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INVESTIGATING THE EFFECTS OF UV FILTERS IN SUNSCREEN ON HUMAN AND ENVIRONMENTAL HEALTH

by

BRITTANY M. THOMPSON

A thesis submitted in partial fulfillment of the requirements
for the Honors in the Major Program in Biology
in the College of the Sciences
and in the Burnett Honors College
at the University of Central Florida
Orlando, Florida

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Thesis Chair: Melinda Donnelly, Ph.D.

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ABSTRACT

Ultraviolet filters are active ingredients in sunscreen that protect us from harmful UV radiation. However, organic UV filters are thought to have adverse effects on the environment and humans. In recent years, fear of harmful impacts of sunscreen has caused a surge of coral reef safe sunscreens to hit the market. These sunscreens, which contain inorganic metal oxides as UV filters, have been accepted as safe for humans and the environment until recently. Metal oxides in reef safe sunscreens may form intermediates in the water that can harm marine life and can absorb through the skin and into the blood, possibly disrupting normal bodily function. In this study, a 48-hour bioassay was run with *Artemia salina* and various UV filters at different concentrations to determine at what levels of exposure and to which UV filters the organism is sensitive. Three trials were run with one organism in each of the 200 bioassay wells and 20 replicates per treatment. At each data collection time, organism survival outcomes were recorded. Results showed significant difference between trials but not between treatments. This project serves to research the impact sunscreen has on *A. salina* and potential environmental and human health impacts.

DEDICATION

To my beloved cousin, Samantha Thompson, who lived with grace and touched so many people with her radiance and positivity. This thesis is in honor of you and your love for the world.

ACKNOWLEDGEMENTS

I would like to acknowledge my thesis chair, Melinda Donnelly, for mentoring me throughout this entire process. Additional thanks to Linda Walters for her guidance as a member of my thesis committee. I would also like to thank my parents, Rachelle and Joseph Thompson, as well as my sisters, Taylor and Carly Thompson, for being my number one supporters.

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CHAPTER ONE: INTRODUCTION

Environmental policies and movements have developed greatly since the 1960s and have grown in strength in the past decade. Climate change, endangered species, and pollution are popular topics in environmental debates and are generally understood as environmental concerns. Pollution can come in various forms including littering, plastic pollution, light pollution, noise pollution, nutrient pollution, and chemical pollution. However, chemical pollution is a form that is not as recognizable to the general public as littering or plastic pollution and therefore can go largely unnoticed (Greve, 1971).

It is a cultural norm to apply sunscreen. What the majority of the public fails to realize is the detrimental environmental impacts the chemicals in some sunscreens are causing once they make their way into oceans. Chemicals such as oxybenzone, metal oxides, and nanoparticles comprise sunscreen, and research indicates these can be a concern to aquatic ecosystems. One study found evidence that oxybenzone was expediting coral bleaching and acting as an endocrine disruptor in young coral (Downs et al., 2015). Another found UV filters radically altering the behavior of fish and causing premature death (Ruszkiewicz et al., 2017). These chemicals may also be a risk to human health once absorbed through the skin and into the bloodstream (Krause et al., 2012). There is additionally a risk of inhalation of these chemicals into the lungs (Krause et al., 2012). The dangers sunscreen may pose are significant, as environmental and human health are found to be highly correlated and, in recent years, to both be declining (Fleming et al., 2019). This project serves to research the impact sunscreen composition has on *A. salina* well as what can be done to minimize or counteract sunscreen’s possible consequences.

CHAPTER TWO: BACKGROUND

Chemical Composition of Sunscreen

Sunscreens function through the use of UV filters. Organic UV filters, which have been utilized in the majority of sunscreen products since the 1920s, are derivatives of para-aminobenzoates (PABA), salicylates, cinnamates, and camphor, which are UV-B absorbers, as well as various UV-A absorbers including benzophenone and dibenzoylmethane derivatives (Jallad et al., 2016). One common organic UV filter is oxybenzone, a benzophenone derivative that is also referred to as benzophenone-3. Oxybenzone makes its way to the blood of humans because it penetrates the epidermis (Dinardo et al., 2017). Oxybenzone is believed to cause various health issues for both the environment and humans (Raffa, 2018). It is also apparent that while oxybenzone can be photostable when combined with other ingredients, oxybenzone is not photostable on its own and can therefore react in the water to produce hazardous by-products which may play a role in coral bleaching (Downs et al., 2015).

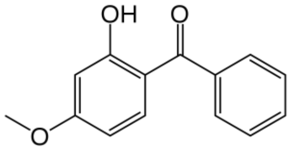


Figure 1: Structure of oxybenzone or benzophenone-3, a benzophenone derivative

Inorganic chemicals in sunscreen, mainly titanium dioxide and zinc oxide, function to protect wearers by both absorbing and reflecting UV radiation from the sun. Nanoparticles of these chemicals, defined as particles ranging from 1-100 nanometers in size, can be a huge risk to wearers. Nanoparticles can absorb into the bloodstream, but likely in insignificant quantities (Cross et al., 2007). Nanoparticles can also accumulate in guts of filter feeders like *Artemia salina*, making it difficult to ingest food and causing lethal oxidative stress (Ates et al., 2012).

Reef Safe Sunscreens

In recent years, fear of the harmful impacts of sunscreen has caused a surge of various environmentally friendly or reef safe sunscreens to hit the market. These sunscreens are supposedly biodegradable and friendly to both the environment and to our own bodies. Metal oxides such as titanium dioxide and zinc oxide are two common inorganic chemicals found in reef friendly sunscreens. These ingredients have been generally deemed safe for both the environment and humans so long as they are not in nanoparticle form (Jallad et al., 2016). Skin irritation reports from these additives are rare and previous studies support the assertions that while titanium dioxide and zinc oxide do not penetrate through the skin and are photostable (Jallad et al., 2016). Other studies show that titanium dioxide is nonbiodegradable and may react to form excessive hydrogen peroxide in warm waters and harm sea life (Sánchez et al., 2014). It should be noted that some products which are advertised as environmentally friendly or biodegradable may still contain potentially toxic chemicals, so consumers should be aware of the ingredients and their health concerns prior to purchasing sun protection products.

Sunscreen Concentrations

Some of the UV filters used in sunscreens are naturally occurring. Oxybenzone is naturally formed in plants but is commercially produced from benzoyl chloride for sunscreen production. Though these UV filters may already be present in certain aquatic habitats, evidence supports that the levels in the water significantly fluctuates with seasonal beach patterns due to the use of sunscreen (Bratkovicks et al., 2015). A yearlong study of the marine waters off the coast of South Carolina found that an increase in beach visitors correlated with substantially higher levels of sunscreen additives in the water (Bratkovicks et al., 2015).

Human and Environmental Health and Sunscreen

Ultraviolet (UV) radiation from the sun interacts with the skin causing cells to mutate and form various types of skin cancer. Sunscreen is known to protect our skin from UVA and UVB radiation, so it is recommended for daily use by dermatologists (Raffa, 2018). There is extensive evidence to support that daily use of sunscreen greatly reduces the risk of sun-related damage to the skin including sunburn and squamous cell carcinomas and melanomas (Jallad et al., 2016). However, Ruszkiewicz et al. (2017) found that the UV filters shielding us from radiation can be toxic themselves. Once absorbed into the blood, these additives can exhibit neurotoxicity because they are able to cross the blood brain barrier and act as endocrine disruptors, altering levels of estrogen, androgen, and progesterone. Nanoparticles, a common ingredient in mineral based and seemingly eco-friendly sunscreens, can be inhaled and lead to asthma and other respiratory illnesses (Dinardo et al., 2017). Apart from its impact on humans, sunscreen accumulation in the water can lead to the unstable UV filters forming free radicals that can play a role in coral bleaching and DNA damage (Downs et al., 2015), alteration of behavior in fish and other organisms (Ruszkiewicz, 2017), and increasing viral production through initiation of the lytic cycle in prophage carrying cells (Danovaro et al., 2003).

Environmental Initiatives

Certain countries and states have begun to enforce new legislation regarding sunscreen to assist in the preservation of the environment. For example, Hawaii has banned two sunscreen ingredients, oxybenzone and octinoxate, and Hanauma Bay in Oahu has new policies to promote the education of the general public on environmental concerns. First time visitors are required to view a nine-minute video on reef conservation and adhere to strict rules (Raffa et al., 2018).

Other Methods of Sun Protection

Aside from sunscreen, there are other ways to protect our bodies from harmful UV rays. For instance, wearing clothing and hats can protect skin by physically blocking UV rays. However, a concern with this approach is that this is a cause of microplastic pollution in the water. Synthetic fibers such as polyester and acrylic make up most the world's clothing today, and when exposed to water these materials can then shed small microplastic fragments (Henry et al., 2019). Microplastics are a significant danger to marine life as they can easily be ingested alongside food and accumulate in the food chain (Waite et al., 2017). Another possible way to protect your skin without the use of sunscreen is to try to avoid being exposed to the sun for extended periods of time during peak UV hours from 11am to 5pm. Additionally, it is important to note that UV exposure is greater at higher altitudes and at lower latitudes (Falk et al., 2012).

Brine Shrimp: A Model Organism

Artemia salina, commonly known as brine shrimp, are filter feeders that are essential to numerous ecosystems such as salt marshes and mangrove swamps. Although in some places they are an invasive species, they often play a functional role in trophic cascades (Sánchez et al., 2016). *A. salina* are important not only a source of food for various species but because of their major roles in nutrient cycling and controlling phytoplankton production levels (Sánchez et al., 2016). *A. salina* have become increasingly common test organisms for ecotoxicity trials. They are used in lethality assays and are beginning to replace animal serums which are more ethically questionable. Since *A. salina* are inexpensive, have a quick 4 week lifespan, and overall make scientific trials relatively convenient, the species is often referred to as a model organism (Rajabi et al., 2015).

CHAPTER THREE: RESEARCH METHODOLOGY

To test the toxicity of various UV filters on *A. salina,* 48-hour bioassays were run in 3 trials. There were 10 test groups: 3 UV filters (oxybenzone, zinc oxide, titanium dioxide) at 3 concentrations (8.0 mg/L, 2.0 mg/L, and 8.0 μg/L) and a control group with no UV filter added. Concentrations were based on a South Carolina study that recorded these levels in aquatic environments (Bratkovics, 2015). Treatment groups had 20 replicates per trial. The salinity was 35 parts per thousand to replicate the environment of *A. salina*. The saltwater and designated amount of UV filter were mixed in a labelled bottle. Each well contained one organism bought as an adult from Top Shelf Aquatics, and well locations were random to ensure no confounding variables due to tray location. Organisms and 2 mL of assigned water treatment were placed in assigned wells with pipettes. At each data collection time (0.5, 1, 2, 3, 6, 24, and 48 hours) organisms were agitated to test survival and those that did not move were considered dead.

Table 1: Treatment Group Assignments for *A. salina* Lethality Assay

Group Number	UV Filter	Concentration of UV Filter
1	Oxybenzone	8.0 mg/L
2	Oxybenzone	2.0 mg/L
3	Oxybenzone	8.0 μg/L
4	Zinc Oxide	8.0 mg/L
5	Zinc Oxide	2.0 mg/L
6	Zinc Oxide	8.0 μg/L
7	Titanium Dioxide	8.0 mg/L
8	Titanium Dioxide	2.0 mg/L
9	Titanium Dioxide	8.0 μg/L
10	None (Control)	0

CHAPTER FOUR: EXPERIMENTAL RESULTS

Table 2: Survival of *A. salina* Upon Exposure to UV Filters Over Time

Treatment Group Number	Hours Elapsed						
	0.5	1	2	3	6	24	48
	Number of *Artemia salina* surviving						
TRIAL 1							
1	19	19	19	19	18	7	6
2	16	16	16	15	14	3	2
3	17	17	17	17	17	7	4
4	18	18	18	18	17	5	2
5	18	18	18	18	17	12	6
6	19	19	19	19	18	11	5
7	19	19	19	19	19	10	4
8	20	19	19	19	19	11	1
9	19	19	19	19	19	5	3
10	19	19	18	17	17	6	1
TRIAL 2							
1	20	20	20	20	20	20	20
2	20	20	20	20	20	20	20
3	20	20	20	20	20	20	20
4	20	20	20	20	20	20	20
5	20	20	20	20	20	20	20
6	20	20	20	20	20	20	20
7	20	20	20	20	19	19	19
8	20	20	20	20	20	20	20
9	20	20	20	20	20	20	20
10	20	20	20	20	20	20	20

Treatment Group Number	Hours Elapsed						
	0.5	1	2	3	6	24	48
	Number of *Artemia salina* surviving						
TRIAL 3							
1	20	19	19	19	19	18	14
2	20	20	20	20	20	18	14
3	20	20	20	20	20	19	16
4	20	20	20	20	20	19	16
5	20	20	20	20	19	19	14
6	20	20	19	18	18	17	14
7	20	19	19	19	17	17	14
8	20	20	20	20	20	19	15
9	20	20	20	20	19	18	16
10	20	20	20	20	20	20	18
AVERAGE							
1	19.67	19.33	19.33	19.33	19	15	13.33
2	18.67	18.67	18.67	18.33	18	13.67	12
3	19	19	19	19	19	15.33	13.33
4	19.33	19.33	19.33	19.33	19	14.67	12.67
5	19.33	19.33	19.33	19.33	18.67	17	13.33
6	19.67	19.67	19.33	19	18.67	16	13
7	19.67	19.33	19.33	19.33	18.33	15.33	12.33
8	20	19.67	19.67	19.67	19.67	16.67	12
9	19.67	19.67	19.67	19.67	19.33	14.33	13
10	19.67	19.67	19.33	19	19	15.33	13

* denotes the total surviving for this group was statistically significant

** no groups displayed a significantly significant total in comparison to the control

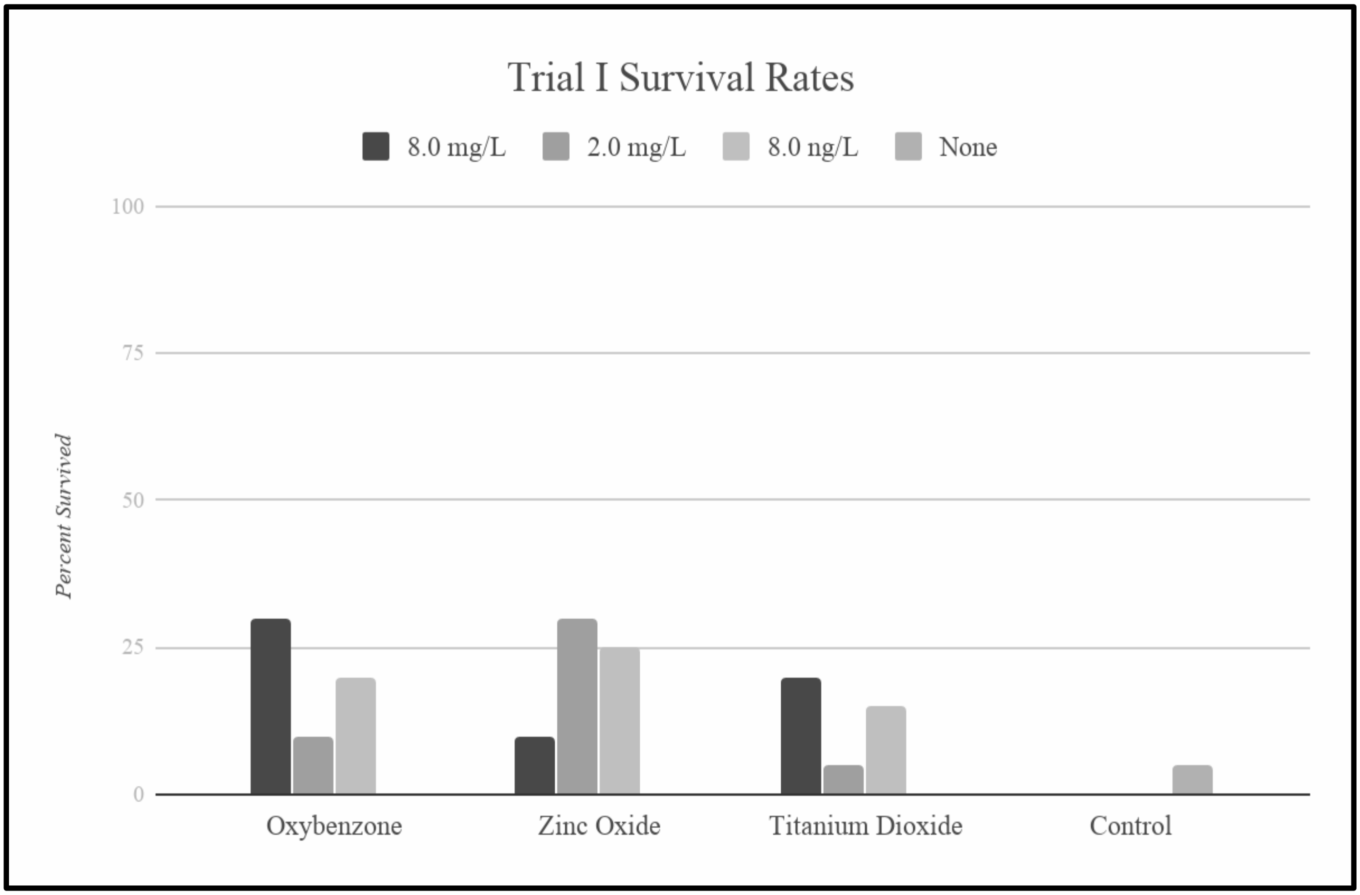


Figure 2: Trial I Survival Rates

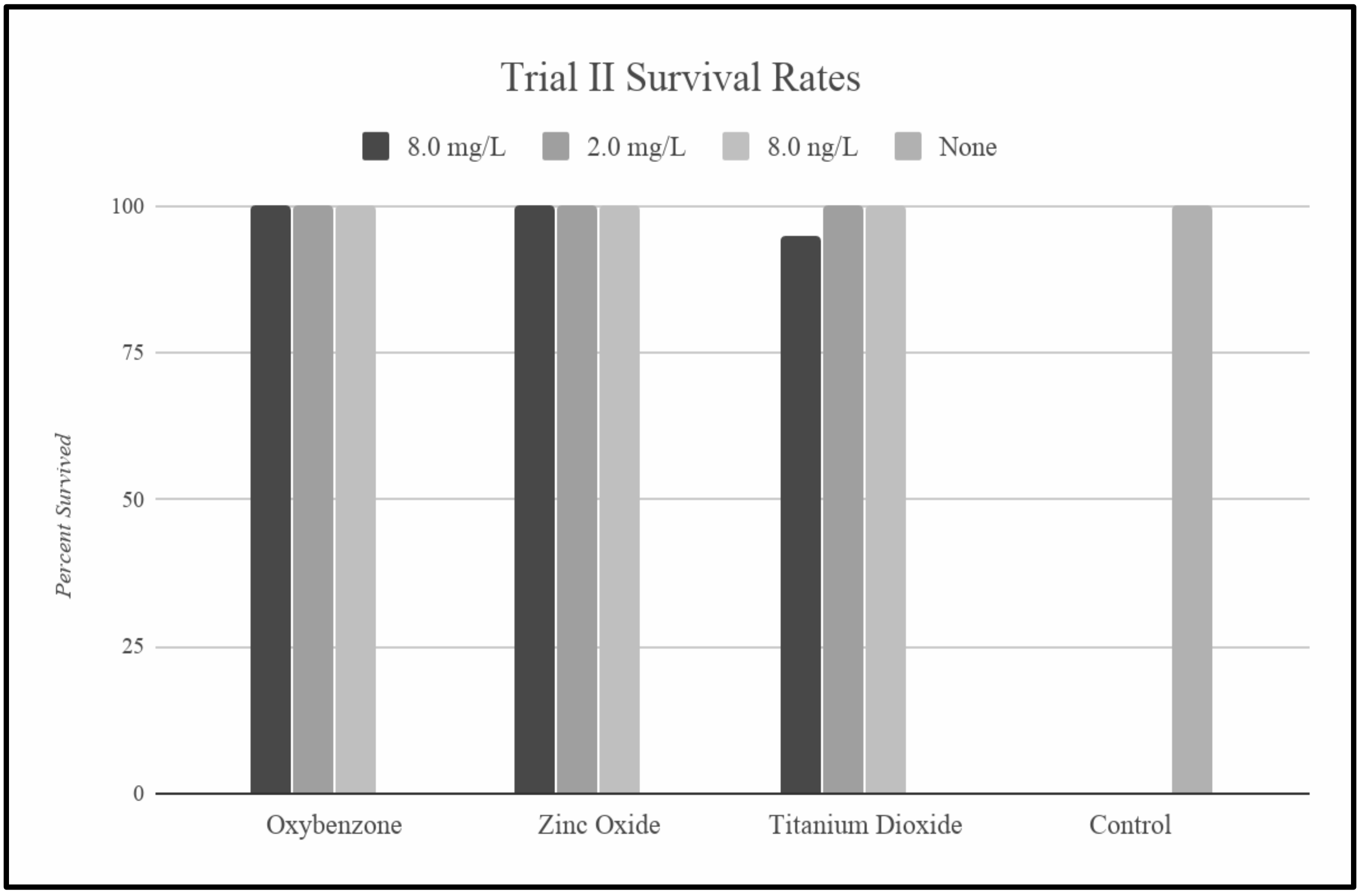


Figure 3: Trial II Survival Rates

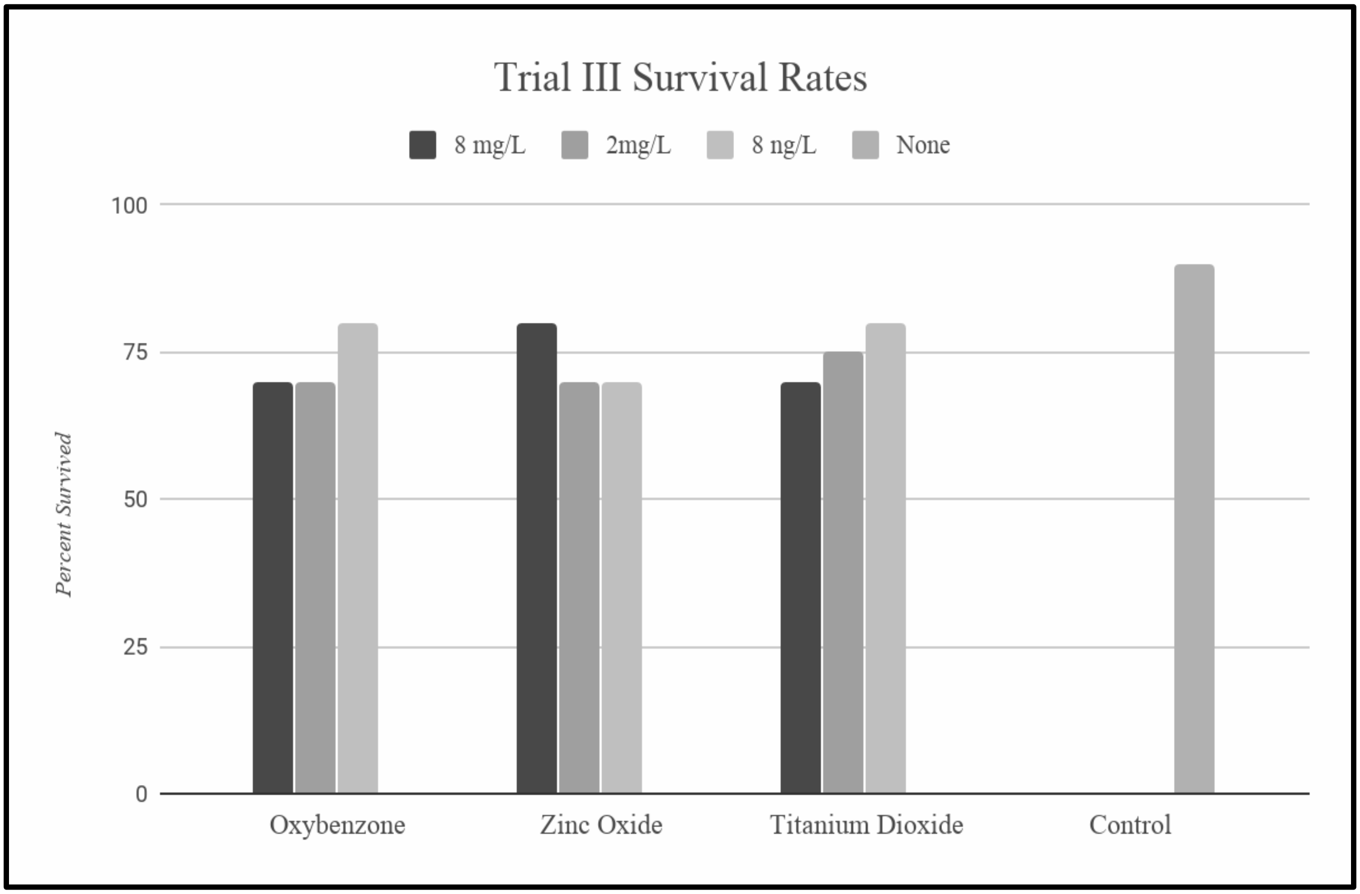


Figure 4: Trial III Survival Rates

Trial I Results

The survival rates for all groups were low in Trial I. This is possibly due to the brine shrimp being stored overnight in the refrigerator to slow their metabolism and help them survive longer. In the following trials, brine shrimp were bought immediately before use in an attempt to reduce the possibility of any confounding variables.

Trial II Results

Only one brine shrimp died in this trial. However, behavioral changes were observed in this trial since the brine shrimp were still alive to observe.

Trial III Results

Brine shrimp exposed to UV filters consistently had lower survival rates in this trial. Exposure to UV filters in high concentrations dropped survival rates by up to twenty percent in comparison to the control group. The control had a survival rate of ninety percent, with the ten percent of deaths likely being due to the short lifespan of the species or salinity shock. High concentrations of zinc oxide did not follow the expected trend and resulted in a higher survival rate than lower concentrations of zinc oxide. Additionally, the behavioral changes observed in Trial II were also observed in this trial since most of the brine shrimp survived and were able to be observed throughout the entirety of the trial.

CHAPTER FIVE: CONCLUSION

Discussion of Results

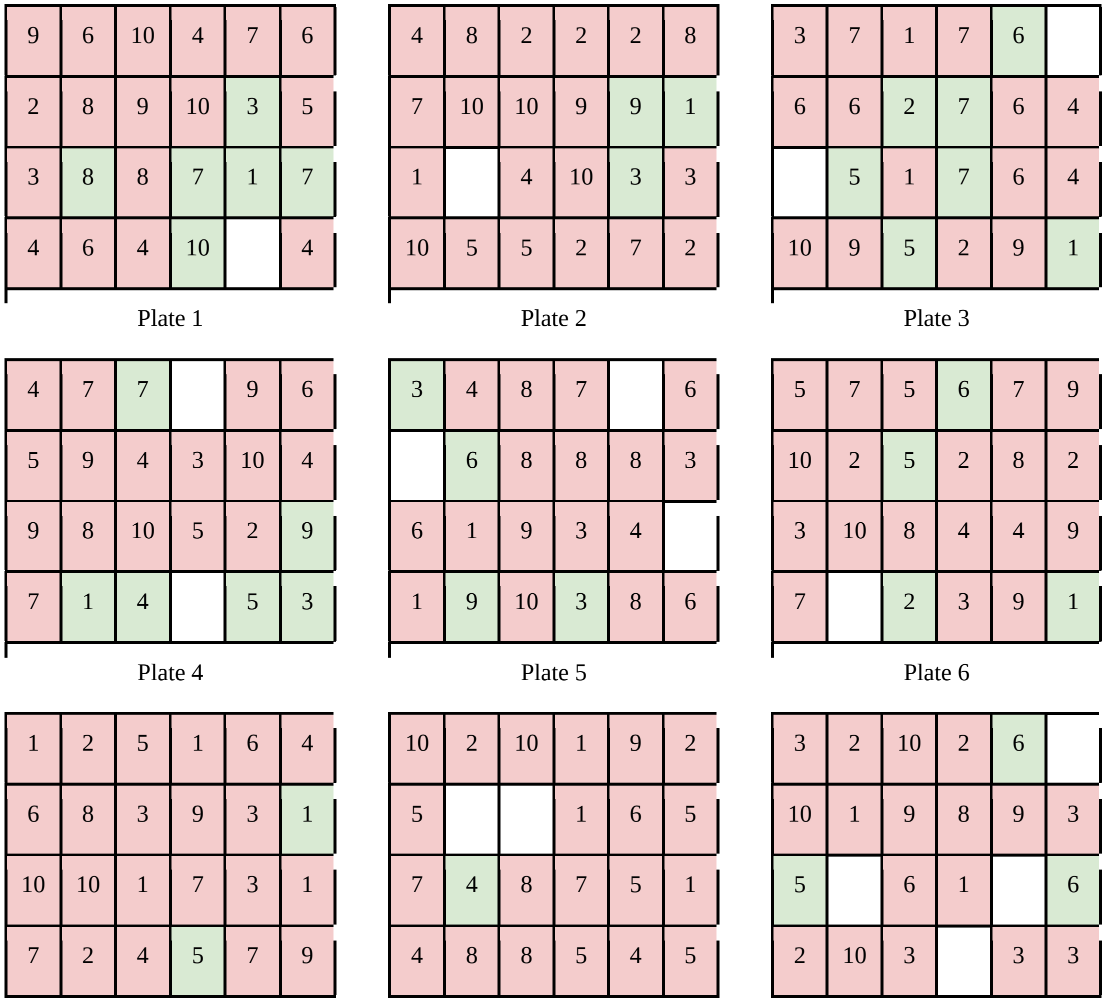
In the first trial, the death rates of all organisms were higher. This is likely due to the fact that they were stored in a refrigerator to slow down their metabolism. We suspect that the death of some of the *A. salina* could be a result of toxic ammonia build up in the water and low oxygen turnover. Because even the control group exhibited a low survival rate, for the second and third trials, the brine shrimp were purchased immediately before lab use to ensure that the time spent without an aerator to move oxygen through the water was minimized. In the following trials, survival rates in all groups were high, yet no statistically significant difference between groups was observed. This leads us to reject the hypothesis that UV filters are detrimental to survival rates of *Artemia salina* and that higher concentrations will have a more pronounced effect. Although no significant difference in survival rates were found, a difference in behavior in Trial II and Trial III were noted. Brine shrimp in the control group swam in the same location of the well throughout the trial, often clinging to the side of the well and maintaining a body position perpendicular to the surface of the water. Those exposed to metal oxides swam around the circumference of the well, often pushing against the plastic and maintaining a body position parallel to the surface of the water. Brine shrimp exposed to oxybenzone seemed to curl and swam sporadically in a flipping motion. This is comparable to other studies where the addition of UV filters can cause an unusual behavioral or physiological change in fishes but not necessarily death. One such study found that oxybenzone caused down regulation of transcription of certain genes and overall antiandrogenic activity in zebrafish (Blüthgen et al., 2012).

Future Research Questions

Further research is necessary to more closely determine the health impacts of UV filters. The question of how the UV filters studied impact survival rates of *A. salina* after a longer period remains. Additionally, the difference in behavioral patterns leads us to question the impact of the UV filters on populations in the wild. It is not yet understood these distinct behaviors occur and what they mean for the organism. Further questions to investigate include how the behavioral changes impact ability to feed, avoid predation, and reproduce. It is also of interest whether these UV filters produce negative impacts after reacting with other toxins.

APPENDIX - DATA COLLECTION

Table 3: Trial I Well Map



🟥 9	🟥 6	🟥 10	🟥 4	🟥 7	🟥 6
🟥 2	🟥 8	🟥 9	🟥 10	🟩 3	🟥 5
🟥 3	🟩 8	🟥 8	🟩 7	🟩 1	🟩 7
🟥 4	🟥 6	🟥 4	🟩 10		🟥 4

Plate 1

🟥 4	🟥 8	🟥 2	🟥 2	🟥 2	🟥 8
🟥 7	🟥 10	🟥 10	🟥 9	🟩 9	🟩 1
🟥 1		🟥 4	🟥 10	🟩 3	🟥 3
🟥 10	🟥 5	🟥 5	🟥 2	🟥 7	🟥 2

Plate 2

🟥 3	🟥 7	🟥 1	🟥 7	🟩 6	
🟥 6	🟥 6	🟩 2	🟩 7	🟥 6	🟥 4
	🟩 5	🟥 1	🟩 7	🟥 6	🟥 4
🟥 10	🟥 9	🟩 5	🟥 2	🟥 9	🟩 1

Plate 3

🟥 4	🟥 7	🟩 7		🟥 9	🟥 6
🟥 5	🟥 9	🟥 4	🟥 3	🟥 10	🟥 4
🟥 9	🟥 8	🟥 10	🟥 5	🟥 2	🟩 9
🟥 7	🟩 1	🟩 4		🟩 5	🟩 3

Plate 4

🟩 3	🟥 4	🟥 8	🟥 7		🟥 6
	🟩 6	🟥 8	🟥 8	🟥 8	🟥 3
🟥 6	🟥 1	🟥 9	🟥 3	🟥 4	
🟥 1	🟩 9	🟥 10	🟩 3	🟥 8	🟥 6

Plate 5

🟥 5	🟥 7	🟥 5	🟩 6	🟥 7	🟥 9
🟥 10	🟥 2	🟩 5	🟥 2	🟥 8	🟥 2
🟥 3	🟥 10	🟥 8	🟥 4	🟥 4	🟥 9
🟥 7		🟩 2	🟥 3	🟥 9	🟩 1

Plate 6

🟥 1	🟥 2	🟥 5	🟥 1	🟥 6	🟥 4
🟥 6	🟥 8	🟥 3	🟥 9	🟥 3	🟩 1
🟥 10	🟥 10	🟥 1	🟥 7	🟥 3	🟥 1
🟥 7	🟥 2	🟥 4	🟩 5	🟥 7	🟥 9

Plate 7

🟥 10	🟥 2	🟥 10	🟥 1	🟥 9	🟥 2
🟥 5			🟥 1	🟥 6	🟥 5
🟥 7	🟩 4	🟥 8	🟥 7	🟥 5	🟥 1
🟥 4	🟥 8	🟥 8	🟥 5	🟥 4	🟥 5

Plate 8

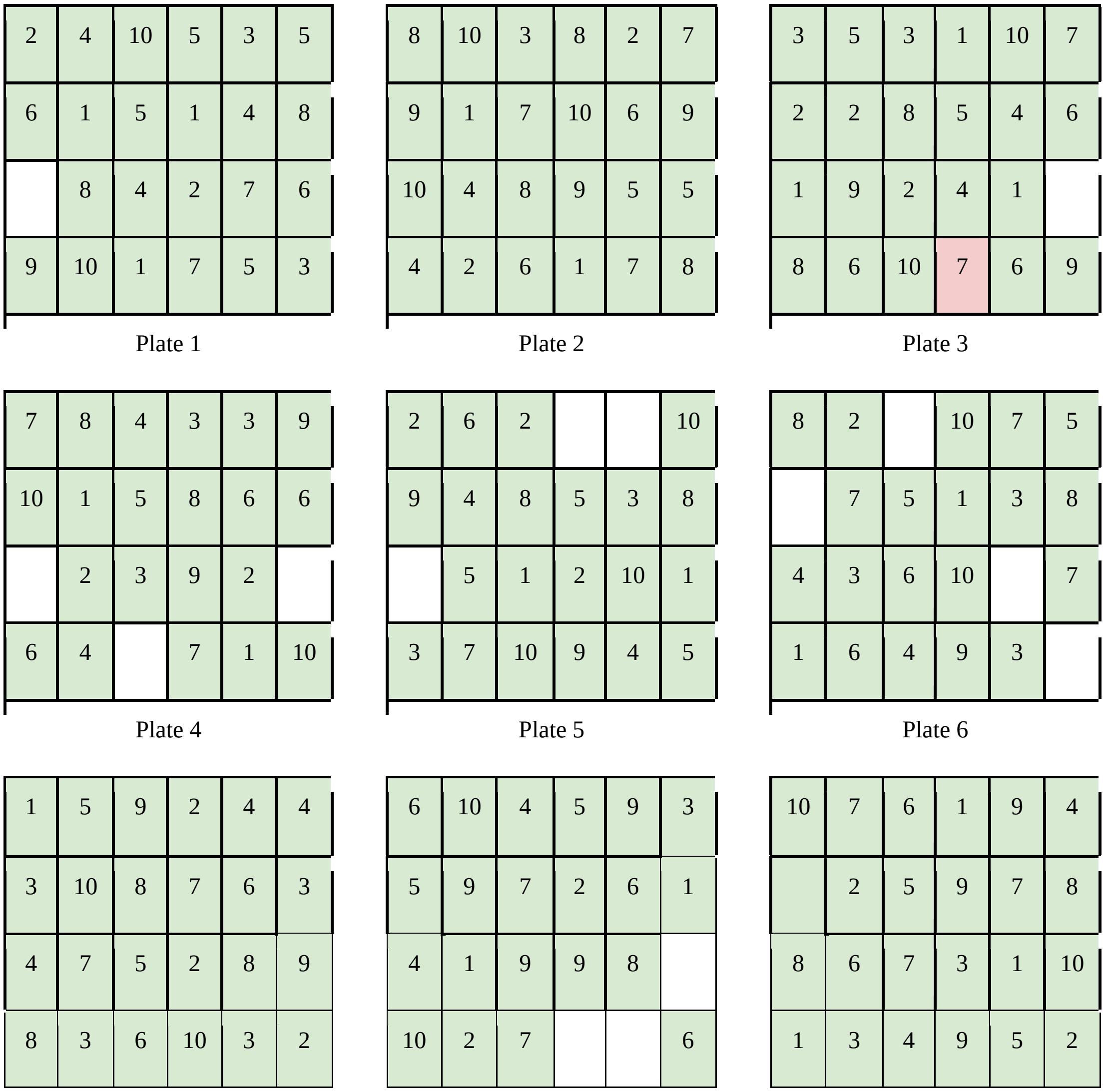
🟥 3	🟥 2	🟥 10	🟥 2	🟩 6	
🟥 10	🟥 1	🟥 9	🟥 8	🟥 9	🟥 3
🟩 5		🟥 6	🟥 1		🟩 6
🟥 2	🟥 10	🟥 3		🟥 3	🟥 3

Plate 9

MAP KEY:

Each box represents a well and is labeled with the assigned treatment group number. Green wells represent that the organism in that well survived throughout the entire 48 hour bioassay, and red wells represent that the organism in that well died by the end of the 48 hour bioassay. Unlabeled boxes represent the wells that were not used, as the plates had 16 additional wells. Well location was randomized for each trial to eliminate confounding variables due to the tray or well location.

Table 4: Trial II Well Map



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6	1	5	1	4	8
	8	4	2	7	6
9	10	1	7	5	3

Plate 1

8	10	3	8	2	7
9	1	7	10	6	9
10	4	8	9	5	5
4	2	6	1	7	8

Plate 2

3	5	3	1	10	7
2	2	8	5	4	6
1	9	2	4	1	
8	6	10	🟥 7	6	9

Plate 3

7	8	4	3	3	9
10	1	5	8	6	6
	2	3	9	2	
6	4		7	1	10

Plate 4

2	6	2			10
9	4	8	5	3	8
	5	1	2	10	1
3	7	10	9	4	5

Plate 5

8	2		10	7	5
	7	5	1	3	8
4	3	6	10		7
1	6	4	9	3	

Plate 6

1	5	9	2	4	4
3	10	8	7	6	3
4	7	5	2	8	9
8	3	6	10	3	2

Plate 7

6	10	4	5	9	3
5	9	7	2	6	1
4	1	9	9	8	
10	2	7			6

Plate 8

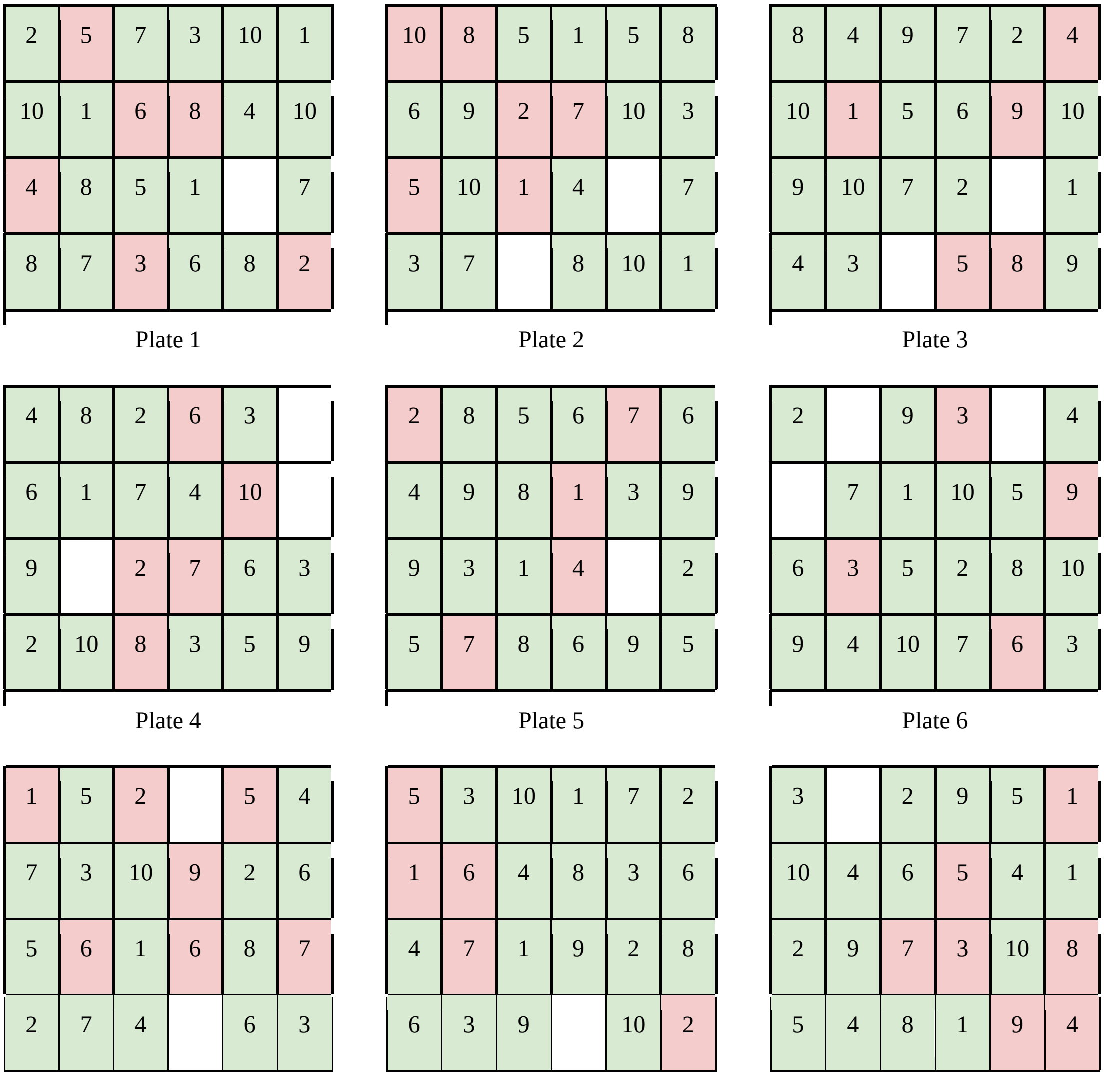
10	7	6	1	9	4
	2	5	9	7	8
8	6	7	3	1	10
1	3	4	9	5	2

Plate 9

MAP KEY:

Each box represents a well and is labeled with the assigned treatment group number. Green wells represent that the organism in that well survived throughout the entire 48 hour bioassay, and red wells represent that the organism in that well died by the end of the 48 hour bioassay. Unlabeled boxes represent the wells that were not used, as the plates had 16 additional wells. Well location was randomized for each trial to eliminate confounding variables due to the tray or well location.

Table 5: Trial III Well Map



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🟥 4	🟩 8	🟩 5	🟩 1		🟩 7
🟩 8	🟩 7	🟥 3	🟩 6	🟩 8	🟥 2

Plate 1

🟥 10	🟥 8	🟩 5	🟩 1	🟩 5	🟩 8
🟩 6	🟩 9	🟥 2	🟥 7	🟩 10	🟩 3
🟥 5	🟩 10	🟥 1	🟩 4		🟩 7
🟩 3	🟩 7		🟩 8	🟩 10	🟩 1

Plate 2

🟩 8	🟩 4	🟩 9	🟩 7	🟩 2	🟥 4
🟩 10	🟥 1	🟩 5	🟩 6	🟥 9	🟩 10
🟩 9	🟩 10	🟩 7	🟩 2		🟩 1
🟩 4	🟩 3		🟥 5	🟥 8	🟩 9

Plate 3

🟩 4	🟩 8	🟩 2	🟥 6	🟩 3	
🟩 6	🟩 1	🟩 7	🟩 4	🟥 10	
🟩 9		🟥 2	🟥 7	🟩 6	🟩 3
🟩 2	🟩 10	🟥 8	🟩 3	🟩 5	🟩 9

Plate 4

🟥 2	🟩 8	🟩 5	🟩 6	🟥 7	🟩 6
🟩 4	🟩 9	🟩 8	🟥 1	🟩 3	🟩 9
🟩 9	🟩 3	🟩 1	🟥 4		🟩 2
🟩 5	🟥 7	🟩 8	🟩 6	🟩 9	🟩 5

Plate 5

🟩 2		🟩 9	🟥 3		🟩 4
	🟩 7	🟩 1	🟩 10	🟩 5	🟥 9
🟩 6	🟥 3	🟩 5	🟩 2	🟩 8	🟩 10
🟩 9	🟩 4	🟩 10	🟩 7	🟥 6	🟩 3

Plate 6

🟥 1	🟩 5	🟥 2		🟥 5	🟩 4
🟩 7	🟩 3	🟩 10	🟥 9	🟩 2	🟩 6
🟩 5	🟥 6	🟩 1	🟥 6	🟩 8	🟥 7
🟩 2	🟩 7	🟩 4		🟩 6	🟩 3

Plate 7

🟥 5	🟩 3	🟩 10	🟩 1	🟩 7	🟩 2
🟥 1	🟥 6	🟩 4	🟩 8	🟩 3	🟩 6
🟩 4	🟥 7	🟩 1	🟩 9	🟩 2	🟩 8
🟩 6	🟩 3	🟩 9		🟩 10	🟥 2

Plate 8

🟩 3		🟩 2	🟩 9	🟩 5	🟥 1
🟩 10	🟩 4	🟩 6	🟥 5	🟩 4	🟩 1
🟩 2	🟩 9	🟥 7	🟥 3	🟩 10	🟥 8
🟩 5	🟩 4	🟩 8	🟩 1	🟥 9	🟥 4

Plate 9

MAP KEY:

Each box represents a well and is labeled with the assigned treatment group number. Green wells represent that the organism in that well survived throughout the entire 48 hour bioassay, and red wells represent that the organism in that well died by the end of the 48 hour bioassay. Unlabeled boxes represent the wells that were not used, as the plates had 16 additional wells. Well location was randomized for each trial to eliminate confounding variables due to the tray or well location.

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