Density 1 (-89.5%, $R^2 = 0.734$).

The ammonium results for Model Application 2 indicated a substantial increase in ammonium concentrations for the control (2,087.0%, $R^2 = 0.520$), Density 2 (874.3%, $R^2 = 0.415$) treatments, and an even larger increase for Density 1 (11,918.7%, $R^2 = 0.917$) (Figure 5.34). The results from mussel Density 2 still correlated better with the control Model Application 2 results (10.3%, $R^2 = 0.990$) than the mussel Density 1 Model Application 2 results (-91.7%, $R^2 = 0.509$).

Organic Nitrogen

The organic nitrogen results for Model Application 1 indicated higher organic nitrogen concentrations in the control (69.5%, $R^2 = 0.777$), Density 1 (90.2%, $R^2 =$

0.750), and Density 2 (120.8%, $R^2 = 0.553$) treatments (Figure 5.35). The results from mussel Density 2 correlated better with the control Model Application 1 results (-14.8%, $R^2 = 0.967$) than the mussel Model Application 1 results for Density 1 (14.8%, $R^2 = 0.954$).

The organic nitrogen results for Model Application 2 indicated a substantial increase in organic nitrogen concentrations in the control (568.2%, $R^2 = 0.037$), Density 1 (651.5%, $R^2 = 0.030$), and Density 2 (862.7%, $R^2 = 0.034$) treatments (Figure 5.36). The results from mussel Density 2 correlated better with the control Model Application 2 results (-6.2%, $R^2 = 0.995$) than the Density 1 Model Application 2 results (25.5%, $R^2 = 0.868$).

Nitrite

The nitrite results for Model Application 1 indicated an increase in ammonium concentrations for the control (274.8%, $R^2 = 0.761$) and Density 2 (70.1%, $R^2 = 0.832$) and a substantial increase in nitrite concentrations for Density 1 (1,585.6%, $R^2 = 0.925$) (Figure 5.37). The results from mussel Density 2 correlated better with the control Model Application 1 results (1.0%, $R^2 = 0.941$) than the mussel Model Application 1 results for Density 1 (-89.4%, $R^2 = 0.802$).

The nitrite results for Model Application 2 indicated a substantial increase in nitrite concentrations for the control (1,699.1%, $R^2 = 0.494$) and Density 2 (792.5%, $R^2 = 0.506$) and an even larger increase for Density 1 (11,340.0%, $R^2 = 0.917$) (Figure 5.38). The results from mussel Density 2 again correlated better with the control Model Application 2 results (7.7%, $R^2 = 0.993$) than the mussel Density 1 Model Application 2 results (-91.8%, $R^2 = 0.618$).

Total Nitrogen

The total nitrogen results indicated a large increase in total nitrogen concentrations in the Density 1 (478.5%, $R^2 = 0.502$) treatments, a slight increase in total nitrogen concentrations for the control (9.6%, $R^2 = 0.993$), and minimal changes for

Density 2 (-0.1%, $R^2 = 0.953$) treatments (Figure 5.39). The results from mussel Density 2 correlated better with the control Model Application 1 results (-27.4%, $R^2 = 0.596$) than the mussel Model Application 1 results for Density 1 (-80.3%, $R^2 = 0.312$).

The total nitrogen results for Model Application 2 indicated an extremely large increase in total nitrogen concentrations for Density 1 (3,455.4%, $R^2 = 0.381$) and a substantial increase in total nitrogen concentrations for the control (85.0%, $R^2 = 0.576$) and Density 2 (154.8%, $R^2 = 0.444$) treatments (Figure 5.40). The results from mussel Density 2 again correlated better with the control Model Application 2 results (0.8%, $R^2 = 0.579$) than the mussel Density 1 Model Application 2 results (-91.8%, $R^2 = 0.387$).

Phytoplankton

As expected, the phytoplankton results for Model Application 1 indicated a substantial increase in phytoplankton concentrations for the control (459.8%, $R^2 = 1$), Density 1 (1,782.8%, $R^2 = 1$), and Density 2 (3,976.2%, $R^2 = 0.983$) treatments (Figure 5.41). The results from mussel Density 2 correlated better with the control Model Application 1 results (-15.5%, $R^2 = 0.998$) than the mussel Model Application 1 results for Density 1 (116.5%, $R^2 = 0.983$).

The phytoplankton results for Model Application 2 indicated an even larger increase in phytoplankton concentrations for the control (3,757.9%, $R^2 = 1$), Density 1 (12,876.8%, $R^2 = 1$), and Density 2 (27,993.7%, $R^2 = 0.983$) treatments (Figure 5.42). The results from mussel Density 2 again correlated better with the control Model Application 2 results (-15.5%, $R^2 = 0.998$) than the mussel Density 1 Model Application 2 results (116.5%, $R^2 = 0.983$).

Discussion

The Effect of Mussels

As expected, the experimental measurements (grab samples, Nitratax, Hydrolabs) obtained from this study indicated that mussels affected the nitrogen cycle in the overlying water of the mesocosms by increasing ammonium concentrations through excretion, indirectly increasing nitrate concentrations via nitrification of the excreted ammonium, and decreasing phytoplankton concentrations via phytoplankton clearance. These results verified the observations made in Chapter 4.

Also similar to Chapter 4, the experimental measurements indicated that mussels increased nitrite and total nitrogen concentrations and demonstrated minimal impact on organic nitrogen. Increases in nitrite were expected given the increase in ammonium and nitrate, and their respective impact on nitrite through nitrification and denitrification. The amount of phytoplankton removed by mussels was too low to influence organic nitrogen concentrations. Increases in total nitrogen indicated mussels were adding more nitrogen (ammonium, nitrate, and nitrite) to the overlying water than they were removing (phytoplankton). It was expected that the increases in total nitrogen were attributable to increased mussel excretion of ammonium due to stress, mussel deposition of organic matter and subsequent hydrolysis to ammonium by heterotrophic bacteria, and increased diffusion of sediment-bound ammonium due to mussel bioturbation.

The experimental results also indicated that the indirect effect of mussels on nitrate resulted in more nitrogen mass being delivered to the overlying water (687.1 to 694.7 mg-N) than the effects of any other nitrogen species. The total mass of nitrogen mussels delivered to the overlying water (by increasing nitrate, ammonium, and nitrite) was greater (729.1 mg-N) than the amount they removed (139.8 mg-N, via phytoplankton clearance). This provided further evidence that mussels produced an increase in total nitrogen concentrations in the overlying water.

The amount of nitrogen mass added to the overlying water due to indirect mussel effects on nitrate was similar between this study (68.6 to 69.3 mg-N d⁻¹) and Chapter 4 (43.3 to 45.3 mg-N d⁻¹). Changes in ammonium concentrations in Chapter 4 resulted in significantly more nitrogen mass added to the overlying water (53.2 to 60.3 mg-N d⁻¹) than this study (3.0 to 3.2 mg-N d⁻¹). This was expected given that the ammonium concentrations were higher in Chapter 4. The amount of nitrogen mass removed from the system via phytoplankton clearance was also higher in Chapter 4 (85.7 to 85.8 mg-N d⁻¹) than this study (14 mg-N d⁻¹), which contributed to the increase in ammonium concentrations observed in Chapter 4. Chapter 4 also added more total nitrogen mass to the overlying water (144.9 mg-N d⁻¹) than this study (71.5 mg-N d⁻¹), which as expected due to the increased nitrogen mass added via mussel ammonium excretion.

Model Performance

In general, the STELLA models correlated well with the experimental measurements, and the flow models tended to correlate better with the experimental measurements than the no flow models. This difference was likely caused by the no flow mesocosms being more sensitive to the model variables given that the mesocosms were not dominated by chemical fluxes in the influent river water. The nitrogen species that was the most difficult for the models to capture was phytoplankton. This was attributable to the variability in Hydrolab measurements for phytoplankton and the difficulty in obtaining accurate results from phytoplankton grab samples. Organic nitrogen and nitrite in the no flow mesocosms was also difficult for the model to accurately predict. The difficulty in predicting organic nitrogen was due to error associated with grab samples used to calibrate the model as the measurements were obtained indirectly by subtracting nitrate, ammonium, and nitrite from total nitrogen. Nitrite was a difficult parameter to model given that it was an intermediate species of both nitrification and denitrification.

The flow and no flow models both tended to underestimate the concentrations of nitrogen species in the mesocosms. Despite these underestimations, the models correlated well with the experimental measurements in predicting that mussels increased ammonium and nitrite, decreased phytoplankton, and did not affect organic nitrogen. However, the models tended to further underestimate nitrogen concentrations in the mussel treatments than the control treatments. This caused the models to slightly underpredict the influence of mussels compared to the experimental measurements for nitrate, ammonium, nitrite, and total nitrogen, and overpredict the influence of mussels on phytoplankton and organic nitrogen.

These differences were especially evident for nitrate and total nitrogen, where the models predicted that mussels slightly decreased nitrate and total nitrogen concentrations, which resulted in removal of nitrogen mass from the overlying water. These were the opposite effects demonstrated by the experimental measurements. However, the correlation between the model results and the experimental measurements was high for nitrate and total nitrogen concentrations. Thus, even though slight changes in the average percent differences were observed, the models were still able to accurately predict nitrate and total nitrogen in the mesocosms. This was important given that nitrate was the most dominant nitrogen species ($\approx 75\%$) and is the most important parameter for downstream impacts on the Gulf of Mexico. It was expected that the slight changes in percent difference were attributable to the models slightly underpredicting the mussel effects and due to the similar nitrate and total nitrogen concentrations observed between the control and mussel treatments. These differences between model outputs and experimental measurements emphasized the importance of obtaining increased experimental measurements for model calibration, especially when modeling complex mesocosm systems.

Sensitivity Analyses

Single Variable

The single variable analysis evaluated the change in model outputs when the observational constraint (i.e. value obtained from calibrating with experimental measurements) was removed from a single model variable (e.g. denitrification rate, temperature, etc.) and replaced with a range of values from the literature. The results of the analysis revealed that the most influential model variables were hydraulic retention time, temperature, denitrification rate, mussel ammonium excretion, and nitrification in the flow-through mesocosms. In the no flow mesocosms, phytoplankton respiration/excretion, maximum phytoplankton growth rate, temperature, and denitrification were the most influential. The influence of light was minimal in both systems. The only difference between the mussel and control treatments was that mussels were not significantly influenced by nitrification in the flow-through mesocosms or by denitrification in the no flow mesocosms. This was due to the mussel models being more sensitive to variables such as mussel ammonium excretion and mussel phytoplankton clearance.

As expected, hydraulic retention time was one of the most influential model variables due to the assumption that the parameters (nitrate, ammonium, etc.) would be sensitive to changes in the chemical fluxes from the influent river water. Similarly, temperature was expected to be influential given that the majority of the model variables that were first-order rate expressions were temperature-dependent. The high denitrification sensitivity was due to its direct influence on nitrate and total nitrogen (as nitrate was the most dominant nitrogen species in the mesocosms). The high sensitivity attributable to mussel ammonium excretion demonstrated the influence of mussels in the mesocosms. It also emphasized the need to develop a better understanding for how ecosystem conditions and mussel behavior affect excretion rates (increased stress = increased excretion, etc.).

The increased influence of phytoplankton characteristics in the no-flow mesocosms was not expected but seemed reasonable given the lack of continuous river water influent. Phytoplankton growth was the only input contributing to increases in phytoplankton concentrations, which would have been very influential in the mesocosms. Phytoplankton respiration/excretion was not expected to be one of the most sensitive model variables, however, studies have shown that phytoplankton respiration can be very influential by consuming over 60% of the nutrients taken up by phytoplankton for growth (Wei et al. 2004). In addition, phytoplankton respiration/excretion was modeled as a direct input for ammonium and a direct output for phytoplankton, which was another source of the high sensitivity in the no-flow mesocosms.

Multiple Variable

The multiple variable analysis evaluated the change in model outputs when the observational constraint was removed from all of the model variables and replaced with random literature values. The results indicated that of the 48,000 total runs completed in the analysis, only 1.15% were able to predict a result comparable to the calibrated model outputs (average within $\pm 5\%$, $R^2 \geq 0.95$) for any of the six parameters (nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton). None of the sensitivity runs were able to accurately predict all six parameters and the most parameters that met the criteria in a single sensitivity run was three. This demonstrated the difficulty in modeling the dynamic nature of the mesocosms and revealed the need to constrain the models with observed experimental measurements.

For the 1.15% of sensitivity runs that did predict results similar to the calibrated models used in this study, the majority were successful for the flow-through mesocosms (85.2%). This was likely due to the no flow systems demonstrating an increased sensitivity to the model variables, thus increasing the difficulty in the unconstrained model variables being able to simulate concentrations comparable to the calibrated

model. In the flow-through mesocosms, the chemical fluxes in the influent river water were expected to decrease the influence of the model variables, thus increasing the ability of the unconstrained model variables to replicate the calibrated model outputs.

The individual parameters that the sensitivity runs were able to accurately predict most often were nitrate, organic nitrogen, and total nitrogen. This was expected given that the concentrations for nitrate and total nitrogen were significantly influenced by the influent river water and therefore less sensitive to changes in model variables. Also, given that organic nitrogen concentrations stayed relatively constant in the mesocosms, it was easier for the sensitivity runs to replicate the model outputs.

Model Application

The model applications predicted that a high mussel density (Density 1) coupled with high phytoplankton concentrations would increase all nitrogen species measured in the mesocosms. Substantial increases were observed for nitrate and total nitrogen in the flow-through mesocosms, as concentrations demonstrated >20% increases for Model Application 1 (average phytoplankton in Iowa River) and more than doubled for Model Application 2 (maximum phytoplankton in Iowa River). The high phytoplankton concentrations resulted in more clearance by mussels, which resulted in increased ammonium excretion, and more nitrate generated through nitrification of the ammonium.

As expected, decreasing the mussel density to a large-scale average (Density 2) decreased the mussel effects on nitrogen dynamics. In general, the low mussel density results correlated well with the control results. For Model Application 1 in the flow-through mesocosms, the control and low mussel density results predicted minimal changes in concentrations of nitrate, organic nitrogen, and total nitrogen, and increases in ammonium, nitrite, and phytoplankton. In Model Application 2, nitrate concentrations were predicted to decrease (\approx -20%), ammonium, organic nitrogen, nitrite, and phytoplankton were predicted to increase, and total nitrogen concentrations were

predicted to stay the same. This indicated that in areas of low or no mussels, high phytoplankton concentrations still caused increases in ammonium (through increased phytoplankton respiration/excretion), organic nitrogen (through increased phytoplankton death), and nitrite (through increased ammonium). Interestingly, there appeared to be a threshold for the low mussel density and control treatments where nitrate concentrations were reduced. However, total nitrogen concentrations were not reduced due to increases in organic nitrogen caused by the high phytoplankton concentrations.

The impact of increasing phytoplankton concentrations was even more pronounced in the no flow mesocosms. The overall trends were similar to the flow-through mesocosm results with the exception of nitrate and total nitrogen. In Model Application 1, the models predicted minimal changes in nitrate concentrations for the control treatments but a substantial decrease in nitrate concentrations for the low mussel density treatments (\approx -29%). This indicated that for the given phytoplankton concentrations, a threshold existed where mussels were able to reduce nitrate concentrations. However, changes in total nitrogen concentrations were minimal due primarily to increases in organic nitrogen concentrations. In Model Application 2, nitrate reductions were predicted in the control and low mussel density treatments, with the models predicting increased reductions in the control treatments. Despite these decreases in nitrate, total nitrogen concentrations were predicted to increase due to substantial increases in organic nitrogen for both treatments.

Model Assumptions

It was expected that the models developed to simulate the complex and dynamic mesocosms could be most improved by obtaining an increased number of experimental measurements for calibration and validation. However, some of the differences observed between the experimental measurements and model predictions in this study could have

been due to the assumptions made in the development and calibration of the STELLA models.

The models assumed that nitrogen and phosphorus were not limiting in the mesocosm system and thus a nutrient attenuation factor was not included in the equation for phytoplankton growth (Equation 5.14). The nitrogen attenuation factor (Equation 4.17) was not included in the phytoplankton growth equation due to the high nitrogen concentrations measured throughout the experiments. To determine if phosphorus was limiting, water samples were sent to the State Hygienic Lab to determine concentrations of ortho-phosphate. Assuming ortho-phosphate was representative of reactive phosphorus, the average measurement (0.3 mg-P L^{-1}) and a reasonable value for phosphorus half-saturation constant ($0.0025 \text{ mg-P L}^{-1}$, Chapra 1997) were used to calculate the phosphorus attenuation factor (Equation 5.18). The equation resulted in an attenuation factor of 0.992, indicating phosphorus was not limiting in the mesocosm system. However, phosphorus concentrations were not measured continuously throughout the experiments so any significant changes in phosphorus concentration were not observed.

Another assumption made in the development of the models was that the overlying water in the mesocosms represented a well-oxygenated system. Oxygen levels were not included in the model as the submersible pumps provided an average oxygen saturation level of $\approx 100\%$ in all of the mesocosms ($\approx 8.3 \text{ mg L}^{-1}$).

The models also assumed that concentrations of ammonia (NH_3) were minimal in the mesocosms. This same reasoning was used to assume that formation of ammonia gas and subsequent transfer out of the system was not significant. However, average pH in the control treatments (8.64) and average pH in the mussel treatments (8.32) resulted in 19.3% and 10.4% ammonia present, respectively, based on the average mesocosm temperatures (control = $24.5 \text{ }^\circ\text{C}$, mussel = $24.7 \text{ }^\circ\text{C}$).

The models may have been limited by assuming the rates influenced by mussels (mussel phytoplankton clearance rate and mussel ammonium excretion rate) were constant. Studies have shown that mussel behaviors can vary diurnally (Bril 2010; Englund and Heino 1996; Wilson et al. 2005) and it is expected that the rate at which mussels remove phytoplankton and excrete ammonium would follow these diurnal patterns. However, the rates obtained from the literature for mussel clearance and mussel excretion were obtained from experiments that lasted for several days. Thus, it was assumed that the studies reported an average rate that captured the changes in the daily behavior of mussels.

Perhaps more importantly, the rates influenced by mussels were not assumed to be dependent on temperature. This assumption was reasonable for model calibration, as the temperature remained relatively constant throughout the experiments. However, temperature has been shown to affect mussel processing rates (Spooner and Vaughn 2008) and the range in temperatures used in the sensitivity runs may have influenced the mussels' ability to remove phytoplankton or excrete ammonium.

The models also assumed that bottom algae would not significantly influence nitrogen dynamics in the overlying water. However, visual observations indicated that significant bottom algae and attached growth accumulated throughout the experiments. It was also assumed that zooplankton predation was minimal as zooplankton grazing is not as prominent in river ecosystems due to low concentrations (Wetzel 2001).

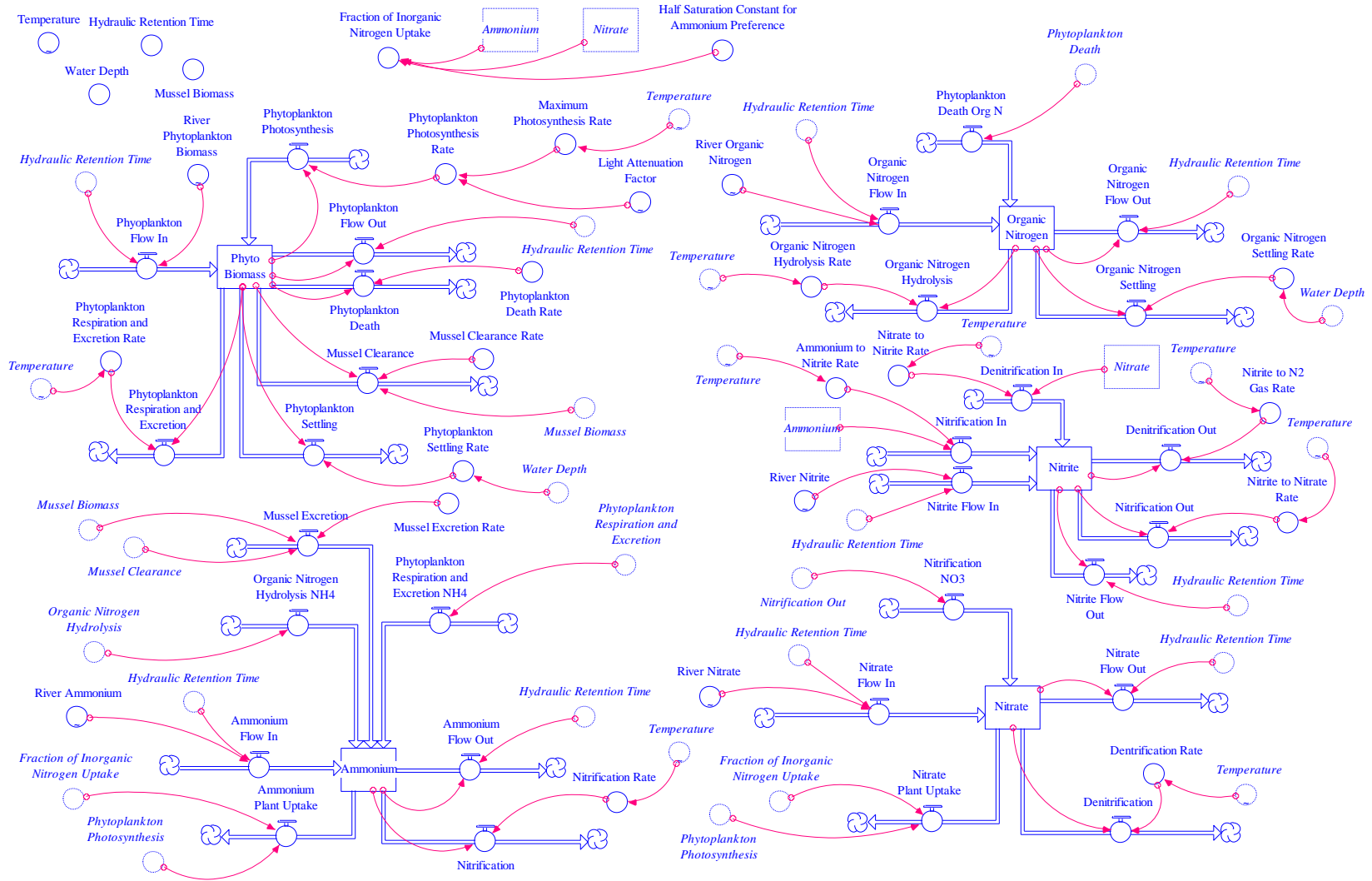


Figure 5.1: STELLA model for laboratory mesocosm experiment with flow.

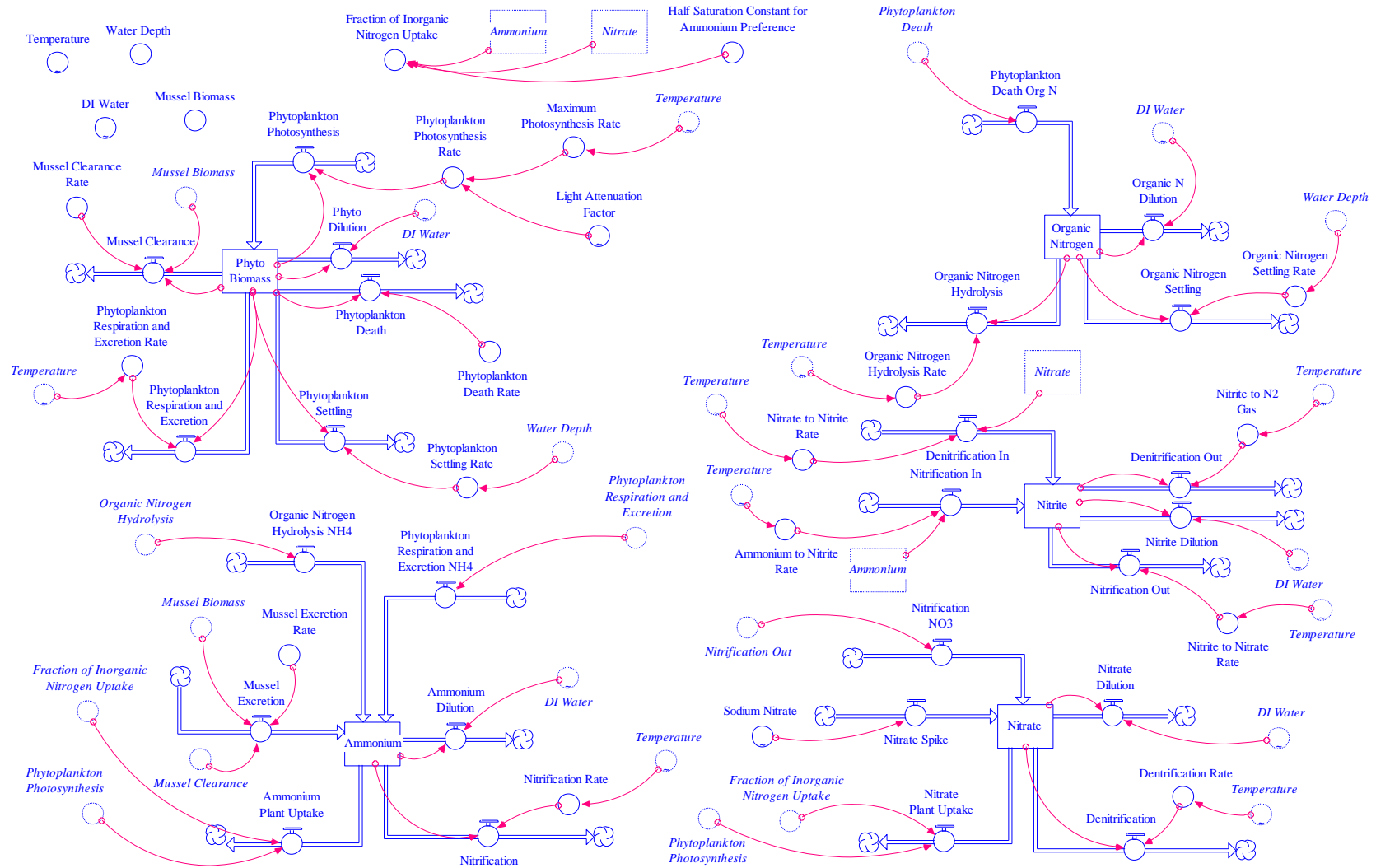


Figure 5.2: STELLA model for laboratory mesocosm experiment without flow.

Table 5.1: Variables used in the development of the STELLA models.

Variable	Definition	Units
a_t	phytoplankton concentration at time t	mg-N L ⁻¹
a_{t-1}	phytoplankton concentration at time $t-1$	mg-N L ⁻¹
F_{am}	preference for ammonium as a nitrogen source for phytoplankton	---
H	water depth	m
$k(20)$	first-order reaction rate at 20 °C	h ⁻¹
$k_{ai}(T)$	temperature-dependent conversion rate of ammonium to nitrite	h ⁻¹
k_{am}	half-saturation constant for ammonium preference	mg-N L ⁻¹
$k_d(T)$	temperature-dependent phytoplankton death rate	h ⁻¹
$k_{dn}(T)$	temperature-dependent denitrification rate	h ⁻¹
$k_g(T, N, I)$	phytoplankton growth rate as a function of temp., nutrients, and light	h ⁻¹
$k_{g,20}$	phytoplankton growth rate at the reference temperature 20 °C	h ⁻¹
$k_{g,T}$	maximum phytoplankton growth rate at temperature T	h ⁻¹
$k_{hn}(T)$	temperature-dependent organic nitrogen hydrolysis rate	h ⁻¹
$k_{ig}(T)$	temperature-dependent conversion rate of nitrite to nitrogen gas	h ⁻¹
$k_{in}(T)$	temperature-dependent conversion rate of nitrite to nitrate	h ⁻¹
$k_n(T)$	temperature-dependent nitrification rate	h ⁻¹
$k_{ni}(T)$	temperature-dependent conversion rate of nitrate to nitrite	h ⁻¹
$k_{ra}(T)$	temperature-dependent phytoplankton respiration and excretion rate	h ⁻¹
k_{sn}	nitrogen half-saturation constant	mg L ⁻¹
k_{sp}	phosphorus half-saturation constant	mg L ⁻¹
M_b	mussel biomass (dry weight)	g
M_{cl}	mussel clearance rate	h ⁻¹ g ⁻¹ dry wt.
M_{ex}	mussel excretion rate of ammonium	h ⁻¹ g ⁻¹ dry wt.
n	nitrogen concentration	mg-N L ⁻¹
$n_{a,t}$	ammonium concentration at time t	mg-N L ⁻¹
$n_{a,t-1}$	ammonium concentration at time $t-1$	mg-N L ⁻¹
$n_{i,t}$	nitrite concentration at time t	mg-N L ⁻¹
$n_{i,t-1}$	nitrite concentration at time $t-1$	mg-N L ⁻¹
$n_{n,t}$	nitrate concentration at time t	mg-N L ⁻¹
$n_{n,t-1}$	nitrate concentration at time $t-1$	mg-N L ⁻¹
$n_{o,t}$	organic nitrogen concentration at time t	mg-N L ⁻¹
$n_{o,t-1}$	organic nitrogen concentration at time $t-1$	mg-N L ⁻¹
$n_{total,t}$	total nitrogen concentration at time t	mg-N L ⁻¹

Table 5.1 continued.

Variable	Definition	Units
p	phosphorus concentration	mg L^{-1}
T	temperature	$^{\circ}\text{C}$
$V_{s,a}$	phytoplankton settling rate	m h^{-1}
$V_{s,o}$	organic nitrogen settling rate	m h^{-1}
θ	temperature effect constant	---
τ	hydraulic retention time	h
φ_L	phytoplankton light attenuation factor	---
φ_N	phytoplankton nutrient attenuation factor	---
φ_n	nitrogen attenuation factor	---
φ_p	phosphorus attenuation factor	---

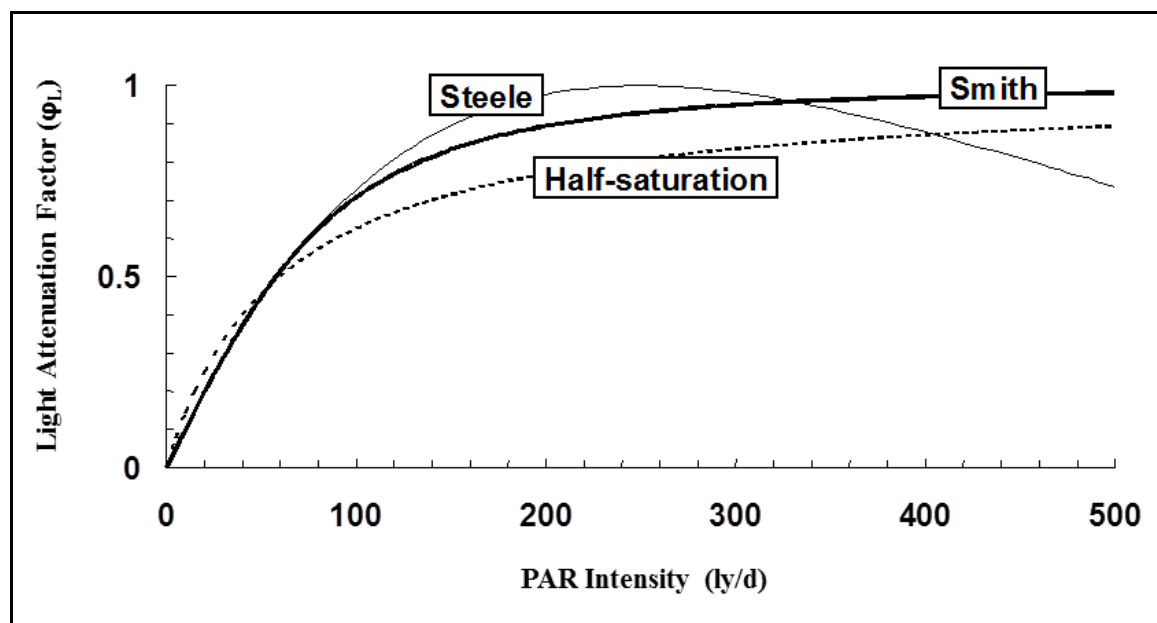


Figure 5.3: The three equations used for phytoplankton light attenuation showing light attenuation factor (φ_L) versus photosynthetically active radiation (Langley day^{-1}).

Table 5.2: Range of model variables and rates used in single variable and multiple variable sensitivity analyses.

Model Variable	Units	Sensitivity Analysis Range
Nitrification Rate	h^{-1}	0.0001 to 0.21
Denitrification Rate	h^{-1}	0.0005 to 0.0996
Light	---	0 to 1
Temperature	$^{\circ}\text{C}$	5 to 35
Hydraulic Retention Time	h	0.5 to 48
Maximum Phytoplankton Growth Rate	h^{-1}	0.0417 to 0.0833
Phytoplankton Death Rate	h^{-1}	0.0021 to 0.0104
Phytoplankton Settling Rate	m h^{-1}	0 to 0.0833
Phytoplankton Respiration/Excretion	h^{-1}	0.0004 to 0.0208
Organic Nitrogen Hydrolysis Rate	h^{-1}	0.00004 to 0.0083
Organic Nitrogen Settling Rate	m h^{-1}	0 to 0.0833
Mussel Biomass	g	0 to 250
Mussel Phytoplankton Clearance Rate	$\text{h}^{-1} \text{g}^{-1}$	0 to 0.000714
Mussel Ammonium Excretion Rate	$\text{h}^{-1} \text{g}^{-1}$	0 to 4

Source: Chapra 1997, Strauss et al. 2004, Bruesewitz et al. 2006, Richardson et al. 2004, Espinosa-Villegas et al. 2003, Schnoor 1996, Baker and Hornbach 2000, Baker and Hornbach 2001, Spooner and Vaughn 2008, Christian et al. 2008

Table 5.3: Model variables used in calibrated STELLA models for each of the experimental conditions and treatments.

Model Variable	Units	With Flow		Without Flow	
		Control	Mussel	Control	Mussel
Nitrification Rate	h^{-1}	0.2	0.2	0.2	0.2
Denitrification Rate	h^{-1}	0.004	0.006	0.004	0.006
Hydraulic Retention Time	h	16.72	16.72	---	---
Maximum Phytoplankton Growth Rate	h^{-1}	0.059	0.059	0.059	0.059
Phytoplankton Death Rate	h^{-1}	0.008	0.008	0.008	0.008
Phytoplankton Settling Rate	m h^{-1}	0.001	0.001	0.001	0.001
Water Depth	m	0.4064	0.4064	0.4064	0.4064
Phytoplankton Respiration/Excretion	h^{-1}	0.02	0.02	0.02	0.02
Organic Nitrogen Hydrolysis Rate	h^{-1}	0.0001	0.0001	0.0001	0.0001
Organic Nitrogen Settling Rate	m h^{-1}	0.001	0.001	0.001	0.001
Nitrate to Nitrite Rate	h^{-1}	0.00005	0.00005	0.00005	0.00005
Ammonium to Nitrite Rate	h^{-1}	0.2	0.2	0.2	0.2
Nitrite to N_2 Gas Rate	h^{-1}	0.0005	0.0005	0.0005	0.0005
Nitrite to Nitrate Rate	h^{-1}	0.2	0.2	0.2	0.2
Ammonium Preference Half-Saturation	mg-N L^{-1}	0.05	0.05	0.05	0.05
Mussel Biomass	g	---	200	---	200
Mussel Phytoplankton Clearance Rate	$\text{h}^{-1} \text{g}^{-1}$	---	0.00002	---	0.000015
Mussel Ammonium Excretion Rate	$\text{h}^{-1} \text{g}^{-1}$	---	0.15	---	1.15

Table 5.4: Percent difference and coefficient of determination (R^2) values between control and mussel treatments for grab samples and model outputs.

Parameter	Grab Samples				Model Outputs			
	Percent Difference		Coefficient of Determination (R^2)		Percent Difference		Coefficient of Determination (R^2)	
	Flow	No Flow	Flow	No Flow	Flow	No Flow	Flow	No Flow
Nitrate ^a	10.2% (11.1%)	160.4% (77.5%)	0.973 (0.992)	0.241 (0.089)	-1.8%	-7.0%	0.996	0.416
Ammonium	123.7%	2768.9%	0.469	0.857	101.4%	241.8%	0.525	0.943
Organic Nitrogen	1.8%	18.9%	0.914	0.000	0.0%	-33.6%	1.000	0.997
Nitrite	36.1%	623.4%	0.862	0.539	56.4%	208.1%	0.655	0.922
Total Nitrogen	9.4%	76.7%	0.968	0.251	-0.8%	-14.5%	0.995	0.505
Phytoplankton Biomass ^b	[-67.4%]	[-86.9%]	[0.067]	[0.012]	-7.7%	-85.5%	0.884	0.982

^a Percent difference and R^2 values for Nitratex measurements are shown in parentheses

^b Percent difference and R^2 values for Hydrolab measurements are shown in brackets

Table 5.5: Average percent difference and coefficient of determination (R^2) values between grab sample measurements and corresponding model outputs for each of the model scenarios.

Parameter	Percent Difference				Coefficient of Determination (R^2)			
	Flow		No Flow		Flow		No Flow	
	Control	Mussel	Control	Mussel	Control	Mussel	Control	Mussel
Nitrate ^a	-0.5% (22.2%)	-8.5% (7.5%)	25.1% (9.7%)	-35.7% (-23.5%)	0.962 (0.963)	0.979 (0.916)	0.965 (0.943)	0.874 (0.832)
Ammonium	-13.0%	-13.4%	44.0%	-63.8%	0.759	0.569	0.804	0.976
Organic Nitrogen	-4.5%	-6.7%	-14.4%	-49.3%	0.417	0.669	0.023	0.148
Nitrite	-0.7%	19.4%	-13.3%	-28.0%	0.398	0.652	0.021	0.083
Total Nitrogen	-1.4%	-8.6%	1.9%	-39.8%	0.919	0.962	0.909	0.881
Phytoplankton Biomass ^b	[-44.0%]	[82.7%]	[-48.4%]	[3.2%]	[0.383]	[0.076]	[0.037]	[0.217]

^a Percent difference and R^2 values between Nitratex measurements and model outputs are shown in parentheses

^b Percent difference and R^2 values between Hydrolab measurements and model outputs are shown in brackets

Table 5.6: Grab sample measurements^a and corresponding model results for nitrate, ammonium, organic nitrogen, nitrite, and total nitrogen for each of the model scenarios^b (mg-N L⁻¹).

Model Scenario	Day	Nitrate		Ammonium		Organic Nitrogen		Nitrite		Total Nitrogen	
		Grab Sample	Model	Grab Sample	Model	Grab Sample	Model	Grab Sample	Model	Grab Sample	Model
Control Flow	0.1	1.95 (0.04)	1.95	0.016 (0.004)	0.015	0.88 (0.08)	0.82	0.024 (0.001)	0.023	2.87 (0.12)	2.82
	1.9	3.38 (0.10)	3.74	0.022 (0.001)	0.014	0.79 (0.09)	0.88	0.029 (0.001)	0.022	4.23 (0.01)	4.66
	3.9	5.01 (1.03)	5.12	0.028 (0.008)	0.029	0.82 (0.16)	1.00	0.025 (0.011)	0.036	5.89 (1.21)	6.18
	8.1	7.59 (0.39)	6.41	0.008 (0.004)	0.008	0.76 (0.13)	0.47	0.019 (0.004)	0.014	8.38 (0.52)	6.90
	10.0	1.95 (0.14)	1.95	0.016 (0.003)	0.010	0.63 (0.04)	0.55	0.013 (0.003)	0.013	2.61 (0.02)	2.53
Mussel Flow	0.1	2.18 (0.05)	2.27	0.052 (0.021)	0.033	0.95 (0.15)	0.84	0.037 (0.003)	0.036	3.21 (0.13)	3.18
	1.9	3.64 (0.30)	3.70	0.039 (0.021)	0.042	0.85 (0.18)	0.88	0.036 (0.007)	0.046	4.57 (0.15)	4.68
	3.9	6.11 (0.31)	5.04	0.047 (0.018)	0.052	0.87 (0.08)	1.00	0.037 (0.010)	0.054	7.07 (0.42)	6.14
	8.1	7.69 (0.04)	6.21	0.019 (0.005)	0.016	0.71 (0.06)	0.47	0.027 (0.001)	0.021	8.44 (0.09)	6.72
	10.0	2.12 (0.05)	1.86	0.032 (0.001)	0.020	0.60 (0.04)	0.55	0.014 (0.008)	0.021	2.76 (0.08)	2.45
Control No Flow	0.2	3.78 (0.15)	3.40	0.020 (0)	0.011	0.82 (0.07)	0.87	0.020 (0.001)	0.016	4.64 (0.08)	4.29
	3.0	2.75 (0.11)	2.28	0.007 (0.005)	0.008	0.67 (0.02)	0.78	0.005 (0.003)	0.010	3.44 (0.12)	3.08
	8.2	0.38 (0.01)	1.00	0.002 (0.001)	0.003	0.57 (0.04)	0.58	0.003 (0.001)	0.004	0.96 (0.04)	1.58
	14.1	2.87 (0.05)	2.46	0.001 (0.001)	0.001	0.61 (0.17)	0.40	0.026 (0.020)	0.002	3.51 (0.25)	2.86
	18.0	1.31 (0.45)	1.41	0.001 (0.001)	0.001	0.81 (0.05)	0.32	0.021 (0.016)	0.001	2.15 (0.42)	1.73
Mussel No Flow	0.2	4.51 (0.11)	4.27	0.114 (0.011)	0.093	0.77 (0.18)	0.64	0.049 (0.002)	0.089	5.45 (0.28)	5.09
	3.0	4.45 (0.18)	3.36	0.090 (0.046)	0.052	1.11 (0.08)	0.55	0.041 (0.012)	0.056	5.69 (0.21)	4.02
	8.2	3.26 (0.11)	1.52	0.042 (0.024)	0.012	0.63 (0.16)	0.39	0.067 (0.066)	0.013	4.00 (0.15)	1.94
	14.1	2.25 (0.26)	1.32	0.033 (0.002)	0.003	0.83 (0.15)	0.26	0.027 (0.006)	0.003	3.14 (0.11)	1.59
	18.0	1.26 (0.26)	0.57	0.038 (0.014)	0.001	0.73 (0.20)	0.20	0.028 (0.001)	0.001	2.05 (0.48)	0.78

^a Standard deviations for grab samples are shown in parentheses

^b Grab samples for phytoplankton biomass were not included due to error in sample analysis

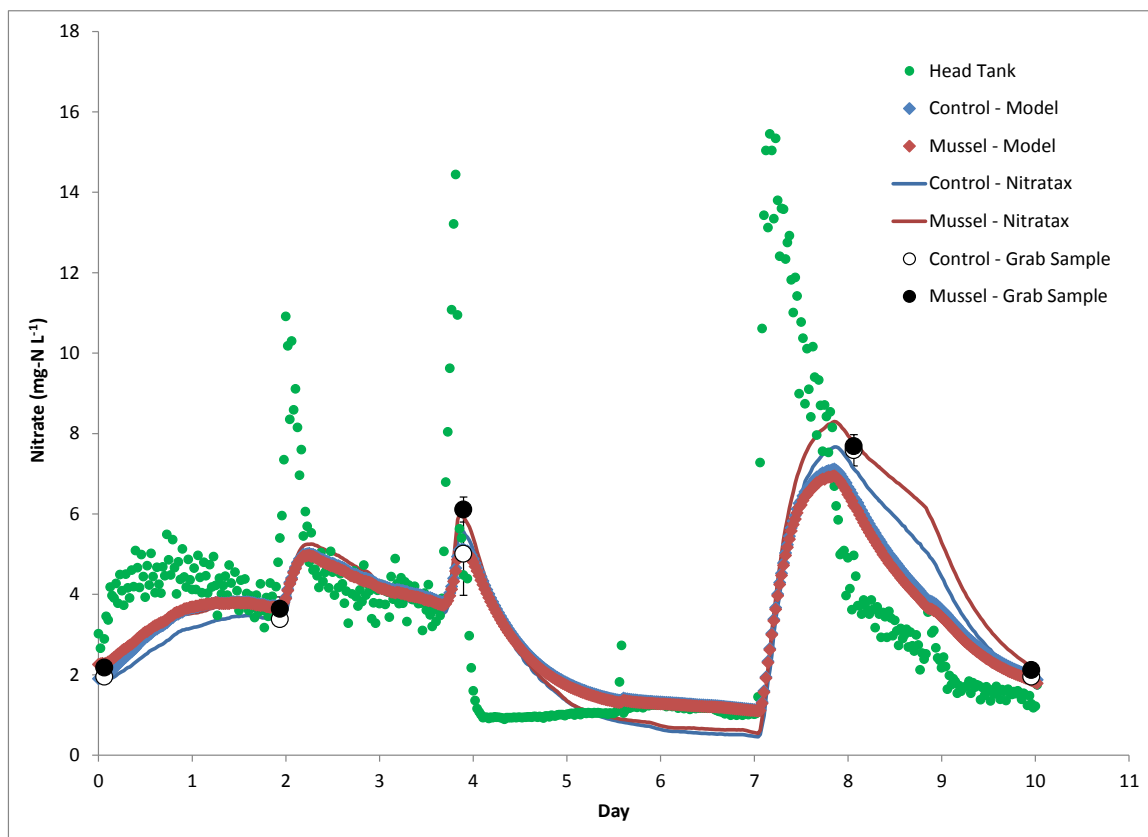


Figure 5.4: Nitrate (mg-N L^{-1}) results for control and mussel treatments with flow showing head tank (river influent) Hydrolab measurements, STELLA model simulations, treatment Nitratax sensor measurements, and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

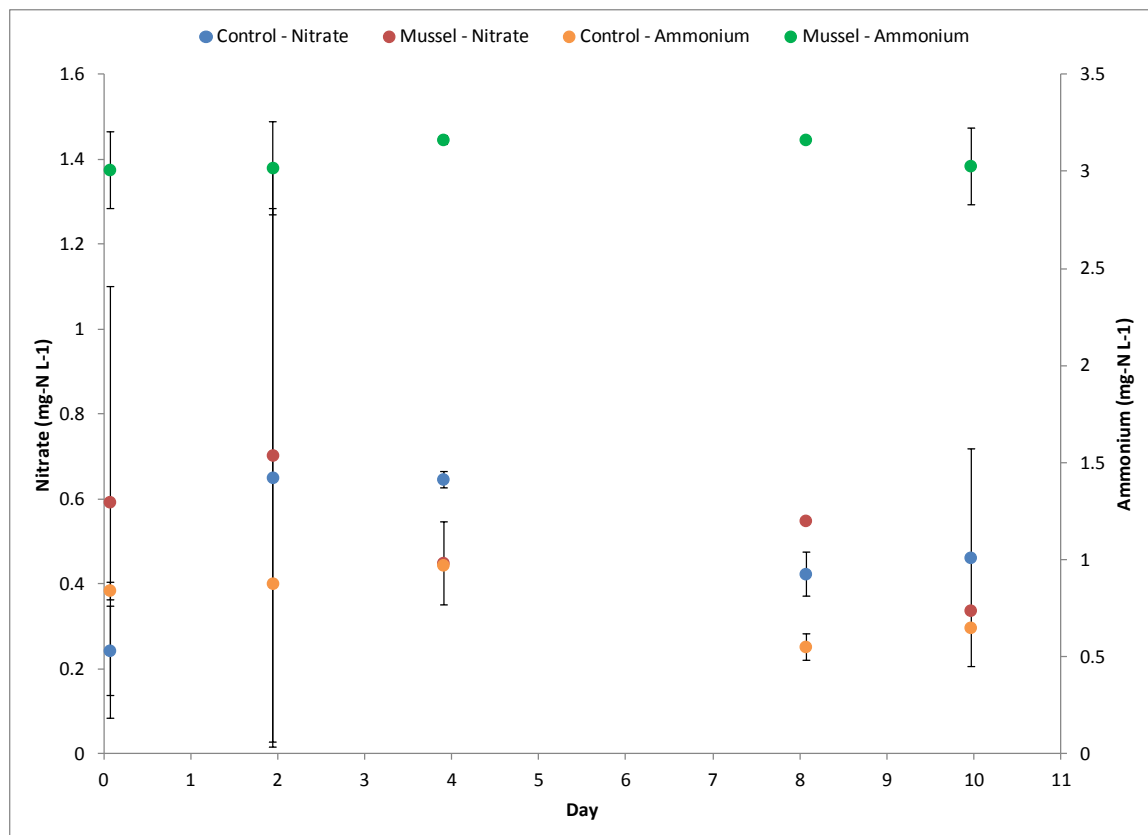


Figure 5.5: Grab sample measurements for nitrate and ammonium concentrations (mg-N L⁻¹) in the pore water of the flow-through mesocosms.

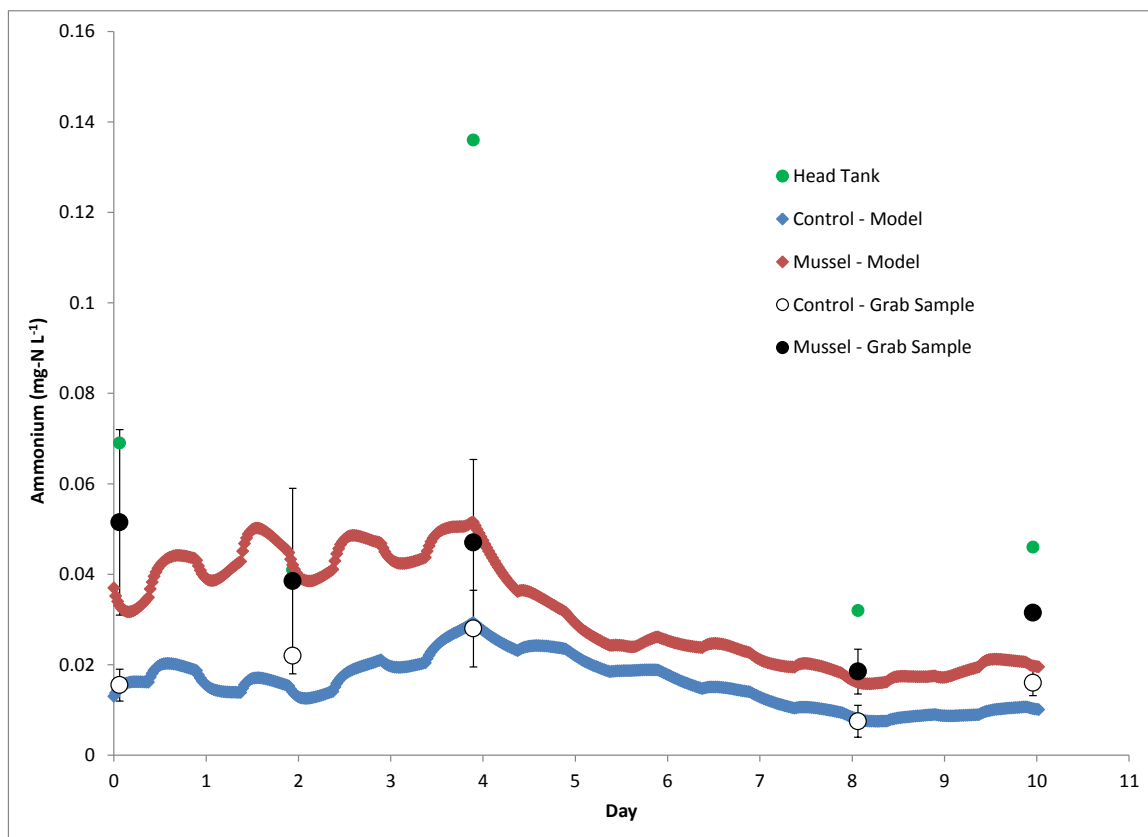


Figure 5.6: Ammonium (mg-N L⁻¹) results for control and mussel treatments with flow showing head tank (river influent) grab sample measurements, STELLA model simulations, and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

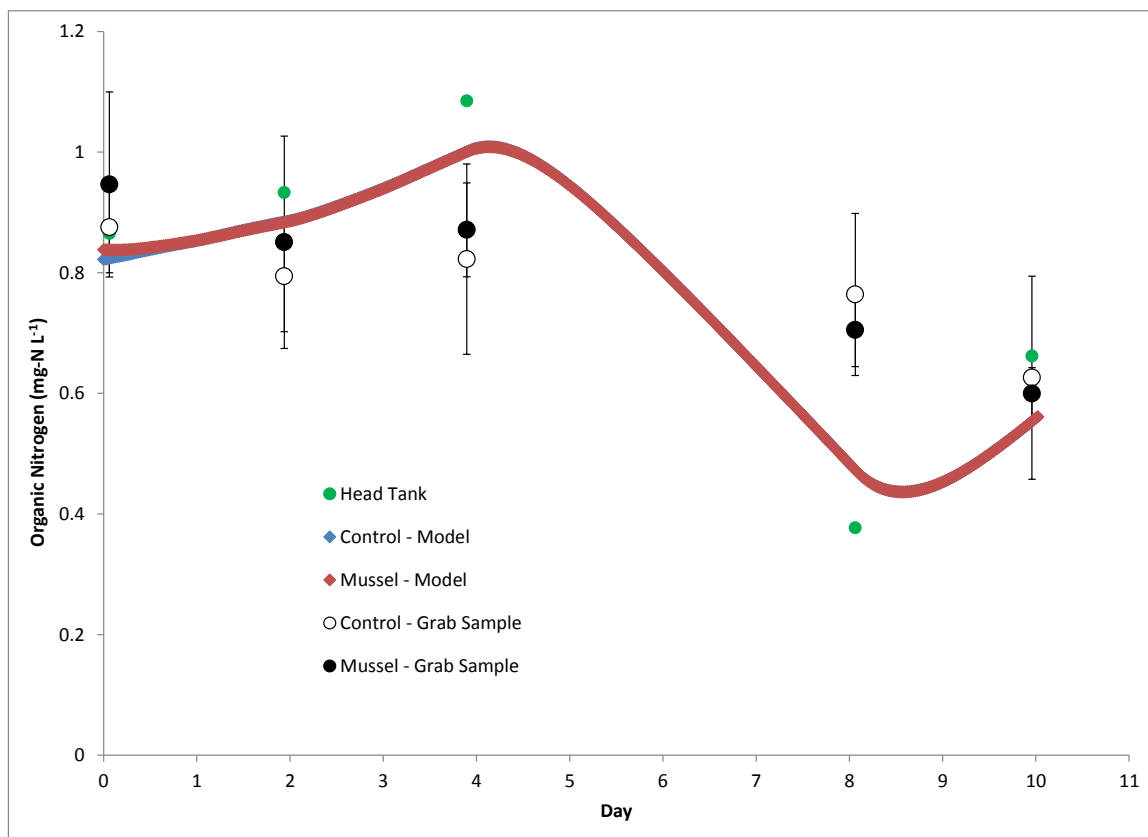


Figure 5.7: Organic nitrogen (mg-N L⁻¹) results for control and mussel treatments with flow showing head tank (river influent) grab sample calculations, STELLA model simulations, and treatment grab sample calculations. Error bars on grab sample calculations represent ± 1 SD.

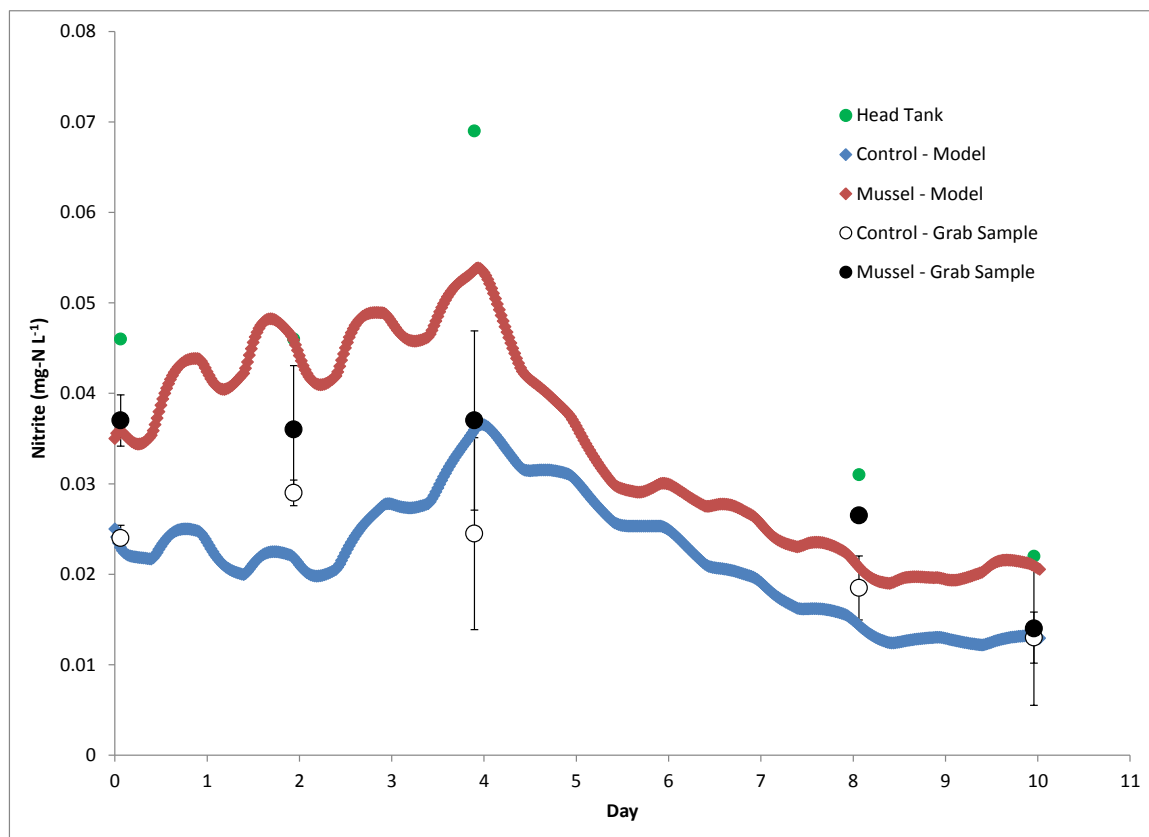


Figure 5.8: Nitrite (mg-N L^{-1}) results for control and mussel treatments with flow showing head tank (river influent) grab sample measurements, STELLA model simulations, and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

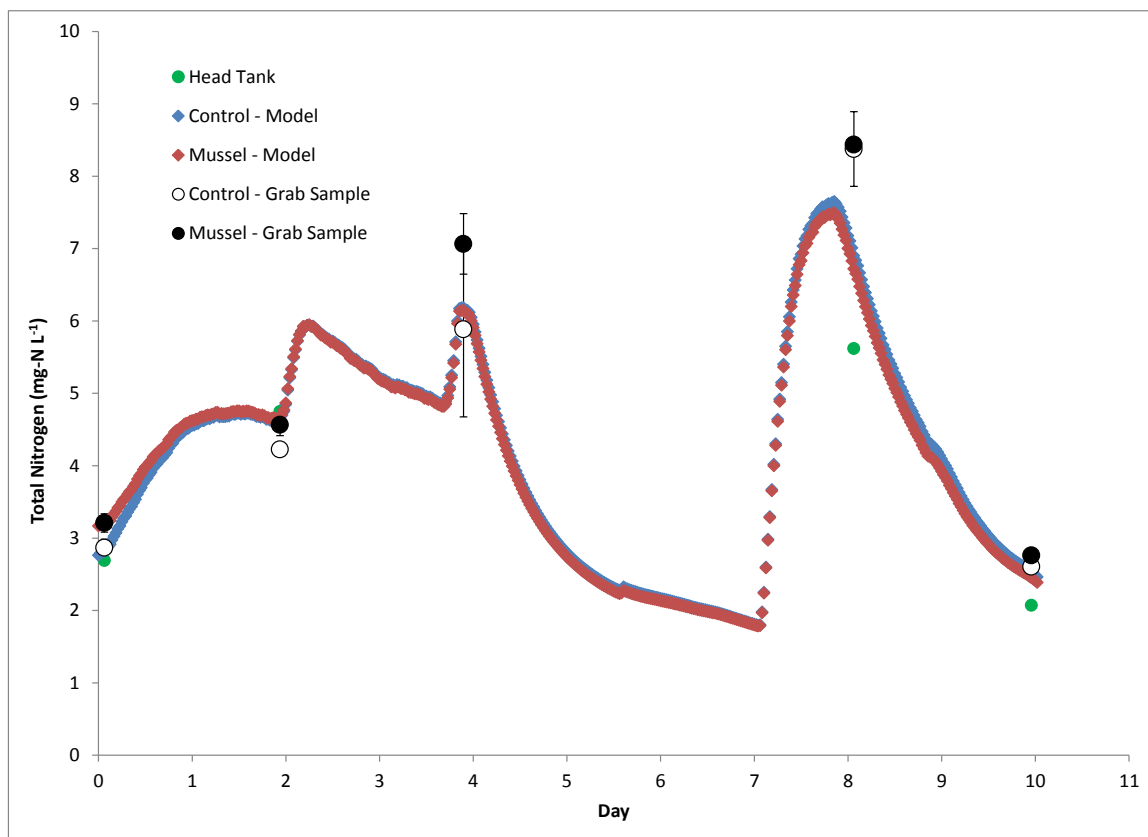


Figure 5.9: Total nitrogen (mg-N L⁻¹) results for control and mussel treatments with flow showing head tank (river influent) grab sample measurements, STELLA model simulations, and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

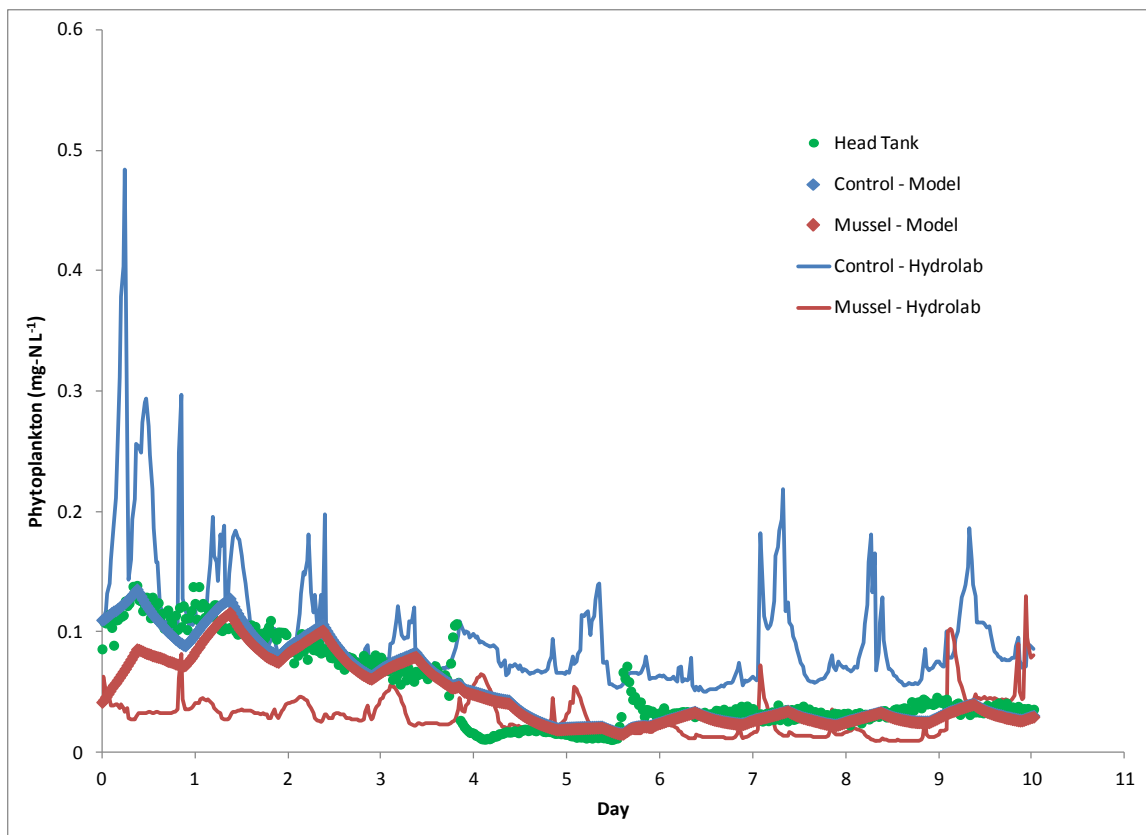


Figure 5.10: Phytoplankton (mg-N L^{-1}) results for control and mussel treatments with flow showing head tank (river influent) Hydrolab measurements, STELLA model simulations, and treatment Hydrolab measurements.

Table 5.7: The amount of mass mussels added or removed from the overlying water of the mesocosms was estimated for nitrate, ammonium, phytoplankton, organic nitrogen, nitrite, and total nitrogen.

Parameter	Measurement	Mussel Effect on Mass of Nitrogen		
		(mg-N)	(mg-N d ⁻¹)	(mg-N d ⁻¹ g ⁻¹ dry mass)
Nitrate	Nitratrax	687.1	68.6	0.343
	Grab Sample	694.7	69.3	0.347
	Model	-126.7	-12.6	-0.063
Ammonium	Grab Sample	30.3	3.0	0.015
	Model	31.9	3.2	0.016
Organic Nitrogen	Grab Sample	-10.7	-1.1	-0.005
	Model	0.5	0.05	0.0002
Nitrite	Grab Sample	14.8	1.5	0.007
	Model	24.9	2.5	0.012
Total Nitrogen	Grab Sample	716.7	71.5	0.358
	Model	-39.4	-3.9	-0.020
Phytoplankton	Hydrolab	-139.8	-14.0	-0.070
	Model	-12.9	-1.3	-0.006

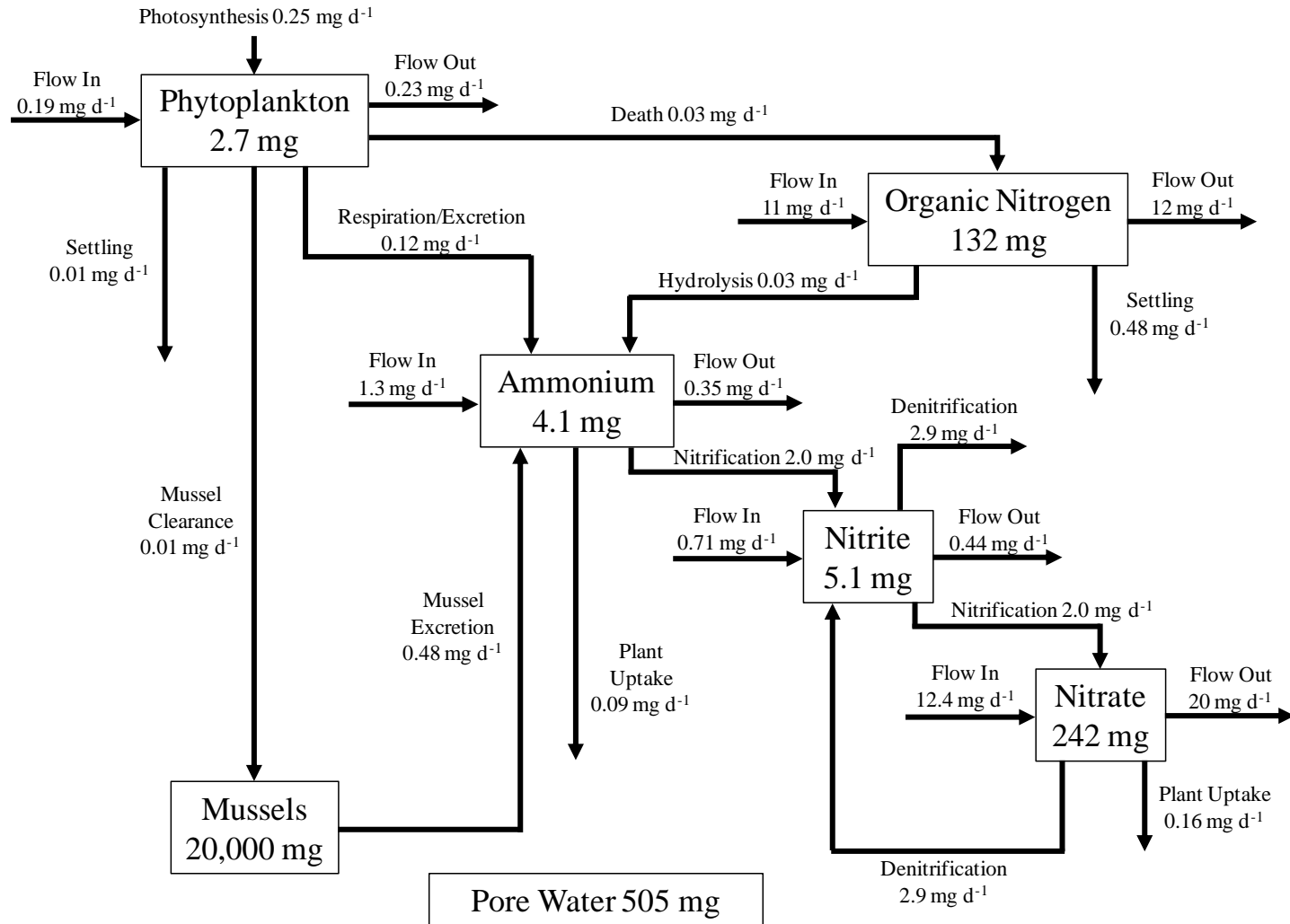


Figure 5.11: Dynamic equilibrium diagram of the nitrogen cycle simulated by the STELLA model with flow for Day 5 of the mesocosm experiment. Total nitrogen mass in the overlying water was estimated to be 386 mg.

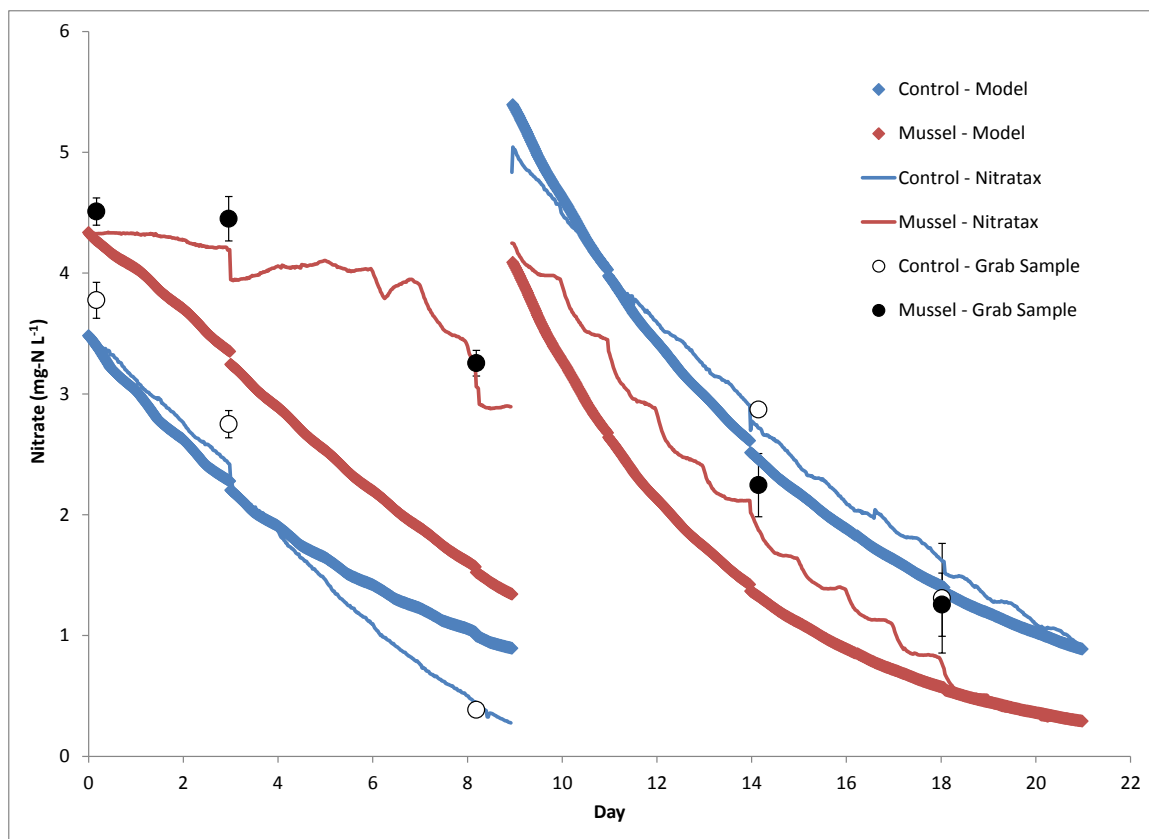


Figure 5.12: Nitrate (mg-N L^{-1}) results for control and mussel treatments without flow showing STELLA model simulations, treatment Nitratax sensor measurements, and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

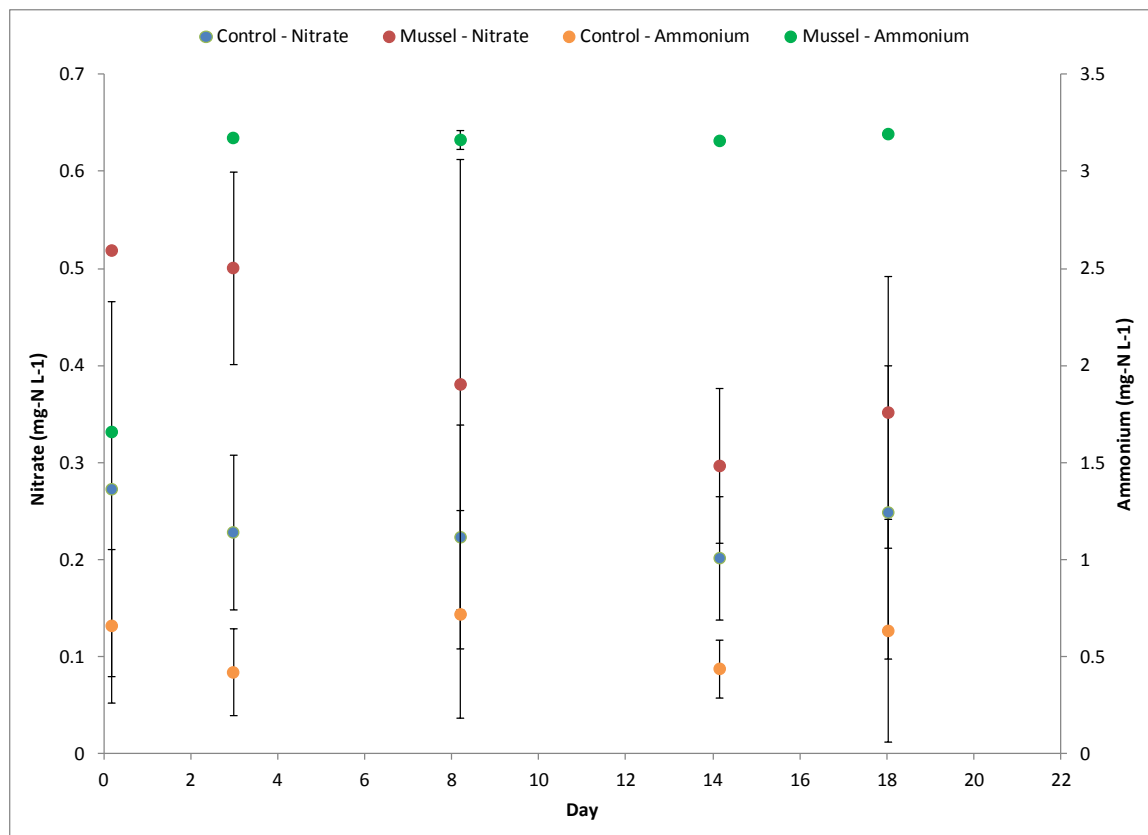


Figure 5.13: Grab sample measurements for nitrate and ammonium concentrations (mg-N L^{-1}) in the pore water of the mesocosms without flow.

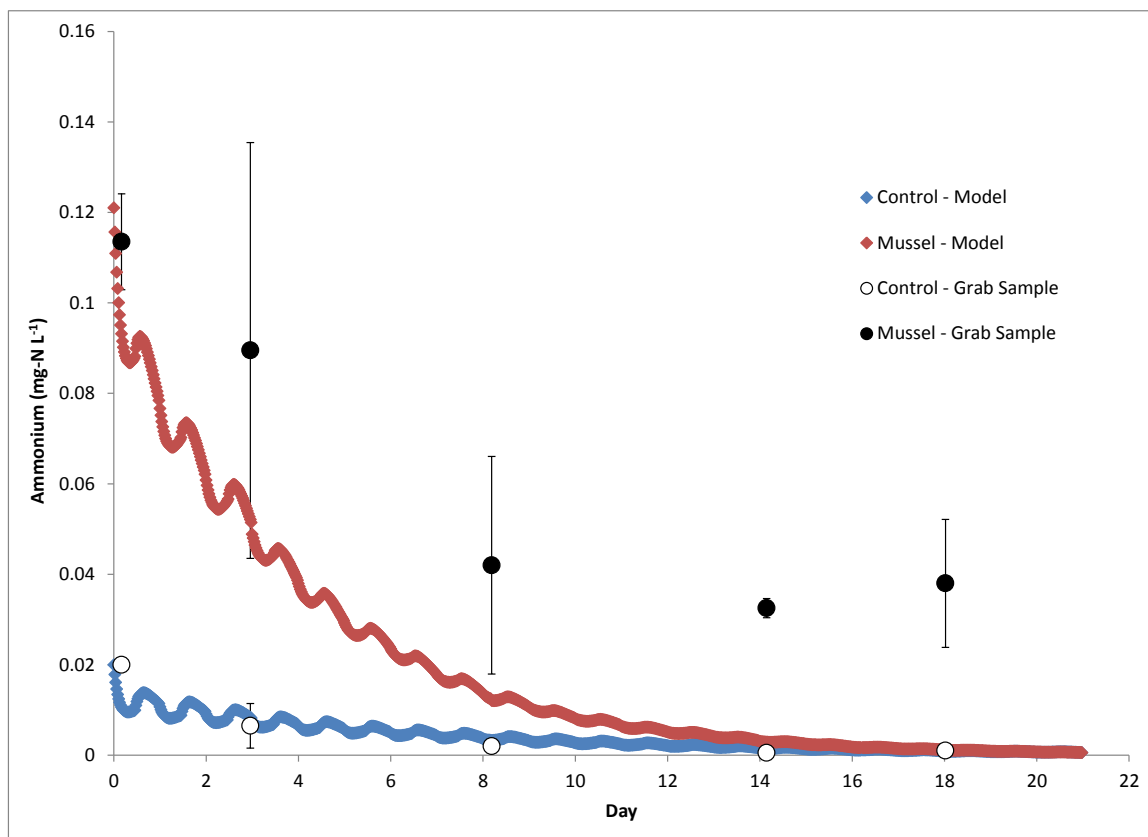


Figure 5.14: Ammonium (mg-N L⁻¹) results for control and mussel treatments without flow showing STELLA model simulations and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

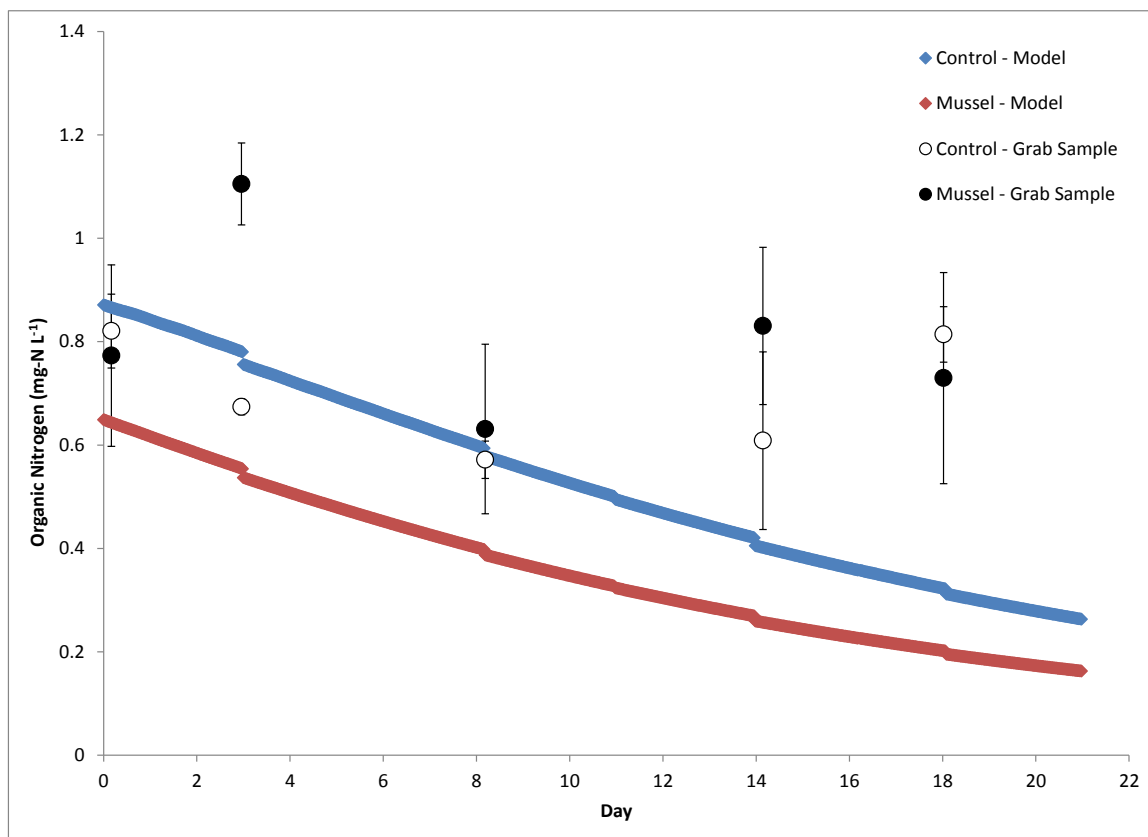


Figure 5.15: Organic nitrogen (mg-N L⁻¹) results for control and mussel treatments without flow showing STELLA model simulations and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

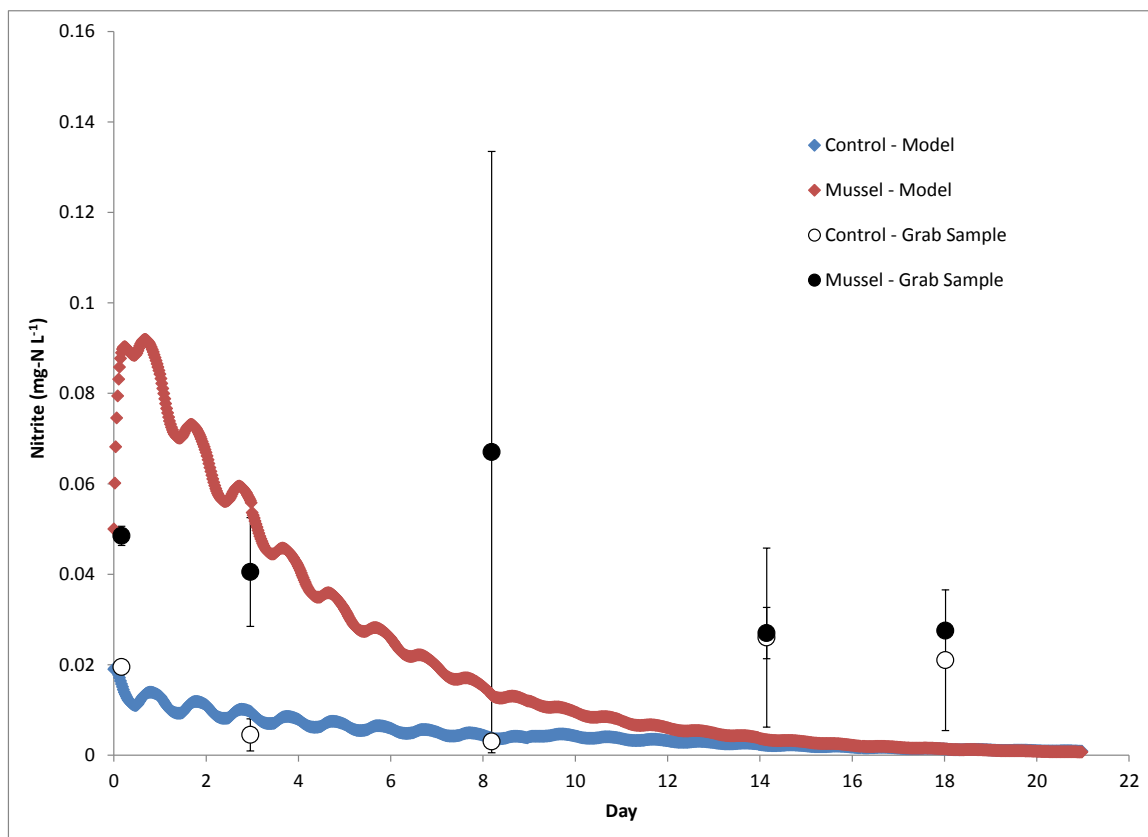


Figure 5.16: Nitrite (mg-N L⁻¹) results for control and mussel treatments without flow showing STELLA model simulations and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

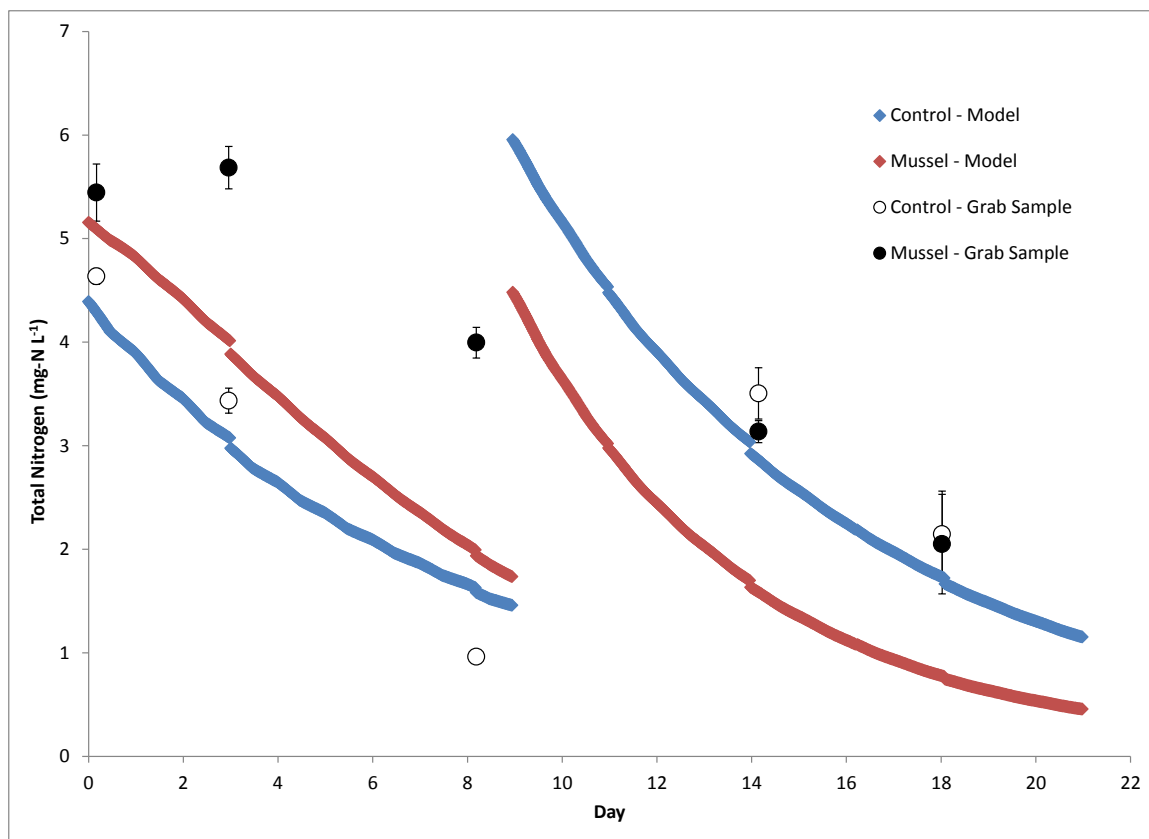


Figure 5.17: Total nitrogen (mg-N L⁻¹) results for control and mussel treatments without flow showing STELLA model simulations and treatment grab sample measurements. Error bars on grab sample measurements represent ± 1 SD.

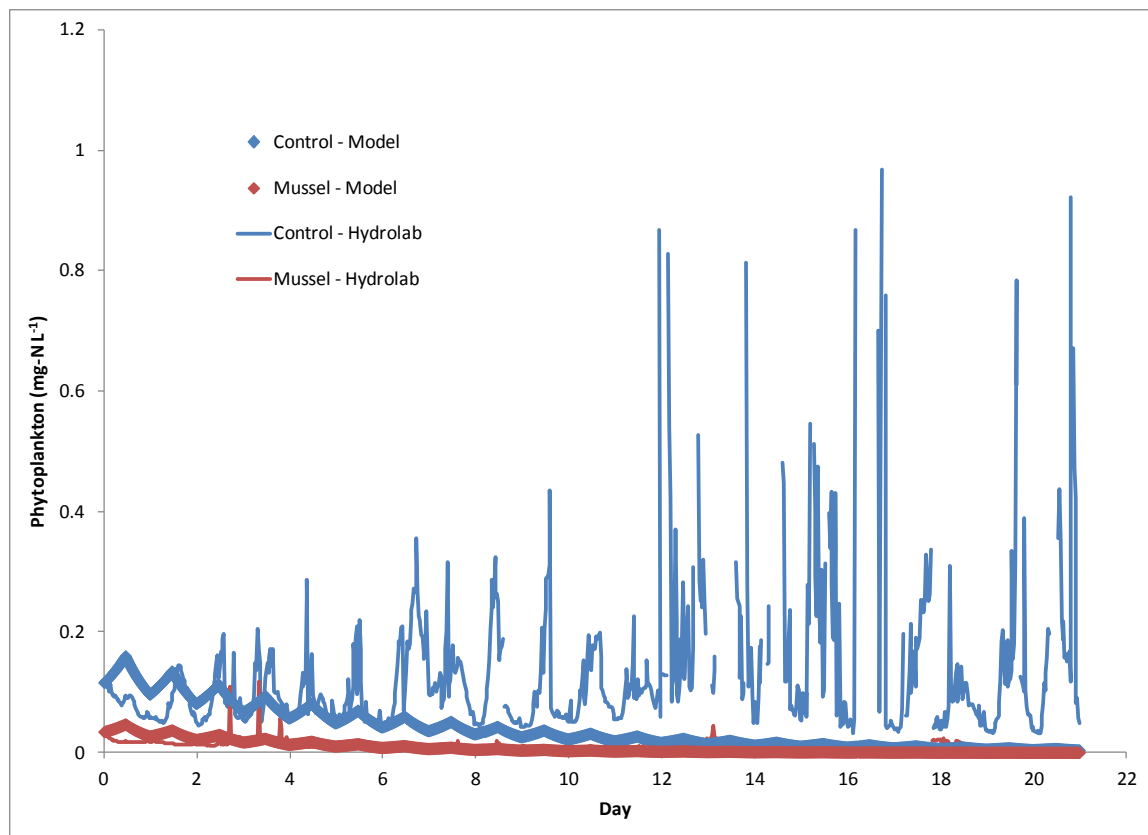


Figure 5.18: Phytoplankton (mg-N L⁻¹) results for control and mussel treatments without flow showing STELLA model simulations and treatment Hydrolab measurements.

Table 5.8: Results for the single variable sensitivity analysis on nitrate showing the normalized sensitivity coefficient (NSC), the coefficient of determination (R^2), and percent difference.

Parameter	Control (flow)			Mussel (flow)			Control (no flow)			Mussel (no flow)		
	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference
Nitrification Rate	0.014	1	-1.2%	0.023	1	-1.8%	0.009	1	-1.0%	0.065	0.981	-6.3%
Denitrification Rate	0.051	0.860	-39.2%	0.077	0.873	-36.8%	0.397 ^a	0.695 ^a	83.7% ^a	0.732	0.299	55.9%
Light	0.007	1	0.3%	0.001	1	0%	0.090	0.999	0.8%	0.678	0.964	-4.7%
Temperature	0.105	0.998	0.1%	0.141	0.997	7.0%	1.096	0.956	39.6%	1.690	0.669	103.8%
Hydraulic Retention Time	0.082	0.708	0.6%	0.093	0.724	1.0%	---	---	---	---	---	---
Maximum Phytoplankton Growth Rate	0.009	1	-0.1%	0.001	1	0%	0.338 ^a	0.999 ^a	-11.5% ^a	2.601	0.892	220.2%
Phytoplankton Death Rate	0	1	0%	0.002	1	0%	0.014	1	-0.7%	0.250	0.990	14.8%
Phytoplankton Settling Rate	0	1	0.1%	0.000	1	-0.7%	0.001	0.999	0.7%	0.023	0.947	-18.8%
Phytoplankton Respiration/Excretion	0.007	1	-0.4%	0.002	1	0.2%	0.241 ^a	0.992 ^a	-12.9% ^a	352.681	0.661	165323.2%
Organic Nitrogen Hydrolysis Rate	0	1	1.5%	0.000	1	1.5%	0.002	0.999	8.1%	0.001	0.999	3.6%
Organic Nitrogen Settling Rate	0	1	0%	0.000	1	0%	0.001	1	-0.3%	0	1	-0.2%
Mussel Biomass	---	---	---	0.021	1	-0.8%	---	---	---	0.335	0.963	-13.3%
Mussel Phytoplankton Clearance Rate	---	---	---	0.010	0.981	11.5%	---	---	---	0.089	0.816	22.5%
Mussel Ammonium Excretion Rate	---	---	---	0.016	0.965	14.8%	---	---	---	0.283	0.931	6.1%

^a Model did not run for complete simulation time due to an error caused by a division by zero or a value that became too large to represent

Table 5.9: Results for the single variable sensitivity analysis on ammonium showing the normalized sensitivity coefficient (NSC), the coefficient of determination (R^2), and percent difference.

Parameter	Control (flow)			Mussel (flow)			Control (no flow)			Mussel (no flow)		
	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference
Nitrification Rate	1.743	0.903	124.2%	1.843	0.917	133.8%	8.973	0.942	1800.8%	24.545	0.967	17343.3%
Denitrification Rate	0	1	0.1%	0	1	0.1%	0.080 ^a	0.913 ^a	-1.8% ^a	0	1	-0.2%
Light	0.026	0.983	-0.9%	0.237	0.974	-7.1%	2.802	0.685	-1.4%	2.501	0.795	57.7%
Temperature	1.073	0.851	33.5%	1.304	0.920	66.9%	0.491	0.822	-21.5%	2.159	0.943	86.3%
Hydraulic Retention Time	1.404	0.900	98.8%	0.552	0.726	39.4%	---	---	---	---	---	---
Maximum Phytoplankton Growth Rate	0.035	0.993	0.4%	0.239	0.991	2.2%	12.410 ^a	0.776 ^a	830.2% ^a	11.951	0.820	4400.9%
Phytoplankton Death Rate	0.023	1	0.6%	0.066	0.999	1.5%	1.319	0.817	115.3%	0.918	0.971	143.3%
Phytoplankton Settling Rate	0.004	0.947	-9.9%	0.011	0.806	-25.9%	0.114	0.530	-46.8%	0.084	0.493	-47.9%
Phytoplankton Respiration/Excretion	0.225	0.931	-12.6%	0.137	0.981	7.5%	3.642 ^a	0.518 ^a	313.3% ^a	3706.004	0.509	8223792.6%
Organic Nitrogen Hydrolysis Rate	0.017	0.978	69.1%	0.009	0.979	36.5%	0.032	0.630	59.3%	0.005	0.999	9.2%
Organic Nitrogen Settling Rate	0	1	-0.9%	0	1	-0.5%	0.012	0.999	-4.4%	0.002	1	-1.3%
Mussel Biomass	---	---	---	0.633	0.794	-20.4%	---	---	---	1.070	0.735	-36.6%
Mussel Phytoplankton Clearance Rate	---	---	---	0.294	0.597	324.0%	---	---	---	0.280	0.388	-44.4%
Mussel Ammonium Excretion Rate	---	---	---	0.511	0.735	408.3%	---	---	---	0.918	0.781	18.2%

^a Model did not run for complete simulation time due to an error caused by a division by zero or a value that became too large to represent

Table 5.10: Results for the single variable sensitivity analysis on organic nitrogen showing the normalized sensitivity coefficient (NSC), the coefficient of determination (R^2), and percent difference.

Parameter	Control (flow)			Mussel (flow)			Control (no flow)			Mussel (no flow)		
	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference
Nitrification Rate	0	1	0%	0	1	0%	0.000	1	0%	0	1	0%
Denitrification Rate	0	1	0%	0	1	0%	0 ^a	1 ^a	0% ^a	0	1	0%
Light	0.004	1	-0.1%	0.004	1	-0.1%	0.339	0.997	-4.2%	0.098	1	-1.3%
Temperature	0.004	1	0%	0.003	1	0.1%	0.056	1	-2.1%	0.040	1	-0.2%
Hydraulic Retention Time	0.007	0.953	0.5%	0.007	0.953	0.4%	---	---	---	---	---	---
Maximum Phytoplankton Growth Rate	0.004	1	0%	0.004	1	0%	1.291 ^a	0.996 ^a	44.3% ^a	0.332	0.872	15.1%
Phytoplankton Death Rate	0.008	1	-0.2%	0.007	1	-0.2%	0.036	0.998	-1.5%	0.020	1	-0.7%
Phytoplankton Settling Rate	0	1.000	-0.4%	0	1	-0.3%	0.013	0.999	-9.2%	0.003	0.999	-3.1%
Phytoplankton Respiration/Excretion	0.005	1	0.2%	0.004	1	0.2%	0.873 ^a	0.688 ^a	27.3% ^a	35.767	0.711	6775.8%
Organic Nitrogen Hydrolysis Rate	0.002	0.993	-7.9%	0.002	0.994	-8.0%	0.017	0.988	-51.9%	0.018	0.867	-54.1%
Organic Nitrogen Settling Rate	0.020	0.687	-47.5%	0.020	0.687	-47.5%	0.188	0.470	-51.0%	0.191	0.329	-49.6%
Mussel Biomass	---	---	---	0	1	0.0%	---	---	---	0.010	1	0.7%
Mussel Phytoplankton Clearance Rate	---	---	---	0	1	-0.3%	---	---	---	0.005	0.999	-2.9%
Mussel Ammonium Excretion Rate	---	---	---	0	1	0%	---	---	---	0	1	0%

^a Model did not run for complete simulation time due to an error caused by a division by zero or a value that became too large to represent

Table 5.11: Results for the single variable sensitivity analysis on nitrite showing the normalized sensitivity coefficient (NSC), the coefficient of determination (R^2), and percent difference.

Parameter	Control (flow)			Mussel (flow)			Control (no flow)			Mussel (no flow)		
	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference
Nitrification Rate	0.997	0.901	58.3%	0.740	0.847	36.2%	3.546	0.906	572.1%	2.659	0.902	1139.3%
Denitrification Rate	0.002	0.999	-1.3%	0.001	1	-0.8%	0.111 ^a	0.966 ^a	20.9% ^a	0.018	1	6.8%
Light	0.015	0.994	-0.6%	0.177	0.984	-5.3%	2.366	0.742	-4.5%	2.419	0.796	48.6%
Temperature	0.895	0.869	23.4%	0.918	0.882	44.0%	0.432	0.795	-6.2%	2.145	0.889	102.8%
Hydraulic Retention Time	0.810	0.940	46.5%	0.333	0.834	17.1%	---	---	---	---	---	---
Maximum Phytoplankton Growth Rate	0.020	0.997	0.2%	0.178	0.994	1.6%	10.460 ^a	0.741 ^a	613.0% ^a	11.436	0.829	3808.0%
Phytoplankton Death Rate	0.014	1	0.3%	0.049	1	1.1%	1.115	0.861	84.7%	0.887	0.970	128.4%
Phytoplankton Settling Rate	0.002	0.977	-5.8%	0.008	0.856	-19.3%	0.097	0.743	-39.2%	0.081	0.500	-46.4%
Phytoplankton Respiration/Excretion	0.134	0.967	-7.4%	0.101	0.987	5.5%	3.025 ^a	0.589 ^a	222.7% ^a	3346.768	0.509	6680778.7%
Organic Nitrogen Hydrolysis Rate	0.010	0.974	40.3%	0.007	0.983	26.4%	0.028	0.443	51.1%	0.004	0.999	8.8%
Organic Nitrogen Settling Rate	0	1	-0.5%	0	1	-0.4%	0.010	0.999	-3.5%	0.002	1	-1.2%
Mussel Biomass	---	---	---	0.471	0.841	-15.2%	---	---	---	1.037	0.745	-35.0%
Mussel Phytoplankton Clearance Rate	---	---	---	0.218	0.568	241.9%	---	---	---	0.271	0.412	-37.5%
Mussel Ammonium Excretion Rate	---	---	---	0.380	0.713	304.0%	---	---	---	0.890	0.788	17.3%

^a Model did not run for complete simulation time due to an error caused by a division by zero or a value that became too large to represent

Table 5.12: Results for the single variable sensitivity analysis on total nitrogen showing the normalized sensitivity coefficient (NSC), the coefficient of determination (R^2), and percent difference.

Parameter	Control (flow)			Mussel (flow)			Control (no flow)			Mussel (no flow)		
	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference
Nitrification Rate	0.001	1	0.1%	0.002	1	0.1%	0.011	0.999	1.3%	0.168	0.926	30.2%
Denitrification Rate	0.041	0.842	-30.4%	0.062	0.857	-28.2%	0.314 ^a	0.709*	66.7% ^a	0.612	0.447	38.0%
Light	0.005	1	0.2%	0.005	1	-0.1%	0.007	0.999	-0.4%	0.621	0.970	-4.4%
Temperature	0.094	0.998	0.4%	0.131	0.996	6.3%	0.887	0.955	30.8%	1.453	0.745	79.0%
Hydraulic Retention Time	0.077	0.709	1.1%	0.083	0.724	1.2%	---	---	---	---	---	---
Maximum Phytoplankton Growth Rate	0.006	1	-0.1%	0.005	1	0%	0.024 ^a	0.999 ^a	-0.7% ^a	2.414	0.907	178.7%
Phytoplankton Death Rate	0.002	1	0%	0.001	1	0%	0.015	1	-0.7%	0.221	0.992	11.9%
Phytoplankton Settling Rate	0	1	0%	0	1	-1.0%	0.002	0.999	-1.5%	0.021	0.956	-16.4%
Phytoplankton Respiration/Excretion	0.007	1	-0.4%	0.004	1	0.3%	0.051 ^a	0.995 ^a	-4.0% ^a	358.178	0.681	137870.0%
Organic Nitrogen Hydrolysis Rate	0	1	0.0%	0	1	-0.1%	0.001	1	-4.3%	0.001	0.999	-7.2%
Organic Nitrogen Settling Rate	0.004	0.994	-10.1%	0.004	0.994	-10.2%	0.036	0.951	-11.5%	0.029	0.997	-8.2%
Mussel Biomass	---	---	---	0.025	1	-0.9%	---	---	---	0.296	0.971	-11.0%
Mussel Phytoplankton Clearance Rate	---	---	---	0.012	0.965	13.2%	---	---	---	0.078	0.865	19.0%
Mussel Ammonium Excretion Rate	---	---	---	0.020	0.947	16.8%	---	---	---	0.251	0.947	5.1%

^a Model did not run for complete simulation time due to an error caused by a division by zero or a value that became too large to represent

Table 5.13: Results for the single variable sensitivity analysis on phytoplankton showing the normalized sensitivity coefficient (NSC), the coefficient of determination (R^2), and percent difference.

Parameter	Control (flow)			Mussel (flow)			Control (no flow)			Mussel (no flow)		
	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference	NSC	R^2	% Difference
Nitrification Rate	0	1	0%	0	1	0%	0	1	0%	0	1	0%
Denitrification Rate	0	1	0%	0	1	0%	0 ^a	1 ^a	0% ^a	0	1	0%
Light	0.403	0.976	-14.3%	0.507	0.971	-15.4%	3.301	0.722	13.0%	2.683	0.788	68.9%
Temperature	0.071	0.983	-2.2%	0.094	0.979	5.7%	0.521	0.978	-26.6%	0.451	0.983	-24.2%
Hydraulic Retention Time	0.005	0.941	1.6%	0.112	0.889	3.6%	---	---	---	---	---	---
Maximum Phytoplankton Growth Rate	0.511	0.992	5.2%	0.515	0.991	5.2%	20.920 ^a	0.671 ^a	1877.1% ^a	13.353	0.802	5347.0%
Phytoplankton Death Rate	0.118	0.999	3.1%	0.114	0.999	2.9%	1.529	0.840	158.6%	0.977	0.967	159.4%
Phytoplankton Settling Rate	0.019	0.821	-47.5%	0.019	0.861	-46.4%	0.128	0.464	-49.1%	0.089	0.454	-49.0%
Phytoplankton Respiration/Excretion	0.525	0.967	33.0%	0.503	0.974	30.6%	12.900 ^a	0.586 ^a	911.7% ^a	4564.796	0.453	11182896.0%
Organic Nitrogen Hydrolysis Rate	0	1	0%	0	1	0%	0	1	0%	0	1	0%
Organic Nitrogen Settling Rate	0	1	0%	0	1	0%	0	1	0%	0	1	0%
Mussel Biomass	---	---	---	0.047	1	2.4%	---	---	---	0.271	0.994	45.8%
Mussel Phytoplankton Clearance Rate	---	---	---	0.034	0.904	-39.1%	---	---	---	0.122	0.522	-39.4%
Mussel Ammonium Excretion Rate	---	---	---	0	1	0%	---	---	---	0	1	0%

^a Model did not run for complete simulation time due to an error caused by a division by zero or a value that became too large to represent

Table 5.14: The normalized sensitivity coefficient (NSC) values were averaged for the sensitivity runs^a that successfully met the conditions established by the multiple variable sensitivity analysis(average within $\pm 5\%$, $R^2 \geq 0.95$).

Parameter	Flow							
	3	Control	Flow		Mussel		No Flow	
		2	1	2	1	Control	Mussel	
						1	1	
Nitrification Rate	0.050	0.135	0.205	0.055	1.374	0.093	0.082	
Denitrification Rate	0.034	0.025	0.019	0.014	0.030	0.101	0.025	
Light	0.191	0.500	0.353	0.122	0.550	0.077	0.185	
Temperature	0.029	0.064	0.252	0.036	0.130	0.167	0.058	
Hydraulic Retention Time	0.113	0.322	0.326	0.177	0.423	---	---	
Maximum Phytoplankton Growth Rate	0.294	0.223	1.711	0.279	0.320	0.488	0.197	
Phytoplankton Death Rate	0.102	0.146	0.270	0.122	0.258	5.793	0.167	
Phytoplankton Settling Rate	0.000	0.001	0.002	0.001	0.001	0.001	0.001	
Phytoplankton Respiration/Excretion	0.084	0.798	0.270	1.084	0.281	0.092	0.053	
Organic Nitrogen Hydrolysis Rate	0.001	0.001	0.002	0.002	0.005	0.022	0.001	
Organic Nitrogen Settling Rate	0.008	0.006	0.012	0.008	0.004	0.009	0.026	
Mussel Biomass	---	---	---	0.051	0.155	---	0.063	
Mussel Phytoplankton Clearance Rate	---	---	---	0.005	0.003	---	0.003	
Mussel Ammonium Excretion Rate	---	---	---	0.005	0.012	---	0.043	

^a The results were grouped together by the number of parameters that successfully met the conditions for a given sensitivity run

Table 5.15: Average values of model variables for sensitivity runs^a that met the criteria established by the multiple variable sensitivity analysis (average within $\pm 5\%$, $R^2 \geq 0.95$).

Parameter	Control		Flow		No Flow		
	3	2	1	2	1	Control 1	Mussel 1
Nitrification Rate	0.069	0.104	0.106	0.036	0.099	0.084	0.130
Denitrification Rate	0.044	0.022	0.030	0.031	0.038	0.027	0.040
Light	0.73	0.47	0.46	0.51	0.47	0.47	0.62
Temperature	-0.92	11.26	14.96	2.12	11.97	11.30	10.04
Hydraulic Retention Time	15.95	17.03	17.32	17.68	16.46	---	---
Maximum Phytoplankton Growth Rate	0.060	0.062	0.063	0.063	0.061	0.064	0.067
Phytoplankton Death Rate	0.0066	0.0066	0.0063	0.0063	0.0064	0.0067	0.0063
Phytoplankton Settling Rate	0.057	0.029	0.037	0.062	0.046	0.053	0.041
Phytoplankton Respiration/Excretion	0.012	0.010	0.010	0.008	0.010	0.012	0.011
Organic Nitrogen Hydrolysis Rate	0.0030	0.0046	0.0033	0.0032	0.0033	0.0033	0.0038
Organic Nitrogen Settling Rate	0.000	0.001	0.009	0.019	0.011	0.017	0.021
Mussel Biomass	---	---	---	91.0	115.4	---	109.1
Mussel Phytoplankton Clearance Rate	---	---	---	0.00038	0.00033	---	0.00031
Mussel Ammonium Excretion Rate	---	---	---	1.22	1.15	---	1.44

^a The results were grouped together by the number of parameters that successfully met the conditions for a given sensitivity run

Table 5.16: Average percent difference and coefficient of determination (R²) results calculated between the control and mussel treatment model outputs and respective results from Model Application 1 and Model Application 2.

Model Scenario	Parameter	Percent Difference						Coefficient of Determination (R ²)					
		Model Application 1			Model Application 2			Model Application 1			Model Application 2		
		Control	Mussel (Density 1)	Mussel (Density 2)	Control	Mussel (Density 1)	Mussel (Density 2)	Control	Mussel (Density 1)	Mussel (Density 2)	Control	Mussel (Density 1)	Mussel (Density 2)
Flow	Nitrate	-3.0%	20.9%	-5.2%	-19.9%	157.5%	-24.0%	0.999	0.993	0.993	0.952	0.748	0.748
	Ammonium	187.0%	670.2%	54.4%	1111.3%	4702.2%	556.1%	0.153	0.093	0.062	0.028	0.057	0.019
	Organic Nitrogen	9.3%	9.1%	9.6%	69.1%	67.1%	70.7%	0.996	0.997	0.996	0.829	0.846	0.822
	Nitrite	108.8%	483.5%	38.6%	656.2%	3399.9%	407.3%	0.266	0.092	0.146	0.013	0.033	0.010
	Total Nitrogen	1.0%	26.1%	-1.2%	7.1%	191.8%	4.5%	0.998	0.986	0.997	0.912	0.618	0.892
	Phytoplankton Biomass	1438.1%	1487.8%	1573.3%	10500.5%	10843.5%	11432.4%	0.140	0.095	0.087	0.140	0.095	0.087
No Flow	Nitrate	-6.9%	551.3%	-29.3%	-45.0%	3981.5%	-20.8%	0.997	0.410	0.918	0.828	0.292	0.757
	Ammonium	340.1%	1667.4%	81.0%	2087.0%	11918.7%	874.3%	0.809	0.925	0.760	0.520	0.917	0.415
	Organic Nitrogen	69.5%	90.2%	120.8%	568.2%	651.5%	862.7%	0.777	0.750	0.553	0.037	0.030	0.034
	Nitrite	274.8%	1585.6%	70.1%	1699.1%	11340.0%	792.5%	0.761	0.925	0.832	0.494	0.917	0.506
	Total Nitrogen	9.6%	478.5%	-0.1%	85.0%	3455.4%	154.8%	0.993	0.502	0.953	0.576	0.381	0.444
	Phytoplankton Biomass	459.8%	1782.8%	3976.2%	3757.9%	12876.8%	27993.7%	1	1	0.983	1	1	0.983

Table 5.17: The Density 2 Model Application results were compared to the control Model Application results and the Density 1 Model Application Results using average percent difference and coefficient of determination (R^2).

Model Scenario	Parameter	Percent Difference				Coefficient of Determination (R^2)			
		Model Application 1		Model Application 2		Model Application 1		Model Application 2	
		Control	Mussel Density 1	Control	Mussel Density 1	Control	Mussel Density 1	Control	Mussel Density 1
Flow	Nitrate	-4.1%	-20.4%	-8.5%	-64.9%	0.996	0.993	0.996	0.761
	Ammonium	3.1%	-80.2%	2.2%	-87.7%	0.991	0.891	0.999	0.904
	Organic Nitrogen	0.3%	0.5%	1.0%	2.0%	1	1	1	0.999
	Nitrite	1.0%	-75.7%	1.2%	-86.1%	0.984	0.739	0.998	0.824
	Total Nitrogen	-2.9%	-20.8%	-3.4%	-61.4%	0.996	0.990	0.996	0.748
	Phytoplankton Biomass	2.1%	5.3%	2.1%	5.3%	0.998	0.994	0.998	0.994
No Flow	Nitrate	-32.3%	-86.0%	511.4%	-96.6%	0.732	0.150	0.489	0.081
	Ammonium	2.2%	-89.5%	10.3%	-91.7%	0.930	0.734	0.990	0.509
	Organic Nitrogen	-14.8%	14.8%	-6.2%	24.5%	0.967	0.954	0.995	0.868
	Nitrite	1.0%	-89.4%	7.7%	-91.8%	0.941	0.802	0.993	0.618
	Total Nitrogen	-27.4%	-80.3%	0.8%	-91.8%	0.596	0.312	0.579	0.387
	Phytoplankton Biomass	-15.5%	116.5%	-15.5%	116.5%	0.998	0.983	0.998	0.983

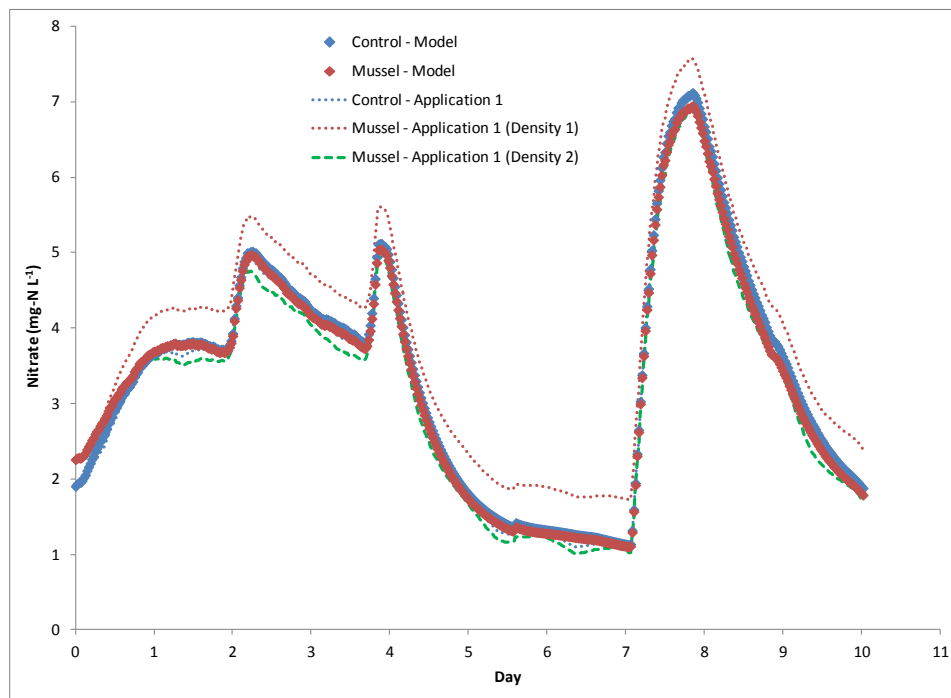


Figure 5.19: Nitrate (mg-N L⁻¹) results for control and mussel treatments with flow showing model outputs and Model Application 1 simulations.

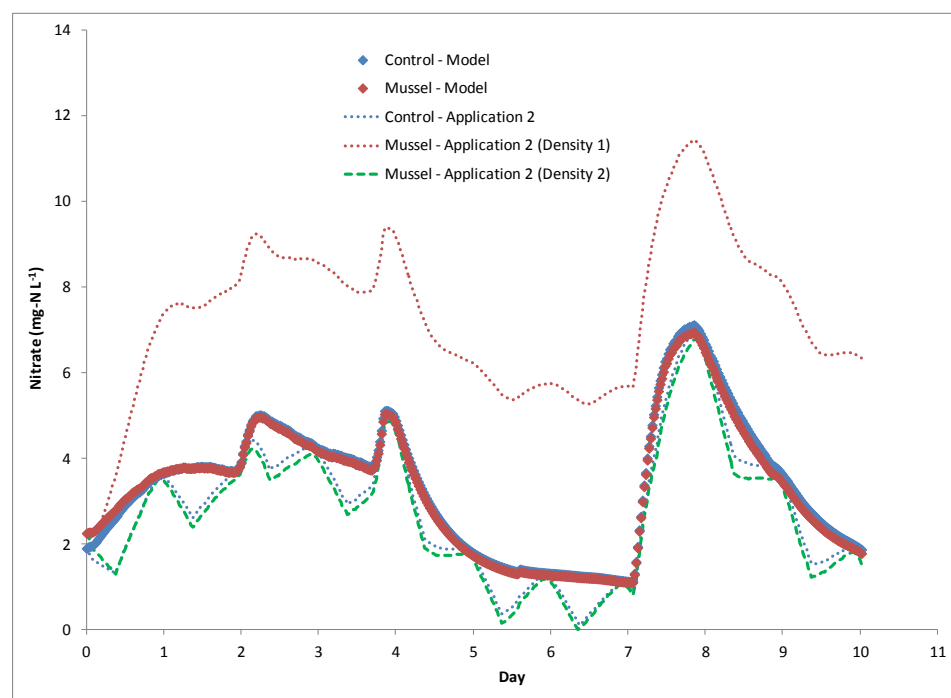


Figure 5.20: Nitrate (mg-N L⁻¹) results for control and mussel treatments with flow showing model outputs and Model Application 2 simulations.

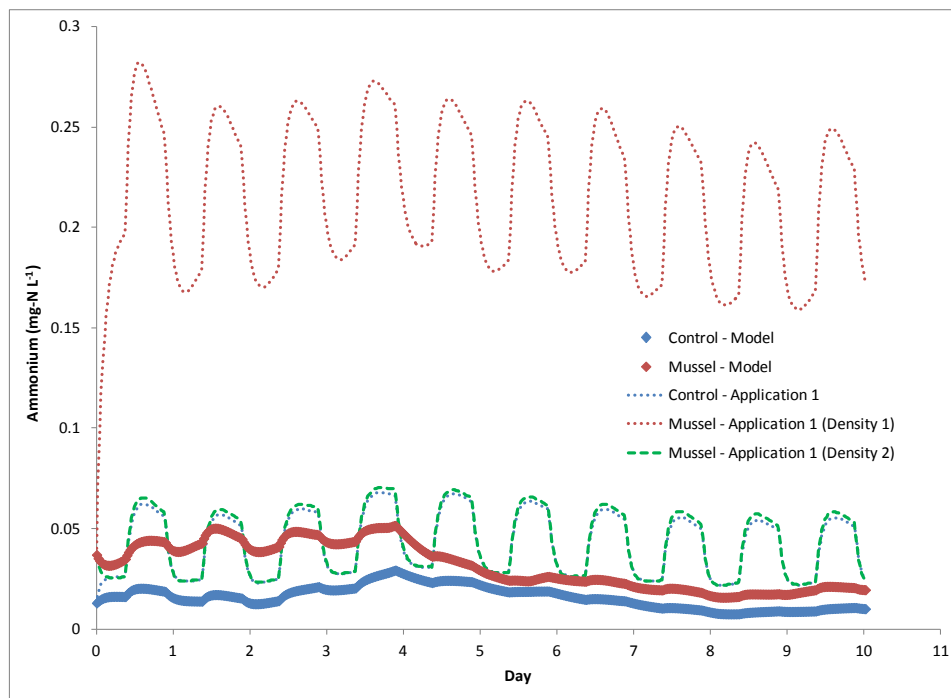


Figure 5.21: Ammonium (mg-N L⁻¹) results for control and mussel treatments with flow showing model outputs and Model Application 1 simulations.

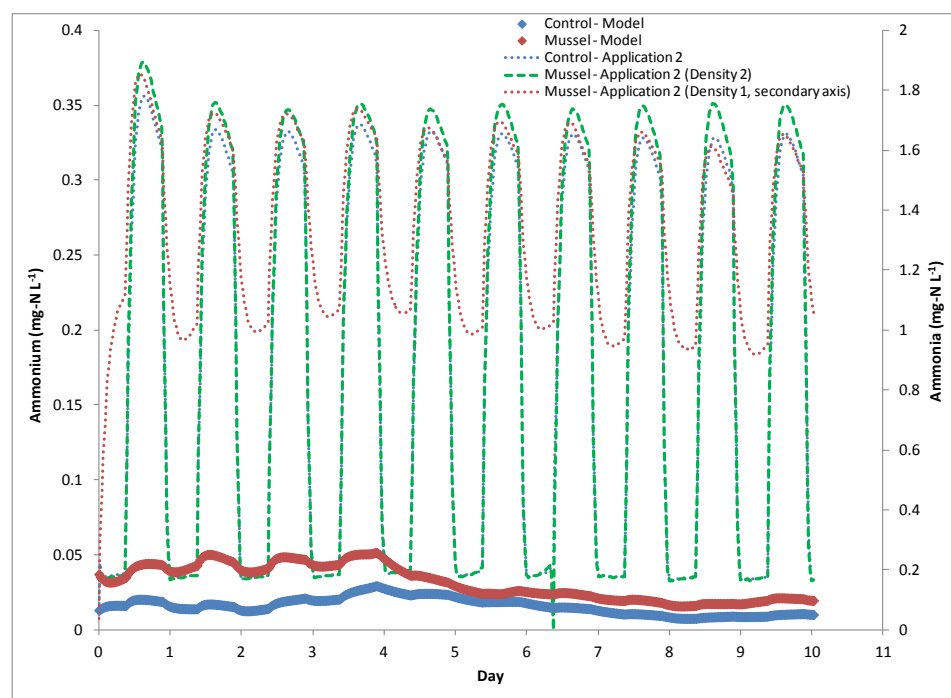


Figure 5.22: Ammonium (mg-N L⁻¹) results for control and mussel treatments with flow showing model outputs and Model Application 2 simulations.

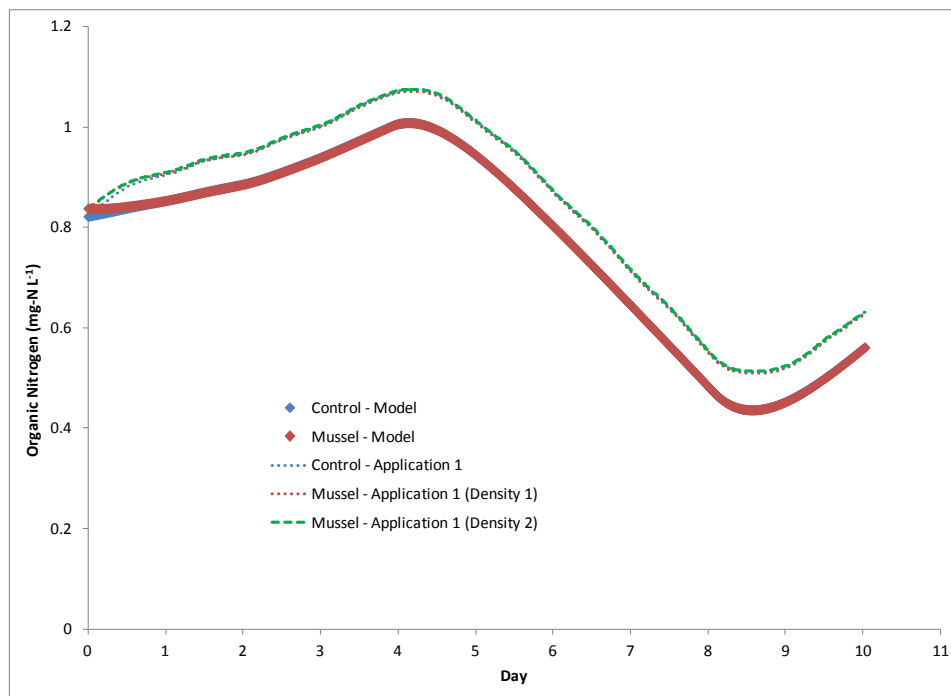


Figure 5.23: Organic nitrogen (mg-N L^{-1}) results for control and mussel treatments with flow showing model outputs and Model Application 1 simulations.

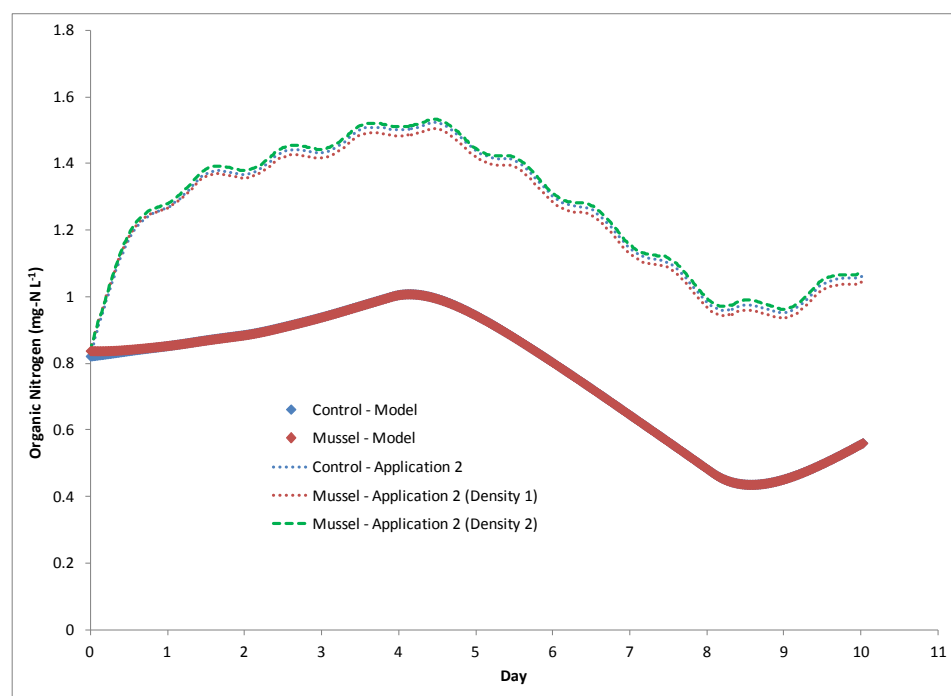


Figure 5.24: Organic nitrogen (mg-N L^{-1}) results for control and mussel treatments with flow showing model outputs and Model Application 2 simulations.

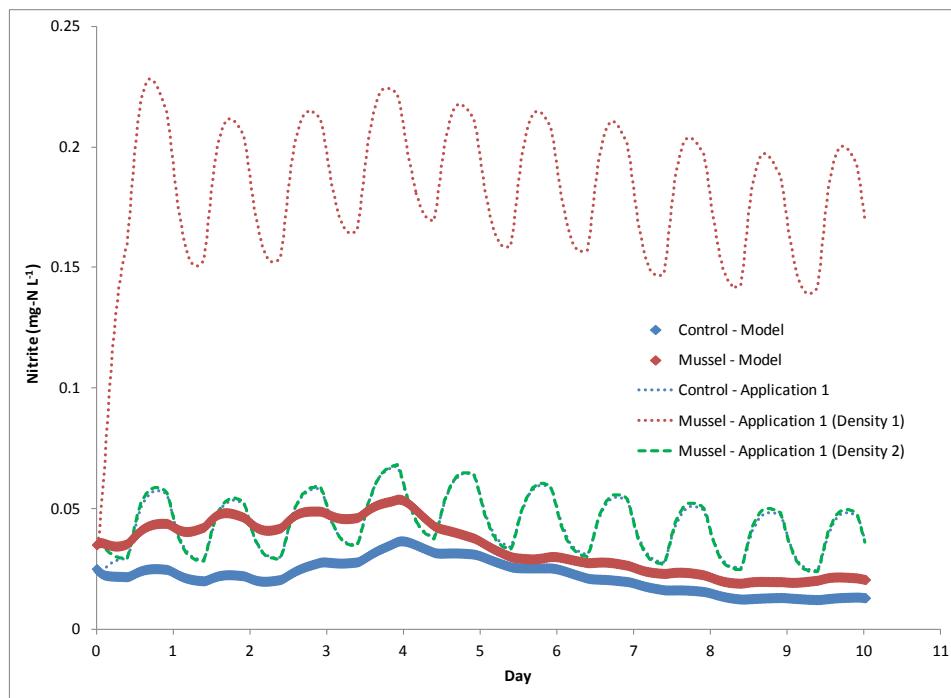


Figure 5.25: Nitrite (mg-N L⁻¹) results for control and mussel treatments with flow showing model outputs and Model Application 1 simulations.

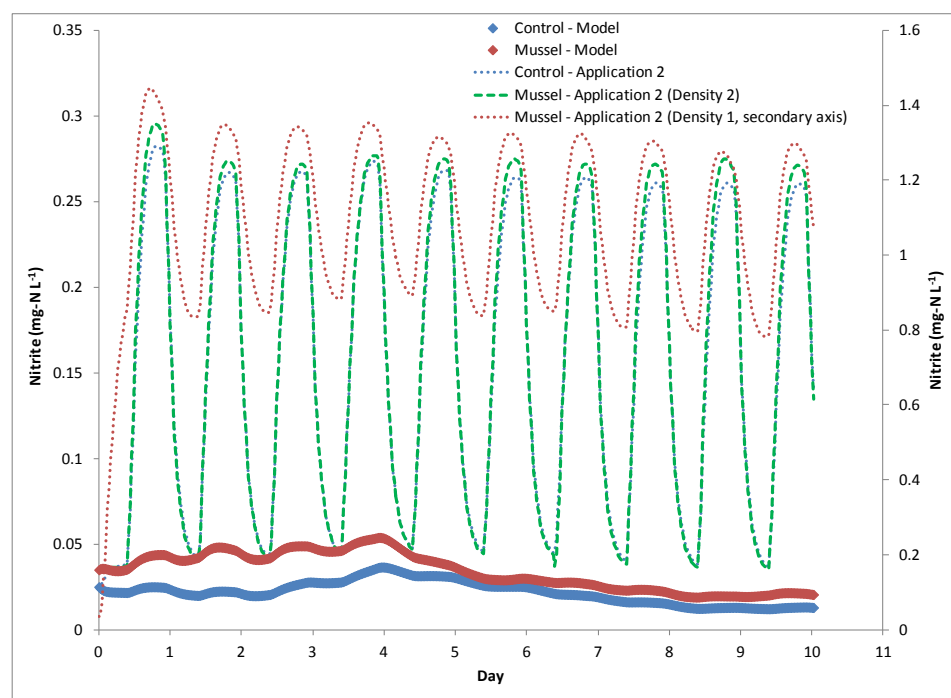


Figure 5.26: Nitrite (mg-N L⁻¹) results for control and mussel treatments with flow showing model outputs and Model Application 2 simulations.

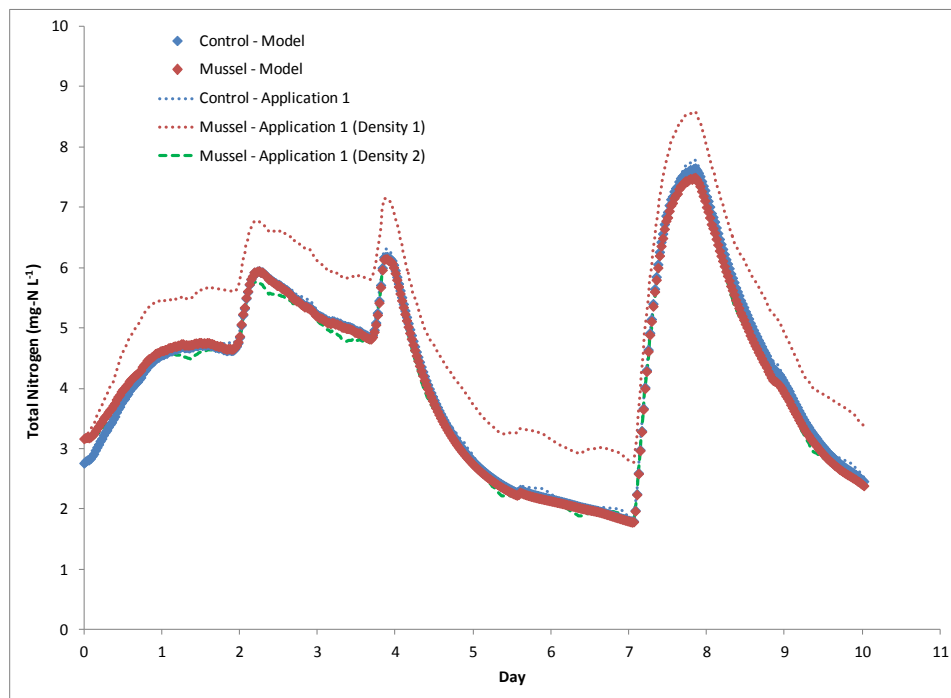


Figure 5.27: Total nitrogen (mg-N L⁻¹) results for control and mussel treatments with flow showing model outputs and Model Application 1 simulations.

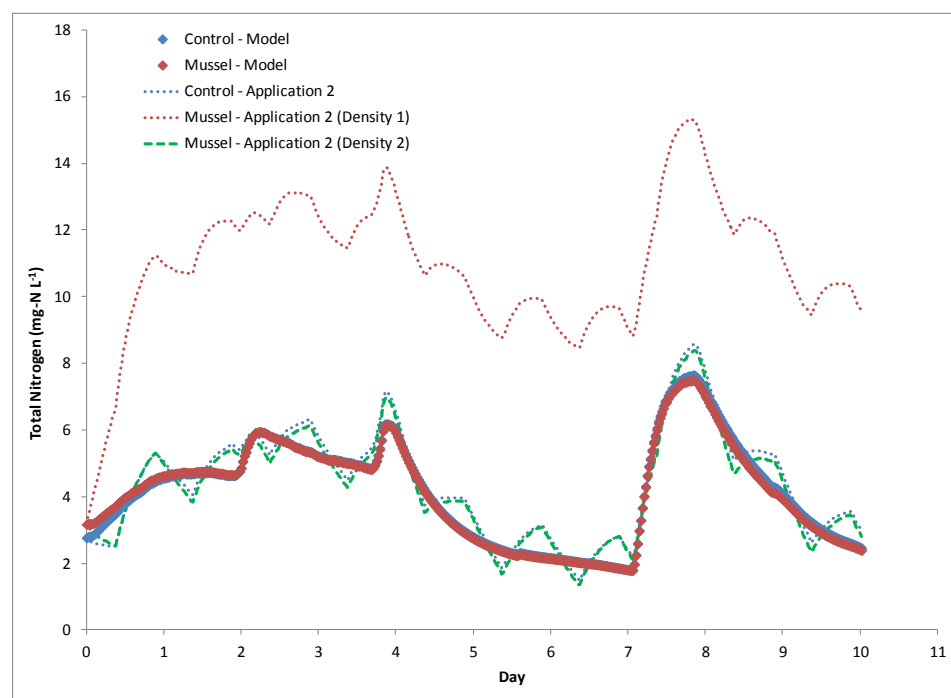


Figure 5.28: Total nitrogen (mg-N L⁻¹) results for control and mussel treatments with flow showing model outputs and Model Application 2 simulations.

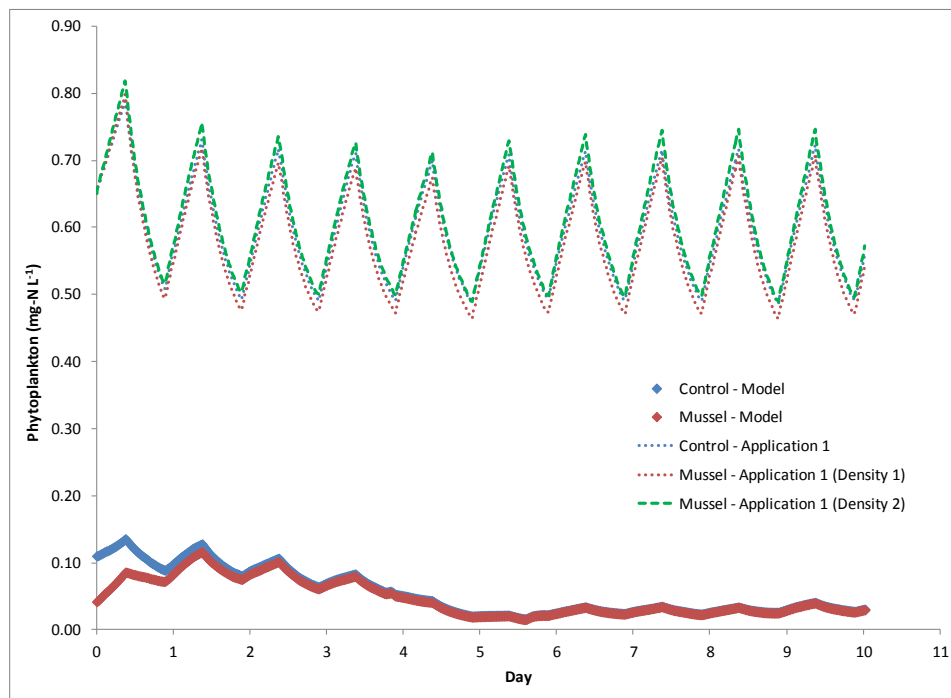


Figure 5.29: Phytoplankton (mg-N L^{-1}) results for control and mussel treatments with flow showing model outputs and Model Application 1 simulations.

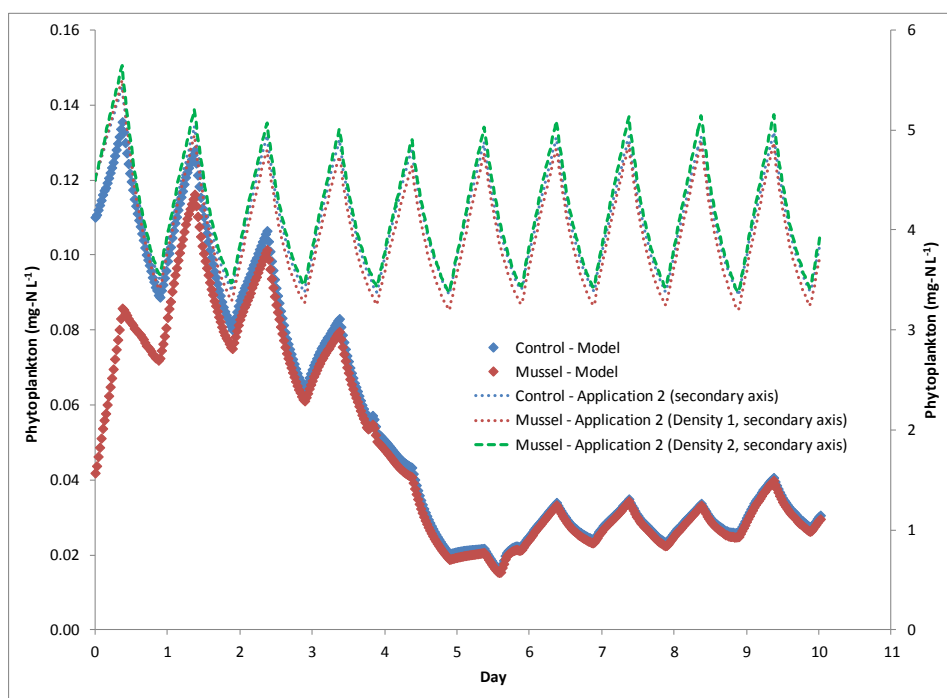


Figure 5.30: Phytoplankton (mg-N L^{-1}) results for control and mussel treatments with flow showing model outputs and Model Application 2 simulations.

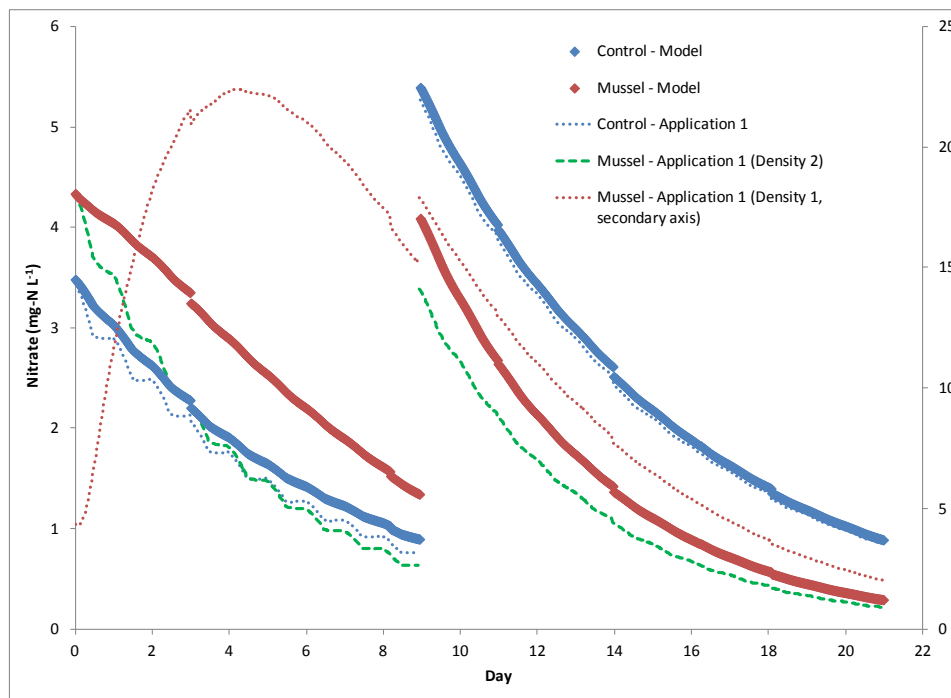


Figure 5.31: Nitrate (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 1 simulations.

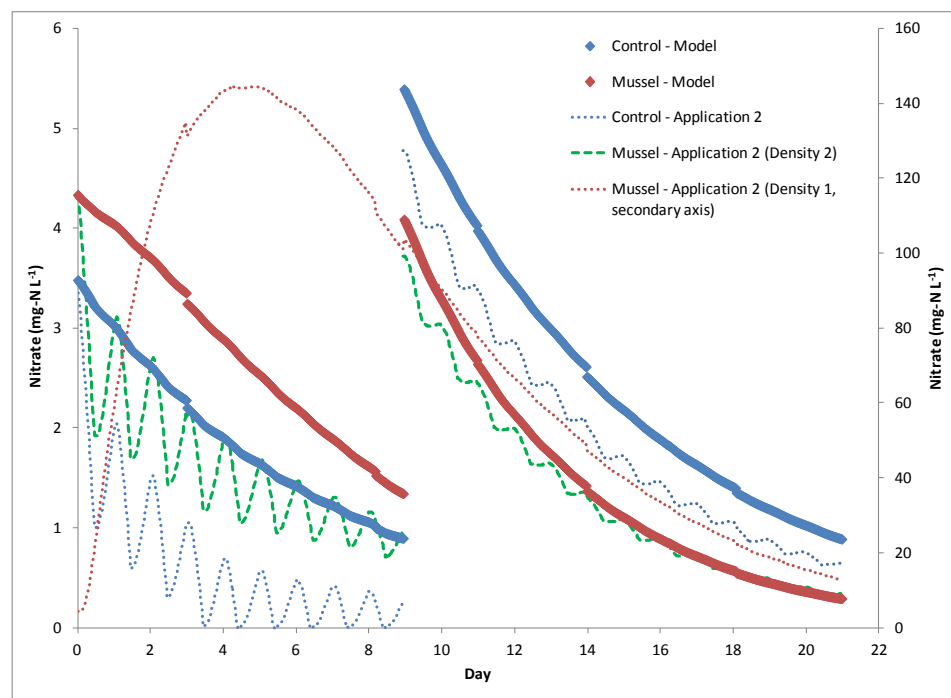


Figure 5.32: Nitrate (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 2 simulations.

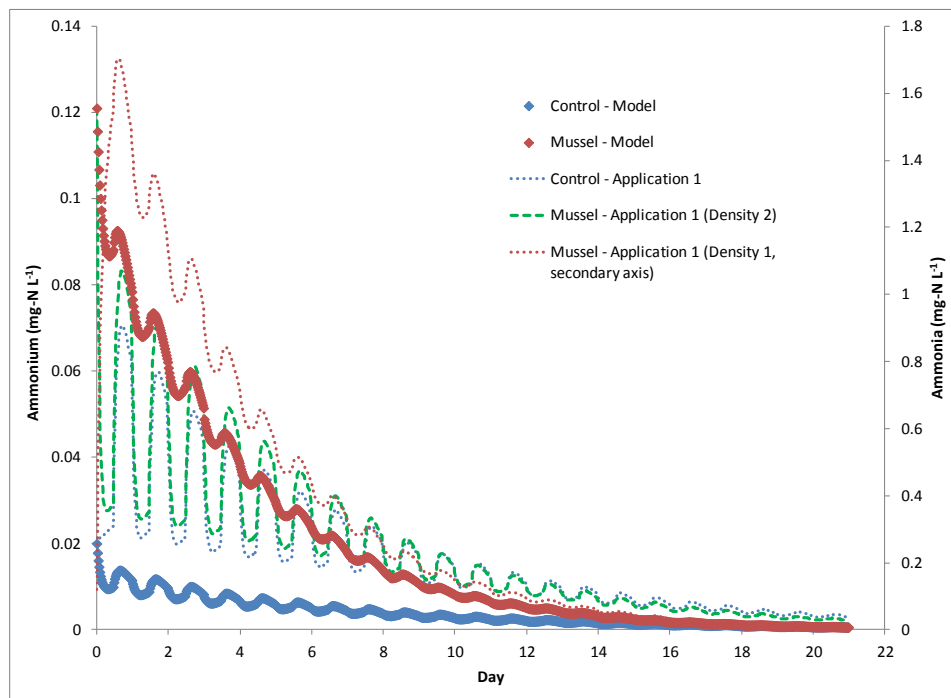


Figure 5.33: Ammonium (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 1 simulations.

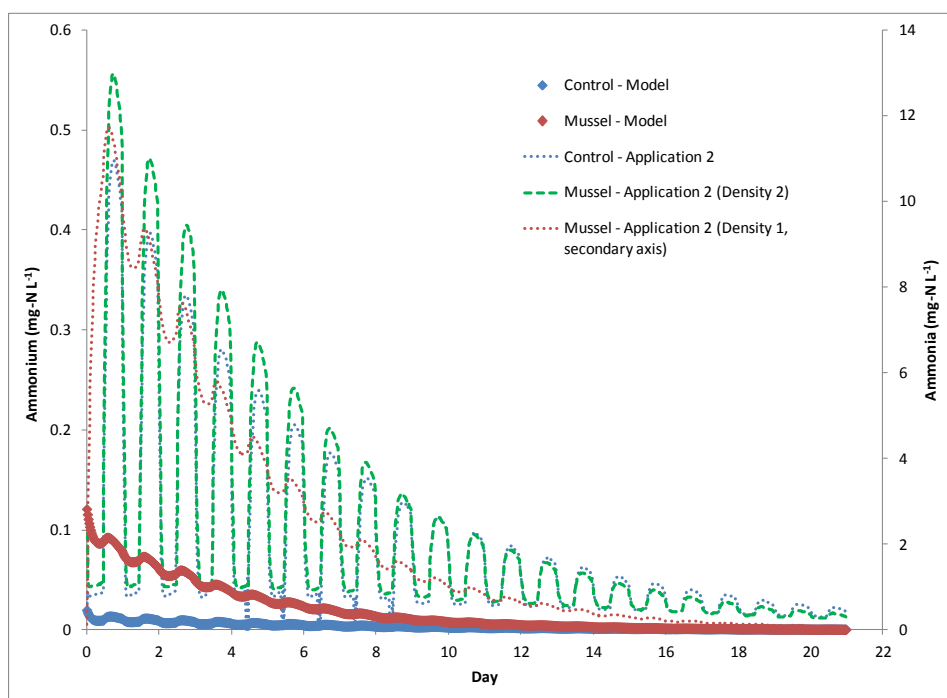


Figure 5.34: Ammonium (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 2 simulations.

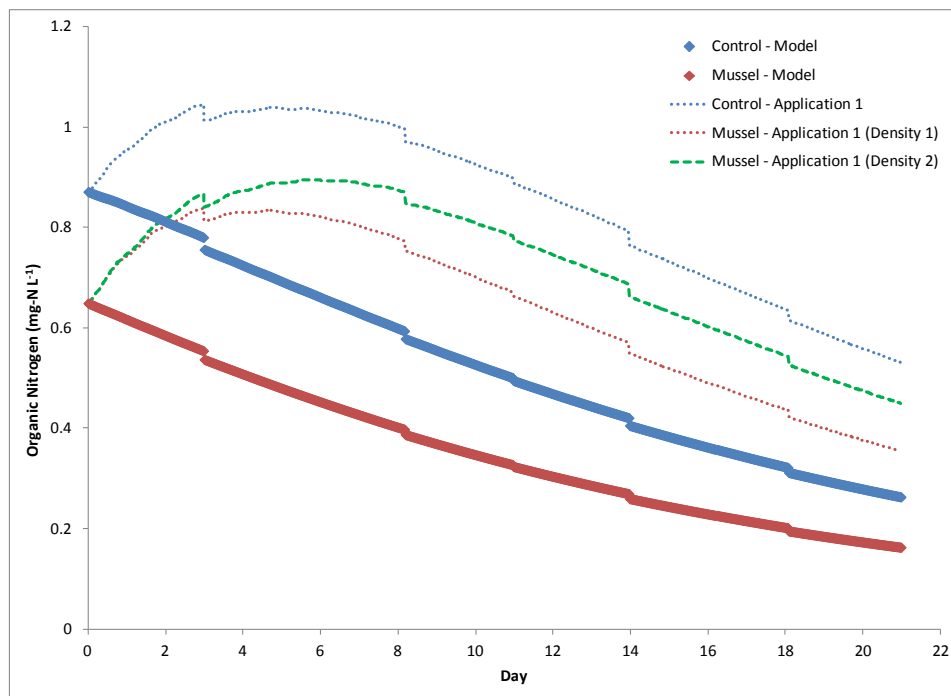


Figure 5.35: Organic nitrogen (mg-N L^{-1}) results for control and mussel treatments without flow showing model outputs and Model Application 1 simulations.

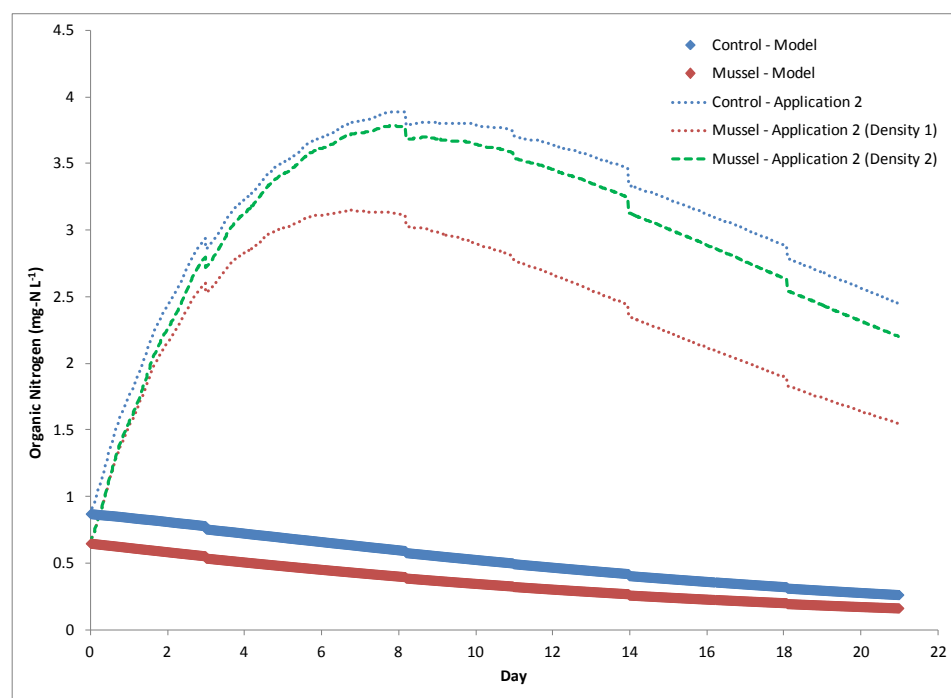


Figure 5.36: Organic nitrogen (mg-N L^{-1}) results for control and mussel treatments without flow showing model outputs and Model Application 2 simulations.

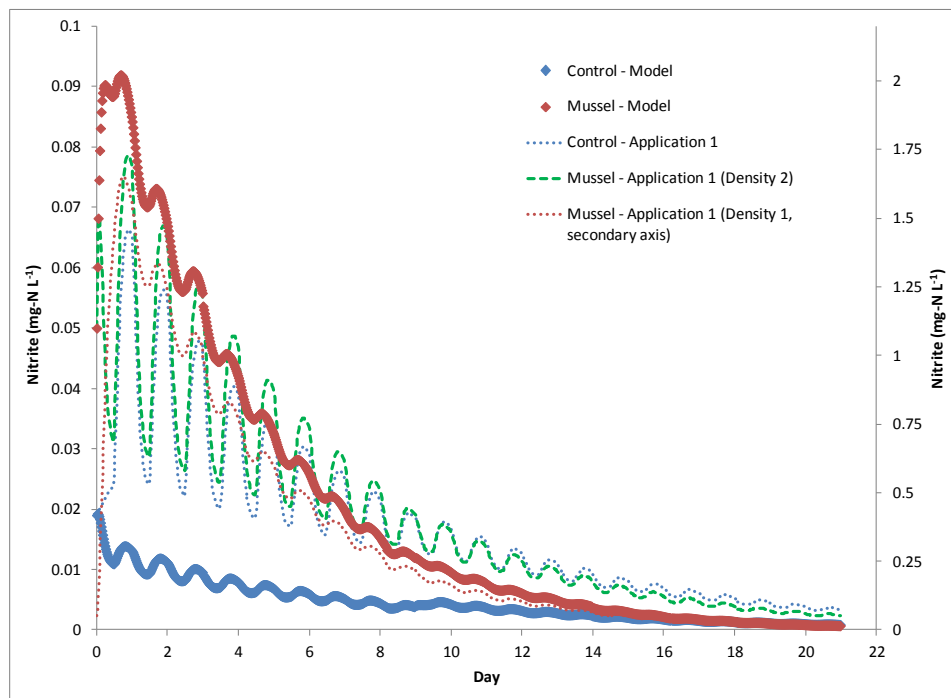


Figure 5.37: Nitrite (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 1 simulations.

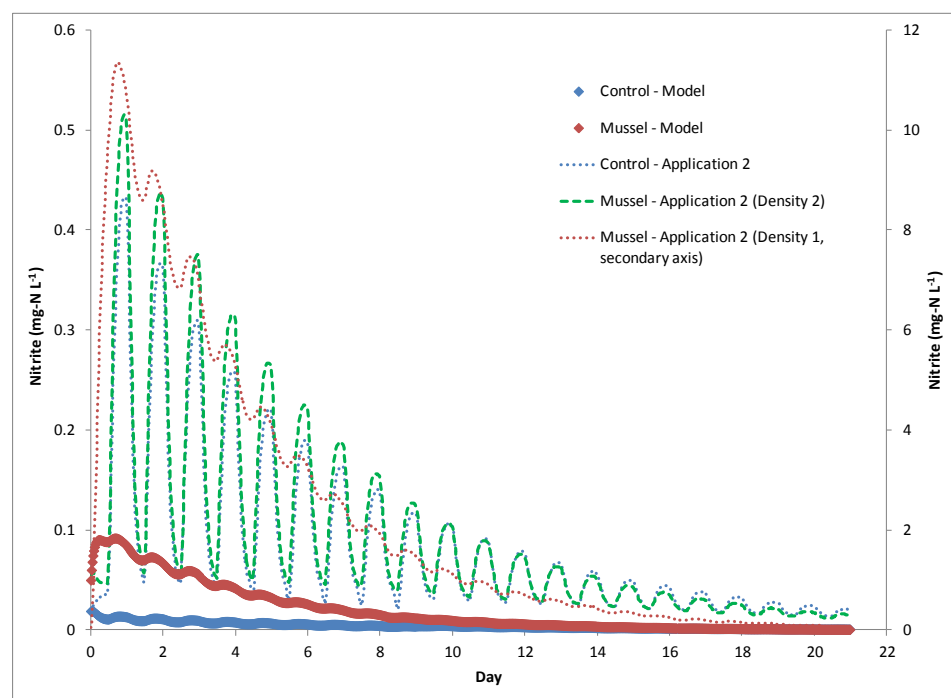


Figure 5.38: Nitrite (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 2 simulations.

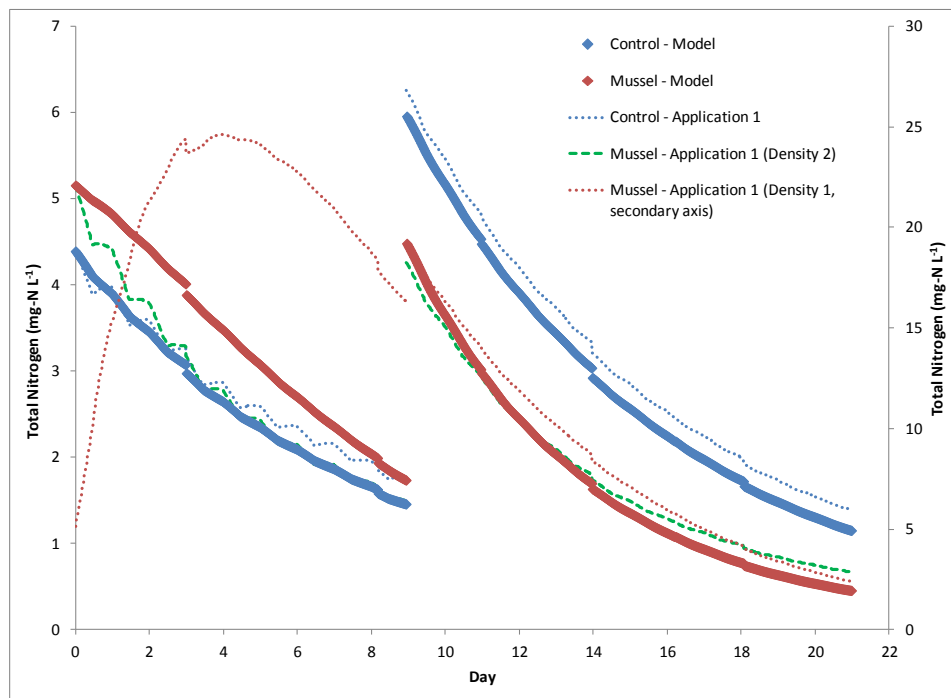


Figure 5.39: Total nitrogen (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 1 simulations.

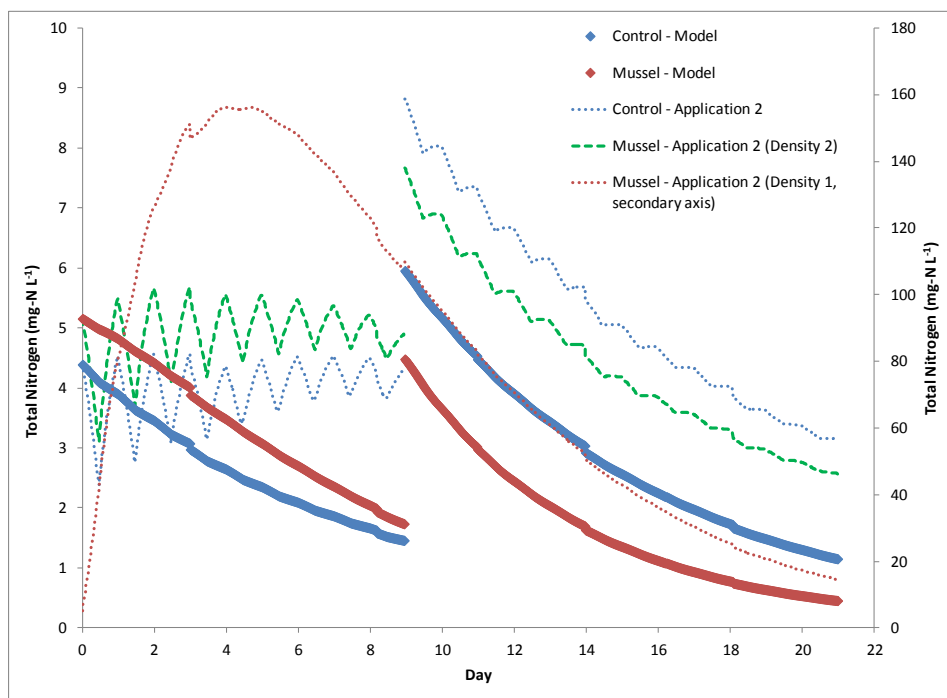


Figure 5.40: Total nitrogen (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 2 simulations.

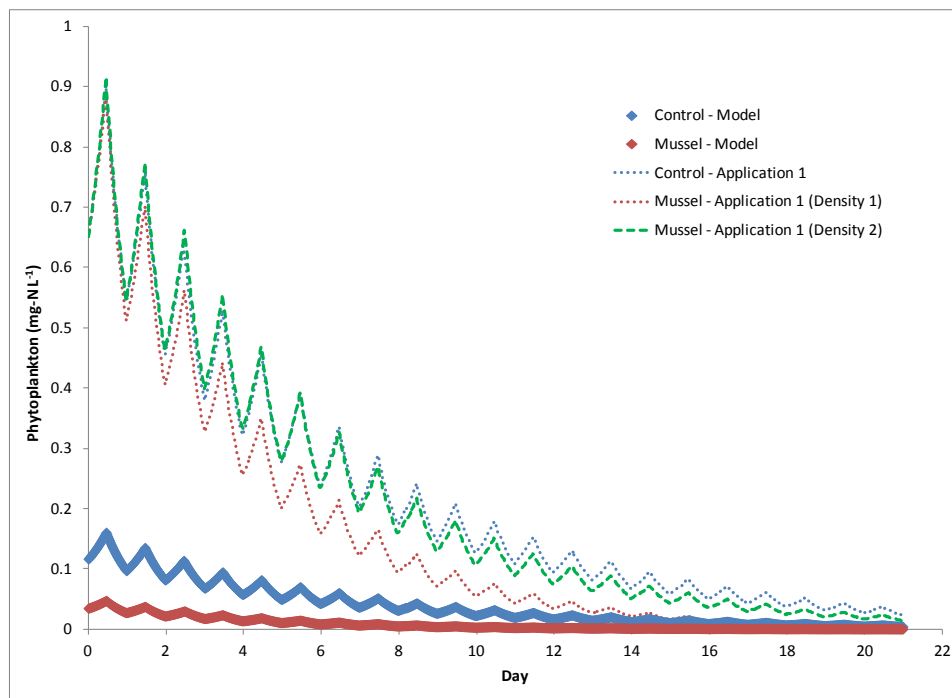


Figure 5.41: Phytoplankton (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 1 simulations.

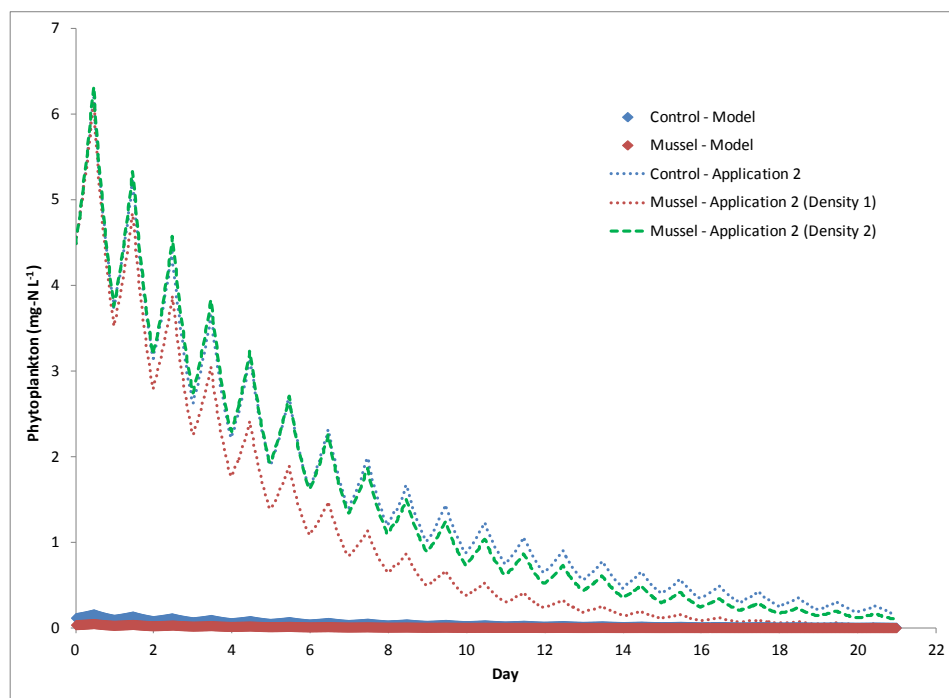


Figure 5.42: Phytoplankton (mg-N L⁻¹) results for control and mussel treatments without flow showing model outputs and Model Application 2 simulations.

CHAPTER 6

CONCLUSIONS AND FUTURE WORK

Summary of Findings

Hypothesis 1

Laboratory-based mesocosms containing native freshwater mussels exhibit increased concentrations of ammonium and nitrate and decreased concentrations of phytoplankton in the overlying water compared to mesocosms with no mussels.

The effects of native freshwater mussels on nitrate, ammonium, and phytoplankton in the overlying water were investigated using flow-through mesocosms fed with a continuous supply of untreated Iowa River water. Highly time resolved (30 min) water chemistry data and grab sample measurements were collected in mesocosms containing mussels and mesocosms without mussels. The flow-through mesocosms design was determined to sufficiently mimic natural conditions for temperature, photosynthetically active radiation, and phytoplankton composition and biomass.

Concentration changes for nitrate, ammonium, and phytoplankton were determined to be significantly different (ANCOVA, $p < 0.05$) between the mussel treatments and control treatments. Results from this study indicated that mussels affected the nitrogen cycle in the overlying water of the mesocosms by increasing ammonium concentrations through excretion, indirectly increasing nitrate concentrations via nitrification of the excreted ammonium, and decreasing phytoplankton concentrations via phytoplankton clearance. Mussels were also determined to increase nitrite and total nitrogen concentrations, but they demonstrated minimal impact on organic nitrogen. Increases in total nitrogen indicated mussels were adding more nitrogen (ammonium, nitrate, and nitrite) to the overlying water than they were removing (phytoplankton). The majority of nitrogen mass delivered to the overlying water by mussels was in the form of

ammonium and nitrate (nitrate mass was added via nitrification of the excreted ammonium).

Hypothesis 2

In laboratory-based mesocosms, the effect of native freshwater mussels on aquatic nitrogen dynamics is most sensitive to changes in flow, temperature, and light.

A deterministic mass balance model was developed to better understand the effects of mussels on nitrogen dynamics in the overlying water of laboratory mesocosms. The model was developed using STELLA modeling software and was calibrated with literature values and highly time resolved data and grab samples obtained from laboratory mesocosm experiments. The model simulated nitrate, ammonium, organic nitrogen, nitrite, total nitrogen, and phytoplankton concentrations in the overlying water of the mesocosms. The model correlated well with the experimental measurements and predicted that changes in nitrate and total nitrogen concentrations attributable to mussels were small relative to overall the concentrations present in the mesocosms. The models also predicted that mussels increased ammonium and nitrite, decreased phytoplankton, and did not significantly affect organic nitrogen.

Sensitivity analyses identified hydraulic retention time (flow), temperature, denitrification rate, and mussel ammonium excretion rate as the most influential variables in mesocosms containing mussels. Changes in light intensity did not significantly influence the effect of mussels on nitrogen dynamics in the mesocosms. The sensitivity analyses also demonstrated the difficulty in modeling the dynamic nature of the mesocosms and emphasized the need to constrain the model variables with observed experimental measurements. Application of the model predicted that increases in phytoplankton concentrations significantly influenced the effect of mussels on nitrogen dynamics in the overlying water of the mesocosms.

Conclusions

Many studies evaluating the functional roles of mussels have been conducted in small systems with high hydraulic retention times, and re-circulating mesocosms have been used to obtain more precise estimates of mussel effects at shorter time scales. To our knowledge, this is the first study to couple the continuous input of untreated river water in flow-through mesocosms with highly time resolved water chemistry data to assess the effects of mussels on nitrogen dynamics. Coupling the results of these mesocosm experiments with a deterministic mass balance model allowed us to identify the most significant environmental conditions and processing rates that would affect the scalability of the observed mussel effects to rivers and streams.

Given the significant influence of nitrate on Gulf of Mexico hypoxia, the effects of mussels on nitrate concentrations are especially important. The results of this study indicated that mussels demonstrated statistically significant increases in nitrate concentrations, but these differences were small in comparison to the overall nitrate concentrations present in the mesocosms. However, model simulations revealed that when phytoplankton concentrations increase in areas of high mussel populations, mussels demonstrate substantial increases in nitrate concentrations in the overlying water. These phenomena require further investigation, but the results reveal the importance of including the effects of mussels on aquatic nitrogen dynamics in the development of strategies for nitrogen management.

Future Research

The results obtained from this study provide opportunities for several future research areas. The models could be used to simulate the effects of mussels on nitrogen dynamics for various scenarios. For example, the model could be used to evaluate how historic populations of mussels and pre-settlement land use influenced nitrogen dynamics and how this compared to present-day observations. The models could also be used to

explore how the diurnal behaviors of mussels and ecosystem perturbations (e.g. changes in temperature) affect the ability of mussels to process nitrogen.

Research could also be done to improve model performance. Obtaining experimental measurements for first-order reaction rates in the mesocosms (e.g. denitrification rate) would help increase the robustness of the model. Improvements could also be made to the model by using measurements from field-scale experiments for model calibration. Comparing the nitrogen dynamics in a known mussel bed to a segment of a river or stream that does not contain mussels would further improve the scalability of observed mussel effects. The results of our study could help to inform the development of these experiments by identifying the most important measurements needed to assess the effect of mussels on nitrogen dynamics. This is especially important given the financial limitations to measuring highly time resolved data in the field.

Improving model performance and scalability of the mussel effects would provide opportunities for placing an economic value on the ecosystem services provided by mussels. For example, our study demonstrated that under certain conditions, mussel-facilitated changes in nitrate concentrations were minimal relative to overall nitrate concentrations, but mussels were still able to remove significant amounts of phytoplankton. Thus, research could be done to investigate how mussels decrease the adverse effects of high phytoplankton populations (e.g. decreased oxygen concentrations, cyanobacteria blooms) without increasing problems associated with nitrogen cycle management. This would be especially valuable for river managers and policy makers attempting to develop ecologically based restoration strategies.

APPENDIX A:
SENSOR SPECIFICATIONS

Table A.1: Measurement method, range, and accuracy for Hydrolab, Nitratax plus sc, Apogee, and LiCor sensors used in this study.

Sensor	Parameter	Measurement Method	Range	Accuracy
Hydrolab Multi- Probe Sonde	pH	Potassium chloride (KCl) impregnated glass bulb is permeable to hydrogen ions; reference filled with 3M KCl and has a porous Teflon junction. Salt bridge is formed between the two, and a potential is measured.	0 to 14 pH units	± 0.02 pH units
	Temperature	The Hydrolab temperature sensor is a 30k ohm variable resistance thermistor.	(-)5 to 50 °C	± 0.1 °C
	Conductivity	The probe measures the current between 2 electrodes held at a fixed potential.	0 to 100 mS cm ⁻¹	± 0.05%
	Dissolved Oxygen	Luminescent dissolved oxygen (LDO) technology. Oxygen reactive luminophor is excited by blue light from an LED. The resulting emission from the luminophor is translated to a dissolved oxygen reading via a photodiode.	0 to 60 mg L ⁻¹	± 0.1 mg L ⁻¹ at <8 mg L ⁻¹ ± 0.2 mg L ⁻¹ at >8 mg L ⁻¹ ± 10% reading >20 mg L ⁻¹
	Chlorophyll <i>a</i>	Compact fluorometer with an excitation wavelength of 460 nanometer and emission wavelength of 685 nanometer.	0.03 to 500 µg L ⁻¹	± 3%
	Nitrate	An ion selective electrode is a reference electrode immersed in a solution of fixed ion concentration separated by a membrane containing a chemical compound that reacts with the ion of interest, measuring electrical potential that varies with concentration.	0 to 100 mg-N L ⁻¹	Greater of ± 5% of reading, Or ± 2 mg-N L ⁻¹
	Ammonium	Two beam UV adsorption technology with a one millimeter path length. A 210 nanometer wavelength beam is used to measure absorbance, and a 355 nanometer wavelength beam is used to filter out other ionic influences on the generated signal.	0 to 100 mg-N L ⁻¹	Greater of ± 5% of reading, Or ± 2 mg-N L ⁻¹
Nitratax plus sc	Nitrate	Two beam UV adsorption technology with a one millimeter path length. A 210 nanometer wavelength beam is used to measure absorbance, and a 355 nanometer wavelength beam is used to filter out other ionic influences on the generated signal.	0.1 to 100 mg-N L ⁻¹	Greater of ± 3% of reading, Or ± 0.5 mg-N L ⁻¹
Apogee	PAR	A filtered photodiode to produce a voltage calibrated to incident radiation within the photosynthetically active range.	400 to 650 nm	± 5%
LiCor	PAR	A filtered photodiode to produce a voltage calibrated to incident radiation within the photosynthetically active range.	400 to 700 nm	± 5%

Source: Durst 2012

APPENDIX B:
WATER CHEMISTRY DATA

Table B.1: Average nitrate and ammonium results (mg-N L^{-1}) in the pore water of the mesocosms used in the experiment in Chapter 4 with standard deviations shown in parentheses.

Day	Nitrate (mg-N L^{-1})		Ammonium (mg-N L^{-1})	
	Control	Mussel	Control	Mussel
0.2	0.47 (0.00)	0.31 (0.06)	1.69 (0.18)	2.00 (0.00)
0.3	0.56 (0.25)	0.36 (0.06)	0.77 (0.84)	1.25 (1.06)
0.6	0.28 (0.02)	0.37 (0.10)	1.13 (0.40)	2.98 (0.37)
1.2	0.27 (0.06)	0.24 (0.09)	1.14 (0.06)	2.19 (0.44)
1.3	0.17 (0.12)	0.63 (0.07)	1.08 (0.13)	2.60 (0.40)
1.6	0.48 (0.27)	0.30 (0.01)	0.66 (0.48)	1.47 (1.41)
2.2	0.21 (0.09)	0.20 (0.04)	1.06 (0.04)	3.26 (0.03)
2.3	0.11 (0.00)	0.43 (0.29)	1.02 (0.09)	3.20 (0.06)
2.6	0.21 (0.06)	0.23 (0.01)	0.87 (0.37)	3.08 (0.19)
3.2	0.23 (0.10)	0.30 (0.11)	1.38 (0.29)	2.65 (0.69)
3.3	0.23 (0.02)	0.23 (0.02)	1.80 (1.00)	2.32 (1.29)
3.6	0.32 (0.01)	0.53 (0.05)	0.99 (0.17)	2.01 (0.12)
4.2	0.44 (0.20)	0.53 (0.19)	1.09 (0.26)	2.67 (0.74)
4.3	0.25 (0.04)	0.27 (0.01)	1.13 (0.39)	3.27 (0.02)
4.6	0.25 (0.08)	0.45 (0.21)	1.04 (0.09)	2.64 (0.43)
5.2	0.42 (0.06)	0.48 (0.01)	0.94 (0.14)	3.00 (0.20)
5.3	0.42 (0.23)	0.58 (0.14)	0.67 (0.26)	2.60 (0.04)
5.6	0.32 (0.08)	0.42 (0.08)	0.79 (0.05)	3.23 (0.00)
6.2	0.34 (0.12)	0.46 (0.06)	0.93 (0.15)	2.59 (0.55)
6.3	0.36 (0.22)	0.49 (0.06)	0.88 (0.09)	2.54 (0.44)
6.6	0.33 (0.002)	0.64 (0.41)	0.49 (0.16)	1.70 (1.68)

Table B.2: Average nitrate and ammonium results (mg-N L^{-1}) in the pore water of the flow-through and no flow mesocosms used in the experiments in Chapter 5 with standard deviations shown in parentheses.

Mesocosm	Day	Nitrate (mg-N L^{-1})		Ammonium (mg-N L^{-1})	
		Control	Mussel	Control	Mussel
Flow	0.1	0.24 (0.11)	0.59 (0.50)	0.84 (0.05)	3.01 (0.20)
	1.9	0.65 (0.63)	0.70 (0.67)	0.88 (0.02)	3.02 (0.24)
	3.9	0.65 (0.02)	0.45 (0.10)	0.97 (0.01)	3.17 (0.02)
	8.1	0.42 (0.05)	0.55 (0.001)	0.55 (0.07)	3.17 (0.01)
	10.0	0.46 (0.26)	0.34 (0.01)	0.65 (0.004)	3.03 (0.20)
No Flow	0.2	0.27 (0.19)	0.52 (0)	0.66 (0.40)	1.66 (0)
	3.0	0.23 (0.08)	0.50 (0.10)	0.42 (0.22)	3.18 (0.02)
	8.2	0.22 (0.06)	0.38 (0.23)	0.72 (0.54)	3.17 (0.05)
	14.1	0.20 (0.06)	0.30 (0.08)	0.44 (0.15)	3.16 (0.01)
	18.0	0.25 (0.15)	0.35 (0.14)	0.64 (0.57)	3.20 (0.01)

APPENDIX C:
STELLA MODEL INPUTS

Table C.1: STELLA model inputs for control and mussel treatments with flow.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
0.00	23.55	24.68	0.83	0.88	0.086	0.069	3.02	0.865	0.046
0.02	23.68	24.3	0.83	0.88	0.108	0.069	2.66	0.865	0.046
0.04	23.81	24.46	0.83	0.88	0.107	0.069	2.28	0.865	0.046
0.06	23.93	24.6	0.83	0.88	0.109	0.069	2.89	0.865	0.046
0.08	24.05	24.72	0.83	0.88	0.115	0.069	3.45	0.866	0.046
0.10	24.17	24.85	0.83	0.88	0.104	0.068	3.36	0.866	0.046
0.12	24.29	24.99	0.83	0.88	0.089	0.068	4.18	0.867	0.046
0.15	24.42	25.11	0.83	0.88	0.110	0.068	3.97	0.868	0.046
0.17	24.53	25.24	0.83	0.88	0.110	0.067	3.91	0.869	0.046
0.19	24.65	25.34	0.83	0.88	0.113	0.067	4.27	0.870	0.046
0.21	24.76	25.45	0.83	0.88	0.113	0.067	3.78	0.870	0.046
0.23	24.86	25.57	0.83	0.88	0.114	0.066	4.49	0.871	0.046
0.25	24.97	25.67	0.83	0.88	0.126	0.066	4.09	0.872	0.046
0.27	25.07	25.77	0.83	0.88	0.122	0.066	3.73	0.873	0.046
0.29	25.17	25.86	0.83	0.88	0.124	0.066	4.50	0.873	0.046
0.31	25.26	25.95	0.83	0.88	0.129	0.065	4.16	0.874	0.046
0.33	25.35	26.03	0.83	0.88	0.138	0.065	3.91	0.875	0.046
0.35	25.43	26.1	0.83	0.88	0.133	0.065	4.60	0.876	0.046
0.37	25.47	26.13	0	0	0.139	0.064	4.19	0.876	0.046
0.40	25.37	26.03	0	0	0.127	0.064	5.09	0.877	0.046
0.42	25.24	25.86	0	0	0.126	0.064	4.66	0.878	0.046
0.44	25.13	25.69	0	0	0.118	0.063	4.17	0.879	0.046
0.46	25.01	25.54	0	0	0.122	0.063	4.99	0.879	0.046
0.48	24.91	25.41	0	0	0.129	0.063	4.44	0.880	0.046
0.50	24.82	25.27	0	0	0.125	0.062	3.93	0.881	0.046
0.52	24.73	25.15	0	0	0.112	0.062	4.71	0.882	0.046
0.54	24.64	25.03	0	0	0.129	0.062	4.23	0.882	0.046
0.56	24.57	24.93	0	0	0.119	0.062	5.02	0.883	0.046
0.58	24.5	24.83	0	0	0.123	0.061	4.44	0.884	0.046
0.60	24.42	24.73	0	0	0.124	0.061	4.04	0.885	0.046
0.62	24.36	24.65	0	0	0.113	0.061	4.67	0.885	0.046
0.65	24.3	24.56	0	0	0.116	0.060	4.25	0.886	0.046
0.67	24.24	24.48	0	0	0.103	0.060	4.03	0.887	0.046

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
0.69	24.18	24.41	0	0	0.103	0.060	4.68	0.888	0.046
0.71	24.13	24.34	0	0	0.118	0.059	4.46	0.888	0.046
0.73	24.08	24.27	0	0	0.113	0.059	5.49	0.889	0.046
0.75	24.03	24.2	0	0	0.108	0.059	4.86	0.890	0.046
0.77	23.98	24.14	0	0	0.099	0.058	4.48	0.891	0.046
0.79	23.94	24.08	0	0	0.114	0.058	5.36	0.891	0.046
0.81	23.9	24.03	0	0	0.102	0.058	4.66	0.892	0.046
0.83	23.88	23.99	0	0	0.120	0.057	4.01	0.893	0.046
0.85	23.85	23.94	0	0	0.104	0.057	4.81	0.894	0.046
0.87	23.82	23.94	0.05	0.2	0.122	0.057	4.37	0.894	0.046
0.90	24	24.17	0.83	0.87	0.111	0.057	5.13	0.895	0.046
0.92	24.17	24.39	0.83	0.87	0.102	0.056	4.43	0.896	0.046
0.94	24.33	24.57	0.83	0.87	0.112	0.056	4.18	0.897	0.046
0.96	24.47	24.74	0.83	0.87	0.118	0.056	4.87	0.897	0.046
0.98	24.61	24.89	0.83	0.87	0.138	0.055	4.36	0.898	0.046
1.00	24.73	25.04	0.83	0.87	0.124	0.055	4.12	0.899	0.046
1.02	24.85	25.17	0.83	0.87	0.111	0.055	4.65	0.900	0.046
1.04	24.96	25.3	0.83	0.87	0.138	0.054	4.12	0.901	0.046
1.06	25.07	25.42	0.83	0.87	0.121	0.054	4.97	0.901	0.046
1.08	25.16	25.53	0.83	0.87	0.124	0.054	4.42	0.902	0.046
1.10	25.25	25.59	0.83	0.87	0.112	0.053	4.04	0.903	0.046
1.12	25.33	25.65	0.83	0.87	0.121	0.053	4.80	0.904	0.046
1.15	25.39	25.69	0.83	0.87	0.118	0.053	4.46	0.904	0.046
1.17	25.44	25.73	0.83	0.87	0.116	0.053	4.03	0.905	0.046
1.19	25.5	25.77	0.83	0.86	0.113	0.052	4.74	0.906	0.046
1.21	25.54	25.8	0.83	0.86	0.123	0.052	4.18	0.907	0.046
1.23	25.59	25.84	0.83	0.86	0.122	0.052	4.94	0.907	0.046
1.25	25.64	25.88	0.83	0.86	0.108	0.051	4.22	0.908	0.046
1.27	25.69	25.91	0.83	0.86	0.102	0.051	3.48	0.909	0.046
1.29	25.73	25.95	0.83	0.86	0.101	0.051	4.40	0.910	0.046
1.31	25.76	25.97	0.83	0.86	0.104	0.050	4.01	0.910	0.046
1.33	25.8	26	0.83	0.86	0.103	0.050	4.22	0.911	0.046
1.35	25.84	26.03	0.83	0.86	0.103	0.050	4.45	0.912	0.046
1.37	25.83	26.02	0	0	0.104	0.049	3.98	0.913	0.046
1.40	25.69	25.85	0	0	0.104	0.049	4.73	0.913	0.046
1.42	25.54	25.63	0	0	0.104	0.049	4.28	0.914	0.046
1.44	25.39	25.42	0	0	0.101	0.048	3.85	0.915	0.046
1.46	25.25	25.23	0	0	0.098	0.048	4.55	0.916	0.046

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
1.48	25.12	25.05	0	0	0.111	0.048	4.09	0.916	0.046
1.50	25	24.88	0	0	0.107	0.048	3.60	0.917	0.046
1.52	24.88	24.72	0	0	0.107	0.047	4.35	0.918	0.046
1.54	24.78	24.57	0	0	0.103	0.047	3.84	0.919	0.046
1.56	24.69	24.44	0	0	0.096	0.047	4.38	0.919	0.046
1.58	24.59	24.31	0	0	0.098	0.046	4.02	0.920	0.046
1.60	24.49	24.18	0	0	0.106	0.046	3.60	0.921	0.046
1.62	24.4	24.06	0	0	0.097	0.046	3.96	0.922	0.046
1.65	24.33	23.96	0	0	0.105	0.045	3.67	0.922	0.046
1.67	24.26	23.86	0	0	0.098	0.045	3.42	0.923	0.046
1.69	24.19	23.77	0	0	0.093	0.045	3.98	0.924	0.046
1.71	24.12	23.68	0	0	0.099	0.044	3.56	0.925	0.046
1.73	24.06	23.6	0	0	0.091	0.044	4.26	0.925	0.046
1.75	23.99	23.52	0	0	0.095	0.044	3.60	0.926	0.046
1.77	23.93	23.44	0	0	0.101	0.044	3.17	0.927	0.046
1.79	23.89	23.38	0	0	0.104	0.043	3.92	0.928	0.046
1.81	23.85	23.32	0	0	0.110	0.043	3.45	0.928	0.046
1.83	23.81	23.27	0	0	0.099	0.043	4.28	0.929	0.046
1.85	23.75	23.21	0	0	0.098	0.042	3.95	0.930	0.046
1.87	23.73	23.2	0.05	0.2	0.094	0.042	3.64	0.931	0.046
1.90	23.89	23.42	0.83	0.86	0.100	0.042	4.19	0.932	0.046
1.92	24	23.6	0.83	0.86	0.100	0.041	4.80	0.932	0.046
1.94	24.15	23.8	0.83	0.86	0.100	0.041	5.40	0.933	0.046
1.96	24.33	24.02	0.83	0.86	0.100	0.042	5.96	0.935	0.046
1.98	24.45	24.19	0.83	0.86	0.098	0.043	7.35	0.936	0.046
2.00	24.58	24.34	0.83	0.86	0.087	0.044	10.91	0.938	0.047
2.02	24.7	24.48	0.83	0.86	0.083	0.045	10.18	0.939	0.047
2.04	24.79	24.61	0.83	0.86	0.087	0.046	8.35	0.941	0.047
2.06	24.88	24.73	0.83	0.86	0.074	0.047	10.30	0.943	0.047
2.08	24.97	24.83	0.83	0.86	0.087	0.048	8.59	0.944	0.048
2.10	25.05	24.93	0.83	0.86	0.081	0.049	9.11	0.946	0.048
2.12	25.13	25.02	0.83	0.86	0.083	0.050	8.15	0.947	0.048
2.15	25.19	25.11	0.83	0.86	0.099	0.051	6.96	0.949	0.048
2.17	25.26	25.18	0.83	0.86	0.084	0.052	7.60	0.951	0.049
2.19	25.32	25.26	0.83	0.86	0.088	0.053	5.45	0.952	0.049
2.21	25.39	25.34	0.83	0.86	0.077	0.054	6.06	0.954	0.049
2.23	25.45	25.41	0.83	0.86	0.092	0.055	5.69	0.956	0.049
2.25	25.5	25.47	0.83	0.86	0.089	0.056	4.80	0.957	0.050

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
2.27	25.56	25.53	0.83	0.86	0.085	0.057	5.53	0.959	0.050
2.29	25.61	25.59	0.83	0.86	0.089	0.058	4.60	0.960	0.050
2.31	25.65	25.64	0.83	0.86	0.085	0.059	4.62	0.962	0.050
2.33	25.69	25.68	0.83	0.86	0.091	0.060	4.46	0.964	0.050
2.35	25.72	25.71	0.83	0.86	0.083	0.061	4.17	0.965	0.051
2.37	25.71	25.71	0	0.05	0.086	0.062	5.04	0.967	0.051
2.40	25.56	25.54	0	0	0.086	0.063	4.32	0.969	0.051
2.42	25.41	25.32	0	0	0.083	0.064	4.54	0.970	0.051
2.44	25.25	25.1	0	0	0.083	0.065	4.64	0.972	0.052
2.46	25.09	24.89	0	0	0.079	0.066	4.16	0.973	0.052
2.48	24.95	24.7	0	0	0.079	0.067	5.07	0.975	0.052
2.50	24.82	24.53	0	0	0.083	0.068	4.55	0.977	0.052
2.52	24.7	24.36	0	0	0.083	0.069	3.98	0.978	0.053
2.54	24.58	24.2	0	0	0.073	0.070	4.73	0.980	0.053
2.56	24.47	24.06	0	0	0.077	0.071	4.17	0.981	0.053
2.58	24.37	23.93	0	0	0.075	0.072	4.51	0.983	0.053
2.60	24.28	23.81	0	0	0.069	0.073	4.26	0.985	0.054
2.62	24.18	23.68	0	0	0.072	0.074	3.78	0.986	0.054
2.65	24.08	23.56	0	0	0.080	0.075	4.08	0.988	0.054
2.67	24	23.46	0	0	0.079	0.076	3.28	0.990	0.054
2.69	23.92	23.35	0	0	0.079	0.077	4.47	0.991	0.055
2.71	23.88	23.31	0	0	0.074	0.078	4.01	0.993	0.055
2.73	23.84	23.24	0	0	0.075	0.079	4.58	0.994	0.055
2.75	23.77	23.17	0	0	0.072	0.080	3.94	0.996	0.055
2.77	23.7	23.08	0	0	0.072	0.081	3.71	0.998	0.056
2.79	23.63	23	0	0	0.074	0.082	4.11	0.999	0.056
2.81	23.51	22.88	0	0	0.081	0.083	3.82	1.001	0.056
2.83	23.41	22.77	0	0	0.069	0.084	4.73	1.002	0.056
2.85	23.31	22.67	0	0	0.077	0.085	3.98	1.004	0.057
2.87	23.26	22.63	0.05	0.15	0.077	0.086	4.25	1.006	0.057
2.90	23.4	22.83	0.83	0.86	0.071	0.087	4.09	1.007	0.057
2.92	23.55	23.03	0.83	0.86	0.075	0.088	3.39	1.009	0.057
2.94	23.69	23.21	0.83	0.86	0.081	0.089	3.79	1.011	0.058
2.96	23.83	23.38	0.83	0.86	0.076	0.090	3.28	1.012	0.058
2.98	23.96	23.56	0.83	0.86	0.075	0.091	4.10	1.014	0.058
3.00	24.08	23.7	0.83	0.86	0.079	0.092	3.77	1.015	0.058
3.02	24.19	23.85	0.83	0.86	0.068	0.094	4.25	1.017	0.059
3.04	24.29	23.97	0.83	0.86	0.071	0.095	4.13	1.019	0.059

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
3.06	24.39	24.09	0.83	0.86	0.074	0.096	3.75	1.020	0.059
3.08	24.48	24.21	0.83	0.86	0.068	0.097	4.06	1.022	0.059
3.10	24.58	24.32	0.83	0.86	0.072	0.098	3.43	1.023	0.060
3.12	24.67	24.43	0.83	0.86	0.061	0.099	4.44	1.025	0.060
3.15	24.75	24.52	0.83	0.86	0.069	0.100	3.88	1.027	0.060
3.17	24.82	24.6	0.83	0.86	0.063	0.101	4.89	1.028	0.060
3.19	24.88	24.68	0.83	0.86	0.067	0.102	4.26	1.030	0.060
3.21	24.95	24.76	0.83	0.86	0.057	0.103	3.77	1.032	0.061
3.23	25.02	24.83	0.83	0.86	0.068	0.104	4.41	1.033	0.061
3.25	25.08	24.9	0.83	0.86	0.067	0.105	3.78	1.035	0.061
3.27	25.15	24.98	0.83	0.86	0.060	0.106	4.31	1.036	0.061
3.29	25.21	25.06	0.83	0.86	0.070	0.107	3.32	1.038	0.062
3.31	25.28	25.13	0.83	0.86	0.064	0.108	4.23	1.040	0.062
3.33	25.34	25.2	0.83	0.86	0.065	0.109	4.09	1.041	0.062
3.35	25.39	25.26	0.83	0.86	0.059	0.110	3.87	1.043	0.062
3.37	25.39	25.28	0	0.05	0.067	0.111	4.20	1.044	0.063
3.40	25.27	25.15	0	0	0.065	0.112	3.93	1.046	0.063
3.42	25.12	24.94	0	0	0.067	0.113	3.77	1.048	0.063
3.44	24.98	24.75	0	0	0.066	0.114	3.78	1.049	0.063
3.46	24.83	24.56	0	0	0.065	0.115	3.10	1.051	0.064
3.48	24.71	24.4	0	0	0.071	0.116	4.03	1.053	0.064
3.50	24.6	24.25	0	0	0.061	0.117	3.61	1.054	0.064
3.52	24.5	24.11	0	0	0.069	0.118	4.24	1.056	0.064
3.54	24.39	23.97	0	0	0.069	0.119	3.49	1.057	0.065
3.56	24.29	23.85	0	0	0.065	0.120	3.20	1.059	0.065
3.58	24.2	23.73	0	0	0.072	0.121	3.62	1.061	0.065
3.60	24.11	23.6	0	0	0.069	0.122	3.32	1.062	0.065
3.62	24.02	23.49	0	0	0.062	0.123	3.66	1.064	0.066
3.65	23.93	23.39	0	0	0.061	0.124	3.47	1.066	0.066
3.67	23.91	23.35	0	0	0.059	0.125	3.90	1.067	0.066
3.69	23.85	23.28	0	0	0.065	0.126	5.07	1.069	0.066
3.71	23.74	23.15	0	0	0.061	0.127	6.79	1.070	0.067
3.73	23.62	23.02	0	0	0.047	0.128	8.04	1.072	0.067
3.75	23.52	22.92	0	0	0.074	0.129	9.62	1.074	0.067
3.77	23.44	22.83	0	0	0.096	0.130	11.08	1.075	0.067
3.79	23.37	22.75	0	0	0.106	0.131	13.21	1.077	0.068
3.81	23.28	22.65	0	0	0.107	0.132	14.44	1.078	0.068
3.83	23.12	22.5	0	0	0.058	0.133	10.95	1.080	0.068

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
3.85	23.03	22.41	0	0	0.027	0.134	5.63	1.082	0.068
3.87	22.99	22.39	0.05	0.05	0.024	0.135	5.40	1.083	0.069
3.90	23.12	22.6	0.81	0.83	0.021	0.136	4.48	1.085	0.069
3.92	23.24	22.8	0.81	0.83	0.020	0.135	5.07	1.082	0.069
3.94	23.36	22.98	0.81	0.83	0.018	0.135	4.39	1.078	0.069
3.96	23.49	23.15	0.81	0.83	0.017	0.134	2.97	1.074	0.068
3.98	23.63	23.36	0.81	0.83	0.016	0.134	2.17	1.071	0.068
4.00	23.77	23.55	0.81	0.83	0.016	0.133	1.60	1.067	0.068
4.02	23.89	23.72	0.81	0.83	0.014	0.133	1.36	1.064	0.068
4.04	24	23.88	0.81	0.83	0.014	0.132	1.16	1.060	0.068
4.06	24.1	24.03	0.81	0.83	0.012	0.132	1.08	1.057	0.068
4.08	24.21	24.17	0.81	0.83	0.011	0.131	1.01	1.053	0.067
4.10	24.3	24.31	0.81	0.83	0.011	0.131	0.93	1.050	0.067
4.12	24.4	24.45	0.81	0.83	0.011	0.130	0.94	1.046	0.067
4.15	24.49	24.57	0.81	0.83	0.012	0.130	0.94	1.043	0.067
4.17	24.57	24.68	0.81	0.83	0.011	0.129	0.91	1.039	0.067
4.19	24.65	24.8	0.81	0.83	0.012	0.129	0.94	1.036	0.066
4.21	24.73	24.91	0.81	0.83	0.014	0.128	0.93	1.032	0.066
4.23	24.81	25.01	0.81	0.83	0.013	0.127	0.95	1.028	0.066
4.25	24.88	25.11	0.81	0.83	0.014	0.127	0.94	1.025	0.066
4.27	24.94	25.21	0.81	0.83	0.016	0.126	0.94	1.021	0.066
4.29	25.01	25.3	0.81	0.83	0.016	0.126	0.93	1.018	0.065
4.31	25.08	25.39	0.81	0.83	0.016	0.125	0.92	1.014	0.065
4.33	25.16	25.48	0.81	0.83	0.017	0.125	0.89	1.011	0.065
4.35	25.23	25.58	0.81	0.83	0.017	0.124	0.93	1.007	0.065
4.37	25.25	25.62	0	0.05	0.017	0.124	0.93	1.004	0.065
4.40	25.12	25.51	0	0	0.017	0.123	0.93	1.000	0.064
4.42	24.97	25.33	0	0	0.017	0.123	0.93	0.997	0.064
4.44	24.82	25.15	0	0	0.018	0.122	0.94	0.993	0.064
4.46	24.69	24.99	0	0	0.017	0.122	0.93	0.990	0.064
4.48	24.57	24.84	0	0	0.016	0.121	0.94	0.986	0.064
4.50	24.45	24.69	0	0	0.018	0.121	0.94	0.982	0.064
4.52	24.34	24.56	0	0	0.018	0.120	0.93	0.979	0.063
4.54	24.23	24.43	0	0	0.019	0.120	0.94	0.975	0.063
4.56	24.14	24.32	0	0	0.019	0.119	0.94	0.972	0.063
4.58	24.06	24.21	0	0	0.018	0.119	0.95	0.968	0.063
4.60	23.98	24.11	0	0	0.019	0.118	0.95	0.965	0.063
4.62	23.9	24.01	0	0	0.019	0.118	0.94	0.961	0.062

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
4.65	23.83	23.92	0	0	0.019	0.117	0.96	0.958	0.062
4.67	23.76	23.84	0	0	0.018	0.117	0.96	0.954	0.062
4.69	23.7	23.76	0	0	0.019	0.116	0.94	0.951	0.062
4.71	23.65	23.69	0	0	0.019	0.115	0.96	0.947	0.062
4.73	23.6	23.62	0	0	0.019	0.115	0.95	0.944	0.061
4.75	23.55	23.55	0	0	0.017	0.114	0.92	0.940	0.061
4.77	23.49	23.49	0	0	0.017	0.114	0.97	0.936	0.061
4.79	23.43	23.42	0	0	0.018	0.113	0.97	0.933	0.061
4.81	23.38	23.35	0	0	0.017	0.113	0.95	0.929	0.061
4.83	23.34	23.29	0	0	0.018	0.112	0.99	0.926	0.061
4.85	23.3	23.24	0	0	0.016	0.112	0.98	0.922	0.060
4.87	23.27	23.23	0.05	0.08	0.016	0.111	0.97	0.919	0.060
4.90	23.44	23.44	0.81	0.83	0.016	0.111	1.00	0.915	0.060
4.92	23.59	23.63	0.81	0.83	0.016	0.110	1.01	0.912	0.060
4.94	23.73	23.8	0.81	0.83	0.016	0.110	1.01	0.908	0.060
4.96	23.86	23.97	0.81	0.83	0.017	0.109	1.01	0.905	0.059
4.98	23.98	24.12	0.81	0.83	0.015	0.109	0.98	0.901	0.059
5.00	24.09	24.26	0.81	0.83	0.015	0.108	1.02	0.898	0.059
5.02	24.2	24.39	0.81	0.83	0.015	0.108	1.02	0.894	0.059
5.04	24.3	24.5	0.84	0.88	0.014	0.107	1.04	0.890	0.059
5.06	24.35	24.53	0.84	0.88	0.014	0.107	1.04	0.887	0.058
5.08	24.39	24.55	0.84	0.88	0.014	0.106	1.00	0.883	0.058
5.10	24.45	24.66	0.84	0.88	0.013	0.106	1.06	0.880	0.058
5.12	24.51	24.77	0.84	0.88	0.013	0.105	1.06	0.876	0.058
5.15	24.56	24.88	0.84	0.88	0.013	0.105	1.01	0.873	0.058
5.17	24.63	24.99	0.84	0.88	0.013	0.104	1.06	0.869	0.057
5.19	24.68	25.09	0.84	0.88	0.013	0.104	1.05	0.866	0.057
5.21	24.74	25.19	0.84	0.88	0.012	0.103	1.04	0.862	0.057
5.23	24.81	25.29	0.84	0.88	0.013	0.102	1.06	0.859	0.057
5.25	24.86	25.38	0.84	0.88	0.013	0.102	1.05	0.855	0.057
5.27	24.92	25.47	0.84	0.88	0.012	0.101	1.04	0.851	0.057
5.29	24.97	25.55	0.84	0.88	0.013	0.101	1.06	0.848	0.056
5.31	25.03	25.64	0.84	0.88	0.013	0.100	1.05	0.844	0.056
5.33	25.07	25.71	0.84	0.88	0.012	0.100	1.06	0.841	0.056
5.35	25.11	25.77	0.84	0.88	0.013	0.099	1.05	0.837	0.056
5.37	25.1	25.8	0	0.2	0.013	0.099	1.04	0.834	0.056
5.40	24.97	25.67	0	0	0.012	0.098	1.04	0.830	0.055
5.42	24.82	25.48	0	0	0.013	0.098	1.05	0.827	0.055

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
5.44	24.69	25.3	0	0	0.012	0.097	1.02	0.823	0.055
5.46	24.57	25.14	0	0	0.011	0.097	1.05	0.820	0.055
5.48	24.45	24.99	0	0	0.011	0.096	1.04	0.816	0.055
5.50	24.33	24.84	0	0	0.011	0.096	1.04	0.813	0.054
5.52	24.22	24.7	0	0	0.012	0.095	1.07	0.809	0.054
5.54	24.1	24.55	0	0	0.012	0.095	1.11	0.805	0.054
5.56	23.94	24.36	0	0	0.022	0.094	1.82	0.802	0.054
5.58	23.81	24.2	0	0	0.030	0.094	2.73	0.798	0.054
5.60	23.7	24.09	0	0	0.067	0.093	1.05	0.795	0.054
5.62	23.66	24.03	0	0	0.062	0.093	1.12	0.791	0.053
5.65	23.61	23.96	0	0	0.072	0.092	1.17	0.788	0.053
5.67	23.55	23.88	0	0	0.059	0.092	1.17	0.784	0.053
5.69	23.48	23.79	0	0	0.051	0.091	1.19	0.781	0.053
5.71	23.45	23.74	0	0	0.044	0.090	1.21	0.777	0.053
5.73	23.42	23.68	0	0	0.046	0.090	1.21	0.774	0.052
5.75	23.37	23.61	0	0	0.043	0.089	1.19	0.770	0.052
5.77	23.31	23.53	0	0	0.040	0.089	1.23	0.767	0.052
5.79	23.25	23.45	0	0	0.042	0.088	1.23	0.763	0.052
5.81	23.11	23.29	0	0	0.036	0.088	1.18	0.759	0.052
5.83	22.95	23.13	0	0	0.030	0.087	1.24	0.756	0.051
5.85	22.86	23.03	0	0	0.036	0.087	1.24	0.752	0.051
5.87	22.82	23.01	0.2	0.25	0.035	0.086	1.23	0.749	0.051
5.90	22.96	23.2	0.84	0.88	0.033	0.086	1.25	0.745	0.051
5.92	23.1	23.38	0.84	0.88	0.034	0.085	1.25	0.742	0.051
5.94	23.2	23.5	0.84	0.88	0.033	0.085	1.25	0.738	0.050
5.96	23.3	23.7	0.84	0.88	0.030	0.084	1.25	0.735	0.050
5.98	23.49	23.87	0.84	0.88	0.028	0.084	1.25	0.731	0.050
6.00	23.61	24.01	0.84	0.88	0.033	0.083	1.25	0.728	0.050
6.02	23.73	24.14	0.84	0.88	0.031	0.083	1.26	0.724	0.050
6.04	23.84	24.28	0.84	0.88	0.037	0.082	1.25	0.721	0.050
6.06	23.96	24.41	0.84	0.88	0.031	0.082	1.21	0.717	0.049
6.08	24.06	24.54	0.84	0.88	0.032	0.081	1.25	0.713	0.049
6.10	24.17	24.66	0.84	0.88	0.032	0.081	1.24	0.710	0.049
6.12	24.27	24.78	0.84	0.88	0.029	0.080	1.21	0.706	0.049
6.15	24.37	24.89	0.84	0.88	0.033	0.080	1.24	0.703	0.049
6.17	24.46	25	0.84	0.87	0.033	0.079	1.23	0.699	0.048
6.19	24.55	25.1	0.84	0.87	0.033	0.079	1.17	0.696	0.048
6.21	24.63	25.19	0.84	0.87	0.032	0.078	1.24	0.692	0.048

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
6.23	24.72	25.28	0.84	0.87	0.034	0.077	1.23	0.689	0.048
6.25	24.8	25.37	0.84	0.87	0.034	0.077	1.16	0.685	0.048
6.27	24.88	25.47	0.84	0.87	0.031	0.076	1.21	0.682	0.047
6.29	24.96	25.55	0.84	0.87	0.034	0.076	1.21	0.678	0.047
6.31	25.04	25.63	0.84	0.87	0.032	0.075	1.14	0.675	0.047
6.33	25.12	25.72	0.84	0.87	0.032	0.075	1.20	0.671	0.047
6.35	25.19	25.8	0.84	0.87	0.034	0.074	1.19	0.667	0.047
6.37	25.22	25.84	0	0.1	0.030	0.074	1.16	0.664	0.046
6.40	25.11	25.73	0	0	0.031	0.073	1.19	0.660	0.046
6.42	24.99	25.54	0	0	0.032	0.073	1.17	0.657	0.046
6.44	24.87	25.37	0	0	0.031	0.072	1.19	0.653	0.046
6.46	24.78	25.21	0	0	0.031	0.072	1.17	0.650	0.046
6.48	24.7	25.06	0	0	0.033	0.071	1.17	0.646	0.046
6.50	24.63	24.93	0	0	0.029	0.071	1.17	0.643	0.045
6.52	24.54	24.79	0	0	0.031	0.070	1.17	0.639	0.045
6.54	24.46	24.66	0	0	0.032	0.070	1.17	0.636	0.045
6.56	24.38	24.53	0	0	0.029	0.069	1.17	0.632	0.045
6.58	24.31	24.42	0	0	0.033	0.069	1.13	0.628	0.045
6.60	24.24	24.34	0	0	0.035	0.068	1.11	0.625	0.044
6.62	24.17	24.28	0	0	0.035	0.068	1.09	0.621	0.044
6.65	24.13	24.24	0	0	0.030	0.067	1.08	0.618	0.044
6.67	24.15	24.25	0	0	0.033	0.067	1.07	0.614	0.044
6.69	24.13	24.22	0	0	0.036	0.066	1.03	0.611	0.044
6.71	24.09	24.17	0	0	0.032	0.065	1.06	0.607	0.043
6.73	24.04	24.13	0	0	0.034	0.065	1.05	0.604	0.043
6.75	23.99	24.08	0	0	0.034	0.064	0.99	0.600	0.043
6.77	23.94	24.03	0	0	0.033	0.064	1.04	0.597	0.043
6.79	23.89	23.98	0	0	0.032	0.063	1.04	0.593	0.043
6.81	23.77	23.85	0	0	0.036	0.063	0.99	0.590	0.043
6.83	23.6	23.7	0	0	0.031	0.062	1.04	0.586	0.042
6.85	23.53	23.63	0	0	0.036	0.062	1.03	0.582	0.042
6.87	23.49	23.63	0.2	0.25	0.038	0.061	0.99	0.579	0.042
6.90	23.64	23.85	0.83	0.87	0.033	0.061	1.03	0.575	0.042
6.92	23.8	24.07	0.83	0.87	0.033	0.060	1.04	0.572	0.042
6.94	23.96	24.27	0.83	0.87	0.039	0.060	1.01	0.568	0.041
6.96	24.1	24.46	0.83	0.87	0.032	0.059	1.04	0.565	0.041
6.98	24.24	24.64	0.83	0.87	0.030	0.059	1.04	0.561	0.041
7.00	24.37	24.8	0.83	0.87	0.036	0.058	1.02	0.558	0.041

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
7.02	24.48	24.95	0.83	0.87	0.029	0.058	1.04	0.554	0.041
7.04	24.57	25.09	0.83	0.87	0.029	0.057	1.45	0.551	0.040
7.06	24.69	25.21	0.83	0.87	0.028	0.057	7.28	0.547	0.040
7.08	24.75	25.24	0.83	0.87	0.032	0.056	10.61	0.544	0.040
7.10	24.84	25.35	0.83	0.87	0.026	0.056	13.43	0.540	0.040
7.12	24.93	25.45	0.83	0.87	0.028	0.055	15.04	0.536	0.040
7.15	25.02	25.56	0.83	0.87	0.033	0.055	13.12	0.533	0.039
7.17	25.1	25.66	0.83	0.87	0.026	0.054	15.45	0.529	0.039
7.19	25.18	25.76	0.83	0.87	0.029	0.054	15.04	0.526	0.039
7.21	25.26	25.84	0.83	0.87	0.034	0.053	13.34	0.522	0.039
7.23	25.34	25.92	0.83	0.87	0.027	0.052	15.34	0.519	0.039
7.25	25.43	26	0.83	0.87	0.031	0.052	13.80	0.515	0.039
7.27	25.51	26.09	0.83	0.87	0.039	0.051	12.41	0.512	0.038
7.29	25.6	26.18	0.83	0.87	0.027	0.051	13.60	0.508	0.038
7.31	25.69	26.26	0.83	0.87	0.031	0.050	13.58	0.505	0.038
7.33	25.78	26.36	0.83	0.87	0.034	0.050	12.34	0.501	0.038
7.35	25.86	26.44	0.83	0.87	0.036	0.049	12.75	0.498	0.038
7.37	25.89	26.48	0	0.05	0.026	0.049	12.92	0.494	0.037
7.40	25.76	26.33	0	0	0.032	0.048	11.82	0.490	0.037
7.42	25.6	26.12	0	0	0.036	0.048	11.01	0.487	0.037
7.44	25.45	25.92	0	0	0.027	0.047	11.88	0.483	0.037
7.46	25.3	25.72	0	0	0.028	0.047	11.42	0.480	0.037
7.48	25.17	25.54	0	0	0.037	0.046	8.99	0.476	0.036
7.50	25.03	25.37	0	0	0.029	0.046	10.77	0.473	0.036
7.52	24.91	25.21	0	0	0.031	0.045	10.37	0.469	0.036
7.54	24.78	25.05	0	0	0.039	0.045	8.74	0.466	0.036
7.56	24.67	24.9	0	0	0.029	0.044	10.11	0.462	0.036
7.58	24.55	24.76	0	0	0.036	0.044	9.10	0.459	0.035
7.60	24.44	24.62	0	0	0.036	0.043	8.41	0.455	0.035
7.62	24.34	24.5	0	0	0.029	0.043	10.16	0.452	0.035
7.65	24.25	24.38	0	0	0.030	0.042	9.40	0.448	0.035
7.67	24.16	24.27	0	0	0.034	0.042	7.96	0.444	0.035
7.69	24.07	24.16	0	0	0.027	0.041	9.33	0.441	0.035
7.71	23.98	24.05	0	0	0.025	0.040	8.70	0.437	0.034
7.73	23.9	23.95	0	0	0.034	0.040	7.56	0.434	0.034
7.75	23.81	23.84	0	0	0.025	0.039	8.71	0.430	0.034
7.77	23.73	23.74	0	0	0.028	0.039	8.42	0.427	0.034
7.79	23.65	23.65	0	0	0.031	0.038	7.53	0.423	0.034

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
7.81	23.57	23.56	0	0	0.031	0.038	8.54	0.420	0.033
7.83	23.49	23.47	0	0	0.027	0.037	8.15	0.416	0.033
7.85	23.42	23.39	0	0	0.031	0.037	6.69	0.413	0.033
7.87	23.39	23.37	0.2	0.25	0.033	0.036	6.20	0.409	0.033
7.90	23.57	23.62	0.83	0.87	0.026	0.036	5.85	0.405	0.033
7.92	23.75	23.85	0.83	0.87	0.032	0.035	4.99	0.402	0.032
7.94	23.92	24.07	0.83	0.87	0.032	0.035	5.04	0.398	0.032
7.96	24.08	24.27	0.83	0.87	0.031	0.034	5.09	0.395	0.032
7.98	24.22	24.45	0.83	0.87	0.032	0.034	3.97	0.391	0.032
8.00	24.35	24.63	0.83	0.87	0.031	0.033	4.91	0.388	0.032
8.02	24.47	24.79	0.83	0.87	0.033	0.033	4.14	0.384	0.032
8.04	24.59	24.96	0.83	0.87	0.023	0.032	3.62	0.381	0.031
8.06	24.7	25.12	0.83	0.87	0.030	0.032	4.97	0.377	0.031
8.08	24.8	25.24	0.83	0.87	0.030	0.032	4.45	0.380	0.031
8.10	24.9	25.38	0.83	0.87	0.032	0.032	3.72	0.383	0.031
8.12	25	25.52	0.83	0.87	0.030	0.033	3.72	0.386	0.031
8.15	25.11	25.66	0.83	0.87	0.033	0.033	3.51	0.389	0.031
8.17	25.22	25.8	0.83	0.87	0.025	0.033	3.86	0.392	0.031
8.19	25.32	25.93	0.83	0.87	0.031	0.033	3.79	0.396	0.031
8.21	25.41	26.05	0.83	0.87	0.032	0.033	3.62	0.399	0.031
8.23	25.51	26.16	0.83	0.87	0.031	0.033	3.51	0.402	0.031
8.25	25.59	26.26	0.83	0.87	0.028	0.034	3.86	0.405	0.031
8.27	25.67	26.36	0.83	0.87	0.032	0.034	3.63	0.408	0.030
8.29	25.75	26.47	0.83	0.87	0.030	0.034	3.17	0.411	0.030
8.31	25.84	26.57	0.83	0.87	0.032	0.034	3.69	0.414	0.030
8.33	25.92	26.68	0.83	0.87	0.032	0.034	3.51	0.417	0.030
8.35	26	26.77	0.83	0.87	0.030	0.034	2.93	0.421	0.030
8.37	26.03	26.82	0	0.05	0.032	0.034	3.55	0.424	0.030
8.40	25.92	26.72	0	0	0.034	0.035	3.44	0.427	0.030
8.42	25.77	26.55	0	0	0.035	0.035	2.93	0.430	0.030
8.44	25.62	26.38	0	0	0.029	0.035	3.58	0.433	0.030
8.46	25.47	26.22	0	0	0.033	0.035	3.41	0.436	0.030
8.48	25.34	26.08	0	0	0.033	0.035	2.97	0.439	0.029
8.50	25.22	25.95	0	0	0.033	0.035	3.35	0.443	0.029
8.52	25.12	25.83	0	0	0.036	0.036	3.09	0.446	0.029
8.54	25.02	25.7	0	0	0.036	0.036	2.73	0.449	0.029
8.56	24.91	25.58	0	0	0.036	0.036	3.15	0.452	0.029
8.58	24.82	25.47	0	0	0.036	0.036	2.90	0.455	0.029

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
8.60	24.74	25.37	0	0	0.036	0.036	2.99	0.458	0.029
8.62	24.66	25.26	0	0	0.037	0.036	3.13	0.461	0.029
8.65	24.57	25.17	0	0	0.037	0.036	2.69	0.464	0.029
8.67	24.5	25.07	0	0	0.033	0.037	3.06	0.468	0.029
8.69	24.42	24.97	0	0	0.033	0.037	2.72	0.471	0.028
8.71	24.35	24.88	0	0	0.042	0.037	2.59	0.474	0.028
8.73	24.28	24.8	0	0	0.035	0.037	2.99	0.477	0.028
8.75	24.22	24.71	0	0	0.040	0.037	2.74	0.480	0.028
8.77	24.16	24.64	0	0	0.042	0.037	2.12	0.483	0.028
8.79	24.11	24.56	0	0	0.042	0.038	2.54	0.486	0.028
8.81	24.05	24.5	0	0	0.037	0.038	2.39	0.490	0.028
8.83	24	24.41	0	0	0.044	0.038	2.52	0.493	0.028
8.85	23.93	24.27	0	0	0.043	0.038	3.56	0.496	0.028
8.87	23.89	24.19	0.05	0.15	0.040	0.038	3.66	0.499	0.028
8.90	24.02	24.34	0.84	0.87	0.041	0.038	3.04	0.502	0.027
8.92	24.14	24.48	0.84	0.87	0.041	0.038	3.10	0.505	0.027
8.94	24.25	24.61	0.84	0.87	0.040	0.039	2.67	0.508	0.027
8.96	24.35	24.73	0.84	0.87	0.041	0.039	2.42	0.511	0.027
8.98	24.45	24.85	0.84	0.87	0.046	0.039	2.36	0.515	0.027
9.00	24.55	24.96	0.84	0.87	0.042	0.039	2.17	0.518	0.027
9.02	24.64	25.06	0.84	0.87	0.042	0.039	2.44	0.521	0.027
9.04	24.7	25.13	0.85	0.87	0.043	0.039	2.20	0.524	0.027
9.06	24.76	25.19	0.85	0.87	0.040	0.040	1.64	0.527	0.027
9.08	24.86	25.29	0.85	0.87	0.044	0.040	1.98	0.530	0.027
9.10	24.96	25.36	0.85	0.89	0.040	0.040	1.75	0.533	0.027
9.12	25.07	25.48	0.85	0.89	0.036	0.040	1.90	0.536	0.026
9.15	25.17	25.6	0.85	0.89	0.034	0.040	1.83	0.540	0.026
9.17	25.26	25.69	0.85	0.89	0.036	0.040	1.54	0.543	0.026
9.19	25.35	25.78	0.85	0.89	0.040	0.040	1.73	0.546	0.026
9.21	25.44	25.88	0.85	0.89	0.041	0.041	1.59	0.549	0.026
9.23	25.52	25.97	0.85	0.89	0.032	0.041	1.68	0.552	0.026
9.25	25.6	26.06	0.85	0.89	0.036	0.041	1.69	0.555	0.026
9.27	25.67	26.13	0.85	0.89	0.035	0.041	1.73	0.558	0.026
9.29	25.75	26.21	0.85	0.89	0.038	0.041	1.84	0.562	0.026
9.31	25.81	26.27	0.85	0.89	0.034	0.041	1.54	0.565	0.026
9.33	25.87	26.33	0.85	0.89	0.031	0.042	1.80	0.568	0.025
9.35	25.93	26.4	0.85	0.89	0.033	0.042	1.69	0.571	0.025
9.37	25.95	26.43	0	0	0.034	0.042	1.75	0.574	0.025

Table C.1 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor	Phytoplankton (mg-N L ⁻¹)	Ammonium (mg-N L ⁻¹)	Nitrate (mg-N L ⁻¹)	Organic N (mg-N L ⁻¹)	Nitrite (mg-N L ⁻¹)
9.40	25.81	26.3	0	0	0.034	0.042	1.73	0.577	0.025
9.42	25.62	26.09	0	0	0.035	0.042	1.38	0.580	0.025
9.44	25.46	25.9	0	0	0.033	0.042	1.68	0.583	0.025
9.46	25.31	25.73	0	0	0.037	0.042	1.49	0.587	0.025
9.48	25.18	25.58	0	0	0.033	0.043	1.70	0.590	0.025
9.50	25.05	25.43	0	0	0.037	0.043	1.59	0.593	0.025
9.52	24.94	25.29	0	0	0.039	0.043	1.35	0.596	0.025
9.54	24.84	25.17	0	0	0.037	0.043	1.62	0.599	0.024
9.56	24.73	25.04	0	0	0.037	0.043	1.52	0.602	0.024
9.58	24.63	24.93	0	0	0.036	0.043	1.71	0.605	0.024
9.60	24.55	24.82	0	0	0.039	0.044	1.58	0.609	0.024
9.62	24.47	24.72	0	0	0.038	0.044	1.39	0.612	0.024
9.65	24.39	24.62	0	0	0.041	0.044	1.63	0.615	0.024
9.67	24.31	24.53	0	0	0.037	0.044	1.59	0.618	0.024
9.69	24.24	24.43	0	0	0.030	0.044	1.36	0.621	0.024
9.71	24.15	24.34	0	0	0.034	0.044	1.64	0.624	0.024
9.73	24.08	24.26	0	0	0.041	0.044	1.54	0.627	0.024
9.75	24.02	24.17	0	0	0.038	0.045	1.51	0.630	0.023
9.77	23.95	24.09	0	0	0.032	0.045	1.58	0.634	0.023
9.79	23.89	24.02	0	0	0.038	0.045	1.53	0.637	0.023
9.81	23.83	23.95	0	0	0.034	0.045	1.60	0.640	0.023
9.83	23.78	23.88	0	0	0.034	0.045	1.55	0.643	0.023
9.85	23.72	23.81	0	0	0.038	0.045	1.39	0.646	0.023
9.87	23.69	23.81	0.25	0.55	0.031	0.046	1.54	0.649	0.023
9.90	23.86	24.03	0.85	0.89	0.031	0.046	1.50	0.652	0.023
9.92	24.03	24.23	0.85	0.89	0.036	0.046	1.24	0.655	0.023
9.94	24.17	23.98	0.87	0.89	0.031	0.046	1.48	0.659	0.023
9.96	24.26	24.13	0.87	0.89	0.037	0.046	1.28	0.662	0.022
9.98	24.39	24.32	0.86	0.89	0.034	0.046	1.18	0.662	0.022
10.00	24.52	24.51	0.86	0.89	0.029	0.046	1.22	0.662	0.022
10.02	24.66	24.69	0.86	0.89	0.036	0.046	1.75	0.662	0.022

Table C.2: STELLA model inputs for control and mussel scenarios without flow.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
0.00	24.12	24.44	0.84	0.85
0.02	24.29	24.64	0.84	0.85
0.04	24.48	24.86	0.84	0.85
0.06	24.63	25.05	0.84	0.85
0.08	24.77	25.22	0.84	0.85
0.10	24.91	25.4	0.84	0.85
0.12	25.03	25.56	0.84	0.85
0.15	25.16	25.72	0.84	0.85
0.17	25.29	25.88	0.84	0.85
0.19	25.4	26.01	0.84	0.85
0.21	25.5	26.12	0.84	0.85
0.23	25.6	26.23	0.84	0.85
0.25	25.69	26.35	0.84	0.85
0.27	25.8	26.49	0.84	0.85
0.29	25.89	26.61	0.84	0.85
0.31	25.99	26.72	0.84	0.85
0.33	26.06	26.8	0.84	0.84
0.35	26.14	26.9	0.84	0.85
0.37	26.22	26.98	0.84	0.84
0.40	26.28	27.06	0.84	0.85
0.42	26.35	27.13	0.84	0.85
0.44	26.43	27.22	0.84	0.85
0.46	26.47	27.27	0	0
0.48	26.35	27.15	0	0
0.50	26.2	26.95	0	0
0.52	26.05	26.75	0	0
0.54	25.92	26.59	0	0
0.56	25.82	26.46	0	0
0.58	25.69	26.29	0	0
0.60	25.56	26.12	0	0
0.62	25.43	25.96	0	0
0.65	25.32	25.8	0	0
0.67	25.2	25.65	0	0
0.69	25.13	25.57	0	0
0.71	25.01	25.43	0	0
0.73	24.9	25.28	0	0
0.75	24.79	25.14	0	0
0.77	24.68	25.01	0	0
0.79	24.58	24.89	0	0
0.81	24.51	24.8	0	0
0.83	24.42	24.7	0	0
0.85	24.33	24.58	0	0
0.87	24.24	24.47	0	0
0.90	24.15	24.37	0	0
0.92	24.06	24.26	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
0.94	23.99	24.18	0	0
0.96	23.97	24.19	0.05	0.1
0.98	24.12	24.39	0.84	0.85
1.00	24.27	24.59	0.84	0.85
1.02	24.41	24.78	0.84	0.85
1.04	24.54	24.94	0.84	0.85
1.06	24.68	25.1	0.84	0.85
1.08	24.82	25.26	0.84	0.85
1.10	24.95	25.41	0.84	0.85
1.12	25.09	25.53	0.84	0.85
1.15	25.22	25.66	0.84	0.84
1.17	25.33	25.8	0.84	0.84
1.19	25.43	25.93	0.84	0.84
1.21	25.52	26.05	0.84	0.85
1.23	25.61	26.17	0.84	0.85
1.25	25.7	26.29	0.84	0.84
1.27	25.81	26.41	0.83	0.84
1.29	25.9	26.52	0.83	0.84
1.31	25.98	26.62	0.83	0.84
1.33	26.06	26.72	0.83	0.84
1.35	26.14	26.81	0.83	0.84
1.37	26.23	26.92	0.84	0.84
1.40	26.32	27.01	0.84	0.84
1.42	26.39	27.09	0.84	0.84
1.44	26.46	27.17	0.84	0.84
1.46	26.49	27.21	0	0.1
1.48	26.39	27.12	0	0
1.50	26.25	26.97	0	0
1.52	26.11	26.81	0	0
1.54	25.99	26.62	0	0
1.56	25.86	26.45	0	0
1.58	25.75	26.3	0	0
1.60	25.63	26.14	0	0
1.62	25.51	25.97	0	0
1.65	25.4	25.82	0	0
1.67	25.29	25.67	0	0
1.69	25.2	25.56	0	0
1.71	25.1	25.41	0	0
1.73	24.99	25.27	0	0
1.75	24.89	25.13	0	0
1.77	24.8	25.02	0	0
1.79	24.72	24.92	0	0
1.81	24.63	24.82	0	0
1.83	24.55	24.73	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
1.85	24.47	24.63	0	0
1.87	24.38	24.55	0	0
1.90	24.3	24.44	0	0
1.92	24.22	24.33	0	0
1.94	24.14	24.23	0	0
1.96	24.09	24.2	0.05	0.1
1.98	24.22	24.39	0.84	0.84
2.00	24.35	24.56	0.84	0.84
2.02	24.47	24.73	0.84	0.84
2.04	24.6	24.89	0.83	0.84
2.06	24.73	25.05	0.84	0.84
2.08	24.85	25.21	0.84	0.84
2.10	24.97	25.35	0.84	0.84
2.12	25.09	25.51	0.84	0.84
2.15	25.2	25.64	0.84	0.84
2.17	25.29	25.76	0.84	0.84
2.19	25.39	25.89	0.84	0.84
2.21	25.48	26.01	0.84	0.84
2.23	25.58	26.12	0.84	0.84
2.25	25.67	26.23	0.84	0.84
2.27	25.75	26.34	0.84	0.84
2.29	25.84	26.44	0.84	0.84
2.31	25.91	26.53	0.84	0.84
2.33	25.99	26.63	0.84	0.84
2.35	26.08	26.73	0.84	0.84
2.37	26.16	26.82	0.84	0.84
2.40	26.22	26.91	0.84	0.84
2.42	26.28	26.98	0.84	0.84
2.44	26.35	27.06	0.84	0.84
2.46	26.37	27.11	0.01	0.84
2.48	26.26	26.99	0	0
2.50	26.12	26.81	0	0
2.52	25.98	26.62	0	0
2.54	25.85	26.43	0	0
2.56	25.72	26.25	0	0
2.58	25.6	26.13	0	0
2.60	25.48	25.96	0	0
2.62	25.36	25.81	0	0
2.65	25.26	25.68	0	0
2.67	25.14	25.53	0	0
2.69	25.04	25.39	0	0
2.71	24.95	25.28	0	0
2.73	24.85	25.15	0	0
2.75	24.75	25.02	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
2.77	24.66	24.89	0	0
2.79	24.58	24.8	0	0
2.81	24.49	24.69	0	0
2.83	24.4	24.58	0	0
2.85	24.33	24.5	0	0
2.87	24.24	24.38	0	0
2.90	24.16	24.28	0	0
2.92	24.1	24.2	0	0
2.94	24.02	24.1	0	0
2.96	23.97	24.07	0.08	0.08
2.98	24.13	24.25	0.85	0.84
3.00	24.21	24.4	0.85	0.84
3.02	24.4	24.64	0.85	0.84
3.04	24.6	24.87	0.85	0.84
3.06	24.75	25.07	0.85	0.84
3.08	24.91	25.25	0.85	0.84
3.10	25.04	25.43	0.85	0.84
3.12	25.17	25.59	0.85	0.84
3.15	25.3	25.75	0.85	0.84
3.17	25.43	25.92	0.85	0.84
3.19	25.54	26.06	0.85	0.84
3.21	25.66	26.2	0.85	0.84
3.23	25.77	26.34	0.85	0.84
3.25	25.87	26.46	0.85	0.84
3.27	25.99	26.61	0.85	0.84
3.29	26.08	26.71	0.85	0.84
3.31	26.18	26.82	0.85	0.84
3.33	26.27	26.91	0.85	0.84
3.35	26.36	27.03	0.85	0.84
3.37	26.45	27.13	0.84	0.84
3.40	26.55	27.25	0.85	0.83
3.42	26.65	27.35	0.85	0.83
3.44	26.74	27.46	0.85	0.83
3.46	26.78	27.51	0.03	0.06
3.48	26.65	27.39	0	0
3.50	26.53	27.24	0	0
3.52	26.38	27.04	0	0
3.54	26.22	26.84	0	0
3.56	26.07	26.65	0	0
3.58	25.93	26.46	0	0
3.60	25.81	26.33	0	0
3.62	25.68	26.16	0	0
3.65	25.55	25.99	0	0
3.67	25.42	25.83	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
3.69	25.29	25.67	0	0
3.71	25.18	25.54	0	0
3.73	25.09	25.42	0	0
3.75	24.97	25.28	0	0
3.77	24.86	25.14	0	0
3.79	24.75	25.01	0	0
3.81	24.65	24.88	0	0
3.83	24.58	24.8	0	0
3.85	24.48	24.68	0	0
3.87	24.38	24.55	0	0
3.90	24.29	24.44	0	0
3.92	24.2	24.34	0	0
3.94	24.14	24.28	0	0
3.96	24.08	24.25	0.3	0.3
3.98	24.24	24.44	0.85	0.83
4.00	24.42	24.68	0.85	0.83
4.02	24.62	24.92	0.85	0.83
4.04	24.8	25.12	0.85	0.83
4.06	24.92	25.29	0.85	0.83
4.08	25.03	25.43	0.85	0.83
4.10	25.18	25.62	0.85	0.83
4.12	25.32	25.8	0.85	0.83
4.15	25.47	25.98	0.85	0.83
4.17	25.6	26.13	0.85	0.83
4.19	25.72	26.27	0.85	0.83
4.21	25.84	26.4	0.85	0.83
4.23	25.95	26.54	0.85	0.83
4.25	26.07	26.67	0.85	0.83
4.27	26.17	26.78	0.85	0.83
4.29	26.26	26.89	0.85	0.83
4.31	26.36	27	0.85	0.83
4.33	26.46	27.11	0.84	0.83
4.35	26.55	27.21	0.85	0.83
4.37	26.63	27.31	0.84	0.83
4.40	26.72	27.41	0.85	0.83
4.42	26.82	27.53	0.84	0.83
4.44	26.92	27.63	0.85	0.83
4.46	26.95	27.68	0.03	0.07
4.48	26.82	27.56	0	0
4.50	26.69	27.41	0	0
4.52	26.54	27.21	0	0
4.54	26.38	27.01	0	0
4.56	26.23	26.82	0	0
4.58	26.12	26.69	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
4.60	25.98	26.52	0	0
4.62	25.85	26.36	0	0
4.65	25.72	26.2	0	0
4.67	25.63	26.1	0	0
4.69	25.51	25.95	0	0
4.71	25.4	25.81	0	0
4.73	25.29	25.69	0	0
4.75	25.2	25.58	0	0
4.77	25.1	25.46	0	0
4.79	25	25.33	0	0
4.81	24.9	25.22	0	0
4.83	24.81	25.11	0	0
4.85	24.69	24.98	0	0
4.87	24.58	24.85	0	0
4.90	24.49	24.75	0	0
4.92	24.4	24.64	0	0
4.94	24.31	24.53	0	0
4.96	24.24	24.48	0.3	0.3
4.98	24.4	24.69	0.85	0.83
5.00	24.56	24.88	0.85	0.83
5.02	24.71	25.07	0.85	0.83
5.04	24.86	25.24	0.85	0.83
5.06	25.01	25.43	0.85	0.83
5.08	25.16	25.61	0.85	0.83
5.10	25.29	25.76	0.85	0.83
5.12	25.41	25.91	0.85	0.83
5.15	25.56	26.08	0.84	0.83
5.17	25.68	26.22	0.85	0.83
5.19	25.8	26.36	0.85	0.83
5.21	25.91	26.49	0.85	0.83
5.23	26.03	26.63	0.85	0.82
5.25	26.14	26.76	0.85	0.82
5.27	26.25	26.9	0.84	0.82
5.29	26.35	27.01	0.84	0.82
5.31	26.45	27.13	0.84	0.82
5.33	26.54	27.24	0.85	0.82
5.35	26.63	27.34	0.85	0.82
5.37	26.72	27.44	0.85	0.82
5.40	26.8	27.54	0.85	0.82
5.42	26.88	27.63	0.84	0.82
5.44	26.95	27.71	0.85	0.82
5.46	26.98	27.76	0.03	0.07
5.48	26.83	27.61	0	0
5.50	26.63	27.38	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
5.52	26.46	27.16	0	0
5.54	26.32	26.99	0	0
5.56	26.15	26.78	0	0
5.58	25.98	26.58	0	0
5.60	25.82	26.38	0	0
5.62	25.7	26.23	0	0
5.65	25.55	26.06	0	0
5.67	25.41	25.89	0	0
5.69	25.27	25.72	0	0
5.71	25.17	25.6	0	0
5.73	25.04	25.44	0	0
5.75	24.91	25.29	0	0
5.77	24.8	25.15	0	0
5.79	24.71	25.05	0	0
5.81	24.6	24.92	0	0
5.83	24.5	24.79	0	0
5.85	24.39	24.67	0	0
5.87	24.32	24.59	0	0
5.90	24.23	24.47	0	0
5.92	24.13	24.36	0	0
5.94	24.04	24.26	0	0
5.96	24	24.25	0.3	0.3
5.98	24.17	24.46	0.85	0.82
6.00	24.34	24.66	0.85	0.82
6.02	24.5	24.86	0.84	0.82
6.04	24.67	25.07	0.85	0.82
6.06	24.84	25.26	0.85	0.82
6.08	24.99	25.45	0.84	0.82
6.10	25.13	25.61	0.85	0.82
6.12	25.28	25.79	0.85	0.82
6.15	25.42	25.95	0.85	0.82
6.17	25.55	26.1	0.84	0.82
6.19	25.67	26.24	0.84	0.82
6.21	25.8	26.4	0.84	0.82
6.23	25.92	26.52	0.84	0.82
6.25	26.03	26.66	0.85	0.82
6.27	26.14	26.78	0.84	0.82
6.29	26.25	26.91	0.85	0.82
6.31	26.35	27.02	0.85	0.81
6.33	26.44	27.12	0.84	0.82
6.35	26.54	27.24	0.84	0.82
6.37	26.65	27.36	0.85	0.81
6.40	26.74	27.47	0.85	0.82
6.42	26.83	27.57	0.85	0.82

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
6.44	26.93	27.69	0.84	0.82
6.46	26.98	27.76	0.03	0.05
6.48	26.86	27.64	0	0
6.50	26.7	27.45	0	0
6.52	26.57	27.3	0	0
6.54	26.43	27.11	0	0
6.56	26.28	26.93	0	0
6.58	26.14	26.76	0	0
6.60	26.03	26.63	0	0
6.62	25.9	26.46	0	0
6.65	25.77	26.3	0	0
6.67	25.63	26.14	0	0
6.69	25.54	26.03	0	0
6.71	25.42	25.89	0	0
6.73	25.3	25.74	0	0
6.75	25.19	25.62	0	0
6.77	25.1	25.51	0	0
6.79	24.99	25.38	0	0
6.81	24.89	25.26	0	0
6.83	24.8	25.15	0	0
6.85	24.72	25.05	0	0
6.87	24.62	24.93	0	0
6.90	24.52	24.82	0	0
6.92	24.45	24.73	0	0
6.94	24.37	24.65	0	0
6.96	24.32	24.61	0.3	0.3
6.98	24.47	24.8	0.84	0.82
7.00	24.65	25.01	0.84	0.82
7.02	24.81	25.21	0.85	0.82
7.04	24.96	25.39	0.84	0.82
7.06	25.09	25.55	0.85	0.82
7.08	25.24	25.73	0.85	0.81
7.10	25.38	25.89	0.84	0.81
7.12	25.51	26.03	0.84	0.81
7.15	25.63	26.18	0.84	0.81
7.17	25.76	26.33	0.84	0.82
7.19	25.88	26.47	0.84	0.81
7.21	25.99	26.6	0.84	0.81
7.23	26.12	26.74	0.85	0.81
7.25	26.24	26.88	0.84	0.81
7.27	26.34	26.99	0.84	0.81
7.29	26.43	27.09	0.85	0.81
7.31	26.54	27.21	0.85	0.81
7.33	26.64	27.32	0.84	0.81

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
7.35	26.72	27.42	0.84	0.81
7.37	26.81	27.52	0.85	0.81
7.40	26.9	27.62	0.85	0.81
7.42	26.98	27.71	0.84	0.81
7.44	27.06	27.81	0.84	0.81
7.46	27.1	27.86	0.04	0.04
7.48	26.97	27.74	0	0
7.50	26.78	27.52	0	0
7.52	26.62	27.32	0	0
7.54	26.48	27.17	0	0
7.56	26.33	26.99	0	0
7.58	26.19	26.81	0	0
7.60	26.05	26.64	0	0
7.62	25.93	26.51	0	0
7.65	25.81	26.35	0	0
7.67	25.68	26.2	0	0
7.69	25.56	26.06	0	0
7.71	25.47	25.95	0	0
7.73	25.36	25.82	0	0
7.75	25.25	25.68	0	0
7.77	25.16	25.57	0	0
7.79	25.06	25.46	0	0
7.81	24.96	25.34	0	0
7.83	24.87	25.22	0	0
7.85	24.8	25.14	0	0
7.87	24.7	25.03	0	0
7.90	24.62	24.93	0	0
7.92	24.53	24.82	0	0
7.94	24.47	24.75	0	0
7.96	24.44	24.76	0.3	0.3
7.98	24.64	25	0.85	0.81
8.00	24.83	25.23	0.85	0.81
8.02	25.03	25.45	0.85	0.81
8.04	25.18	25.63	0.84	0.82
8.06	25.32	25.79	0.84	0.81
8.08	25.45	25.94	0.84	0.81
8.10	25.59	26.09	0.84	0.81
8.12	25.73	26.28	0.85	0.81
8.15	25.86	26.43	0.84	0.81
8.17	25.99	26.58	0.84	0.81
8.19	25.98	26.58	0.85	0.82
8.21	26.09	26.72	0.85	0.82
8.23	26.2	26.86	0.85	0.82
8.25	26.22	26.88	0.85	0.82

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
8.27	26.31	27	0.85	0.81
8.29	26.41	27.12	0.85	0.81
8.31	26.48	27.2	0.84	0.82
8.33	26.53	27.27	0.85	0.82
8.35	26.58	27.33	0.85	0.82
8.37	26.64	27.41	0.85	0.81
8.40	26.73	27.5	0.85	0.82
8.42	26.8	27.59	0.85	0.82
8.44	26.87	27.67	0.85	0.82
8.46	26.91	27.71	0.04	0.03
8.48	26.78	27.59	0	0
8.50	26.61	27.39	0	0
8.52	26.46	27.2	0	0
8.54	26.32	27.03	0	0
8.56	26.17	26.86	0	0
8.58	26.04	26.69	0	0
8.60	25.91	26.54	0	0
8.62	25.78	26.37	0	0
8.65	25.64	26.21	0	0
8.67	25.51	26.05	0	0
8.69	25.38	25.9	0	0
8.71	25.26	25.75	0	0
8.73	25.14	25.61	0	0
8.75	25.02	25.46	0	0
8.77	24.91	25.33	0	0
8.79	24.8	25.2	0	0
8.81	24.71	25.08	0	0
8.83	24.61	24.96	0	0
8.85	24.51	24.84	0	0
8.87	24.42	24.73	0	0
8.90	24.33	24.62	0	0
8.92	24.24	24.52	0	0
8.94	24.17	24.42	0	0
8.96	24.12	24.39	0.3	0.3
8.98	24.26	24.59	0.85	0.81
9.00	24.43	24.8	0.85	0.82
9.02	24.6	25	0.85	0.81
9.04	24.75	25.2	0.85	0.82
9.06	24.9	25.38	0.85	0.81
9.08	25.04	25.56	0.85	0.81
9.10	25.18	25.73	0.85	0.81
9.12	25.35	25.93	0.85	0.81
9.15	25.51	26.12	0.85	0.81
9.17	25.67	26.3	0.85	0.81

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
9.19	25.83	26.49	0.85	0.81
9.21	25.98	26.67	0.85	0.81
9.23	26.13	26.84	0.85	0.81
9.25	26.25	26.97	0.85	0.81
9.27	26.36	27.1	0.85	0.81
9.29	26.46	27.23	0.85	0.81
9.31	26.56	27.34	0.85	0.82
9.33	26.66	27.45	0.85	0.82
9.35	26.76	27.57	0.85	0.82
9.37	26.86	27.68	0.85	0.81
9.40	26.95	27.79	0.85	0.83
9.42	27.03	27.88	0.85	0.83
9.44	27.1	27.97	0.85	0.83
9.46	27.15	28.04	0.04	0.03
9.48	27.02	27.92	0	0
9.50	26.85	27.72	0	0
9.52	26.69	27.53	0	0
9.54	26.52	27.33	0	0
9.56	26.36	27.15	0	0
9.58	26.25	27.02	0	0
9.60	26.1	26.85	0	0
9.62	25.95	26.67	0	0
9.65	25.81	26.5	0	0
9.67	25.67	26.33	0	0
9.69	25.54	26.17	0	0
9.71	25.45	26.07	0	0
9.73	25.32	25.91	0	0
9.75	25.18	25.75	0	0
9.77	25.05	25.6	0	0
9.79	24.93	25.45	0	0
9.81	24.81	25.3	0	0
9.83	24.71	25.19	0	0
9.85	24.62	25.08	0	0
9.87	24.5	24.94	0	0
9.90	24.4	24.81	0	0
9.92	24.3	24.69	0	0
9.94	24.2	24.57	0	0
9.96	24.14	24.51	0.3	0.3
9.98	24.3	24.71	0.85	0.83
10.00	24.45	24.9	0.85	0.83
10.02	24.59	25.08	0.85	0.83
10.04	24.73	25.26	0.85	0.84
10.06	24.85	25.42	0.85	0.83
10.08	24.97	25.57	0.85	0.83

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
10.10	25.1	25.72	0.85	0.83
10.12	25.24	25.88	0.85	0.83
10.15	25.39	26.06	0.85	0.83
10.17	25.54	26.23	0.85	0.84
10.19	25.68	26.38	0.85	0.83
10.21	25.78	26.51	0.85	0.84
10.23	25.88	26.64	0.85	0.83
10.25	25.98	26.76	0.85	0.84
10.27	26.06	26.87	0.85	0.83
10.29	26.17	26.99	0.85	0.83
10.31	26.26	27.1	0.85	0.83
10.33	26.35	27.21	0.85	0.83
10.35	26.43	27.31	0.85	0.84
10.37	26.51	27.4	0.85	0.83
10.40	26.6	27.51	0.85	0.83
10.42	26.68	27.59	0.85	0.83
10.44	26.74	27.68	0.85	0.83
10.46	26.76	27.71	0.05	0.05
10.48	26.63	27.58	0	0
10.50	26.49	27.41	0	0
10.52	26.33	27.2	0	0
10.54	26.16	27	0	0
10.56	26.01	26.81	0	0
10.58	25.89	26.67	0	0
10.60	25.74	26.48	0	0
10.62	25.59	26.3	0	0
10.65	25.45	26.13	0	0
10.67	25.35	26	0	0
10.69	25.22	25.84	0	0
10.71	25.1	25.69	0	0
10.73	24.98	25.54	0	0
10.75	24.89	25.43	0	0
10.77	24.79	25.29	0	0
10.79	24.68	25.15	0	0
10.81	24.59	25.05	0	0
10.83	24.5	24.93	0	0
10.85	24.41	24.82	0	0
10.87	24.31	24.69	0	0
10.90	24.23	24.6	0	0
10.92	24.18	24.54	0	0
10.94	24.16	24.51	0	0
10.96	24.15	24.53	0.3	0.3
10.98	24.31	24.75	0.85	0.83
11.00	24.51	24.99	0.85	0.83

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
11.02	24.69	25.19	0.85	0.83
11.04	24.83	25.36	0.85	0.83
11.06	24.97	25.53	0.85	0.83
11.08	25.11	25.69	0.85	0.83
11.10	25.24	25.84	0.85	0.83
11.12	25.39	26.01	0.85	0.83
11.15	25.51	26.15	0.85	0.83
11.17	25.62	26.29	0.85	0.83
11.19	25.73	26.43	0.85	0.83
11.21	25.83	26.57	0.85	0.83
11.23	25.94	26.71	0.85	0.83
11.25	26.05	26.83	0.85	0.83
11.27	26.15	26.94	0.85	0.83
11.29	26.23	27.04	0.85	0.83
11.31	26.31	27.15	0.85	0.83
11.33	26.4	27.25	0.85	0.83
11.35	26.48	27.35	0.85	0.83
11.37	26.56	27.44	0.85	0.83
11.40	26.63	27.52	0.85	0.83
11.42	26.69	27.59	0.84	0.83
11.44	26.76	27.68	0.84	0.83
11.46	26.78	27.71	0.05	0.05
11.48	26.63	27.57	0	0
11.50	26.46	27.37	0	0
11.52	26.29	27.17	0	0
11.54	26.15	27.01	0	0
11.56	25.98	26.82	0	0
11.58	25.81	26.62	0	0
11.60	25.65	26.44	0	0
11.62	25.53	26.3	0	0
11.65	25.39	26.13	0	0
11.67	25.24	25.96	0	0
11.69	25.09	25.79	0	0
11.71	25	25.68	0	0
11.73	24.93	25.59	0	0
11.75	24.83	25.47	0	0
11.77	24.72	25.34	0	0
11.79	24.61	25.21	0	0
11.81	24.52	25.11	0	0
11.83	24.41	24.98	0	0
11.85	24.3	24.85	0	0
11.87	24.2	24.72	0	0
11.90	24.11	24.63	0	0
11.92	24.01	24.51	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
11.94	23.92	24.4	0	0
11.96	23.86	24.35	0.3	0.3
11.98	24.02	24.55	0.85	0.83
12.00	24.2	24.76	0.85	0.83
12.02	24.31	24.92	0.85	0.83
12.04	24.38	25.04	0.85	0.83
12.06	24.47	25.17	0.85	0.83
12.08	24.58	25.32	0.85	0.83
12.10	24.68	25.46	0.85	0.83
12.12	24.78	25.6	0.85	0.83
12.15	24.9	25.74	0.85	0.83
12.17	25.01	25.87	0.85	0.83
12.19	25.11	26	0.85	0.83
12.21	25.21	26.12	0.85	0.83
12.23	25.31	26.23	0.85	0.83
12.25	25.41	26.35	0.85	0.83
12.27	25.5	26.46	0.85	0.83
12.29	25.6	26.57	0.85	0.83
12.31	25.69	26.66	0.85	0.83
12.33	25.77	26.76	0.85	0.83
12.35	25.87	26.86	0.85	0.83
12.37	25.96	26.95	0.85	0.83
12.40	26.03	27.04	0.85	0.83
12.42	26.1	27.12	0.85	0.83
12.44	26.18	27.2	0.85	0.83
12.46	26.2	27.24	0.05	0.05
12.48	26.07	27.13	0	0
12.50	25.91	26.94	0	0
12.52	25.75	26.76	0	0
12.54	25.61	26.6	0	0
12.56	25.46	26.43	0	0
12.58	25.34	26.28	0	0
12.60	25.19	26.12	0	0
12.62	25.05	25.96	0	0
12.65	24.95	25.83	0	0
12.67	24.82	25.69	0	0
12.69	24.7	25.54	0	0
12.71	24.6	25.42	0	0
12.73	24.48	25.28	0	0
12.75	24.41	25.19	0	0
12.77	24.33	25.09	0	0
12.79	24.24	24.98	0	0
12.81	24.17	24.88	0	0
12.83	24.07	24.77	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
12.85	23.99	24.67	0	0
12.87	23.9	24.56	0	0
12.90	23.8	24.45	0	0
12.92	23.73	24.36	0	0
12.94	23.66	24.26	0	0
12.96	23.63	24.24	0.3	0.3
12.98	23.81	24.45	0.85	0.83
13.00	23.94	24.6	0.85	0.83
13.02	24.02	24.73	0.85	0.83
13.04	24.13	24.88	0.85	0.83
13.06	24.26	25.03	0.85	0.83
13.08	24.38	25.19	0.85	0.83
13.10	24.52	25.34	0.85	0.83
13.12	24.64	25.49	0.85	0.83
13.15	24.76	25.63	0.85	0.83
13.17	24.88	25.77	0.85	0.83
13.19	25	25.9	0.85	0.83
13.21	25.11	26.03	0.85	0.83
13.23	25.22	26.16	0.85	0.83
13.25	25.33	26.28	0.85	0.83
13.27	25.44	26.39	0.85	0.83
13.29	25.54	26.5	0.85	0.83
13.31	25.64	26.6	0.85	0.83
13.33	25.74	26.7	0.85	0.83
13.35	25.83	26.8	0.85	0.83
13.37	25.93	26.89	0.85	0.83
13.40	26.01	26.99	0.85	0.83
13.42	26.1	27.08	0.85	0.83
13.44	26.19	27.18	0.85	0.83
13.46	26.22	27.23	0.05	0.05
13.48	26.11	27.14	0	0
13.50	25.97	26.98	0	0
13.52	25.82	26.83	0	0
13.54	25.69	26.69	0	0
13.56	25.55	26.54	0	0
13.58	25.44	26.4	0	0
13.60	25.31	26.25	0	0
13.62	25.19	26.13	0	0
13.65	25.06	25.99	0	0
13.67	24.95	25.86	0	0
13.69	24.83	25.73	0	0
13.71	24.74	25.61	0	0
13.73	24.66	25.51	0	0
13.75	24.61	25.44	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
13.77	24.52	25.34	0	0
13.79	24.46	25.25	0	0
13.81	24.37	25.15	0	0
13.83	24.29	25.06	0	0
13.85	24.22	24.96	0	0
13.87	24.15	24.88	0	0
13.90	24.07	24.78	0	0
13.92	24.01	24.71	0	0
13.94	23.98	24.67	0	0
13.96	23.99	24.69	0.3	0.3
13.98	24.06	24.75	0.86	0.83
14.00	24.16	24.87	0.86	0.83
14.02	24.27	25.01	0.86	0.83
14.04	24.41	25.18	0.86	0.83
14.06	24.54	25.34	0.86	0.83
14.08	24.67	25.49	0.86	0.83
14.10	24.8	25.64	0.86	0.83
14.12	24.93	25.78	0.86	0.83
14.15	25.04	25.9	0.86	0.83
14.17	25.15	26.03	0.86	0.83
14.19	25.27	26.17	0.86	0.83
14.21	25.38	26.3	0.86	0.83
14.23	25.48	26.42	0.86	0.83
14.25	25.6	26.55	0.86	0.83
14.27	25.72	26.66	0.86	0.83
14.29	25.82	26.77	0.86	0.83
14.31	25.92	26.88	0.86	0.83
14.33	26.01	26.98	0.86	0.83
14.35	26.11	27.08	0.86	0.83
14.37	26.2	27.18	0.86	0.83
14.40	26.28	27.27	0.86	0.83
14.42	26.37	27.37	0.86	0.83
14.44	26.44	27.46	0.86	0.83
14.46	26.48	27.51	0.05	0.05
14.48	26.35	27.4	0	0
14.50	26.17	27.21	0	0
14.52	26	27.01	0	0
14.54	25.83	26.83	0	0
14.56	25.69	26.66	0	0
14.58	25.56	26.51	0	0
14.60	25.42	26.35	0	0
14.62	25.29	26.2	0	0
14.65	25.16	26.05	0	0
14.67	25.04	25.91	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
14.69	24.93	25.78	0	0
14.71	24.81	25.64	0	0
14.73	24.69	25.5	0	0
14.75	24.57	25.36	0	0
14.77	24.47	25.25	0	0
14.79	24.37	25.12	0	0
14.81	24.27	25	0	0
14.83	24.17	24.87	0	0
14.85	24.06	24.75	0	0
14.87	23.98	24.65	0	0
14.90	23.89	24.53	0	0
14.92	23.8	24.42	0	0
14.94	23.72	24.33	0	0
14.96	23.69	24.31	0.3	0.3
14.98	23.87	24.51	0.86	0.83
15.00	24.04	24.7	0.86	0.83
15.02	24.2	24.88	0.86	0.83
15.04	24.36	25.05	0.86	0.83
15.06	24.5	25.22	0.86	0.83
15.08	24.63	25.37	0.86	0.83
15.10	24.74	25.52	0.86	0.83
15.12	24.87	25.68	0.86	0.83
15.15	25.01	25.84	0.86	0.83
15.17	25.14	25.98	0.86	0.83
15.19	25.29	26.14	0.83	0.83
15.21	25.42	26.29	0.85	0.83
15.23	25.55	26.43	0.85	0.83
15.25	25.69	26.57	0.86	0.83
15.27	25.81	26.71	0.86	0.83
15.29	25.94	26.84	0.86	0.83
15.31	26.06	26.98	0.86	0.83
15.33	26.18	27.11	0.86	0.83
15.35	26.3	27.23	0.86	0.83
15.37	26.42	27.35	0.86	0.83
15.40	26.53	27.46	0.86	0.83
15.42	26.64	27.59	0.85	0.83
15.44	26.75	27.7	0.86	0.83
15.46	26.8	27.76	0.05	0.05
15.48	26.73	27.72	0	0
15.50	26.6	27.57	0	0
15.52	26.5	27.45	0	0
15.54	26.37	27.31	0	0
15.56	26.27	27.19	0	0
15.58	26.14	27.05	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
15.60	26.05	26.95	0	0
15.62	25.93	26.81	0	0
15.65	25.81	26.68	0	0
15.67	25.75	26.6	0	0
15.69	25.67	26.5	0	0
15.71	25.59	26.41	0	0
15.73	25.51	26.31	0	0
15.75	25.44	26.22	0	0
15.77	25.31	26.08	0	0
15.79	25.26	26.01	0	0
15.81	25.19	25.93	0	0
15.83	25.13	25.86	0	0
15.85	25.08	25.77	0	0
15.87	25	25.68	0	0
15.90	24.93	25.6	0	0
15.92	24.86	25.51	0	0
15.94	24.82	25.46	0	0
15.96	24.76	25.42	0.3	0.3
15.98	24.93	25.61	0.86	0.83
16.00	25.08	25.77	0.86	0.83
16.02	25.22	25.93	0.86	0.83
16.04	25.35	26.08	0.86	0.83
16.06	25.48	26.22	0.86	0.83
16.08	25.6	26.36	0.86	0.83
16.10	25.73	26.5	0.86	0.83
16.12	25.84	26.62	0.85	0.83
16.15	25.94	26.73	0.86	0.83
16.17	26.04	26.84	0.85	0.83
16.19	26.14	26.95	0.85	0.83
16.23	26.34	27.18	0.85	0.83
16.25	26.43	27.27	0.86	0.83
16.27	26.51	27.37	0.86	0.83
16.29	26.6	27.46	0.85	0.83
16.31	26.69	27.57	0.86	0.83
16.33	26.77	27.65	0.85	0.83
16.35	26.84	27.74	0.86	0.83
16.37	26.91	27.81	0.85	0.83
16.40	26.97	27.89	0.85	0.83
16.42	27.05	27.98	0.86	0.83
16.44	27.1	28.05	0.85	0.83
16.46	27.11	28.09	0.05	0.05
16.48	26.96	27.96	0	0
16.50	26.79	27.79	0	0
16.52	26.6	27.59	0	0

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
16.54	26.41	27.4	0	0
16.56	26.23	27.21	0	0
16.58	26.09	27.06	0	0
16.60	25.94	26.89	0	0
16.62	25.79	26.73	0	0
16.65	25.64	26.57	0	0
16.67	25.52	26.44	0	0
16.69	25.38	26.29	0	0
16.71	25.26	26.15	0	0
16.73	25.15	26.02	0	0
16.75	25.05	25.9	0	0
16.77	24.96	25.8	0	0
16.79	24.9	25.71	0	0
16.81	24.81	25.59	0	0
16.83	24.72	25.49	0	0
16.85	24.62	25.37	0	0
16.87	24.51	25.26	0	0
16.90	24.43	25.16	0	0
16.92	24.33	25.04	0	0
16.94	24.24	24.94	0	0
16.96	24.18	24.89	0.3	0.3
16.98	24.35	25.09	0.86	0.83
17.00	24.56	25.32	0.86	0.83
17.02	24.71	25.48	0.86	0.83
17.04	24.84	25.63	0.86	0.83
17.06	24.94	25.76	0.86	0.83
17.08	25.05	25.9	0.86	0.83
17.10	25.17	26.05	0.86	0.83
17.12	25.3	26.2	0.86	0.83
17.15	25.42	26.32	0.85	0.83
17.17	25.54	26.46	0.86	0.83
17.19	25.65	26.59	0.86	0.83
17.21	25.76	26.72	0.84	0.83
17.23	25.8	26.8	0.85	0.83
17.25	25.88	26.91	0.85	0.83
17.27	25.97	27.02	0.85	0.83
17.29	26.08	27.14	0.85	0.83
17.31	26.18	27.25	0.85	0.83
17.33	26.26	27.35	0.85	0.83
17.35	26.34	27.45	0.85	0.83
17.37	26.42	27.55	0.85	0.83
17.40	26.5	27.65	0.85	0.83
17.42	26.6	27.76	0.85	0.83
17.44	26.65	27.83	0.85	0.83

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
17.46	26.71	27.91	0.05	0.05
17.48	26.61	27.84	0	0
17.50	26.47	27.67	0	0
17.52	26.33	27.5	0	0
17.54	26.21	27.35	0	0
17.56	26.08	27.2	0	0
17.58	25.97	27.06	0	0
17.60	25.85	26.91	0	0
17.62	25.72	26.76	0	0
17.65	25.61	26.62	0	0
17.67	25.5	26.49	0	0
17.69	25.39	26.37	0	0
17.71	25.29	26.24	0	0
17.73	25.18	26.1	0	0
17.75	25.08	25.98	0	0
17.77	24.98	25.86	0	0
17.79	24.88	25.76	0	0
17.81	24.78	25.65	0	0
17.83	24.69	25.52	0	0
17.85	24.6	25.41	0	0
17.87	24.52	25.31	0	0
17.90	24.43	25.21	0	0
17.92	24.36	25.11	0	0
17.94	24.29	25	0	0
17.96	24.24	24.95	0.3	0.3
17.98	24.33	25.09	0.86	0.83
18.00	24.44	25.24	0.86	0.83
18.02	24.54	25.37	0.86	0.83
18.04	24.65	25.42	0.86	0.83
18.06	24.77	25.54	0.86	0.83
18.08	24.75	25.45	0.86	0.83
18.10	24.87	25.56	0.86	0.83
18.12	25	25.72	0.86	0.83
18.15	25.12	25.87	0.85	0.83
18.17	25.24	26.02	0.84	0.83
18.19	25.35	26.16	0.83	0.83
18.21	25.45	26.29	0.84	0.83
18.23	25.55	26.42	0.84	0.83
18.25	25.65	26.54	0.85	0.83
18.27	25.76	26.67	0.85	0.83
18.29	25.86	26.79	0.85	0.83
18.31	25.96	26.91	0.85	0.83
18.33	26.05	27.01	0.85	0.83
18.35	26.14	27.13	0.85	0.83

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
18.37	26.25	27.24	0.85	0.83
18.40	26.34	27.35	0.85	0.83
18.42	26.44	27.46	0.85	0.83
18.44	26.53	27.57	0.85	0.83
18.46	26.56	27.63	0.05	0.05
18.48	26.46	27.53	0	0
18.50	26.33	27.35	0	0
18.52	26.21	27.18	0	0
18.54	26.08	27.02	0	0
18.56	25.97	26.85	0	0
18.58	25.85	26.7	0	0
18.60	25.75	26.55	0	0
18.62	25.64	26.4	0	0
18.65	25.54	26.28	0	0
18.67	25.46	26.17	0	0
18.69	25.38	26.06	0	0
18.71	25.27	25.92	0	0
18.73	25.18	25.79	0	0
18.75	25.08	25.69	0	0
18.77	24.98	25.59	0	0
18.79	24.89	25.47	0	0
18.81	24.8	25.35	0	0
18.83	24.71	25.25	0	0
18.85	24.62	25.16	0	0
18.87	24.52	25.07	0	0
18.90	24.44	24.98	0	0
18.92	24.37	24.87	0	0
18.94	24.3	24.77	0	0
18.96	24.25	24.72	0.3	0.3
18.98	24.35	24.88	0.84	0.83
19.00	24.49	25.07	0.84	0.83
19.02	24.65	25.26	0.84	0.83
19.04	24.79	25.44	0.85	0.83
19.06	24.94	25.61	0.85	0.83
19.08	25.08	25.77	0.85	0.83
19.10	25.2	25.93	0.85	0.83
19.12	25.32	26.08	0.84	0.83
19.15	25.45	26.23	0.85	0.83
19.17	25.56	26.36	0.83	0.83
19.19	25.66	26.49	0.84	0.83
19.21	25.76	26.62	0.84	0.83
19.23	25.85	26.74	0.84	0.83
19.25	25.95	26.85	0.85	0.83
19.27	26.04	26.96	0.84	0.83

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
19.29	26.14	27.08	0.85	0.83
19.31	26.22	27.19	0.84	0.83
19.33	26.3	27.29	0.84	0.83
19.35	26.39	27.4	0.84	0.83
19.37	26.48	27.51	0.84	0.83
19.40	26.58	27.61	0.84	0.83
19.42	26.66	27.71	0.85	0.82
19.44	26.75	27.81	0.84	0.82
19.46	26.79	27.87	0.05	0.05
19.48	26.68	27.77	0	0
19.50	26.55	27.6	0	0
19.52	26.42	27.42	0	0
19.54	26.3	27.24	0	0
19.56	26.18	27.07	0	0
19.58	26.06	26.91	0	0
19.60	25.95	26.75	0	0
19.62	25.84	26.6	0	0
19.65	25.73	26.45	0	0
19.67	25.62	26.31	0	0
19.69	25.51	26.2	0	0
19.71	25.4	26.1	0	0
19.73	25.36	26.01	0	0
19.75	25.26	25.88	0	0
19.77	25.16	25.78	0	0
19.79	25.07	25.67	0	0
19.81	24.99	25.55	0	0
19.83	24.91	25.43	0	0
19.85	24.82	25.32	0	0
19.87	24.72	25.24	0	0
19.90	24.64	25.16	0	0
19.92	24.56	25.06	0	0
19.94	24.49	24.96	0	0
19.96	24.44	24.92	0.3	0.3
19.98	24.53	25.07	0.84	0.83
20.00	24.66	25.24	0.84	0.83
20.02	24.81	25.43	0.86	0.83
20.04	24.96	25.6	0.85	0.83
20.06	25.1	25.77	0.86	0.83
20.08	25.23	25.93	0.86	0.83
20.10	25.36	26.08	0.85	0.83
20.12	25.48	26.22	0.84	0.83
20.15	25.59	26.37	0.84	0.83
20.17	25.7	26.5	0.85	0.83
20.19	25.81	26.63	0.83	0.83

Table C.2 continued.

Day	Control Temperature (°C)	Mussel Temperature (°C)	Control Light Attenuation Factor	Mussel Light Attenuation Factor
20.21	25.92	26.76	0.83	0.83
20.23	26.02	26.89	0.84	0.83
20.25	26.12	27.01	0.83	0.83
20.27	26.22	27.13	0.83	0.83
20.29	26.32	27.25	0.83	0.83
20.31	26.41	27.36	0.83	0.83
20.33	26.49	27.47	0.83	0.82
20.35	26.59	27.57	0.83	0.82
20.37	26.68	27.68	0.83	0.82
20.40	26.76	27.78	0.83	0.82
20.42	26.83	27.87	0.83	0.82
20.44	26.91	27.96	0.83	0.82
20.46	26.95	28.02	0.05	0.05
20.48	26.84	27.91	0	0
20.50	26.71	27.74	0	0
20.52	26.55	27.55	0	0
20.54	26.39	27.36	0	0
20.56	26.22	27.17	0	0
20.58	26.07	26.99	0	0
20.60	25.94	26.85	0	0
20.62	25.84	26.7	0	0
20.65	25.73	26.54	0	0
20.67	25.63	26.4	0	0
20.69	25.53	26.27	0	0
20.71	25.44	26.13	0	0
20.73	25.34	25.99	0	0
20.75	25.25	25.87	0	0
20.77	25.16	25.74	0	0
20.79	25.06	25.62	0	0
20.81	24.98	25.5	0	0
20.83	24.9	25.39	0	0
20.85	24.82	25.28	0	0
20.87	24.73	25.17	0	0
20.90	24.65	25.07	0	0
20.92	24.58	24.99	0	0
20.94	24.51	24.9	0	0
20.96	24.47	24.86	0.3	0.3
20.98	24.61	25.06	0.83	0.83

APPENDIX D:
MULTIPLE VARIABLE SENSITIVITY ANALYSIS RESULTS

Table D.1: Control flow model variables for the 263 sensitivity runs that met the criteria established by the multiple variable sensitivity analysis.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
1988	Organic N	0.75	0.999	-0.019	0.069	0.92	13.81	18.56	0.052	0.0091	0.023	0.012	0.0060	-0.010
1972	Nitrate	3.41	0.968	0.153	0.006	0.21	21.68	11.71	0.062	0.0091	-0.024	-0.013	0.0035	0.047
1954	Organic N	0.77	0.997	0.147	0.046	0.72	15.21	19.74	0.070	0.0048	0.100	0.023	0.0026	-0.015
1932	Organic N	0.80	0.989	0.106	0.021	0.73	16.76	22.59	0.031	0.0087	0.088	0.007	-0.0006	-0.043
1917	Nitrate	3.39	0.992	0.142	0.016	0.70	6.95	13.90	0.066	0.0133	0.039	0.009	0.0062	0.058
1914	Organic N	0.74	0.951	0.219	-0.026	0.40	22.49	4.30	0.080	0.0038	-0.060	0.011	0.0028	0.004
1911	Nitrate	3.43	0.959	0.120	0.004	-0.57	14.79	23.73	0.063	0.0053	0.092	0.002	0.0050	0.021
1900	Organic N	0.73	0.960	0.142	0.092	0.24	31.23	41.32	0.058	0.0067	0.022	0.002	0.0015	-0.011
1897	Total N	4.22	0.995	0.031	-0.008	0.57	17.94	16.53	0.095	0.0104	0.030	0.001	0.0091	0.016
1889	Total N	4.18	0.958	0.156	-0.002	0.42	44.95	21.74	0.080	0.0033	0.048	0.009	0.0010	0.010
1885	Organic N	0.76	0.971	0.012	0.069	0.56	3.72	33.54	0.049	0.0049	0.037	0.005	0.0081	-0.037
1883	Organic N	0.78	0.999	0.055	0.053	0.83	7.23	17.68	0.061	0.0023	0.123	0.025	0.0031	-0.018
1873	Organic N	0.78	0.997	0.097	0.106	0.82	11.61	19.40	0.063	0.0064	0.073	0.011	0.0027	-0.001
1871	Organic N	0.73	0.997	0.174	-0.014	0.83	8.60	19.95	0.051	0.0048	0.033	-0.001	0.0120	-0.004
1868	Total N	4.00	0.993	0.152	0.013	0.85	13.42	14.68	0.053	0.0026	0.040	0.000	0.0068	0.007
1868	Nitrate	3.31	0.994	0.152	0.013	0.85	13.42	14.68	0.053	0.0026	0.040	0.000	0.0068	0.007
1851	Organic N	0.77	0.968	0.161	0.007	0.65	21.36	6.07	0.075	0.0064	0.017	-0.005	0.0021	0.000
1844	Nitrate	3.25	0.960	0.135	0.006	0.70	17.54	25.10	0.066	0.0055	0.006	0.024	0.0037	0.046
1841	Organic N	0.74	0.998	-0.069	0.055	0.38	20.74	14.08	0.066	0.0031	0.073	0.022	0.0049	-0.020
1824	Organic N	0.78	0.983	0.103	0.010	0.71	-2.33	26.68	0.057	-0.0035	0.074	0.012	0.0084	-0.014
1800	Organic N	0.78	0.965	0.150	0.064	0.63	17.67	5.59	0.058	0.0118	0.042	0.005	0.0009	-0.007
1797	Organic N	0.80	0.982	0.120	0.081	0.54	8.69	26.01	0.065	0.0111	0.077	0.002	0.0013	-0.029
1793	Total N	4.15	0.988	-0.006	0.102	1.14	-11.55	13.91	0.064	0.0090	0.073	-0.003	0.0061	0.000
1793	Organic N	0.79	0.999	-0.006	0.102	1.14	-11.55	13.91	0.064	0.0090	0.073	-0.003	0.0061	0.000
1793	Nitrate	3.24	0.987	-0.006	0.102	1.14	-11.55	13.91	0.064	0.0090	0.073	-0.003	0.0061	0.000
1776	Nitrate	3.52	0.971	0.126	0.003	0.75	12.82	21.63	0.078	0.0023	0.055	0.007	0.0037	0.050
1756	Total N	3.99	0.993	0.150	0.020	0.21	8.51	21.31	0.032	0.0084	0.085	0.012	0.0053	-0.040
1756	Organic N	0.77	0.996	0.150	0.020	0.21	8.51	21.31	0.032	0.0084	0.085	0.012	0.0053	-0.040

Table D.1 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
1753	Total N	4.06	0.985	-0.045	-0.004	0.51	36.66	17.97	0.051	0.0066	0.014	0.010	0.0027	0.034
1753	Nitrate	3.56	0.991	-0.045	-0.004	0.51	36.66	17.97	0.051	0.0066	0.014	0.010	0.0027	0.034
1750	Organic N	0.78	0.997	0.087	0.063	0.44	9.15	19.46	0.079	0.0044	0.033	0.016	0.0035	-0.002
1737	Organic N	0.79	0.982	0.144	0.056	0.36	11.24	26.20	0.073	0.0050	0.070	0.020	0.0016	-0.020
1733	Organic N	0.81	0.955	0.184	0.131	0.47	2.15	33.59	0.064	0.0003	-0.037	0.012	0.0012	-0.036
1730	Organic N	0.75	0.997	0.007	-0.004	0.46	-8.32	13.28	0.065	0.0020	0.017	-0.001	0.0042	0.002
1726	Nitrate	3.28	0.975	-0.154	0.083	1.15	-8.92	12.53	0.033	0.0080	0.085	0.021	0.0089	0.090
1721	Nitrite	0.02	0.965	0.120	0.021	0.89	26.51	22.79	0.076	0.0074	0.042	0.022	-0.0022	0.051
1718	Total N	3.99	0.973	0.073	0.009	-0.16	2.98	21.71	0.091	0.0076	0.096	0.022	0.0028	0.015
1718	Nitrate	3.43	0.974	0.073	0.009	-0.16	2.98	21.71	0.091	0.0076	0.096	0.022	0.0028	0.015
1714	Organic N	0.77	0.991	0.137	0.113	-0.13	4.65	26.11	0.054	0.0127	-0.013	-0.003	0.0083	0.000
1695	Organic N	0.75	1.000	0.060	0.068	0.87	15.91	17.03	0.067	0.0147	0.056	0.009	0.0053	-0.011
1694	Nitrate	3.27	0.998	0.173	0.036	0.51	-2.46	18.37	0.073	0.0081	0.103	0.010	0.0016	0.011
1690	Nitrate	3.42	1.000	0.232	0.017	0.74	3.12	15.87	0.072	0.0070	0.035	0.007	-0.0009	0.027
1680	Organic N	0.75	0.999	0.063	0.050	0.42	21.60	19.33	0.085	0.0105	0.047	0.002	0.0035	-0.011
1659	Organic N	0.78	1.000	0.068	0.163	0.34	3.46	15.82	0.034	0.0087	0.031	0.017	0.0044	-0.013
1649	Organic N	0.81	0.989	0.283	-0.079	0.37	6.37	22.73	0.065	0.0115	0.026	0.016	-0.0045	-0.034
1647	Organic N	0.81	0.997	-0.053	0.052	0.90	20.41	17.08	0.090	0.0052	0.012	0.011	-0.0004	-0.022
1646	Total N	4.14	0.988	0.101	-0.012	0.47	18.77	12.95	0.086	0.0079	0.075	-0.002	0.0023	0.033
1644	Organic N	0.76	1.000	0.021	0.053	-0.09	19.54	15.13	0.043	0.0056	0.035	0.014	-0.0035	0.001
1635	Total N	4.06	0.966	0.007	-0.003	0.13	30.33	10.93	0.071	0.0018	0.002	-0.007	0.0002	0.060
1625	Total N	4.06	0.961	0.205	-0.006	0.12	-1.56	21.57	0.025	0.0074	0.049	0.003	0.0023	0.025
1605	Organic N	0.75	0.989	0.252	0.127	0.49	20.41	10.00	0.072	0.0078	0.045	-0.002	0.0044	-0.027
1595	Organic N	0.78	0.992	0.041	0.086	0.88	6.75	10.60	0.084	0.0085	0.105	-0.008	0.0034	-0.004
1591	Nitrate	3.40	0.996	0.239	0.003	0.92	22.46	14.58	0.068	0.0047	0.005	0.007	0.0059	0.053
1586	Nitrate	3.51	1.000	0.036	0.004	0.32	13.21	15.44	0.084	0.0036	0.045	0.014	-0.0006	0.146
1585	Nitrite	0.02	0.955	0.220	0.095	1.06	34.51	5.66	0.040	0.0064	0.035	0.015	-0.0005	0.013
1569	Nitrate	3.40	0.997	0.014	0.069	0.89	-18.16	17.86	0.094	0.0047	0.033	0.013	-0.0005	0.025
1556	Total N	4.19	0.980	0.071	-0.017	0.25	14.20	11.81	0.042	0.0106	-0.009	0.004	0.0073	0.031
1553	Total N	4.16	0.981	0.221	0.002	0.33	29.90	21.93	0.038	0.0043	0.062	0.008	0.0125	-0.001
1548	Nitrate	3.26	0.992	0.114	0.021	0.77	3.24	20.32	0.064	0.0128	0.082	0.009	0.0066	0.023
1547	Organic N	0.79	0.987	0.070	0.026	0.48	31.54	9.12	0.088	0.0033	0.028	0.024	-0.0030	-0.004
1531	Total N	4.02	0.994	0.153	0.023	0.63	10.50	15.47	0.081	0.0125	-0.016	0.015	0.0028	-0.001
1531	Organic N	0.79	0.999	0.153	0.023	0.63	10.50	15.47	0.081	0.0125	-0.016	0.015	0.0028	-0.001
1530	Phyto	0.05	0.953	0.168	-0.004	0.85	21.60	15.69	0.020	0.0047	-0.012	0.018	0.0035	0.003

Table D.1 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/ Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
1527	Organic N	0.76	0.953	0.066	0.078	0.51	21.19	4.45	0.054	0.0119	0.029	0.019	0.0075	-0.023
1508	Organic N	0.77	0.999	0.017	0.062	0.24	11.38	17.96	0.077	0.0022	-0.020	0.014	0.0040	-0.015
1501	Organic N	0.74	0.984	0.227	0.007	0.15	14.25	28.28	0.068	0.0086	0.083	0.024	0.0051	0.000
1500	Nitrate	3.45	0.962	-0.070	-0.003	0.40	28.70	22.04	0.075	0.0068	-0.009	0.008	0.0048	0.043
1497	Total N	4.38	0.963	0.249	0.003	0.78	12.33	22.46	0.049	0.0056	0.067	0.023	0.0020	-0.005
1497	Organic N	0.78	0.992	0.249	0.003	0.78	12.33	22.46	0.049	0.0056	0.067	0.023	0.0020	-0.005
1497	Nitrate	3.54	0.963	0.249	0.003	0.78	12.33	22.46	0.049	0.0056	0.067	0.023	0.0020	-0.005
1485	Organic N	0.76	0.982	0.092	0.036	0.56	11.45	8.27	0.056	-0.0023	-0.024	0.000	0.0090	-0.031
1477	Total N	4.02	0.987	0.060	0.000	0.71	6.65	13.11	0.036	0.0117	0.054	0.006	0.0022	0.064
1473	Organic N	0.77	0.963	0.038	-0.001	0.68	15.06	5.41	0.090	0.0069	0.053	0.009	0.0046	-0.067
1471	Total N	4.09	0.961	0.095	-0.003	0.45	12.27	21.63	0.054	0.0006	0.031	0.020	-0.0023	0.021
1468	Phyto	0.05	0.953	0.166	-0.027	0.26	5.25	15.95	0.068	0.0057	-0.004	0.022	-0.0009	0.089
1459	Organic N	0.77	0.987	0.148	0.057	1.31	18.58	9.36	0.055	0.0095	0.088	0.013	0.0026	-0.004
1446	Nitrite	0.02	0.950	0.126	0.040	0.53	27.41	19.96	0.088	0.0052	0.055	0.018	0.0023	0.077
1445	Nitrate	3.30	0.958	0.095	0.015	0.97	1.69	24.55	0.081	0.0052	0.014	-0.002	0.0042	0.116
1442	Nitrate	3.37	0.999	0.137	0.038	0.66	-5.64	15.95	0.076	-0.0006	0.049	0.010	0.0097	0.108
1429	Total N	4.18	0.992	0.050	-0.045	-0.34	35.41	13.43	0.057	0.0054	0.044	0.008	0.0009	0.030
1414	Organic N	0.79	0.996	-0.038	0.012	0.32	38.71	11.64	0.056	0.0043	0.093	0.028	-0.0027	-0.001
1410	Nitrate	3.51	0.960	0.058	0.005	0.09	17.70	10.69	0.050	0.0091	0.047	0.008	0.0062	0.054
1390	Nitrate	3.43	0.991	0.024	0.005	0.49	19.56	13.48	0.037	0.0011	-0.023	0.007	0.0097	0.051
1374	Organic N	0.80	0.992	0.110	0.040	0.39	6.32	21.03	0.053	0.0087	0.117	0.016	-0.0034	-0.009
1372	Organic N	0.77	0.979	0.217	0.079	1.02	16.29	30.02	0.082	0.0050	0.040	0.016	0.0027	-0.033
1361	Organic N	0.79	0.994	0.063	0.127	0.65	11.72	11.20	0.064	0.0023	0.063	0.005	0.0004	-0.002
1354	Organic N	0.75	0.995	0.065	0.012	0.77	23.70	12.04	0.062	0.0033	-0.004	0.006	0.0035	-0.004
1347	Nitrate	3.30	0.986	0.120	0.015	0.68	13.18	13.63	0.060	-0.0010	0.096	-0.003	0.0060	0.044
1343	Organic N	0.78	0.969	0.123	0.078	0.59	35.54	32.77	0.061	0.0018	0.035	0.016	0.0005	-0.008
1338	Organic N	0.78	0.992	0.043	0.028	0.44	8.46	10.45	0.062	0.0032	0.017	0.008	0.0035	-0.026
1336	Organic N	0.73	0.997	-0.062	-0.015	0.37	3.94	20.19	0.043	0.0097	0.089	0.010	-0.0072	0.002
1332	Organic N	0.79	0.960	0.211	0.036	0.61	14.23	34.91	0.079	0.0088	0.069	-0.010	0.0015	-0.001
1323	Organic N	0.77	1.000	-0.059	0.093	0.07	22.39	16.91	0.094	0.0057	-0.006	0.014	0.0019	-0.017
1309	Organic N	0.80	0.979	0.134	-0.003	0.03	29.95	27.36	0.079	0.0054	0.024	0.010	0.0003	-0.011
1303	Organic N	0.78	0.978	0.367	0.046	0.65	16.32	7.36	0.069	0.0013	-0.025	0.006	0.0014	-0.006
1299	Nitrite	0.02	0.954	0.101	-0.041	0.62	29.07	24.31	0.074	0.0083	0.059	0.010	0.0015	0.056
1297	Organic N	0.81	0.991	0.111	0.021	0.77	21.13	20.70	0.087	0.0075	0.002	0.021	0.0013	-0.002
1295	Total N	4.37	0.977	0.073	-0.004	0.82	30.04	11.39	0.057	0.0037	0.043	0.001	0.0109	0.010

Table D.1 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/ Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
1291	Total N	4.18	0.964	-0.129	-0.042	0.52	0.68	21.46	0.059	0.0134	0.103	0.009	0.0021	0.013
1288	Total N	4.25	0.954	-0.023	-0.010	1.10	12.33	10.05	0.038	0.0036	0.009	0.019	0.0066	0.024
1268	Organic N	0.75	1.000	0.131	0.101	0.59	18.91	17.29	0.073	0.0105	0.094	0.000	0.0037	-0.047
1234	Organic N	0.80	0.988	0.097	0.074	-0.40	7.28	22.86	0.064	0.0000	0.048	0.022	0.0006	-0.039
1231	Organic N	0.80	0.962	0.102	0.104	0.49	8.50	33.97	0.032	0.0051	0.001	-0.004	0.0021	-0.026
1226	Organic N	0.76	0.977	0.095	0.043	0.94	15.42	7.55	0.053	0.0063	-0.004	0.014	0.0043	0.001
1218	Organic N	0.77	1.000	0.069	0.101	0.99	16.66	17.62	0.082	0.0072	0.026	0.006	0.0034	-0.003
1215	Organic N	0.79	0.999	0.188	0.007	1.05	2.42	16.31	0.054	0.0060	-0.020	0.013	0.0024	-0.007
1215	Nitrate	3.54	0.999	0.188	0.007	1.05	2.42	16.31	0.054	0.0060	-0.020	0.013	0.0024	-0.007
1210	Organic N	0.79	0.994	0.190	0.047	0.67	45.28	11.02	0.046	0.0052	-0.048	0.028	-0.0015	-0.012
1181	Organic N	0.76	0.987	0.168	0.048	-0.02	17.17	26.51	0.070	0.0082	0.051	0.018	0.0033	-0.011
1179	Organic N	0.74	0.999	0.104	0.103	0.60	22.30	17.51	0.059	0.0029	0.039	0.033	0.0037	-0.007
1167	Total N	4.01	0.954	0.089	-0.025	0.82	13.35	22.15	0.048	0.0065	0.084	0.021	0.0039	0.032
1164	Total N	4.14	0.958	0.196	-0.003	0.93	13.08	22.04	0.070	0.0041	0.040	0.003	0.0028	0.015
1144	Organic N	0.75	0.988	0.172	0.060	-0.05	28.75	26.34	0.067	0.0052	0.029	0.000	0.0018	-0.010
1143	Nitrate	3.41	0.953	0.068	0.013	0.06	12.16	10.64	0.054	0.0096	-0.028	0.015	0.0048	0.050
1140	Total N	4.05	0.953	0.113	0.072	0.25	-2.32	11.42	0.043	0.0130	0.040	0.005	0.0106	0.002
1140	Organic N	0.74	0.991	0.113	0.072	0.25	-2.32	11.42	0.043	0.0130	0.040	0.005	0.0106	0.002
1132	Organic N	0.78	0.978	0.142	0.036	0.33	-0.78	7.49	0.078	0.0064	-0.018	0.026	0.0024	0.000
1121	Organic N	0.78	0.993	0.078	0.065	0.29	3.96	22.63	0.080	0.0084	0.065	-0.017	0.0053	-0.035
1118	Organic N	0.75	0.999	-0.029	0.026	0.33	9.25	17.80	0.055	0.0079	0.036	-0.001	0.0086	-0.046
1107	Organic N	0.78	0.978	0.153	0.072	0.77	-1.54	7.37	0.052	0.0067	0.057	0.010	0.0074	-0.029
1102	Nitrate	3.48	0.975	0.096	0.017	-0.11	-9.82	21.20	0.034	-0.0029	0.062	0.020	0.0003	0.038
1101	Organic N	0.77	0.990	0.141	0.007	0.34	9.85	10.26	0.088	0.0094	0.008	0.017	0.0060	-0.003
1101	Nitrate	3.56	0.954	0.141	0.007	0.34	9.85	10.26	0.088	0.0094	0.008	0.017	0.0060	-0.003
1097	Total N	4.26	0.998	0.075	0.002	0.82	-1.48	15.72	0.060	0.0079	0.023	0.009	0.0006	0.013
1080	Phyto	0.06	0.950	0.070	-0.016	0.87	4.62	13.48	0.053	0.0018	0.008	-0.002	0.0010	0.070
1079	Organic N	0.74	0.998	0.312	0.100	-0.26	29.79	19.20	0.052	0.0076	0.088	0.014	0.0019	-0.006
1077	Organic N	0.79	0.998	0.120	0.024	-0.16	31.32	18.22	0.075	0.0047	0.030	0.014	0.0003	-0.021
1069	Organic N	0.79	0.998	0.199	0.015	0.22	22.42	13.48	0.052	0.0019	0.002	0.015	-0.0034	-0.001
1065	Total N	4.00	0.954	0.075	-0.003	-0.46	26.53	22.01	0.044	0.0008	0.064	0.002	0.0065	0.042
1060	Nitrate	3.36	0.985	0.084	0.016	0.69	1.82	20.81	0.102	0.0080	0.038	0.012	0.0083	0.044
1058	Phyto	0.05	0.953	0.182	0.035	0.10	24.85	19.42	0.078	0.0095	-0.023	0.005	0.0061	0.078
1058	Nitrite	0.02	0.957	0.182	0.035	0.10	24.85	19.42	0.078	0.0095	-0.023	0.005	0.0061	0.078
1030	Total N	4.16	0.989	-0.117	-0.002	-0.30	7.20	17.96	0.095	0.0072	0.067	0.008	-0.0029	0.020

Table D.1 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/ Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
1017	Organic N	0.79	0.995	0.194	-0.013	0.17	16.56	11.52	0.046	0.0010	0.039	0.012	-0.0015	-0.018
1012	Organic N	0.75	0.981	0.065	0.029	0.92	23.71	8.62	0.062	0.0087	0.015	0.009	0.0029	0.001
999	Nitrite	0.02	0.951	0.204	0.112	0.29	26.00	15.13	0.082	0.0073	0.051	0.003	0.0039	0.047
994	Organic N	0.77	0.978	-0.004	0.074	0.50	3.79	7.54	0.077	0.0073	0.070	0.009	0.0073	-0.003
991	Phyto	0.05	0.954	0.158	0.087	0.03	2.25	14.29	0.071	0.0073	-0.002	0.006	0.0039	0.105
988	Nitrate	3.54	0.953	0.073	0.002	0.25	5.65	23.07	0.041	-0.0001	0.011	0.003	0.0035	0.092
969	Total N	4.28	0.981	0.061	0.021	0.24	4.47	12.64	0.058	0.0094	0.043	0.022	0.0080	-0.040
969	Organic N	0.77	0.997	0.061	0.021	0.24	4.47	12.64	0.058	0.0094	0.043	0.022	0.0080	-0.040
969	Nitrate	3.38	0.981	0.061	0.021	0.24	4.47	12.64	0.058	0.0094	0.043	0.022	0.0080	-0.040
961	Total N	4.10	0.979	0.187	0.003	0.70	15.70	20.97	0.096	0.0033	0.052	0.008	0.0021	0.009
961	Nitrate	3.50	0.978	0.187	0.003	0.70	15.70	20.97	0.096	0.0033	0.052	0.008	0.0021	0.009
953	Nitrate	3.35	1.000	0.135	0.005	0.46	23.99	16.57	0.060	0.0076	0.106	0.012	0.0084	0.026
946	Organic N	0.74	0.997	0.124	0.033	-0.09	20.36	20.40	0.086	0.0003	0.070	-0.005	0.0040	-0.014
945	Nitrate	3.34	0.990	0.125	0.015	0.66	4.59	20.15	0.069	0.0055	0.100	0.006	0.0008	0.044
943	Organic N	0.75	1.000	0.016	0.042	0.29	27.72	16.25	0.027	0.0075	0.037	0.008	0.0021	-0.010
936	Organic N	0.81	0.972	0.060	0.128	0.36	20.29	30.02	0.060	0.0056	-0.007	0.011	0.0007	-0.029
925	Organic N	0.81	0.955	0.175	0.055	0.55	1.88	36.55	0.014	0.0066	-0.025	0.023	0.0032	-0.037
923	Organic N	0.76	0.975	0.044	0.015	0.46	11.16	7.14	0.056	0.0068	0.011	0.003	0.0089	-0.008
921	Nitrite	0.02	0.955	0.158	0.040	0.57	26.64	19.18	0.057	0.0053	0.060	0.017	0.0033	0.083
915	Nitrite	0.02	0.963	0.248	0.085	0.27	28.30	10.52	0.077	0.0056	0.066	0.012	0.0026	0.039
912	Total N	4.05	0.968	0.076	-0.046	0.17	33.72	20.57	0.043	0.0042	0.038	0.012	0.0040	0.038
905	Nitrite	0.02	0.958	0.153	-0.028	0.30	46.03	5.90	0.046	0.0068	0.092	0.005	0.0030	0.054
904	Organic N	0.78	0.977	0.108	0.059	1.21	6.40	7.28	0.036	0.0056	0.074	-0.007	0.0038	-0.009
903	Organic N	0.78	0.988	0.111	0.077	1.14	0.60	9.40	0.081	0.0061	0.048	0.014	0.0012	-0.003
882	Organic N	0.78	0.958	0.087	0.011	0.36	24.99	4.86	0.077	0.0117	-0.010	0.010	0.0014	-0.008
879	Organic N	0.76	0.983	0.069	0.029	0.46	2.08	8.53	0.063	0.0098	0.076	-0.002	0.0056	0.001
878	Total N	4.04	0.988	0.125	-0.014	0.48	1.08	13.25	0.078	0.0148	0.038	0.017	0.0004	0.055
867	Phyto	0.05	0.953	-0.006	0.001	0.23	13.01	16.93	0.077	0.0054	-0.016	0.020	0.0082	-0.004
867	Organic N	0.74	0.999	-0.006	0.001	0.23	13.01	16.93	0.077	0.0054	-0.016	0.020	0.0082	-0.004
854	Organic N	0.75	0.982	0.166	-0.005	0.35	29.65	30.14	0.056	0.0095	0.018	0.011	0.0016	-0.010
846	Organic N	0.77	0.997	0.154	0.052	0.34	23.86	12.57	0.042	0.0053	0.031	0.013	0.0017	-0.014
844	Phyto	0.05	0.954	0.186	0.062	0.14	14.45	21.13	0.053	0.0032	-0.022	0.015	0.0073	-0.015
844	Organic N	0.73	0.996	0.186	0.062	0.14	14.45	21.13	0.053	0.0032	-0.022	0.015	0.0073	-0.015
834	Organic N	0.74	0.999	0.022	0.101	0.13	19.91	15.53	0.060	0.0108	0.041	0.000	0.0051	-0.031
832	Organic N	0.73	0.995	0.073	0.045	1.45	28.50	21.57	0.042	0.0071	0.114	-0.005	0.0024	-0.016

Table D.1 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/ Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
811	Organic N	0.76	0.981	0.082	0.060	0.85	12.83	8.10	0.049	0.0070	0.082	0.011	0.0074	-0.010
808	Organic N	0.77	0.999	0.067	0.065	0.42	17.46	14.01	0.096	0.0044	0.020	0.003	0.0033	-0.013
804	Nitrate	3.34	0.975	0.176	0.007	0.85	21.93	12.44	0.053	0.0062	0.010	0.016	-0.0018	0.060
785	Nitrite	0.02	0.959	0.289	0.038	-0.14	22.56	12.47	0.068	0.0079	0.051	0.015	0.0013	0.057
781	Organic N	0.78	0.984	0.023	0.120	0.27	6.15	8.51	0.082	0.0033	0.003	0.002	0.0009	-0.012
776	Organic N	0.80	0.985	0.023	0.013	0.45	13.73	24.77	0.071	0.0093	0.026	0.011	0.0005	0.000
775	Organic N	0.75	0.952	0.218	0.157	0.34	29.90	4.30	0.018	0.0038	0.017	0.005	0.0052	-0.017
770	Organic N	0.78	0.996	-0.044	0.091	0.21	19.79	12.17	0.089	0.0024	-0.002	0.009	0.0008	-0.024
767	Total N	4.37	0.989	0.195	-0.043	0.69	10.18	12.58	0.087	0.0065	0.014	0.013	0.0027	0.008
765	Organic N	0.81	0.982	0.249	0.134	0.31	9.88	24.90	0.060	0.0047	0.029	-0.006	-0.0002	-0.004
741	Organic N	0.81	0.979	0.072	0.033	0.59	25.25	27.12	0.036	0.0093	0.026	-0.008	0.0002	-0.012
740	Nitrate	3.27	0.976	0.118	0.015	0.27	5.62	22.83	0.071	0.0006	0.030	0.015	0.0057	0.044
739	Total N	4.18	0.970	0.168	-0.007	-0.11	12.59	11.05	0.055	0.0037	0.013	-0.005	0.0045	0.033
723	Total N	4.27	0.963	0.098	-0.013	-0.18	24.09	10.52	0.056	0.0080	0.012	0.009	0.0109	0.026
720	Organic N	0.73	0.980	0.177	0.070	0.85	32.74	8.44	0.045	0.0034	0.068	0.010	0.0034	-0.053
713	Total N	4.08	0.991	0.280	-0.022	0.88	33.75	17.05	0.036	0.0100	-0.019	0.010	0.0012	0.020
703	Nitrite	0.02	0.950	0.342	-0.022	0.46	16.61	18.04	0.079	0.0105	0.065	0.021	0.0055	0.075
683	Nitrite	0.02	0.950	0.107	0.042	0.05	31.30	25.99	0.021	0.0124	0.031	-0.002	0.0013	-0.041
683	Organic N	0.75	0.990	0.107	0.042	0.05	31.30	25.99	0.021	0.0124	0.031	-0.002	0.0013	-0.041
679	Organic N	0.78	0.998	0.205	0.075	0.68	3.25	12.98	0.070	0.0071	0.066	0.004	0.0050	0.000
676	Organic N	0.74	0.982	0.214	0.029	0.23	14.25	8.98	0.055	0.0083	-0.013	0.006	0.0078	0.001
672	Phyto	0.05	0.953	-0.045	-0.023	0.45	12.26	13.70	0.062	0.0075	0.005	0.010	0.0071	0.041
672	Total N	4.09	0.991	-0.045	-0.023	0.45	12.26	13.70	0.062	0.0075	0.005	0.010	0.0071	0.041
668	Nitrate	3.48	0.997	0.100	0.010	-0.20	2.72	17.58	0.122	0.0061	0.048	0.005	0.0063	0.036
648	Nitrate	3.27	0.987	0.103	0.006	0.21	19.01	21.39	0.057	0.0035	0.035	0.002	0.0010	0.019
637	Nitrate	3.30	0.970	0.044	0.018	0.43	0.24	23.17	0.085	0.0105	-0.021	0.008	0.0032	0.086
631	Organic N	0.77	0.992	0.013	0.085	1.00	8.42	22.96	0.055	0.0003	0.023	0.008	0.0043	-0.017
616	Organic N	0.75	0.994	0.089	-0.009	0.67	14.95	22.68	0.055	0.0026	0.019	0.015	0.0051	-0.005
603	Nitrite	0.02	0.966	0.260	0.040	0.50	24.12	23.60	0.071	-0.0003	0.099	0.010	0.0044	-0.012
601	Phyto	0.05	0.953	0.078	-0.005	0.16	33.95	15.46	0.046	0.0045	-0.057	0.006	-0.0003	-0.020
601	Organic N	0.80	0.999	0.078	-0.005	0.16	33.95	15.46	0.046	0.0045	-0.057	0.006	-0.0003	-0.020
595	Organic N	0.77	1.000	0.207	0.055	0.07	29.84	16.88	0.067	0.0051	0.034	0.001	0.0010	-0.017
592	Organic N	0.75	0.994	0.332	0.104	0.36	16.22	11.72	0.065	0.0082	-0.011	0.035	0.0062	-0.002
587	Total N	4.40	0.983	0.003	-0.055	0.55	36.87	19.14	0.027	0.0105	0.066	0.020	0.0062	0.007
577	Organic N	0.73	0.994	0.199	0.086	0.48	27.29	22.64	0.070	0.0067	0.044	0.004	0.0027	-0.047

Table D.1 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
571	Total N	4.09	0.961	0.162	-0.035	0.65	26.57	10.59	0.030	0.0139	0.041	0.000	0.0011	0.054
564	Organic N	0.75	1.000	0.099	0.093	1.11	9.00	16.59	0.105	0.0055	0.053	0.001	0.0094	-0.019
552	Phyto	0.06	0.951	0.033	0.045	0.20	14.79	14.25	0.051	0.0116	-0.009	-0.001	-0.0016	0.051
541	Organic N	0.78	1.000	0.158	0.071	0.67	28.33	14.73	0.057	0.0080	0.097	0.000	0.0007	-0.008
519	Organic N	0.80	0.999	0.103	-0.088	0.29	11.91	16.66	0.094	0.0081	0.088	0.025	-0.0013	-0.022
511	Organic N	0.79	0.970	0.184	0.032	0.09	1.32	31.39	0.060	0.0055	0.054	0.003	0.0046	-0.002
509	Total N	4.11	0.992	0.015	-0.050	0.64	18.00	13.86	0.071	0.0064	0.057	0.004	0.0059	0.037
471	Nitrate	3.23	0.976	0.127	0.080	0.92	-6.60	12.91	0.051	0.0011	0.034	0.034	0.0039	0.060
469	Total N	4.32	0.992	0.037	-0.005	0.69	23.60	17.63	0.078	0.0059	0.077	0.014	-0.0020	0.008
465	Organic N	0.76	0.988	0.118	0.016	0.67	15.68	25.24	0.057	0.0003	0.011	0.019	0.0034	-0.016
456	Nitrate	3.25	0.998	0.072	0.038	-0.06	-2.72	18.65	0.091	0.0078	0.132	0.025	0.0007	0.057
448	Organic N	0.75	0.999	0.038	0.033	0.27	23.49	15.36	0.061	0.0069	0.065	0.019	0.0028	-0.002
430	Total N	4.22	0.997	0.137	-0.013	0.01	27.09	14.88	0.060	0.0123	0.028	0.006	0.0030	0.021
424	Organic N	0.79	0.997	0.050	0.070	0.64	11.18	19.50	0.057	0.0064	0.070	-0.003	0.0017	-0.011
394	Organic N	0.80	0.996	0.213	0.092	0.50	27.57	19.38	0.051	0.0049	0.032	0.009	-0.0027	-0.022
367	Organic N	0.80	0.999	0.124	-0.051	0.39	16.23	17.24	0.059	0.0104	0.027	0.021	-0.0019	-0.002
353	Nitrate	3.53	0.999	0.178	-0.020	0.62	41.40	15.96	0.051	0.0084	0.003	0.011	0.0020	0.044
351	Organic N	0.77	0.997	0.050	-0.011	0.84	5.82	12.71	0.069	0.0052	0.052	0.004	0.0010	0.001
350	Total N	4.16	0.995	0.224	-0.028	0.27	30.30	14.96	0.054	0.0044	0.026	0.000	0.0083	0.031
350	Nitrite	0.02	0.950	0.224	-0.028	0.27	30.30	14.96	0.054	0.0044	0.026	0.000	0.0083	0.031
329	Phyto	0.05	0.953	0.173	0.022	0.17	10.82	23.62	0.091	0.0048	-0.012	0.024	0.0065	0.049
328	Total N	4.03	0.991	-0.005	0.000	0.61	36.54	17.38	0.065	0.0007	0.073	-0.001	0.0110	0.035
328	Nitrate	3.50	0.996	-0.005	0.000	0.61	36.54	17.38	0.065	0.0007	0.073	-0.001	0.0110	0.035
309	Total N	4.08	0.991	0.247	0.028	0.49	-18.57	18.09	0.086	0.0027	0.031	0.001	0.0025	0.019
309	Nitrate	3.53	0.994	0.247	0.028	0.49	-18.57	18.09	0.086	0.0027	0.031	0.001	0.0025	0.019
275	Total N	4.04	0.966	0.125	-0.025	0.85	40.37	10.99	0.059	0.0094	0.039	0.020	-0.0015	0.057
261	Nitrate	3.27	0.999	0.204	0.058	-0.33	-7.25	16.70	0.066	-0.0001	0.056	0.008	0.0033	0.020
255	Organic N	0.73	0.979	0.050	0.048	0.91	14.23	30.87	0.061	0.0050	0.044	0.007	0.0061	-0.010
249	Phyto	0.05	0.954	0.179	0.051	0.39	7.58	14.93	0.069	0.0126	-0.006	0.017	0.0065	0.006
231	Nitrate	3.25	0.980	0.053	0.023	-0.01	1.00	22.34	0.062	0.0055	0.057	0.001	0.0039	0.036
228	Nitrate	3.53	1.000	0.190	0.008	-0.16	5.02	15.39	0.036	0.0083	0.081	0.005	-0.0003	0.062
219	Organic N	0.76	0.994	0.081	0.043	0.25	22.21	11.66	0.066	0.0088	0.034	0.019	0.0030	-0.012
206	Organic N	0.75	0.975	0.022	-0.067	0.49	45.19	33.31	0.060	0.0133	0.080	0.005	0.0004	-0.018
202	Organic N	0.73	0.992	-0.005	0.034	-0.09	21.35	11.57	0.075	0.0087	0.100	0.010	0.0064	-0.001
194	Total N	4.28	0.997	-0.027	0.050	0.78	-8.92	14.78	0.070	0.0025	0.045	0.007	-0.0040	-0.035

Table D.1 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
194	Nitrate	3.37	0.996	-0.027	0.050	0.78	-8.92	14.78	0.070	0.0025	0.045	0.007	-0.0040	-0.035
194	Organic N	0.79	0.999	-0.027	0.050	0.78	-8.92	14.78	0.070	0.0025	0.045	0.007	-0.0040	-0.035
186	Total N	4.02	0.989	0.015	-0.002	-0.05	15.07	13.51	0.064	0.0062	0.010	-0.004	0.0082	0.065
185	Organic N	0.74	0.993	0.080	0.129	0.25	16.39	12.27	0.041	0.0122	0.002	0.017	-0.0010	0.003
168	Organic N	0.77	1.000	0.006	0.055	0.07	18.41	15.11	0.058	0.0016	0.069	0.019	0.0022	-0.075
164	Organic N	0.78	0.999	0.005	0.091	0.45	8.02	13.69	0.105	0.0040	0.049	0.008	0.0026	-0.009
149	Total N	4.18	0.988	0.086	-0.007	1.13	24.86	12.99	0.068	-0.0134	0.013	0.024	0.0018	0.021
138	Organic N	0.79	0.982	0.123	0.041	0.35	25.98	26.68	0.078	0.0019	-0.005	0.014	0.0007	-0.006
136	Organic N	0.80	0.996	0.067	-0.041	0.40	26.77	18.51	0.075	0.0009	0.068	0.014	-0.0023	-0.009
132	Nitrate	3.37	0.969	0.121	0.003	-0.15	39.28	12.36	0.035	0.0073	0.053	0.020	0.0075	0.065
123	Organic N	0.80	0.973	0.061	0.004	0.36	10.72	29.49	0.102	0.0054	-0.021	0.015	0.0016	0.000
109	Nitrate	3.23	0.968	0.100	0.020	0.31	2.50	24.20	0.078	0.0103	0.033	0.016	0.0070	0.120
95	Organic N	0.77	0.968	0.041	-0.012	1.19	6.22	34.04	0.099	0.0024	0.108	-0.005	0.0060	-0.001
65	Organic N	0.79	0.987	0.049	-0.020	1.09	16.97	8.98	0.068	0.0069	0.091	0.014	-0.0012	-0.021
62	Total N	4.11	0.980	0.167	-0.012	-0.12	3.58	11.94	0.072	0.0061	-0.014	0.025	-0.0016	0.044
61	Organic N	0.73	0.957	0.220	0.036	0.40	39.75	4.98	0.077	0.0083	0.086	0.021	-0.0012	0.006
53	Organic N	0.75	0.989	0.052	0.050	0.48	20.26	25.75	0.079	0.0051	0.056	0.011	0.0032	-0.018
49	Nitrate	3.47	0.970	0.190	0.009	0.29	1.97	22.06	0.099	0.0053	0.065	0.016	0.0091	0.051
48	Organic N	0.80	0.992	-0.011	0.031	0.11	13.88	22.11	0.070	0.0135	0.034	0.012	0.0007	-0.013
39	Total N	4.06	0.992	0.118	-0.017	1.13	19.86	14.56	0.045	0.0068	0.004	0.014	0.0122	0.043
38	Nitrate	3.24	0.989	0.069	0.037	0.77	1.32	14.23	0.069	0.0042	0.035	0.004	0.0078	0.035
35	Total N	4.24	0.985	0.184	0.006	0.25	10.22	12.52	0.027	0.0066	-0.020	0.020	-0.0014	0.011
32	Organic N	0.79	0.973	-0.015	0.054	0.59	0.09	30.66	0.027	0.0038	0.009	0.011	0.0058	-0.007
6	Organic N	0.73	0.996	0.136	0.022	0.34	23.21	21.08	0.057	0.0043	0.027	0.017	0.0038	-0.005
3	Phyto	0.05	0.954	0.044	0.037	0.07	20.84	18.09	0.038	0.0056	-0.029	0.004	0.0008	0.036

Table D.2: Mussel flow model variables for the 209 sensitivity runs that met the criteria established by the multiple variable sensitivity analysis.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)	Mussel Biomass (g)	Mussel Clearance Rate (h ⁻¹ g ⁻¹)	Mussel Excretion Rate (h ⁻¹ g ⁻¹)
1996	Total N	4.14	0.990	0.175	-0.053	0.65	22.22	14.88	0.076	0.0023	0.006	0.012	0.0050	0.040	6.2	0.00052	3.31
1976	Organic N	0.78	0.993	0.054	0.095	0.31	33.52	10.87	0.050	0.0070	0.073	0.020	0.0002	-0.007	309.4	0.00036	3.02
1970	Organic N	0.75	0.998	-0.040	-0.041	0.38	16.06	14.63	0.048	0.0083	-0.022	0.011	0.0066	-0.006	45.6	0.00063	0.17
1967	Nitrate	3.41	0.961	0.179	0.001	0.18	35.35	23.91	0.060	0.0053	0.090	0.017	0.0048	0.074	41.9	0.00057	-0.10
1966	Nitrate	3.21	0.996	0.088	0.034	0.54	3.55	15.36	0.036	0.0089	-0.027	0.014	0.0064	0.065	73.8	-0.00006	-0.10
1965	Organic N	0.75	0.981	0.035	0.066	0.09	20.66	8.43	0.059	0.0059	0.110	0.019	0.0061	-0.007	97.3	0.00071	-0.12
1953	Organic N	0.78	0.967	0.105	0.025	0.46	1.97	34.34	0.050	0.0041	-0.020	-0.001	0.0066	-0.035	53.5	0.00000	2.01
1940	Total N	4.03	0.973	0.097	-0.030	0.51	25.59	11.60	0.067	0.0105	0.060	0.018	0.0031	0.076	15.9	0.00004	-0.69
1932	Nitrate	3.25	0.991	0.011	0.073	0.34	-11.46	19.76	0.058	0.0041	0.058	0.010	0.0061	0.001	290.0	0.00057	1.08
1932	Organic N	0.75	0.998	0.011	0.073	0.34	-11.46	19.76	0.058	0.0041	0.058	0.010	0.0061	0.001	290.0	0.00057	1.08
1923	Nitrate	3.26	0.991	0.040	0.062	0.86	-9.77	19.58	0.064	0.0073	0.114	0.008	0.0043	0.010	80.0	0.00021	2.18
1922	Nitrate	3.18	0.997	-0.046	0.041	0.93	1.45	15.66	0.054	0.0076	0.074	0.006	0.0001	0.058	72.3	-0.00002	1.23
1898	Total N	4.05	0.985	0.164	-0.008	0.41	22.19	15.64	0.023	0.0082	0.045	0.015	0.0040	0.053	-55.0	0.00054	1.00
1897	Organic N	0.75	0.951	0.086	0.038	0.73	23.72	4.16	0.056	0.0058	0.056	0.012	0.0087	-0.022	78.9	0.00019	2.56
1877	Organic N	0.75	0.985	0.152	0.069	-0.03	13.62	28.25	0.063	0.0085	0.037	0.004	0.0055	-0.004	40.5	0.00012	2.45
1876	Organic N	0.79	0.996	-0.066	0.065	0.23	6.32	11.92	0.049	0.0078	0.033	0.005	0.0009	-0.010	39.2	0.00078	1.17
1874	Organic N	0.76	0.950	0.211	0.069	0.99	16.58	43.74	0.059	0.0066	0.048	0.014	0.0028	-0.005	94.3	0.00080	0.41
1833	Organic N	0.77	0.999	0.105	0.029	-0.07	24.46	18.17	0.073	0.0062	0.092	0.010	0.0005	0.000	283.0	0.00025	-1.54
1829	Total N	4.05	0.951	0.109	-0.049	-0.30	7.83	9.87	0.064	0.0101	0.000	0.011	-0.0004	0.081	196.6	0.00018	-1.00
1822	Organic N	0.75	0.960	0.161	0.079	-0.04	20.30	5.11	0.076	-0.0047	0.042	0.013	0.0068	0.000	-13.2	0.00030	2.17
1803	Organic N	0.79	0.985	0.236	0.024	1.09	19.82	26.54	0.083	0.0104	0.040	0.023	0.0011	-0.013	56.1	0.00005	1.04
1798	Total N	4.18	0.976	-0.070	0.069	0.66	-3.50	15.22	0.061	0.0014	0.041	0.031	0.0039	0.074	78.4	0.00058	0.78
1794	Nitrate	3.31	0.969	0.112	0.028	0.14	16.73	16.24	0.051	0.0015	0.066	0.019	-0.0013	0.070	220.4	0.00008	2.86
1781	Organic N	0.78	0.957	-0.026	0.039	0.92	2.49	4.67	0.045	0.0061	0.060	0.011	0.0061	-0.007	84.3	-0.00016	0.20
1775	Nitrate	3.34	0.990	0.173	0.048	0.38	-6.72	19.73	0.062	0.0052	0.040	0.006	0.0036	0.065	54.4	0.00037	2.31
1775	Total N	4.37	0.962	0.173	0.048	0.38	-6.72	19.73	0.062	0.0052	0.040	0.006	0.0036	0.065	54.4	0.00037	2.31
1772	Organic N	0.76	0.988	0.252	0.064	0.85	9.51	9.72	0.068	0.0030	-0.030	0.022	0.0093	-0.019	166.9	0.00019	4.02
1764	Organic N	0.73	0.975	-0.007	0.059	0.62	32.49	7.47	0.075	0.0020	0.073	0.016	0.0036	-0.009	234.7	0.00003	-1.96
1757	Nitrate	3.25	0.981	0.072	0.003	-0.23	34.80	22.97	0.024	0.0038	0.078	0.021	0.0066	0.020	130.5	-0.00014	-0.14
1751	Total N	4.25	0.980	0.091	0.006	0.80	14.32	12.20	0.104	0.0069	0.045	0.006	0.0058	0.129	81.4	0.00018	1.23
1746	Organic N	0.75	0.982	0.052	0.051	0.37	17.42	30.49	0.068	0.0061	-0.023	0.000	0.0044	-0.029	175.5	0.00009	2.21
1739	Total N	4.22	0.978	-0.009	0.000	0.43	35.53	18.36	0.042	0.0073	0.092	-0.011	0.0092	0.024	259.5	0.00029	-0.81
1737	Organic N	0.80	0.970	0.215	0.046	-0.30	-15.81	31.62	0.032	0.0105	0.022	0.015	0.0119	-0.043	126.0	0.00026	-2.91
1731	Nitrate	3.37	0.955	0.153	0.035	-0.05	2.15	10.45	0.046	0.0040	0.049	0.006	0.0042	0.037	81.8	0.00023	0.19
1728	Organic N	0.73	0.998	0.018	-0.002	-0.09	23.68	17.18	0.049	0.0110	0.054	0.011	0.0041	-0.042	74.3	0.00017	1.38
1725	Nitrate	3.35	0.969	0.154	0.069	0.79	2.42	12.30	0.077	0.0047	0.050	0.010	0.0060	0.016	130.9	0.00098	1.34
1723	Organic N	0.78	0.999	0.149	0.064	0.50	1.86	14.70	0.050	0.0051	-0.004	0.003	0.0061	-0.007	179.0	0.00051	-0.11
1719	Total N	3.96	0.977	0.085	-0.023	0.39	35.48	16.97	0.053	0.0067	0.037	0.006	0.0048	0.092	223.2	0.00063	-0.10
1697	Organic N	0.79	0.967	0.195	0.037	-0.02	13.62	33.07	0.047	0.0024	0.016	0.019	0.0019	-0.005	89.9	-0.00008	4.54
1693	Organic N	0.74	0.999	0.205	0.074	1.03	15.60	16.57	0.075	0.0045	0.064	0.018	0.0061	-0.002	66.0	0.00052	-3.93
1669	Organic N	0.79	0.984	0.029	0.027	-0.07	7.61	25.72	0.065	0.0022	0.102	0.019	0.0021	-0.028	183.9	0.00013	-2.13
1648	Organic N	0.80	0.971	0.210	0.160	0.92	3.18	30.68	0.053	0.0064	0.023	0.002	0.0020	-0.019	48.3	-0.00036	1.35

Table D.2 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)	Mussel Biomass (g)	Mussel Clearance Rate (h ⁻¹ g ⁻¹)	Mussel Excretion Rate (h ⁻¹ g ⁻¹)
1646	Organic N	0.75	0.979	0.233	0.069	0.65	23.01	30.63	0.089	0.0026	0.035	0.010	0.0024	-0.024	96.5	0.00022	0.61
1597	Total N	4.35	0.955	-0.018	-0.035	0.84	28.25	9.68	0.044	0.0145	0.073	0.015	0.0002	0.045	88.0	0.00023	0.59
1590	Organic N	0.78	0.999	0.072	0.033	0.53	7.73	17.14	0.084	0.0049	0.009	0.009	0.0028	-0.002	167.0	0.00072	1.20
1571	Nitrate	3.28	0.996	0.066	0.033	-0.15	8.10	17.47	0.065	0.0073	0.070	0.016	0.0005	0.073	204.4	0.00060	0.96
1562	Total N	4.02	0.983	0.182	-0.006	0.64	30.66	13.24	0.065	0.0022	0.073	0.025	0.0039	0.075	102.5	-0.00039	-1.02
1547	Organic N	0.73	0.996	0.021	0.024	0.31	-13.32	13.26	0.077	0.0096	-0.060	0.010	0.0059	0.002	218.9	0.00040	6.84
1525	Nitrate	3.24	0.998	0.066	0.009	0.27	23.08	18.53	0.055	0.0081	0.018	0.017	0.0000	0.055	176.3	0.00054	0.12
1498	Total N	4.31	0.977	0.225	-0.046	0.40	14.21	11.17	0.063	0.0146	0.043	0.016	0.0062	0.024	40.3	0.00065	0.18
1496	Nitrate	3.24	0.991	0.156	0.018	0.36	14.99	14.24	0.076	0.0109	0.022	0.013	-0.0016	0.033	35.7	0.00081	0.61
1488	Organic N	0.73	0.972	0.097	0.094	0.55	6.35	6.95	0.073	0.0019	0.038	0.003	0.0050	0.003	258.9	0.00035	0.03
1479	Organic N	0.73	0.966	0.163	0.058	0.33	8.61	6.18	0.055	0.0090	0.027	0.024	-0.0008	0.005	94.7	0.00023	-0.45
1473	Nitrate	3.24	0.980	-0.133	0.032	0.89	5.43	12.68	0.085	0.0056	0.024	0.014	0.0008	0.102	94.1	0.00021	0.87
1473	Total N	4.17	0.974	-0.133	0.032	0.89	5.43	12.68	0.085	0.0056	0.024	0.014	0.0008	0.102	94.1	0.00021	0.87
1470	Total N	4.18	0.989	0.184	-0.008	1.43	17.32	15.48	0.071	-0.0010	0.007	0.019	0.0020	0.017	30.4	0.00096	-0.67
1468	Organic N	0.74	0.975	0.224	0.057	0.53	16.06	7.45	0.100	0.0076	0.022	0.000	0.0119	-0.004	67.3	0.00085	0.03
1462	Organic N	0.78	0.951	0.013	-0.013	-0.14	6.09	4.01	0.091	0.0085	0.093	0.008	0.0007	-0.024	188.8	0.00063	-2.14
1460	Organic N	0.75	0.968	0.167	0.108	0.31	18.63	6.23	0.068	0.0062	0.043	0.013	0.0051	0.001	240.5	-0.00023	2.82
1451	Nitrate	3.25	0.981	0.154	0.083	0.28	-9.25	22.10	0.053	0.0008	-0.011	0.015	-0.0003	0.087	138.4	0.00011	1.64
1449	Organic N	0.77	0.970	0.066	0.014	-0.15	3.54	33.84	0.089	0.0027	0.086	0.000	0.0075	-0.046	117.8	0.00025	1.05
1445	Nitrate	3.50	0.981	0.053	0.019	-0.30	3.93	11.77	0.050	0.0059	0.047	0.007	0.0028	0.029	159.5	0.00054	0.88
1428	Organic N	0.80	0.995	-0.059	0.089	0.27	19.62	19.60	0.063	0.0095	0.058	-0.002	-0.0008	-0.020	390.4	0.00040	-0.36
1426	Total N	4.12	0.986	0.094	-0.017	0.57	9.36	16.46	0.084	0.0089	0.081	0.018	0.0044	0.033	113.1	0.00049	-1.96
1413	Total N	4.06	0.983	0.129	-0.056	0.07	9.00	16.76	0.038	0.0102	0.008	0.014	0.0026	0.043	161.8	0.00035	-0.70
1399	Organic N	0.74	0.972	0.205	-0.029	0.61	29.18	6.90	0.093	0.0080	0.041	0.033	-0.0016	0.003	-4.7	0.00037	2.41
1398	Organic N	0.79	0.999	0.054	0.075	0.34	14.27	17.15	0.050	0.0031	-0.018	0.011	0.0010	-0.040	119.1	0.00045	1.50
1389	Organic N	0.75	0.999	0.076	0.022	0.31	30.07	15.28	0.074	0.0017	0.032	0.018	0.0020	-0.037	250.7	0.00117	-2.07
1387	Organic N	0.77	0.999	0.159	0.115	0.19	19.12	18.09	0.058	0.0028	0.003	0.009	0.0027	-0.041	144.5	-0.00031	0.82
1382	Nitrate	3.24	0.996	-0.001	0.053	0.54	-6.21	18.58	0.049	0.0059	0.094	0.008	0.0011	0.014	59.6	-0.00018	1.26
1381	Organic N	0.77	0.985	0.171	0.116	0.70	1.24	8.74	0.054	0.0093	0.049	0.014	0.0094	-0.014	-164.6	-0.00044	1.76
1368	Total N	4.09	0.960	-0.154	-0.012	0.55	3.12	20.46	0.060	0.0021	0.087	0.002	0.0084	0.029	-4.3	0.00061	3.68
1367	Nitrate	3.34	0.985	0.069	0.034	0.30	0.93	12.77	0.073	0.0072	0.080	-0.005	0.0017	0.035	264.0	-0.00006	4.21
1348	Total N	4.28	0.994	0.197	0.008	0.22	10.51	15.07	0.024	0.0054	0.008	0.022	0.0023	0.053	239.8	0.00001	2.52
1339	Organic N	0.78	0.997	-0.018	0.121	-0.07	0.26	19.19	0.051	0.0034	0.052	0.020	0.0048	-0.001	82.9	0.00013	3.19
1337	Total N	3.97	0.982	0.124	-0.017	0.82	8.76	13.56	0.057	0.0085	0.059	0.010	0.0041	0.094	-110.1	0.00044	0.68
1334	Organic N	0.79	0.999	0.111	0.087	0.80	-3.24	15.25	0.072	0.0040	-0.039	0.016	0.0009	-0.006	118.7	0.00011	1.16
1328	Organic N	0.75	0.998	-0.026	0.026	0.66	18.89	13.95	0.073	0.0113	0.066	0.008	0.0053	-0.031	23.5	-0.00018	4.33
1315	Organic N	0.77	0.954	0.155	-0.004	0.52	0.13	41.63	0.076	0.0092	0.067	0.020	0.0097	-0.010	135.9	0.00056	2.20
1296	Organic N	0.75	0.999	0.211	0.092	0.45	20.05	18.95	0.037	0.0072	0.025	0.015	0.0027	0.000	112.6	0.00029	5.68
1284	Organic N	0.77	0.997	0.120	0.151	0.26	14.18	12.51	0.084	0.0044	0.020	0.008	0.0032	-0.029	-95.5	0.00028	3.46
1280	Organic N	0.74	0.994	0.090	0.039	0.67	17.90	22.79	0.074	0.0109	0.064	0.008	0.0048	-0.018	3.6	0.00046	1.27
1265	Organic N	0.74	0.964	0.057	-0.006	1.05	27.83	37.70	0.077	0.0012	0.051	0.037	0.0017	-0.002	199.2	-0.00001	1.46
1263	Organic N	0.78	0.974	0.169	0.074	0.52	7.68	6.89	0.060	0.0077	0.019	0.006	0.0013	0.000	62.5	0.00019	-0.31
1241	Organic N	0.80	0.994	0.109	0.039	0.64	29.87	20.47	0.060	0.0090	0.075	-0.006	-0.0040	-0.025	90.5	0.00039	3.99

Table D.2 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/ Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)	Mussel Biomass (g)	Mussel Clearance Rate (h ⁻¹ g ⁻¹)	Mussel Excretion Rate (h ⁻¹ g ⁻¹)
1240	Total N	4.14	0.989	0.060	-0.012	-0.26	18.41	15.22	0.061	0.0037	0.048	0.006	0.0019	0.033	6.4	0.00004	0.98
1229	Organic N	0.76	0.977	0.158	0.020	-0.36	16.22	7.50	0.066	0.0029	0.060	0.015	0.0008	0.002	135.2	0.00059	0.10
1220	Total N	4.11	0.954	0.140	-0.024	0.42	25.97	21.07	0.097	0.0041	0.040	0.010	0.0097	0.027	-35.0	0.00059	4.94
1217	Organic N	0.78	0.991	0.096	0.061	-0.07	0.83	10.04	0.072	0.0040	0.021	0.021	0.0023	-0.013	216.5	0.00038	-0.28
1210	Nitrate	3.34	0.994	0.064	0.006	0.87	18.85	18.50	0.098	0.0047	0.036	0.005	0.0020	0.036	167.2	0.00003	-0.35
1198	Total N	4.10	0.988	-0.008	-0.033	0.26	9.71	14.60	0.064	0.0032	0.070	0.030	0.0014	0.041	-36.4	0.00055	1.46
1188	Organic N	0.77	0.973	0.010	0.070	0.58	6.65	32.60	0.079	0.0083	0.053	-0.006	0.0059	-0.022	169.4	0.00029	-1.42
1170	Total N	4.27	0.965	-0.087	-0.021	0.28	17.54	10.37	0.057	0.0081	-0.014	0.009	0.0054	0.025	70.3	-0.00004	1.73
1167	Nitrate	3.44	0.984	0.090	0.014	0.68	0.95	19.73	0.081	0.0072	0.072	0.010	0.0013	0.023	41.6	0.00024	0.35
1167	Total N	3.96	0.979	0.090	0.014	0.68	0.95	19.73	0.081	0.0072	0.072	0.010	0.0013	0.023	41.6	0.00024	0.35
1163	Organic N	0.76	0.986	-0.073	-0.005	0.51	33.06	9.51	0.057	0.0097	0.016	0.003	-0.0022	0.002	66.6	0.00031	1.08
1152	Organic N	0.78	0.998	0.031	0.050	-0.03	14.63	13.21	0.086	0.0084	0.040	0.015	0.0017	-0.002	147.0	0.00026	0.34
1148	Organic N	0.78	0.994	0.158	0.017	0.30	7.05	11.57	0.069	0.0092	0.014	0.004	0.0051	-0.043	131.8	0.00012	1.68
1145	Nitrate	3.43	0.998	0.019	0.060	0.69	-13.30	14.79	0.053	0.0043	0.030	0.004	-0.0006	0.022	69.3	0.00022	2.37
1141	Organic N	0.78	0.985	0.096	0.016	0.66	-4.17	8.73	0.065	0.0092	0.079	0.009	0.0026	-0.009	22.0	0.00033	3.02
1138	Total N	4.16	0.958	-0.019	-0.037	0.52	-5.21	20.95	0.060	0.0091	0.019	0.003	0.0097	0.019	203.4	0.00072	-0.05
1129	Organic N	0.79	0.999	0.010	0.063	0.16	20.99	15.40	0.069	0.0077	0.037	-0.001	0.0000	-0.023	329.1	0.00024	1.97
1125	Organic N	0.78	0.987	0.102	0.021	0.98	6.09	9.01	0.047	0.0015	0.086	0.012	0.0008	-0.042	230.1	0.00081	0.41
1097	Total N	4.10	0.989	0.189	0.002	0.02	0.07	15.76	0.049	0.0095	0.049	0.001	0.0091	0.050	186.3	0.00012	0.07
1075	Organic N	0.78	0.979	0.123	0.102	0.83	7.25	7.52	0.078	0.0044	-0.001	0.032	0.0007	-0.011	54.1	0.00015	2.89
1058	Total N	4.17	0.960	0.127	-0.059	0.78	25.30	10.20	0.027	0.0027	0.038	0.012	0.0058	0.043	-38.5	0.00028	1.22
1053	Organic N	0.80	0.999	0.105	0.085	0.56	6.77	16.34	0.020	0.0059	0.002	-0.006	0.0003	-0.008	-3.7	0.00084	-0.20
1052	Organic N	0.76	0.995	0.121	0.070	-0.29	31.90	22.10	0.029	0.0071	0.037	-0.002	0.0012	-0.013	61.6	0.00021	2.56
1047	Nitrate	3.45	0.954	0.160	0.041	-0.10	1.86	22.84	0.047	0.0052	0.042	0.014	0.0096	0.022	117.1	0.00045	1.62
1041	Organic N	0.79	0.997	0.164	0.025	0.33	31.70	12.37	0.042	0.0143	0.113	-0.003	-0.0047	-0.044	196.0	0.00024	-0.17
1036	Organic N	0.78	0.989	0.133	0.037	0.87	4.77	9.70	0.076	0.0072	0.053	0.021	0.0048	-0.003	217.5	0.00051	3.76
1006	Total N	4.09	0.950	0.110	-0.009	-0.23	18.75	21.54	0.027	0.0060	0.051	0.021	0.0055	0.029	51.1	-0.00007	0.56
997	Organic N	0.80	0.999	0.167	0.059	0.73	27.00	17.19	0.051	0.0084	0.056	0.020	-0.0010	-0.022	218.2	0.00024	3.95
995	Nitrate	3.28	0.970	0.108	0.077	0.53	-6.11	11.64	0.069	0.0031	0.034	0.008	0.0003	0.038	237.2	0.00046	-1.14
987	Organic N	0.78	0.987	0.007	0.074	0.12	10.62	9.13	0.083	0.0083	0.063	0.017	0.0033	-0.001	49.6	-0.00015	2.79
974	Total N	3.99	0.952	0.101	-0.038	0.48	23.72	20.89	0.068	0.0036	0.106	0.019	0.0005	0.047	115.8	0.00014	-2.17
968	Organic N	0.77	0.995	0.128	0.028	0.36	13.73	11.76	0.085	0.0073	0.031	0.014	0.0045	-0.019	103.0	-0.00003	2.18
959	Nitrate	3.29	0.970	0.043	0.021	0.12	20.19	12.96	0.087	0.0034	0.013	-0.006	0.0069	0.018	179.0	0.00040	1.00
958	Nitrate	3.43	0.993	0.110	0.011	0.03	11.70	13.55	0.027	0.0012	0.069	0.009	0.0043	0.023	250.0	0.00048	-1.31
958	Total N	3.97	0.986	0.110	0.011	0.03	11.70	13.55	0.027	0.0012	0.069	0.009	0.0043	0.023	250.0	0.00048	-1.31
937	Nitrate	3.26	0.965	0.086	0.041	0.21	13.39	16.97	0.053	0.0130	-0.045	-0.002	0.0040	0.092	60.7	0.00103	2.68
920	Organic N	0.75	0.991	0.085	0.121	0.57	31.74	22.28	0.077	0.0028	0.009	0.006	0.0026	-0.024	-6.0	-0.00010	2.05
895	Nitrate	3.22	0.996	0.093	0.012	0.54	22.14	15.94	0.068	0.0099	0.110	0.021	0.0040	0.070	150.3	0.00018	0.77
885	Total N	3.96	0.955	0.200	0.062	0.57	-15.52	10.44	0.067	0.0116	0.073	0.013	0.0037	0.056	204.9	0.00086	-0.65
879	Nitrate	3.40	0.999	0.139	0.008	0.73	14.50	16.70	0.046	0.0063	0.061	0.004	-0.0007	0.068	-60.1	0.00047	0.59
873	Organic N	0.79	0.999	0.114	0.005	0.76	7.15	17.97	0.036	0.0089	0.067	0.025	0.0021	-0.003	164.7	0.00065	-0.33
870	Nitrate	3.19	0.977	0.029	0.024	0.66	3.80	22.74	0.070	0.0096	0.048	0.009	0.0007	0.068	273.6	0.00029	0.16
848	Total N	4.18	0.984	0.169	-0.034	0.01	26.39	12.47	0.059	0.0065	0.134	0.003	0.0010	0.033	122.6	0.00030	-0.06

Table D.2 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)	Mussel Biomass (g)	Mussel Clearance Rate (h ⁻¹ g ⁻¹)	Mussel Excretion Rate (h ⁻¹ g ⁻¹)
812	Total N	4.00	0.993	0.195	0.002	0.76	27.30	16.01	0.023	0.0088	0.027	0.003	0.0034	0.034	27.2	0.00058	0.56
802	Organic N	0.78	0.995	0.039	0.113	0.98	9.37	11.79	0.050	0.0094	-0.012	0.025	0.0039	-0.009	64.8	0.00020	2.81
800	Organic N	0.77	0.981	-0.040	0.042	-0.22	24.59	29.31	0.048	0.0085	0.047	0.007	0.0015	-0.010	-22.9	0.00061	1.18
797	Organic N	0.77	0.981	0.041	-0.003	0.53	23.46	8.12	0.047	0.0058	-0.022	0.009	0.0025	-0.070	75.9	0.00075	0.22
766	Total N	4.01	0.982	-0.107	0.001	0.25	1.92	13.02	0.077	0.0054	0.030	0.003	0.0033	0.072	67.9	-0.00003	1.00
751	Nitrate	3.23	0.968	0.132	0.026	0.37	10.94	11.83	0.018	0.0115	0.045	0.024	0.0074	0.062	59.8	0.00013	1.06
744	Organic N	0.77	0.987	-0.002	0.065	0.58	6.20	26.19	0.075	0.0005	0.039	0.005	0.0061	-0.025	74.9	0.00000	0.68
729	Nitrate	3.17	0.999	-0.004	0.038	1.00	1.70	16.81	0.076	0.0088	0.034	0.005	0.0045	0.082	96.8	0.00038	2.99
715	Organic N	0.80	0.989	0.117	0.131	1.20	27.84	10.18	0.056	0.0100	-0.016	0.005	-0.0022	-0.015	91.2	0.00033	2.91
714	Organic N	0.78	0.979	0.159	0.021	0.11	35.61	7.59	0.038	0.0038	0.068	0.023	-0.0024	-0.030	127.7	0.00044	-0.10
696	Total N	4.06	0.955	0.239	-0.016	0.74	42.72	20.41	0.082	0.0042	0.106	0.006	0.0083	0.041	9.7	0.00021	2.85
695	Total N	4.03	0.954	0.139	0.022	0.61	-17.82	10.17	0.032	0.0035	0.037	0.017	0.0065	0.068	165.1	0.00009	-1.15
688	Total N	4.36	0.967	0.043	-0.035	0.18	22.36	20.37	0.070	0.0121	0.051	0.004	0.0044	0.009	22.3	0.00024	1.06
681	Organic N	0.78	0.997	0.048	0.132	0.73	17.19	19.61	0.081	0.0047	-0.007	0.015	0.0016	-0.004	104.7	0.00060	-0.07
677	Organic N	0.79	0.996	0.153	0.111	1.17	27.60	20.24	0.042	0.0122	0.044	0.020	0.0003	-0.076	230.3	0.00051	2.07
667	Nitrate	3.35	0.953	0.158	0.038	0.80	10.93	10.97	0.067	0.0041	0.010	0.013	0.0051	0.035	103.0	0.00007	4.17
666	Organic N	0.75	0.985	0.177	0.047	0.96	13.89	9.17	0.053	0.0014	0.044	0.008	0.0089	-0.004	205.4	0.00027	2.57
654	Organic N	0.76	0.997	0.216	0.030	0.73	10.04	21.13	0.042	0.0076	-0.036	0.015	0.0064	-0.017	-25.4	0.00011	-1.26
631	Total N	4.16	0.984	0.193	-0.017	0.70	14.56	12.44	0.040	0.0028	0.077	0.008	0.0070	0.049	114.6	0.00002	1.53
622	Nitrate	3.49	0.950	0.250	0.041	0.95	4.51	10.17	0.034	0.0077	0.021	0.030	-0.0017	0.051	117.4	0.00015	1.93
591	Nitrate	3.44	0.999	0.030	0.012	0.50	6.20	15.75	0.079	0.0073	0.059	-0.003	0.0071	0.013	-92.6	0.00055	-1.51
591	Total N	4.09	0.995	0.030	0.012	0.50	6.20	15.75	0.079	0.0073	0.059	-0.003	0.0071	0.013	-92.6	0.00055	-1.51
590	Nitrate	3.32	0.976	0.050	0.017	1.01	20.36	13.08	0.059	0.0065	0.102	0.008	0.0018	0.020	105.7	0.00082	1.85
584	Organic N	0.81	0.986	0.055	0.125	0.51	6.58	24.18	0.025	0.0096	0.018	0.002	-0.0005	-0.027	176.0	0.00066	-0.80
554	Total N	3.98	0.987	0.001	0.003	0.28	13.57	15.73	0.050	0.0075	0.032	0.030	0.0073	0.047	237.6	0.00033	-0.29
553	Nitrate	3.43	0.951	0.099	0.049	0.72	-4.25	10.00	0.049	0.0114	0.129	0.011	0.0044	0.008	71.3	0.00021	6.48
551	Total N	3.99	0.984	0.081	-0.014	0.66	11.17	13.79	0.055	0.0047	0.067	0.005	0.0052	0.080	79.5	0.00027	-1.83
544	Organic N	0.79	0.989	0.138	0.016	0.00	15.73	23.89	0.046	0.0019	0.065	0.009	0.0013	-0.031	278.1	0.00018	2.75
533	Organic N	0.77	0.964	0.113	0.087	0.70	15.78	5.45	0.045	0.0026	0.037	0.014	0.0045	-0.017	144.5	0.00085	2.14
518	Organic N	0.77	0.988	0.197	0.058	0.76	18.84	9.60	0.047	0.0072	0.068	0.007	0.0027	-0.020	170.1	0.00066	2.41
515	Organic N	0.78	1.000	0.095	0.049	0.43	4.42	15.91	0.075	0.0030	0.109	0.019	0.0046	-0.043	89.1	0.00023	0.00
509	Organic N	0.75	0.960	0.154	0.129	0.26	35.76	5.15	0.080	0.0115	0.013	0.009	0.0029	-0.030	234.7	0.00122	4.08
500	Nitrate	3.43	0.996	0.062	0.004	0.81	20.74	14.14	0.053	0.0011	-0.041	0.009	0.0013	0.026	343.6	-0.00009	1.12
496	Organic N	0.73	0.979	0.182	0.030	0.90	11.46	31.29	0.065	0.0039	0.018	0.009	0.0079	-0.032	-17.8	0.00050	2.89
475	Organic N	0.78	0.950	0.056	0.039	-0.05	3.42	3.86	0.059	0.0054	0.106	0.016	0.0031	-0.039	366.9	0.00039	0.51
472	Total N	4.20	0.955	0.028	0.007	1.06	14.70	10.16	0.046	0.0057	0.040	0.011	0.0062	0.015	162.1	0.00028	-1.03
467	Nitrate	3.23	0.994	-0.014	0.020	0.76	10.09	14.65	0.057	0.0048	0.058	0.020	0.0081	-0.099	62.5	0.00058	1.16
467	Organic N	0.75	0.999	-0.014	0.020	0.76	10.09	14.65	0.057	0.0048	0.058	0.020	0.0081	-0.099	62.5	0.00058	1.16
465	Organic N	0.78	0.997	0.011	0.085	0.15	16.46	19.93	0.073	0.0067	0.050	0.007	0.0018	-0.021	103.7	0.00004	-1.40
456	Nitrate	3.35	0.999	0.210	0.061	1.05	-10.71	16.77	0.069	0.0060	0.061	0.003	0.0029	0.094	33.2	0.00021	-0.61
440	Organic N	0.78	0.993	0.216	0.070	0.84	2.43	22.69	0.070	0.0070	0.053	0.013	0.0058	-0.031	123.7	0.00050	0.85
416	Organic N	0.75	1.000	-0.082	0.142	0.65	14.08	15.81	0.087	0.0062	0.020	0.002	0.0057	-0.023	149.7	0.00086	0.74
415	Organic N	0.79	0.955	0.167	0.170	0.42	38.42	38.64	0.040	0.0062	0.057	0.016	-0.0005	0.001	53.7	0.00054	2.84

Table D.2 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	HRT (h)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)	Mussel Biomass (g)	Mussel Clearance Rate (h ⁻¹ g ⁻¹)	Mussel Excretion Rate (h ⁻¹ g ⁻¹)
409	Nitrate	3.26	0.962	0.357	0.022	0.28	14.82	23.57	0.021	0.0037	0.068	0.007	0.0000	0.035	43.3	0.00039	4.98
394	Nitrate	3.20	0.979	-0.023	0.025	0.62	2.40	22.23	0.072	0.0093	0.156	0.014	-0.0023	0.084	79.8	0.00024	3.22
394	Total N	4.05	0.963	-0.023	0.025	0.62	2.40	22.23	0.072	0.0093	0.156	0.014	-0.0023	0.084	79.8	0.00024	3.22
381	Organic N	0.81	0.973	0.026	0.036	0.49	-19.38	28.62	0.078	0.0053	0.071	-0.003	0.0044	-0.041	209.7	0.00040	-1.16
380	Organic N	0.80	0.996	0.094	0.106	0.23	6.65	18.93	0.087	0.0061	0.074	-0.001	-0.0013	-0.023	115.5	0.00011	2.19
377	Nitrate	3.23	0.993	0.034	0.026	0.54	10.09	14.52	0.037	0.0138	0.049	-0.002	-0.0014	-0.053	100.2	0.00058	2.60
377	Organic N	0.80	0.999	0.034	0.026	0.54	10.09	14.52	0.037	0.0138	0.049	-0.002	-0.0014	-0.053	100.2	0.00058	2.60
362	Organic N	0.77	0.954	0.139	0.019	0.46	12.56	41.01	0.077	0.0027	-0.047	0.016	0.0034	-0.018	197.8	0.00028	1.93
345	Organic N	0.77	0.999	0.318	0.127	0.56	7.37	14.60	0.027	0.0038	0.017	0.004	0.0063	-0.005	139.2	0.00070	2.76
342	Organic N	0.79	0.991	-0.119	0.079	0.85	5.70	10.39	0.060	0.0081	0.016	0.011	0.0009	-0.001	172.5	0.00015	0.92
341	Organic N	0.76	0.989	0.144	0.108	0.32	9.78	9.79	0.055	0.0071	0.081	0.007	0.0081	-0.011	-8.5	0.00032	3.46
337	Nitrate	3.36	0.990	0.089	0.043	0.07	-1.19	13.37	0.061	0.0138	0.041	-0.003	0.0003	0.061	161.5	0.00061	0.54
329	Nitrate	3.22	0.974	0.066	0.039	0.34	-2.44	23.02	0.054	0.0049	0.094	0.003	0.0046	0.088	168.9	0.00024	1.36
315	Organic N	0.79	0.998	0.122	-0.023	0.79	25.17	13.63	0.054	0.0113	0.058	0.012	-0.0025	-0.031	221.0	0.00035	-0.69
310	Organic N	0.78	0.986	0.261	0.037	0.99	18.73	25.91	0.038	0.0072	0.072	0.007	0.0016	-0.007	59.4	0.00050	3.42
305	Organic N	0.78	0.993	0.168	0.041	1.25	7.98	22.94	0.061	0.0104	0.083	-0.001	0.0038	-0.042	20.8	0.00065	1.02
283	Organic N	0.79	0.994	0.213	0.065	0.14	6.84	11.34	0.060	0.0091	0.036	0.004	0.0014	-0.044	123.8	-0.00013	0.88
274	Organic N	0.80	0.999	0.067	0.009	-0.27	15.23	16.84	0.069	0.0045	0.024	0.010	-0.0013	-0.006	122.1	0.00052	2.88
261	Organic N	0.78	0.988	0.241	0.030	1.60	18.75	9.43	0.061	0.0050	0.043	0.013	0.0015	-0.014	295.4	0.00036	4.13
245	Organic N	0.80	0.992	0.215	0.026	0.05	15.12	21.40	0.066	0.0072	0.076	-0.003	-0.0025	-0.016	278.5	0.00069	4.49
235	Nitrate	3.23	0.984	0.135	0.024	0.75	8.84	21.92	0.076	0.0056	0.086	0.006	0.0004	0.042	53.4	0.00036	3.68
235	Total N	4.12	0.952	0.135	0.024	0.75	8.84	21.92	0.076	0.0056	0.086	0.006	0.0004	0.042	53.4	0.00036	3.68
211	Total N	4.24	0.981	0.283	0.009	0.30	15.38	13.90	0.063	0.0075	0.049	-0.008	0.0054	0.125	125.2	0.00019	0.81
207	Nitrate	3.33	0.997	0.154	0.017	0.32	8.19	18.28	0.045	0.0080	-0.036	0.023	-0.0033	0.049	80.2	0.00018	0.23
201	Organic N	0.79	0.991	0.031	0.071	0.78	-2.87	10.04	0.092	0.0044	0.099	0.010	-0.0020	-0.016	81.4	-0.00005	0.85
191	Organic N	0.76	0.965	0.176	0.069	0.53	26.69	5.71	0.045	0.0054	0.084	0.003	0.0027	-0.014	15.4	0.00013	1.26
177	Organic N	0.75	0.983	0.178	0.031	0.09	17.78	8.71	0.080	0.0072	-0.007	0.013	0.0072	-0.004	273.4	0.00070	2.77
167	Organic N	0.80	0.991	0.006	0.094	0.86	4.58	22.47	0.069	0.0056	-0.001	0.012	0.0020	-0.026	122.1	-0.00031	-0.05
144	Nitrate	3.29	0.959	0.042	0.049	0.57	0.95	10.87	0.049	0.0020	0.099	0.005	-0.0015	0.046	229.9	0.00022	2.07
135	Organic N	0.76	0.992	0.321	0.071	0.64	18.89	10.80	0.063	0.0052	0.049	0.018	0.0043	-0.001	220.4	0.00037	-0.17
127	Total N	4.07	0.971	0.196	-0.007	0.09	15.72	18.89	0.069	0.0080	0.070	0.004	0.0007	0.034	130.5	0.00061	0.00
114	Organic N	0.79	0.969	0.156	0.053	0.35	3.62	32.07	0.052	0.0088	0.083	0.005	0.0033	-0.001	140.9	0.00063	0.03
105	Nitrate	3.35	0.986	-0.022	0.062	0.09	-14.14	19.99	0.063	0.0053	0.011	0.006	0.0076	0.012	67.4	0.00001	0.96
105	Total N	4.01	0.984	-0.022	0.062	0.09	-14.14	19.99	0.063	0.0053	0.011	0.006	0.0076	0.012	67.4	0.00001	0.96
91	Nitrate	3.49	0.970	0.205	0.008	0.85	15.35	11.03	0.056	0.0010	0.045	0.010	0.0093	0.054	-32.8	0.00042	1.41
51	Nitrate	3.28	0.979	0.229	0.008	0.34	16.69	22.25	0.089	0.0084	0.078	-0.005	-0.0005	0.052	131.2	0.00055	-1.82
44	Organic N	0.74	0.950	0.109	0.083	0.47	23.60	4.05	0.083	0.0022	0.025	0.008	0.0095	-0.024	206.3	0.00031	-2.64
34	Organic N	0.75	0.954	0.130	0.127	0.36	45.92	4.40	0.062	0.0126	0.059	0.022	0.0011	-0.025	137.7	0.00078	2.52

Table D.3: Control no flow model variables for the 46 sensitivity runs that met the criteria established by the multiple variable sensitivity analysis.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
1984	Organic N	0.54	0.998	0.073	-0.016	0.38	9.87	0.065	0.0103	0.088	0.004	0.0041	-0.014
1893	Nitrite	0.00	0.964	0.262	0.061	0.56	24.68	0.080	0.0095	0.055	0.006	0.0045	-0.009
1861	Organic N	0.52	0.998	0.195	0.105	0.72	3.34	0.052	0.0119	0.011	0.027	0.0082	0.000
1850	Nitrate	2.33	1.000	0.071	0.004	0.09	25.15	0.050	0.0090	0.064	0.005	0.0002	0.062
1818	Nitrate	2.30	1.000	0.114	0.012	0.07	10.64	0.055	0.0061	0.082	0.002	0.0007	0.079
1804	Organic N	0.53	0.998	0.076	0.087	0.52	9.83	0.084	0.0091	0.069	0.001	0.0043	-0.011
1715	Nitrate	2.27	1.000	0.096	0.006	1.14	19.53	0.043	0.0067	0.060	-0.003	0.0030	0.048
1627	Nitrate	2.17	0.997	0.158	0.004	-0.25	24.94	0.059	0.0117	0.046	0.029	0.0018	0.056
1621	Organic N	0.51	0.997	-0.043	-0.026	0.91	15.87	0.025	0.0043	0.060	0.013	0.0001	0.001
1592	Nitrate	2.20	0.999	0.154	0.032	0.19	-1.15	0.091	0.0079	0.068	0.014	-0.0007	-0.014
1511	Total N	2.70	0.995	0.268	0.032	1.40	1.65	0.077	0.0054	0.030	0.002	-0.0004	-0.011
1501	Organic N	0.53	0.998	0.107	0.042	0.46	14.27	0.062	0.0084	0.104	0.006	0.0030	-0.002
1454	Organic N	0.52	0.997	0.224	0.005	0.44	17.61	0.064	0.0071	0.084	0.029	0.0025	-0.034
1413	Nitrate	2.32	1.000	-0.075	0.029	0.49	-0.73	0.093	0.0086	0.056	0.012	0.0046	0.025
1382	Nitrate	2.30	1.000	0.109	0.012	-0.03	10.47	0.092	0.0068	0.049	0.021	0.0058	0.032
1275	Total N	2.82	0.998	0.084	0.033	0.31	-0.04	0.100	0.0067	0.016	0.017	0.0037	-0.005
1241	Phyto	0.04	0.960	0.047	0.122	0.66	38.54	0.049	0.0002	0.013	0.019	0.0067	-0.013
1166	Nitrate	2.23	0.992	0.046	0.008	0.57	18.20	0.018	0.0091	0.095	0.003	0.0073	-0.012
1140	Nitrate	2.16	0.999	0.000	0.013	1.12	11.07	0.057	0.0028	0.038	0.011	0.0050	0.047
1018	Nitrate	2.18	0.998	0.233	0.010	0.14	13.87	0.082	0.0080	0.077	0.014	0.0056	0.132
1007	Phyto	0.04	0.961	0.140	0.027	0.40	6.96	0.066	0.0067	-0.009	0.027	0.0098	0.069
981	Organic N	0.53	0.998	0.029	0.046	0.84	3.85	0.089	0.0056	0.054	0.018	-0.0028	0.001
971	Organic N	0.56	0.999	0.244	0.089	0.43	25.07	0.069	0.0043	0.035	0.018	0.0012	-0.046
960	Nitrate	2.31	1.000	0.208	0.022	0.42	2.70	0.040	0.0122	0.092	0.023	-0.0005	-0.017
910	Nitrate	2.17	0.999	0.012	0.032	0.59	-0.91	0.096	0.0049	0.021	0.017	-0.0025	0.011
896	Organic N	0.54	0.998	0.016	0.029	0.59	0.94	0.043	0.0007	0.012	0.006	0.0082	-0.019
815	Phyto	0.04	0.962	0.187	-0.030	1.39	3.20	0.058	0.0074	0.010	0.004	0.0001	0.028
780	Nitrate	2.17	0.998	0.101	0.047	0.62	-5.88	0.080	0.0062	0.069	0.017	0.0064	0.050
763	Nitrate	2.28	1.000	0.090	0.010	0.59	14.02	0.085	0.0073	0.085	0.005	0.0051	0.035
751	Organic N	0.54	0.999	0.066	0.068	-0.44	20.44	0.063	0.0041	0.079	0.021	0.0018	-0.017
699	Organic N	0.51	0.997	-0.014	0.011	0.60	7.27	0.073	0.0057	0.107	0.010	0.0056	-0.001
633	Total N	2.89	0.994	-0.098	0.004	0.63	27.12	0.048	0.0035	0.065	0.022	0.0061	-0.024
619	Total N	2.66	0.986	-0.016	0.047	0.69	-4.77	0.058	0.0018	-0.001	-0.002	-0.0038	-0.006

Table D.3 continued.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)
603	Organic N	0.54	0.998	0.001	0.017	0.29	16.82	0.048	0.0057	0.034	0.018	0.0024	-0.047
512	Nitrate	2.32	1.000	0.129	0.033	-0.04	-2.59	0.067	0.0038	0.017	0.029	0.0035	0.077
473	Nitrate	2.24	1.000	-0.066	0.010	0.10	13.37	0.066	0.0093	0.097	0.003	0.0065	0.061
418	Nitrate	2.34	1.000	0.260	0.021	0.40	3.23	0.071	0.0111	0.032	0.011	0.0030	0.103
397	Nitrate	2.24	1.000	0.027	0.023	0.33	2.83	0.055	0.0025	0.046	0.009	0.0073	0.038
386	Organic N	0.55	0.999	0.097	-0.009	-0.17	11.24	0.056	0.0075	0.066	0.002	0.0035	-0.018
156	Nitrate	2.32	1.000	0.125	0.006	0.65	20.11	0.029	0.0087	0.075	0.007	0.0071	0.082
132	Organic N	0.54	0.996	0.156	-0.028	0.23	24.14	0.071	0.0047	-0.043	0.013	0.0019	-0.019
115	Organic N	0.55	0.999	-0.034	0.019	0.16	6.58	0.082	0.0063	0.113	0.003	0.0050	-0.023
100	Organic N	0.51	0.997	0.097	0.030	0.63	18.27	0.040	0.0044	0.069	0.014	0.0024	-0.001
54	Phyto	0.04	0.960	0.087	0.079	1.16	23.66	0.080	0.0072	0.043	0.007	0.0001	0.037
25	Organic N	0.55	1.000	-0.042	0.050	0.77	10.26	0.037	0.0095	0.008	-0.002	0.0045	-0.004
7	Nitrate	2.34	0.999	-0.147	0.019	-0.08	4.14	0.094	0.0059	0.098	0.017	-0.0011	0.063

Table D.4: Mussel no flow model variables for the 36 sensitivity runs that met the criteria established by the multiple variable sensitivity analysis.

Sensitivity Run #	Parameter	Average (mg-N L ⁻¹)	R ²	Nitrification Rate (h ⁻¹)	Denitrification Rate (h ⁻¹)	Light	Temperature (°C)	Maximum Phytoplankton Growth Rate (h ⁻¹)	Phytoplankton Death Rate (h ⁻¹)	Phytoplankton Settling Rate (m h ⁻¹)	Phytoplankton Respiration/ Excretion Rate (h ⁻¹)	Organic Nitrogen Hydrolysis Rate (h ⁻¹)	Organic Nitrogen Settling Rate (m h ⁻¹)	Mussel Biomass (g)	Mussel Clearance Rate (h ⁻¹ g ⁻¹)	Mussel Excretion Rate (h ⁻¹ g ⁻¹)
1217	Ammonia	0.02	0.981	0.075	0.062	0.71	-2.79	0.072	0.0064	0.077	0.028	0.0059	0.037	31.5	0.00090	-0.01
620	Ammonia	0.02	0.981	0.026	0.077	0.34	10.95	0.072	0.0124	0.025	0.002	0.0066	0.049	-20.8	0.00000	-0.73
373	Ammonia	0.02	0.986	0.046	-0.015	0.66	2.48	0.045	0.0122	0.085	0.012	0.0017	0.097	-42.4	0.00089	4.51
1976	Nitrate	2.06	0.988	0.113	0.028	0.71	2.77	0.074	0.0019	0.062	0.007	0.0046	0.043	89.3	0.00017	3.45
1600	Nitrate	1.95	0.953	0.330	0.028	0.87	1.66	0.065	0.0078	0.086	0.007	0.0020	0.046	135.7	0.00013	0.58
1482	Nitrate	1.97	0.978	0.262	0.047	-0.02	-3.82	0.081	0.0059	0.032	-0.001	0.0042	-0.024	165.0	0.00005	1.28
854	Nitrate	1.98	0.954	0.090	0.038	0.88	-1.34	0.058	0.0072	0.017	0.014	-0.0039	0.000	41.1	0.00045	1.89
803	Nitrate	2.01	0.956	0.101	0.061	0.49	-6.16	0.051	0.0061	0.107	0.021	0.0080	0.034	113.8	0.00054	2.42
338	Nitrate	2.08	0.961	0.217	0.002	0.90	22.20	0.108	0.0119	0.038	-0.004	0.0042	0.010	93.4	-0.00029	-2.42
308	Nitrate	2.05	0.995	0.098	0.019	0.18	8.49	0.088	0.0040	0.083	0.017	0.0022	-0.004	157.8	0.00033	1.24
156	Nitrate	2.00	0.986	0.118	0.050	0.74	-2.53	0.041	0.0033	0.021	0.014	0.0018	0.074	137.2	0.00030	1.05
78	Nitrate	1.96	0.972	0.026	0.013	0.78	14.41	0.088	0.0107	0.033	0.024	0.0032	0.044	90.6	0.00039	1.58
1964	Organic N	0.35	0.999	0.080	0.024	0.69	15.95	0.097	0.0079	0.026	0.023	0.0035	-0.001	49.9	0.00038	1.75
1963	Organic N	0.37	1.000	-0.022	0.025	0.04	22.50	0.070	0.0075	0.078	0.035	0.0019	-0.009	187.4	0.00020	1.46
1896	Organic N	0.36	1.000	0.120	0.026	1.20	2.09	0.055	0.0055	0.095	0.002	0.0095	-0.016	100.4	0.00034	0.09
1675	Organic N	0.36	1.000	0.059	0.051	-0.07	21.63	0.044	0.0133	0.076	0.009	0.0021	-0.004	-1.4	0.00031	3.46
1530	Organic N	0.37	1.000	0.083	0.077	0.48	12.01	0.082	0.0059	0.041	0.003	0.0039	0.000	-43.9	0.00039	2.57
1484	Organic N	0.36	1.000	0.154	0.057	0.43	7.84	0.052	0.0047	0.066	-0.002	0.0061	-0.007	17.5	0.00027	3.31
1205	Organic N	0.37	1.000	0.147	0.052	1.33	9.45	0.064	0.0050	0.015	0.023	0.0055	-0.030	156.1	0.00001	-0.52
1167	Organic N	0.37	1.000	0.246	0.026	0.13	21.50	0.077	0.0085	0.045	0.002	0.0021	-0.030	233.3	0.00027	-1.15
1032	Organic N	0.35	0.999	0.089	0.079	0.58	17.55	0.083	0.0124	0.039	0.011	0.0031	0.000	214.3	0.00054	2.45
825	Organic N	0.35	0.999	0.214	0.063	0.71	12.56	0.065	0.0034	0.018	0.002	0.0045	-0.055	90.4	0.00049	2.18
820	Organic N	0.37	1.000	0.153	0.108	1.44	11.27	0.064	-0.0033	-0.013	0.011	0.0044	-0.013	315.1	0.00075	3.69
499	Organic N	0.36	1.000	0.189	0.048	0.29	5.76	0.059	0.0104	0.070	-0.002	0.0070	-0.004	243.1	0.00045	1.94
462	Organic N	0.35	0.999	0.101	0.006	0.35	19.54	0.082	0.0084	0.069	0.023	-0.0006	0.001	158.3	0.00046	1.99
375	Organic N	0.35	1.000	0.120	0.023	0.67	3.88	0.031	0.0074	-0.012	-0.006	0.0089	-0.012	111.8	0.00028	0.90
1481	Phyto	0.01	0.968	0.148	0.005	0.86	33.52	0.079	0.0051	0.018	0.016	-0.0003	0.042	342.3	0.00022	-0.35
1404	Phyto	0.01	0.966	0.218	0.095	0.21	38.07	0.049	0.0000	-0.016	0.004	0.0058	0.067	93.1	0.00027	2.48
904	Phyto	0.01	0.968	0.104	0.005	1.28	6.35	0.077	0.0038	0.016	0.014	0.0096	0.015	6.1	-0.00008	-1.17
612	Phyto	0.01	0.971	0.271	0.011	0.45	34.21	0.078	0.0005	0.035	0.003	0.0021	0.061	-65.8	0.00039	1.59
571	Phyto	0.01	0.971	0.086	0.086	0.61	6.30	0.062	0.0057	-0.080	0.012	0.0029	0.082	135.1	0.00010	-0.11
1747	Total N	2.35	0.970	0.165	0.040	0.57	-3.97	0.032	0.0062	0.028	0.031	0.0044	0.062	77.4	0.00009	3.16
1332	Total N	2.46	0.988	0.057	0.040	0.90	1.10	0.081	0.0041	0.063	0.014	0.0046	0.038	159.7	0.00013	2.68
890	Total N	2.44	0.957	0.257	0.025	0.35	4.18	0.043	0.0010	0.071	0.006	0.0021	0.046	126.6	0.00046	1.96
156	Total N	2.45	0.982	0.118	0.050	0.74	-2.53	0.041	0.0033	0.021	0.014	0.0018	0.074	137.2	0.00030	1.05
78	Total N	2.44	0.992	0.026	0.013	0.78	14.41	0.088	0.0107	0.033	0.024	0.0032	0.044	90.6	0.00039	1.58

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