Stony Brook University

Impacts of the Lobate Ctenophore *Mnemiopsis leidyi* on Zooplankton

Community Dynamics in the Long Island Sound, NY

A Thesis Presented

by

David Michael Rawitz

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Master of Science

in

Marine and Atmospheric Sciences

Stony Brook University

December 2014

Stony Brook University

The Graduate School

David Michael Rawitz

We, the thesis committee for the above candidate for the

Master of Science degree, hereby recommend

acceptance of this thesis.

Darcy J. Lonsdale – Thesis Advisor
Professor, School of Marine and Atmospheric Sciences

Christopher J. Gobler – Second Reader
Professor, School of Marine and Atmospheric Sciences

Jackie L. Collier – Third Reader
Professor, School of Marine and Atmospheric Sciences

Abstract of the Thesis

Impacts of the Lobate Ctenophore *Mnemiopsis leidyi* on Zooplankton

Community Dynamics in the Long Island Sound, NY

by

David Michael Rawitz

Master of Science

in

Marine and Atmospheric Sciences

Stony Brook University

2014

The impact of the lobate ctenophore, *Mnemiopsis leidyi,* on zooplankton community structure has been noted on a variety of ecosystems. This impact arises primarily through high predation rates on copepods. Eutrophication appears to enhance *M. leidyi* abundance through bottom-up effects. This study investigated the effects of an eutrophication gradient (west to east) on *M. leidyi* abundance, and the effects of *M. leidyi* predation on zooplankton populations in the Long Island Sound (LIS). Bi-weekly samples of zooplankton, microplankton, and *M. leidyi* were obtained from three distinct sites in the Central, Middle, and Western LIS across the eutrophication gradient in 2011 and 2012. An ANOVA was used to compare the *M. leidyi* abundances and biovolumes at the three sampling sites. Cross-correlation analysis was used to compare abundances of organisms at different trophic levels. *M. leidyi* consumption rates were

also compared to copepod daily growth rates. Abundances of *M.* leidyi were greater in 2011 than in 2012. The data did not reveal any significantly greater *M. leidyi* abundance or biovolume in the western LIS than in the eastern LIS. The study also indicated that *M. leidyi* predation did not significantly reduce the copepod population nor bring about an increase of microplankton as would be expected in a top-down trophic cascade.

Table of Contents

List of Figures

List of Tables

Acknowledgments

I would like to express my deepest appreciation to my committee members, Dr. Darcy Lonsdale, Dr. Chris Gobler and Dr. Jackie Collier for their guidance, wisdom, ongoing support and infinite patience.

Special thanks to Dr. Robert Cerrato for his assistance with statistical design and analysis; Lee Holt for his technical assistance in the laboratory and on the boat; and Laura Treible for her instructions and practical training. I would like to thank the boat captains who were always helpful and courteous without whom I could not collect the samples for this study.

I would also like to thank the New York/Connecticut Sea Grant Program for providing funding for this project.

Finally, I would like to thank Ilya Kopysitsky for his statistics expertise and unwavering support.

INTRODUCTION

The lobate ctenophore, *Mnemiopsis leidyi* (Agassiz, 1865) (also once referred to as *Mnemiopsis maccradyi* in the southeast Atlantic coast), has expanded well beyond its natural habitat of North and South American coastlines to estuarine and coastal areas all around the world (Condon et al. 2011). In the past decade alone, *M. leidyi* has been found in the North and Baltic Seas, the Adriatic and Caspian Seas, the coastlines of Belgium and the Netherlands, the French Coast, and the Danish Limfjorden (Purcell 2009, Colin et al. 2010, Antajan et al. 2014, Riisgard et al. 2012). The dramatic expansion has been attributed to several factors including eutrophication, climate change and overfishing (Mills 2001, Purcell 2007, Condon 2008).

One area where *M. leidyi* had a strong impact on plankton communities is the Black Sea, where it caused a substantial decline in zooplankton and increased phytoplankton blooms (Purcell et al. 2001). First found in Sudak Bay in 1982, *M. leidyi* reached peak levels throughout the entire basin in 1988 (Vinogradov, 1989 as cited by Shiganova 1998). During this peak, which lasted to 1992, *M. leidyi* consumed 30% to 40% of the zooplankton per day (Finenko et al. 2006, Finenko 2009), and reached abundances as high as 304 individuals m^{-3} (Purcell et al. 2001). From 1990 to 1992, *M. leidyi* caused zooplankton and fish eggs to decline so dramatically that some species almost disappeared (Shiganova 1998). A second peak in *M. leidyi* abundance in 1994-1995 reduced herbivorous zooplankton, resulting in phytoplankton blooms primarily in coastal waters (Finenko 2009). Furthermore, the effect of eutrophication was seen here in that the increased *M. leidyi* abundance induced a particularly sharp decline in zooplankton abundance in the northern portion of the sea where anthropogenic input is highest (Shiganova 1998).

In the US, *M. leidyi* has been studied extensively because of the significant mortality it can exert on zooplankton and ichthyoplankton populations in estuaries and coastal areas (Kremer 1994, Mills 1995, Purcell et al. 1994, 2001b, McNamara et al. 2010). Like many gelatinous zooplankton, *M. leidyi* biomass follows annual cycles of blooms dependent on seawater temperature, and earlier seasonal blooms have been associated with increasing seawater temperatures (Sullivan et al. 2001, Condon and Steinberg 2008). In the Northeast US, blooms occur in summer and early fall when seawater temperatures exceed 19 ^{o}C; between 24 and 28 ^{o}C, reproduction spikes at which time *M. leidyi* can produce thousands of eggs per day (Kremer 1994, Purcell and Arai 2001).

Mnemiopsis leidyi reaches adult stage at lengths greater than 0.5 cm (McNamara et al. 2013). An adult uses its cilia to generate continuous water currents to ingest zooplankton which adhere to the sticky inner surfaces of the ctenophore's oral lobes (Colin et al. 2010, Waggett and Costello 1999). Because these water currents are almost undetectable by zooplankton prey, *M. leidyi* is a particularly effective predator on a wide variety of organisms, but crustacean zooplankton predominate the adult *M. leidyi* diet (Colin et al. 2010). The prey-capture efficiency of *M. leidyi* on *Acartia tonsa* adults, for example, has been measured at 74%, and 94% on *Acartia* nauplii (Waggett and Costello 1999). The diet of larval *M. leidyi* (individuals < 0.5 cm) differs from that of the adults due to different morphologies; i.e., tentaculate larvae versus lobate adults, and microplankton dominate the larval diet (Rapoza et al. 2005, Waggett and Sullivan 2006, Sullivan, 2010). *M. leidyi* larvae will consume diatoms, flagellates, autotrophic and heterotrophic dinoflagellates, naked and tintinnid ciliates, and rotifers (Stoecker et al. 1987, Sullivan and Gifford, 2007), and larvae have been found to consume copepodite

and nauplii stages (Sullivan 2010). Larval ctenophore consumption of adult copepods is difficult because metazoan prey can escape from, damage, and even kill the larvae (Reeve et al. 1978, Waggett and Sullivan 2006).

Mnemiopsis leidyi consumption patterns have been measured in various estuarine systems. McNamara et al. (2013) reported that adult ctenophores consumed between 20% and 89% per day of copepods, bivalve veligers and tintinnids in the Great South Bay and Peconic Bay estuaries where *M. leidyi* larval abundance corresponded with lows (and complete absence of some species) of dinoflagellates and ciliates. In Chesapeake Bay, *M. leidyi* was capable of clearing up to 100% d^{-1} of fish eggs (Purcell et al. 2001) and adult ctenophores consumed 59% of copepod nauplii, 38% of copepods (i.e., copepodites and adults), and 1.6% of bivalve veligers in the water column per day (Purcell and Arai 2001). In Narragansett Bay, high abundances of *M. leidyi* larvae (100 m^{-3}) could potentially clear up to 60% of the water column of nanoplankton and microplankton on a daily basis (Deason 1982).

The heavy predation that *M. leidyi* exerts on zooplankton is capable of altering planktonic community structure primarily through its consumption of copepods (Sullivan and Gifford 2004, Purcell and Decker 2005, Colin et al. 2010, McNamara et al. 2013). *M. leidyi* predation has been examined in multiple studies demonstrating an inverse correlation between *M. leidyi* abundance and zooplankton abundance over time (Purcell 1988). In the York River, bivalve larval biomass was inversely proportional to *M. leidyi* biomass (Burrell and Van Engel 1976) and in Narragansett Bay an inverse correlation was observed between *M. leidyi* abundance and average zooplankton biomass (Deason and Smayda 1982). When *M. leidyi* are abundant, their predation on copepods reduces the predation pressure that copepods place on microplankton (McNamara et al. 2013). In this way, high abundances of *M. leidyi* can initiate a top-down trophic cascade

whereby the reduced copepod predation allows the abundance of microplankton to increase (Sullivan and Gifford 2004, Purcell and Decker 2005, McNamara et al. 2010). Most recently, temporal abundance of adult *M. leidyi* was positively correlated with microplankton temporal abundance in Great South Bay (McNamara et al. 2013).

Mnemiopsis leidyi is the predominant gelatinous zooplankton predator in Long Island Sound (LIS), one of the largest estuaries in the US covering 1320 square miles with an average water depth of 25m (Capriulo et al. 2002). Eutrophication affects microplankton and phytoplankton growth and community structure in LIS (Murdoch et al. 1998 as cited by Capriulo et al. 2002). Nutrients and sediment enter from rivers and coastlines all along LIS, though the major source of nutrient input is New York City sewage (Bowman 1977). Cervetto (1999) estimated 65% of nitrogen runoff into LIS originates in Queens and the Bronx, making dissolved nutrients such as dissolved inorganic nitrogen (DIN) higher in the western portion of LIS (Bowman 1977). Chlorophyll *a*, microplankton, nanoplankton and dissolved nutrients showed higher concentrations in the western part of LIS relative to the eastern portion (Goebel 2006). In 2011 and 2012, there was a gradient of concentrations declining from west to east in LIS of dissolved nutrients (nitrate, nitrite, orthophosphate, total dissolved nitrogen and total dissolved phosphate) and chlorophyll a (CT DEEP). Because nutrient loads, particularly nitrogen input, are higher in western LIS, both primary and secondary production (in particular, copepod biomass), are higher here than further east in the LIS as well (Capriulo et al. 2002). Because of this increased production, Capriulo et al. (2002) predicted that ctenophores were likely to reach greater abundances in the west than in the east of LIS.

To date, no study has examined the impact of *M. leidyi* on the copepod community in LIS nor the impact of the eutrophication gradient on *M. leidyi*. The current investigation was

undertaken to explore these questions during 2011 and 2012. *M. leidyi* and copepod and microplankton samples were taken bi-weekly from three LIS sites to estimate the *M. leidyi* community consumption rate on copepods using a predictive equation (Purcell 2009). The easternmost site is referred to as central Long Island Sound (CLIS), while the westernmost site is designated western Long Island Sound (WLIS). A third site, approximately mid-way between these two, is labeled as MLIS. The CLIS and WLIS sampling sites are approximately 56 km (0.51 degrees longitude) apart.

The hypothesis was that *M. leidyi* will have a significant impact on the LIS zooplankton community through predation, defined as *M. leidyi* consuming copepods at a greater daily rate than copepod community daily growth rate. Hence, an inverse correlation between abundance of *M. leidyi* and copepods was expected. Also expected was a positive correlation between the abundance of *M. leidyi* and the abundance of microplankton, as evidence of a trophic cascade. Lastly, a second hypothesis predicted that higher eutrophication in the WLIS will result in higher microplankton, copepod, and *M. leidyi* abundances than in the CLIS.

METHODS

Sampling

Sampling was performed at three sites in Long Island Sound: Western Long Island Sound (WLIS; 40˚52.320N, 73˚44.040W), Central Long Island Sound (CLIS; 41˚3.572 N, 73˚8.674 W), and a site in between, referred to as the Middle Long Island Sound (MLIS; 40˚59.085N, 73˚27.038W) site. Bi-weekly sampling was conducted from May to October of 2011 (n=14) and 2012 (n=13). There was one exception to sampling in 2011 and three exceptions to sampling in 2012 when data was not collected at all three sites due to poor weather.

Plankton collection

      Abundances of *M. leidyi* and copepods were measured using samples collected from short (2-4 minutes) oblique net tows, using three mesh nets. Copepod samples were collected from a 64-µm mesh net (0.5-m diameter opening), and gelatinous zooplankton samples were collected with a 202-µm mesh net (0.5-m diameter opening) and a 1000-µm mesh net (1.0-m diameter opening). Flow meters on each net allowed for an estimate of the total volume (m^3) of seawater sampled (Smith et al. 1968). Attached to the end of each net was a flexible cod end that collected the organisms caught. Net tows were performed twice for each net at each site. The process of each net tow was as follows: The net was released and retracted gradually for the duration of the tow so that the water column from surface to maximum sampling depth (about 15m) was evenly sampled. Immediately after each tow, the cod end was emptied onto a 64-µ sieve and rinsed with 20µm-filtered seawater (ICES, 2000) then placed into containers with buffered formalin (f/2, final concentration 5%) for preservation.

      Ctenophores were immediately sorted by size on the boat (larvae < 0.5 cm and adults > 0.5 cm), and numbers in each size class counted. Adults were also sorted into three size classes (0.5-3.0cm, 3.0-5.0cm, 5.0-7.0cm) to investigate the size structure of the population. *M. leidyi* was the only gelatinous species observed in net tows. Total live biovolume per cubic meter (mL m^{-3}) of *M. leidyi* from each tow was subsequently measured by placing the gelatinous zooplankton into a graduated cylinder.

      Mesoplankton samples were later enumerated by Lee Holt with an Olympus SZX12 dissecting microscope to the lowest possible taxonomic level. In order to measure microplankton abundance, seawater samples (100 mL) were also collected using a Niskin bottle from 1m depth (labeled as sub-surface) and from 6m depth and stored in amber glass jars with

acidic Lugol's (5% final concentration) and transported in a dark environment to the laboratory. Standard settling techniques and inverted light microscopy (Hasle 1978 as cited by Hamer et al. 2011) were used by Lee Holt to count the microplankton. The measure of microplankton abundance used in this study is the sum of the total number of ciliates, flagellates, diatoms, and dinoflagellates per m^3 at each site on each sampling date.

Select adult *M. leidyi* were gently collected bi-weekly at the three sampling sites from the surface with dip nets (Raskoff et al. 2003) for gut contents analysis and for wet-weight measurements. Adult *M. leidyi* specimens of three sizes (0.5-3.0cm, 3.0-5.0cm, 5.0-7.0cm) were then preserved separately from each other in buffered 5% formalin where the soft bodies of *M. leidyi* dissolved, but the gut-contents did not. The remaining specimens were placed in jars containing seawater to be weighed in the laboratory in order to estimate their consumption rate based on their wet weight.

Estimation of copepod consumption rates and comparison to copepod growth rates

The *M. leidyi* samples collected from the surface water were used for estimation of consumption rates from clearance rate (CR) in liters of water cleared per ctenophore per day using wet weight (WW) of *M. leidyi* in grams. Purcell (2009) provided the following relationship based on regression analysis of clearance rate vs. wet weight performed on adult *M. leidyi* data:

$$Log_{10}CR = 0.766*Log_{10}WW + 0.423$$

Due to the fact that *M. leidyi* larvae have a different feeding morphology than adults, this equation does not apply to *M. leidyi* larvae (Purcell 2009). This equation relates the wet weight of each adult *M. leidyi* to the clearance rate of single organism of that size. In this equation wet weight (WW) is measured in grams and clearance rate (CR) is L individual^{-1} day^{-1} (liters per

individual per day). After the clearance rate was computed, the consumption rate for each *M. leidyi* was calculated. The consumption rate (copepods consumed per cubic meter per day) was computed in several steps. First, the units for clearance rate were converted from liters to m^3 by dividing the CR computed in the equation above by 1000. After this conversion, the units for CR were m^3 per indivdual^{-1} day^{-1}. Second, this new clearance rate was multiplied by number of ambient copepods per meter cubed in order to calculate the number of copepods consumed by each adult *M. leidyi* per day. The units for this consumption rate were copepods individual *M. leidyi*$^{-1}$ day^{-1}. Finally, the number of copepods consumed by *M. leidyi* per m^3 was computed by multiplying the consumption for each individual *M. leidyi*, computed in the previous step, by the number of *M. leidyi* adults per m^3 (abundance).

Growth rates for copepods were estimated using daily percent *Acartia tonsa* growth rates taken at temperatures corresponding ambient temperatures measured during sampling from Huntley and Lopez (1992). Huntley and Lopez (1992) showed that temperature explains 90% of the variation in daily copepod growth rates and compiled results from 181 studies where ambient temperature was linked to daily percent copepod growth rate.

Gut contents analysis

The gut contents from the *M. leidyi* that were preserved in Formalin solution were counted by Lee Holt. Because *M. leidyi* of different sizes were preserved separately (0.5-3.0cm, 3.0-5.0cm, 5.0-7.0cm), it was possible to enumerate prey for each *M. leidyi* size class. For each *M. leidyi* size class, proportions of each copepod type found in the *M. leidyi* gut with respect to the total number of copepods found in the *M. leidyi* gut were determined. Then, percentages of each copepod type for each *M. leidyi* size class were compared to the proportions of copepods in the ambient environment and the electivity indexes proposed by Ivlev (1955).

Determination of eutrophication effects and the relationships between abundance of M. leidyi, copepods, and microplankton

Copepod and microplankton abundances were compared to *M. leidyi* abundance and biovolume in order to detect direct and indirect trophic impacts. In order to test for effects of eutrophication, abundances for the years 2011 and 2012 were analyzed with a two-way ANOVA performed using SPSS. Post-hoc tests were performed in order to compare abundance of organisms at WLIS to that at the CLIS and MLIS sites. Pearson correlations with lag between abundance of microplankton, copepods, and *M. leidyi* were computed to analyze the relationships between abundances of organisms. Analysis was also performed to understand the relationship of *M. leidyi* biovolume with copepod and microplankton abundances.

RESULTS

M. leidyi abundance

There was a dramatic interannual difference in abundance of all of planktonic groups investigated in this study (Figures 2 and 3). *M. leidyi* abundance was greater in 2011 than in 2012 (see Table 2). In 2011, *M. leidyi* was abundant from mid-June through August and abundance peaked twice, after which the population declined. Abundance was highest at the MLIS site: the first peak of 14.6 adult ctenophores m^{-3} occurred on June 21, the second peak was 17.9 ctenophores m^{-3} on August 3. Peak larval abundance of *M. leidyi* was 36.7 ctenophores m^{-3} on July 6 at the MLIS site. The highest biovolume of *M. leidyi* adults and larvae of 71.2 mL m^{-3} was recorded on August 3 at the WLIS site (Figure 2). Adult *M. leidyi* abundance varied by site and date and the effects of the two variables were non-additive (*df* =18,86; F=40.430; p=0.047; two-way ANOVA with site and date as fixed variables). Post-hoc tests revealed significantly lower adult *M. leidyi* abundance in WLIS relative to the other sites on July 6 (*df* =1,86; F=18.103; p<0.001; contrast comparing abundance at the WLIS site and the CLIS and MLIS

sites). Differences in larval abundance of *M. leidyi* were also analyzed. Larval abundance varied by site and date (*df = 10,96;* F=3.346; p=0.001 and *df*=2,96; F=6.555, p=0.002; two-way ANOVA with site and date as fixed variables). Post-hoc tests revealed significantly lower larval abundance at the WLIS site relative to the other sites on July 6 (*df = 1,96;* F=19.936; p<0.001; contrast comparing abundance at the WLIS site and the CLIS and MLIS sites).

Overall in 2012 there were markedly fewer ctenophores, copepods and microplankton than in 2011. *M. leidyi* was most abundant from early July to late October. The highest abundance of *M. leidyi* adults (3.5 ctenophores m^{-3}) was recorded on August 29 in CLIS. Peak larval abundance occurred on July 3 at all three sites followed by a dramatic decline by the next sampling date. The highest peak of larval abundance was 165.3 ctenophores m^{-3} at the CLIS site, which contradicts the overall lower measurements. The highest biovolume of total *M. leidyi* adults and larvae of 9.8 mL m^{-3} was recorded on October 18 at the CLIS site. Total adult *M. leidyi* abundance varied by site and date and the effects of the two variables were non-additive (*df* =20,55; F=3.246; p=0.001; two-way ANOVA with site and date as fixed variables). There was a significantly lower abundance of *M. leidyi* at WLIS than at the other sites on October 18. (*df* =1,86; F=18.103; p<0.001; contrast comparing abundance at the WLIS site and the CLIS and MLIS sites). Analysis of larval *M. leidyi* abundance was also performed. Larval abundance varied by site and date and the effects of the two variables were non-additive (*df*=18,30; F=2.212; p<0.026.; two-way ANOVA with site and date as fixed variables). The data showed significantly fewer larvae at the WLIS site than at other sites on July 3 (*df = 1,30;* F=10.747; p=0.003; contrast comparing abundance at the WLIS site and the CLIS and MLIS sites).

Copepods

At all three sampling sites, copepod nauplii comprised between 60% and 80% of copepod abundance in both 2011 and 2012. The mean abundance of total copepods (adults plus nauplii) in 2011 ranged from 4.5 individuals L^{-1} to 207.4 individuals per L^{-1}. At the MLIS and WLIS sites, the highest copepod abundance occurred on September 13 (582.6 individuals L^{-1} and 525.9 individuals L^{-1}, respectively); at the CLIS site, it occurred on the last sampling date, October 11 (849.3 individuals L^{-1}). The predominant genera of copepod at all three sites were *Acartia* and *Oithona*.

In 2012, total mean copepod abundance ranged from 19.4 individuals L^{-1} to 1358.5 individuals per L^{-1}. At the WLIS site, two peaks occurred with abundances of 278.9 individuals L^{-1} on May 3 and 306.7 individuals L^{-1} on August 29. At the MLIS site, three peak abundances of 338.5 individuals L^{-1} on May 23, 268.0 individuals L^{-1} on July 31, and 311.1 individuals L^{-1} on August 29 occurred. Finally, at the CLIS site, two peak abundances of 207.7 individuals L^{-1} on May 23 and 184.2 individuals L^{-1} on August 14 were found.

Microplankton

However, microplankton abundance was higher in 2011 than in 2012 at the WLIS and MLIS sites, and higher in 2012 than in 2011 at the CLIS site (see Table 2). In 2011, microplankton was abundant throughout the sampling period at all three sites. The highest abundances of microplankton were observed on June 21 at WLIS (18,418 cells mL^{-1}), on September 13 at MLIS (13,223 mL^{-1}), and on September 13 at CLIS (11,573 mL^{-1}). In 2012, peak microplankton abundance was lower than in the previous year. Peak abundances were observed on June 19 at MLIS (7563.7 cells mL^{-1}), on June 19 at CLIS (5278.4 mL^{-1}), and on June 19 at WLIS (2022.1 mL^{-1}).

Trophic interactions

The effect of *M. leidyi* on copepod abundance was analyzed using estimates of consumption rates derived from wet weight analysis. Wet-weights and gut-contents data were analyzed only for 2011 because the numbers of adult *M. leidyi* in 2012 were so low that none were seen at the surface for collection with dip nets. Copepod population growth rates (estimated using methods described in Huntley and Lopez 1992) far exceeded consumption of copepods by *M. leidyi* (Table 1), indicating no significant impact of *M. leidyi* grazing on copepod abundance.

Cross correlation analysis was conducted to detect relationships between *M. leidyi* abundance and copepod abundance, and relationships between *M. leidyi* abundance and microplankton abundance. Analysis was also performed to compare *M. leidyi* biovolume with copepod and microplankton abundances. In 2011, at the WLIS site, there was a statistically significant inverse correlation between copepod abundance and microplankton abundance measured two weeks after the copepod abundance measurement was taken (correlation coefficient r=-.609, p<.05). At the CLIS site, there was a statistically significant positive correlation between microplankton abundance and copepod abundance measured four weeks after the copepod abundance measurement was taken (correlation coefficient r=.536, p<.05). In 2012, there was a statistically significant positive relationship between *M. leidyi* biovolume and the abundance of copepod nauplii measured four weeks after the biovolume measurement was taken at the CLIS site (correlation coefficient r=.798, p<.05). In 2012, a peak abundance of copepod nauplii followed a peak in the *M. leidyi* biovolume at all three sites (see Figure 3). Another statistically significant relationship observed in 2012 at the WLIS site was a positive

correlation between copepod abundance and *M. leidyi* biovolume taken two weeks later (correlation coefficient r=.588, p<.05).

Gut contents analysis

To determine if there was any relationship between size class and prey type, gut contents for each *M. leidyi* size class were enumerated. For each size class, the percentage of each prey type found in the *M. leidyi* gut and subsequently the electivity indexes were computed (Table 3). Prey electivity was different for *M. leidyi* of varying sizes. This was demonstrated in several ways. Larger (3cm to 5cm and 5cm to 7cm categories) *M. leidyi* preferred *Acartia* adults first and *Parvocalanus crassirostris* second as prey in both the CLIS and WLIS. In the WLIS, smaller *M. leidyi* (0.5cm-3cm) displayed a preference for *Oithiona* as prey. In the CLIS, smaller *M. leidyi* (0.5cm-3cm) displayed a preference for copepod nauplii as prey.

DISCUSSION

Eutrophication and bottom-up control of ctenophore abundance

It has been suggested that over the past three decades, anthropogenic eutrophication may be associated with the proliferation of gelatinous zooplankton (Shiganova 1998, Riisgard et al. 2012, Dinasquet et al. 2012, Purcell et al. 2001b, 2007, Mills 2001, Parsons and Lalli, 2002). Elevated levels of nitrogen and phosphorous can influence phytoplankton communities from diatoms to flagellates and other autotrophs, leading to an increase in the abundance of copepods which in turn fosters the growth of *M. leidyi* and other gelatinous species (Daskalov et al. 2002, Purcell et al. 2007).

A postulate of the current study was that eutrophication in Long Island Sound, one of the most urbanized estuaries in the world, impacts planktonic communities, including the ctenophore *Mnemiopsis leidyi*. The peak mean biovolumes recorded in this study were comparable to measurements taken in other urban estuaries. Measurements were lower, however, than those taken in the Long Island estuaries Peconic Bay and Great South Bay in 2006 (McNamara, 2010), but slightly higher than those taken in the Chesapeake Bay in 1995, 1996, and 1998 (Purcell et al. 2001a). Yet, the original hypothesis that ctenophore abundance would be greatest in the western part of the LIS (as also posed by Capriulo et al. 2002) and would decrease gradually towards the eastern portion was not upheld. Several factors could play a role in this unexpected observation. It is important to consider other differences between the three sampling sites. Ctenophore biomass is typically greater in stratified rather than unstratified waters due to the fact that turbulence may interfere with adult *M. leidyi* feeding currents (Mianzan et al. 2010, Purcell et al. 2001b). Models of the LIS water column predict greater stability at the easternmost site, CLIS, relative to WLIS (Bowman 1977). The water column is impacted by wind and turbulence,

which can influence *M. leidyi* distribution. Ctenophores have been observed to retreat from surface waters during wave turbulence and high winds (Miller 1974). Furthermore, *Mnemiopsis* is sensitive to increases of only 3-5 decibars of pressure and will "sound" or move away from areas of such water turbulence (Graham 2001). Although oblique tows were used in this study, the depth of the LIS did not permit the entire water column to be sampled. This finding does lend credence to the assertion by Condon (2012) that anthropogenic input does not impact gelatinous zooplankton abundance.

Top-Down Trophic Effects of *M. leidyi*

During seasonal blooms, *M. leidyi* can dominate zooplankton biomass and exert strong predation pressure on mesoplankton and microplankton communities (Deason and Smayda 1982, Graneli and Turner 2002, Sullivan and Gifford 2004, Purcell and Decker 2005). Recent studies have also suggested a top-down cascade whereby *M. leidyi* grazing pressure upon copepods allows microplankton to proliferate in response to reduced copepod predation (Dinasquet et al. 2012, McNamara et al. 2010, 2013). More specifically, studies in the LIS area have concluded that *M. leidyi* does exert top-down influences on the planktonic food web. McNamara et al. (2013) reported two trophic responses to *M. leidyi* as: high adult ctenophore to low mesoplankton with enhanced microplankton abundance; and high larval ctenophore to low microplankton with increased nanoplankton abundance.

The results of the current study do not support the hypothesis that *M. leidyi* grazing reduces copepod abundance, which in turn increases microplankton abundance in LIS. In both 2011 and 2012, no statistically significant correlation between *M. leidyi* abundance and adult copepod abundance was detected with up to a 4 week lag. Furthermore, consumption rates as estimated by wet weight analysis in 2011 revealed that growth rates for the copepod population

greatly exceeded grazing rates by *M. leidyi.* There was no evidence of a relationship between *M. leidyi* abundance and microplankton abundance at any of the sampling sites in either 2011 or 2012. Nor was there any evidence of a relationship between *M. leidyi* biovolume and microplankton abundance at any of the sites in either sampling year indicating the absence of a top-down cascade.

Water depth may be a factor accounting for the contradictory results between LIS and Great South Bay (McNamara et al. 2010, 2013). In Great South Bay, depths average less than 2m, and maximum depths reach roughly 6m. In the LIS, the average water depth is 25m, and the depths at the three sampling sites in this study ranged from 30m to 40m (CT DEEP). The use of oblique net tows that sample only the top 15m of the water column prevented the complete vertical range of ctenophore density from being sampled. In deeper bodies of water, ctenophores may be concentrated near the surface or at the bottom (Riisgard et al. 2012, Costello and Mianzan, 2003) and net sampling may be inadequate if organisms are sparse and unevenly distributed (Purcell 2009, Purcell and Decker 2005).

Other possible explanations for the data demonstrating no top-down effects of *M. leidyi* abundance on copepod abundance include predation on *M. leidyi* by other species and competing predation on copepods by other predators in the LIS. The LIS contains predators of *M. leidyi* that would not have been detected by the sampling methods used in this study, such as dogfish and sea turtles (*Caretta caretta*) (CT DEEP). According to McMillan and Morse (1999), *M. leidyi* comprise a large percentage of the diet of dogfish (*Squalus acanthias*) in the Long Island Sound. Similarly, Loggerhead turtles (*C. caretta*) consume *M. leidyi* and are also present in the LIS. Another factor that could have led to the results of the current study is the presence of other zooplanktovores in the LIS that affect copepod abundance. For example, Atlantic Manhaden (*B.*

tyrannus) also consume copepods in the LIS.

There were some findings in the current study that were expected. In 2011, there was an inverse correlation between copepod abundance and microplankton abundance two weeks later, indicating that there may be a predation effect of copepods on microplankton. Another finding from 2011 was a correlation between microplankton and copepod abundance four weeks later, suggesting a positive response in copepod abundance due to an increase in prey availability. The data also demonstrated bottom-up effects. In 2012, increased copepod abundance was associated with increased *M. leidyi* abundance two weeks to one month later. The data also demonstrated that greater average copepod abundance in 2011 than in 2012 was associated with greater *M. leidyi* abundance, supporting the possibility of a bottom-up effect.

Conclusion

In the Long Island Sound, *Mnemiopsis leidyi* biomass does not show the expected response to eutrophication. Abundances of both adult and larval *M. leidyi* were greater in the eastern part of the LIS where eutrophication is less pronounced relative to the west in both 2011 and 2012. *M. leidyi* did not appear to elicit a trophic effect upon the LIS planktonic community in either year. *M. leidyi* grazing did not significantly reduce the copepod population nor bring about an increase of microplankton. Several factors may account for the absence of these effects, mainly the water depth and possibly the sampling technique employed in this study. Further investigation with modified techniques would be worthwhile.

REFERENCES

Antajan, E., T. Bastian, T. Raud , J.M. Brylinski, S. Hoffman, G. Breton, V. Cornille, A. Delegrange, and D. Vincent. 2104. The invasive ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 along the English Channel and the North Sea French coasts: another introduction pathway in northern European water? Aquatic Invasions 9:167-173.

Bowman, M.J. 1977. Nutrient distributions and transport in Long Island Sound. Estuarine and Coastal Marine Science 5: 531-548.

Burrell, V. G., and W.A.VanEngel. 1976. Predation by and Distribution of a Ctenophore Mnemiopsis-Leidyi a Agassiz, in York River Estuary. Estuarine and Coastal Marine Science 4:235-242.

Capriulo, G.M., and E.J. Carpenter. 1980. Grazing by 35 to 202 µm micro-zooplankton in Long Island Sound. Marine Biology 56:319-326.

Capriulo, G.M., G. Smith, R. Troy, G.H. Wikfors, J. Pellet, and C.Yarish. 2002. The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. Hydrobiologia 475: 263-333.

Cervetto, G., R. Gaudy, and M. Pagano. 1999. Influence of salinity on the distribution of *Acartia tonsa* (Copepoda, Calanoida). Journal of Experimental Marine Biology and Ecology 239:33-45.

Colin, S. P., J. H. Costello, L.J. Hansson, J.Titelman, and J.O. Dabiri. 2010. Stealth predation and   the predatory success of the invasive ctenophore Mnemiopsis leidyi. Proceedings of the National Academy of Sciences of the United States of America 107:17223-17227.

Condon, R. H., W. M. Graham, C. M. Duarte, K. A. Pitt, C. H. Lucas, S. H. Haddock, K. R. Sutherland, K. L. Robinson, M. N. Dawson, and M. B. Decker. 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. BioScience 62:160-169.

Condon, R.H., and D.K. Steinberg. 2008. Development, biological regulation, and fate of ctenophore blooms in the York River estuary, Chesapeake Bay. Marine Ecology Progress Series 369: 153-168.

Condon, R. H., Steinberg, D.K., Bronk, D.A. (2010) Production of dissolved organic matter and inorganic nutrients by gelatinous zooplankton in the York River estuary, Chesapeake Bay. Journal of Plankton Research 32:153-170.

Condon, R., D.K. Steinberg, P. del Giorgio, T. Bouvier, D. Bronk, W.M.Graham, and H. Ducklow. 2011. Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. Proceedings of the National Academy of Sciences 108: 10225-10230. doi:10.1073/pnas.1015782108

Costello, J.H., and H.W. Mianzan. 2003. Sampling field distributions of Mnemiopsis leidyi (Ctenophore, Lobata): planktonic or benthic methods? Journal of Plankton Research 25(4):455-459.

Daskalov, G., A. Grishin, S. Rodionov, V. Mihneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proceedings of the National Academy of Sciences 104: 10518-10523.

Deason, E.E. 1982. *Mnemiopsis leidyi* (Ctenophora) in Narragansett Bay, 1975–1979: Abundance, size composition and estimation of grazing. Estuarine, Coastal and Shelf Science 15.2: 121-134.

Deason, E.E., and T.J. Smayda. 1982. Ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA, during 1972–1977. Journal of Plankton Research 4.2: 203-217.

Dinasquet, J., J. Titelman, L. Moller, O. Setala, L. Granhag, R. Andersen, U. Bamstedt, M. Haraldsson, A. Hosia, T. Katajisto, T. Kragh, J. Kuparinen, M. Schroter, M. Sondergaard, P. Tiselius, and L. Riemann. 2012. Cascading effects of the Ctenophore *Mnemiopsis leidyi* on the planktonic food web in a nutrient-limited estuarine system. Marine Ecology-Progress Series 460: 49-61.

Finenko, G.A., Z.A. Romanova, G.I. Abolmasova, B.E. Amminsky, T.V. Pavlovkaya, L. Bat and A. Kideys. 2006. Ctenophores-Invaders and Their Role in the Trophic Dynamics of the Planktonic Community in the Coastal Regions off the Crimean Coasts of the Black Sea (Sevastopol Bay). Oceanology 46:472-482.

Goebel, N., J. Kremer, and C. Edwards. 2006. Primary production in Long Island Sound. Estuaries and Coasts 29:232-245.

Graham, E. M., F. Pages, W.M. Hamner. 2001. Physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451:199-212.

Granéli, E., and J. Turner. 2002. Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study. Mar Ecol Prog Ser 239: 57-68.

Hamer, H., A. Makzahn, and M. Boersma. 2011. The invasive ctenophore *Mnemiopsis leidyi*: a threat to fish recruitment in the North Sea. Journal of Plankton Research 37: 137-144.

Huntley, M.E., and M. Lopez. 1992. Temperature-dependent production of marine copepods: a global synthesis. American Naturalist 140: 201-242.

Ivlev, V.S. 1955. Experimental ecology and nutrition of fishes. Pishchemizdat, Moscow [Yale Univ. 1961]

Kremer, P. 1994. Patterns of abundance for *Mnemiopsis* in US coastal waters: a comparative overview. ICES Journal of Marine Science 51: 347-354.

McMillan, D. G., and W.W. Morse. 1999. Essential Fish Habitat Source Document: Spiny Dogfish, *Squalus acanthias,* Life History and Habitat Characteristics. NOAA Technical Memorandum NMFS-NE-150.

McNamara, M.E., D.L. Lonsdale, and R. Cerrato. 2010. Shifting abundance of the ctenophore *Mnemiopsis leidyi* and the implications for larval bivalve mortality. Marine Biology 157.2: 401-412.

McNamara, M.E., D.L. Lonsdale, and R. Cerrato. 2013. Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* A. Agassiz 1865 influences microplankton abundance and composition enhancing prey conditions for larval ctenophores. Estuarine and Coastal Shelf Science 133:2-10. http://dx.doi.org/10.1016/j.ecss.2013.04.019.

Mianzan, H.W., P. Martos, J.H. Costello, and R.A. Guerrero. 2010. Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (Ctenophors: Lobata) in open-sea populations from Patagonia, Argentina. Hydrobiologia 645:113-124.

Miller, R. J. 1974. Distribution and Biomass of an Estuarine Ctenophore Population, *Mnemiopis leidyi* (A. Agassiz). Chesapeake Science 15(1): 1-8.

Mills, C. 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES Journal of Marine Science 52:575-581.

Mills, C. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451:55-68.

Parsons, T.R, and C.M. Lalli. 2002. Jellyfish population explosions: revisiting a hypothesis of possible causes. La Mer 40:111–121.

Purcell, J.E, D.A. Nemazie, S.E. Dorsey., E.D. Houde, and J.C. Gamble. 1994. Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphozoan medusae and ctenophores in Chesapeake Bay. Marine Ecology-Progress Series 114:47-58.

Purcell, J.E., T.A. Shiganova, M.B. Decker, and E.D. Houde. 2001a. The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. Hydrobiologia 451: 145-176. doi: 10.1023/A:1011826618539

Purcell, J. E., D.L. Breitburg, M.B. Decker, W.M. Graham, M.J. Youngbluth, and K.A. Raskoff. 2001b. Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review.

Rabalais, N. N. & R. E. Turner (eds), Coastal Hypoxia: Consequences for Living Resources and Ecosystems, America

Purcell, J.E., and M.N. Arai. (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451: 27-44.

Purcell, J.E., and M.B. Decker. 2005. Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987-2000. Limnology and Oceanography 50:376-387.

Purcell, J.E, S. Uye S, and W.T. Lo. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Marine Ecology Progress Series 350:154-174. doi: 10.3354/meps07093

Purcell, J.E. 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. Hydrobiologia 616:23 – 50.

Rapoza, R., D. Novak, J.H. Costello. 2005. Life-stage dependent, in situ dietary patterns of the lobate ctenophore *Mnemiopsis leidyi* Agassiz 1865. Journal of Plankton Research 27: 951-956.

Raskoff, K.A., F. A. Sommer, W.M. Hammer, and K.M Cross. 2003. Collection and culture techniques for gelatinous zooplankton. The Biological Bulletin 204:68-80.

Reeve, M. R., M. A. Walter, and T. Ikeda. 1978. Laboratory studies of ingestion and food utilization in lobate and tentaculate ctenophores. Limnology and Oceanography 23: 740-751.

Riisgård, H.U, C.V. Madsen, C. Barth-Jensen, and J.E. Purcell. 2012. Population dynamics and zooplankton-predation impact of the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark). Aquat. Inv. 7: 147-162

Shiganova, T.A. 1998. Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. Fisheries Oceanography 7:305-310.

Smith, P. E., R. C. Counts, and R. I. Clutter. 1968. Changes in Filtering Efficiency of Plankton Nets Due to Clogging Under tow. J. Cons. int. Explor. Mer **32**:232-248.

Stoecker, D., P. Verity, A. Michaels, and L. Davis. 1987. Feeding by larval and post-larval ctenophores on microzooplankton. Journal of Plankton Research 9: 667-683. doi: 10.1093/plankt/9.4.667

Sullivan, B. K., D. Van Keuren, and M. Clancy. 2001. Timing and size of blooms of the ctenophore Mnemiopsis leidyi in relation to temperature in Narragansett Bay, RI. Hydrobiologia 451:113-120.

Sullivan, L., and J. Gifford. 2004. Diet of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). Journal of Plankton Research 26: 417-431. doi: 10.1093/plankt/fbh033

Sullivan, L., and J. Gifford. 2007. Growth and feeding rates of the newly hatched larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). Journal of Plankton Research 29:949-965.

Sullivan L. 2010. Gut evacuation of larval *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). Journal of Plankton Research 32.1: 69-74.

Waggett, R., and J. H. Costello. 1999. Capture mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, preying on the copepod *Acartia tonsa*. Journal of Plankton Research 21.11: 2037-2052.

Waggett, R. J., and L.J. Sullivan. 2006 Feeding efficiency of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). Journal of Plankton Research 28: 719-723.
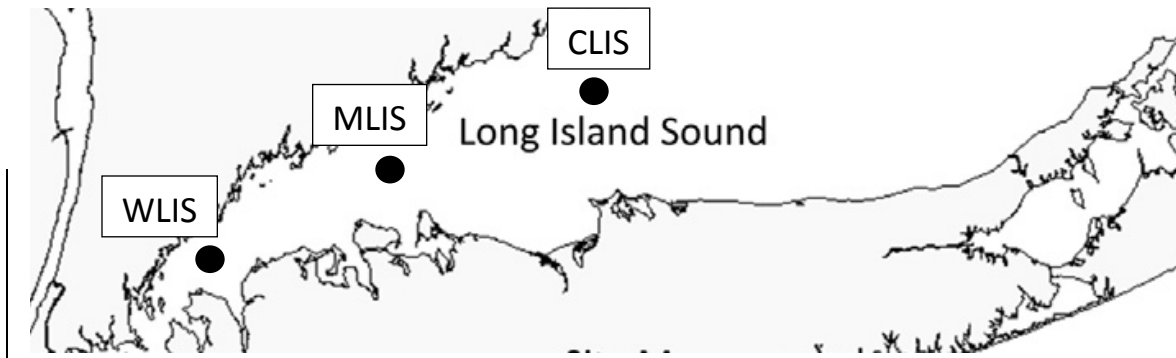
FIGURES

Figure. 1. Sampling locations (WLIS, MLIS, and CLIS) in the Long Island Sound, NY, USA

Figure 2. *M. leidyi*, copepod adult, copepod nauplii and microplankton abundances in 2011 by site (left panels CLIS, middle panels MLIS, right panels WLIS)

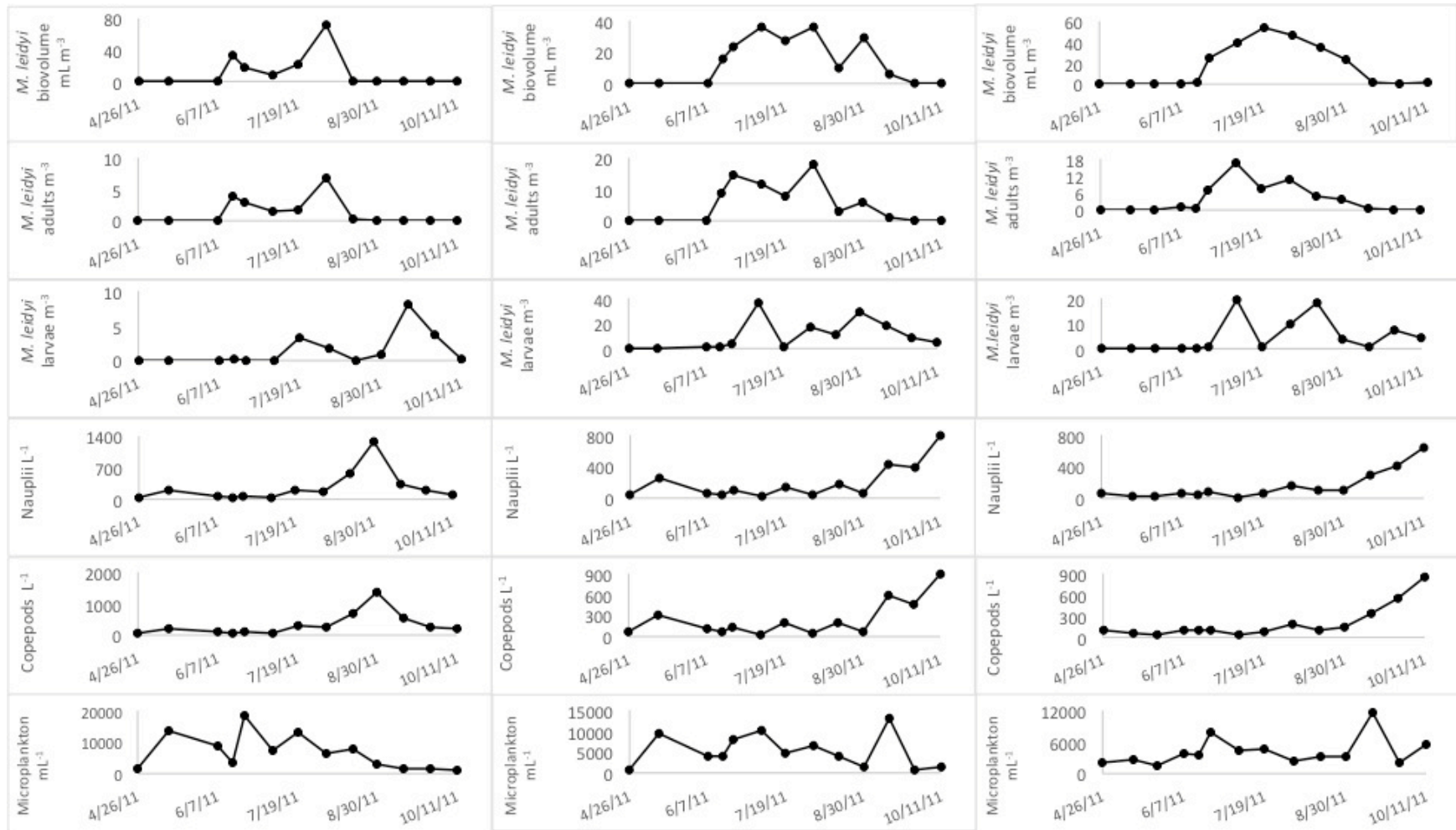**Figure. 3.** *M. leidyi*, copepod adult, copepod nauplii and microplankton abundances in 2012 by site (left panels CLIS, middle panels MLIS, right panels WLIS)

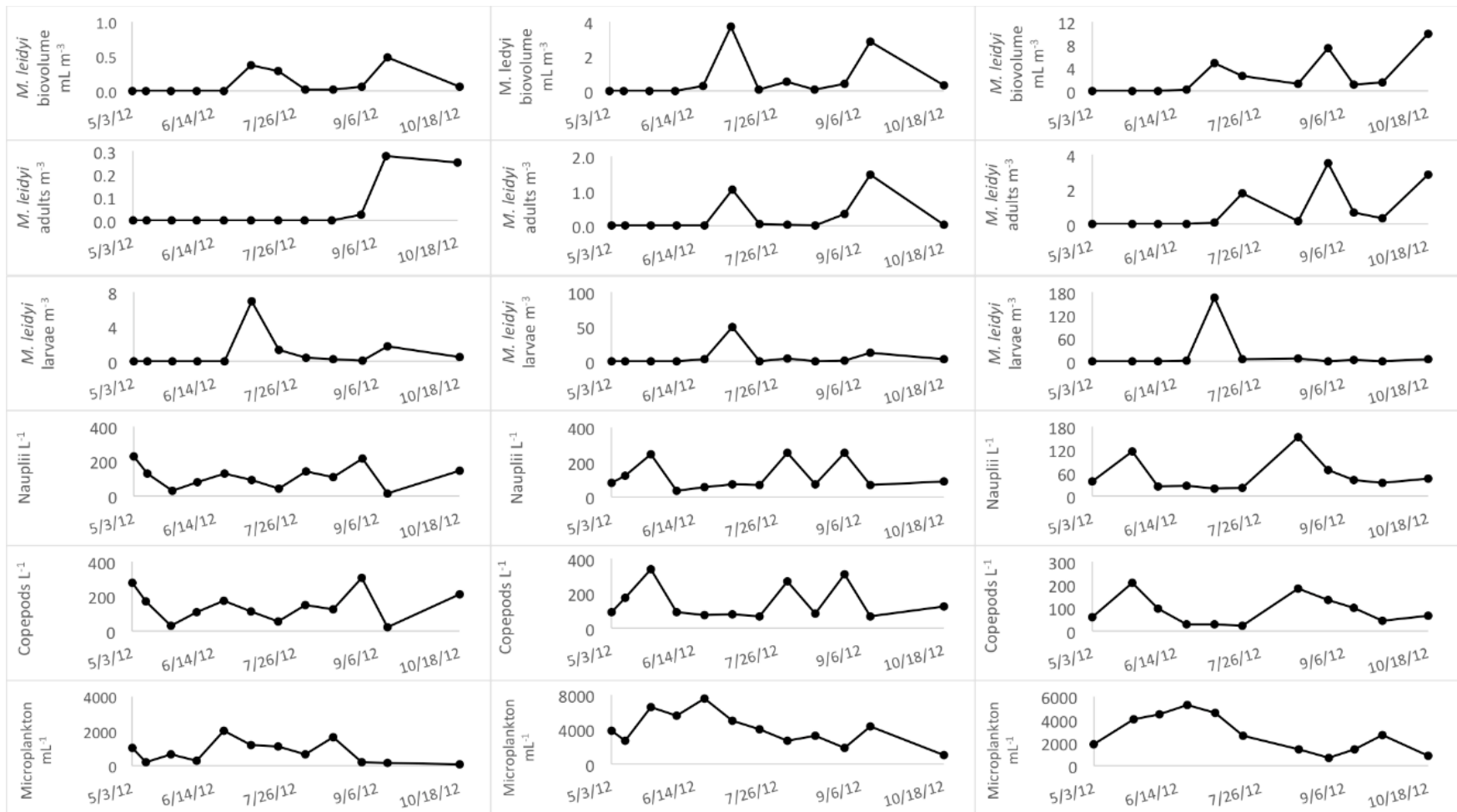**Table 1.** Abundance, growth and consumption of copepods in 2011 at the WLIS and CLIS sites

CLIS					
Date	Abundance (m^{-3}) Copepods	*M. leidyi* adult abundance (no. m^{-3})	Copepod Growth Rate (no. m^{-3} day^{-1})	Consumption Rate (no. m^{-3} day^{-1})	Percent of Growth Consumed per Day
June 15	102389.6	1.5	14232.2	315.4	2.22%
June 21	109894.8	25.2	15275.4	791.8	5.18%
July 6	26907.8	40.0	7695.6	1070.9	13.92%
July 19	78699.3	53.4	24869.0	677.1	2.72%
August 3	187141.5	46.8	70365.2	1184.9	1.68%
August17	105029.5	34.5	42536.9	202.8	0.48%
August 30	139273.6	23.4	61419.7	442.0	0.72%
September 13	340679.6	2.3	150239.7	160.3	0.11%
WLIS					
June 21	126962.2	17.9	25138.5	1569.8	6.24%
July 6	63086.4	8.5	12491.1	225.6	1.81%
July 19	310263.7	21.7	88735.4	2407.2	2.71%
August 3	228949.6	71.2	72348.1	2097.7	2.90%
August 17	667672.7	0.6	270407.4	65.2	0.02%

Note. Growth rates were estimated using the copepod growth rate model described in Huntley and Lopez (1992)

Table 2. Mean Seasonal Abundance for Each Group by Site and Year

	2011 WLIS	2011 MLIS	2011 CLIS	2012 WLIS	2012 MLIS	2012 CLIS
M. leidyi adults abundance	1.3	5.4	3.8	0.046	0.2	0.9
M. leidyi larvae abundance	1.4	10.3	4.8	0.930	6.0	17.3
Copepods abundance	320307	244131	199492	145412	147813	88695
M. leidyi biovolume	11.93	14.24	16.41	0.11	0.73	2.61
Microplankton abundance	6767.0	5248.02	4179.7	7708.76	4048.40	2709.54

Table 3. Proportion of each prey type for each M. leidyi size class and electivity indexes for each M. leidyi size class and prey type.

WLIS

Prey type	0.5-3cm	3-5cm	5-7cm	Ambient Abundance
Acartia adults	0.00%	32.91%	42.95%	8.44%
Acartia copopedites	0.00%	10.13%	36.58%	6.54%
Oithona adults	100.00%	16.46%	16.44%	24.12%
Nauplii	0.00%	40.51%	2.01%	66.99%
*Parvocalanu*s *crassirostris* adults	0.00%	0.00%	0.34%	0.09%

CLIS

Prey type	0.5-3cm	3-5cm	5-7cm	Ambient Abundance
Acartia adults	16.00%	23.08%	34.39%	12.83%
Acartia copopedites	4.00%	30.77%	18.10%	9.00%
Oithona adults	0.00%	0.00%	27.15%	7.98%
Nauplii	80.00%	38.46%	4.52%	77.87%
Parvocalanus crassirostris adults	0.00%	7.69%	9.05%	0.50%

Electivity Index - WLIS

Prey Type	0.5-3cm	3-5cm	5-7cm
Acartia adults	-1.00	0.59	0.67
Acartia copopedites	-1.00	0.22	0.70
Oithona adults	0.61	-0.19	-0.19
Nauplii	-1.00	-0.25	-0.94
Parvocalanus crassirostris adults	-1.00	-1.00	0.59

Electivity Index - CLIS

Prey Type	0.5-3cm	3-5cm	5-7cm
Acartia adults	0.11	0.29	0.46
Acartia copopedites	-0.38	0.55	0.34
Oithona adults	-1.00	-1.00	0.55
Nauplii	0.01	-0.34	-0.89
Parvocalanus crassirostris adults	-1.00	0.88	0.90

Note. Positive values represent selection for and negative values represent avoidance