Mnemiopsis microcosm: will jelly blooms lead to trophic cascades?

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Abstract

The Ctenophore, Mnemiopsis leidyi, is a ctenophore zooplankton grazer that is invasive in eastern Atlantic and prevalent along the western Atlantic coast. I conducted a three week microcosm experiment to assess the potential for Mnemiopsis blooms to cause trophic cascades. I set up six tanks containing 10 cm of sediment and 67 liters of 30 µm filtered seawater. After 3 days, a phytoplankton inoculum was added to all tanks. There were three treatments: one that contained only algal inoculation; one that contained both algae and zooplankton Zooplankton (density 20.1/liter, 95% copepod Acratrons), and one that contained algae, zooplankton, and Mnemiopsis (2 individuals per tank). Concentration of nutrients, chlorophyll, and zooplankton abundances were measured over three weeks. Zooplankton showed significant decline in the Mnemiopsis treatment from 20.1/liter to 1.8/liter while densities in the zooplankton treatment were unchanged during the 20 day experiment. Effects on lower trophic levels were less clear. While there were no significant differences between treatments in chlorophyll concentrations, the algal treatment and Mnemiopsis treatment had almost double average chlorophyll concentrations of the zooplankton treatment. Nutrients also showed no significant differences, but some important trends. Dissolved inorganic nitrogen increased to up to 30 µM was on average 200% higher after the addition of zooplankton. Although there were only significant differences for the first level of a trophic cascade, Mnemiopsis affected the lower trophic levels and has potential to generate trophic cascades in the western Atlantic.

Key Words and Phrases

Mnemiopsis leidy, ctenophores, trophic cascades, jelly blooms, algal blooms

Introduction

Even though the concept of trophic cascades has been around since 1960, many of these interactions have not been understood (Hairston et al. 1960). With the current reshaping of the climate, understanding these ecosystem shifts spurred by a single species is an important direction of study. Species are changing in prevalence, either increasing or declining from anthropogenic disturbance. With this disturbance, species that were previously dominant and causes of top down trophic control might disappear. In the oceans, overfishing and shifting chemistry have removed dominant species in food webs. What will fill this trophic vacuum? One type of organism that could benefit are ctenophores. Eutrophication, reduction in competing fish stocks, and increased temperatures all favor the production of ctenophores (Purcell 2005). Other work has explored how declining population stocks of calcifying zooplankton might open up niches to be filled by noncalcified jellies (Richardson and Gibbons 2008). Work is still inconclusive on this replacement, but there is a trend of historically dominant ocean
species being depleted and then being replaced by jellies (Purcell 2005). Ctenophores and other jellies might become a stronger control in marine ecosystems of production. This is a concern because jellies are not the ideal organisms to fill empty niches. Jelly blooms can be a danger to swimmers. This decreases the value of ocean properties. They also compete with economically important fish species and maintain dominance of food webs by eating the larvae and eggs of competing predators (Purcell and Sturdevant 2001). This could be a threat to recovery of protected fisheries and lead to miscalculations of the maximum sustainable yield. Ecologically, jellies are considered a trophic dead end. The energy jellies consume from lower trophic levels is not transferred and upper level consumers such as marine mammals and sharks. These groups are already under threat from other anthropogenic pressures, so decreased food stocks could inhibit their recovery.

One important marine trophic interaction that might be impacted by jelly blooms is the grazing of herbivorous zooplankton. Aquatic herbivores are an important control on producers. Biomass stocks of phytoplankton are lower than herbivores in many aquatic systems because phytoplankton are consumed almost as quickly as they reproduce. As a result, most phytoplankton have a high production rate. Without a control on phytoplankton growth from an herbivore, this high production rate can lead to algal blooms. In Carpenter et al. 1987, removal of an herbivore showed this result. A fish that consumes larger herbivorous zooplankton was introduced into ponds that lacked such a predator. Compared to ponds that did not have this introduction, the chlorophyll in the water was much higher. This shows how removal of an herbivore can drastically increase phytoplankton biomass. Waquoit Bay, MA showed this depletion of zooplankton herbivores in September 2014. Non-gelatinous zooplankton biomass was 0.002 g/m² as compared to 3.53 g/m² observed in nearby West Falmouth Harbor. The difference between these harbors was a bloom of ctenophore, *Mnemiopsis leidyi*, a voracious zooplankton grazer. To test if jelly blooms can lead to herbivore removal and phytoplankton blooms, I used a microcosm experiment. This experiment intends to test if *Mnemiopsis* can lead to a trophic cascade in northwest Atlantic systems by overgrazing zooplankton.

**Methods**

The experiment was run from 11 November 2014 to 5 December 2014 at the Marine Biological Laboratory (MBL) in Woods Hole, MA.

**Microcosm Tanks**

Six tanks were placed inside a larger half cylinder container to reduce stress on organisms and to ensure more constant temperature. The conglomeration of six tanks was lit on a 16:8 light dark cycle. Microcosm tanks were eighty liters and filled with 10 cm of sediment from Waquoit Bay, MA and 67 liters of seawater filtered through 30 μm mesh from the MBL sea water system. Sediment was homogenized and added on 10 November 2014. Sediment was allowed to settle for three days. Sediment concentrations of phosphate, nitrate, and ammonia were collected for several days to estimate nutrient addition from the sediment (see measurement protocols). Tanks were
aerated with a bubbler to maintain currents and to facilitate ctenophore feeding. Phytoplankton inoculation containing *Chaetoceros neogracile*, *Isochrysis galbana*, *Tetraselmis chui*, and *Pavolva sp.* were added on 14 November 2014. Phytoplankton were cultured for three days before addition of zooplankton and *Mnemiopsis* on 17 November 2014.

**Treatments**

There were three treatments in duplicate. The first treatment contained only algae as a control. The second treatment was dosed with 1400 ± 500 zooplankton collected from a 330 μm tow around Woods Hole, MA. Species included mostly the copepod, *Acartra tonsa*. Small amounts of another copepod *Temora longicornis*, cladocerans, crab zoe and megalopa, and an amphipod were also observed. The third treatment was also dosed with 1400 ± 500 zooplankton and two *Mnemiopsis*. This is based off peak abundances of *Mnemiopsis* in Narragansett Bay Rhode Island (Kremer and Nixon 1976).

**Measurement Protocols**

Water samples were taken daily to analyze the concentration of phosphate, ammonium, and nitrate. Water column nutrient samples were filtered through a 25 mm GFF filter. Phosphate was analyzed using a modified version of the Murphy and Riley 1962 method. The 3 mL of sample was mixed with 0.3 mL Murphy and Riley reagent. This was incubated for 30 minutes in the dark and then measured in a spectrophotometer at the 885 nm wavelength. The absorbance was compared to a standard curve to calculate concentration. Ammonium was analyzed by using methods of Solaranzo 1969. 3 mL of sample was reacted with Solaranzo’s phenol solution, sodium nitroprusside solution, and oxidizing solution. Sample will incubate for an hour in the dark. Concentration was determined using a standard curve. Nitrate was analyzed using a Lachat Flow Injection Analyzer.

Chlorophyll a was measured by filtering 400-1000 mL of the water column into a 47 mm GFF filter. The filter was washed in 35 mL 90% acetone and the solution was sonicated. The product was placed on ice and allowed to extract overnight. Analysis was performed on a modified method based on Lorenzen 1969. Absorbance at the 750 nm and 665 nm wavelength was measured in a spectrophotometer. The sample will be acidified and measured again at these wavelengths. Chlorophyll concentration will be calculated using the equation

$$ Chl \ a \ (\mu g \ l^{-1}) = \frac{26.7 \times [(665_o - 750_o) - (665_a - 750_a)] \times V \times L}{V} $$

Where V is the volume filtered, v is the volume of acetone and 665/750o is the original absorbance and 665/750a is the acidified absorbance. Zooplankton were collected by a 330 μm mesh tow in Great Harbor outside of Woods Hole, MA. The zooplankton were concentrated into buckets and samples fixed by Lugol’s iodine. These were counted to estimate the amount of zooplankton collected and species were identified. At the termination of the experiment, the water was siphoned through a 63 μm filter. Zooplankton were diluted and counted to get an estimate of the final concentration.
Results

Zooplankton counts decreased significantly from the initial to final counts in the *Mnemiopsis* treatment from 20.1 individuals/L to 1.8 individuals/L (Figure 1). Zooplankton treatment did not have any significant changes of zooplankton (Figure 1). Attempts to count while the experiment was running did not find a representative sample of the tanks, so all statistical testing was done on initial and final counts.

Chlorophyll showed no significant difference between treatments (ANOVA F=0.72, P=0.49 Figure 2). However, there was a trend showing highest concentration in the phytoplankton treatment and *Mnemiopsis* treatment. Average chlorophyll a concentration in zooplankton treatments was half the concentration of the other treatments (Figure 2). The largest amount of chlorophyll were observed in the A replicate of the phytoplankton treatment (Figure 3). The B replicate of the phytoplankton treatment had very low chlorophyll (Figure 3). Zooplankton treatment chlorophyll responded to the addition of zooplankton with several peaks before leveling out near zero (Figure 4). The *Mnemiopsis* treatment showed similar peaks, but replicate F had larger increases in chlorophyll than the zooplankton treatment (Figures 4 and 5).

Nutrients also showed no significant difference between treatments. Dissolved inorganic nitrogen (DIN) did not have statistical differences between treatment (ANOVA F=0.25, P=0.78, Figure 6). The averages were very similar. However, treatments showed differences over time. Phytoplankton replicates had very little DIN variation with time (Figure 7). In the treatments with animals added in, there was variation with time. The zooplankton treatment showed an immediate spike of DIN from 10 μM to 30 μM after the addition of zooplankton (Figure 8). The *Mnemiopsis* treatment showed the same spike when the zooplankton and *Mnemiopsis* were added, but the DIN decreased after a few days. Average phosphate concentrations were lowest in the phytoplankton treatments (0.76 ± 0.94 μM). The zooplankton treatment had an average phosphate concentration of (0.97 ± 1.12 μM) and the *Mnemiopsis* treatment had an average of (1.40 ± μM). The time series showed no differences between treatments.

Discussion

*Mnemiopsis leidyi* shows potential for trophic cascades. The strongest evidence was the complete depletion of zooplankton in treatments that contained *Mnemiopsis*. This depletion was the same as observed in Waquoit Bay, with the presence of *Mnemiopsis*. Another microcosm experiment with *Mnemiopsis* found the same affect on zooplankton as well. This microcosm was conducted in a low nutrient environment by Dinasquet et al. 2012. They found that trophic cascading effects were most obvious in zooplankton and larger phytoplankton such as dinoflagellates. This is consistent with this experiment, because statistically significant changes were only observed in the upper levels. However, there was a notable difference in the zooplankton species they used. Their study had a cladoceran dominating the zooplankton, whereas this one was dominated by a copepod, *Arcatia tonsa*. Since *Arcatia* has strong selective grazing on phytoplankton it seems there would be more evidence of a trophic cascade than the Baltic study. In addition to strong effects on the zooplankton level, stronger impacts on phytoplankton might be expected. However, unlike the Baltic study, lower trophic levels lacked statistical differences between treatments. Only trends were observed:
Chlorophyll was almost double in the treatments that lacked zooplankton, dissolved inorganic nitrogen showed an increase to zooplankton presence and a decline after *Mnemiopsis* grazed them. Since the trophic cascading should be stronger with the copepod than the cladoceran it further supports that these trends are representative.

Another interesting similarity between the Baltic study was the effect of juvenile *Mnemiopsis*. Replicate F of the *Mnemiopsis* treatment generated juveniles. This replicate also had the highest chlorophyll concentration of its treatment group. In the Baltic study, there was a treatment that included juveniles. Like replicate F, this had the largest algal blooms and strongest trophic responses. Therefore it could be important to understand *Mnemiopsis* reproduction to assess the potential of trophic cascades.

The lack of statistical significance could be due to several design problems. First, there were only two replicates in each treatment. If there was a problem with a replicate it was impossible to do statistical testing on the entire treatment. For example, in the phytoplankton treatment, one replicate had extremely low chlorophyll. This contrasted strongly with the other replicate that had immediate and strong phytoplankton blooms. That made statistical testing between all treatments difficult. In addition, there was variable light reaching different tanks. Some tanks had as much as 600 μE and others had only 300 μE. This could be fixed with several light banks or measurement of the light above tanks and adjustment before the beginning of the experiment. Additionally, to ensure differences were not due to variation in nutrients, it would be interesting to do a nutrient addition experiment.

Since chlorophyll and nutrients responded to *Mnemiopsis*, it would be worthwhile to conduct an expanded experiment that addressed these concerns. Understanding this interaction could be vital to the already stressed systems of the western Atlantic. As eutrophication, overfishing, and rising temperatures continue, jelly trophic cascades become a more urgent field of study. *Mnemiopsis* has the potential to spur drastic short term effects on ecosystems and should be examined further.

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**Literature Cited**


**Figures**

Figure 1. Initial and final abundance of zooplankton in *Mnemiopsis* and zooplankton treatments.

Figure 2. Average chlorophyll concentration of treatments.

Figure 3. Chlorophyll a concentration in the phytoplankton treatment

Figure 4. Chlorophyll a concentration in the zooplankton treatment

Figure 5. Chlorophyll a concentration in the *Mnemiopsis* treatment

Figure 6: Average dissolved inorganic nitrogen in treatments.

Figure 7. Dissolved inorganic nitrogen of replicates in the phytoplankton treatment

Figure 8. Dissolved inorganic nitrogen of replicates in the zooplankton treatment

Figure 9. Dissolved inorganic nitrogen of replicates in the *Mnemiopsis* treatment
Figure 1: Average abundance of zooplankton when added to the tanks (6 days), and at the conclusion of the experiment (21 days).
Figure 2: Average chlorophyll a concentration on both replicates in each treatment. Error bars are standard error.

Figure 3: Chlorophyll a concentration in treatments containing only phytoplankton.

Figure 4: Chlorophyll a concentration in treatments containing zooplankton. Circle shows addition of zooplankton.
Figure 5: Chlorophyll a concentration in treatments containing zooplankton and *Mnemiopsis*. Circle shows addition of zooplankton and *Mnemiopsis*.

Figure 6: Average dissolved inorganic nitrogen (DIN) calculated from the measured ammonium and nitrate. Error bars are standard error.
Figure 7: Dissolved inorganic nitrogen of replicates in the phytoplankton treatment.

Figure 8: Dissolved inorganic nitrogen of replicates in the zooplankton treatment. Circle shows addition of zooplankton.
Figure 9: Dissolved inorganic nitrogen of replicates in the *Mnemiopsis* treatment. Circle shows addition of zooplankton and *Mnemiopsis*. 