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# Sustainable Aquaponics

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## Trophic controls for optimization of sustainable food production methods

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*A thesis submitted in fulfilment of the  
requirements for the degree of Masters of  
Science in the*

Department of Biology



## *Abstract*

Aquaponics has the potential to be a superior food production method compared to traditional agriculture through its potential for sustainability. This is particularly important in advanced aquaponic systems that integrate waste disposal (e.g., kitchen waste) and involve several steps linking waste decomposition to protein production. In such systems a success of one type of organism propagates down the food chain and may have negative impact on contribution of other organisms, which reduces system efficiency. I hypothesised that a combination of top-down and bottom-up regulations, concepts borrowed from resilient natural ecosystems, would allow to optimize environment for aquaponics systems to avoid such negative impacts. First, I conducted an experiment using simplified systems with two trophic levels only to determine productivity, resistance and resilience of the various combinations of top-down and bottom-up forces. The simple systems contained algae and *Daphnia magna* and were placed under a light removal disturbance to observe the abilities of these different combinations to resist and recover from a generic negative environmental impact. Next, a similar light disturbance was implemented on a large complex aquaponics system to discover if it would react differently from the smaller ones.

The resistance and resilience of algae in the small systems was not found to have any relationship to predation. The resilience of algae was better at low nutrient levels compared to high ones. There was evidence that low nutrient treatments had better resistance and resilience of abiotic factors. The larger systems appeared to have inferior resistance and resilience as compared to the simple, small systems. However, a time series analysis indicates that these large systems, in contrast to the simpler systems, actually improved in the amount of algae after the disturbance. New methods for accounting for this in resilience calculations are needed to eliminate potential statistical artifacts that might lead to some of my observations.

Department of Biology

Masters of Science

Sustainable Aquaponics:

Examination of trophic controls for optimization of sustainable food production methods

By: Michael Tadashi Sullivan Takahashi

## *Acknowledgements*

**Dr. Jurek Kolasa** for supervising the project

**Dr. Matt Hammond** for assisting with ideas and understanding of the project

**(Dr.) Jo Werba** for assisting with the project and for statistical advice and guidance

**Dr. Jonathon Stone** for guidance and ideas

**Dr. Susan Dudley** for statistical ideas and methods

**Claire Layton** for editing and offering writing advice

**Shay Freger** for volunteer assistance with data collection

**Sean Takahashi** for assistance with data collection

**Jaki Peters** for assistance with data collection

**Erin Smith** for assistance with data collection

**Sandra Smith** for building the equipment necessary for the experimental methods

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## *Abbreviations*

$\Omega$  Resistance

$\Delta$  Resilience

$Y_n$  expected ecosystem productivity during normal periods (mean across all pre-disturbance periods)

$Y_e$  during a disturbance event

$Y_{e+1}$  during the period after a disturbance event.

## 1.0 Introduction

Designer ecosystems have been a relatively new trend within the realm of applied ecology and urban agriculture. One of the major unsettled questions is how productive and stable such systems can be. My study focuses on fundamental aspects of optimizing modular designer ecosystems. I take advantage of a system available at McMaster (designed and operated by Dr. Kolasa and Dr. Hammond). They have built aquaponic ecosystems that are partitioned into four tiers that roughly correspond to trophic levels in a hypothetical trophic cascade.

The four tiers consist, from top, of a recycling module, a primary production module containing algae, the third containing *Daphnia magna* as the primary consumer, and the bottom tank containing Tilapia as the secondary consumer. This modular architecture enables easy control of interactions among these components. Water flow from the primary production module into the primary consumer module can be regulated to adjust feeding of the *D. magna*. In turn, the *D. magna* can be taken from the primary consumer module in nets and fed to the tilapia. Finally, the water from the tilapia tank can be pumped up to the primary consumer module where the algae can use the tilapia waste the water contains. Chlorophyll concentration was measured to calculate productivity in this experiment because chlorophyll is associated with algal growth. To assess the stability of the systems, resistance and resilience metrics were calculated. These two measures are relevant because resistance describes the system ability to maintain its characteristics despite variation in conditions while resilience describes its ability to return to the characteristic state after a disturbance.





**Fig 1.** The aquaponic systems used in the study. The components of the system include a terrestrial composting unit (top shelf), primary producing algal unit (second from top), the primary consumer unit, and a secondary consumer unit at the bottom. Photograph taken by Dr. Jurek Kolasa.

### **Significance**

This study aimed at providing information on approaches and methods for overcoming an inherent challenge associated with designing self-sustainable, productive, and stable indoor aquaponic systems. Recycling and relatively closed aquaponic systems have the potential for broader applications, with environmental benefits alongside, through the reduction of pollution and land degradation associated with current forms of agriculture. This project contributes to the discipline of ecology by testing the idea that top-down and bottom-up controls are not independent, but rather represent two facets of the same process, and that it is feasible to determine the relative magnitudes of each control at any point in time.

While the research question has a broader meaning in the field of ecology, the specific results my experiments are intended to apply to aquaponics research. Aquaponics is the combination of hydroponics and aquaculture: The wastewater from the aquaculture provides the nutrients for hydroponic growth (Blidariu & Grozea, 2011; Tyson, Simonne, White, & Lamb, 2004). Hydroponic plant cultivation involves plants that are grown in nutrient solutions, typically without a solid component (Jensen, 1997). These nutrients can derive solely from the aquaculture waste or in combination with human-introduced nutrients, depending on the system. The rate of nitrate, nitrogen and phosphorus removal from the fish waste depends on the number of plants and amount of waste. The plants are crucial for the recycling of this waste, and benefit from the subsequent intake of nutrients through this process (Blidariu & Grozea, 2011; Adler, Harper, Takeda, Wade, & Summerfelt, 2000).

The contained recycling of waste in an aquaponics system is beneficial when considered at a larger scale, as there are increasing environmental regulations regarding water use and disposal (Blidariu & Grozea, 2011; Enduta, Jusoh, Ali, & Nik, 2011). Effluent, excess nutrients, and surplus fish food contribute to waste produced through aquaculture that can be damaging to the environment (Enduta, Jusoh, Ali, & Nik, 2011). This situation of excess nutrients is the cause of eutrophication, polluting natural environments and creating dead zones. Aquaponics allows for better management of water which can benefit businesses as well as the environment.

An additional benefit of using aquaponics for growing crops is the ability to label food grown in this method as organic because there is no need for pesticides and more control how the products are grown (Blidariu & Grozea, 2011). The results from these experiments can aid to maximize production and efficiency of aquaponics systems. They can also be used to inform

interventions that can reduce previously observed fluctuations in the system – to increase its stability.

After the initial experimentation on the lower trophic levels, which includes the nutrients, algae, and *D. magna*, I extended my results and methodology to an entire aquaponics system that was built by Dr. Hammond and Dr. Kolasa.

### **Situating this research in relation to other experiments**

Previous experimental studies have shown that individual aquaponics systems exhibit variability that negatively affects their productivity, efficiency and stability (Tyson, Simonne, White, & Lamb, 2004). I have proposed that this variability can be reduced because of the very nature of the trophic cascades at the core of the multitrophic aquaponic system. Specifically, I would like to determine if there are points in the trophic cascade relationship that allow for optimization of performance aspects of a system. The aspects I focus on in this experiment are predation and nutrient flow.

#### **1.1 Background Information on Trophic Cascades and Regulation**

Trophic cascades occur when changes in a community at one trophic level have effects on other trophic levels (Heath, Speirs, & Steele, 2014). Trophic cascades are situations where the effects of the amount of consumption on the higher trophic level (such as a predator) spread down to the levels preyed on such that an increase in production of a higher trophic level results in a decrease of one immediately below. For example, the producers (algae) in the aquaponic system are directly responsible for feeding the primary consumers (*D. magna*) – overgrazing by *D. magna* however can reduce the algal population well below its ability to grow at optimum rates. Trophic cascades are highly variable in different ecosystems, with the effect of cascades fading over successive trophic levels (Heath, Speirs, & Steele, 2014). In the study presented here

inorganic nutrients are important for the growth of algae - the primary producer of concern. Algae are the resource that *D. magna* needs as food. It is known that in different systems predators (top-down controllers) or resources (bottom-up controllers) can dominate the initial effects that propagate down or up the trophic chain, which regulates the size of populations within ecosystems (Power, 1992; Hunter & Price, 1992). Top-down regulation can occur through one or multiple linkages in food webs (Baum & Worm, 2009). In natural environments there are often many trophic links between trophic levels (instances of resources consumed), but for the simplified system in this experiment, as well as the larger aquaponic ecosystems in our lab, there was only one link between each level. In the simplified experiment one link was the flux of dissolved nutrients to algae, which then was consumed (another link) by *Daphnia*. In the large complex systems there were controlled single links: compost to algae, algae to *Daphnia* and *Daphnia* to tilapia. The tilapia water was also recycled back to the algae. Limiting links allows for increased control of the energy flow through trophic levels and thus the whole system.

Trophic cascades are best revealed after a perturbation in the environment (Baum & Worm, 2009). An example given by Baum & Worm (2009) was the sea otter overexploitation that, in the 1970's, led to the growth of urchin populations that are normally consumed by the sea otters. Therefore, I suggest, as a research strategy, the creation of a gradient of top-down and bottom-up regulated systems. Such a gradient should allow to determine at which combination of resources levels of productivity, efficiency and stability can be maximized.

It is often difficult to generate experimental data for ecological systems with large predators due to financial, ethical and time constraints (Baum & Worm, 2009). This study omits large predators (tertiary predators such as piscivorous fish, turtles, or birds), because our interests are focused on aquaponic systems. Like with most laboratory representations, the manufactured

relationships are only representative of what may but not necessary does occur in nature. Nevertheless, they will provide a glimpse into how trophic cascades can operate. Additionally, while the experiments may not provide a complete representation of natural phenomena, they are directly applicable to aquaponics research, as closed recirculating ecosystems are completely controlled by anthropogenic intervention. Such intervention is not much unlike the experiments themselves. Researchers demonstrated that the aquaponics approach to recycling waste can be used to manage sewage waste as well, thus giving another opportunity for application of this research (Rana, et al., 2011) to management of immediate human environment.

Bottom-up regulation, in contrast to the top-down regulations, refers to situations where changes in availability of resources at the basis of the trophic pyramid (e.g., nutrients, primary production) affect the dynamics of the higher trophic levels (Davis, Cook, Collins, & Hall, 2015; Heath, Speirs, & Steele, 2014). When there is an increase of predation pressure at higher trophic levels, it results in less predation at a level immediately below the predator, and a corresponding increase in abundance at the next trophic level down, and so on, resulting in a chain of alternating (decrease-increase) effects on production of the consecutive levels (Heath, Speirs, & Steele, 2014).

Past experiments and models have manipulated resources and consumers in order to affect species performance (usually abundance) in food web interactions (Polishchuck, Vijverberg, & Voronov, 2013; Turner, 1992; Turkington, 2009; Brett & Goldman, 1997; Kratina, Hamish, Carvalho-Pereira & Shurin, 2012). The strongest evidence for the existence of predation-regulated assemblages is found within aquatic ecosystems (Heath, Speirs, & Steele, 2014; Strong, 1992).

Bottom-up regulation constrains define the amount of energy that can be transferred up to higher trophic levels, while top-down regulation determines the distribution of the energy throughout the trophic levels (Terborgh, 2015). Terborgh (2015) argues that ecosystems cannot exist with only either top-down or bottom-up regulation, as this would go against ‘undisputed reality.’ This idea however is neither clear nor inevitably correct as there is no logical or empirical evidence that this always must be the case. Terborgh (2015) appears to conflate the notion of limitation with the notion of control.

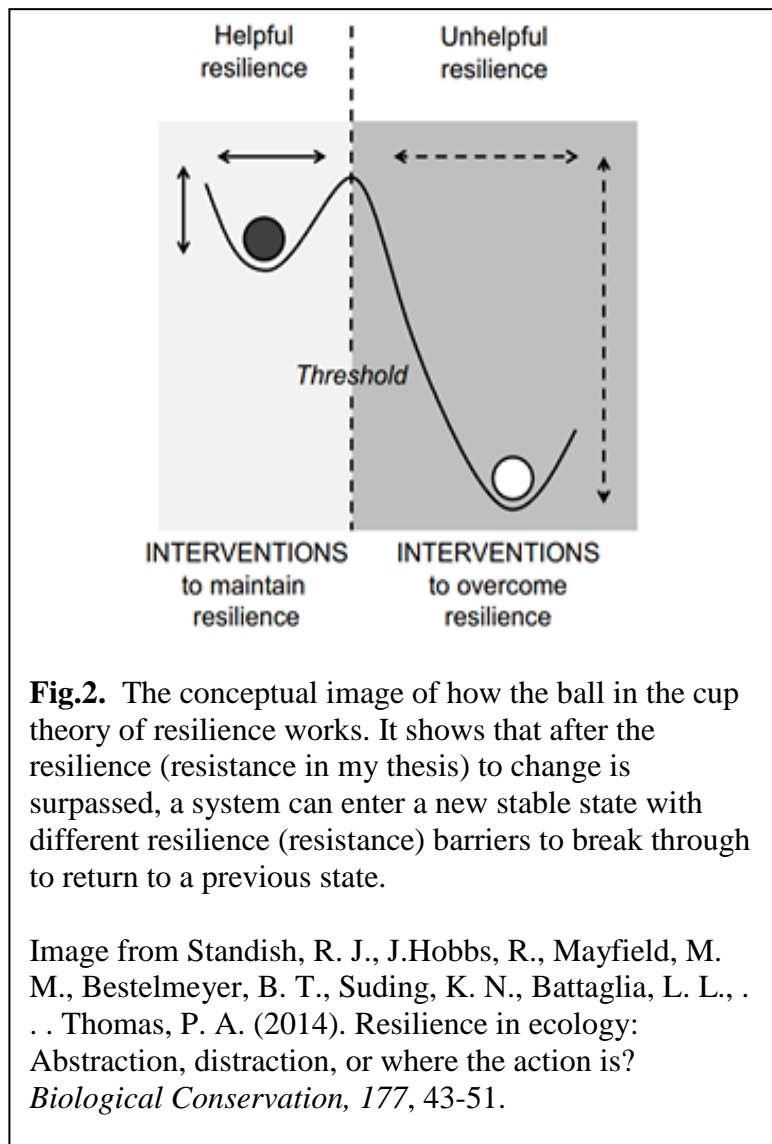
## **1.2 Background on Resistance and Resilience**

Holling (1973) is credited with introducing the term ‘resilient’ to ecology. Since then, there have been many interpretations of what resilience in ecology might mean (Standish, et al., 2014). The measures of how to evaluate resilience can also vary. Since the initial use of ‘resilience’ in ecology, the many interpretations of what it could be used for, have often led to individuals redefining it (Standish, et al., 2014), or coming up with working definitions for a particular study (Carpenter, Walker, Anderies, & Abel, 2001). Understanding ‘resilience’ becomes difficult due to these numerous definitions. There have also been attempts to define ‘resistance’ in literature (Carpenter, Walker, Anderies, & Abel, 2001), though the general meaning of resistance seems to be more consistent over time, with it currently being defined as a description of a systems ability to avoid change when under pressure (Isbell at al., 2015). Other researchers have broken stability measures into resilience and recovery components, where resilience is resistance to change, while recovery is the ability to return after a disturbance (Hodgson, McDonald, & Hosken, 2015). If authors do not define their use of these highly contested terms, interpretation of their research becomes difficult. It is therefore important to outline the terms of resilience and resistance employed in this study, calculated according to

Isbell et al. (2015). I follow an engineering resilience definition for the ability of a system to recover after a disturbance, while resistance will measure the ability to stop change from happening while under stress.

Researchers have attempted to relate the complexity of an ecosystem to its ability to endure a disturbance (Pimm, 1984; Isbell F, 2015). Relevant here, is the earlier discussion and the associated assumption that more pathways are beneficial for increasing stability (Pimm, 1984).

Resilience has been broken down into several sub-types by some authors, which has proved useful when thinking about the way resilience can influence a system. Standish et. al (2014) have noted that there can be *helpful* and *unhelpful* resilience. This recognition comes from the often discussed ‘ball in a cup’ model (Gunderson, 2000); once a system passes a threshold, it might enter a new stable state that is entirely different from the previous one (Fig. 2). Helpful resilience in this case is the resilience that prevents



the ecosystem from passing this threshold, while unhelpful resilience is the resilience that prevents a system from returning to a previous state once through the initial threshold (Standish, et al., 2014). This has been conceptualised in the past as shifting of stable states through the term bifurcation (Dakos, Nes, D’Odorico, & Scheffer, 2012). The concept of helpful or beneficial resilience versus unhelpful resilience was separately introduced discussed by Angeler and Allen (2016). They question whether resilience is a desirable aspect of an ecosystem in all cases. For example systems such as macro-algae dominated reefs could be considered highly resilient by some researchers, but that this may not be a situation that is beneficial (Angeler & Allen, 2016). They also note that a problem in the literature is understanding why authors generally view resilience and resistance to change as a positive trait, as there are limited examples or instruction on how to use it in a form of ecosystem management (Angeler & Allen, 2016). Another problem that is noted is that resilience measures are often focused on small subgroups of species in an ecosystem and that they might not be representative of the entire ecosystem at a bigger scale. It was also observed that resilience is measured in environments through correlations and that there are limitations due to the “local scale of the ecosystem” (Angeler & Allen, 2016).

This study attempts to address both of these problems - as previously mentioned the resistance and resilience will be calculated and assessed for small and simplified systems before scaling it up into a larger more diverse ecosystem. Additionally, this study demonstrates an active use for resilience and a tangible example of why resilience might be a desirable trait to use in creating designed ecosystems.

### **1.3 Hypothesis**

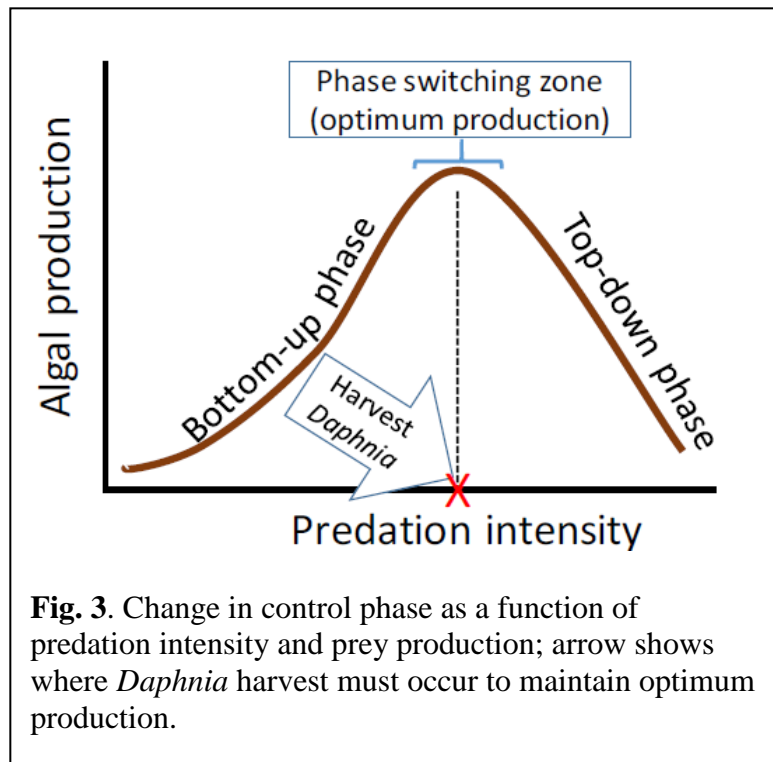
The project addresses whether the stability and production management of the indoor ecosystems is affected by top-down and/or bottom-up manipulations. I posit that the most stable



and productive system will result from the balanced control of equal top-down and bottom-up forces. I specifically hypothesise that when neither top-down or bottom-up dominate (i.e., the two mechanisms are maintained at equilibrium), a system will be more sustainable than systems controlled through either resources or predation (Fig. 3). This hypothesis can be tested because it makes quantitative predictions: I predict that a) limited predation with sufficient nutrients (bottom-up control occurring) will lead to rapid rises and crashes in algal density and that b) when predation intensity causes bottom-up control to fade away, algal production will be optimal under a given nutrient delivery regime. I use algae populations as they form the base of the food web in the aquaponics systems in the lab.

In short, this project focuses on testing the idea that the stable production of a consumer species (e.g., fish) will occur at close-to-maximum production of its prey. This is based on my theoretical proposition, unpublished, that bottom-up control of a two species food chain switches to a top-down control when predation reaches a threshold that surpasses control

effectuated through resource availability. I am focusing on the trophic control of production because this is essential for designing aquaponics systems that are self-sustaining and self-regulating.



**Fig. 3.** Change in control phase as a function of predation intensity and prey production; arrow shows where *Daphnia* harvest must occur to maintain optimum production.

Stability of the system in this study is measured with reference to resistance and resilience. As stated in my hypothesis, an active balancing of top-down and bottom-up ecological pressures should contribute to the system's stability. Top-down control can occur through one or multiple linkages in food webs (Baum & Worm, 2009). This is convenient in that it assists in designing my experimental approach.

## **2. Methods**

### **Experiment Outline**

To test the hypothesis, I proposed manipulating the relative strengths of top-down and bottom-up controls in a replicated aquaponics structure that produces its own food for fish and requires household compost as the only nutrient input. In a multilevel aquaponic system available for experimentation, I selected a particular point where manipulation and observation were to occur. This point of interjection focused on the trophic where primary production and consumption consisted solely of algae and *Daphnia magna*. I used a single linkage between the nutrient input to algae and subsequently to *D. magna*, as the grazer. This single linkage is defined as only one trophic chain starting with a single source of nutrient input for the algae and only one type of grazer eating the algae. I chose to focus on *D. magna* because it provides essential proteins for *Tilapia* fish, which is one of the products harvested for consumption within the designed indoor ecosystem.

To advance understanding of how and whether specific type of controls operate in aquaponic systems. I have conducted two experiments. The purpose of the first, factorial experiment has been to determine productivity and stability differences between systems with varying bottom-up and top-down regulations. The different levels of predation and nutrients were combined in a factorial design to determine if there was a combination that provided an

optimal environment for maintaining human built ecosystems. The productivity of algae was measured through the abundance of chlorophyll whereas to measure stability, a light disturbance was introduced. Resistance and resilience to the disturbance were calculated using approach described in section 2.3. A similar treatment of nutrient loading and light disturbance was subsequently applied to a larger, more complex, aquaponics structure to compare how resistant and resilient the larger complex system was compared to the simpler ones used in the factorial experiment.

To determine the various levels of top-down and bottom-up regulation I designed a factorial experiment with both nutrient concentration levels and grazing intensity as treatments. In addition, to generate baseline data for the proposed work, I experimentally quantified zooplankton grazing effects on algal growth (with predation enclosure controls) obtained from McMaster aquaponics systems. These experiments involved 7 replicates for each treatment (based on the power analysis of a pilot experiment), with 3 nutrient levels and 30 *D. magna* individuals placed into each replicate. The experiment intended to determine the best combinations of top-down and bottom-up controls in terms of population stability and productivity, for potential use in aquaponics systems. Specifically, the experiment aimed to determine how base trophic levels of primary consumers and primary consumers should be manipulated (Fig. 1), including nutrient delivery, frequency of intervention, and harvest rates for algae and *D. magna*. Such guided manipulations should help stabilize aquaponics systems at the optimal rates of energy transfer to and thus production of the target organism (Tilapia).

## **2.1 Methods for factorial experiment on simple ecosystems**

This experiment tested all the hypotheses stated previously. Productivity was evaluated by the cumulative amount of chlorophyll produced throughout the entire experiment

The factorial experiment used a design of three nutrient levels and three predation levels. The nutrient levels were high, medium and low. Analogously, the predation levels were high, medium, and low. The experimental treatments had seven replicates, with three balanced treatments of high, medium and low predation and nutrients. There were also two other experimental treatments of high predation with low nutrients and low predation with high nutrients (Table 2). Control treatments involved the same nutrient levels but no predation. The number of replicates was determined by a power analysis on data from an earlier experiment (not described in the thesis) which used nearly identical procedures to determine relationships between nutrients, chlorophyll and *Daphnia*. The nutrient ingredients and concentrations were obtained from the combination of a nutrient enhancement mixture named COMBO and tap water (details in Appendix 18). COMBO is based on Kilham, Kreeger, Lynn, Goulden, & Herrera's (1998) recipe and was used as the basis for the nutrient additions in all the experiments due to its suitability for growing algae in the presence of *D. magna*. The amount of the media required to grow algae was estimated using a Trophic State Index (TSI; Kratzer & Brezonik, 1981). The index relates the values of TSI to the amount of chlorophyll that can be expected and the amount of nitrogen in the environment. These estimates were used as guidelines for the experiment - one could expect concentrations of chlorophyll to be higher than expected based on the TSI because there were no other consumer of nutrients that might be present in a natural environment.

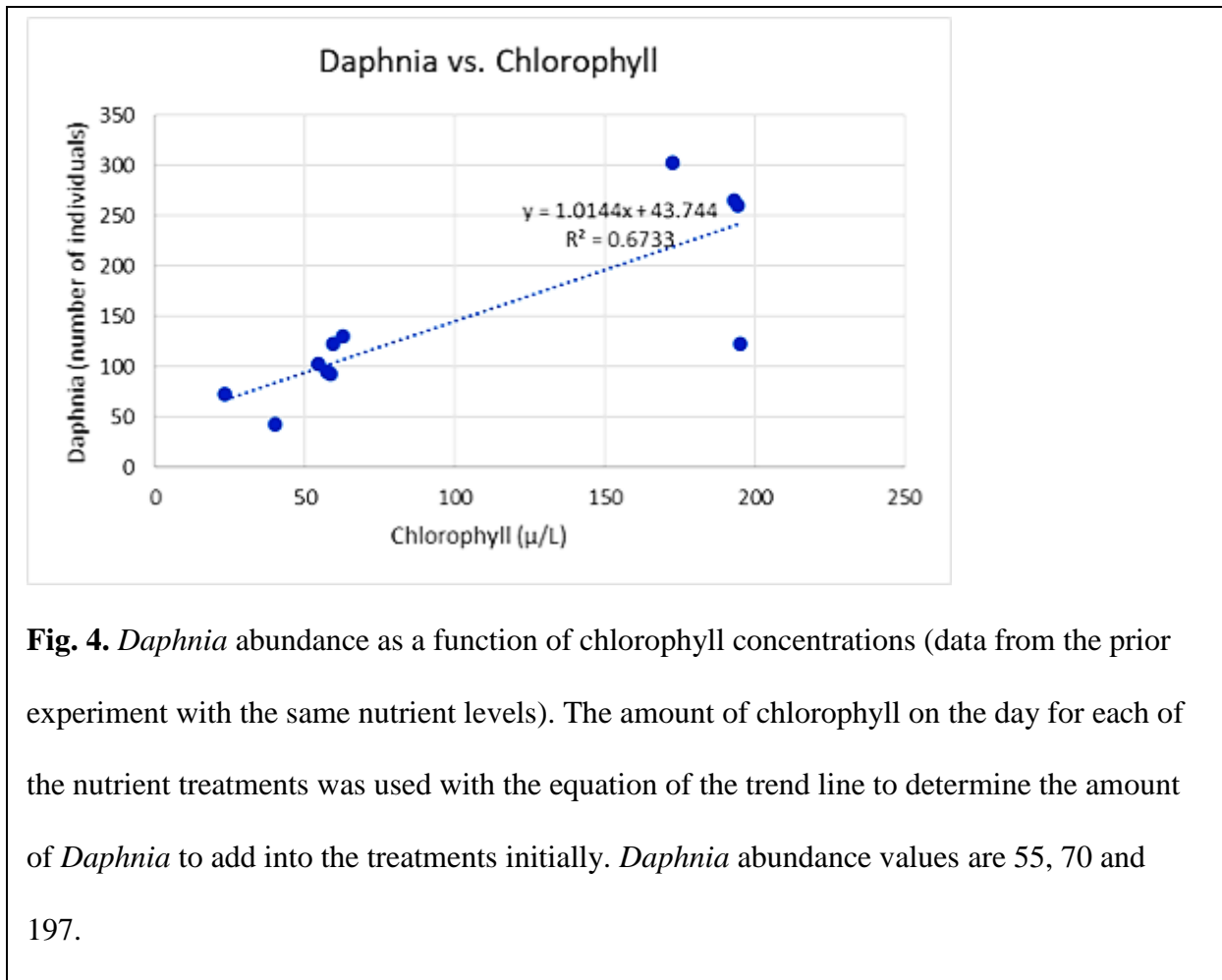
**Table 2.1.** Nutrients added to each treatment level along with, projected TSI value, projected chlorophyll concentration and the volume of 100 times concentrated solution added to each container on nutrient replacement days.

TSI Expected	N(mg/L)	Proportion of COMBO	Chlorophyll expected	mL of solution to add per L	mL solution per 5 L container
80-90	3.55129	0.25	126	2.5	12.5
60-70	0.789239	0.05556	60	0.5556	2.778
40-45	0.175391	0.012347	2.6	0.12347	0.61735

**Table 2.2** Factorial design for experimental treatments with predation and nutrients factors and the three treatments without predation. The number of replicates for each treatment is in parenthesis. The grey boxes indicate possible combinations of nutrients and predation that were not included in the experiment. There were also three nutrient only treatments for each of the low, medium and high nutrient levels.

	Nutrients			
		low	medium	High
Predation	none	(7)	(7)	(7)
	low	(7)		(7)
	medium		(7)	
	high	(7)		(7)

I determined the number of *D. magna* individuals employed in grazing treatments from a relationship between the chlorophyll concentrations and Daphnia density sustained by this

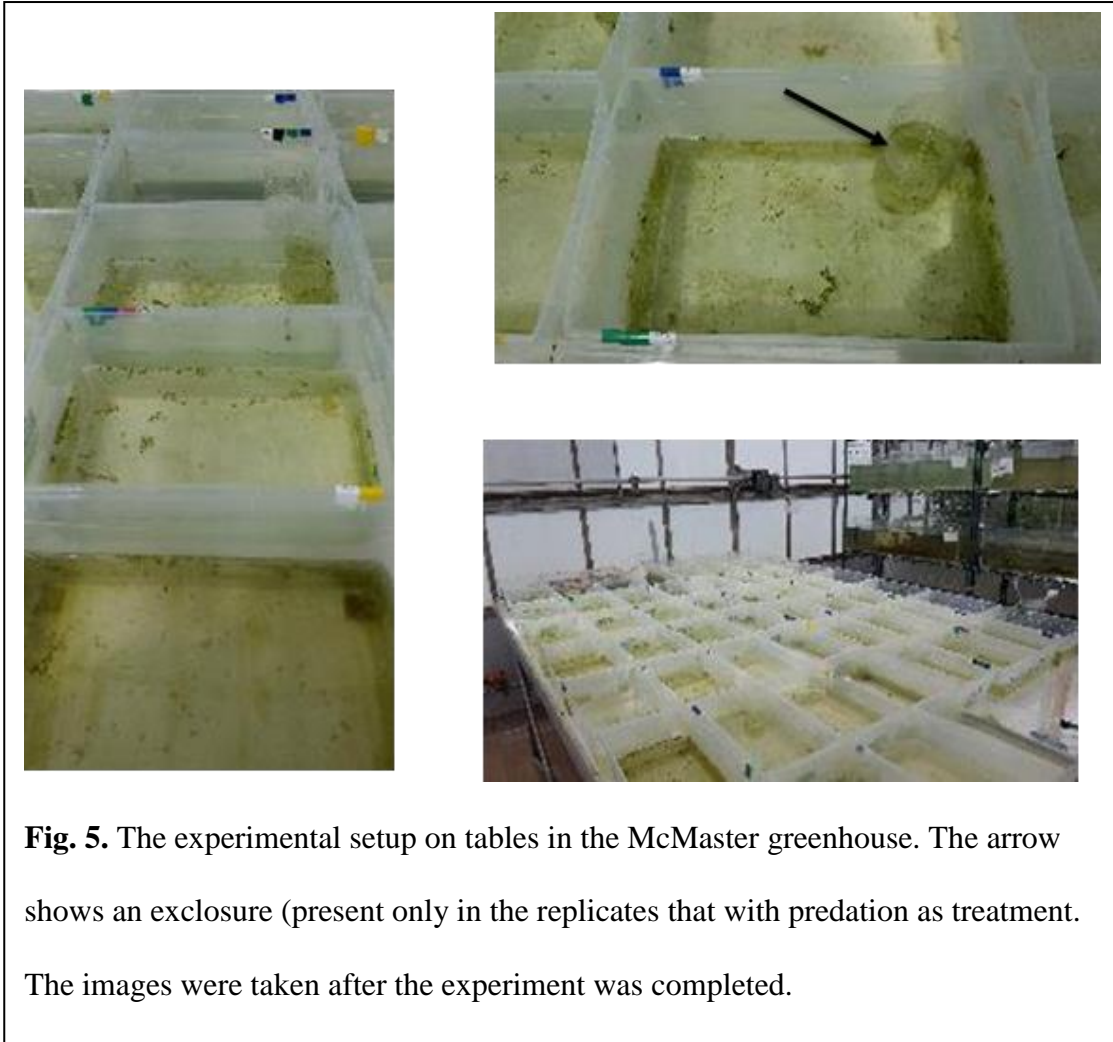


concentration (data taken from the first experiment shown in Fig. 4). In that earlier experiment, I used the same nutrient levels and allowed *D. magna* to graze and reproduce with the chlorophyll. This allowed me to estimate the level of predation at which the chlorophyll stops increasing. The corresponding predation amounts constituted 55, 70 and 197 *Daphnia* for low, medium and high treatments respectively. This was accomplished using the chlorophyll amount averaged for each treatment on the *D. magna* introduction to containers with chlorophyll. From that point onward, I maintained the constant number of *D. magna* by removing the excess of individuals (by straining out all of the *D. magna* through 250-micron mesh net on every third day and replacing them with the target number. I chose this length of adjustment interval to limit the effect of *D. magna* reproduction within each replicate. To increase density if it fell below the experimentally

mandated level I strained *D. magna* into a 500 mL container, added some *D. magna* from stock culture grown in similar nutrient solutions and transferred the whole population back to the original container. Eight 25 mL sample counts were taken of *D. magna* and averaged. The number of replicates was determined using a power analysis on a data from a similar pilot experiment. The total estimated number of *D. magna* to be inserted in the container was calculated. I used water volume as a proxy for the number of individuals to eliminate size bias for *D. magna*. Size bias in this case would be the preference to select the largest *D. magna* out of a container as they are easier to see and capture, than younger, smaller juveniles. By using sample counts and then distributing a volume of water containing *D. magna* it was no longer likely that large *D. magna* would be preferentially selected for. This also added further robustness to the experiment as selecting for a certain size of *D. magna* would have led to a skewing of observed predation as larger individuals consume more algae than smaller ones.

The colonies of algae were obtained from a local pond and cultured in the lab. The stock populations for different nutrient treatments were cultured in water with their respective nutrient treatment levels, (Table 1, with 0.25, 0.05556, 0.012347 proportions of COMBO being high, medium and low nutrient treatments). Five litres of water containing the algal populations were then distributed to the individual replicates in the treatments, *D. magna* was added to the treatments with the predation treatment. The replicate containers - clear, rectangular boxes 38.4 x 24.1 x 14 cm had a maximum volume of 9 L. To determine the daily gross change of chlorophyll within the replicate without *Daphnia*, I added small predation exclosures containing 250 mL of water from the larger replicate to each *D. magna* treatment. These exclosures were fashioned from cut plastic water bottles (arrow in Fig. 5) and then were placed upright into the larger replicate container. Clear thin plastic helped minimize the differences in exposure to light

and maintain an environment like that of the larger, hosting replicate. Every day I measured the chlorophyll in the enclosure, returned the water into the hosting replicate and another strained another volume of water was strained into it.



I reintroduced nutrients every 11 days. The same amount of nutrients that were initially added to each treatment were then added to each replicate of that treatment. The 11-day interval was determined from data obtained in the pilot experiment mentioned earlier that used the same nutrient levels. Those data indicated that nutrients were depleted in 11 days (that is 11 days was the average period for the three treatments with the same nutrient levels moving average to reach zero). The corresponding period length was 10 days for low and medium nutrient levels and 13



for high. To increase the nutrients back to the prescribed level, I prepared the COMBO solution at 100 times concentration per liter to minimize the additional volume to add. The volume of nutrients added to each replicate was 12.5mL, 2.78mL, and 0.62mL of COMBO to high, medium and low nutrient treatments, respectively. To counter evaporation, once a week I added tap water to bring it back up to 5 liters.

Initially, I measured chlorophyll, pH, dissolved oxygen, nitrate, ammonium and temperature daily. After I verified that all treatments were showing an even distribution of nutrients across them, on day 5 I have reduced the frequency of measurements to alternate days, with chlorophyll on one day and then dissolved oxygen, pH, ammonium and nitrate being measured on the other. This continued until the start of disturbance (Day 32) that lasted for 2 day and ended on day 34. The disturbance was a light disruption where all the replicates of all the treatments were covered with black plastic sheets to eliminate natural light necessary for the algal photosynthesis and so to impede algal population reproduction and growth. Following the disturbance, water and populations condition measurements were taken every day a until the end of the experiment on day 43. Chlorophyll was measured in  $\mu\text{L}$  using an AquaFluor® Handheld Fluorometer and Turbidimeter. Dissolved oxygen was measured in mg/L using an Extech DO600. pH was measured using a Hach Pocket Pro Tester and ammonium and nitrate were measured in mg/L using a YSI Proplus Multiparameter Meter.

## **2.2 Methods for experiment on complex aquaponic ecosystems**

As previously mentioned the inspiration for manipulation top-down and bottom-up pressures on systems and for evaluating them was derived from observing nutrient re-cycling aquaponic systems that were designed for sustainability. The availability of such systems

allowed for the next step of experimentation where effects of the disturbance could be examined for more realistic, more complex systems built in an indoor setting.

These systems consisted of four separate modular components, with regimented movement of organisms and materials between them. The trophic base of the ecosystems contained a community of algae that was based on the same algal stocks as those used in the factorial experiment. Additionally, and unlike the previous experiment, the algal tank contained two types of snails that helped recycle detritus, and approximately two dozen guppies at any given time that were there to provide insurance against any algal grazers that might invade the algal component. The second module (grazers or secondary producers) consisted of a tank that contained *D. magna*. These *D. magna* were accompanied by snails as well. The third component consisted of a tank containing 6 tilapia and also had a mixed species snail population.

These three components were on top of each other. Water from the bottom tilapia tank containing the fish waste was moved up to the top algal tank food to replenish nutrients. The excess volume of water in the algal tank was drained over a flood valve into the middle tank containing the *D. magna*. The water in the *D. magna* tank was then drained into the bottom tilapia tank.



**Fig. 6.** the experimental aquaponic systems before experimentation began. For the experiment the top terrestrial component was detached and the hydroponic planters were removed.

A light deprivation disturbance was applied to the entire system (Fig. 6). All hydroponic plants were removed to reduce the number of nutrient uptake pathways and to divert most nutrients to the algae. Additionally, to ensure that nutrients were added in consistent amounts, the composting component at the top in the image was disconnected from the rest of the system. Instead, the same nutrient mix as in the factorial experiment was added on a regular schedule (Appendix 22) to the algal tank. Approximately 1/7th of the total *D. magna* were collected every week by removing population from one of the seven partitions each zooplankton tank was divided into. These removed *Daphnia* were then fed to the tilapia. In addition, 15 mL of fish food was added to the tilapia tank every day to ensure adequate nutrition. There were 6 tilapia in the system which was the estimated maximum number that could be supported by the system as approved animal utilization protocol (#15-10-42) by the Animal research ethics board.

The experiment involved two of such three trophic level systems, with one acting as the control and the other as the experimental treatment to which the disturbance was applied. First, the contents of the matching modules (e.g., algae-algae) of the two systems were mixed to create

two almost identical replicates. 60% of the water and sediments from each module was reciprocally exchanged with that of the other system. This continued 3 times a week, for 4 weeks until values of chlorophyll, nitrates, ammonium and pH were the same across each level of tanks between the systems. Once this was accomplished, the nutrient addition regime was started and the light system of 12-hour days was implemented for the tanks.

Chlorophyll measurements were taken daily, with some exceptions. The only breaks in the collection of these measurements was on day 6, 23, 24, 42, 43, 55 and 56. Additionally, pH, dissolved oxygen, nitrates and ammonium data were collected twice a week on Tuesdays and Thursdays.

The disturbance was applied to the experimental system on day 9 and continued to day 25. Like the disturbance in the factorial experiment, lights within the system were turned off and the system was wrapped in black plastic sheets to shade it from external lights. Unlike the factorial experiment, the systems had to have some light allowed through because of fish needs. This disturbance was selected for because it was similar to one used in the experiment with simpler and smaller systems. The disturbance is also realistic with respect to the needs of a designed ecosystem as light supplied to the system might be disrupted during power outages. On the 25th day the lights were returned to the 12-hour cycle and the plastic sheets were removed.

The calculations of resistance and resilience indices followed the same method as for the factorial experiment (section 2.3). Means of the daily chlorophyll measurements for the entire periods for before, during and after the experiment were used to derive resistance and resilience values. Although only one system was disturbed, these values were also calculated for the control using the same time frames as the treatment system. The before-disturbance values were

defined as values collected from Day 1-9, the during-disturbance values were collected on days 10-25 and the after-disturbance values were collected on days 26-57.

As there was only one experimental and one control replicate in each treatment, there was no variability in these groups to compare. However, as resilience and resistance are relative metrics, I was justified to examine their behavior with respect to temporal dynamics (before, during, and after the disturbance) using ANOVA on combined data from both experiments with time periods and experiment ID being treatments.

### **2.3 Method for calculating Resistance and Resilience**

Resistance and resilience quantification follow Isbell et al. (2015). Resistance is the change within the system that follows a disturbance – the small relative change indicates high resistance. Resilience captures the ability of a system to return to the pre-disturbance state and is assessed by measuring the difference in values of state variables recorded before disturbance and after the recovery ends. I calculated the resistance and resilience for chlorophyll concentrations inside and outside of the *Daphnia* enclosures, when applicable as not all treatments contained the enclosures. I also calculated the resistance and resilience for the abiotic measures: dissolved oxygen, pH, nitrate and ammonium. Then, I used their estimates to determine the abilities of the systems to resist and recover from a disturbance as a function of treatment (Analysis of Variance – ANOVA Type III). I also conducted a contrast analysis on the effects of predation and nutrients on variables measured in the factorial experiment with simple systems. This last contrast analysis looked for interactions between nutrients and predation.

Potential problems with the method of calculating resistance and resilience I used could arise when the variables are unusually resistant to a disturbance, or when the disturbance is not strong enough to trigger a meaningful response. If a system is perfectly resistant to disturbance-

induced change for some variable(s), or the disturbance is very weak, then the system would lack the need for, and would not demonstrate resilience. The method of calculating both resistance and resilience as proportional change from before a disturbance means that systems with perfect resistance or resilience should have a value of 1.

### **Equations 1 and 2**

Following (Isbell et al. 2015), we define resistance and resilience as:

$$\Omega \equiv \frac{\bar{Y}_n}{|Y_e - \bar{Y}_n|} \quad (1)$$

$$\Delta \equiv \left| \frac{Y_e - \bar{Y}_n}{Y_{e+1} - \bar{Y}_n} \right| \quad (2)$$

where  $\bar{Y}_n$  is the expected ecosystem productivity pre-disturbance,  $Y_e$  during a disturbance event, and  $Y_{e+1}$  after the disturbance event.

I have evaluated predation and nutrient effects on all the variables that I selected to characterize systems resistance and resilience in order to gain resolution as to contributions of various processes to system stability. I quantified these effects through the `lm` (linear model) function in RStudio.

### **2.4 Method for calculating productivity in simple ecosystems**

I used the amount of chlorophyll produced as a measure of productivity in the individual replicates. To find out this amount, I fitted fifth order polynomials to the chlorophyll time-series curves. Then, I found the integral to estimate the total area under the curve, which I used as a

proxy measure for the total algal production in each replicate. I carried out those calculations for the outside of the exclosures for all the treatments over the duration of the experiment (details in Appendix 16).

### **3 Results**

#### **3.1 Resistance and resilience analysis of factorial experiment**

##### **Resistance and Resilience of Chlorophyll**

**Table 3.1** Resistance and resilience of chlorophyll from algae grown in the glasshouse and exposed to predation by *Daphnia* from an ANOVA (Type III). Analysis was done to determine if there were differences between nutrient and predation treatments on the ability of simple systems to resist or recover from a light disturbance. A contrast analysis was applied to nutrients and predation in order to determine if either or an interaction was responsible for the differences in resistance and resilience. Nutrients and Predation were independent variables while chlorophyll was dependent.

<b>resistance of chlorophyll exposed to predation.</b>					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	4.418835	7	2.111595	0.06016	
Residuals	14.34962	48			
contrast	estimate	SE	df	t ratio	p value
Nutrients	-0.7118180	0.5062047	48	-1.406	0.4201
Predation	-0.8169504	0.4133144	48	-1.977	0.1530
Interaction	0.2189304	0.4133144	48	0.530	0.9354
<b>resilience</b>					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	0.487812	7	0.822561	0.573481	
Residuals	4.066569	48			
Contrast	estimate	SE	df	t ratio	p value
Nutrient	-0.5653625	0.2694760	48	-2.098	0.1186
Predation	0.0822825	0.2200262	48	0.374	0.9756
Interaction	0.1840768	0.2200262	48	0.837	0.7914



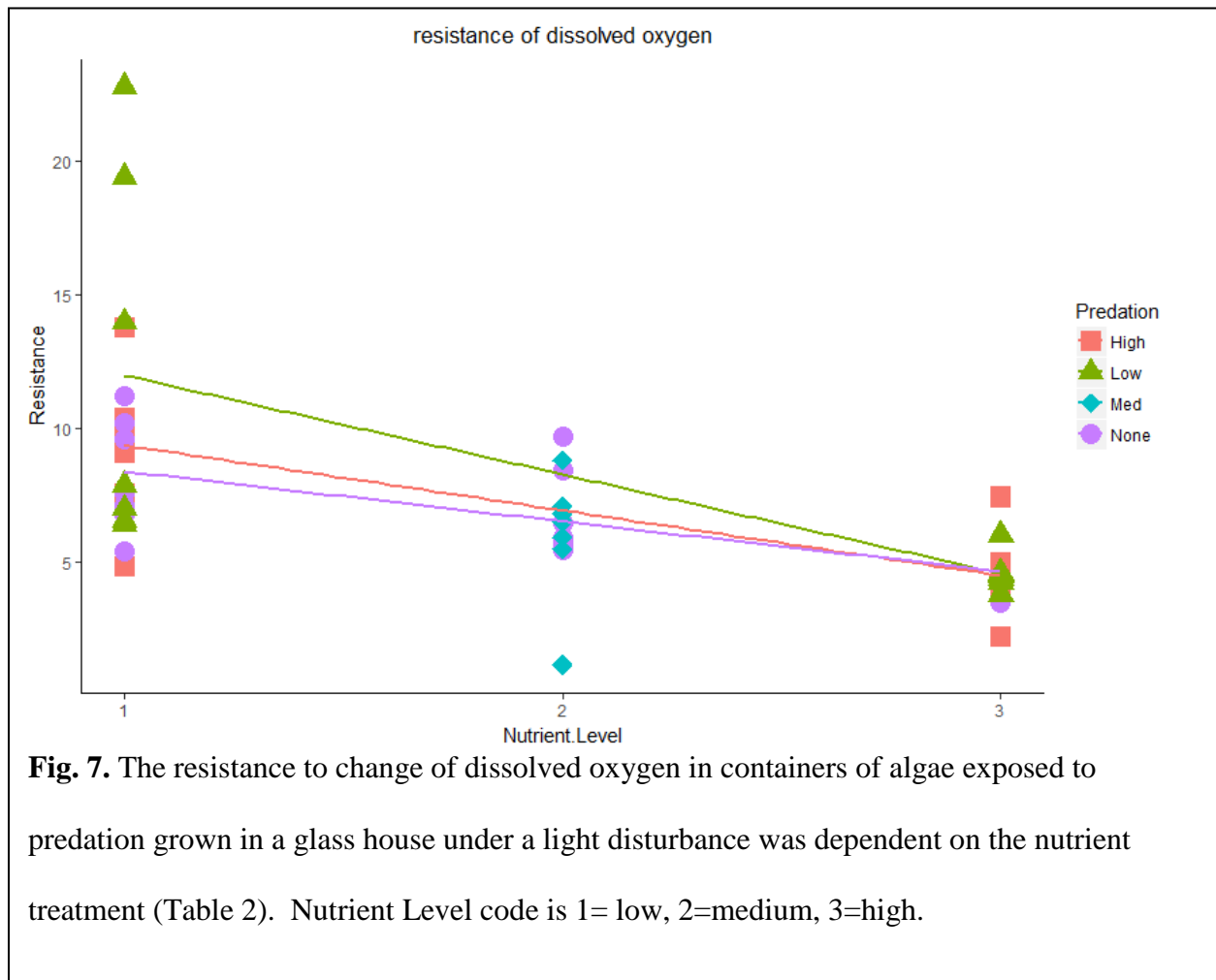
There were no significant differences between the algae exposed to predation to resist or recover from a light disturbance across nutrient or predation treatments. No interactions between nutrient or predation effects on the resistance or resilience of algae were found, either.

### Resistance and Resilience of dissolved oxygen

**Table 3.2** Resistance and resilience of dissolved oxygen from containers containing algae grown in the glasshouse and exposed to predation by *Daphnia* from an ANOVA (Type III). Analysis was done to determine if there were differences between nutrient and predation treatments on the ability of simple systems to resist or recover from a disturbance. A contrast analysis was applied to nutrients and predation in order to determine if either or an interaction was responsible for the differences in resistance and resilience. Nutrients and Predation were independent variables while dissolved oxygen was dependent.

resistance of dissolved oxygen					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	361.7664	7	5.913472	5.47E-05	
Residuals	419.497	48			
contrast	estimate	SE	df	t ratio	p value
Nutrients	-16.056097	2.736972	48	-5.866	<.0001
Predation	-2.667246	2.234729	48	-1.194	0.5585
Interaction	2.582067	2.234729	48	1.155	0.5842
resilience					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	117.7451	7	1.791899	0.110719	
Residuals	450.5807	48			
Contrast	estimate	SE	df	t ratio	p value
Nutrients	3.025523	2.836562	48	1.067	0.6443
Predation	3.598182	2.316043	48	1.554	0.3343
Interaction	2.187429	2.316043	48	0.944	0.7249

There were no determinable differences in the ability for dissolved oxygen in the simple systems to recover from a light disturbance due to nutrient or predation. The resistance of dissolved oxygen to change from a light disturbance was dependent on the nutrient level (Fig. 7). No interaction between nutrient or predation effects on the resistance or resilience of dissolved oxygen were determined. As identified in Fig.7 as the amount of nutrients increases, the



resistance trends negatively towards 1. This indicates that higher nutrient levels have an increasingly better ability to resist dissolved oxygen change due to a light disturbance.

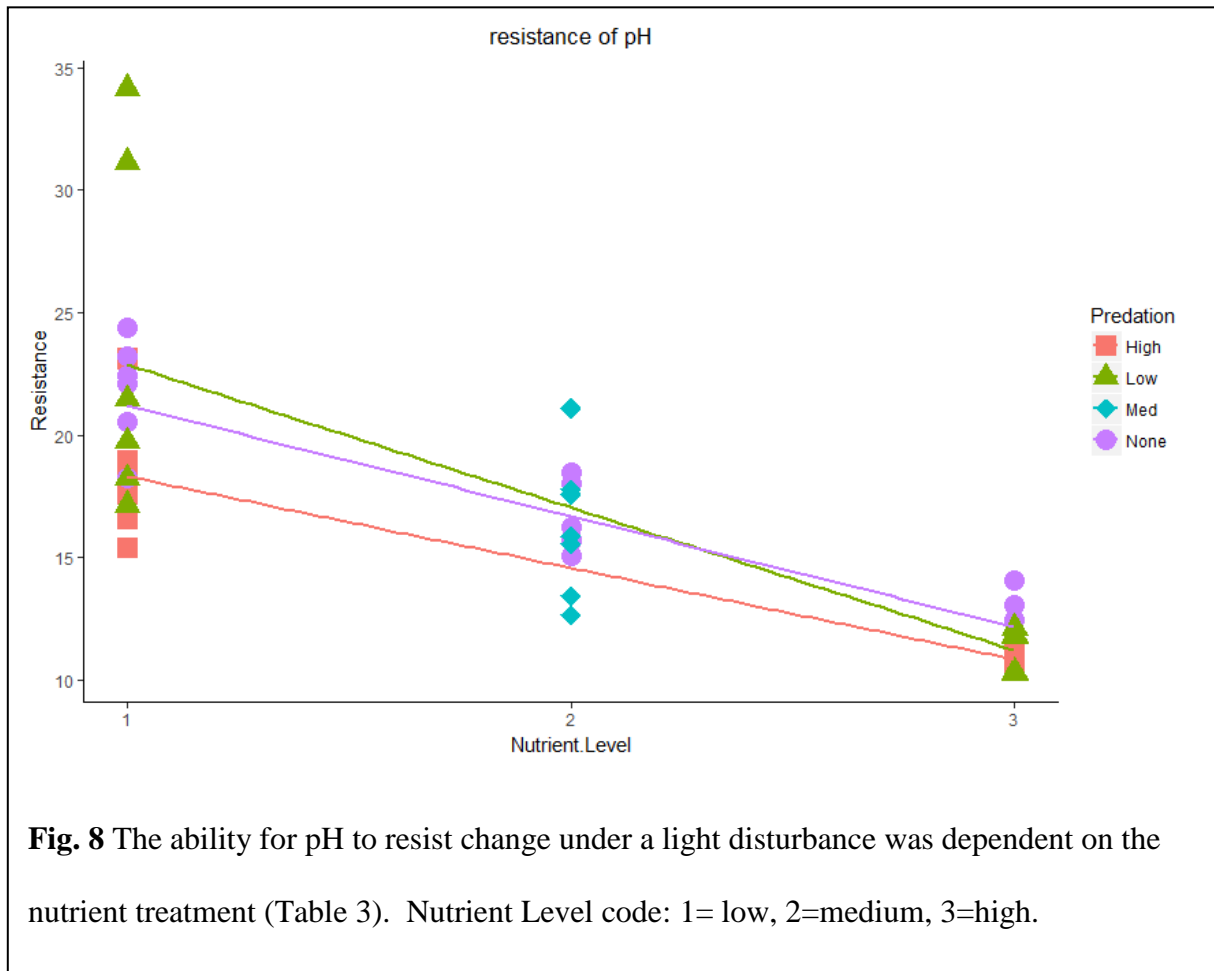
## Resistance and Resilience of pH

**Table 3.3** Resistance and resilience of pH from containers containing algae grown in the glasshouse and exposed to predation by *Daphnia* from an ANOVA (Type III). Analysis was done to determine if there were differences between nutrient and predation treatments on the ability of simple systems to resist or recover from a disturbance. A contrast analysis was applied to nutrients and predation in order to determine if either or an interaction was responsible for the differences in resistance and resilience. Nutrients and Predation were independent variables while pH was dependent.

Resistance of pH					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	1009.992	7	16.34341	8.68E-11	
Residuals	423.7583	48			
contrast	estimate	SE	df	t ratio	p value
Nutrients	-28.182872	2.750839	48	-10.245	<.0001
Predation	-3.499562	2.246050	48	-1.558	0.3319
Interaction	5.603899	2.246050	48	2.495	0.0475
Resilience of pH.					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	3733.345	7	1.009424	0.436606	
Residuals	25361.07	48			
contrast	estimate	SE	df	t ratio	p value
Nutrients	-8.620649	21.28089	48	-0.405	0.9694
Predation	-2.211448	17.37577	48	-0.127	0.9990
Interaction	0.804156	17.37577	48	0.046	1.0000

There were no significant differences between the ability of pH in the simple systems to recover from a light disturbance across nutrient and predation treatments. The resistance of pH to change from a light disturbance depended on the nutrient level, with treatments differing significantly

from each other (Fig. 8). An interaction between nutrient or predation effects on the resistance pH was determined. As identified by the regression line in Fig. 8, as the amount of nutrients increases, the resistance trends negatively towards 1. This indicates that higher nutrient levels have an increasingly better ability to resist pH change due to a light disturbance. Additionally, the interaction indicates that at increasing nutrient levels predation might further reduce the resistance value making the resistance better.



### Resistance and Resilience of Nitrate

**Table 3.4.** Resistance and resilience of nitrate in algal cultures exposed to predation by *Daphnia* (Experiment NAME here). ANOVA (Type III) aimed to determine if nutrient and predation levels affected the ability of algal systems to resist and recover from a light disturbance. A contrast analysis was applied to nutrients and predation to determine if either or an interaction was responsible for the differences in resistance and resilience. Nutrients and predation were independent variables while nitrate was dependent.

<b>resistance of nitrate</b>					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	0.362148	7	2.143124	0.056613	
Residuals	1.158731	48			
contrast	estimate	SE	df	t ratio	p value
Nutrients	0.01746892	0.1438458	48	0.121	0.9991
Predation	-0.18862169	0.1174496	48	-1.606	0.3065
Interaction	0.19163498	0.1174496	48	1.632	0.2934
<b>resilience</b>					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	0.827607	7	1.593589	0.160191	
Residuals	3.561158	48			
contrast	estimate	SE	df	t ratio	p value
Nutrients	-0.58473918	0.2521747	48	-2.319	0.0723
Predation	-0.02029882	0.2058998	48	-0.099	0.9995
Interaction	-0.00847318	0.2058998	48	-0.041	1.0000

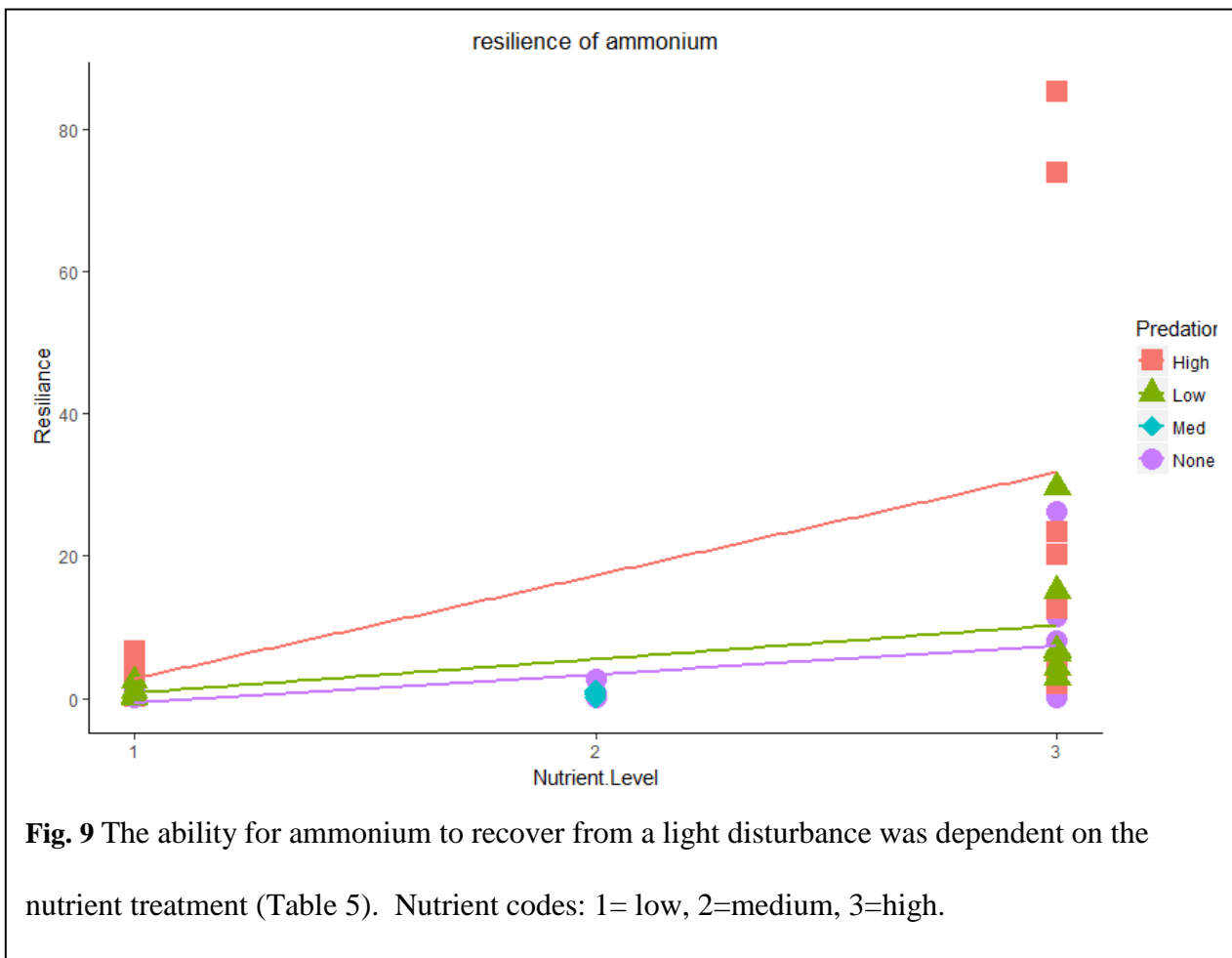
There were no determinable differences in the ability for nitrates in the simple systems of algae exposed to predation to resist or recover from a light disturbance due to nutrient or predation.

No interaction between nutrient or predation effects on the resistance or resilience of nitrates in these systems were determined.

**Table 3.5** Resistance and resilience of chlorophyll from algae grown in the glasshouse and exposed to predation by *Daphnia* from an ANOVA (Type III). Analysis was done to determine if there were differences between nutrient and predation treatments on the ability of simple systems to resist or recover from a light disturbance. A contrast analysis was applied to nutrients and predation in order to determine if either or an interaction was responsible for the differences in resistance and resilience. Nutrients and Predation were independent variables while chlorophyll was dependent.

<b>resistance of ammonium</b>					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	6786.096	7	0.965659	0.466757	
Residuals	48188.04	48			
contrast	estimate	SE	df	t ratio	p value
Nutrients	16.44624	29.33429	48	0.561	0.9247
Predation	33.25211	23.95135	48	1.388	0.4312
Interaction	39.60547	23.95135	48	1.654	0.2825
<b>resilience</b>					
	Sum Sq	Df	F value	Pr(>F)	
Treatment	5624.895	7	4.891255	0.000318	
Residuals	7885.646	48			
contrast	estimate	SE	df	t ratio	p value
Nutrients	46.4719269	11.866554	48	3.916	0.0009
Predation	0.3891419	9.689001	48	0.040	1.0000
Interaction	-3.6310806	9.689001	48	-0.375	0.975

There were no significant differences in the ability of ammonium to resist change from a light disturbance between nutrient and predation treatments. The resilience of ammonium to change from a light disturbance depended on the nutrient level (Fig. 9). No interaction between nutrient or predation effects on the resistance or resilience of ammonium were determined. As identified by the regression line, as the amount of nutrients increases, the resilience trends positively away from 1. This indicates that ammonium has an increasingly better ability to recover after a light disturbance at low nutrient levels.



### **3.2 Results of aquaponics experiment on large complex systems compared against systems in the factorial experiment**

#### **Resistance of chlorophyll**

The test on the resistance values indicated (Table 3.1) that there were differences between the chlorophyll across the treatments from the factorial experiment and the aquaponics experiment [p-value of 0.0001]. The resistance in the aquaponics systems were much further from 1 than the simple factorial systems in the first experiment. This indicates that the resistance of the large aquaponics system was not weaker than the small ones.

Both the control and the disturbance had resistance values much larger than 1 when compared to the rest of the previous treatments (Appendix 19). The disturbance treatment has the largest resistance when compared against the control.

#### **Resilience of chlorophyll**

The resilience of the larger systems and the treatment groups from the factorial simple experiment. There is lower resilience to change in both the control and experimental across all the treatments (Appendix 20).

### **3.3 Primary productivity of small systems in factorial experiment**

The amount of chlorophyll produced depended on the nutrient treatment, with the high nutrient treatment producing more chlorophyll than the other treatments [ $p < 2e-16$ , F value 326]. The amount of chlorophyll produced depended on the amount of nutrient with all like nutrient treatments grouping together (Appendix 20). Additionally, the predation level tends to have a negative effect on chlorophyll production. In general, exposure to predation leads to less measured biomass in all nutrient treatments. In the low nutrient with high predation (LN-HP) treatment production is lower than in the combination of the low nutrient and low predation



treatments. In the high nutrient treatments an opposite situation developed: the high nutrient and low predation produced slightly more chlorophyll than the high nutrient and high predation.

Interestingly, there are differences between low nutrient treatments between the varying predation levels. This could indicate that having top-down forces at lower nutrient constraints might not affect production as greatly as it would happen in high nutrient treatments. This could potentially be explained by the fact that recycling of nutrients at low nutrient concentrations having a greater impact than at high nutrient levels. Low levels of predation and the effects of recycling on the production of algae at low nutrient levels could be further investigated in future studies.

### **Main observations from both experiments**

Both experiments yielded several results. The most relevant to my hypothesis are:

- No evidence to support that equivalent top-down and bottom-up produced better stability or productivity in the factorial experiment
- Nutrient availability (bottom-up regulation) was the most important factor in boosting productivity
- Resilience of ammonia at low nutrient levels is stronger than at high nutrient levels, indicating that some nutrient recycling might be more important at lower nutrient levels.
- Treatments with higher nutrient levels were better able to resist changes in their dissolved oxygen and pH content, indicating that higher nutrients might provide better resistance for certain measurements
- Predation did not explain the differences in the ability of what? to resist and recover from a disturbance and any significance for what? was due to nutrient levels. This strongly

suggests that bottom-up controls are more important for these stability measures in the experimental systems.

## **4. Discussion**

### **4.1 Interpretation of results for the factorial experiment on small systems**

The factorial experiment testing the hypothesis that balancing top-down and bottom-up controls would lead to greater ecosystem stability and productivity were inconclusive. I found no evidence that predation affected the ability for the systems to resist or recover after a light disturbance given the range of indicators I used (chlorophyll production, ammonia, oxygen, and pH). Additionally, the treatments with equivalent nutrients and predation did not have better resistance and/or resilience to unbalanced treatments for any of the variables measured.

In only one case resilience, that of ammonium, was significant (Table 3.5 and Fig.9). This shows there is resilience closer to 1 at lower nutrient levels and that higher nutrient levels have much greater resilience values and that the systems become more variable. This suggests that systems at lower nutrient levels have a greater ability for ammonium levels to return to pre-disturbance levels after a disturbance than higher nutrient levels. This could indicate that nutrient recycling at lower nutrient levels is relatively more important to the recovery of production and associated processes than at higher levels.

Some of the findings from the factorial experiment may be useful when designing a sustainable aquaponics system. Designers of these systems should expect that at low nutrient levels there will be lower resistance of dissolved oxygen and pH from a disturbance, but could also expect a better ability to recover ammonium. While the opposite is true for high nutrient systems, where resistance as measured by pH and dissolved oxygen dynamics is stronger and the resilience of ammonium is weaker.

## **4.2 Interpretation of results for aquaponics experiment on complex systems compared against the factorial experiment**

This experiment aimed to test whether larger and more diverse systems are more stable than simpler and smaller systems. As I found no evidence the larger system resisted disturbance better than the smaller systems, I conclude that they hypothesized difference is not supported by the data. Although in the large aquaponic system nutrient recycling may have been quite effective (snail freed nutrients from o and fish releasing nutrients from Daphnia and duckweed via waste in addition to bacterial action). Furthermore, nutrients were directly added to water. However, the lack of light for an extended time appeared to counteract all these nutrient pathways and severely negatively affect the system's ability to resist change. As the disturbance to the aquaponics system ran for much longer than the disturbance on the smaller systems in the factorial experiment, the aquaponics systems had to resist change from the disturbance for a much longer time than the smaller systems. This could have been the cause for the lowered resistance in larger aquaponics ecosystems.

There was no evidence to comment on the resilience of a large and diverse system to recover after a disturbance. It is implied that the absolute resilience values are lower than those of the treatments in the factorial experiment. This might be a drawback to the use of large and highly diverse systems in aquaponics as it might take longer for them to recover after a large-scale disturbance than a smaller and simpler system.

Some of the differences between the design of the aquaponics experiment and the factorial experiment could lead to difficulties interpreting the results. First the large aquaponic systems were not in the same environment as the factorial experiment. They were placed in a sealed laboratory and only under artificial light, whereas the factorial experiment was set in a

greenhouse with natural, glass-filtered daylight. The second major distinction between the two experiments is that the large systems are completely modular where the *D. magna* populations are not directly exposed to the algal growth tank and are only fed according to a water exchange regime. In the factorial experiment the *D. magna* were constantly exposed to the algae as their population was growing. In both cases there were methods to control the ability for *D. magna* to predate on the algae, however the methods differed significantly. Additionally, some algal species form colonies and sediment out of the water column when exposed to *D. magna* which could also make it difficult to gain accurate chlorophyll readings when comparing combined and modular systems (Rocuzzo, Beckerman, & Pandhal, 2016).

A general expectation based on theoretical and empirical studies is that species diversity can contribute to stability of ecosystem metrics. However, I found no evidence that this applies to my experimental treatments. When comparing the values of resistance and resilience they trend farther from 1 than the replicates in the factorial experiment. Aspects of stability need to be separated out and defined. Importantly, stability, when measured by resistance appears to be higher in the more complex system, as compared to the simpler systems, while the recovery after a disturbance (resilience) was in fact somewhat weakened. However, chlorophyll concentrations before the disturbance of the large system are higher than those after the disturbance. This would give a resilience value far from 1 when the system has surpassed the algal density from before the disturbance. This indicates that disturbances on large, modular ecosystems, might not be as detrimental as to simpler systems in the factorial experiment. As observed by the algae growing very rapidly to higher than pre-disturbance levels. The observation could indicate an intriguing possibility that applying disturbances to larger designed aquaponic systems could be beneficial for creating rapid algal growth. Such benefits might be explained by the additional

recycling pathways that larger more diverse systems have. The recycling of nutrients through the fish waste and the presence of snails might have generated a surplus of nutrients for the algae. Once the light disturbance ended, algae were able to rapidly grow back and overshoot the pre-disturbance levels. This could be beneficial when attempting to maximize the rapid algal growth or for harvesting and exporting algae for other purposes.

A major problem with this design of the experiment was that there was no replication of the disturbance. I would be recommended that multiple replicates be used in any future study to improve the ability to determine the differences in the resistance and resilience. Though this is difficult to implement, as there are many financial and space constraints for designing an experiment of this scale. Differences in circadian rhythms were not addressed in this experimental design and all organisms were under 12-hour light cycles. It is unknown if this light cycle would have affected organisms in any way. Another issue with the design of this experiment was the presence of snails at all trophic levels. Their presence allowed for detritus to be recycled at all levels and might make the levels less distinct, at least with respect to nutrient availability. Although, this may not have been a major issue as the nutrients were primarily used by algae and all the water from all levels was recycled back to the algal tank.

#### **4.3 Interpretation of result of the productivity analysis on the small systems**

While not definitive, it appears that predation has less of an effect on the production of chlorophyll than nutrients. One might expect these results, though at the lowest nutrient level differences in primary production with and without low levels of predation are similar. This might be of interest to increasing production of algae at low nutrient levels as exposure to low levels of predation might boost production. This remains a hypothesis that might be interesting to test. It could be that exposure to very low levels of *D. magna* could enhance growth as there

would be a release of nutrients from *D. magna* waste. Overall, controlling nutrients in these simple systems is the best method for managing chlorophyll production.

In the broader picture, the results might mean that, as far as the switch between the bottom-up control to top-down control is concerned (Fig. 3.), the transition may be driven by different sets of mechanisms depending on whether the system is nutrient limited or not.

Specifically, it is possible that in the aquatic environments the nutrients interact with grazers in determining algal population dynamics when nutrients are limited but this interaction is disrupted in nutrient-rich system such that the growth of primary production would be a simpler function of the algal growth rates and grazing (predation) intensity.

## **5. Conclusion**

The factorial experiment indicates that predation has a smaller effect on the production of chlorophyll than nutrients do. This observation is supported by fewer differences between groups that can be statistically attributed to predation rather than nutrients. The prevalence of nutrient causing differences between treatments implies that bottom-up regulation had a more prominent distinction between the treatment groups. These results should be expected as *D. magna* would initially reduce the density of algae present through direct grazing.

Overall, nutrients were more important for the variation in resistance and resilience metrics to disturbance than predation for both abiotic and biotic measures. This finding can be linked to the general hypothesis as the two metrics, resistance and resilience, are important traits of both sides of the bottom-up and top-down control model. Interestingly, the low predation levels provided better resilience of some system parameters than higher predation levels. This could indicate importance of direct recycling feedback to design of ecosystems.

Additionally, if resistance is higher for some parameters at low nutrients but productivity is better at high nutrients, it can be argued that there is a stability/productivity trade off when designing these systems. There were trends for better stability at lower nutrient levels (4.1) while higher production was observed at higher nutrient levels (4.3)

The physical and organizational scale of the system appears to matter as well: the larger and more complex systems were better at recovering from the light disturbance than the smaller and simpler ones. The small systems in the factorial experiment never returned back to pre-disturbance levels, whereas the experimental treatment in the larger system surpassed the pre-disturbance values and continued to grow. The method for calculating the resilience, while



excellent for measuring the recovery of a system in relation to pre-disturbance levels does not handle well situations where post-disturbance values may be higher after a disturbance. Yet, such situations may be more desirable from the management perspective. When designing an ecosystem with high productivity as the main aim, it would be important to maintain consistently large concentrations of organisms contributing to each trophic level. The large ecosystems surpassed the pre-disturbance levels by a large amount, which made them have a resilience value far from 1 (nominally poor considering the index used) even though the system recovered beyond the chlorophyll values prior to the disturbance. A different method for describing resilience might be needed to account for recovery exceeding pre-disturbance levels. As mentioned in the introduction, researchers have discussed helpful resilience and unhelpful resilience. A measure for calculating resilience beyond what might be expected of a system could be useful when designing an ecosystem.

### **Next Steps**

Future work needed to advance the understanding of the relationships between top-down and bottom-up regulations in ecosystems might require experiments similar to those I conducted with modifications. One would be to impose a disturbance (light deprivation) at different time points in the algal bloom. I suggest that imposing a disturbance at the peak of the bloom or in the growth phase of the bloom might yield different results than performing the disturbance after the bloom. If timing mattered, it would help elucidate mechanisms underlying some of the patterns detected in my research.

Another alternative to the light-based disturbance would be to perform a different ecological disruption to the systems. A use of direct nutrient deprivation as a disturbance or some form of chemical disturbance are likely to produce different outcomes. Again, this can be applied at various points throughout the growth of the algal bloom.

I recommend that repeating the final experiment on the larger systems with more replicates would strengthen the conclusions. Using a design that blocked certain pathways such as snail recycling might also add further dimension to that study. It might allow for clear quantification of the effect of each nutrient pathway on the ability of algae to withstand a disturbance event.

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## Appendices

### **Appendix 1: Resistance and Resilience for variables measured in factorial experiment**

Treatment	Nutrient	Predation	Tank	Resistance of Chl out	Resilience of Chl out	Resistance of Chl in	Resilience of Chl in
High	High	None	1	1.748528942	0.762355281	1.461349677	0.805572902
High	High	None	2	1.302550987	1.019931003	1.029344633	0.995337142
High	High	None	3	1.338254793	0.910211971	1.118161489	1.081812184
High	High	None	4	2.083200365	0.586347785	1.204075075	1.015127884
High	High	None	5	1.413167829	0.885492578	1.151718325	1.018001376
High	High	None	6	1.522892527	1.002801371	1.193656772	1.099591709
High	High	None	7	1.52476791	0.827708266	1.283677952	0.943691345
High-High	High	High	1	1.106556464	1.048314527	1.172077656	0.991631872
High-High	High	High	2	1.084692042	1.05946413	1.219445242	0.911969302
High-High	High	High	3	1.103634619	1.128300416	1.12270872	1.017002414
High-High	High	High	4	1.128682499	1.041797542	1.186924679	0.950741962
High-High	High	High	5	1.571551031	0.763492527	1.224251519	1.026487644
High-High	High	High	6	1.775129636	0.73029207	1.148498068	1.03728152
High-High	High	High	7	1.070047054	1.155444669	1.196939949	0.980668068
HN-LP	High	Low	1	1.071079539	1.133023063	1.109042099	1.103294405
HN-LP	High	Low	2	1.06192237	1.021530725	1.341868341	0.941649935
HN-LP	High	Low	3	1.442414754	0.851691997	1.392824497	1.056637943
HN-LP	High	Low	4	1.086236618	1.054783272	1.130020185	1.090205452
HN-LP	High	Low	5	1.507653771	0.801589446	1.194002036	1.250523294
HN-LP	High	Low	6	1.106481721	1.100192503	1.172296907	1.087616584
HN-LP	High	Low	7	1.150929348	1.047877026	1.244936158	1.051449233
LN-HP	Low	High	1	1.789676497	0.720974194	3.004903917	0.519007384
LN-HP	Low	High	2	1.225910558	1.054315342	1.350564004	0.972869528
LN-HP	Low	High	3	2.565929884	0.469777812	1.601952042	0.813742417
LN-HP	Low	High	4	1.227224076	1.129390851	1.456533415	0.972430517
LN-HP	Low	High	5	1.465211773	1.275175951	1.22110404	1.059338165
LN-HP	Low	High	6	1.092762906	1.673331307	1.19275483	1.096070979
LN-HP	Low	High	7	1.208866741	1.428100593	1.287052407	0.979052638
Low	Low	None	1	1.222732305	1.174539829	1.144396859	1.052069064
Low	Low	None	2	1.336464363	1.218918325	1.165792618	1.112072864
Low	Low	None	3	1.765254598	1.818325959	1.038881564	1.002542384
Low	Low	None	4	1.378593757	1.912328914	1.17514255	1.024900857
Low	Low	None	5	4.935752167	0.353764267	1.186693883	1.029606862
Low	Low	None	6	1.660044798	0.83432607	1.195162088	1.038899559
Low	Low	None	7	1.902323108	0.795142834	1.325583301	1.076829753
Low-Low	Low	Low	1	1.25131268	0.99467868		
Low-Low	Low	Low	2	1.141064534	1.162626651		
Low-Low	Low	Low	3	1.088010696	1.119233758		
Low-Low	Low	Low	4	1.192473475	1.216339229		
Low-Low	Low	Low	5	1.159492471	1.450348439		

Low-Low	Low	Low	6	1.146393251	1.194112631		
Low-Low	Low	Low	7	1.42760635	0.894428269		
Med	Med	None	1	1.447135269	1.542628386		
Med	Med	None	2	1.753595575	0.849882033		
Med	Med	None	3	1.479283609	1.069674522		
Med	Med	None	4	1.646823811	0.95121874		
Med	Med	None	5	1.24990095	1.214583706		
Med	Med	None	6	2.06705568	0.696903236		
Med	Med	None	7	2.517694466	0.788575084		
Med-Med	Med	Med	1	1.145132713	1.008869973		
Med-Med	Med	Med	2	1.327031199	0.914117827		
Med-Med	Med	Med	3	1.137059139	1.06009217		
Med-Med	Med	Med	4	1.575914388	0.82531894		
Med-Med	Med	Med	5	1.12048875	1.135525368		
Med-Med	Med	Med	6	1.168896422	1.076980751		
Med-Med	Med	Med	7	1.229372862	0.979414667		

Treatment	Nutrient	Predation	Tank	Resistance of DO	Resilience of DO	Resistance of pH	Resilience of pH
High	High	None	1	4.766332982	3.869520897	13.05454545	2.946428571
High	High	None	2	3.467981155	14.30762829	10.76865672	4.7109375
High	High	None	3	4.777777778	3.198307774	11.95867769	2.469387755
High	High	None	4	4.170189344	6.616704435	14.03883495	1.73271028
High	High	None	5	4.977290731	3.605140681	11.608	2.378435518
High	High	None	6	4.840985733	2.321512211	11.95867769	1.887348354
High	High	None	7	4.65806927	5.543803904	12.43103448	2.007692308
High-High	High	High	1	2.171513976	1.245104614	10.41726619	4.720754717
High-High	High	High	2	4.202161914	2.610192102	10.96992481	3.288461538
High-High	High	High	3	4.110766504	2.991825613	11.04545455	3.514792899
High-High	High	High	4	3.890349076	6.106157704	10.96992481	8.370629371
High-High	High	High	5	7.417398244	1.407338076	11.359375	6.939759036
High-High	High	High	6	4.950832886	2.531207496	10.67883212	5.788732394
High-High	High	High	7	4.641619969	3.43849747	10.40425532	3.799401198
HN-LP	High	Low	1	5.987043189	1.759776536	11.744	2.855329949
HN-LP	High	Low	2	4.541320293	1.602385513	11.83064516	2.559633028
HN-LP	High	Low	3	4.375408306	1.954301348	12.09917355	2.662591687
HN-LP	High	Low	4	4.246153846	3.732057416	11.83064516	3.72
HN-LP	High	Low	5	4.457627119	2.711159737	10.27272727	3.334196891
HN-LP	High	Low	6	3.758556701	3.344827586	10.33802817	3.55
HN-LP	High	Low	7	4.590646216	4.108471074	10.33802817	4.376712329
LN-HP	Low	High	1	9.872624912	2.503229595	17.575	1.493775934
LN-HP	Low	High	2	9.040201005	1.592	23.1	1.607142857
LN-HP	Low	High	3	4.829787234	2.521609538	18.22368421	2.091743119



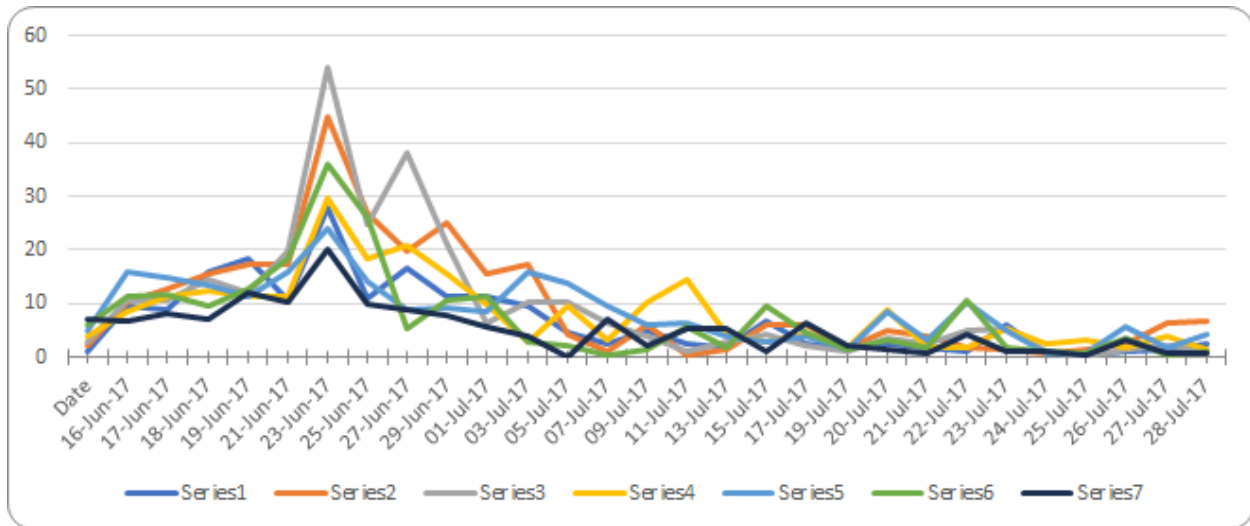
LN-HP	Low	High	4	10.39181287	1.649517685	15.35555556	2.862190813
LN-HP	Low	High	5	7.518518519	3.871602624	16.56626506	7.396039604
LN-HP	Low	High	6	10.16814159	3.743558282	18.45333333	4.560810811
LN-HP	Low	High	7	13.75568744	1.654664484	18.93150685	5.814159292
Low	Low	None	1	6.737028825	2.041339771	22.45901639	3.137142857
Low	Low	None	2	5.410548824	2.805376583	18.22666667	4.560810811
Low	Low	None	3	7.577679449	2.7	18.22666667	6.958762887
Low	Low	None	4	9.609677419	9.368703828	23.18644068	40.84615385
Low	Low	None	5	7.097652582	5.510204082	20.53731343	6.483870968
Low	Low	None	6	11.2154195	2.9133839	22.11290323	5.636363636
Low	Low	None	7	10.2185567	2.353522646	24.375	8.129032258
Low-Low	Low	Low	1	6.979859485	1.614027719	34.15	2.307692308
Low-Low	Low	Low	2	7.861340206	1.587272727	18.22666667	3.125
Low-Low	Low	Low	3	6.420392812	1.967568061	18.22666667	2.7
Low-Low	Low	Low	4	6.537933991	2.997002569	19.72463768	2.7
Low-Low	Low	Low	5	19.39130435	0.816568047	17.15	6.666666667
Low-Low	Low	Low	6	22.79623824	1.444891797	21.453125	8.727272727
Low-Low	Low	Low	7	13.96229972	2.171214188	31.13636364	10.15384615
Med	Med	None	1	6.445472837	3.180913099	16.22093023	3.948979592
Med	Med	None	2	5.621077763	2.882327883	15.70786517	5.804347826
Med	Med	None	3	5.884642604	2.066125102	15.07526882	4.810344828
Med	Med	None	4	5.423557206	20.73639191	16.22093023	4.807453416
Med	Med	None	5	5.831261101	2.920461095	18	7.237113402
Med	Med	None	6	8.418839808	3.920027816	18.44736842	171
Med	Med	None	7	9.713261649	2.031553398	15.73333333	5.510204082
Med-Med	Med	Med	1	7.071428571	1.453287197	13.42307692	3.916317992
Med-Med	Med	Med	2	5.480404964	1.841989172	12.63963964	3.30794702
Med-Med	Med	Med	3	1.145436752	1.007368469	15.875	2.506329114
Med-Med	Med	Med	4	6.500570994	1.21915124	15.54444444	2.7
Med-Med	Med	Med	5	5.91354055	1.929901172	21.09090909	6.906976744
Med-Med	Med	Med	6	6.803857201	1.762111352	17.575	31.30434783
Med-Med	Med	Med	7	8.785216926	1.351375261	17.78481013	7.181818182

Treatment	Nutrient	Predation	Tank	Resistance of Nitrate	Resilience of Nitrate	Resistance of Ammonium	Resilience of Ammonium
High	High	None	1	0.657805044	0.500967558	232.75	0.03930131
High	High	None	2	0.640506329	0.501339726	7.253623188	8.064935065
High	High	None	3	0.55695478	0.541518857	4.478672986	11.50909091
High	High	None	4	0.611793612	0.500478207	7.882882883	26.28947368
High	High	None	5	0.527041357	0.543794451	3.948356808	1.796626054
High	High	None	6	0.491803279	0.582184517	6.951612903	11.625
High	High	None	7	0.69347079	0.465434512	7.169354839	1.015468608

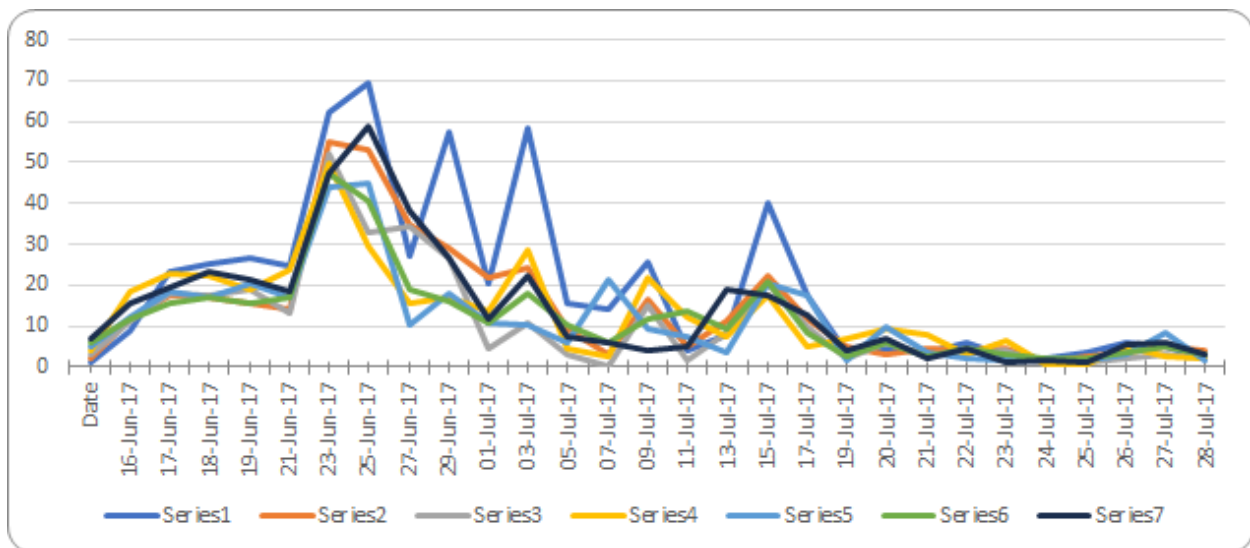
High-High	High	High	1	0.546529563	0.619492515	1.881355932	2.113241679
High-High	High	High	2	0.503355705	0.71226952	2.126033058	12.6627907
High-High	High	High	3	0.375206612	0.963750929	1.784482759	5.112634672
High-High	High	High	4	0.222929936	1.594139832	1.377308707	85.275
High-High	High	High	5	0.803921569	0.481132075	2.317073171	73.8
High-High	High	High	6	0.644418193	0.486292407	1.424962853	23.29615385
High-High	High	High	7	0.57696567	0.534706231	1.221216041	20.22383721
HN-LP	High	Low	1	0.55695478	0.563891977	3.554716981	6.58839779
HN-LP	High	Low	2	0.603729604	0.55054898	3.373188406	4.282758621
HN-LP	High	Low	3	0.546666667	0.529965977	1.41025641	2.900826446
HN-LP	High	Low	4	0.599091425	0.545896049	1.026490066	6.789342215
HN-LP	High	Low	5	0.605411499	0.548923881	1.78957529	29.69426752
HN-LP	High	Low	6	0.627439385	0.509422594	1.483146067	15.11320755
HN-LP	High	Low	7	0.629535328	0.48777038	2.795597484	6.317880795
LN-HP	Low	High	1	0.465495609	0.955253696	2.504615385	1.774878641
LN-HP	Low	High	2	0.403933434	1.064920341	1.582692308	6.023166023
LN-HP	Low	High	3	0.195352994	1.070767857	1.202328967	6.577659574
LN-HP	Low	High	4	0.277589454	0.916535614	1.458928571	4.087591241
LN-HP	Low	High	5	0.546273546	0.554411987	25.96551724	0.149570201
LN-HP	Low	High	6	0.451546392	0.65036007	3.074074074	0.574468085
LN-HP	Low	High	7	0.491311216	0.647312805	19.275	0.180722892
Low	Low	None	1	0.507335907	0.694783905	4.985915493	0.684520621
Low	Low	None	2	0.480597015	0.636747624	3.3507109	1.357398142
Low	Low	None	3	0.299973097	1.709838998	11.41269841	0.301435407
Low	Low	None	4	0.86784141	0.560801537	4.467105263	0.709175739
Low	Low	None	5	0.892857143	0.493150685	6.281553398	0.694382022
Low	Low	None	6	1.028169014	0.470198675	4.194630872	0.602696629
Low	Low	None	7	0.828571429	0.531059525	15.82051282	0.191803279
Low-Low	Low	Low	1	0.715242881	1.120075047	3.808080808	2.4
Low-Low	Low	Low	2	0.618525289	1.102740237	6.157894737	0.557548093
Low-Low	Low	Low	3	0.771469127	1.020603622	16.55737705	0.204774338
Low-Low	Low	Low	4	0.564444444	0.922911648	4.071428571	1.105263158
Low-Low	Low	Low	5	0.509859155	0.594861292	33.64	0.110078278
Low-Low	Low	Low	6	0.489526765	0.57679113	6.4453125	0.478008299
Low-Low	Low	Low	7	0.493333333	0.562969141	6.619834711	0.441605839
Med	Med	None	1	0.680190931	0.551934429	19	0.207692308
Med	Med	None	2	0.679087452	0.590952215	5.404145078	0.593440383
Med	Med	None	3	0.474022496	0.777808638	20.83333333	0.32
Med	Med	None	4	0.668356264	0.578496626	7.181818182	0.445444319
Med	Med	None	5	0.69470405	0.547055482	4.916230366	0.639508929
Med	Med	None	6	0.565217391	0.620689655	5.021505376	0.711129992
Med	Med	None	7	0.540106952	0.533438986	4.661538462	2.631184408
Med-Med	Med	Med	1	1	0.636363636	59.35	0.067694622
Med-Med	Med	Med	2	0.662633452	0.658422286	6.813664596	0.918833228
Med-Med	Med	Med	3	0.659090909	0.64495114	6.8625	0.888888889
Med-Med	Med	Med	4	0.299212598	1.532171582	3.809210526	1.157360406

Med-Med	Med	Med	5	0.594684385	0.561916615	4.526970954	0.743572163
Med-Med	Med	Med	6	0.564444444	0.59944179	6.858108108	0.497943925
Med-Med	Med	Med	7	0.539149888	0.653190453	20.59322034	0.203838772

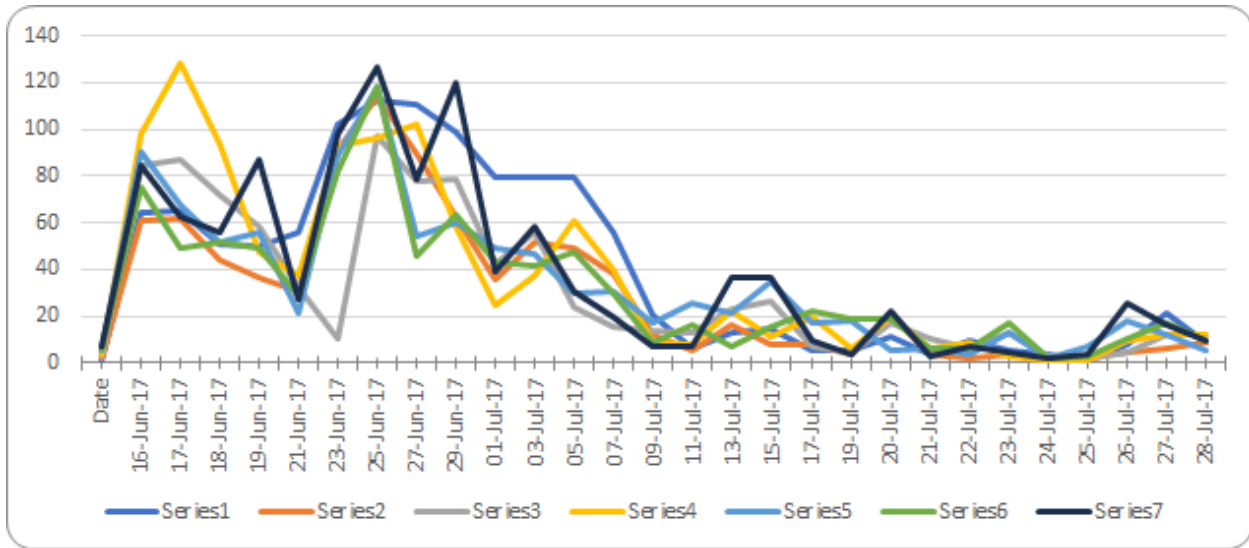
**Appendix 8: Time series of Low Nutrient and Low Predation Chlorophyll Out**



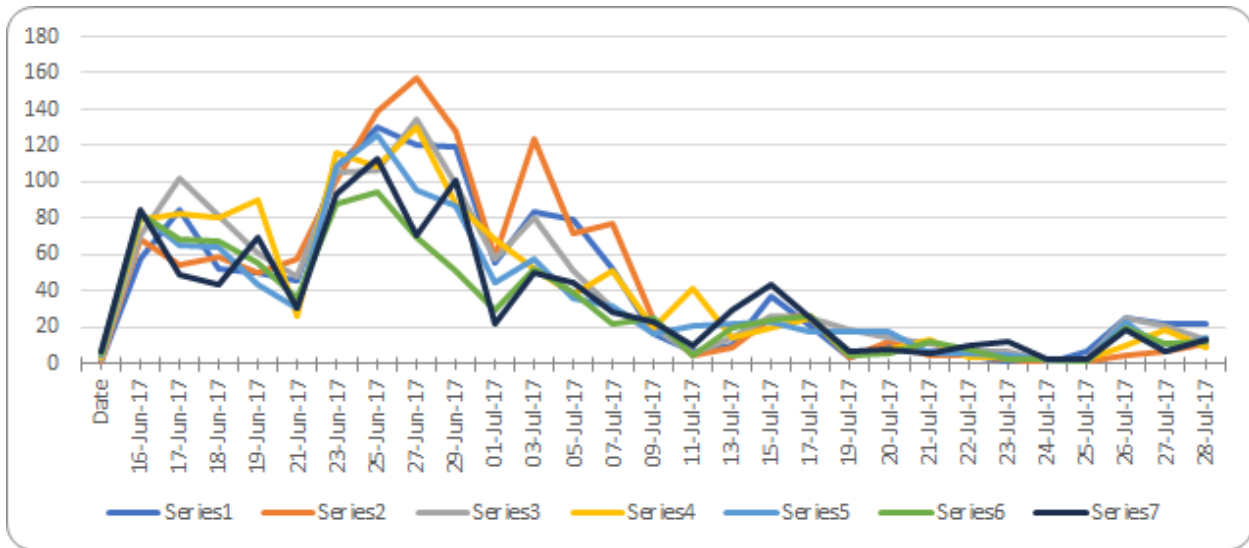
**Appendix 9: Time series of Medium Nutrient and Medium Predation Chlorophyll Out**



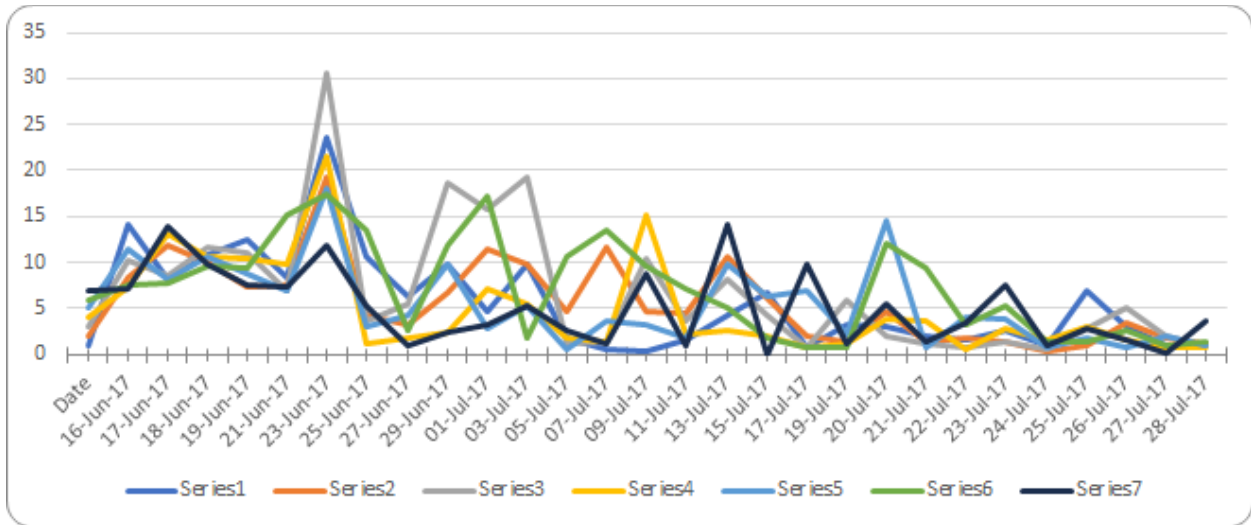
**Appendix 10: Time series of High Nutrient and High Predation Chlorophyll Out**



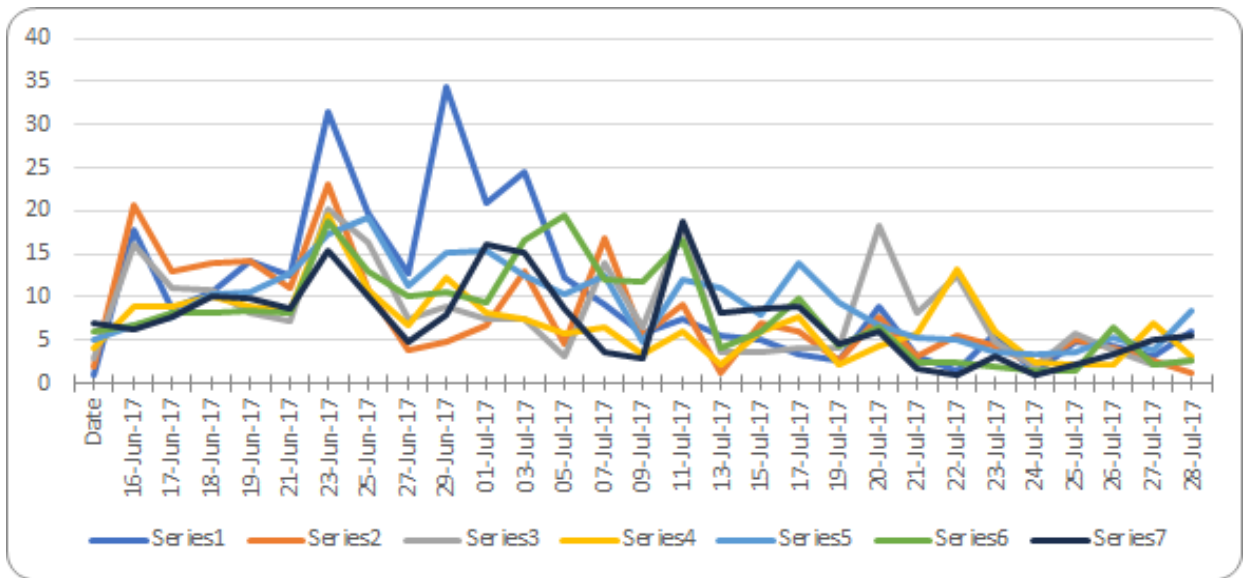
**Appendix 11: Time series of High Nutrient and Low Predation Chlorophyll Out**



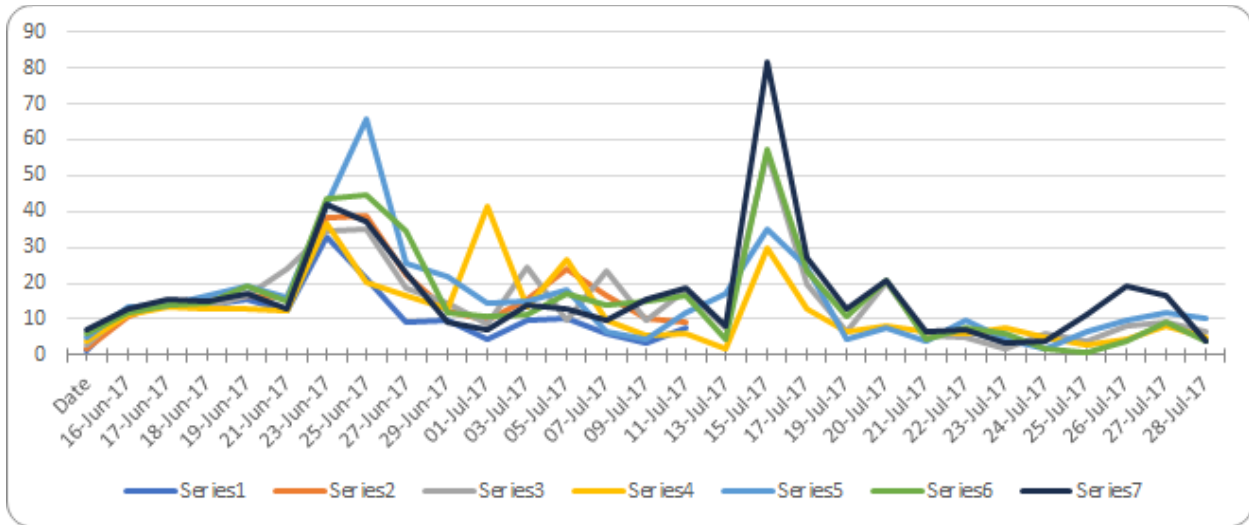
**Appendix 12: Time series of Low Nutrient and High Predation Chlorophyll Out**



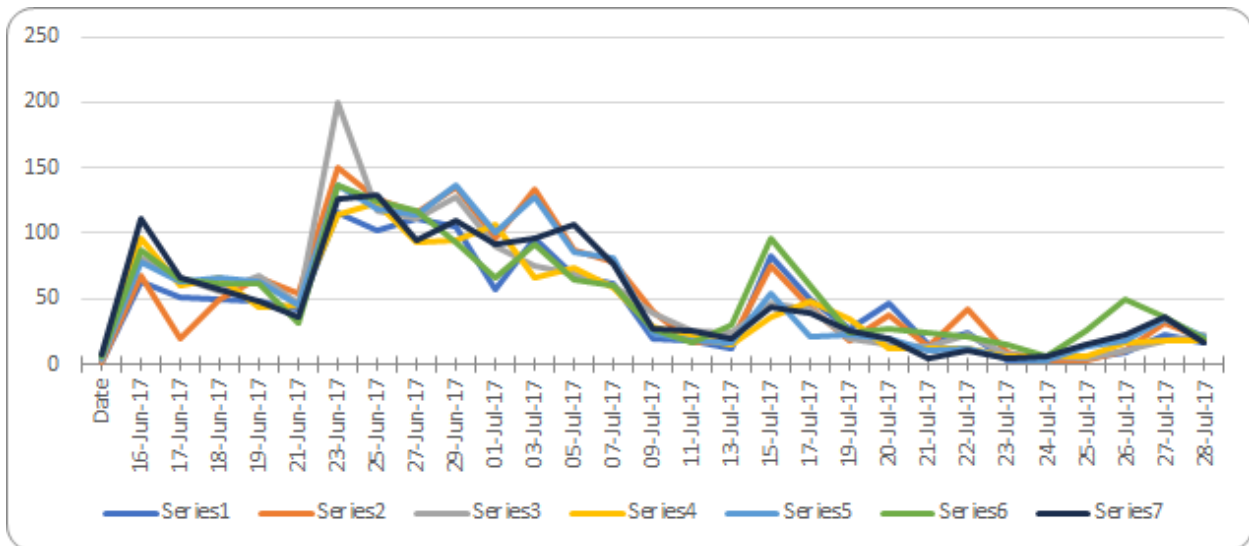
**Appendix 13: Time series of Low Nutrient and no Predation Chlorophyll**



**Appendix 14: Time series of Medium Nutrients and no Predation Chlorophyll**



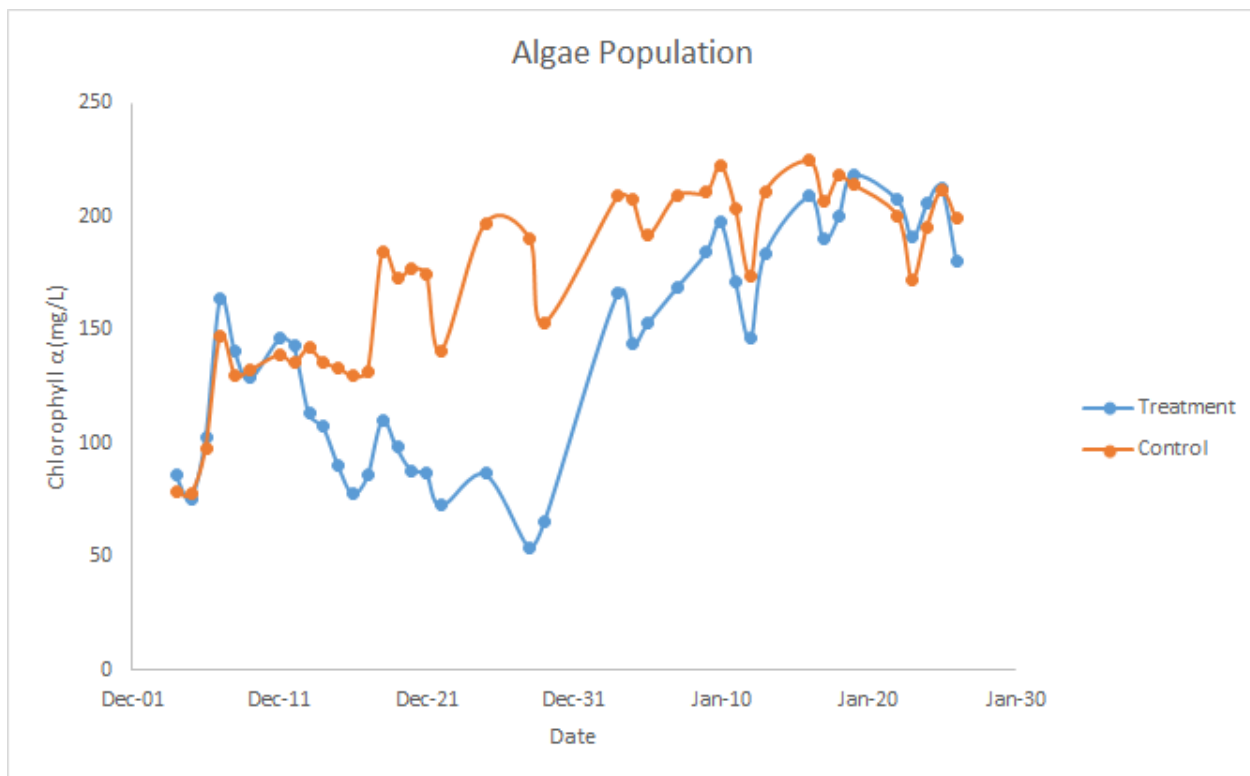
**Appendix 15: Time series of High Nutrients and no Predation Chlorophyll**



**Appendix 16: Integrals of chlorophyll outside of exclosures**

Treatment	Replicate	Fit Functio	R-Squared	Integral
Low-Low	1	#NAME?	0.89324	197.4209
Low-Low	2	#NAME?	0.862806	284.5317
Low-Low	3	#NAME?	0.776962	284.8968
Low-Low	4	#NAME?	0.847811	237.2277
Low-Low	5	12.677571	0.891055	237.9464
Low-Low	6	#NAME?	0.762734	209.7496
Low-Low	7	#NAME?	0.864845	144.8952
Med-Med	9	#NAME?	0.805713	580.4148
Med-Med	10	#NAME?	0.80925	417.6424
Med-Med	11	#NAME?	0.768665	331.4915
Med-Med	12	2.8855035	0.843708	376.9481
Med-Med	13	#NAME?	0.789165	346.1092
Med-Med	14	#NAME?	0.824188	347.0568
Med-Med	15	#NAME?	0.82208	417.1456
High-High	17	50.354865	0.930732	1145.991
High-High	18	42.900523	0.856666	871.4082
High-High	19	100.03734	0.851451	880.0368
High-High	20	113.79746	0.883348	1036.22
High-High	21	83.968333	0.868243	955.7548
High-High	22	53.886222	0.855469	896.3912
High-High	23	53.970737	0.83556	1076.735
HN-LP	25	46.885578	0.88991	1240.274
HN-LP	26	42.359579	0.876851	1300.978
HN-LP	27	59.170432	0.902129	1238.053
HN-LP	28	58.918825	0.901382	1203.014
HN-LP	29	59.413475	0.865652	1071.105
HN-LP	30	71.239431	0.913135	919.8696
HN-LP	31	57.281788	0.845825	1013.192
LN-HP	33	6.5300651	0.816418	159.5147
LN-HP	34	9.7277632	0.821252	160.3793
LN-HP	35	6.4267574	0.706929	194.9443
LN-HP	36	5.4383856	0.699256	134.9902
LN-HP	37	5.2438588	0.770931	151.2968
LN-HP	38	1.0927646	0.807782	202.8258
LN-HP	39	6.03475 +	0.784632	91.2687
Low	41	11.372090	0.858136	299.3162
Low	42	19.667397	0.849489	219.4753
Low	43	11.520329	0.793406	237.3426
Low	44	2.4988666	0.86644	196.827
Low	45	#NAME?	0.952044	267.8799
Low	46	7.2354996	0.908547	230.7514
Low	47	4.7779598	0.847205	204.8813
Med	49	1.0239249	0.602673	367.2121
Med	50	#NAME?	0.812222	410.3899
Med	51	#NAME?	0.754414	437.0376
Med	52	3.7839410	0.768584	360.4306
Med	53	#NAME?	0.751814	456.4834
Med	54	#NAME?	0.728993	452.4433
Med	55	#NAME?	0.626559	488.0341
High	57	28.368990	0.86131	1331.322
High	58	16.422463	0.883014	1582.161
High	59	33.814396	0.868153	1492.785
High	60	82.234397	0.902911	1327.602
High	61	69.468605	0.91285	1514.969
High	62	64.742256	0.861512	1538.33
High	63	119.74269	0.905541	1453.232

## Appendix 17: Time series of Chlorophyll



Appendix 17 note: Control indicates the system that did not undergo a disturbance while treatment indicates the system that did have the disturbance

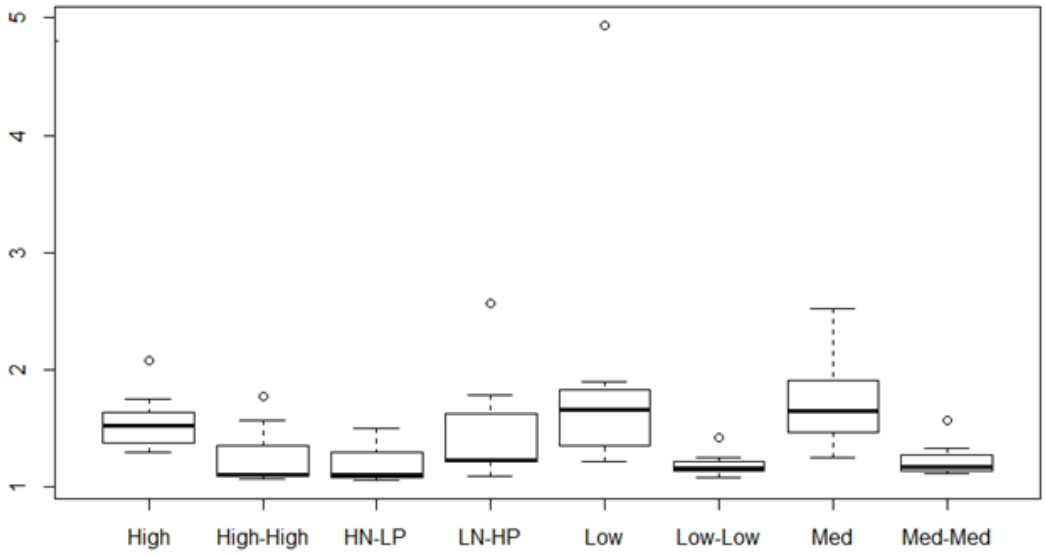
### Appendix 18: COMBO and Lake Ontario components

	Ammonia	Nitrate	Nitrite	TN	Phosphorus	Potassium	Sodium	Calcium	Sulphate	Iron	Magnesium	
Lake Ontario / municipal water + supplements	50	280	10	14205	1585	7776	31180	34000	26000	79.5	9000	
COMBO media				14000	1550	7821	31589	10000	14400	210	3910	
	Manganese	Silicon	Cadmium	Barium	Molybdenum	Boron	Zinc	Strontium	Lithium	Rubidium	Vanadium	
Lake Ontario / municipal water + supplements	29.75	139	0.1	22	8.67	5428	28.4	165			0.34	
COMBO media	50	2810	0	0	8.6	4600	5	50	50	50	0.5	
	Selenium	Chromium	Cobalt	Copper	Chlorine	Bromine	Iodine	DIC	DOC	B12	Biotin	Thiamin
Lake Ontario / municipal water + supplements	2	1	0.07	1	23520	47	2.9	22000	Likely 0	0.56	1.6	560
COMBO media	1	0	3	0.25	18240	12.5	2.5	9000	0	0.55	0.5	100

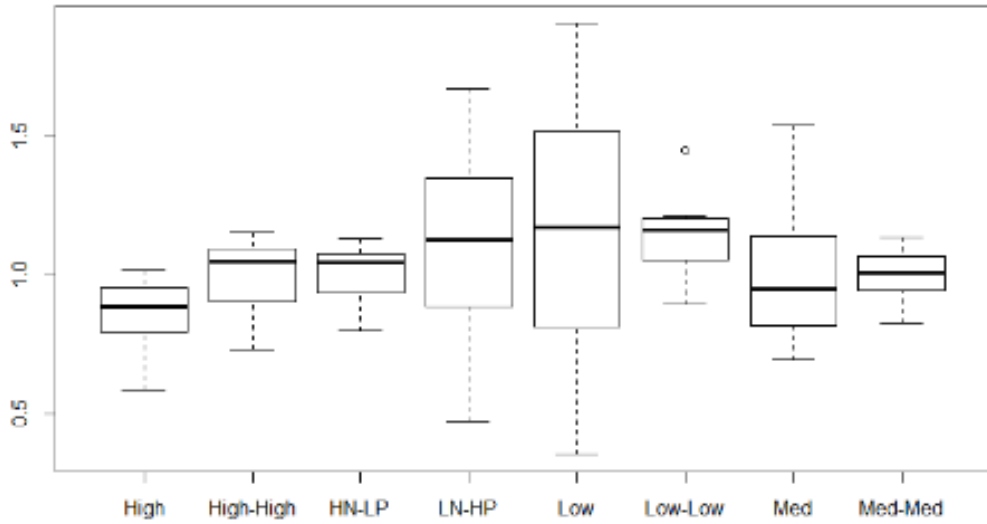
### Appendix 19: Boxplots of resistance and resilience for experiment one



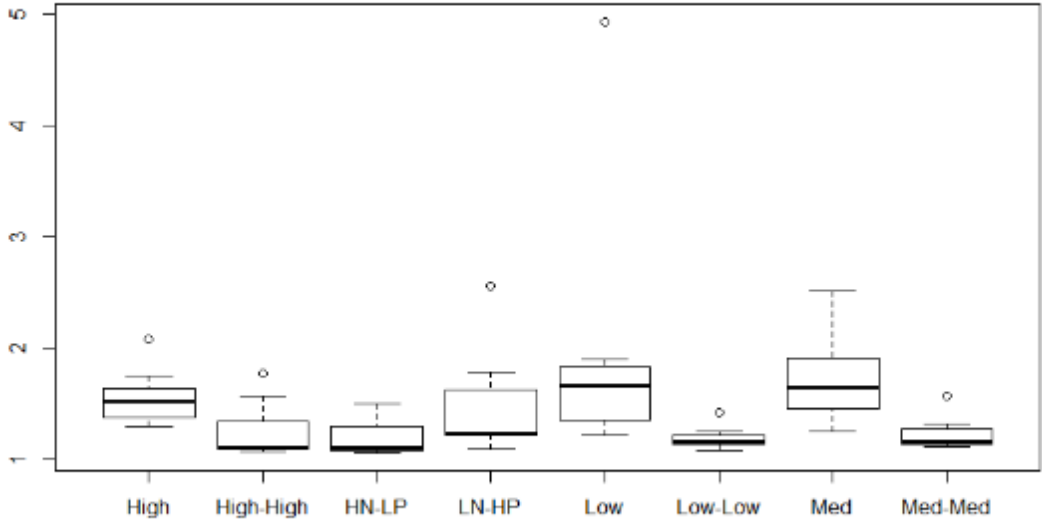
**Boxplot of resistance for chlorophyll outside of the exclosures**



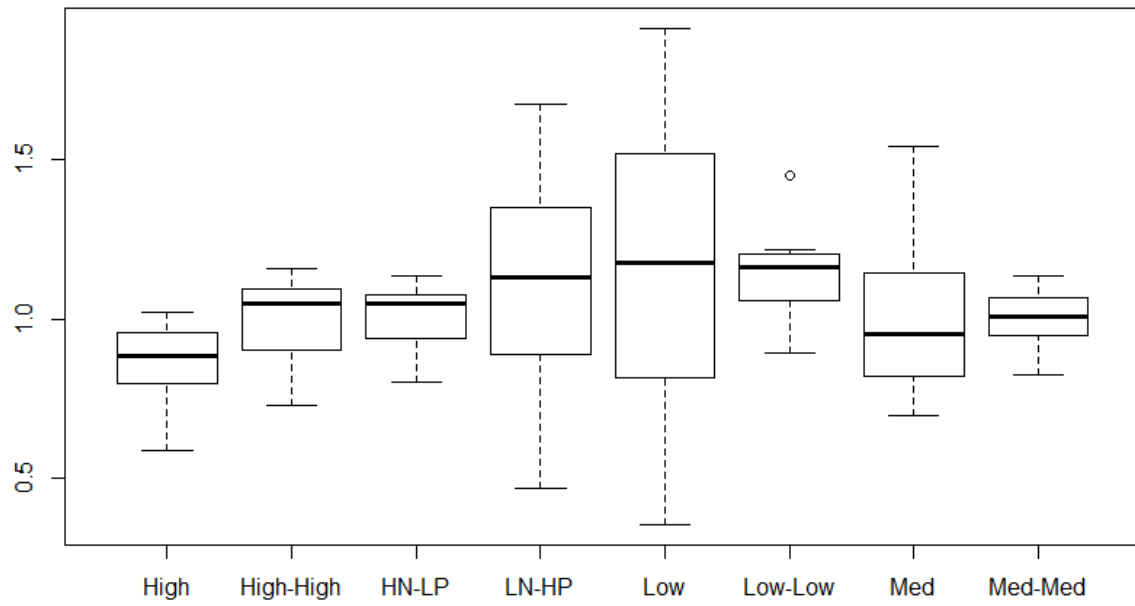
**Resilience for chlorophyll outside of exclosures**



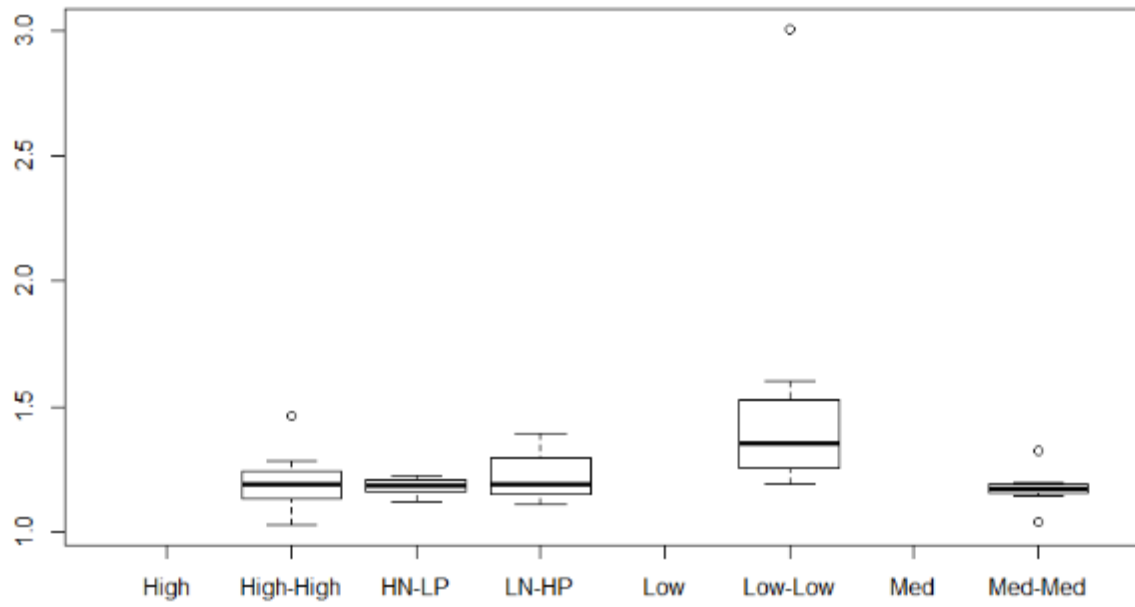
**Resistance of chlorophyll inside exclosures**



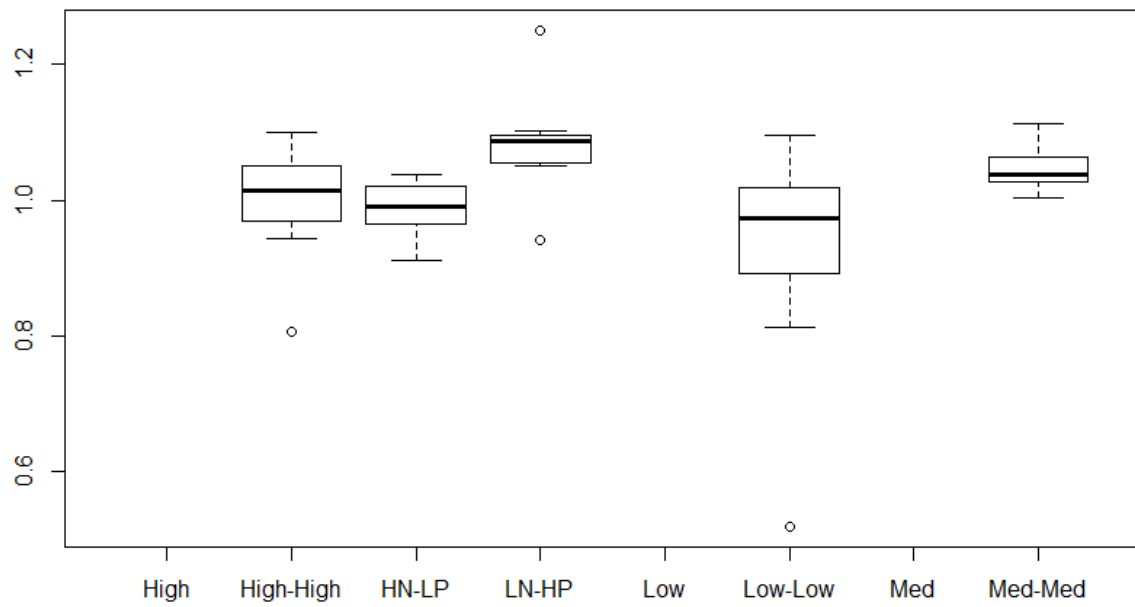
### Resilience of chlorophyll outside of the exclosures



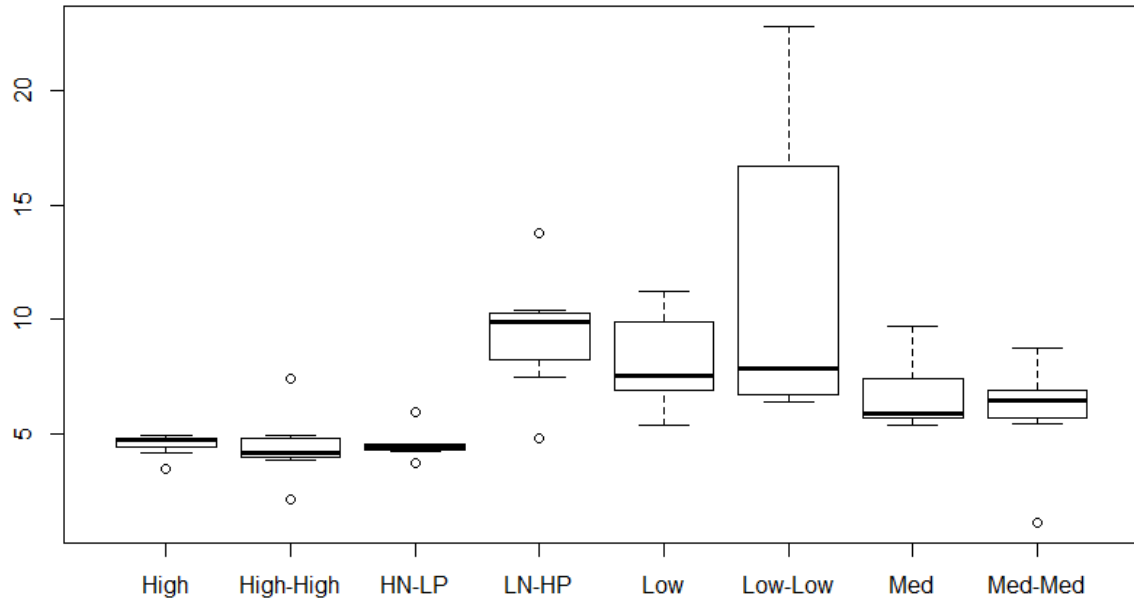
### Resistance of chlorophyll inside of exclosures



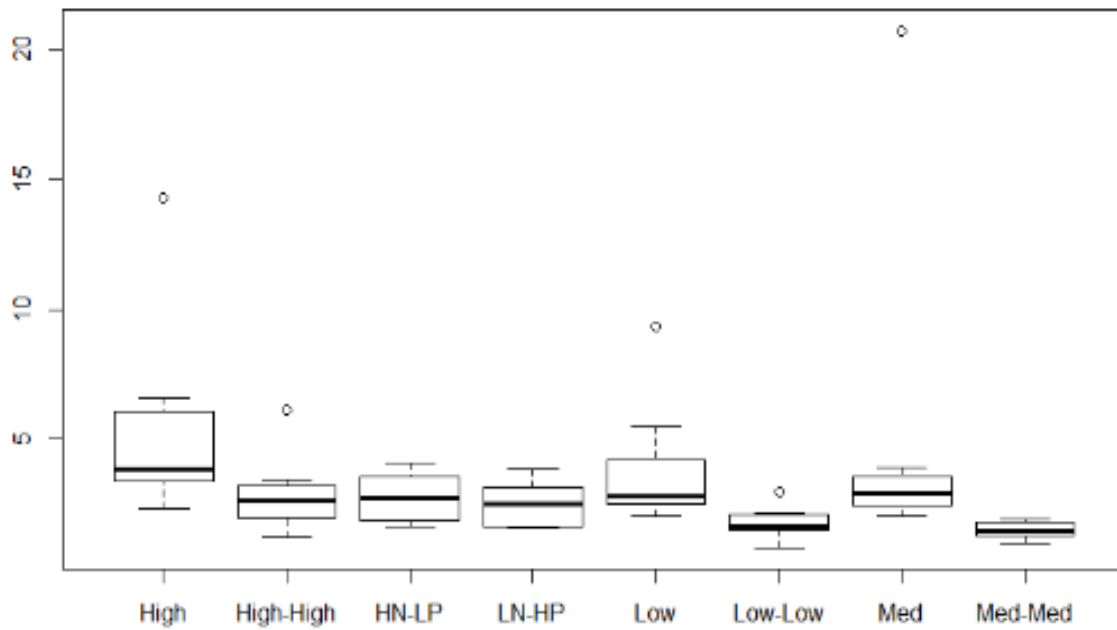
**Resilience of chlorophyll inside of exclosures**



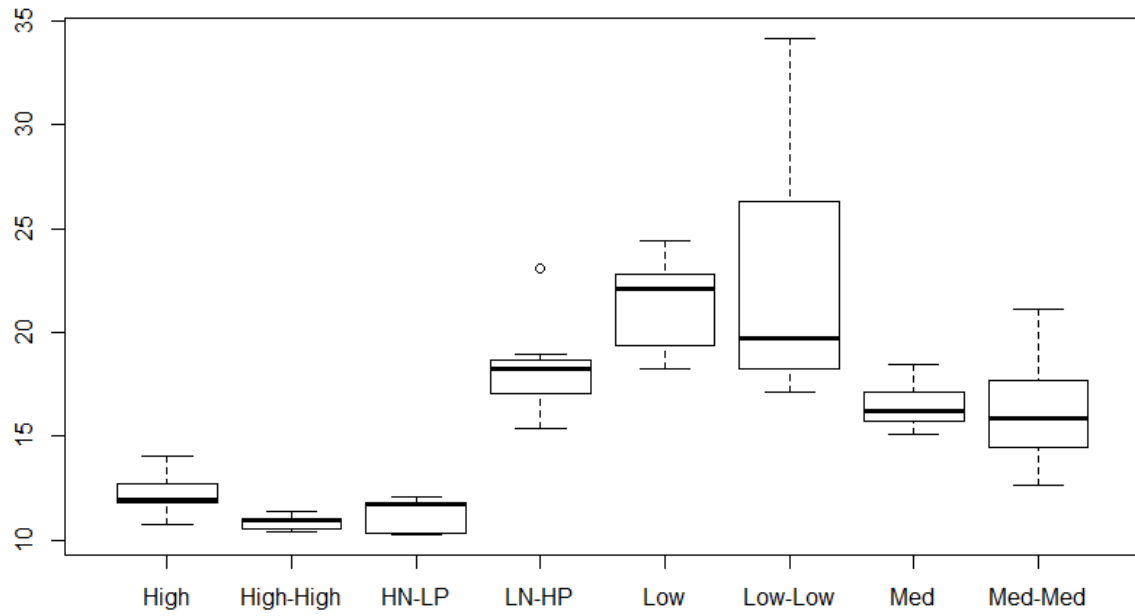
### Resistance of oxygen



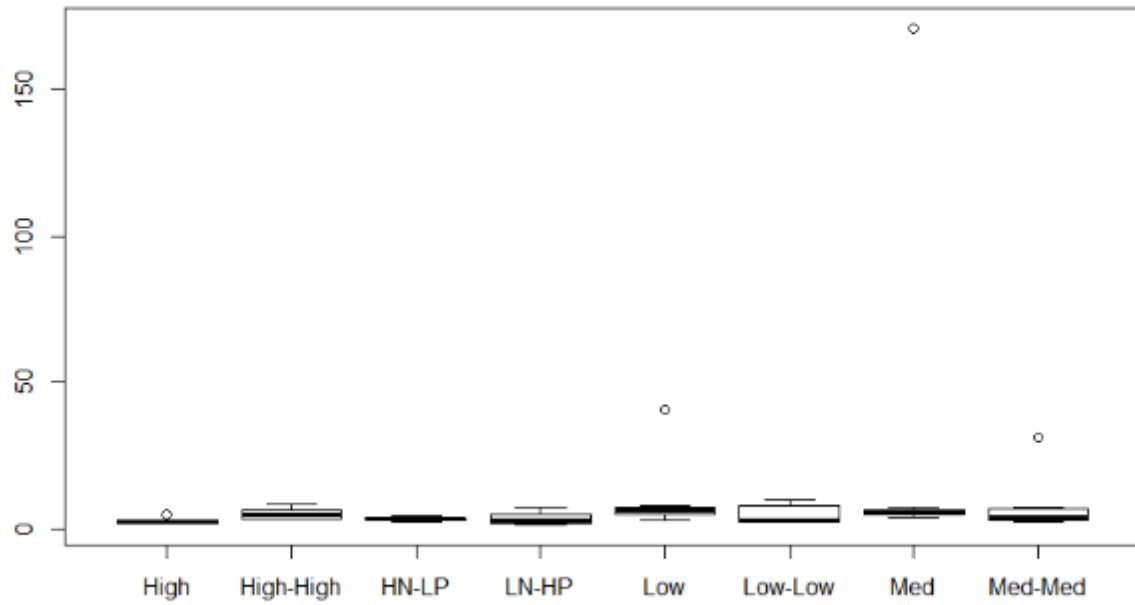
### Resilience of oxygen



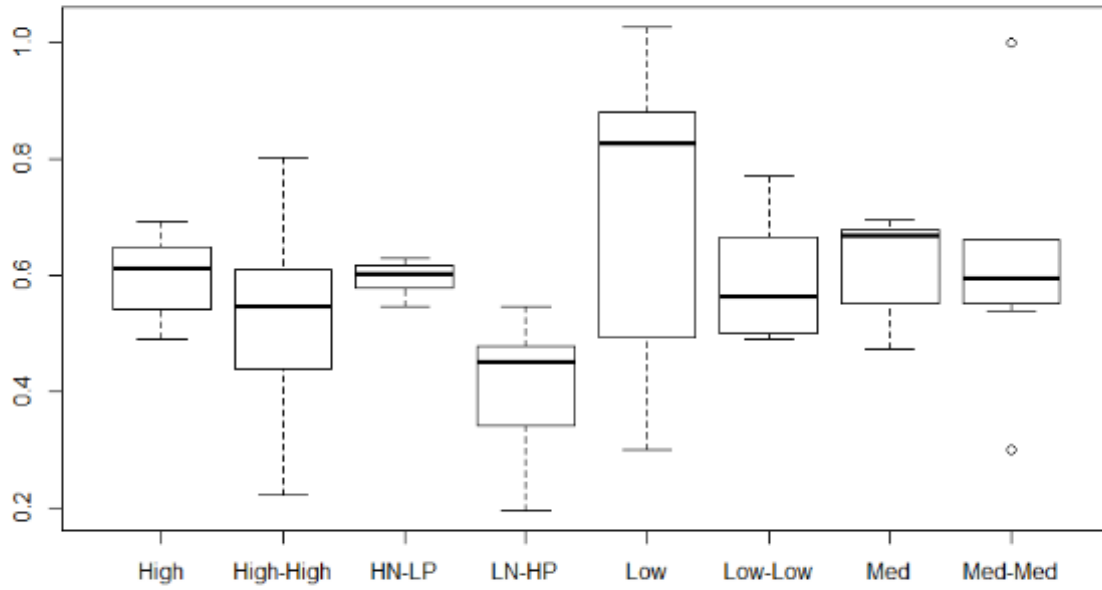
## Resistance of pH



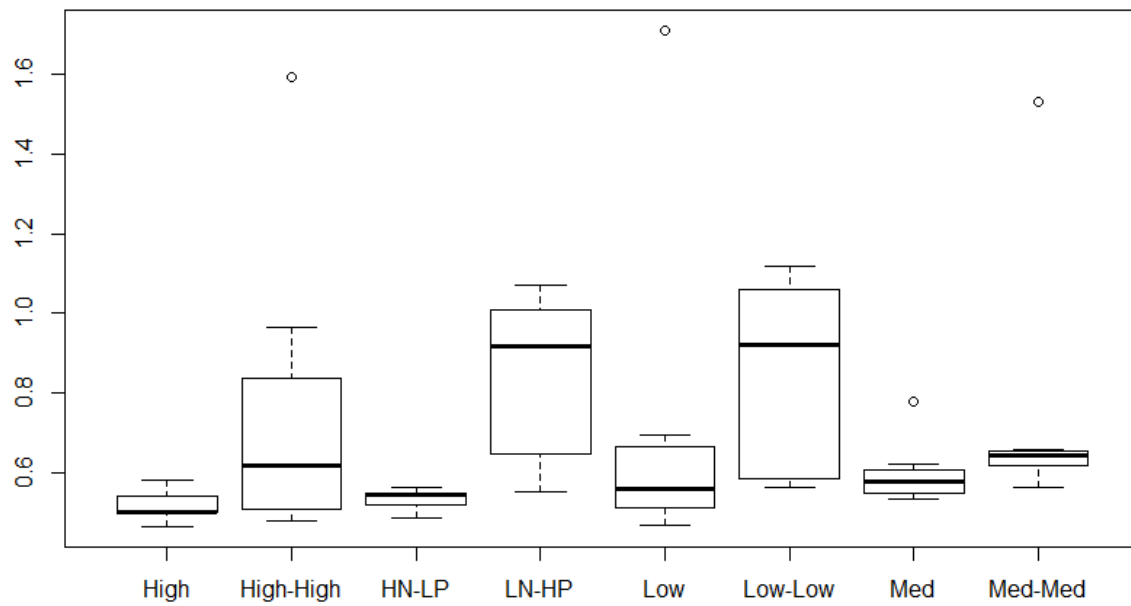
## Resilience of pH



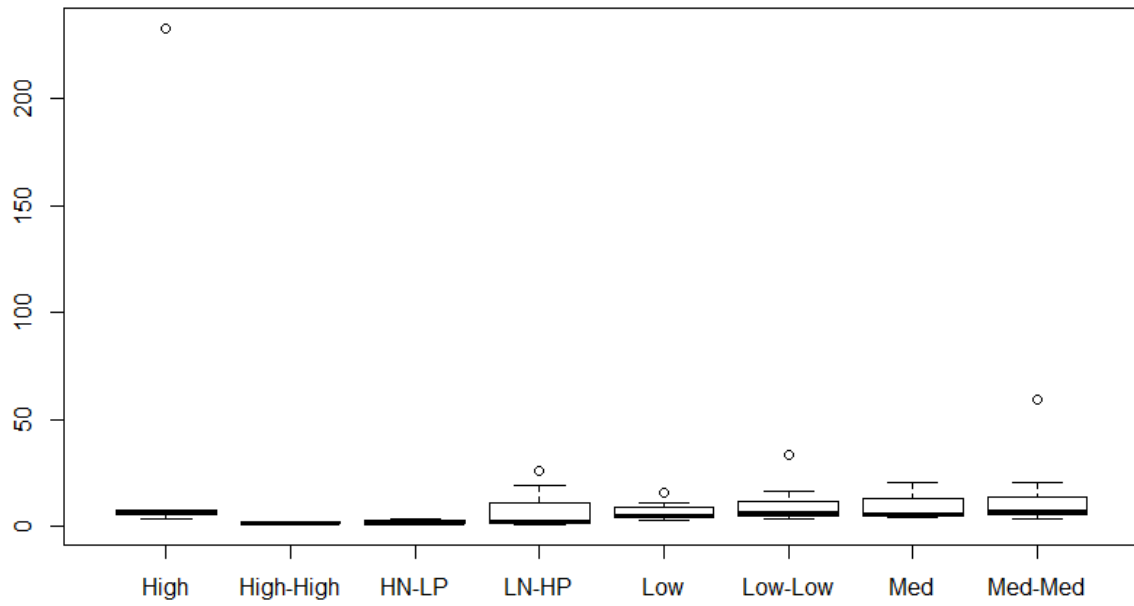
### Resistance of nitrate



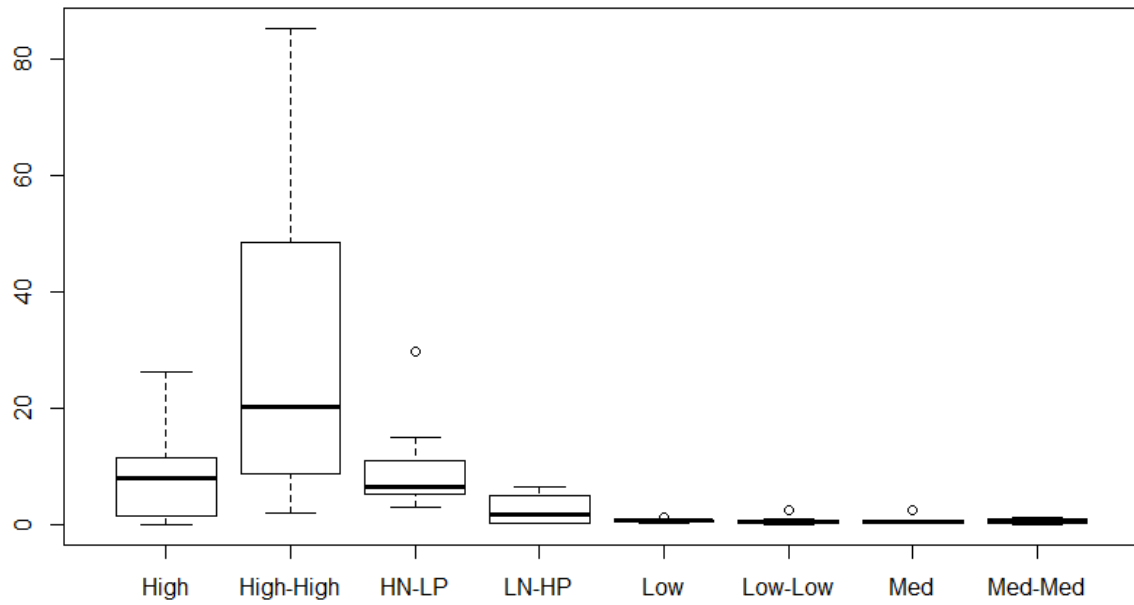
### Resilience of nitrate



### Resistance of ammonium

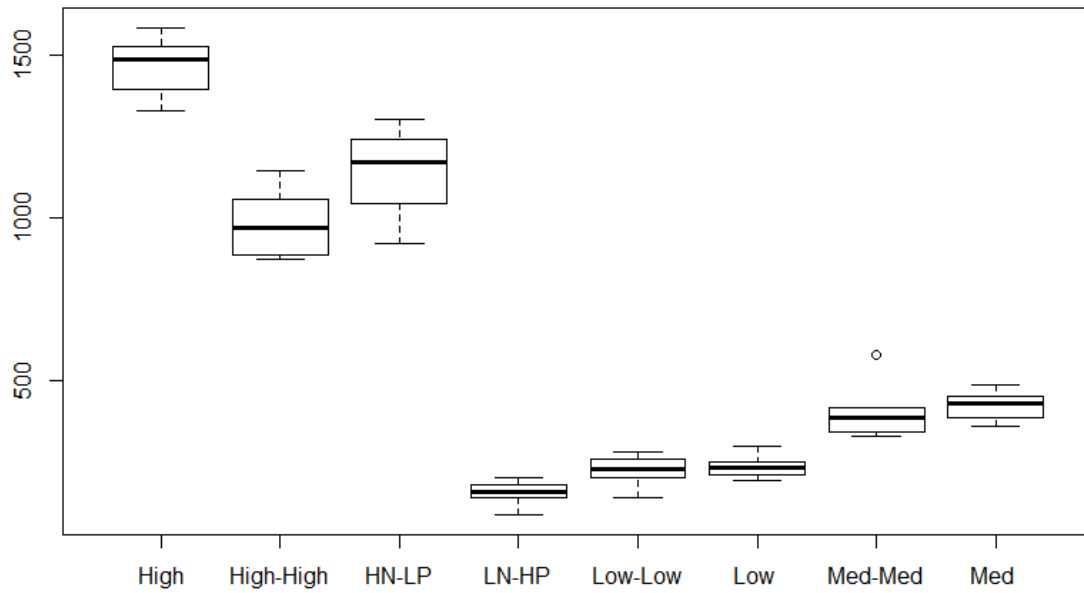


### Resilience of ammonium

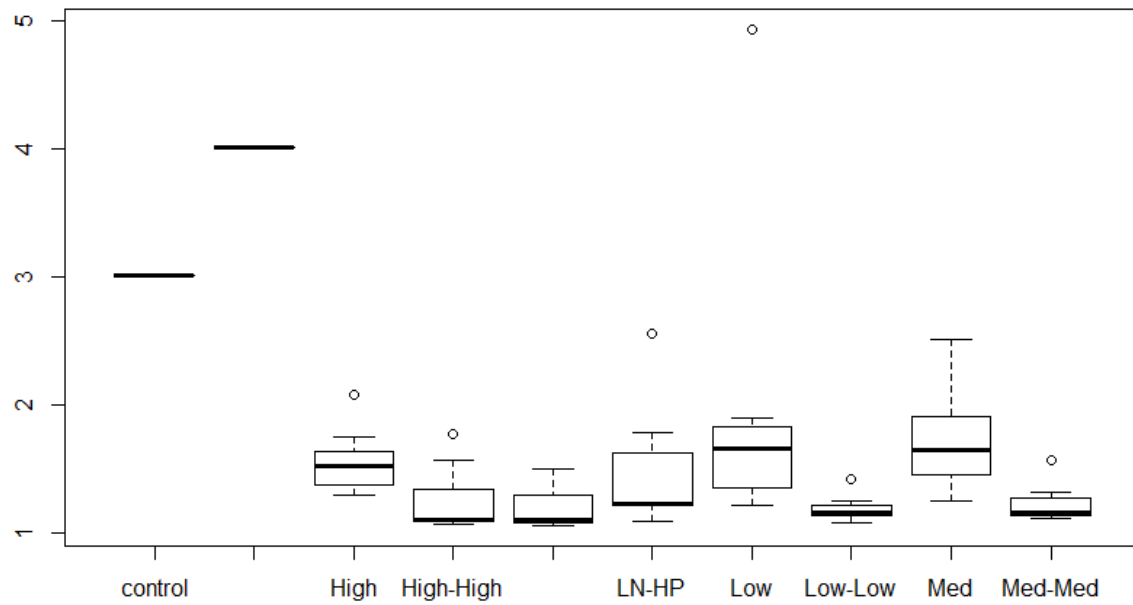




**Appendix 20: Integrals of chlorophyll values outside of the exclosures for productivity**



**Appendix 20: Resistance analysis on chlorophyll including the large aquaponic structures**



**Appendix 21: Resilience analysis on chlorophyll including the large aquaponic structures**

