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**Population dynamics of the ctenophore *Mnemiopsis leidyi* and implications for bottom-up and top-down controls of the plankton community**

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by

**Marianne E. McNamara**

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**Marianne Elizabeth McNamara**

We, the dissertation committee for the above candidate for the
Doctor of Philosophy degree, hereby recommend
acceptance of this dissertation.

**Dr. Darcy J. Lonsdale – Dissertation Adviser**
**Professor, School of Marine and Atmospheric Science**

**Dr. Robert C. Aller - Chairperson of Defense**
**Distinguished Professor, School of Marine and Atmospheric Science**

**Dr. Robert M. Cerrato**
**Associate Professor, School of Marine and Atmospheric Science**

**Dr. Joseph D. Warren**
**Associate Professor, School of Marine and Atmospheric Science**

**Dr. John H. Costello**
**Professor, Providence College**

This dissertation is accepted by the Graduate School

Charles Taber
Interim Dean of the Graduate School

Abstract of the Dissertation

**Population dynamics of the ctenophore *Mnemiopsis leidyi* and implications for bottom-up and top-down controls of the plankton community**

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This dissertation investigated the ecology of the ctenophore *Mnemiopsis leidyi* in Great South Bay, New York *via* field and laboratory studies. The research focused on the role of *M. leidyi* in controlling plankton community structure and the influence of the plankton community in regulating seasonal population blooms of *M. leidyi*. First, this study documented top-down control of microplankton by larval *M. leidyi* in Great South Bay. A relationship between high adult *M. leidyi*/low mesozooplankton with high microplankton abundance was also identified, and preceded an increase in larval ctenophores, suggesting that intense feeding on mesozooplankton by adult *M. leidyi* enhances prey conditions for their larvae. Secondly, this study found significant interannual differences in *M. leidyi* abundance, fecundity and recruitment. Ctenophores contained nearly three times as many prey items and produced twice as many eggs in 2008 during a brown tide (*Aureococcus anophagefferens*) than in 2009, a non-bloom year, implying bottom-up regulation of the ctenophore population. However, *M. leidyi* abundance was five times lower in 2008 than in 2009 and field data identified a mismatch between maximum ctenophore egg production and microplankton abundance in 2008, whereas the two coincided in 2009, further demonstrating the importance of microplankton for larval *M. leidyi*. Thirdly, field-based mesocosm experiments examined the individual and interactive roles of *M. leidyi* predation and eutrophication (*i.e.*, nutrient loading) on the microplankton community. Ciliates, an important prey item for larval *M. leidyi*, exhibited an order of magnitude increase in tanks receiving nutrients and in those containing *M. leidyi*, but increased by two orders of magnitude in treatments receiving both ctenophore and nutrient additions, which may help explain recently documented shifts in *M. leidyi* population dynamics in coastal estuaries. *Mnemiopsis* populations interact with estuarine nutrient distributions in multiple ways, including biomass production, excretion, and decomposition. The elemental composition (carbon, nitrogen, and phosphorous) of *M. leidyi* demonstrated a significant dependence on ctenophore size and zooplankton prey abundance; percentages of C, N, and P declined 30-60% from the onset of the *M. leidyi* population bloom to their collapse, when prey were fewer. This study documented *in situ* seasonal patterns in ctenophore elemental stoichiometry and suggests that previous estimates of nutrients remineralized during population crashes are likely over-estimated.

## Dedication Page

*When I woke today, suddenly nothing happened, but in my dreams I slew the dragon*

"Waiting for my real life to begin", Colin Hay

This thesis is dedicated to the brave men and women of the United States Armed Forces who have sacrificed so much for so little so that we may live in peace and freedom.

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**Acknowledgments**

It is said that 'it takes a village' to raise a child. Certainly, the same can be said for a Ph.D degree. My experience at Stony Brook University began one afternoon in 2004 with an email from Anne McElroy congratulating me on my acceptance to the university. I could not have possibly known then how that moment would change and shape the rest of my life forever. I have spent the last nine years as a graduate student at Stony Brook Universiy, first as a Masters student when SoMAS was formerly known as MSRC, and later as a full-time, and then part-time, Ph.D. student. There are so many people who have given me their support, time, assistance, and encouragement, in large ways and in small. I could not have made it this far without their support and am truly grateful to include these individuals in these acknowledgements.

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# INTRODUCTION

This dissertation focused on the bottom-up and top-down control of the plankton community by the ctenophore *Mnemiopsis leidyi* in a Long Island estuary. *Mnemiopsis leidyi* (A. Agassiz 1865) is an ecologically-important gelatinous predator in temperate coastal environments. Populations of *M. leidyi* exhibit significant intra- and interannual variation in abundance (e.g., Costello et al. 2006). Blooms of the ctenophore are made up of lobate adults and cydippid larvae, which exert strong predation pressure on mesozooplankton (e.g., Kremer 1979; Deason and Smayda 1982; Purcell et al. 2001; Purcell and Decker 2005; McNamara et al. 2010) and microplankton (Stoecker et al. 1987; Sullivan and Gifford 2004; Rapoza et al. 2005; Sullivan and Gifford 2007), respectively. Recent evidence suggests that *M. leidyi* has increased in abundance and shifted towards an earlier seasonal maximum in mid-Atlantic estuaries (Narragansett Bay; Sullivan et al. 2001, Costello et al. 2006, Chesapeake Bay; Condon and Steinberg 2008, and Long Island estuaries; McNamara et al. 2010).

Since larval *M. leidyi* depend on microplankton for prey, its availability may regulate the survival and growth, and subsequent recruitment, of the larvae into mesozooplankton-feeding adults (Sullivan and Gifford 2004; Rapoza et al. 2005). Previous studies have demonstrated the importance of certain microplanktonic taxa (e.g., dinoflagellates and ciliates) as prey for larval *M. leidyi* and the potential of larvae to exert significant predatory control on microzooplankton, but have done so only experimentally (Stoecker et al. 1987; Sullivan and Gifford 2004; 2007). Despite a preponderance of data on the predatory influence of adult *M. leidyi* on mesozooplankton, little is known about the changes in microplankton communities during blooms of *M. leidyi*. Further, high densities of adult *M. leidyi* during seasonal population blooms may increase microplankton abundance through reduction of mesozooplankton predators, potentially enhancing prey conditions for the larvae.

The magnitude of *M. leidyi* blooms varies from year to year and is regulated by biotic and abiotic factors. Ctenophore fecundity correlates positively with ctenophore size and prey density (Baker and Reeve 1974; Kremer 1976; Reeve et al. 1989; Grove and Breitburg 2005) and is also temperature-dependent (Kremer 1976; Purcell et al. 2001; Costello et al. 2006). In order for a *M. leidyi* bloom to persist, however, sufficient egg production must be paired with an adequate supply of microplanktonic prey for the hatching larvae. Relatively-little attention has been paid to the bottom-up processes that regulate ctenophore fecundity and recruitment, or how differences in these regulatory processes, between and within years, influences *M. leidyi* population dynamics.

Increasing evidence has implicated anthropogenic activities (*i.e.*, eutrophication) as favoring the development of gelatinous zooplankton blooms in coastal waters (e.g., Mills 1995; Mills 2001; Purcell et al. 2007). The ecological role of *M. leidyi* in disturbed habitats is likely to differ from that in natural, undisturbed environments as the plankton community responds to combined top-down (predatory) and bottom-up (nutrient enrichment) processes. Experimental mesocosms have demonstrated substantial increases in microplankton (*i.e.*, dinoflagellates) exposed to simultaneous predation by a gelatinous predator and nutrient enhancement, compared to treatments receiving nutrient or predator amendments alone (Pitt 2007). The interactive influence of *M. leidyi* predation and eutrophication could result in unique consequences for the plankton community, which may feedback to ctenophore population dynamics by increasing microplanktonic prey for their larvae.

Although ctenophores and other gelatinous zooplankton were previously considered to be trophic dead ends, some research suggests that the release of dissolved organic matter *via*

decomposition of collapsing populations can stimulate the microbial community and transfer carbon across spatial gradients (e.g., Hansson and Norrman 1995; Titelman 2006). Since *M. leidyi* is characterized by seasonal population blooms and subsequent demise (e.g. Turner 1982; Turner et al. 1983; Quaglietta 1987; McNamara et al. 2010), the release of carbon, nitrogen and phosphorus following seasonal population collapse may provide a significant source of nutrients for the planktonic and microbial community. However, since C, N, and P content of *M. leidyi* varies temporally along with changes in ctenophore size and nutritional status (e.g., Kremer 1975; Reeve et al. 1989), estimates of their release during population collapse based on the elemental composition of well-fed, laboratory-reared individuals or a one-time field collection of specimens (see Pitt et al. 2009 for a summary) may be overestimated.

The main objectives of this dissertation were to:

1. Determine the seasonal abundance and size distribution of *Mnemiopsis leidyi* over two sampling years in Great South Bay (GSB), New York.
2. Determine the seasonal (late spring to early fall) abundance and composition of mesozooplankton and microplankton in GSB.
3. Determine the fecundity (egg production) of *M. leidyi* in GSB, and identify correlations between egg production and ctenophore size, mesozooplankton abundance (and composition), and temperature.
4. Document the gut contents of *M. leidyi* in GSB, and identify correlations between gut contents and ctenophore size and mesozooplankton abundance; investigate prey selectivity by *M. leidyi*, and identify other biotic or abiotic factors that may influence intra- and interannual differences in *M. leidyi* egg production and their gut contents.
5. Determine the role of microplankton as a limiting factor to larval *M. leidyi* recruitment in GSB.
6. Determine if/how predatory (top-down) impacts of adult *M. leidyi* influence planktonic food web structure, and whether such influences feedback to ctenophore population dynamics by enhancing or limiting recruitment of their larvae.
7. Determine the impact of larval *M. leidyi* on microplankton abundance and composition, and whether this cascades down the food web to influence nanoplankton abundance and composition.
8. Determine how nutrient enrichment and predation by adult *M. leidyi*, individually and interactively, alter planktonic community structure in GSB.
9. Determine if/how the elemental composition (carbon, nitrogen, and phosphorus) of *M. leidyi* varies temporally and seasonally in GSB; determine if/how percent C, N, and P and molecular ratios of C/N/P vary with ctenophore size and nutritional status (zooplankton abundance) in GSB.
10. Calculate and contrast the contribution of C, N, and P by *M. leidyi via* excretion and population collapse in GSB.

Field sampling and experimental studies were conducted over two sampling years (May-October; 2008 and 2009) in Great South Bay, New York, USA. Great South Bay is a

lagoonal estuary, located on the south shore of Long Island. The bay is approximately 40 km in length extending from South Oyster Bay on the west to Moriches Bay on the east, and varies in width from 300 m to 11 km. The bay is shallow, averaging only 2 m in depth with a maximum depth of 4 m, and is well-mixed (Schubel et al. 1991). The bottom of Great South Bay is primarily sandy, with muddy sections on its northern side (Hinga 2005). Temperatures within the bay vary seasonally and salinity typically ranges from 20 to 30 (Hinga 2005). Water exchange between the bay and Atlantic Ocean is driven by coastal sea level and tidal forcing through Fire Island and Moriches Inlets primarily (Schubel et al. 1991), and is typical of other shallow coastal lagoons found along the eastern (Hinga 2005) and Gulf coasts (Wilson et al. 1991) of the United States. A third inlet formed during Hurricane Sandy (2012) and remains opened at Old Inlet, Fire Island. Because it is shallow, Great South Bay is well-mixed and is generally considered to be unstratified with only slight differences between surface and bottom water temperature and salinity (pers. obs.; Hinga 2005). Residence time within the estuary varies with climatic conditions, but typically averages around 50 days (Hinga 2005).

Great South Bay is considered to be one of the world's most productive marine habitats (Carpenter et al. 1991), but has experienced a 120-year decline in ecosystem maturity, loss of dominant species, and a switch from migratory (*i.e.*, finfish) to lower trophic ecosystem dominance. The shift in ecosystem structure within the bay has been attributed to habitat loss, warmer winter temperatures, overfishing and eutrophication (Nutall et al. 2011). Loss of its three major planktivores (eastern oysters, hard clams, and Atlantic menhaden; Nutall et al. 2011) and intermittent blooms of the brown tide alga *Aureococcus anophagefferens* have plagued Great South Bay in recent decades, during which the time the bay has also experienced shifts in the abundance and seasonal distribution of *M. leidyi* (McNamara et al. 2010).

This dissertation examined top-down control of *M. leidyi* on the mesozooplankton, microplankton and nanoplankton communities through weekly sampling at two sampling locations in the bay. Exploration into the top-down control of adult *M. leidyi* on the mesozooplankton and microplankton communities was achieved through weekly sampling and through experimental mesocosms situated within the bay. The regulatory role of the plankton community in influencing seasonal and interannual differences in *M. leidyi* population dynamics was also examined; ctenophores were regularly collected for gut contents and egg production studies and compared to size-specific abundance estimates of *M. leidyi* and to the abundance and composition of lower (planktonic) trophic assemblages. The relative impacts of eutrophication and ctenophore predation on the zooplankton community were compared using historic (low) and recent (high) abundances of *M. leidyi via* experimental mesocosms. Finally, ctenophores were collected and analyzed for elemental composition to estimate the contribution of C, N, and P by *M. leidyi* excretion and decomposition during seasonal population blooms in the bay.

# CHAPTER ONE

Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance and composition enhancing prey conditions for larval ctenophores

## Abstract

The ctenophore *Mnemiopsis leidyi* is an ecologically-important, gelatinous predator capable of exerting strong regulatory control on the plankton community. Ctenophore populations are comprised of lobate adults and cydippid larvae. Since the larvae depend on microplankton for prey, its availability may determine the magnitude of larval survivorship and growth, and their subsequent recruitment into mesozooplankton-feeding adults. Ctenophore population data were used alongside mesozooplankton and microplankton abundances to interpret predatory impacts of *M. leidyi* in a Long Island, New York estuary over two years. Field data suggested significant top-down control of mesozooplankton and microplankton during peak abundances of adult and larval ctenophores, respectively. Abundances of dinoflagellates and ciliates declined by 45-56% and 83-97%, during highest larval abundances in 2008 and 2009, respectively. Furthermore, the dramatic reduction of mesozooplankton by adult *M. leidyi* resulted in a cascading effect on microplankton. A relationship between high adult *M. leidyi*/low mesozooplankton with high microplankton abundances was identified, and preceded an increase in ctenophore larvae. These data suggest that blooms of *M. leidyi* result in a direct feedback system, wherein intense feeding activity by adults on mesozooplankton releases certain microplanktonic taxa from predation pressure, enhancing prey conditions for larval ctenophores.

## Introduction

The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 is a planktonic predator capable of exerting significant mortality on the zooplankton community in temperate coastal environments (e.g., Kremer 1979; Deason and Smayda 1982; Purcell et al. 2001; Purcell and Decker 2005; McNamara et al. 2010). Ctenophore blooms may consist of both adults and larvae, the latter of which must pass through distinct morphological stages. After hatching, *M. leidyi* undergo a tentaculate (cydippid) stage during which they possess two tentacles which are used to seize and capture microplanktonic (20-200 μm) prey (Sullivan and Gifford 2007). As the larva grows, it develops lobes and the tentacles are resorbed. The transformation from a tentaculate to lobate body plan is marked by a transitional stage, in which both tentacles and lobes are used to capture microplanktonic and mesozooplanktonic prey (Reeve et al. 1978; Sullivan and Gifford 2004). *Mnemiopsis leidyi* typically enter the transitional stage between 0.5-1.5 cm and the transformation to lobate form is usually complete when the ctenophore reaches lengths greater than 1.5 cm (Stoecker et al. 1987; Sullivan and Gifford 2004; Rapoza et al. 2005; Sullivan and Gifford 2007).

The survival of larval *M. leidyi* depends, in part, on the availability and composition of microplanktonic prey. In laboratory incubations, a diet consisting entirely of microplankton (diatoms, flagellates, autotrophic and heterotrophic dinoflagellates, naked and tintinnid ciliates, and rotifers) supported significant growth of larval ctenophores (Stoecker et al. 1987; Sullivan and Gifford 2007). Larvae incubated in low concentrations of microplankton were smaller than larvae incubated in medium and high concentrations during long-term feeding experiments, and those fed a diet consisting predominantly of mixotrophic dinoflagellates exhibited significantly higher growth rates than those fed other microplanktonic taxa (Sullivan and Gifford 2007). Larval *M. leidyi* experienced significant differences in growth and survival rates when fed ciliates and copepod nauplii compared to those fed high amounts of phytoplankton alone, which did not survive (Stoecker et al. 1987). Larval *M. leidyi* frequently dominate during high ctenophore densities (Costello et al. 2006; Condon and Steinberg 2008), and it has been

suggested that the abundance and composition of microplankton may ultimately explain the timing and magnitude of ctenophore recruitment into mesozooplankton-feeding adults (Sullivan and Gifford 2004; Rapoza et al. 2005).

While the abundance and composition of zooplankton communities are likely to influence the population dynamics of *M. leidyi* differently across life stages, the influence of *M. leidyi* on the plankton community will depend on the magnitude and size-distribution of the ctenophore population. Clearance rates of larval *M. leidyi* obtained experimentally indicated that larvae, when abundant, have the potential to exert significant predatory control over microzooplankton (Stoecker et al. 1987; Sullivan and Gifford 2004; 2007). Larvae fed *in situ* concentrations of microplankton significantly reduced the abundance of aloricate ciliates, rotifers and copepod nauplii (Stoecker et al. 1987). Sullivan and Gifford (2004) estimated that high abundances of the larvae could potentially clear up to ~60% of the water column $d^{-1}$ of microplankton. Further, the ingestion rates of larvae increased with increasing prey density, like those of adult *M. leidyi* on mesozooplankton (e.g., Kremer 1979). For these reasons, it has been suggested that regions of high microplankton abundance may serve as "nurseries" for ctenophores during their earliest life-history stage (Sullivan and Gifford 2007).

The larvae of *M. leidyi* may also benefit from the presence of adult ctenophores that feed on crustacean zooplankton. Firstly, high densities (100 $L^{-1}$) of copepod nauplii have been shown to damage the tentacles of developing ctenophores (Reeve et al. 1978) and newly-hatched *M. leidyi* suffered 84-100% mortality in the presence of copepods > 200 μm (Stanlaw et al. 1981). Waggett and Sullivan (2006) observed that ctenophores < 0.8 cm were frequently damaged by encounters with copepodites. Secondly, high densities of adult *M. leidyi* may increase microplankton abundance through reduction of the latter's crustacean predators. Mesocosm experiments performed with a ctenophore (*Pleurobrachia pileus* Müller 1776; Granéli and Turner 2002) or non-zooxanthellate jellyfish (*Catostylus mosaicus*, Scyphozoa; West et al. 2009; Pitt et al. 2007) documented significant increases in ciliate and dinoflagellate abundances, respectively, in the presence of the gelatinous species compared to control tanks or those with mesozooplankton additions. In contrast, ciliates decreased in the absence of ctenophores, presumably due to increased predation by copepods (Granéli and Turner 2002).

Despite a preponderance of data on the predatory influence of adult *M. leidyi* on mesozooplankton, little is known about the changes in microplankton communities during blooms of *M. leidyi*. The aim of this study was to identify and interpret changes in microplankton abundance and composition in response to top-down control of mesozooplankton by adult *M. leidyi* and microplankton by larval *M. leidyi in situ*. I hypothesized that blooms of *M. leidyi* are involved in a direct feedback system in which intense feeding activity by adults on mesozooplankton enhances prey conditions for larval ctenophores by removing crustacean predators and increasing microplanktonic prey. To my knowledge, this is the first study to compare temporal changes in mesozooplankton and microplankton to *M. leidyi* abundance and size composition *in situ*.

## Methods

### *Temporal and spatial distribution of M. leidyi*

Collections for *Mnemiopsis leidyi* were made weekly from May through October in 2008 and 2009 in Great South Bay, New York, USA (Figure 1). Sampling was conducted by boat and

occurred weekly at site M and biweekly at site A (except during high *M. leidyi* abundance when weekly collections were made) using a 1.0-m diameter, 1000-µm mesh net (n=2) and a 0.5-m diameter, 250-µm mesh net (n=2) equipped with flow meters. An exception to weekly sampling at site M occurred in 2008 when one potential sampling date (Aug 21) was canceled due to severe weather. To minimize damage to ctenophores during collection, both nets were equipped with soft, flexible cod ends and tow times restricted to short intervals. Tows were conducted obliquely to sample the entire water column (~1.5 m and 3 m at sites A and M, respectively). Collected ctenophores were rinsed of debris and any surface-attached zooplankton (e.g., crab zoea) with 20-µm filtered seawater and then poured through a 500-µm sieve to remove excess water (Purcell, 1988). Total live volume (biovolume) of ctenophores was then measured in graduated cylinders. Collected ctenophores were counted individually and measured (length, including lobes) to the nearest 0.5 cm (when smaller individuals dominated) or 1.0 cm (when larger individuals dominated) and divided into length-based size-classes. Depending upon ctenophore abundance, either the entire sample or only a subsample was measured. All species of ctenophores and other gelatinous zooplankton were counted and recorded.

*Mesozooplankton and microplankton sampling and enumeration*

Sampling of mesozooplankton and micrometazoa (*i.e.*, copepod eggs and nauplii, rotifers) was conducted as described for ctenophores but using a 0.5-m diameter, 64-µm mesh net (n=2) equipped with a flow meter. Samples were preserved immediately in 5% (final concentration) buffered formalin. In the laboratory, all mesozooplankton were identified (a minimum of 200; Omori and Ikeda 1992) to the lowest possible taxonomic group using a dissecting microscope.

Collections for microplankton (defined herein as unicellular protists 20-200 µm) were also made bi-weekly or weekly. Twenty liters of whole seawater were gently collected from ~ 0.5 m beneath the surface, from which a 90-mL sample was immediately preserved in 10% acidic Lugol's solution (100 mL final sample volume). Samples were collected in amber glass jars and stored immediately in the dark. Microplankton were isolated following standard settling techniques (Stoecker et al. 1994) in 10-mL Utermöhl chambers, and identified to the lowest possible taxonomic level using an inverted light microscope. Taxa were characterized into one of the following categories: centric or pennate diatoms, flagellates, dinoflagellates, loricate ciliates, aloricate ciliates (e.g., oligotrichs) and other (e.g., heliozoans, acantharians, etc). Individual linear measurements (length and width) of the first 25 representatives of each group were used to convert sizes into biovolume using calculations established by Sun and Liu (2003). Biovolume and abundance (cells $mL^{-1}$) values of each taxon were converted into biomass estimates (µg C $L^{-1}$) using conversion factors published by Strathmann (1967; centric and pennate diatoms), Børsheim and Bratbak (1987; flagellates), Putt and Stoecker (1989; ciliates) and Menden-Deuer and Lessard (2000; dinoflagellates). Chains of small centric diatoms were counted as single microorganisms when chain lengths exceeded 20 µm.

Additionally, taxa smaller than 20 µm in the 2009 microplankton samples were enumerated and recorded separately to provide a measure of nanoplankton (2-20 µm) abundance. Nanoplankton identification was rarely made to the genus level and was typically limited to placement into one of the following groups: centric or pennate diatoms, flagellates, dinoflagellates, or aloricate ciliates. Possible cyanobacteria, cryptophytes and other very small protozoa were excluded from identification, and differences between autotrophic and heterotrophic nanoplankton were not determined.

*Determination of top-down influences of planktonic food web structure by M. leidyi*

Mesozooplankton abundance and microplankton abundances and biomasses were compared to size-specific *M. leidyi* abundances to detect possible direct and indirect trophic impacts by tentaculate, transitional, and lobate ctenophores. Microplankton community structure (abundance and composition) before, during, and following peaks in larval ctenophore abundance was examined to determine preference for microplanktonic prey (if any) by larval *M. leidyi*, and to identify responses of microplankton to adult *M. leidyi* predation on mesozooplankton in Great South Bay. Similarly, nanoplankton community structure (2009) before, during, and following the highest larval abundances was also examined and compared to microplankton abundances to determine any cascading impacts within the plankton community.

*Statistical Analysis*

Data were analyzed by two-way ANOVA using BIOMstat: Statistical Software for Biologists, Version 3.30 by Applied Biostatistics, Inc., 10 Inwood Road, Port Jefferson, NY 11777. Homogeneity of variances was tested prior to doing ANOVAs using Bartlett, $F_{max}$, Scheffé-Box (log-anova) and Levene tests for homogeneity of variances (BIOMstat). No transformations of data were necessary.

## Results

*Ctenophore and zooplankton dynamics*

Population densities ($m^{-3}$) of *Mnemiopsis leidyi* differed significantly between 2008 and 2009 (df= 1, 209; F= 10.384; p = 0.0015; two-way ANOVA with station and year as fixed variables). In 2008, the highest ctenophore abundance (and biovolume) occurred on Jul 17 with 8.7 ctenophores $m^{-3}$ (13.7 mL $m^{-3}$) at site M (Figure 2a), and 13.5 $m^{-3}$ (56.1 mL $m^{-3}$) at site A (Figure 2b). In 2009, peak abundance (and biovolume) of *M. leidyi* occurred on Jul 29 at site M and Aug 05 at site A with 43.8 $m^{-3}$ (170.7 mL $m^{-3}$) and 65.5 (181.1 mL $m^{-3}$) $m^{-3}$, respectively (Figure 3). Adult (> 1.5 cm) *M. leidyi* dominated numerical abundances in both years with the exception of site M in 2008, when transitional stage (0.5-1.5 cm) ctenophores dominated during the highest ctenophore densities. Peaks in transitional-stage forms coincided with the highest adult densities, and preceded observed larval maxima by one week during both years (site M). In 2008, the arrival of the predatory ctenophore *Beroe ovata* coincided with the decline of *M. leidyi*. *Mnemiopsis*, which was already in low abundance (< 1 ctenophore $m^{-3}$) prior to the appearance of *B. ovata* on Aug 14, was undetectable at site M on the last day of sampling (Oct 09). However, unconstrained by an absence of *B. ovata* in 2009, *M. leidyi* exhibited a second (but reduced) population increase in the fall reaching a peak in abundance on Oct 9 at site M, and to a lesser extent at site A on Sep 18 (Figure 3). Once again, adult *M. leidyi* dominated during the second population increase at site M, but transitional-stage ctenophores were most abundant at site A. Total *M. leidyi* abundances did not differ by site in 2008 or 2009 (df= 1, 209; F= 2.597; p= 0.1086; two-way ANOVA with station and year as fixed variables). *Mnemiopsis* was the most common gelatinous predator in Great South Bay during both sampling years, with the exception of *B. ovata* from Aug to Oct in 2008.

Total mean mesozooplankton and micrometazoa abundances (collectively referred to as mesozooplankton) ranged from 16.2 individuals $L^{-1}$ to 743.1 $L^{-1}$ in 2008, and from 2.8 $L^{-1}$ to

1718.2 $L^{-1}$ in 2009 (Table 1). Mesozooplankton abundance did not differ significantly between the two sampling years (df= 1, 107; F= 0.977; p= 0.3252; two-way ANOVA with station and year as fixed variables), but varied substantially within the sampling period in both years. Mesozooplankton abundance varied in the presence (≥ 0.1 ctenophores $m^{-3}$) or relative absence (< 0.1 ctenophores $m^{-3}$) of *M. leidyi* in both years (df= 1, 113; F= 32.558; p= <0.0001; two-way ANOVA with ctenophore abundance and year as fixed variables). Copepods (adults, copepodites, and nauplii) comprised between 55 and 65% of total mesozooplankton averaged over the sampling period in 2008 (~ 9 to 99%) and 2009 (~ 3 to 95%; Table 1). *Acartia tonsa* and *Oithona similis* were the dominant copepods in Great South Bay during both sampling years. Other copepod species included *Centropages hamatus, Centropages typicus*, *Labridocera aestiva*, *Paracalanus pavus, Parvocalanus crassirostris*, *Temora turbinata* and *Temora longicornis*. Meroplankton averaged ~ 25% of the mesozooplankton community in 2008 (~ 0.3 to 82%) and 2009 (~ 0.5 to 95%), and consisted largely of bivalve and gastropod veligers, naupliar- and cyprid-stage barnacles, and polychaete larvae. Tintinnids and to a lesser extent rotifers were also identified in mesozooplankton samples and together comprised approximately 5% of the mesozooplankton community. Tintinnids were dominated by *Tintinnopsis* sp. and *Favella* sp. and occurred only sporadically in both years, occurring in high abundances (up to 73 $L^{-1}$) in the spring, and intermittently in lower abundances (0 to 35 $L^{-1}$) through the end of sampling (Table 1).

Total density of microplankton ranged from 174 to 5387 cells $mL^{-1}$ (54 to 4284 μg C $L^{-1}$) in 2008 and from 85 to 3965 cells $mL^{-1}$ (69 to 2303 μg C $L^{-1}$) in 2009 (Table 2). Dinoflagellates (site M) and flagellates (site A) dominated in 2008, comprising 55% and 47% of the total biomass, respectively, when averaged over the entire sampling period. In 2009, aloricate ciliates dominated at both sites, contributing ~ 35% of the total microplankton biomass. Dominant dinoflagellates in both years included *Gyrodinium sp.* (particularly *G. spirale, G. dominans, and G. aurelium*), *Gymnodinium sanguineum, Akashiwo sanguinea, Scripsiella trochoidea, Prorocentrum minimum, Prorocentrum micans, Polykrikos schwartzii* and *Polykrikos kofoidii, Pyrophacus horologicum, Protoperidinium crassipes*, and *Gonyaulax scrippsae*. Other species present included *Heterocapsa rotundata, Cochlodinium polykrikoides*, and *Amphidinium* sp., although to a lesser extent. Flagellates were largely euglenoid but also included phytoflagellates and silicoflagellates, and were not identified to genus level. Although flagellates were generally found in low abundances throughout 2008, an extremely high abundance (411.5 cells $mL^{-1}$ and 2886.3 μg C $L^{-1}$) of large euglenoids on Sep 25 occurred at site A. When this date is not considered, dinoflagellates contributed the majority (41%) of total microplanktonic carbon at site A, as they had at site M (Table 2). Aloricate ciliates were dominated in both years by *Strombidinium* sp., and to a lesser extent by *Strobilidium* sp., *Halteria* sp., and *Tontonia* species. Loricate ciliates, while generally low in abundance, were dominated by *Stenosemella* sp. with *Favella* sp., *Stenosemella* sp., *Codonella* sp., and *Tintinnopsis* sp. occurring less frequently.

Abundances of centric diatoms were relatively low and dominated the microplankton community only once in each year. When averaged over the entire sampling period, centric diatoms contributed < 5% and < 10% to total microplankton carbon in 2008 and 2009, respectively. Dominant diatom taxa included *Coscinodiscus sp., Thalassiosira guillardi, Grammatophora angulosa, Thalassionema nitzschoides, Leptocylindrus danicus* (chains), and *Amphora ovalis.* Pennate diatoms, while contributing relatively little to total microplanktonic biomass (~ 3% in 2008 and ~ 9% in 2009), were numerically dominant (cells $mL^{-1}$) on ~ 45% of the dates in 2008 and 75% of the dates in 2009. *Nitzschia longissima* and *Cylindrotheca*

*closterium* dominated the pennate diatom taxa in both years, while *Pleurosigma directum* and *Pleurosigma elongatum* were present in lower abundances. Abundances of all other taxa ranged from 0 to 66 cells $mL^{-1}$ (no biomass was determined) and included heliozoans, Acantharia, fungi, eggs, possible cysts, and microplankton of unknown taxa.

Nanoplankton abundances ranged from 6.1 to 2952.1 cells $mL^{-1}$ (Table 3). Dinoflagellates and, to a lesser extent flagellates dominated nanoplankton abundance, averaging ~ 65% and 25%, respectively, of the total at both sites. Centric and pennate diatoms < 20 μm averaged only about ≤5% of the nanoplankton community. And ciliates were scarce, occurring only sporadically. Biomass conversions were not applied to nanoplankton.

*Evidence of top-down influences of planktonic food web structure by M. leidyi*

In both sampling years, *M. leidyi* abundance corresponded inversely with mesozooplankton abundance. The build-up of *M. leidyi* coincided with an immediate and precipitous decline in mesozooplankton, which plunged from 344.4 to 7.2 individuals $L^{-1}$ in 2008 and 859.6 to 2.8 individuals $L^{-1}$ in 2009 at site M (Figures 2a, 3a), and from 173.0 $L^{-1}$ to 16.8 individuals $L^{-1}$ (2008) and 351.8 $L^{-1}$ to 3.6 individuals $L^{-1}$ (2009) at site A (Figures 2b, 3b). The mesozooplankton recovered fully under reduced *M. leidyi* densities following the arrival of *Beroe ovata* in 2008, but remained low in numbers in 2009 when *M. leidyi* populations persisted in the bay through the end of the sampling period (Figures 2 and 3).

In 2008 and 2009, the highest densities of adult *M. leidyi* coincided with substantial increases in dinoflagellate and especially aloricate ciliate abundances ($mL^{-1}$) and biomasses (μg C $L^{-1}$. During this time, dinoflagellate abundance (and biomass) increased by 261% (and 468%) at site M (Figure 4) and by 1368% (and 262%) at site A in 2008 (Figure 5), and by 864% (and 926%) at site M in 2009 (Figure 6). Aloricate ciliates increased by 681% (and 748%) and 3086% (and 4195%) at sites M and A, respectively, in 2008 (Figures 4 and 5) and by 4455% (and 4687%) at site M in 2009 (Figure 6). At site M in 2009, the highest numbers of adult ctenophores on Jul 29 coincided with the highest biomasses of both dinoflagellates (447 μg C $L^{-1}$) and aloricate ciliates (1407 μg C $L^{-1}$) during the entire six-month sampling period (Table 2). Rapid increases in dinoflagellates and ciliates (837% and 1264%, respectively) in 2009 at site A did not coincide with maximum densities of adult *M. leidyi*, but occurred one week prior when adult ctenophore density was increasing (Figure 7). No increases in diatoms (centric or pennate), flagellates or loricate ciliates were identified alongside the highest density of adult *M. leidyi* in either year.

Predation by adult *M. leidyi* on mesozooplankton appeared to shift planktonic food web structure resulting in enhanced prey conditions for larval ctenophores. During both sampling years, the rapid increase in dinoflagellate and ciliate populations coincident with the highest densities of adult *M. leidyi* preceded an increase in their larvae (< 0.5 cm), which in turn was followed by decreases in dinoflagellate and ciliate concentrations. Ctenophore larvae reached a maximum one week after the highest adult abundance in both years, and during which time dinoflagellate abundance (cells $mL^{-1}$) decreased by 45% in 2008 (Figure 4) and by 56% in 2009 (Figure 6). During the larval bloom, ciliate abundance (cells $mL^{-1}$) decreased by 83% in 2008 (Figure 4) and by 97% in 2009 (Figure 6). Dinoflagellate and ciliate biomasses also decreased during this time (Table 2). Evidence for larval consumption of flagellates and diatoms was not detected. Rather, diatom and flagellate concentrations increased only slightly during highest larval densities (Table 2). Because maximum abundances of larval ctenophores occurred during

bi-weekly sampling at site A, the effect of larvae on microplankton abundance and taxa could only be assessed for site M.

The severe reduction of microplankton during the larval *M. leidyi* bloom in 2009 also appeared to result in a cascading effect on nanoplankton. During maximum larval abundance on Aug 05, total 20-200 μm dinoflagellate and ciliate densities decreased, coincident with a ~ 300% increase in total nanoplankton (2-20 μm) abundance at site M (Figure 8). Moreover, the highest densities of nanoplanktonic dinoflagellate and flagellate abundances observed throughout the study occurred at this time (Table 3), increasing by 316% and 255%, respectively. The contribution of other nanoplanktonic organisms (*e.g.*, diatoms and ciliates) was generally too low to determine any cascading impacts.

## Discussion

To my knowledge, this is the first study to identify *in situ* predatory control of microplankton by larval *M. leidyi*. Also identified was a positive relationship between adult *M. leidyi* abundance and microplankton (*i.e.*, dinoflagellates and ciliates), which preceded an increase in *M. leidyi* larvae. I conclude that blooms of *M. leidyi* are involved in a direct feedback system in which intense feeding activity by adults on mesozooplankton enhances prey conditions for larval ctenophores. Two distinct trophic responses to ctenophore predation were identified: high adult *M. leidyi*/low mesozooplankton with increased microplankton abundance and high larval *M. leidyi*/low microplankton with increased nanoplankton abundance.

*Impact of M. leidyi predation on mesozooplankton and microplankton*

Although densities of *Mnemiopsis leidyi* differed between 2008 and 2009, their impact on mesozooplankton abundance was remarkably similar. High abundances of adult and transitional-stage *M. leidyi* corresponded with considerable decreases in total mesozooplankton (> 95%), and in particular, copepods. Similar predatory impacts by *M. leidyi* on copepods have been documented for Chesapeake and Narragansett Bays (Purcell and Decker 2005; Sullivan et al. 2007; Condon and Steinberg 2008). For instance, declines of *Acartia tonsa* associated with *M. leidyi* blooms ranged from 86% to 98% in Narragansett Bay (Sullivan et al. 2007). In this study, *A. tonsa* adults experienced a 96- 99.8% decline following the onset of the highest ctenophore abundances in 2009 (data not shown). Predation by larval *M. leidyi* on copepod nauplii could not be distinguished from that by adult and transitional-stage ctenophores since decreases in nauplii (*e.g., Acartia, Oithona*) occurred throughout the ctenophore bloom alongside declines in all copepod life stages (Table 1).

Seasonal blooms of adult *M. leidyi* and subsequent reductions in crustacean zooplankton coincided with considerably higher densities of microplanktonic dinoflagellates and aloricate ciliates in Great South Bay. Increases in larval ctenophores followed these surges in microplankton, presumably causing subsequent declines in the latter one week later. These findings strongly support the hypotheses that intense feeding by adult ctenophores on mesozooplankton can influence microplankton abundance and composition and that dinoflagellates and ciliates are important prey items for developing ctenophores. In contrast, concentrations of diatoms and flagellates changed little during high larval abundances suggesting that they do not comprise a significant portion of the prey for larval ctenophores, at least when sufficient quantities of dinoflagellates and ciliates are available.

In Great South Bay, high concentrations of dinoflagellates and aloricate ciliates preceded the highest number of larval *Mnemiopsis* by one week in both sampling years. At this time, these potential protistan prey were each within the upper range of the "high" microplanktonic concentrations found to support significantly-increased growth of larval *M. leidyi*, relative to medium and low concentrations, during 23-day feeding experiments (Sullivan and Gifford 2007). In this study, larval abundance peaks coincided not only with substantial declines in but the total absence of certain dinoflagellates and ciliates. The dinoflagellates *Prorocentrum minimum* and *P. maximum*, otherwise present throughout the sampling period, were completely absent from microplanktonic samples during the highest larval abundances in 2009, and high larval abundance coincided in both years with a total absence of the ciliate *Strobilidium*, which was also otherwise present. Digestion of microplankton by larval *M. leidyi* occurs rapidly; digestion times range from ~ 1 min for aloricate ciliates to 7 min for thecate and athecate dinoflagellates (Sullivan 2009). And, clearance rates of *Strobilidium* by *M. leidyi* supported significant growth of the ctenophores, exceeding those of other ciliates, including *Strombidium*, *Laboea*, and *Favella* (Stoecker et al. 1987). My data demonstrated considerable top-down control of microplanktonic dinoflagellates and ciliates by larval *M. leidyi in situ.* Previous studies investigating the predatory impact of larval *M. leidyi* on microplankton have done so experimentally (e.g., Reeve et al. 1978; Stanlaw et al. 1981; Stoecker et al. 1987; Sullivan and Gifford 2004; 2007; Waggett and Sullivan 2006) and results from my study agree well with these laboratory-based investigations.

*Impact of M. leidyi on planktonic food web structure*

In Great South Bay, high abundances of adult and larval *M. leidyi* coincided with significant declines in mesozooplankton and microzooplankton, respectively. Moreover, predation by *M. leidyi* on mesozooplankton and microplankton prey cascaded down the food web influencing microplankton and nanoplankton, respectively. The greatest densities of adult and transitional-stage *M. leidyi* coincided with substantial increases in dinoflagellates and ciliates, enhancing prey conditions for larval ctenophores. The exception was site A in 2009 when the increase in microplankton coincided with increasing, but not maximum, adult and transitional-stage abundances. However, total adult and transitional-stage abundance at this time exceeded the highest abundances of *M. leidyi* at either site in 2008. In both years, high *M. leidyi* abundance corresponded with substantial declines in copepods, and the subsequent increases in dinoflagellates and aloricate ciliates (Figures 4-7).

The considerable reduction of dinoflagellates and ciliates during larval blooms seems to have resulted in a further effect on nanoplankton. Total nanoplankton abundance increased by nearly 300% during this time in 2009 (site M, Figure 8). Although larvae have been shown to consume nanoplankton such as ciliates and thecate dinoflagellates in laboratory studies (Sullivan and Gifford 2004), my findings suggest that dinoflagellates and flagellates <20 μm are less important prey items for developing ctenophores, at least when sufficient quantities of microplanktonic dinoflagellates and ciliates exist.

Previous studies have documented significant predation on ciliates by copepods (*e.g.*, Stoecker and Egloff 1987; Lonsdale et al. 1996, Calbet and Saiz 2005), but the influence of ctenophore (and copepod) predation on lower trophic levels may be dependent on the individual sizes of the autotrophic community. In mesocosm experiments, copepods grazed heavily on large diatoms when abundant, but fed predominantly on ciliates when smaller algae dominated (Stibor et al. 2004). The authors hypothesized that size-selective feeding by copepods regulates the

responses of the phytoplankton community within food chains of varying length. For example, when larger algae dominate, predation by ctenophores stimulate a trophic cascade transmitted along a three-link food chain (ctenophore-copepod-phytoplankton), whereas when algae are small, their predatory influences are likely to be transmitted along a four-link food chain (ctenophore-copepod-ciliate-phytoplankton). Granéli and Turner (2002) suggested that ciliates serve as a trophic link between their mesozooplankton predators and flagellate prey, and documented increased ciliate abundance and subsequent declines in phytoflagellates in mesocosm treatments containing the cydippid ctenophore *Pleurobrachia pileus*.

In Great South Bay, autotrophic and heterotrophic nanoflagellates (2-20 μm) provide the highest contribution to plankton biomass (Lonsdale et al. 2006), and the trophic structure of the plankton community likely contains four trophic levels from phytoplankton to copepods: picoplankton, nanoplankton, microplankton, and mesozooplankton (Deonarine et al. 2006). The results of my study agree well with those hypothesized by Granéli and Turner (2002) and Stibor et al. (2004) in that predation by ctenophores on mesozooplankton had further influence on microplanktonic ciliates and dinoflagellates. But, the predatory impact of adult ctenophores did not appear to extend further to the nanoplankton community. Rather, direct predation on microplankton by larval ctenophores influenced nanoplanktonic flagellates and dinoflagellates, suggesting that cascading influences of ctenophore predation is limited to three trophic levels in Great South Bay; adult *M. leidyi*-mesozooplankton-microplankton and larval *M. leidyi*-microplankton-nanoplankton (Figure 9). Attempts to quantify picoplankton abundance (i.e., chl *a*, flow cytometry) were not made in this study. Propagation of *M. leidyi* predation along a three-link trophic structure has previously been documented in native (Narragansett Bay; Deason and Smayda 1982) and exotic (Caspian Sea; Kideys et al. 2008, Nasrollahzadeh et al. 2008) habitats of *M. leidyi*, where reductions in mesozooplankton led to increases in phytoplankton during high ctenophore abundances. To my knowledge, this is the first study to document two distinct predatory impacts by *M. leidyi* on lower trophic levels by life stage, and along a four-chain planktonic food web (excluding picoplankton) *in situ*.

## Conclusions

Because populations of *M. leidyi* control, and are controlled by, temporal changes in plankton community structure, mismatches between mesozooplankton prey for adults and microplankton prey for larvae can potentially limit the overall production of *M. leidyi*. I document *in situ* top-down control of microzooplankton (dinoflagellates and aloricate ciliates) by larval *M. leidyi* during ctenophore blooms. My data agrees well with previous, laboratory-based investigations of regulation of microplanktonic prey by developing *M. leidyi* and identifies potential bottom-up control of larval *M. leidyi* by insufficient microplankton densities. This study also identifies two distinct cascading influences on microplankton and nanoplankton by adult and larval *M. leidyi* predation, respectively. These findings suggest that ctenophores are involved in a direct feedback system, wherein intense feeding activity by adults on mesozooplankton releases certain microplankton taxa from grazing pressure, enhancing prey conditions for larval ctenophores.

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Table 1. Mean mesozooplankton abundances (individuals $L^{-1}$) by category at sites M and A 2008 and 2009. The range of values (n=2) is given in parentheses.

| Year | Date | Total mesozooplankton | Copepods (all life stages) | Meroplankton | Tintinnids and rotifers |
|---|---|---|---|---|---|
| 2008 | 8-May | 395 (n/a) | 318 (n/a) | 76 (n/a) | 0 |
| 2008 | 15-May | 256 (56) | 244 (62) | 18 (7) | 17 (11) |
| 2008 | 22-May | 396 (169) | 78 (18) | 10 (6) | 161 (103) |
| 2008 | 28-May | 108 (4) | 83 (9) | 4 (1) | 9 (4) |
| 2008 | 5-Jun | 228 (127) | 206 (111) | 13 (13) | 1 (<1) |
| 2008 | 12-Jun | 143 (95) | 121 (83) | 12 (14) | <1 (<1) |
| 2008 | 19-Jun | 99 (17) | 97 (17) | 1 (<1) | 0 |
| 2008 | 27-Jun | 230 (119) | 216 (108) | 4 (4) | 0 |
| 2008 | 3-Jul | 301 (201) | 274 (181) | 3 (2) | 0 |
| 2008 | 10-Jul | 344 (184) | 328 (173) | 11 (2) | 0 |
| 2008 | 17-Jul | 93 (85) | 57 (54) | 32 (28) | 2 (3) |
| 2008 | 24-Jul | 98 (26) | 59 (11) | 25 (11) | 5 (7) |
| 2008 | 31-Jul | 16 (2) | 5 (2) | 7 (<1) | 2 (2) |
| 2008 | 7-Aug | 77 (n/a) | 7 (n/a) | 11 (n/a) | 39 (n/a) |
| 2008 | 14-Aug | 7 (5) | 5 (4) | 2 (1) | 0 |
| 2008 | 28-Aug | 110 (137) | 43 (41) | 64 (93) | 1 (2) |
| 2008 | 11-Sep | 437 (205) | 118 (69) | 213 (139) | 4 (4) |
| 2008 | 25-Sep | 118 (23) | 93 (16) | 13 (4) | 1 (1) |
| 2008 | 9-Oct | 100 (2) | 35 (<1) | 8 (1) | 36 (1) |
| | | | | | |
| 2009 | 6-May | 785 (n/a) | 647 (n/a) | 47 (n/a) | 0 |
| 2009 | 13-May | 1767 (1467) | 1201 (1046) | 324 (371) | 0 |
| 2009 | 20-May | 745 (184) | 450 (118) | 17 (14) | <1 (<1) |
| 2009 | 27-May | 320 (n/a) | 101 (n/a) | 18 (n/a) | 0 |
| 2009 | 3-Jun | 377 (209) | 723 (19) | 28 (17) | 0 |
| 2009 | 10-Jun | 861 (1438) | 401 (577) | 423 (808) | 0 |
| 2009 | 17-Jun | 847 (1309) | 595 (896) | 162 (265) | 0 |
| 2009 | 24-Jun | 691 (1093) | 624 (988) | 34 (61) | 5 (8) |
| 2009 | 1-Jul | 2249 (742) | 1724 (500) | 20 (9) | 0 |
| 2009 | 8-Jul | 1274 (n/a) | 1213 (n/a) | 6 (n/a) | 7 (n/a) |
| 2009 | 15-Jul | 328 (24) | 294 (<1) | 5 (4.2) | 0 |
| 2009 | 22-Jul | 860 (698) | 779 (615) | 7 (4) | 10 (6) |
| 2009 | 29-Jul | 73 (62) | 57 (60) | 6 (2) | 1 (2) |
| 2009 | 5-Aug | 15 (6) | 11 (3) | 3 (1) | 0 |
| 2009 | 12-Aug | 15 (7) | <1 (<1) | 15 (7) | 0 |
| 2009 | 19-Aug | 7 (5) | <1 (<1) | 7 (5) | 0 |
| 2009 | 26-Aug | 3 (2) | <1 (<1) | 2 (2) | 0 |
| 2009 | 4-Sep | 40 (7) | 29 (12) | 9 (3) | 0 |
| 2009 | 18-Sep | 20 (10) | 11 (4) | 8 (5) | 0 |
| 2009 | 2-Oct | 19 (18) | 7 (1) | 3 (<1) | 9 (18) |
| 2009 | 9-Oct | 5 (n/a) | 4 (n/a) | 1 (n/a) | 0 |
| 2009 | 23-Oct | 34 (9) | 15 (8) | 18 (<1) | <1 (<1) |
| 2009 | 30-Oct | 8 (4) | 5 (2) | 1 (<1) | 1 (1) |

Table 2. Microplankton abundances (cells $mL^{-1}$) and biomasses (µg C $L^{-1}$; given in parenthesis) at sites M and A during 2008 and 2009.

| Year | Date | Site | Centric diatoms | Pennate diatoms | Dinoflagellates | Flagellates | Aloricate ciliates | Loricate ciliates | Other | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| 2008 | 8-May | M | 100.9 (132.5) | 489.1 (79.2) | 225.1 (76.8) | 124.2 (289.5) | 38.8 (117.2) | 23.3 (56.2) | 7.8 | 1009.2 (751.4) |
| 2008 | 15-May | M | 55.0 (21.6) | 128.8 (31.7) | 486.0 (188.3) | 91.4 (85.0) | 12.3 (4.7) | 0.0 | 4.2 | 777.6 (331.3) |
| 2008 | 22-May | M | 43.6 (26.6) | 357.6 (128.8) | 231.1 (66.8) | 61.1 (75.9) | 100.3 (122.1) | 8.7 (134.9) | 8.7 | 811.2 (555.1) |
| 2008 | 28-May | M | 69.8 (52.7) | 401.2 (85.3) | 549.5 (176.3) | 165.7 (76.1) | 279.1 (408.8) | 52.3 (50.2) | 8.7 | 1526.4 (849.4) |
| 2008 | 5-Jun | M | 95.0 (69.0) | 388.6 (18.6) | 941.3 (459.5) | 241.8 (36.3) | 25.9 (29.4) | 8.6 (159.5) | 0.0 | 1701.3 (772.3) |
| 2008 | 12-Jun | M | 32.4 (26.9) | 194.7 (6.4) | 571.1 (220.1) | 142.8 (30.7) | 38.9 (67.6) | 6.5 (7.6) | 0.0 | 986.4 (359.2) |
| 2008 | 19-Jun | M | 22.4 (24.9) | 2253.2 (39.7) | 1129.4 (476.7) | 55.9 (19.7) | 67.1 (49.8) | 5.6 (4.1) | 0.0 | 3533.6 (615.1) |
| 2008 | 27-Jun | M | 43.9 (31.5) | 84.6 (2.4) | 203.8 (146.8) | 15.7 (4.2) | 15.7 (66.6) | 3.1 (51.7) | 0.0 | 366.8 (303.1) |
| 2008 | 3-Jul | M | 50.8 (35.4) | 203.2 (12.1) | 309.1 (757.1) | 25.4 (10.7) | 33.9 (22.4) | 4.2 (3.1) | 0.0 | 626.6 (840.7) |
| 2008 | 10-Jul | M | 55.4 (46.4) | 393.2 (6.4) | 564.9 (273.2) | 16.6 (5.8) | 33.2 (33.3) | 38.8 (51.9) | 0.0 | 1102.0 (417.0) |
| 2008 | 17-Jul | M | 42.5 (28.8) | 1031.9 (17.7) | 2037.8 (1601.5) | 26.0 (12.0) | 259.6 (282.3) | 13.0 (111.1) | 13.0 | 3423.7 (2053.3) |
| 2008 | 24-Jul | M | 60.8 (37.7) | 574.9 (16.2) | 1127.6 (713.3) | 77.4 (91.7) | 44.2 (66.5) | 5.5 (623.6) | 5.5 | 1896.0 (1548.9) |
| 2008 | 31-Jul | M | 117.9 (60.1) | 360.4 (22.8) | 1317.0 (1015.7) | 45.9 (64.8) | 124.5 (150.0) | 0.0 | 0.0 | 1965.6 (1313.5) |
| 2008 | 7-Aug | M | 182.8 (92.4) | 382.1 (9.1) | 2699.7 (2901.4) | 16.6 (2.4) | 822.4 (1278.8) | 0.0 | 8.3 | 4111.9 (4284.1) |
| 2008 | 14-Aug | M | 16.2 (14.7) | 838.8 (16.3) | 439.8 (344.0) | 24.4 (54.2) | 179.2 (187.4) | 0.0 | 0.0 | 1498.5 (616.5) |
| 2008 | 28-Aug | M | 13.6 (10.0) | 265.8 (32.4) | 402.0 (279.6) | 27.3 (15.4) | 224.9 (907.0) | 13.6 (1.8) | 0.0 | 947.2 (1246.1) |
| 2008 | 11-Sep | M | 82.2 (47.9) | 4934.8 (84.0) | 296.1 (175.0) | 33.0 (9.3) | 41.1 (104.4) | 0.0 | 0.0 | 5387.1 (420.6) |
| 2008 | 25-Sep | M | 11.0 (7.2) | 126.5 (2.7) | 247.6 (145.5) | 99.0 (3.8) | 66.0 (55.3) | 5.5 (653.3) | 5.5 | 561.1 (867.8) |
| 2008 | 9-Oct | M | 19.5 (16.8) | 97.3 (2.9) | 227.1 (96.6) | 6.5 (3.8) | 77.9 (61.0) | 0.0 | 0.0 | 428.3 (181.0) |
| | | | | | | | | | | |
| 2008 | 22-May | A | 33.2 (86.6) | 99.7 (33.8) | 207.7 (121.6) | 58.1 (186.8) | 12.5 (12.5) | 4.2 (18.6) | 8.3 | 423.7 (459.9) |
| 2008 | 5-Jun | A | 47.5 (53.8) | 285.5 (82.2) | 584.1 (264.9) | 194.7 (36.0) | 26.0 (57.1) | 13.0 (59.4) | 0.0 | 1150.8 (553.4) |
| 2008 | 19-Jun | A | 42.5 (49.9) | 77.9 (1.8) | 207.7 (63.7) | 0.0 | 51.9 (53.5) | 45.4 (172.7) | 0.0 | 425.4 (341.4) |
| 2008 | 3-Jul | A | 33.2 (38.2) | 132.9 (4.7) | 17.4 (37.7) | 4.2 (10.0) | 4.2 (3.9) | 0.0 | 0.0 | 191.8 (94.5) |
| 2008 | 17-Jul | A | 14.7 (10.6) | 220.5 (4.5) | 254.8 (136.9) | 9.8 (0.2) | 132.3 (169.1) | 4.9 (0.4) | 4.9 | 641.9 (321.6) |
| 2008 | 31-Jul | A | 14.7 (13.3) | 220.5 (7.5) | 14.7 (39.0) | 4.9 (7.5) | 122.5 (7.7) | 0.0 | 0.0 | 377.3 (75.0) |
| 2008 | 14-Aug | A | 86.4 (142.9) | 354.1 (10.2) | 414.5 (324.7) | 34.5 (5.2) | 51.8 (11.6) | 0.0 | 0.0 | 941.3 (494.6) |
| 2008 | 28-Aug | A | 17.5 (17.6) | 169.6 (11.8) | 310.0 (160.2) | 17.5 (31.8) | 70.2 (56.3) | 0.0 | 0.0 | 585.0 (277.7) |
| 2008 | 11-Sep | A | 312.5 (312.5) | 1151.4 (30.8) | 403.0 (308.3) | 65.8 (37.4) | 74.0 (389.6) | 0.0 | 41.1 | 2047.9 (1078.6) |
| 2008 | 25-Sep | A | 159.7 (102.2) | 159.7 (5.7) | 147.4 (93.5) | 411.5 (2886.3) | 24.6 (18.5) | 0.0 | 12.3 | 915.2 (3106.3) |
| 2008 | 9-Oct | A | 101.1 (134.5) | 120.1 (12.8) | 75.8 (41.1) | 63.2 (179.2) | 25.3 (18.4) | 0.0 | 0.0 | 385.5 (386.0) |
| | | | | | | | | | | |
| 2009 | 6-May | M | 0.0 | 607.2 (53.2) | 717.7 (287.0) | 11.0 (7.2) | 0.0 | 0.0 | 0.0 | 1335.9 (347.4) |
| 2009 | 13-May | M | 0.0 | 54.7 (24.2) | 6.1 (1.5) | 18.2 (39.9) | 0.0 | 6.1 (3.0) | 0.0 | 85.1 (68.6) |
| 2009 | 20-May | M | 0.0 | 238.5 (74.4) | 57.6 (26.2) | 16.4 (43.5) | 24.7 (20.0) | 0.0 | 8.2 | 345.4 (164.1) |
| 2009 | 27-May | M | 22.4 (8.5) | 715.7 (125.6) | 279.6 (114.5) | 33.5 (8.5) | 145.4 (228.7) | 268.4 (186.3) | 0.0 | 1464.9 (672.2) |
| 2009 | 3-Jun | M | 7.8 (18.4) | 39.2 (0.9) | 368.3 (148.0) | 47.0 (146.9) | 94.0 (121.3) | 0.0 | 7.8 | 564.2 (435.5) |
| 2009 | 10-Jun | M | 8.1 (5.4) | 193.8 (7.2) | 395.7 (334.8) | 24.2 (6.7) | 16.2 (236.8) | 0.0 | 0.0 | 638.0 (590.9) |
| 2009 | 17-Jun | M | 16.4 (12.0) | 74.0 (1.3) | 65.8 (52.0) | 41.1 (16.9) | 49.3 (61.4) | 0.0 | 0.0 | 246.7 (143.6) |
| 2009 | 24-Jun | M | 16.4 (9.4) | 353.7 (7.0) | 57.6 (20.6) | 16.4 (9.9) | 8.2 (7.2) | 41.1 (17.0) | 16.4 | 509.9 (71.1) |
| 2009 | 1-Jul | M | 13.6 (9.9) | 306.6 (17.7) | 129.5 (55.5) | 6.8 (8.8) | 6.8 (3.4) | 0.0 | 0.0 | 463.4 (95.3) |
| 2009 | 8-Jul | M | 24.8 (11.9) | 371.9 (6.2) | 82.6 (28.7) | 16.5 (54.9) | 8.3 (150.2) | 0.0 | 16.5 | 520.6 (251.9) |
| 2009 | 15-Jul | M | 8.3 (4.0) | 406.9 (6.3) | 157.8 (90.5) | 24.9 (29.8) | 107.9 (141.9) | 0.0 | 0.0 | 705.8 (272.4) |
| 2009 | 22-Jul | M | 24.7 (12.3) | 485.3 (6.2) | 74.0 (43.5) | 41.1 (32.2) | 24.7 (29.4) | 8.2 (67.5) | 8.2 | 666.2 (191.1) |
| 2009 | 29-Jul | M | 19.5 (11.7) | 527.7 (9.8) | 713.4 (446.6) | 0.0 | 1123.9 (1407.0) | 0.0 | 39.1 | 2423.7 (1875.1) |
| 2009 | 5-Aug | M | 22.4 (15.6) | 1610.3 (44.4) | 313.1 (136.3) | 11.2 (8.7) | 33.5 (32.8) | 0.0 | 11.2 | 2001.6 (237.9) |
| 2009 | 12-Aug | M | 8.6 (2.5) | 431.8 (8.2) | 172.7 (114.9) | 0.0 | 69.1 (243.9) | 0.0 | 60.5 | 742.7 (369.4) |
| 2009 | 19-Aug | M | 24.7 (8.6) | 1266.6 (13.9) | 197.4 (216.0) | 8.2 (7.5) | 24.7 (105.9) | 0.0 | 57.6 | 1579.1 (351.9) |
| 2009 | 26-Aug | M | 191.7 (88.3) | 564.4 (19.2) | 266.2 (128.6) | 21.3 (13.1) | 10.6 (90.9) | 0.0 | 31.9 | 1086.3 (340.1) |
| 2009 | 4-Sep | M | 190.1 (263.0) | 2079.9 (52.2) | 55.9 (79.8) | 11.2 (3.6) | 55.9 (265.1) | 11.2 (1639.4) | 22.4 | 2426.6 (2303.1) |
| 2009 | 18-Sep | M | 107.9 (89.7) | 489.9 (12.9) | 166.1 (245.6) | 24.9 (38.0) | 16.6 (13.4) | 0.0 | 26.7 | 832.1 (399.6) |
| 2009 | 2-Oct | M | 8.6 (15.5) | 164.1 (2.6) | 250.4 (185.7) | 17.3 (6.7) | 120.9 (150.9) | 51.8 (541.2) | 34.5 | 647.7 (902.6) |
| 2009 | 9-Oct | M | 174.4 (286.8) | 456.7 (6.4) | 274.0 (160.5) | 66.4 (115.3) | 91.3 (159.2) | 0.0 | 58.1 | 1121.0 (728.1) |
| 2009 | 23-Oct | M | 32.9 (13.7) | 427.7 (17.5) | 213.8 (122.0) | 65.8 (71.4) | 8.2 (11.3) | 8.2 (5.4) | 16.4 | 773.1 (241.4) |
| 2009 | 30-Oct | M | 77.0 (36.1) | 2924.5 (77.9) | 230.9 (129.1) | 0.0 | 64.1 (156.4) | 0.0 | 0.0 | 3296.5 (399.5) |
| | | | | | | | | | | |
| 2009 | 20-May | A | 19.0 (18.5) | 120.1 (9.0) | 12.6 (11.1) | 12.6 (22.1) | 12.6 (11.1) | 0.0 | 0.0 | 177.0 (71.9) |
| 2009 | 17-Jun | A | 7.3 (6.5) | 65.3 (1.2) | 94.4 (40.6) | 14.5 (4.6) | 29.0 (40.4) | 0.0 | 7.3 | 217.7 (93.3) |
| 2009 | 1-Jul | A | 13.0 (9.8) | 97.3 (4.9) | 181.7 (79.5) | 19.5 (12.0) | 0.0 | 0.0 | 0.0 | 311.5 (106.2) |
| 2009 | 15-Jul | A | 25.9 (24.4) | 95.0 (3.0) | 43.2 (100.2) | 25.9 (26.9) | 60.5 (82.2) | 0.0 | 0.0 | 250.4 (236.6) |
| 2009 | 29-Jul | A | 68.0 (34.6) | 2662.0 (63.2) | 589.0 (406.6) | 34.0 (14.6) | 566.4 (938.7) | 11.3 (142.4) | 34.0 | 3964.6 (1600.0) |
| 2009 | 5-Aug | A | 22.2 (31.9) | 830.7 (18.0) | 177.2 (90.1) | 11.1 (10.0) | 99.7 (124.1) | 0.0 | 22.2 | 1163.0 (274.2) |
| 2009 | 12-Aug | A | 49.3 (44.5) | 230.3 (7.2) | 246.7 (271.7) | 24.7 (84.6) | 90.5 (190.4) | 0.0 | 41.1 | 682.6 (598.4) |
| 2009 | 26-Aug | A | 288.9 (205.3) | 1744.2 (107.0) | 181.9 (158.0) | 10.7 (3.5) | 10.7 (46.6) | 0.0 | 42.8 | 2279.3 (520.3) |
| 2009 | 18-Sep | A | 148.0 (99.2) | 674.4 (29.9) | 106.9 (146.3) | 49.3 (158.5) | 8.2 (11.3) | 0.0 | 65.8 | 1052.8 (445.2) |
| 2009 | 30-Oct | A | 16.6 (7.9) | 871.9 (16.2) | 240.8 (129.4) | 8.3 (7.5) | 49.8 (176.2) | 0.0 | 16.6 | 1204.0 (337.2) |

Table 3. Nanoplankton abundances (cells $mL^{-1}$) at sites M and A during 2009.

| Site | Date | Centric diatoms | Pennate diatoms | Dinoflagellates | Flagellates | Aloricate ciliates | Total |
|---|---|---|---|---|---|---|---|
| M | 6-May | 0.0 | 0.0 | 684.5 | 132.5 | 0.0 | 817.0 |
| M | 13-May | 0.0 | 0.0 | 0.0 | 6.1 | 0.0 | 6.1 |
| M | 20-May | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| M | 27-May | 0.0 | 22.4 | 55.9 | 22.4 | 0.0 | 100.6 |
| M | 3-Jun | 0.0 | 0.0 | 0.0 | 0.0 | 54.9 | 54.9 |
| M | 10-Jun | 0.0 | 0.0 | 129.2 | 105.0 | 72.7 | 306.9 |
| M | 17-Jun | 0.0 | 49.3 | 156.2 | 24.7 | 8.2 | 238.4 |
| M | 24-Jun | 0.0 | 24.7 | 90.5 | 16.4 | 8.2 | 139.8 |
| M | 1-Jul | 0.0 | 0.0 | 88.6 | 54.5 | 0.0 | 143.1 |
| M | 8-Jul | 24.8 | 16.5 | 82.6 | 49.6 | 8.3 | 181.8 |
| M | 15-Jul | 16.6 | 8.3 | 91.3 | 41.5 | 0.0 | 157.8 |
| M | 22-Jul | 0.0 | 16.4 | 90.5 | 8.2 | 0.0 | 115.1 |
| M | 29-Jul | 0.0 | 0.0 | 537.5 | 195.5 | 9.8 | 742.7 |
| M | 5-Aug | 22.4 | 0.0 | 2236.5 | 693.3 | 0.0 | 2952.1 |
| M | 12-Aug | 17.3 | 0.0 | 380.0 | 138.2 | 0.0 | 535.4 |
| M | 19-Aug | 8.2 | 238.5 | 255.0 | 148.0 | 0.0 | 649.7 |
| M | 26-Aug | 74.5 | 0.0 | 426.0 | 53.2 | 0.0 | 553.8 |
| M | 4-Sep | 22.4 | 0.0 | 134.2 | 67.1 | 0.0 | 223.6 |
| M | 18-Sep | 33.2 | 8.3 | 99.6 | 174.4 | 8.3 | 323.8 |
| M | 2-Oct | 0.0 | 17.3 | 267.7 | 77.7 | 60.5 | 423.2 |
| M | 9-Oct | 91.3 | 0.0 | 440.1 | 348.8 | 24.9 | 905.1 |
| M | 19-Oct | 0.0 | 57.6 | 115.1 | 0.0 | 0.0 | 172.7 |
| M | 23-Oct | 24.7 | 0.0 | 444.1 | 625.1 | 0.0 | 1093.9 |
| M | 30-Oct | 192.4 | 0.0 | 525.9 | 692.6 | 0.0 | 1410.9 |
| | | | | | | | |
| A | 17-Jun | 0.0 | 0.0 | 239.5 | 65.3 | 21.8 | 326.6 |
| A | 1-Jul | 0.0 | 6.5 | 136.3 | 32.4 | 6.5 | 181.7 |
| A | 15-Jul | 17.3 | 0.0 | 207.3 | 69.1 | 8.6 | 302.3 |
| A | 29-Jul | 0.0 | 0.0 | 838.2 | 158.6 | 34.0 | 1030.8 |
| A | 5-Aug | 11.1 | 11.1 | 697.8 | 110.8 | 0.0 | 830.7 |
| A | 12-Aug | 16.4 | 8.2 | 353.7 | 131.6 | 0.0 | 509.9 |
| A | 26-Aug | 214.0 | 0.0 | 438.7 | 149.8 | 0.0 | 802.6 |
| A | 18-Sep | 0.0 | 8.2 | 74.0 | 74.0 | 0.0 | 156.3 |
| A | 30-Oct | 16.6 | 0.0 | 548.0 | 274.0 | 8.3 | 847.0 |

Figure 1. Sampling locations (sites M and A) in Great South Bay, Long Island, NY, USA.

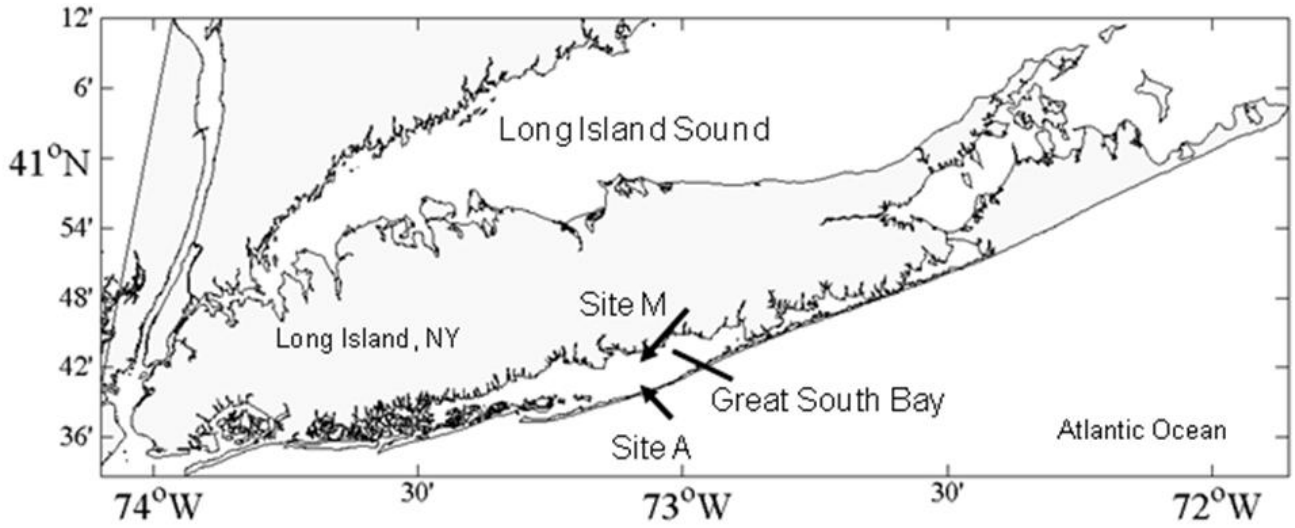
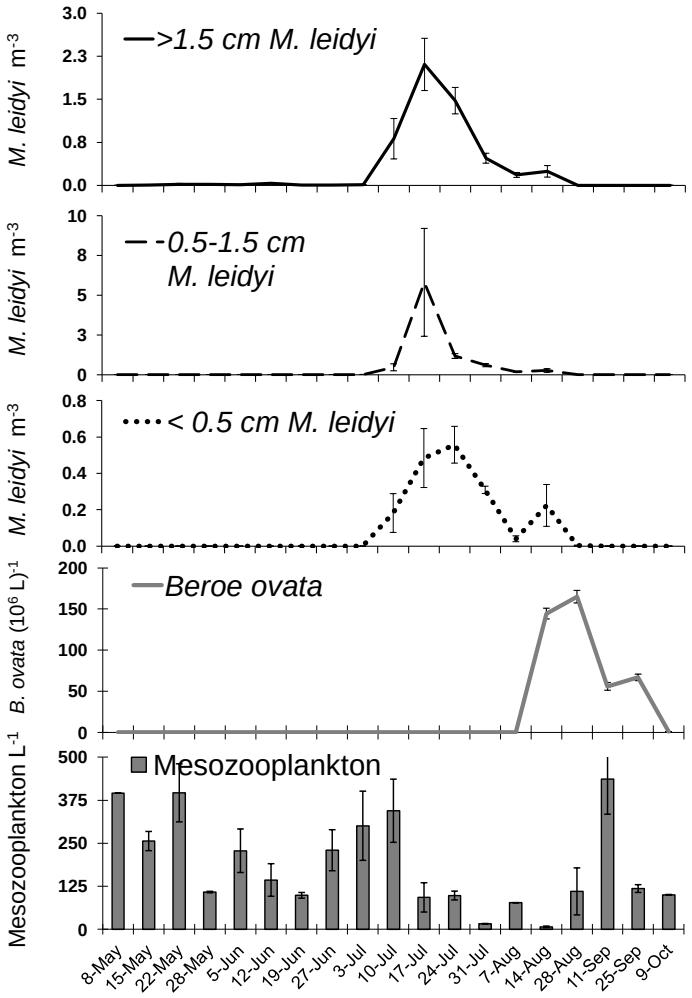
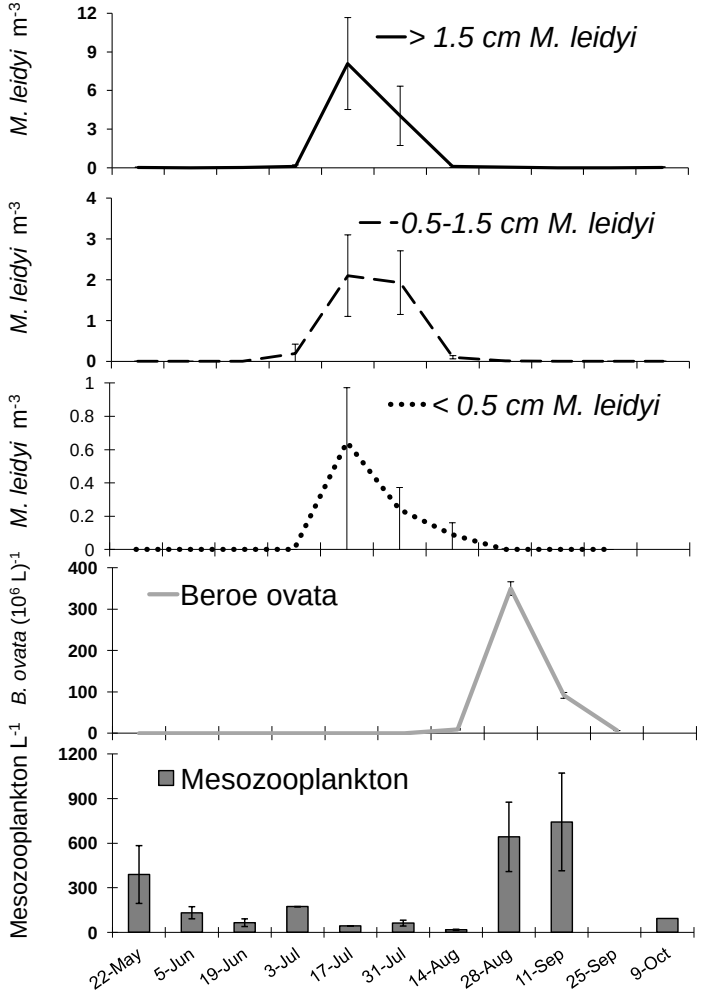


Figure 2. Mean mesozooplankton abundance (individuals $L^{-1}$; +/- range; n=2) and *M. leidyi* abundance (all size classes; individuals $m^{-3}$; +/- s.d.; n=4) in Great South Bay at sampling sites M (a) and A (b) in 2008. Note the differences in the secondary y-axis.

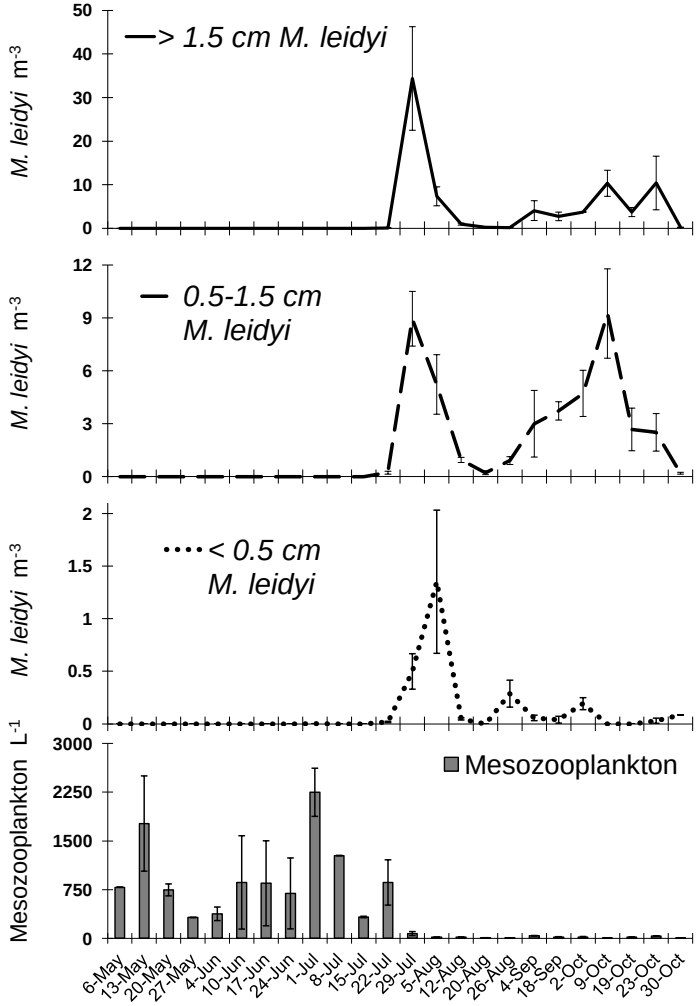



(a)

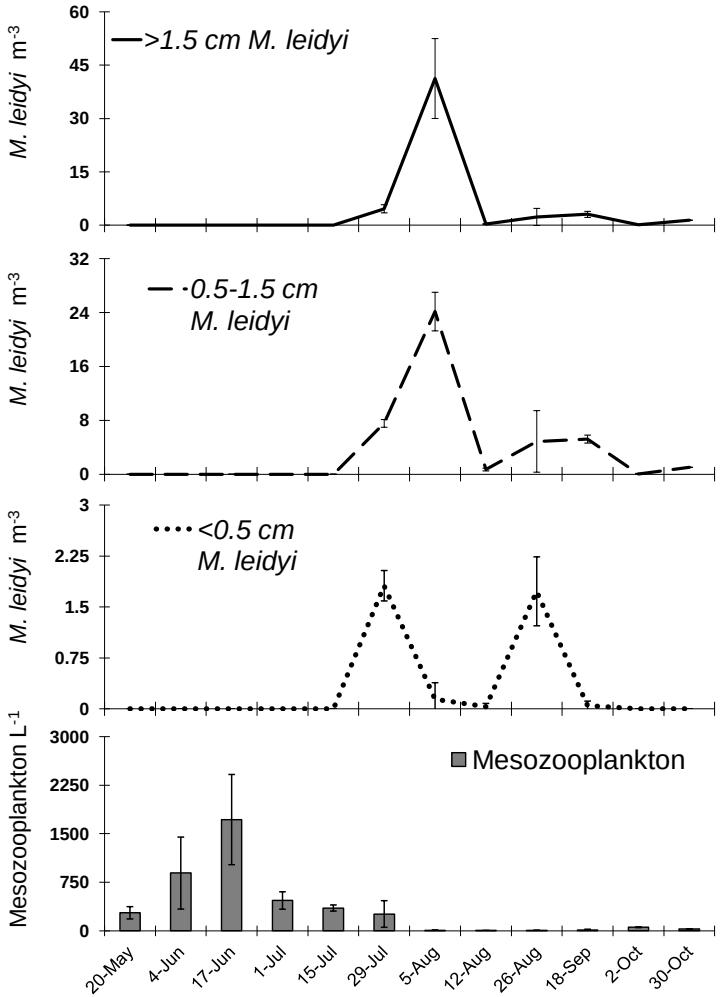



(b)

Figure 3. Mean mesozooplankton abundance (individuals $L^{-1}$; +/- range; n=2) and *M. leidyi* abundance (all size classes; individuals $m^{-3}$; +/- s.d.; n=4) in Great South Bay at sampling sites M (a) and A (b) during 2009.




(a)




(b)

Figure 4. Mean adult (> 1.5 cm), transitional (0.5-1.5 cm), and larval (<0.5 cm) *M. leidyi* abundance (individuals $m^{-3}$; +/- s.d.), microplanktonic dinoflagellate and aloricate ciliate abundance (cells $mL^{-1}$), and total copepod abundance (all life stages; $L^{-1}$; +/- s.d.) in 2008 at site M. The vertical line marks the onset of rapid *M. leidyi* increases.

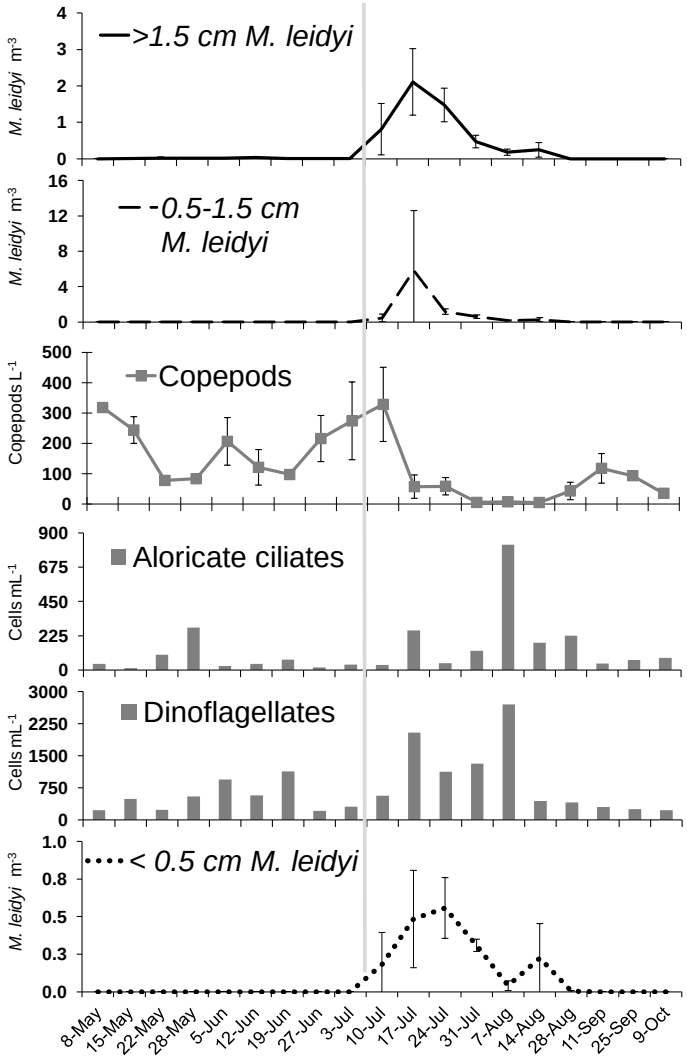


Figure 5. Mean adult (> 1.5 cm) and transitional (0.5-1.5 cm) *M. leidyi* abundance (individuals $m^{-3}$; +/- s.d.), microplanktonic dinoflagellate and aloricate ciliate abundances (cells $mL^{-1}$), and total copepod abundance (all life stages; $L^{-1}$; +/- s.d.) in 2008 at site A. No sampling of mesozooplankton occurred on Sep 25 due to the weather. The vertical line marks the onset of rapid *M. leidyi* increases.

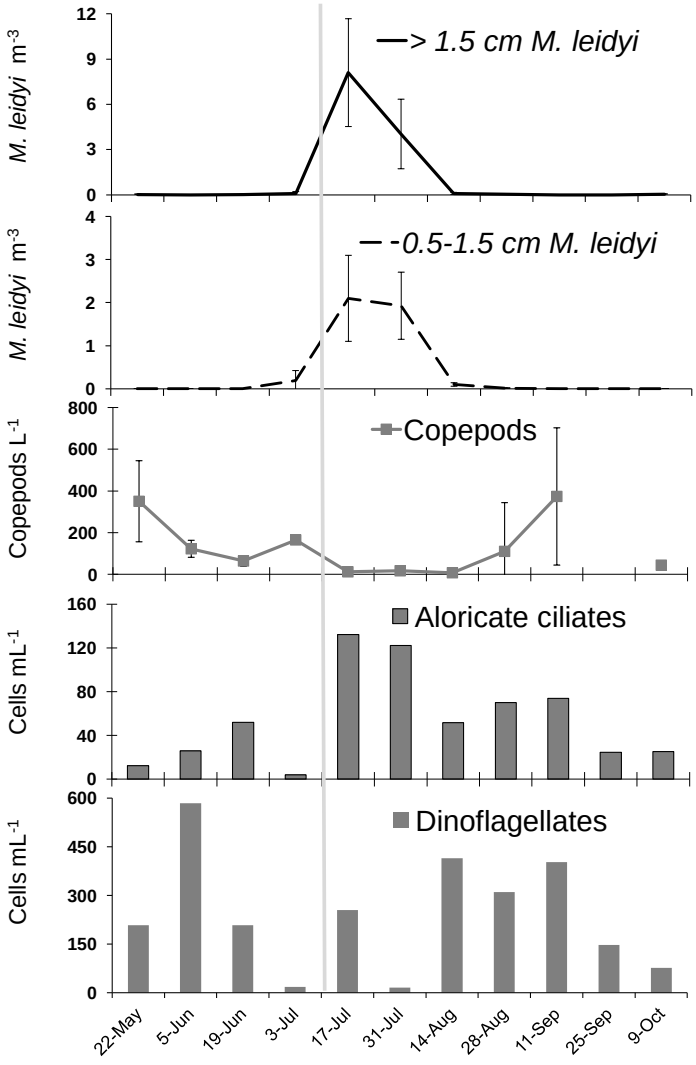


Figure 6. Mean adult (> 1.5 cm), transitional (0.5-1.5 cm), and larval (<0.5 cm) *M. leidyi* abundance (individuals $m^{-3}$; +/- s.d.), microplanktonic dinoflagellate and aloricate ciliate abundance (cells $mL^{-1}$, and total copepod abundance (all life stages; $L^{-1}$; +/- s.d.) in 2009 at site M. The vertical line marks the onset of rapid *M. leidyi* increases.

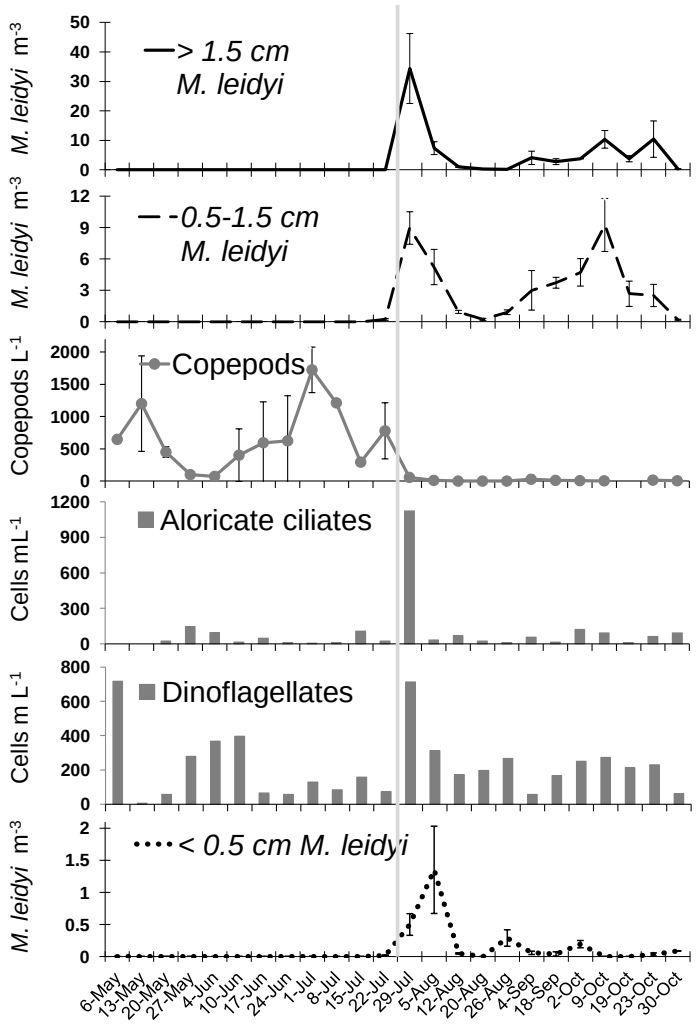


Figure 7. Mean adult (> 1.5 cm) and transitional (0.5-1.5 cm) *M. leidyi* abundance (individuals $m^{-3}$; +/- s.d.), microplanktonic dinoflagellate and aloricate ciliate abundance (cells $mL^{-1}$), and total copepod abundance (all life stages; $L^{-1}$; +/- s.d.) in 2009 at site A. The vertical line marks the onset of rapid *M. leidyi* increases.

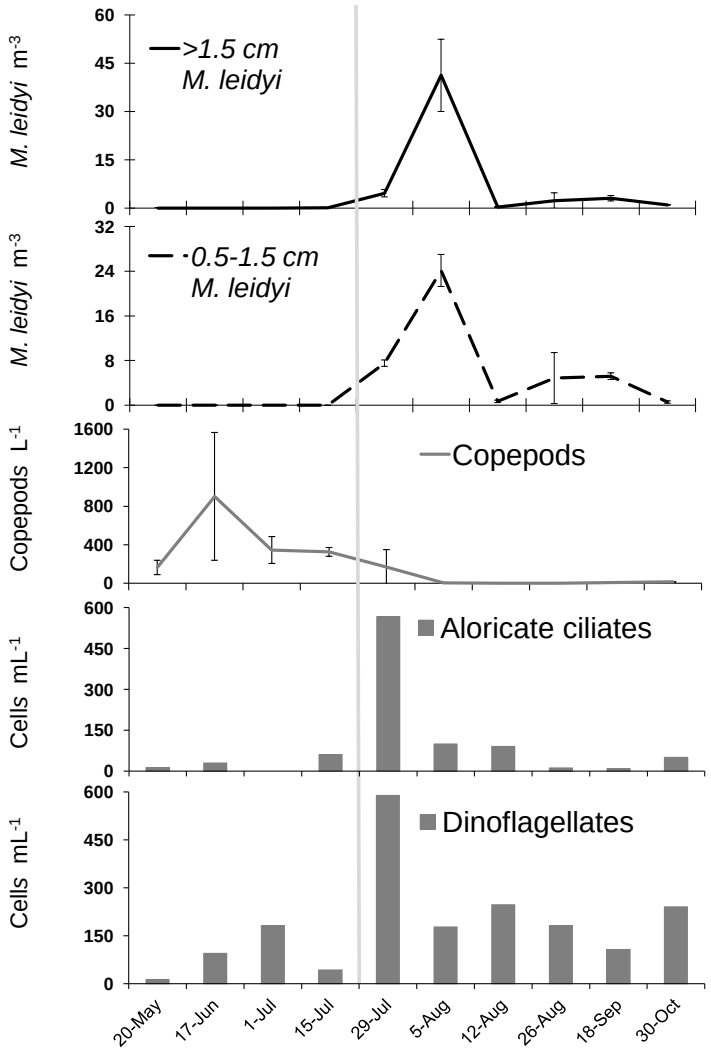


Figure 8. Abundances of microplanktonic dinoflagellates and ciliates (cells $mL^{-1}$), total nanoplankton (cells $mL^{-1}$) and mean < 0.5 cm *M. leidyi* (individuals $m^{-3}$; +/- s.d.) in 2009 at site M.

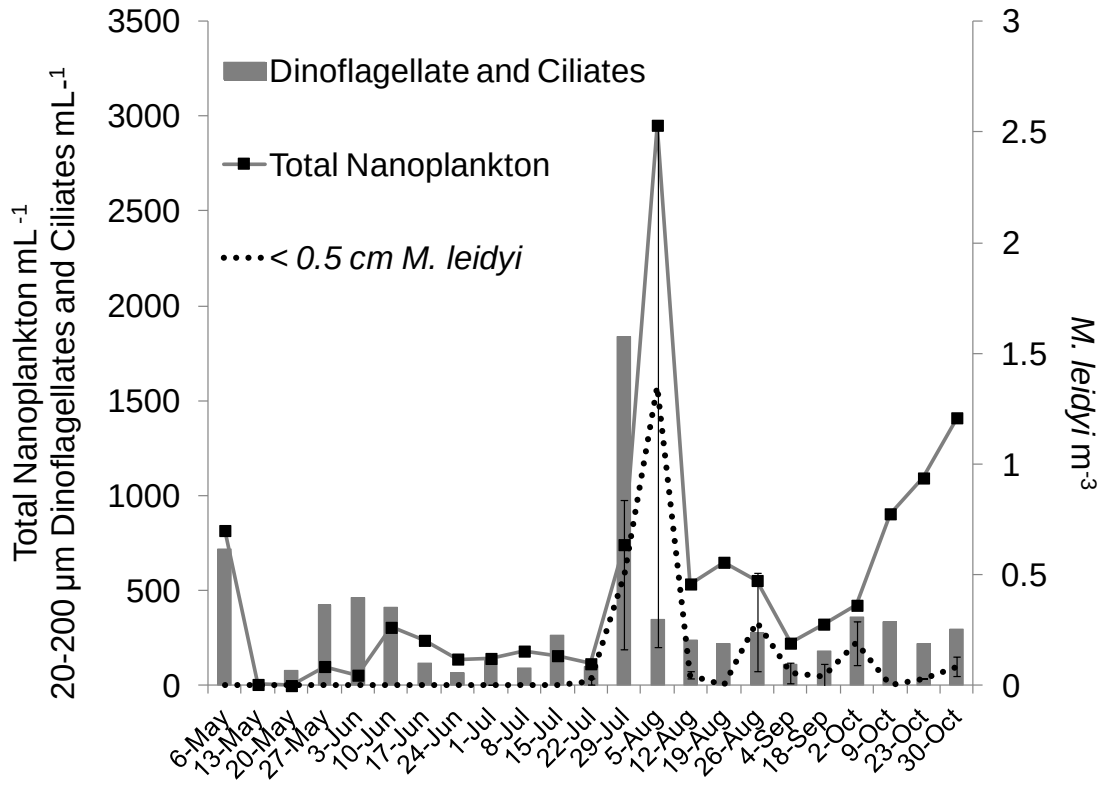
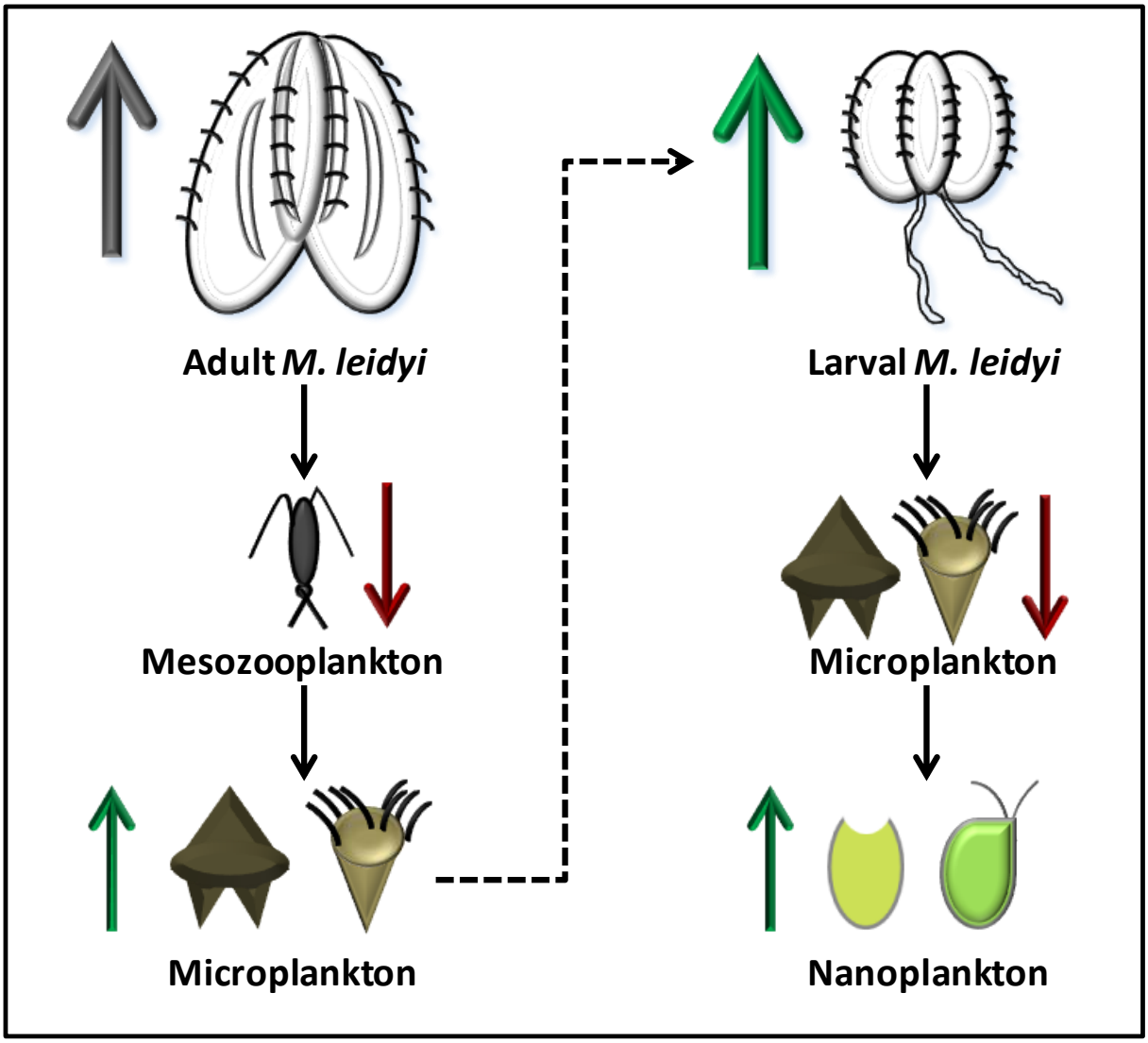


Fig. 9. Planktonic food web of Great South Bay, NY. High abundances of adult *M. leidyi* reduce mesozooplanktonic predation pressure on microplanktonic dinoflagellates and ciliates, which subsequently increase in abundance. As a result, the feeding conditions and survival of larval ctenophores are improved, consequently reducing microplanktonic predation on nanoplankton.



# CHAPTER TWO

Interannual differences in plankton structure drive changes in the fecundity and recruitment of *Mnemiopsis leidyi* in a Long Island estuary

## Abstract

The ctenophore *Mnemiopsis leidyi* is characterized by seasonal population blooms, which can exert significant predatory control on the plankton community. The magnitude of these blooms varies from year to year and is itself controlled by environmental (biotic and abiotic) factors. I examined plankton abundance and composition along with ctenophore egg production rates and gut contents to identify factors influencing the recruitment of *M. leidyi* in a Long Island estuary. Significant interannual differences in *M. leidyi* abundance, fecundity and recruitment were identified. Ctenophores contained nearly three times as many prey items in their guts and produced twice as many eggs in 2008 during a brown tide (*Aureococcus anophagefferens*) than in 2009, a non-bloom year. However, despite the increased fecundity, abundance of *M. leidyi* was five-times lower than in 2009. Field data identified a mismatch between maximum ctenophore egg production (eggs produced $d^{-1}$ $m^{-3}$) and high microplankton (ciliates and dinoflagellates) abundance in 2008, in contrast to 2009 when the two coincided. Since dinoflagellates and ciliates are important prey items for larval *M. leidyi*, insufficient densities of the former can limit successful recruitment of the latter. These data suggest that *A. anophagefferens* indirectly enhanced ctenophore fecundity, however, the mismatch between optimum prey conditions for the larvae and ample egg production by adults ultimately limited recruitment of *M. leidyi* in 2008. This study further documents the importance of microplankton for larval *M. leidyi* and underlines the role of lower trophic levels in influencing *M. leidyi* population dynamics.

## Introduction

The ctenophore *Mnemiopsis leidyi* is an important gelatinous predator characterized by seasonal population blooms which exhibit intra-annual and interannual variation in abundance (e.g., Costello et al. 2006). Blooms of *M. leidyi* are made up of lobate adults and cydippid larvae, which can exert significant regulatory control over mesozooplankton (e.g., Kremer 1979; Deason and Smayda 1982; Purcell et al. 2001; Purcell and Decker 2005; McNamara et al. 2010) and microplankton (Stoecker et al. 1987; Sullivan and Gifford 2004; Rapoza et al. 2005; Sullivan and Gifford 2007; McNamara et al. 2013, Chapter One), respectively. Therefore, the predatory influence of *M. leidyi* varies both within and between years, and is dependent on the magnitude and size-structure of the ctenophore population. Conversely, fecundity and recruitment of *M. leidyi* depends in large part on the abundance and composition of the plankton community. While previous studies have focused on the top down predatory role of *M. leidyi*, relatively-little attention has been paid to the bottom-up processes that regulate their seasonal population dynamics.

Ctenophore fecundity is dependent on biotic and abiotic factors. Egg production rates of *M. leidyi* correlate positively with ctenophore size and prey density (Baker and Reeve 1974; Kremer 1976; Reeve et al. 1989; Grove and Breitburg 2005) and is temperature-dependent; egg production is negligible at <10 °C (Kremer 1976; Purcell et al. 2001; Costello et al. 2006). Under favorable seawater temperatures, *Mnemiopsis* produces eggs within thirteen days of hatching and adults regularly produce 2,000-3,000 eggs $d^{-1}$ at high zooplankton densities, while larger (>4 cm) *M. leidyi* can produce >10,000 eggs $d^{-1}$ under ideal conditions (Baker and Reeve 1974; Kremer 1976; Reeve et al. 1989; Costello et al. 2006). A period of starvation of two to four days resulted in a cessation of egg production in laboratory-reared *M. leidyi*, which was reversible at high food concentrations over the same time period (Reeve et al. 1989). A prey

abundance of >100 copepods $L^{-1}$ (mixed-stage cultures of *Acartia tonsa*) was required in order to successfully maintain egg production in field-collected *M. leidyi* (Sullivan and Gifford 2007).

Field and laboratory studies have demonstrated that survival and growth of hatched *M. leidyi* depend, in part, on the availability and composition of microplanktonic prey. Larvae incubated in low concentrations of microplankton were significantly smaller than larvae incubated in medium and high concentrations (Sullivan and Gifford 2007), and those fed a diet consisting of dinoflagellates, ciliates and/or copepod nauplii exhibited significantly higher growth and survival rates than those fed other microplanktonic taxa (Stoecker et al. 1987; Sullivan and Gifford 2007). In Great South Bay, New York, high abundances of dinoflagellates and ciliates preceded an increase in larval *M. leidyi* by one week, followed by subsequent decreases in the abundance of these microplanktonic taxa (McNamara et al. 2013, Chapter One). While control of microplanktonic dinoflagellates and ciliates by larval *M. leidyi* has been demonstrated *in situ* (McNamara et al. 2013, Chapter One), regulation by the plankton community of ctenophore fecundity and recruitment has not been fully examined.

The aim of this study was to identify and interpret bottom-up controls of *M. leidyi* in a Long Island estuary. Plankton abundance and composition were analyzed alongside egg production rates and gut contents of *M. leidyi* over two years in Great South Bay. Intra- and interannual differences in feeding, fecundity, and recruitment of *M. leidyi* were identified in association with differences in plankton community structure. To my knowledge, this is the first study to examine differences in *M. leidyi* fecundity and recruitment as a function of lower planktonic trophic assemblages *in situ*.

## Methods

*Temporal and spatial distribution of M. leidyi*

Collections for ctenophores were made weekly from May through October in 2008 and 2009 in Great South Bay, New York (Figure 1). Sampling was conducted by boat and occurred weekly at site M and biweekly at site A (except during high *M. leidyi* abundance when weekly collections were made) using a 1.0-m diameter, 1000-µm mesh net and a 0.5-m diameter, 250-µm mesh net equipped with flow meters (n=2 tows for each net). An exception to weekly sampling occurred at site M in 2008 when one planned sampling date (Aug 21) was canceled due to severe weather. Sampling locations were chosen for their nearness to shore (site M) and proximity to Fire Island Inlet (site A). To minimize damage to ctenophores during collection, nets were equipped with soft, flexible cod ends and tow times restricted to short intervals. Tows were conducted obliquely to sample the entire water column (~1.5 m and 3 m water depth at sites A and M, respectively). Collected ctenophores were rinsed of debris and any surface-attached zooplankton (e.g., crab zoea) with 20-µm filtered seawater and then poured through a 500-µm sieve to remove excess water. Total live volume (biovolume) of ctenophores was then measured in graduated cylinders. Collected ctenophores were counted individually and measured (length, including lobes) to the nearest 0.5 cm (when smaller individuals dominated) or 1.0 cm (when larger individuals dominated) and divided into length-based size-classes. Depending upon ctenophore abundance, either the entire sample or only a subsample was measured. All other species of ctenophores were also counted and recorded.

*Temporal and spatial distribution of mesozooplankton and microplankton*

Sampling of mesozooplankton and micrometazoa (*i.e.*, copepod eggs and nauplii, rotifers) was conducted as described for ctenophores but using a 0.5-m diameter, 64-μm mesh net (n=2) equipped with a flow meter. Samples were preserved immediately in 5% (final concentration) buffered formalin. In the laboratory, all mesozooplankton were identified (a minimum of 200; Omori and Ikeda, 1992) to the lowest possible taxonomic group using a dissecting microscope.

Microplankton abundance and composition data were also collected during sampling and are reported in McNamara et al. (2013, Chapter One).

*Fecundity of M. leidyi*

Ctenophores representing all sizes were collected for egg production studies. Collections were made only when *M. leidyi* were sufficiently abundant because all specimens were individually recovered by dip net, making collections difficult during low (<1 $m^{-3}$) abundances. Field-collected *M. leidyi* were transferred to the laboratory where they were placed into individual, gridded, watch glasses containing 0.45-μm filtered seawater and held in an incubator set at ambient temperature and light conditions. After 24 hours, the ctenophores were removed and rinsed with the filtered seawater over the watch glass to allow enumeration of total eggs using a dissecting scope. When egg production was extremely high (>1,000 eggs), a subsample was collected, and a daily egg production rate (eggs produced $individual^{-1}$ $d^{-1}$) was calculated from enumeration of the subsample. Subsamples were accomplished by first measuring and then gently stirring the contents of the watch glass in a graduated cylinder and beaker, respectively. While the mixture was being stirred, a small (~10-20%) aliquot was removed by pipette and transferred to a smaller, gridded watch glass for examination under the microscope.

In order to estimate total (population) egg production rates for Great South Bay, mean daily egg production values (from above) were calculated per size class of ctenophore (*i.e.*, 1-2 cm, 2-3 cm, etc.) and multiplied by the abundances of that size. These values were then tallied to establish an estimate of the number of eggs produced by *M. leidyi* $m^{-3}$ $d^{-1}$ for each sampling site and date.

*Prey consumption and selective feeding by M. leidyi*

Ctenophores of all sizes were also collected for gut content analyses. As above, collections were made by dip net and only when *M. leidyi* were sufficiently abundant. Individual *M. leidyi* were measured to the nearest millimeter, rinsed with 20-μm filtered seawater to remove any surface-attached zooplankton, and preserved immediately in a solution of 5% buffered formalin. In the laboratory, gut contents were identified to the nearest possible taxon using a dissecting scope.

Gut content analyses of *M. leidyi* were compared with zooplankton abundance estimates to determine relative prey selectivity for the most abundant mesozooplankton taxa: *Acartia tonsa* (adults, copepodites and nauplii), *Oithona similis* (adults and copepodites), other copepod nauplii (including *O. similis*), bivalve and gastropod veligers, and polychaetes. Prey preference by *M. leidyi* was estimated using Ivlev's electivity index (*E*) (Ivlev 1955; cited in Omori and Ikeda 1992):

$$E_i = (r_i - n_i) / (r_i + n_i)$$

where $r_i$ and $n_i$ denote the number of prey items in the gut and environment, respectively. Values ranged from -1 to 1, with positive and negative values indicating positive and negative selection for or against a prey item, respectively.

*Statistical Analysis*

Data were analyzed by one- and two-way ANOVAs and by multiple regressions using BIOMstat: Statistical Software for Biologists, Version 3.30 by Applied Biostatistics, Inc., 10 Inwood Road, Port Jefferson, NY 11777. No transformations of data were necessary.

## Results

*Population dynamics of ctenophores and mesozooplankton in Great South Bay*

Population densities of *Mnemiopsis leidyi* differed significantly between sampling years in Great South Bay (*df*= 1, 209; *Fs*= 10.4; *p*= 0.002; two-way ANOVA with station and year as fixed variables; McNamara et al. 2013, Chapter One). Maximum abundance of *M. leidyi* was approximately five times greater in 2009 than in 2008 (Figure 2). *Mnemiopsis* was present in very low concentrations when sampling commenced in May in 2008, and became abundant (>1 individual $m^{-3}$) on Jul 10$^{th}$. In contrast, *M. leidyi* was not detected until mid-June in 2009, and did not become abundant until Jul 29$^{th}$. Population densities did not differ significantly between sampling stations in either year (*df*= 1, 209; *Fs*= 2.60; *p*= 0.109; two-way ANOVA with station and year as fixed variable; McNamara et al. 2013, Chapter One).

In 2008, the arrival of *Beroe ovata* Mayer 1912 coincided with the decline of *M. leidyi* in Great South Bay (Figure 2a, b). The predatory ctenophore was first identified on Aug 14 at both sites and persisted through the end of sampling. Abundances of *B. ovata* were substantially lower than that of *M. leidyi*; maximum densities of the former occurred at site A on Aug 28 with 0.3 individuals $m^{-3}$. *Beroe* was not identified in Great South Bay in 2009. The sea gooseberry, *Pleurobrachia pileus* Müller 1776, was identified in both years, but only once, at site A. Abundances of *P. pileus* were also low, averaging 0.03 individuals $m^{-3}$ on Jun 19$^{th}$ and Jun 17$^{th}$, in 2008 and 2009, respectively. At no time were all three ctenophore species identified at once in Great South Bay.

Mean mesozooplankton and micrometazoa abundances (collectively referred to as mesozooplankton) ranged from 2.8 individuals $L^{-1}$ to 1718.2 individuals $L^{-1}$ and correlated inversely with *M. leidyi* abundance in 2008 and 2009 (Figure 2; McNamara et al. 2013, Chapter One). Mesozooplankton densities did not differ significantly between the two sampling years (df= 1, 107; F= 0.977; p= 0.3252; two-way ANOVA with station and year as fixed variables; McNamara et al. 2013, Chapter One).

Copepods comprised the majority (~60%) of mesozooplankton during both years. *Acartia tonsa* and *Oithona similis* were the dominant copepods in Great South Bay during the sampling period. *Centropages hamatus, Centropages typicus, Labridocera aestiva, Paracalanus parvus, Parvocalanus crassirostris, Temora turbinata* and *Temora longicornis* also occurred, but in smaller quantities. Meroplankton made up about a quarter of the mesozooplankton community, and consisted predominantly of bivalve and gastropod veligers, with naupliar- and cyprid-stage barnacles, crab zoea, nematodes, and larval shrimp, flatworms, fish, polychaetes and ascidians, occurring less frequently. Tintinnids and rotifers comprised ~5% of the mesozooplankton in both years (McNamara et al. 2013, Chapter One).

*Ctenophore fecundity*

The egg production rate (eggs $individual^{-1}$ $d^{-1}$) of *M. leidyi* corresponded positively and significantly with body size and mesozooplankton (copepod) abundance in both years (Table 1).

As *M. leidyi* size increased, so too did ctenophore fecundity, but only during periods of sufficient prey availability. Even large (>5 cm) *M. leidyi* failed to produce eggs within 24 hours under reduced (<100 individuals $L^{-1}$) zooplankton abundances. Conversely, small (<1.5 cm) ctenophores produced very few or no eggs when zooplankton abundances were sufficient (Figure 3). However, the influence of body size and zooplankton abundance on ctenophore egg production rate was not equal between sampling years. In 2008, the greatest egg production occurred in *M. leidyi* >4.0 cm and at zooplankton densities between 100-400 individuals $L^{-1}$ (Figure 3a). In 2009, maximum egg production also occurred in individuals >4.0 cm, but only at zooplankton densities greater than 800 individuals $L^{-1}$ (Figure 3b).

Daily egg production rates (eggs produced individual $d^{-1}$) of *M. leidyi* differed significantly between 2008 and 2009 (*df* = 1, 327; *Fs* = 3.914; *p* = 0.049). Ctenophores produced nearly twice as many eggs individual$^{-1}$ $d^{-1}$ in 2008 than in 2009. Daily egg production averaged 700 (+/- 2087; n= 144) eggs ctenophore$^{-1}$ $d^{-1}$ in 2008, but only 334 (+/- 1244; n= 187) eggs ctenophore$^{-1}$ $d^{-1}$ in 2009. When only non-zero values are considered, egg production averaged 2085 (+/- 3194; n= 48) eggs ctenophore$^{-1}$ $d^{-1}$ in 2008 and 1324 (+/- 2210; n= 46) eggs ctenophore$^{-1}$ $d^{-1}$ in 2009. The size of *M. leidyi* sampled for egg production studies did not differ between sampling years (*df* = 1, 327; *Fs* = 0.161; *p* = 0.688), averaging 3.6 (+/- 1.9) cm in 2008 and 3.7 (+/- 1.6) cm in 2009, yet for any given size and zooplankton abundance, egg production rates were consistently lower in 2009 than in 2008. For instance, *M. leidyi* >4 cm produced 4406 (+/- 3705) eggs individual$^{-1}$ $d^{-1}$ at zooplankton densities between 100-400 individuals $L^{-1}$ in 2008 (Figure 3a). In contrast, similarly-sized ctenophores at these same densities produced only 1080 (+/- 685) eggs individual$^{-1}$ $d^{-1}$ in 2009 (Figure 3b).

Despite interannual differences in the quantity of eggs produced, trends in fecundity were otherwise similar between the two years. Average *M. leidyi* egg production was highest in early summer and sustained relatively high fecundity through mid- to the end July in both years when egg production plummeted alongside reduced zooplankton densities (Figure 4). Extremely low egg production (<10 eggs individual$^{-1}$ $d^{-1}$) persisted through August before slowly recovering in mid-September (2008) and October (2009), although production never exceeded 250 eggs individual$^{-1}$ $d^{-1}$ even amongst large ctenophores at this time. Despite high zooplankton densities following the arrival of *B. ovata* and subsequent decline of *M. leidyi* in 2008, egg production was limited and failed to reflect values observed earlier in the season at similar zooplankton abundances (Figures 2 and 4).

Egg production rates corresponded negatively with temperature in 2008 (Table 1), however collection of *M. leidyi* was limited to Jun-Aug that year, becoming scarce following the arrival of *B. ovata*. Subsequently, the limited range of temperatures (21.8-26.7°C) used in the analysis are not likely to reflect an actual correlation, but may instead be representative of the warming summer temperatures that occurred alongside declining zooplankton abundance while *M. leidyi* was abundant (Figure 2a, b).

*Ctenophore gut contents*

The number of prey items in *M. leidyi* also corresponded with ctenophore size and zooplankton abundance in both sampling years (multiple regression, *df* = 2, 126; *F*s = 64.6 and 19.0 for size and abundance, respectively; *p* = <0.001 in 2008; *df* = 2, 144; *F*s = 19.0 and 43.0 for size and abundance, respectively; *p* = <0.001 in 2009) and demonstrated differences in quantity between 2008 and 2009. Although mesozooplankton abundance did not differ significantly between the two sampling years, the number of zooplankton in ctenophore gut

contents did ($df$ = 1, 274; $F$s = 29.0; $p$ = <0.001). The mean number of prey items was nearly three times greater in 2008 compared to 2009; prey items identified in *M. leidyi* ranged from 0-249 in 2008, but from 0-55 in 2009 (Table 2; Figure 5). The sizes of *M. leidyi* sampled for gut content analyses did not differ significantly between sampling years ($df$ = 1, 267; $Fs$ = 0.342; $p$ = 0.559), and cannot explain the observed differences in gut content quantity between years.

The composition of gut contents by taxon demonstrated significant dependence on the calanoid copepod *Acartia tonsa* by *M. leidyi* in Great South Bay. All life stages of the copepod (adults, copepodites, nauplii and eggs) were identified in *M. leidyi*, and generally comprised >50% of the total identifiable prey items in both years (Table 3). However, the number and percentage of *A. tonsa* adults identified in gut contents was greater in 2008 than in 2009. In 2008, *A. tonsa* adults comprised up to 37% of total gut contents and averaged 15 copepods ctenophore$^{-1}$, whereas in 2009, *A. tonsa* adults comprised ≤16% of total identifiable gut contents and averaged only 2.7 copepods ctenophore$^{-1}$. The cyclopoid copepod *Oithona similis* was identified in *M. leidyi* less frequently; adults and copepodites of this species comprised no more than 9% of total gut contents in either sampling year (Table 3).

Electivity indices identified selective feeding by *M. leidyi* on select zooplankton assemblages in Great South Bay. In both sampling years, *M. leidyi* preferentially selected for *A. tonsa* adults, copepodites, and nauplii, but selected against *O. similis* adults and copepodites, and "other" copepod nauplii. Ctenophores also demonstrated a strong negative selection against polychaetes, which were frequently absent in the gut contents, or found in very low abundances. Selection for bivalve veligers and against gastropod veligers was also identified, although with some inconsistency (Table 4).

## Discussion

*Ctenophore population dynamics in Great South Bay*

In 2008, the decline of *M. leidyi* coincided with the appearance of the predatory ctenophore *Beroe ovata* (Figure 2). *Beroe ovata* is commonly associated with the decline of *M. leidyi* populations in both native and exotic habitats (Reeve et al. 1978; Quaglietta 1987; Kremer 1994; Falkenhaug 1996; Shiganova et al. 2001). In the Black Sea, Finenko et al. (2003) estimated that *B. ovata* removes 5% to 80% of *M. leidyi* d$^{-1}$, although Shiganova et al. (2001) reported daily consumption rates of <10%. Using ingestion rates reported by Shiganova et al. (2001) with ctenophore abundances in Great South Bay, I calculated that populations of *B. ovata* had the potential to consume 5% (at their lowest abundance) to 100% (at their highest abundance) of *M. leidyi* d$^{-1}$ in 2008. These values agree well with observations made in the field (*M. leidyi* was absent from the bay on the last day of sampling). However, it is more likely that decreasing mesozooplankton abundance, and not predation by *B. ovata*, was the principal factor leading to the population's initial demise. *Mnemiopsis* was already in decline when *B. ovata* was first observed (Figure 2a, b). Similarly, Kremer (1976) concluded that inadequate food supply, and not mortality from predation, was the primary factor controlling population densities of *M. leidyi* in Narragansett Bay.

*Beroe ovata* is an oceanic species, appearing irregularly in coastal embayments (Park and Carpenter 1987, Kremer and Nixon 1976). The loss of *M. leidyi* in years when *B. ovata* is present could have significant consequences on the timing and appearance of ctenophore blooms the following year. Since over-wintering *M. leidyi* serve as a source population for reproducing adults in the spring, a decline in their abundance can potentially delay the initiation of their

bloom, and subsequent predatory impacts on the plankton community (Falkenhaug 1996; Costello et al. 2006). In 2009, *M. leidyi* was absent from the bay for six weeks before being identified at either station (Figure 2c, d) and peak abundance occurred two weeks later than in 2008. Similar effects were seen in Narragansett Bay where, following an invasion of *B. ovata* in 2006, *M. leidyi* did not become numerous in 2007 until early August, comparatively late for the region (Beaulieu et al. 2013).

*Regulation of M. leidyi fecundity and recruitment by lower trophic levels*

Ctenophore size and mesozooplankton abundance significantly and positively corresponded with *M. leidyi* egg production and gut contents in 2008 and 2009. However, despite similarities in *M. leidyi* length and zooplankton density between the two years, *per capita* egg production rates and gut contents were both significantly higher in 2008 than 2009. Ctenophores contained nearly three times as many gut contents and produced twice as many eggs individual$^{-1}$ throughout the sampling period in 2008 relative to 2009. Further, copepods, namely *A. tonsa*, comprised a greater percentage of *M. leidyi* prey items in 2008. Although temperature related significantly with egg production in 2008 (Table 1), this correlation was negative and cannot explain the observed increases in egg production relative to 2009.

One notable difference between the two sampling years was the occurrence of an extensive brown tide (*Aureococcus anophagefferens*) in 2008, which reached 1,778,362 cells mL$^{-1}$ at its peak in Great South Bay (Suffolk County Department of Health Services; SCDHS). Since sampling stations M and A correspond well to SCDHS stations 90160 and 90170, respectively, brown tide abundances could be compared to egg production rates of *M. leidyi*. The number of prey items identified in *M. leidyi* was greatest during high ($\geq$ 200.000 cells mL$^{-1}$) abundance of *A. anophagefferens* and corresponded positively and significantly with the alga (Table 5). Present, but in reduced concentrations, *A. anophagefferens* did not bloom in the bay in 2009 (Figure 6). Although concentrations of *A. anophagefferens* declined during summer months alongside declining mesozooplankton abundances, the differences in gut contents and egg production rates between a brown tide year and a non-brown tide year suggest that brown tides may somehow provide a benefit to ctenophore fecundity by enhancing feeding on mesozooplankton.

In order to understand how a brown tide could improve feeding in *M. leidyi*, I considered the feeding mechanisms of *M. leidyi*. Successful consumption of prey by the lobate ctenophore is dependent on capture; adult *M. leidyi* employ ciliary flow fields to entrain and capture prey, but direct encounters with swimming zooplankton can also be significant. Costello et al. (1999) demonstrated the importance of these flow fields in the entrainment of small, slowly-swimming copepods such as *Oithona colcarva*, but found that larger, more active swimmers such as *A. tonsa* were entrained less frequently, and instead were captured by direct swimming encounters with the ctenophore. The majority (82%) of *A. tonsa* captured by *M. leidyi* in their study resulted from the copepod actively swimming into the ctenophore. Could overall differences in the swimming and feeding activities of *A. tonsa* between the two years explain the observed difference in ctenophore gut contents? *Acartia tonsa* are known to switch swimming and feeding behaviors based on prey availability. For example, the copepod utilizes an ambush strategy when ciliates are abundant and switches to suspension-feeding when diatoms and other immobile prey are present (Jonsson and Tiselius 1990; Kiørboe et al. 1996). Specifically, clearance rates of diatoms by *A. tonsa* increased proportionately with copepod swimming activity and correlated negatively with ciliate abundance. In contrast, sinking (ambush) behavior of the copepod

increased with increasing ciliate concentration (Kiørboe et al. 1996). I did not find a significant difference in ciliate abundance between the two years. However, other laboratory studies have demonstrated that *A. tonsa* allocates more time to suspension feeding when exposed to high concentrations of microflagellates (Jonsson and Tiselius 1990). In Great South Bay, microplanktonic flagellate abundance (McNamara et al, 2013, Chapter One) was significantly greater in 2008 than 2009 ($df$= 1, 46; $Fs$= 7.97; $p$= <0.003) and related positively and significantly to *A. anophagefferens* (multiple regression testing for correlations between *A. anophagefferens* abundance and microplanktonic centric diatom, pennate diatom, dinoflagellate, ciliate, and flagellate abundance in 2008 and 2009; $df$= 1, 46; $Fs$= 29.4; $p$= <0.001 for flagellates). Thus, it is possible that the conditions (*i.e.*, abundance of microflagellates) during the brown tide enhanced encounter rates between *A. tonsa* and *M. leidyi* by promoting suspension feeding in *A. tonsa*. In turn, the increased feeding success of *M. leidyi* led to improved fecundity of the ctenophore; *M. leidyi* had significantly higher egg production rates in 2008 than 2009.

Despite the enhanced feeding and fecundity, *M. leidyi* abundances were significantly lower in 2008 than 2009. In order for a ctenophore bloom to persist, increases in egg production must be sufficiently paired with an adequate supply of microplanktonic prey for the developing larvae. A comparison of microplanktonic abundance and composition of Great South Bay (McNamara et al. 2013, Chapter One) with ctenophore egg production rates from this study identified a mismatch between maximum egg production and larval prey availability in 2008 in contrast to 2009 when the two coincided. In 2008, peak egg production occurred on Jul 10 during relatively low (~300 μg C $L^{-1}$) densities of dinoflagellates and aloricate ciliates. Increases in the larvae, however, occurred two weeks later following extremely high (>2000 μg C $L^{-1}$) abundances of dinoflagellates and ciliates, despite an order of magnitude reduction in egg production. In contrast, maximum egg production co-occurred with extremely high densities of dinoflagellates and ciliates in 2009, followed by a surge in larval *M. leidyi* one week later. The coupling of high egg production rates with high microplanktonic abundance in 2009 may explain why ctenophore abundances were ~400% higher than those observed in 2008. Whether *A. anophagefferens* contributed to the mismatch in 2008 is undetermined and warrants further study.

### *Conclusions*

Interannual differences in the fecundity, feeding success, and recruitment of *M. leidyi* were documented and attributed to differences in lower planktonic community structure in Great South Bay. Feeding success was found to be dependent not only on mesozooplankton, but potentially indirectly on picoplankton (*A. anophagefferens*). The presence of a brown tide in 2008 may have helped *M. leidyi* reproductive success by enhancing fecundity, but ultimately a mismatch with prey prevented successful recruitment into larvae. While numerous studies have focused on the top-down control of the plankton community by *M. leidyi*, little attention has been paid to the bottom-up control of this important gelatinous predator. To my knowledge, this is the first study to correlate lower planktonic trophic structure with *M. leidyi* population dynamics *in situ*.

**Acknowledgments**

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Table 1. Dependence of daily egg production rate (eggs produced individual$^{-1}$ d$^{-1}$) of *M. leidyi* on ctenophore size (length), mesozooplankton abundance (copepods including adults, copepodites and nauplii, meroplankton including gastropod and bivalve veligers, crab zoea, but excluding polychaetes, polychaete larvae, and rotifers and tintinnids), and ambient temperature (°C) in Great South Bay determined from multiple regression analysis for 2008 (a) and 2009 (b). The models were significant (*df* = 6; *Fs* = 30.8; *p* = <0.001 for 2008 and *df* = 6; *Fs* = 23.7; *p* = <0.001 for 2009) and explained 76.4% (2008) and 66.5% (2009) of the variance in *M. leidyi* egg production.

| Variable | Standard partial regression coefficient | *Fs* *df* = 1 | *p* |
|---|---|---|---|
| *M. leidyi* size | 0.443 | 59.3 | **<0.001** |
| Copepods | 0.18 | 7.96 | **0.006** |
| Meroplankton | 0.082 | 1.13 | 0.289 |
| Rotifers and tintinnids | 0.054 | 0.707 | 0.402 |
| Polychaetes | 0.134 | 3.23 | 0.075 |
| Temperature | -0.595 | 53 | **<0.001** |

(a)

| Variable | Standard partial regression coefficient | *Fs* *df* = 1 | *p* |
|---|---|---|---|
| *M. leidyi* size | 0.246 | 18.2 | **<0.001** |
| Copepods | 0.533 | 40.9 | **<0.001** |
| Meroplankton | 0.027 | 0.129 | 0.72 |
| Rotifers and tintinnids | 0.048 | 0.313 | 0.577 |
| Polychaetes | 0.3 | 0.257 | 0.613 |
| Temperature | 0.055 | 0.457 | 0.5 |

(b)

Table 2. Mean number (+/- s.d.) and range of gut content items in *M. leidyi*, number and average size (+/- s.d.) of ctenophores sampled, and mean mesozooplankton abundance ($L^{-1}$) in the field.

| Date | Site | Mean no. of contents | Range | No. of ctenophores examined | Average size, cm | Zooplankton abudance |
|---|---|---|---|---|---|---|
| 3-Jul-08 | A | 46.9 (72.9) | 2-249 | 12 | 3.4 (2.0) | 173.0 |
| 10-Jul-08 | M | 49.7 (49.3) | 3-167 | 21 | 3.0 (1.7) | 344.4 |
| 17-Jul-08 | M | 39.3 (39.7) | 1-167 | 31 | 2.9 (1.3) | 92.8 |
| 17-Jul-08 | A | 31.2 (29.8) | 2-100 | 12 | 4.5 (1.5) | 42.9 |
| 31-Jul-08 | M | 4.1 (4.7) | 0-20 | 27 | 2.0 (1.0) | 16.2 |
| 31-Jul-08 | A | 7.7 (17.3) | 1-75 | 19 | 2.9 (1.4) | 62.2 |
| 14-Aug-08 | M | 2.0 (2.4) | 0-5 | 4 | 2.4 (1.2) | 7.2 |
| 14-Aug-08 | A | 3.0 (4.2) | 0-6 | 3 | 2.2 (1.0) | 16.8 |
| 28-Aug-08 | M | 3.0 (0) | n/a | 1 | 2.6 (0) | 110.1 |
| | | | | | | |
| 22-Jul-09 | M | 17.2 (14.9) | 2-55 | 17 | 2.3 (1.1) | 859.6 |
| 29-Jul-09 | M | 18.8 (11.3) | 2-46 | 23 | 3.3 (1.8) | 72.5 |
| 29-Jul-09 | A | 10.9 (7.1) | 0-28 | 24 | 1.8 (0.9) | 259.4 |
| 5-Aug-09 | M | 2.7 (3.2) | 0-12 | 16 | 3.3 (1.2) | 15.2 |
| 5-Aug-09 | A | 3.4 (4.4) | 0-21 | 24 | 3.3 (1.5) | 7.7 |
| 12-Aug-09 | M | 1.9 (1.5) | 0-6 | 15 | 3.4 (1.5) | 15.4 |
| 26-Aug-09 | M | 1.4 (1.5) | 0-6 | 22 | 2.3 (1.4) | 2.8 |
| 26-Aug-09 | A | 2.0 (1.4) | 0-4 | 6 | 2.7 (1.0) | 5.9 |

Table 3. Number (and percentage) of prey items identified in the gut contents of *M. leidyi* collected from Great South Bay in 2008 (a) and 2009 (b).

| Date | 3-Jul-08 | 10-Jul-08 | 17-Jul-08 | 17-Jul-08 | 31-Jul-08 | 31-Jul-08 | 14-Aug-08 | 14-Aug-08 | 28-Aug-08 |
|---|---|---|---|---|---|---|---|---|---|
| Site | A | M | M | A | M | A | M | A | M |
| Acartia adults | 139 (25) | 314 (37) | 100 (14) | 11 (29) | 4 (5) | 5 (4) | 0 | 0 | 0 |
| Acartia copepodites | 52 (9) | 78 (9) | 39 (6) | 8 (2) | 2 (3) | 7 (5) | 0 | 0 | 0 |
| Acartia nauplii | 101 (18) | 264 (31) | 247 (35) | 99 (26) | 1 (1) | 13 (10) | 0 | 0 | 0 |
| Oithona adults | 8 (1) | 10 (1) | 6 (1) | 1 (0.3) | 1 (1) | 0 | 0 | 0 | 0 |
| Oithona copepodites | 24 (4) | 16 (2) | 4 (1) | 0 | 2 (3) | 0 | 0 | 0 | 0 |
| Other nauplii | 9 (2) | 7 (1) | 7 (1) | 0 | 1 (1) | 2 (1) | 1 (13) | 0 | 0 |
| Bivalves | 13 (2) | 9 (1) | 128 (18) | 143 (38) | 1 (1) | 2 (1) | 2 (25) | 1 (17) | 0 |
| Gastropods | 0 | 1 (0.1) | 12 (2) | 13 (3) | 18 (23) | 3 (2) | 0 | 0 | 2 (67) |
| Polychaetes | 3 (1) | 5 (0.6) | 2 (0.3) | 6 (2) | 1 (1) | 1 (1) | 0 | 0 | 0 |
| No. of *M. leidyi* examined | 12 | 21 | 31 | 12 | 27 | 19 | 4 | 3 | 1 |

(a)

| Date | 22-Jul-09 | 29-Jul-09 | 29-Jul-09 | 5-Aug-09 | 5-Aug-09 | 12-Aug-09 | 26-Aug-09 | 26-Aug-09 |
|---|---|---|---|---|---|---|---|---|
| Site | M | M | A | M | A | M | M | A |
| Acartia adults | 46 (16) | 57 (16) | 12 (5) | 1 (2) | 5 (7) | 6 (21) | 4 (15) | 4 (33) |
| Acartia copepodites | 36 (12) | 61 (17) | 22 (10) | 1 (23) | 8 (11) | 6 (21) | 1 (4) | 0 |
| Acartia nauplii | 107 (37) | 125 (34) | 119 (52) | 20 (47) | 11 (15) | 8 (28) | 1 (4) | 0 |
| Oithona adults | 4 (1) | 8 (2) | 21 (9) | 1 (2) | 1 (1) | 0 | 0 | 0 |
| Oithona copepodites | 4 (1) | 10 (3) | 21 (9) | 0 | 0 | 0 | 1 (4) | 0 |
| Other nauplii | 48 (16) | 54 (15) | 28 (12) | 5 (12) | 11 (15) | 3 (10) | 4 (15) | 2 (17) |
| Bivalves | 3 (1) | 17 (4) | 2 (0.9) | 2 (5) | 14 (19) | 2 (7) | 3 (11) | 2 (17) |
| Gastropods | 3 (1) | 1 (0.3) | 0 | 6 (14) | 12 (16) | 1 (3) | 5 (19) | 0 |
| Polychaetes | 0 | 0 | 0 | 2 (5) | 6 (8) | 0 | 0 | 0 |
| No. of *M. leidyi* examined | 17 | 23 | 24 | 16 | 24 | 15 | 22 | 6 |

(b)

Table 4. Ivlev electivity indices for *M. leidyi* feeding on select zooplankton prey. Positive values indicate positive selection, whereas negative values indicate prey avoidance. A value of 1 indicates that the prey was identified in gut content analyses, but was not identified in the zooplankton; a value of -1 indicates that the prey item was not identified in gut content analyses, but was present in the zooplankton samples. 'n/a' denotes when the prey item was identified in neither zooplankton nor gut content samples.

| Date | Site | *Acartia* adults | *Acartia copepodites* | *Acartia* nauplii | *Oithona* adults | *Oithona* copepodites | Other nauplii | Bivalves | Gastropods | Polychaetes |
|---|---|---|---|---|---|---|---|---|---|---|
| 3-Jul-08 | A | 0.8 | 0.7 | 0.8 | -0.8 | -0.2 | 0.0 | n/a | -1.0 | 0.9 |
| 10-Jul-08 | M | 0.9 | 0.8 | 0.9 | -0.6 | -0.8 | -0.8 | 0.98 | 0.5 | 0.7 |
| 17-Jul-08 | M | 1.0 | 0.9 | 0.9 | 0.6 | -0.3 | -0.6 | 0.96 | 0.9 | -0.9 |
| 17-Jul-08 | A | 1.0 | 0.9 | 0.9 | 0.5 | -1.0 | -1.0 | 0.9 | 0.5 | 0.0 |
| 31-Jul-08 | M | 1.0 | 0.8 | -0.1 | 0.0 | 0.3 | -0.1 | 0.2 | 0.8 | -0.6 |
| 31-Jul-08 | A | 0.9 | 0.8 | 0.0 | -1.0 | -1.0 | -0.1 | -0.4 | -0.8 | -0.4 |
| 14-Aug-08 | M | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -0.4 | 0.9 | -1.0 | -1.0 |
| 14-Aug-08 | A | n/a | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | 0.8 | -1.0 | -1.0 |
| 28-Aug-08 | M | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -0.6 | -1.0 |
| ***Mean E*** | | ***0.5*** | ***0.2*** | ***0.05*** | ***-0.5*** | ***-0.7*** | ***-0.6*** | ***0.4*** | ***-0.2*** | ***-0.4*** |
| 22-Jul-09 | M | -0.1 | -0.5 | 0.1 | -0.8 | -1.0 | -0.7 | -0.1 | 0.6 | -1.0 |
| 29-Jul-09 | M | 1.0 | 0.9 | 0.8 | -0.1 | -0.1 | 0.4 | 0.8 | -0.3 | -1.0 |
| 29-Jul-09 | A | 1.0 | 0.3 | 0.7 | 0.1 | -0.6 | -0.1 | 0.3 | -1.0 | -1.0 |
| 5-Aug-09 | M | 0.7 | -0.1 | 0.8 | 0.1 | -1.0 | 0.2 | 0.98 | 0.5 | 0.5 |
| 5-Aug-09 | A | 1.0 | 1.0 | 0.6 | 0.9 | -1.0 | 0.7 | 0.97 | 0.8 | 0.8 |
| 12-Aug-09 | M | 1.0 | 1.0 | 1.0 | -1.0 | -1.0 | 0.8 | 0.7 | -0.9 | -1.0 |
| 26-Aug-09 | M | 1.0 | 0.7 | 0.7 | -1.0 | 1.0 | 1.0 | 0.7 | 0.5 | -1.0 |
| 26-Aug-09 | A | 1.0 | -1.0 | -1.0 | -1.0 | n/a | 0.4 | 0.8 | -1.0 | -1.0 |
| ***Mean E*** | | ***0.8*** | ***0.3*** | ***0.5*** | ***-0.4*** | ***-0.5*** | ***0.3*** | ***0.6*** | ***-0.1*** | ***-0.6*** |

Table 5. Dependence of *M. leidyi* gut contents (number of prey items individual$^{-1}$) on ctenophore size (length), mesozooplankton (individuals L$^{-1}$) and *Aureococcus anophagefferens* abundance (cells mL$^{-1}$) in Great South Bay determined from multiple regression analysis for 2008 and 2009 (combined). The model was significant (*df* = 3; *Fs* = 60.3; *p* = <0.001) and explained 63.7% of the variance in *M. leidyi* gut content.

| Variable | Standard partial regression coefficient | *Fs* *df* = 3 | *p* |
|---|---|---|---|
| *M. leidyi* size | 0.367 | 57.2 | **<0.0001** |
| Zooplankton abundance | 0.173 | 12.8 | **0.0004** |
| *A. anophagefferens* | 0.438 | 82.2 | **<0.0001** |

Figure 1. Sampling locations (sites M and A) in Great South Bay, Long Island, NY, USA.

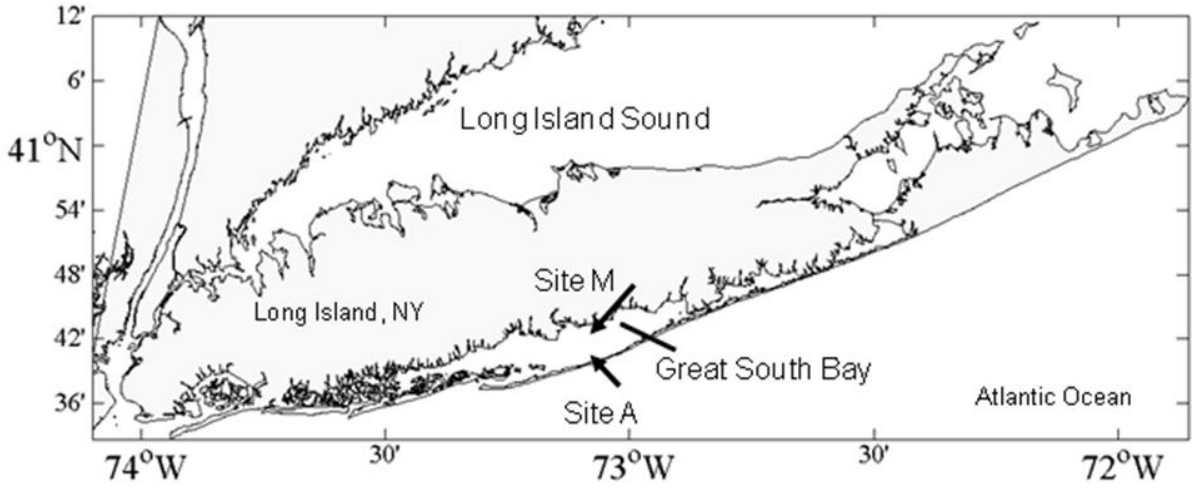


Figure 2. Mean abundances of *M. leidyi* ($m^{-3}$; +/- s.d.), *B. ovata* ($(10^6\ L)^{-1}$; +/- s.d.), and mesozooplankton ($L^{-1}$; +/- range) in Great South Bay in 2008 and 2009 at sites M (a, c) and A (b, d), respectively.

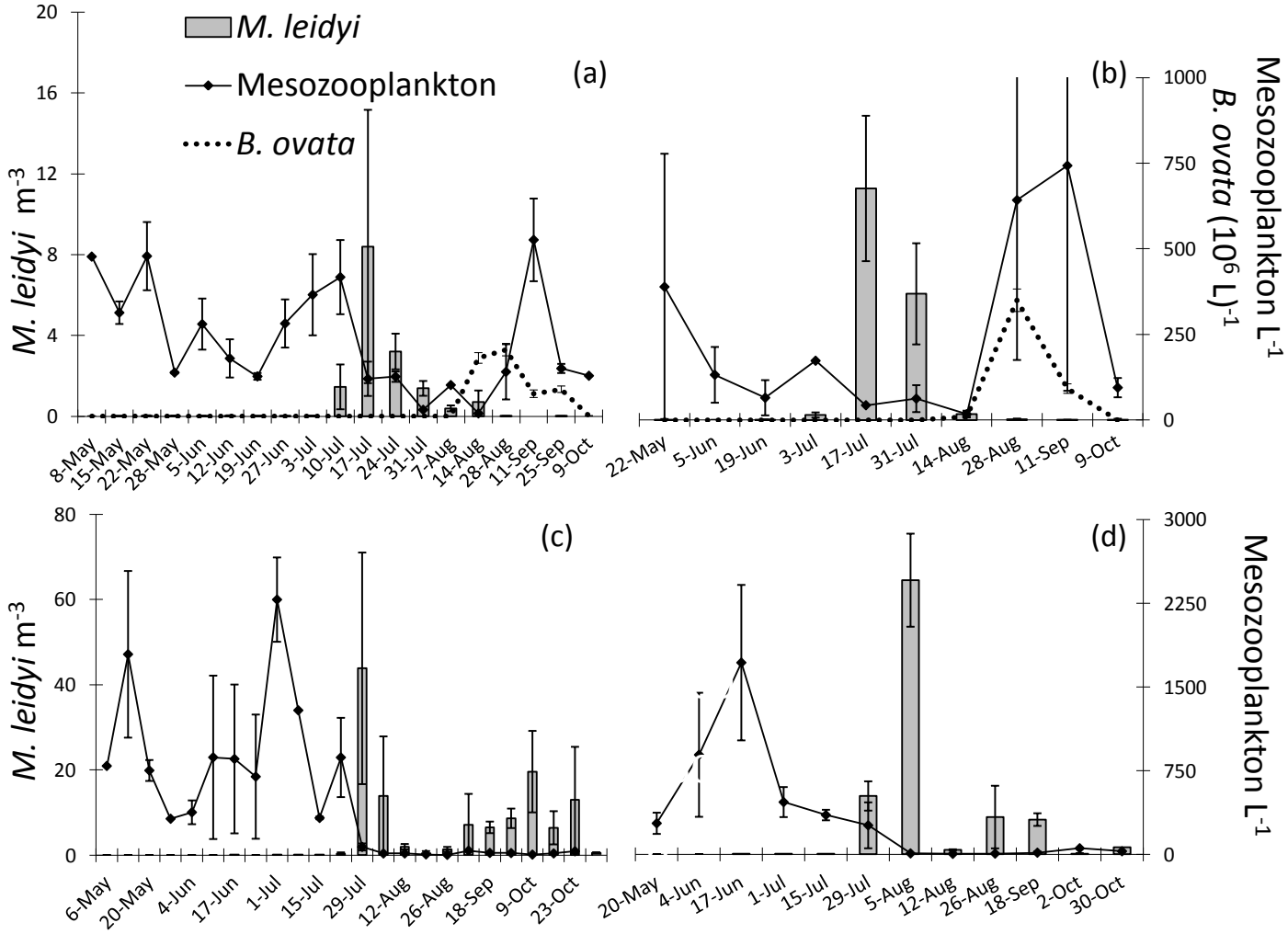
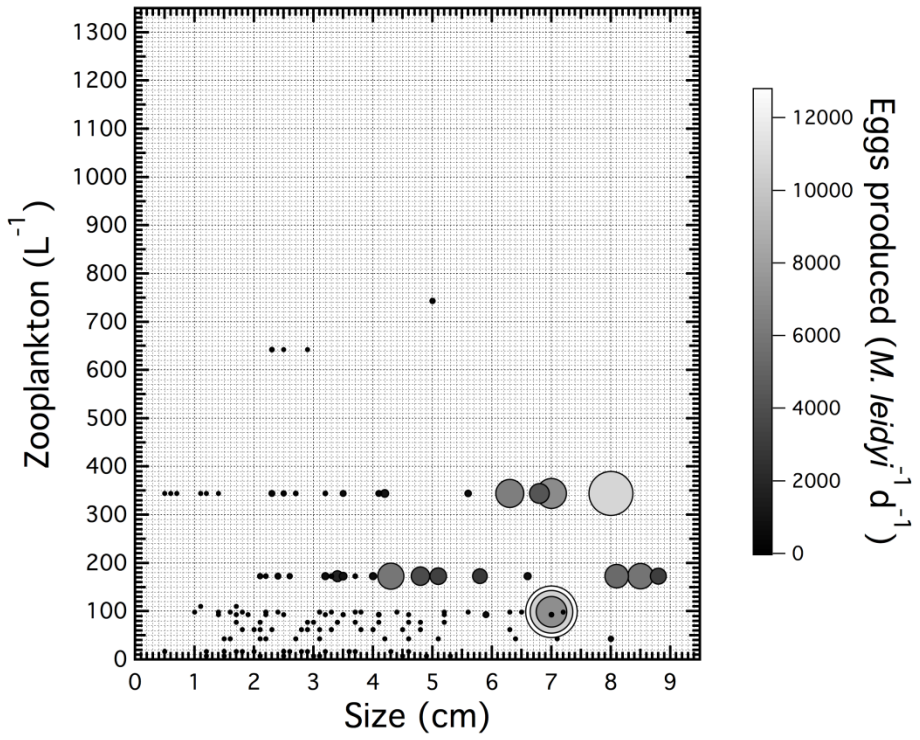
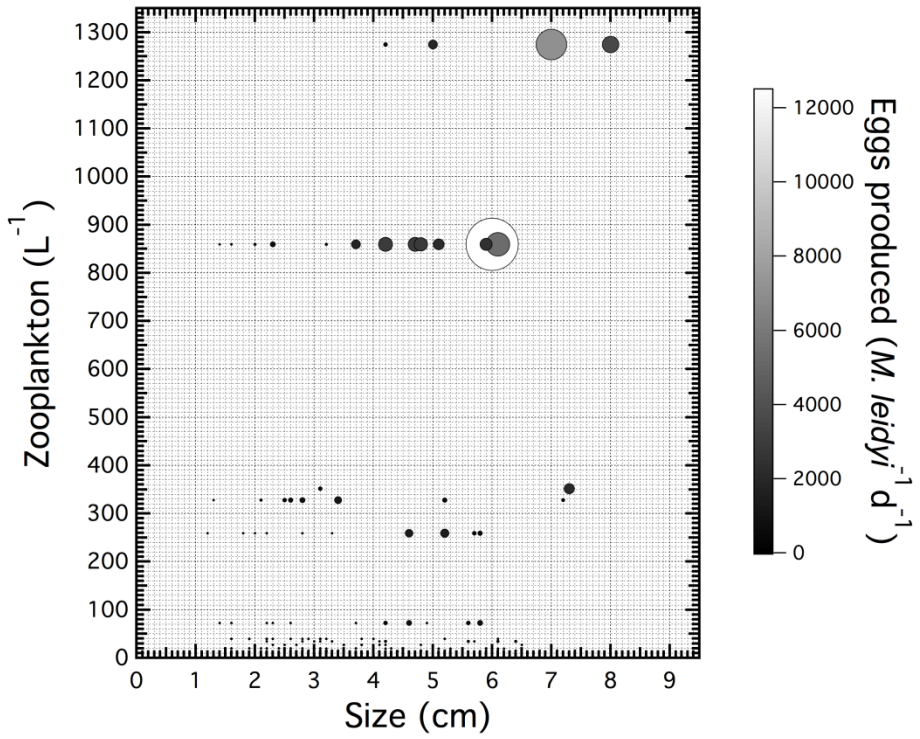


Figure 3. Egg production by *M. leidyi* (eggs individual$^{-1}$ d$^{-1}$) per zooplankton abundance (L$^{-1}$) and ctenophore size in Great South Bay in 2008 (a) and 2009 (b). Note the differences in x- and y- axes between sampling years.

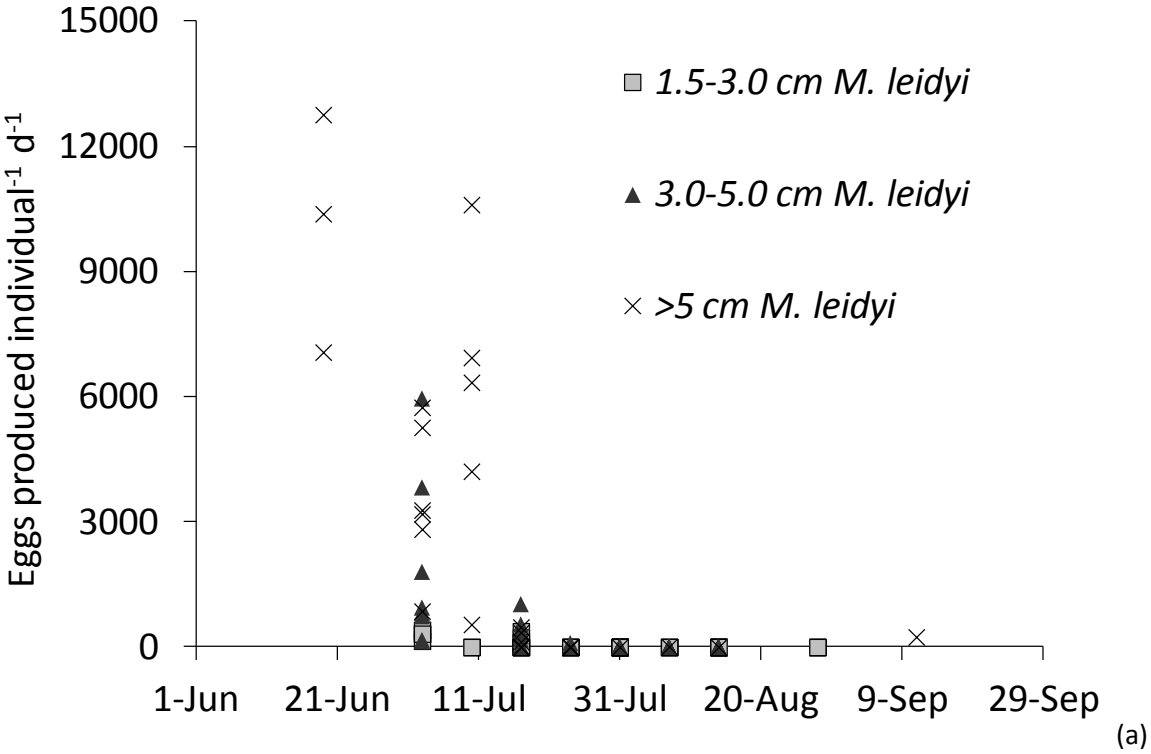



(a)

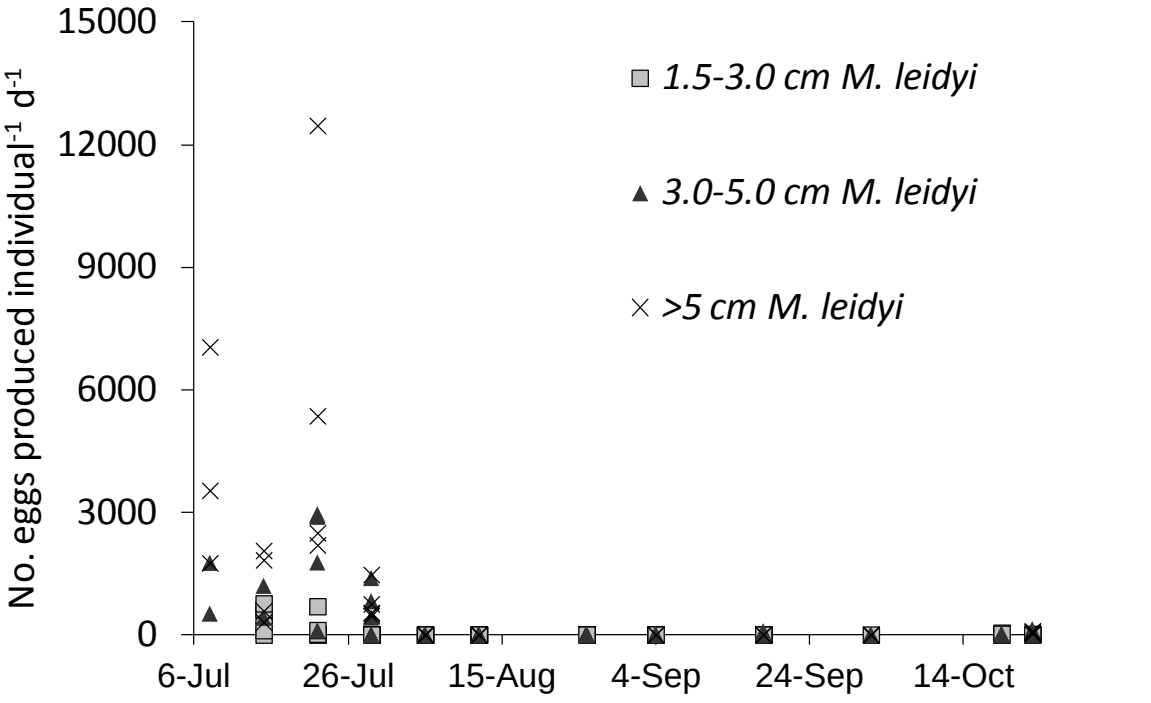



(b)

Figure 4. Egg production (eggs produced individual$^{-1}$ d$^{-1}$) by *M. leidyi* in 2008 (a) and 2009 (b) at both sampling locations in Great South Bay.

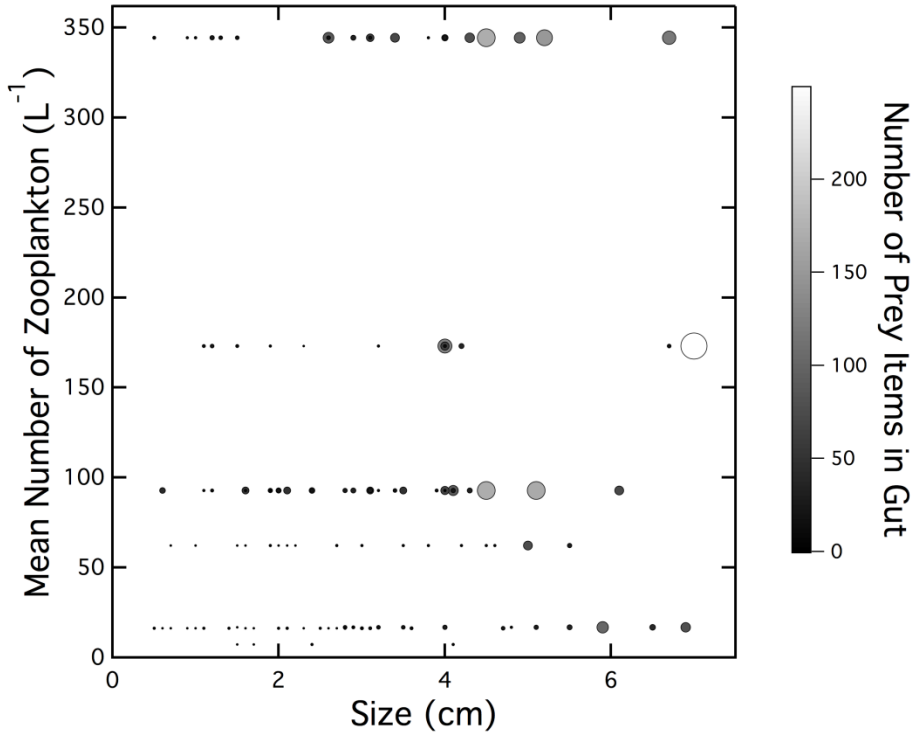



(a)

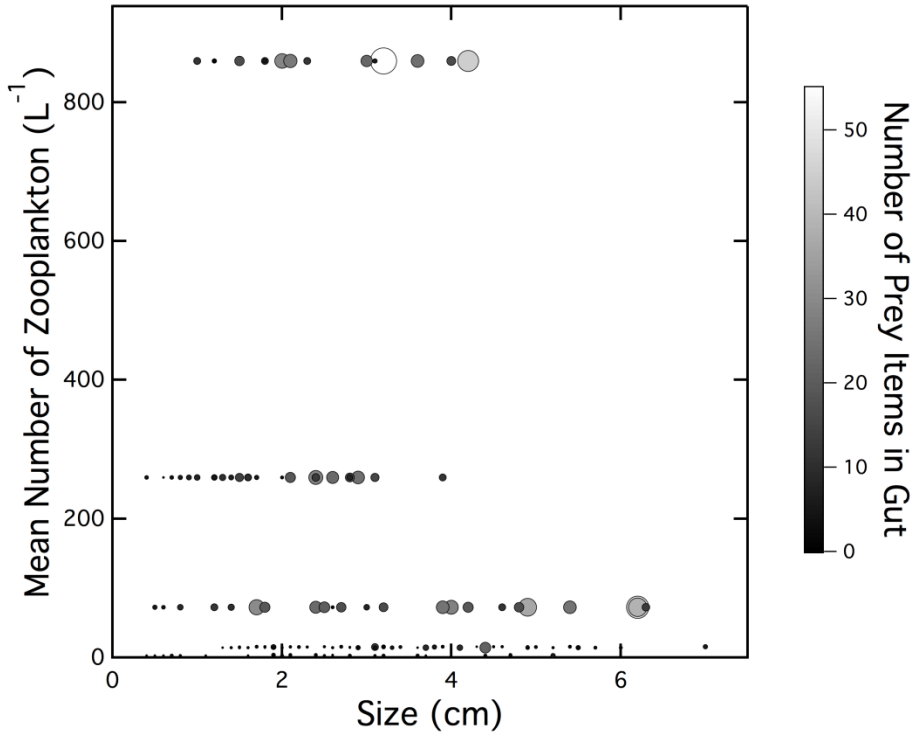



(b)

Figure 5. Gut contents of *M. leidyi* (eggs individual$^{-1}$ d$^{-1}$) per zooplankton abundance (L$^{-1}$) and ctenophore size in Great South Bay in 2008 (a) and 2009 (b). Note the differences in y- axes between sampling years.

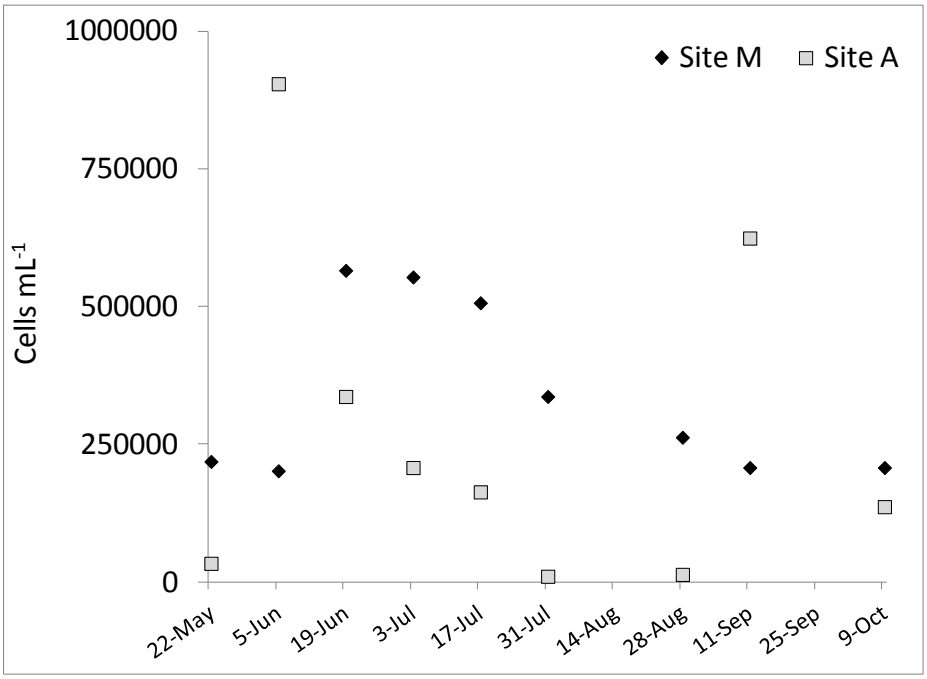



(a)

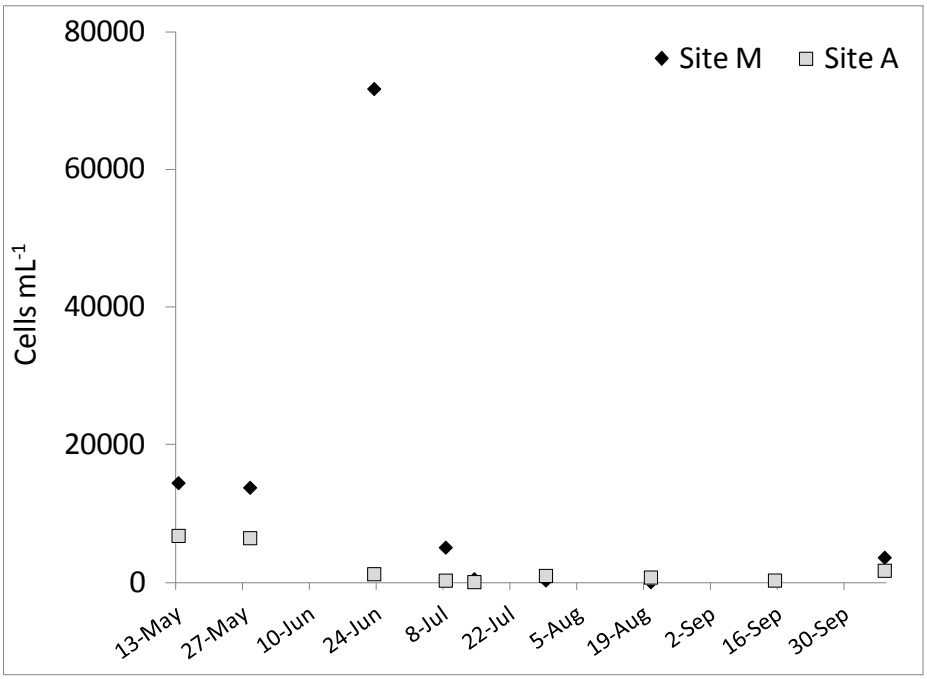



(b)

Figure 6. Concentrations of *A. anophagefferens* ($mL^{-1}$) in Great South Bay near sites M and A in 2008 (a) and 2009 (b). Data courtesy of Suffolk County Department of Health Services (SCDHS), Office of Ecology; sites M and A (this study) roughly correspond to SCDHS sites 90160 and 90170, respectively. Note differences in axes and sampling frequency between sampling years.




(a)




(b)

# CHAPTER THREE

The role of eutrophication in structuring planktonic communities in the presence of the ctenophore *Mnemiopsis leidyi* (Agassiz 1865)

## Abstract

Increasing evidence implicates anthropogenic activities with recently documented shifts in the abundance and seasonal distribution of gelatinous zooplankton in coastal waters. The ctenophore *Mnemiopsis leidyi* occurs in mid-Atlantic estuaries where seasonal blooms occur earlier and in greater magnitude than those studied decades ago. Large densities of adult *M. leidyi* exert significant predation pressure on mesozooplankton, potentially influencing microplankton abundance and composition. Field-based mesocosm experiments were conducted to examine the individual and interactive roles of ctenophore predation and nutrient loading on the microplankton community using historic and recent abundances of *M. leidyi* in Great South Bay, NY, USA. High (recent) abundances of *M. leidyi* exposed to eutrophic conditions influenced plankton community structure in a way that was distinctly different from when the processes occurred separately or under low (historic) abundances. Microplanktonic ciliates exhibited an order of magnitude increase in tanks receiving either nutrient or ctenophore amendments, but increased by two orders of magnitude in treatments receiving both ctenophore and nutrient additions. Since ciliates are an important prey item for developing *M. leidyi*, the combined bottom-up and top-down influences of eutrophication and ctenophore predation, respectively, on microplankton may help explain recently documented shifts in the population dynamics of *M. leidyi* in mid-Atlantic estuaries.

## Introduction

Although global increases in gelatinous zooplankton are subject to debate (Mills 1995; Mills 2001; Purcell et al. 2007; Condon et al. 2013), some regions have experienced shifts in the abundance and seasonal distribution of their gelatinous predators (e.g., scyphomedusae, siphonophores, and ctenophores), which may be taking advantage of localized regime shifts brought about by overfishing, pollution, and/or global climate change (Mills 1995; Mills 2001; Sullivan et al. 2001; Purcell 2005; Purcell et al. 2007). Increasing evidence has linked anthropogenic eutrophication to increased abundances and earlier seasonal appearances of gelatinous zooplankton in coastal waters. The increased hypoxia and turbidity associated with nutrient enrichment can benefit non-visual, oxytolerant gelatinous zooplankton (*i.e.*, ctenophores) over many fish and squid species (Arai 2001; Parsons and Lalli 2002; Grove and Brietburg 2005; Kemp et al. 2005; Thuesen et al. 2005; Purcell et al. 2007; Kimmel et al. 2012). Further, by preferentially elevating levels of nitrogen and phosphorus, but not silica, anthropogenic eutrophication can shift phytoplankton communities from diatoms towards flagellates and other small autotrophs (Daskalov 2002; Parsons and Lalli 2002; Purcell et al. 2007), increasing the abundance of small zooplankton which ctenophores and small scyphomedusae favor (Uye 1994; Daskalov 2002). Although eutrophication has been implicated in the proliferation of small gelatinous zooplankton (e.g., *Aurelia aurita*) in disturbed habitats, it is difficult to attribute these observed increases to nutrient enrichment alone and not to other co-occurring environmental changes (Arai 2001; Purcell et al. 2007; Purcell 2012).

The ctenophore *Mnemiopsis leidyi* Agassiz 1865 is a gelatinous zooplankton predator, occurring in coastal, temperate waters. Once limited in distribution to the Atlantic coasts of North and South America, this species has successfully invaded the Black, Caspian, Mediterranean, Aegean, North and Baltic Seas, and has recently been identified along the Australian coast in the South Pacific Ocean (Costello et al. 2012). In their native mid-Atlantic estuaries, populations of *M. leidyi* have increased in abundance and shifted towards an earlier seasonal maximum (Narragansett Bay; Sullivan et al. 2001, Costello et al. 2006; Chesapeake

Bay; Condon and Steinberg 2008; Long Island estuaries; McNamara et al. 2010). Seasonal blooms of *M. leidyi* can exert strong predation pressure on the surrounding mesozooplankton community as adults (e.g., Kremer 1979; Deason and Smayda 1982; Purcell et al. 2001; Purcell and Decker 2005; McNamara et al. 2010) and on microzooplankton as larvae (Stoecker et al. 1987; Sullivan and Gifford 2004; Rapoza et al. 2005; Sullivan and Gifford 2007; McNamara et al. 2013, Chapter One). Moreover, predation on mesozooplankton and microplankton by large densities of adult and larval *M. leidyi*, respectively, can cascade down the food web influencing lower trophic levels. Correlations between high adult *M. leidyi*/low mesozooplankton with high microzooplankton abundances and high larval *M. leidyi*/low microzooplankton with high nanoplankton abundances have been identified in Great South Bay, NY (McNamara et al. 2013, Chapter One). Such cascading influences on lower trophic levels can feedback to ctenophore population dynamics by enhancing the abundance of certain taxa (*i.e.*, dinoflagellates and ciliates), which serve as prey for developing ctenophores (Stoecker et al. 1987; Sullivan and Gifford 2007; McNamara et al. 2013, Chapter One).

The ecological role of gelatinous zooplankton in disturbed habitats is likely to differ from that in natural, undisturbed environments. When the scyphomedusae *Catostylus mosaicus* was added to mesocosms receiving nutrient additions, the result on the plankton community was distinctly different from that in mesocosms receiving *C. mosaicus* or nutrient additions alone (Pitt et al. 2007). While mesozooplankton abundance was reduced in tanks containing *C. mosaicus*, abundances of the toxic heterotrophic dinoflagellate *Nocticula scintillans* increased by a factor of twenty in tanks containing *C. mosaicus* and receiving nutrient additions. The authors hypothesized that nutrient enrichment increased the diatom prey of *N. scintillans*, while the addition of *C. mosaicus* removed mesozooplankton grazers, enabling the red tide-forming dinoflagellate to increase in abundance (Pitt et al. 2007). Thus, responses of the plankton community to ctenophore predation under eutrophic conditions may differ from when the two processes occur independently.

In this study, I examined the individual and interactive roles of *M. leidyi* predation and nutrient loading on the microplankton community in Great South Bay, NewYork, in experimental mesocosms. Great South Bay is a shallow, lagoonal embayment located on the south shore of Long Island where seasonal population blooms of *M. leidyi* have increased by a factor of two to five and occur two to three months earlier than populations studied two to three decades ago (McNamara et al. 2010; McNamara et al. 2013, Chapter One). The relative impacts of eutrophication and ctenophore predation on the zooplankton community were compared using historic (low) and recent (high) abundances of *M. leidyi* documented in the bay. To my knowledge, this is the first study to experimentally determine the contrasting influences of nutrients with varying densities of *M. leidyi* on the microplanktonic community.

## Methods

*Experimental design and set-up*

Field-based mesocosm experiments were conducted to examine the individual and interactive impacts of *M. leidyi* predation and nutrient loading on the abundance and composition of the plankton community in a coastal marine environment. During 2008 and 2009, two mesocosm experiments (one in each year) were performed at the West Sayville Boat Basin located on Great South Bay, New York, USA (40° 48’ N, 72°, 36’ W). Mesocosms consisted of

twelve 400-L translucent plexiglass cylinders filled with ~300 L of ambient bay water. Cylinders were enclosed within a large floating platform in the bay, with each cylinder secured by line to each other and/or to the platform. Cylinders were somewhat flexible and were mixed by ambient wave activity within the bay. The experimental set-up consisted of four treatments, each with three replicates: control (C), nutrient enrichment (N), ctenophore addition (Ct), and combined ctenophore addition and nutrient enrichment (Ct+N). Three cylinders were randomly assigned to each treatment.

Control treatments (C) consisted of bay water only and received neither nutrient enrichment nor ctenophore addition. To simulate eutrophic conditions, nutrient enrichment treatments (N and Ct+N) received daily additions of ammonium (10 μM final concentration) and orthophosphate (0.625 μM final concentration) as per Wall et al. (2008). In order to achieve final target concentrations of nutrients, the height of water in each of the tanks was regularly measured to calculate total water volume and determine the appropriate nutrient dosages for each tank. Ctenophore addition treatments (Ct and Ct+N) were supplemented with adult (>1.5 cm) *M. leidyi* in quantities reflecting maximum seasonal abundances observed historically and recently in Great South Bay. Five adult *M. leidyi* (~15 individuals $m^{-3}$; ~25 mL $m^{-3}$) were added to Ct and Ct+N treatments in 2008 (M1; Jul 28 - Aug 02), whereas Ct and Ct+N treatments received 20 adult *M. leidyi* (~60 individuals $m^{-3}$; ~100 mL $m^{-3}$) in 2009 (M2; Jul 13-18). Ctenophores were added at $T_0$, marking the beginning of the timed experiment. Ctenophores were collected approximately twelve to twenty-four hours prior by dip net and held in 4-L glass jars containing 0.45-μm filtered seawater within an incubator set to ambient temperature. Mesocosm experiments ran for five full days ending 120 hours after their initiation ($T_0$-$T_{120}$).

*Physical and chemical environmental parameters and chlorophyll a content*

Temperature, salinity, and dissolved oxygen concentration were sampled daily in each tank and the surrounding bay water using a YSI 85. Chlorophyll *a* content was determined from whole (n=2) and <5 μm-fractioned samples (n=2) collected from all cylinders at $T_0$, $T_{48}$, $T_{96}$ and $T_{120}$. Twenty liters of whole seawater were gently collected from ~0.5 m beneath the surface of each cylinder, from which a 250-mL sample was immediately stored in amber bottles inside a cool, dark cooler for chl *a* analysis. The remainder of collected water was then returned to the cylinder. In the laboratory, size fractionation was accomplished by filtering samples through a 5-μm polycarbonate membrane filter. Whole and size-fractionated samples (30 mL) were concentrated onto Whatman GF/F filters and stored in acetone for 24 hours at -20° C. Allowed to thaw for one hour, samples were analyzed using a Turner Designs (model 10-AU) fluorometer after Arar and Collins (1997).

*Mesozooplankton abundance and composition*

Mesozooplankton and micrometazoa (collectively referred to as mesozooplankton) were collected only at the beginning ($T_0$) and end ($T_{120}$) of each experiment due to the large volume of water required for accurate enumeration. At $T_0$, mesozooplankton samples (n=3) were collected (immediately before, after, and during the period) the experimental cylinders were filled. At $T_{120}$, samples were collected individually from each experimental cylinder. To collect mesozooplankton, 20 L of seawater was filtered through a 64-μm sieve and the contents on the mesh preserved in 5% (final concentration) buffered formalin. In the laboratory, all mesozooplankton were enumerated to the lowest possible taxonomic group.

*Microplankton abundance and composition*

Microplankton (20-200 μm) samples were also collected at $T_0$, $T_{48}$, $T_{96}$ and $T_{120}$. A 90-mL sample was carefully removed from the twenty liters of whole seawater previously collected for chl *a* analyses (as above), and preserved in 10% acidic Lugol's solution (100 mL final sample volume) in amber glass jars and stored immediately in the dark. Microplanktonic organisms were isolated following standard settling techniques (Stoecker et al. 1994) in 10-mL Utermöhl chambers, and identified to the lowest possible taxonomic level using an Olympus CK2 inverted light microscope. For data analyses, taxa were characterized into one of the following categories: centric or pennate diatoms, flagellates, dinoflagellates, loricate ciliates, aloricate ciliates (e.g., oligotrichs) and others (e.g., heliozoans, acantharians, etc). Individual length and width measurements of the first 25 representatives of each group were used to convert sizes into biovolume using calculations established by Sun and Liu (2003). In turn, biovolume and abundance values of each taxonomic category were converted into biomass estimates (μg carbon $L^{-1}$) using conversion factors published by Strathmann (1967; centric and pennate diatoms), Børsheim and Bratbak (1987; flagellates), Putt and Stoecker (1989; ciliates) and Menden-Deuer and Lessard (2000; dinoflagellates). Chains of small centric diatoms were counted as single microorganisms when chain lengths exceeded 20 μm.

*M. leidyi abundance, size structure, and fecundity*

Transplanted ctenophores were individually counted and measured (length, including lobes) to the nearest millimeter prior to their addition to the tanks. Ctenophores were recovered at $T_{120}$ by gently stirring and dip-netting the cylinders after the aforementioned samples were collected, and measured. Attempts to recover ctenophores from tanks not having received ctenophore amendments were also made to determine the natural presence of *M. leidyi* from ambient seawater.

In 2009 (M2), a subset of collected ctenophores ($n \approx 18$) from Ct and Ct+N treatments was transferred back to the laboratory and examined for egg production. Recovered ctenophores were placed into individual watch glasses containing 0.45-μm filtered seawater and held in an incubator set at ambient temperature and light conditions. After 24 hours, the ctenophores were removed and rinsed with 0.45-μm filtered seawater over the watch glass to allow enumeration of total eggs using a dissecting scope.

*Statistical analyses*

Microplankton abundance and biomass data at $T_{48}$, $T_{96}$, and $T_{120}$ were analyzed using a repeated measures two-way ANOVA (Statistica 9.0, StatSoft, Inc., Tulsa, OK). Mesozooplankton abundance data at $T_{120}$ were also analyzed by two-way ANOVA with nutrients and ctenophores as fixed factors using BIOMstat: Statistical Software for Biologists (Version 3.30 by Applied Biostatistics, Inc., 10 Inwood Road, Port Jefferson, NY 11777). Homogeneity of variance was tested prior to ANOVAs using $F_{max}$, Scheffé-Box (log-anova) and Levene tests for homogeneity of variance (BIOMstat). Where necessary, data were log-transformed [ $\ln(x+1)$] prior to the ANOVAs. No appropriate transformation could be identified to perform a repeated measures ANOVA on chlorophyll *a* data. Instead, chl *a* data were analyzed by individual two-way ANOVAs with nutrients and ctenophores as fixed factos for $T_{48}$, $T_{96}$, and $T_{120}$ using BIOMstat.

**Results**

*Physical and chemical environmental parameters*

Daily dissolved oxygen (DO) concentration, temperature and salinity measurements taken within experimental cylinders suggested adequate mixing of cylinder water throughout the experiments. DO concentration within the cylinders consistently measured >50% saturation and was routinely higher than concentrations measured simultaneously in ambient water (data not shown). Temperatures within the cylinders ranged from 25.9 to 27.3° C in 2008 and 23.5 to 25.0° C in 2009, but for each experiment varied by less than 0.2° C within and among the cylinders and remained within 0.5° C of ambient temperatures. Cylinder salinity values ranged from 26.0 to 26.5 in 2008 and 22.1 to 22.5 in 2009, varied by ≤0.2 within and among cylinders, and never exceeded more than 1 unit of the salinity of ambient seawater.

*Chlorophyll a*

Whole and size-fractionated chlorophyll levels were significantly elevated in N and Ct+N treatments compared to C and Ct treatments during both experiments (Figure 1, Table 1). Chlorophyll *a* <5 μm comprised 97% and 81% of total chl *a* content at $T_0$ during M1 and M2, respectively, and frequently matched or exceeded whole chlorophyll values throughout both mesocosms (extreme outliers were not discarded when calculating mean treatment values). While chl *a* levels increased with time in N and Ct+N treatments, they exhibited a general trend of decline in C and Ct treatments during the duration of the two experiments. At $T_{96}$ and $T_{120}$, differences in chlorophyll content between N and C+N or between C and Ct treatments were indiscernible (Figure 1).

*Mesozooplankton abundance and composition*

Mean mesozooplankton densities at $T_0$ were 71 (+/- 18) $L^{-1}$ and 81 (+/- 12) $L^{-1}$ during M1 and M2, respectively, and increased substantially in all treatments during the experiments. Copepod nauplii (predominantly *Acartia tonsa*) consistently dominated the mesozooplankton at $T_{120}$ during both mesocosm experiments, comprising 84-95% of total mesozooplankton abundance in all cylinders. Ctenophores significantly reduced mesozooplankton abundance in Ct and Ct+N treatments in both experiments, relative to the control (Figure 2, Table 2). In contrast, nutrients increased mesozooplankton abundance in both experiments, however the differences were only significant in M2 (Figure 2, Table 2).

*Microplankton abundance and composition*

During both experiments, microplanktonic assemblages were dominated numerically (cells $mL^{-1}$) by pennate diatoms (e.g., *Nitzschia longissima, Pleurosigma directum* and *Pleurosigma elongatum*) which initially comprised >93% of the microplanktonic community, but ranged from 80-90% and 35-93% at the end of M1 and M2, respectively. However, diatoms contributed less than 26% to total microplanktonic biomass (μg C $L^{-1}$), which was dominated in both experiments by ciliates (aloricate and loricate). Dinoflagellates and flagellates comprised less than 3% of total microplanktonic abundance at $T_0$, but ranged from 0.2-5.8% and 0.3-57% throughout M1 and M2, respectively. Centric diatoms, while generally low in abundance during M2, were largely absent in M1. Uncategorized (other) microplankton (e.g., *Pterosperma*, heliozoans, and unidentified amoeboids) contributed little to total microplanktonic abundance in M2, but comprised up to 14% of microplanktonic abundance in M1 (data not shown). Biomass conversions for these other microplanktonic taxa were not made.

Nutrients significantly increased densities of all microplanktonic taxa in M2, but only pennate diatoms, flagellates and aloricate ciliates in M1 (Tables 3 and 4; Figures 3 and 4). Increases of microplankton in N treatments were generally limited to between $T_0$ and $T_{48}$ during both experiments, after which abundances remained relatively constant. Nutrients had no detectable influence on dinoflagellates ($mL^{-1}$ or $\mu g\ C\ L^{-1}$) during M1, although increases in these taxa were identified during M2. In M2, the dinoflagellate community was largely autotrophic and dominated by *Protoperidinium crassipes, Scrippsiella trochoidea, Prorocentrum minimum and Prorocentrum micans, and Pyrophacus sp.;* whereas in M1 (2008), heterotrophic dinoflagellates (e.g., *Gyrodinium spirale*, *Gyrodinium dominans*, *Gyrodinium aureolum* and *Akashiwo sanguinea*) dominated the assemblage. Thus, differences in species composition and trophic structure of the dinoflagellate community between the two years likely explain the contradiction. The scarcity of centric diatoms and loricate ciliates during M1 (each taxon averaged <0.6% of total microplankton throughout the experiment), may have precluded a statistically-significant relationship.

The presence of *M. leidyi* in recent (M2), but not historic (M1), abundances altered microplanktonic abundance and composition over the five-day experiments. High abundances of *M. leidyi* significantly influenced ciliate densities (cells $mL^{-1}$ and $\mu g\ C\ L^{-1}$), and marginally influenced flagellate abundance (cells $mL^{-1}$), during M2 (Table 4). At $T_{96}$ and $T_{120}$, loricate (e.g., *Tintinnopsis* sp. and *Favella* sp.) and aloricate ciliates (e.g., *Strombidinium* sp. and *Strobilidium* sp.) were more numerous in ctenophore treatments, relative to the control (Figure 5). Further, increases in aloricate ciliates were substantially greater in ctenophore treatments than in nutrient-amended cylinders. Aloricate ciliates, relative to the control, experienced a three-fold increase in N treatments, but a fourteen-fold increase in Ct treatments at the end of M2 (Figure 5a). Whereas ciliates increased immediately in N treatments, their increases in cylinders containing *M. leidyi* were not detected until $T_{96}$ (Figure 4). Flagellates also increased in the presence of *M. leidyi*, but these increases were not detected until $T_{120}$. Ctenophores significantly influenced densities of pennate diatoms in M2 (Table 3), which were slightly elevated in ctenophore treatments at $T_{120}$, relative to the control (Figure 4b). No significant increases in centric diatoms or dinoflagellates were identified in ctenophore treatments during either experiment.

Moreover, *M. leidyi* predation and nutrient enrichment had a combined and interactive effect on the microplankton community. At $T_{120}$, ciliate and flagellate densities were higher in Ct+N tanks than any other treatment during both experiments, although the differences were only significant in M2 (Figures 3 and 4; Tables 3 and 4). Aloricate ciliates, which had increased by an order of magnitude in N and Ct treatments, were 120X greater in abundance in Ct+N tanks, relative to the control, at $T_{120}$ during M2 (Figure 5a). Dinoflagellates were slightly elevated in Ct+N treatments at the end of both experiments, although neither of these increases was significant. The combined effect of eutrophication and ctenophore predation on pennate diatoms was conflicting; Ct+N treatments contained significantly more pennates than C and Ct treatments, but fewer than N treatments, suggesting that *M. leidyi* may have a reducing influence on this taxon in the presence of nutrient enhancement. The same was observed for centric diatoms, although their low abundance, especially during M1, likely precludes a statistically significant relationship.

*M. leidyi abundance, size structure, and fecundity*

*Mnemiopsis* specimens were seen actively swimming in ctenophore-amended tanks throughout the experiments. The ctenophores were recovered at the end of both experiments, and

appeared in good health with no sign of bodily damage. The average size of *M. leidyi* added to ctenophore treatments was 3.2 (+/- 0.1) cm in M1 and 2.4 (+/- 0.1) cm in M2. Ctenophores recovered from M1 did not vary greatly in size (<10%) between $T_0$ and $T_{120}$, however ctenophores recovered at the end of M2 grew 83% over the course of the five-day experiment. At $T_{120}$, the average size of ctenophores recovered from Ct and Ct+N treatment cylinders was 4.4 cm (+/- 0.4 s.d.) and 4.3 cm (+/- 0.2 s.d.), respectively. No ctenophores were identified in non-ctenophore amended cylinders at $T_f$ during either experiment.

Ctenophores recovered from M2 were transported back to the laboratory for egg production studies. All recaptured *M. leidyi* produced eggs overnight. Ctenophores recovered from Ct cylinders averaged 3.5 (+/- 1.1) cm, whereas ctenophores recovered from Ct+N cylinders averaged 3.8 (+/- 0.8) cm. The size of collected ctenophores did not differ significantly between treatments ($df$= 1, 16; $Fs$= 0.408; $p$= 0.532). However, the number of eggs produced by *M. leidyi* from Ct treatments differed significantly from the number produced by *M. leidyi* from Ct+N treatments ($df$= 1, 16; $Fs$= 7.48; $p$= 0.015). Ctenophores from Ct+N treatments produced nearly three times as many eggs as those reclaimed from Ct treatments; recovered *M. leidyi* produced an average of 466 eggs (+/- 113 s.e.) and 1324 eggs (+/- 293 s.e.) individual$^{-1}$ d$^{-1}$ in Ct and Ct+N treatments, respectively.

## Discussion

*The influence of M. leidyi on the plankton community varies with nutrient availability and ctenophore abundance*

Nutrient enhancement in the presence of adult *M. leidyi* altered plankton community structure in a way that was distinctly different than when nutrient and predatory processes occurred separately. Certain microplanktonic taxa benefited under the combined influence of ctenophore predation and eutrophication. Moreover, these changes appear to be dependent on ctenophore abundance; current (high) densities of *M. leidyi* produced dramatic cascading changes in microzooplankton abundance and composition, whereas historic (low) abundances failed to elicit a significant response in the lower trophic assemblage. For example, where aloricate ciliates increased by nearly 300% in Ct+N treatments containing low densities of *M. leidyi* during M1, the taxa increased by more than 12,000% in Ct+N treatments containing high densities of *M. leidyi* at the end of M2.

The combination of top-down and bottom-up influences of nutrients and ctenophore predation, respectively, revealed an interactive, non-additive influence on the plankton community when *M. leidyi* abundances were high. The response of ciliates to simultaneous nutrient enrichment and ctenophore predation in M2 was significantly greater than the individual influence of nutrients or *M. leidyi*, and exceeded what would be expected if the two effects were additive. Cylinders containing recent abundances of *M. leidyi* or those receiving daily nutrient amendments experienced an order of magnitude increase in ciliates whereas the combination of nutrient enrichment in the presence of *M. leidyi* increased the abundance of ciliates by two orders of magnitude, relative to control treatments (Figure 5). These data demonstrate that predation by current abundances of *M. leidyi* under eutrophic conditions can have significant impacts on the microplanktonic community.

*Nutrient enrichment positively influences ctenophore fecundity and recruitment*

The cascading increases of certain microzooplanktonic taxa during population blooms of adult *M. leidyi* can influence the survival and recruitment of larval ctenophores into mesozooplankton-feeding adults. Ciliates, an important prey item for developing ctenophores (Stoecker et al. 1987; Sullivan and Gifford 2007), increased substantially in treatments containing high densities of *M. leidyi.* Significant increases in ciliate abundance alongside reduced mesozooplankton densities in the presence of the cydippid ctenophore *Pleurobrachia pileus* Müller 1776 have also been documented experimentally (Granéli and Turner 2002). These results agree well with recent observations made in Great South Bay, where seasonal blooms of adult *M. leidyi* corresponded with subsequent and substantial increases in aloricate ciliates in 2008 and 2009 (McNamara et al. 2013, Chapter One). Increases in larval *M. leidyi* followed the microplanktonic surge, during which time dinoflagellate and ciliate abundance subsequently and dramatically declined (McNamara et al. 2013, Chapter One).

Although anticipated, no significant increases in dinoflagellates associated with *M. leidyi* were detected in this mesocosm study. However, large densities of adult *M. leidyi* drastically increased dinoflagellate abundance after reducing mesozooplankton abundance in mesocosms contained within the Baltic Sea (Dinasquet et al. 2012). The region in which Dinasquet et al. (2012) conducted their experiments is considered to be nutrient-limited and the authors noted that the predatory influence of *M. leidyi* on lower trophic levels is likely to be dependent on local nutrient conditions. Moreover, their experiments differed from mine in that cladocera, not copepods, comprised the majority of planktonic biomass, and no ciliate increases were detected within the *M. leidyi* treatments. The link between selective grazing by copepods and ciliate abundance is well-established (e.g., Stoecker and Egloff 1987; Zöllner et al. 2003; Calbet and Saiz 2005), but ciliates also respond very rapidly to increasing nutrient concentrations (e.g., Gismervik et al. 2002). Accompanied by blooms of the indigenous *Aurelia aurita*, the invasion of *M. leidyi* in the heavily eutrophic Limfjorden (Denmark) caused substantial declines in copepods and cladocera, after which ciliates surged in abundance (Riisgård et al. 2012).

Eutrophication also appears to enhance the fecundity of *M. leidyi* by increasing mesozooplanktonic prey for adults. Ctenophores taken from nutrient-enriched treatments produced significantly more eggs than those from treatments not receiving nutrient amendments. *Mnemiopsis* from Ct+N treatments produced three times as many eggs as those from Ct treatments. These values agree well with differences in mesozooplankton abundance between the two *M. leidyi* treatments; at $T_{120}$, mean mesozooplankton abundance in Ct+N cylinders was nearly three times greater than in Ct treatments (Figure 2).

When (or where) seasonal population blooms of *M. leidyi* coincide with periods of nutrient enrichment, the combined influence of (top-down) ctenophore predation and (bottom-up) eutrophication processes could result in unique consequences for the plankton community, which can feedback to ctenophore population dynamics by increasing microplanktonic prey for their larvae, and enhancing fecundity of the adults. In Great South Bay (GSB), NY, major losses of eastern oysters, hard clams, and Atlantic menhaden (*via* salinity changes and overexploitation) has led to a decline in ecosystem maturity and increasing dominance of lower trophic level organisms (Nuttall et al. 2011). Warmer winter temperatures and increased nutrient enrichment have also been implicated in the decline of ecosystem structure in GSB (Nuttall et al. 2011) where increases in *M. leidyi* abundance and shifts to an earlier seasonal maximum have occurred over the past two decades (McNamara et al. 2010; McNamara 2013, Chapter One). GSB contains relatively high levels of inorganic nutrients, which are spatially and temporally influenced by freshwater discharge (groundwater seepage, fluvial discharge, storm drainage, and

sewage effluents), anthropogenic influences, and physical, biological and benthic processes (Clark et al. 2006). Higher concentrations of $NH_4^+$, $NO_3^-$, and $PO_4^{-3}$ have been observed in rivers and groundwater, and at stations located near river mouths during high flow periods (April and September; Clark et al. 2006). The release of nutrients and subsequent increases in certain mesozooplanktonic and microplanktonic taxa may help explain the increased abundance and earlier population blooms of *M. leidyi* in Great South Bay and other coastal estuaries.

**Conclusions**

This is the first study to document interactive effects by nutrient enrichment and *M. leidyi* predation on the microplanktonic community using recent (high) and historic (low) ctenophore abundances. My results agree well with previously-conducted mesocosm experiments wherein nutrient enrichment and gelatinous zooplankton predation resulted in cascading, positive impacts on microplankton (Pitt et al. 2007; Graneli and Turner 2002). The role of gelatinous zooplankton in disturbed habitats is likely to differ from that in natural, undisturbed environments. Large blooms of *M. leidyi* occurring during periods or in regions of nutrient enrichment may elicit unique responses within the microplanktonic community, as top-down predatory influences coincide with bottom-up nutrient processes. Since microplankton are important prey for developing *M. leidyi*, the combined bottom-up and top-down influences of eutrophication and predation, respectively, may help explain recently-documented shifts in the population dynamics of *M. leidyi* in Great South Bay.

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Table 1. Results of two-way ANOVA testing for differences in whole (a) and <5 μm chl *a* (b) content among treatments (with nutrients and ctenophores as fixed variables) at $T_{48}$, $T_{96}$, and $T_{120}$ during M1 and M2.

| M1 (whole chl *a*) | Time, h | *df* | *MS* | *F* | *p* |
|---|---|---|---|---|---|
| Nutrients | 48 | 1 | 192 | 26.7 | **<0.001** |
| | 96 | 1 | 514 | 69.2 | **<0.001** |
| | 120 | 1 | 588 | 71.9 | **<0.001** |
| Ctenophore | 48 | 1 | 36 | 5 | **0.036** |
| | 96 | 1 | 15.8 | 2.1 | 0.160 |
| | 120 | 1 | 10.1 | 1.23 | 0.279 |
| Ctenophore*Nutrients | 48 | 1 | 7.8 | 1.1 | 0.310 |
| | 96 | 1 | 18.2 | 2.4 | 0.133 |
| | 120 | 1 | 17.7 | 2.16 | 0.157 |
| M2 (whole chl *a*) | | | | | |
| Nutrients | 48 | 1 | 699 | 124 | **<0.001** |
| | 96 | 1 | 700 | 405 | **<0.001** |
| | 120 | 1 | 1280 | 7150 | **<0.001** |
| Ctenophore | 48 | 1 | 41.7 | 7.41 | **0.013** |
| | 96 | 1 | 2.84 | 1.65 | 0.214 |
| | 120 | 1 | 14 | 1.65 | 0.213 |
| Ctenophore*Nutrients | 48 | 1 | 37.4 | 6.64 | **0.018** |
| | 96 | 1 | 3.26 | 1.88 | 0.185 |
| | 120 | 1 | 14 | 1.65 | 0.213 |

(a)

| M1 (<5 μm chl *a*) | Time, h | *df* | *MS* | *F* | *p* |
|---|---|---|---|---|---|
| Nutrients | 48 | 1 | 21.2 | 1.2 | 0.296 |
| | 96 | 1 | 617 | 78.1 | **<0.001** |
| | 120 | 1 | 739 | 122 | **<0.001** |
| Ctenophore | 48 | 1 | 6 | 0.33 | 0.574 |
| | 96 | 1 | 6.7 | 0.85 | 0.368 |
| | 120 | 1 | 0.36 | 0.06 | 0.810 |
| Ctenophore*Nutrients | 48 | 1 | 0.72 | 0.04 | 0.845 |
| | 96 | 1 | 23 | 2.91 | 0.103 |
| | 120 | 1 | 0.004 | 0.001 | 0.979 |
| M2 (<5 μm chl *a*) | | | | | |
| Nutrients | 48 | 1 | 706 | 133 | **<0.001** |
| | 96 | 1 | 560 | 350 | **<0.001** |
| | 120 | 1 | 1190 | 4140 | **<0.001** |
| Ctenophore | 48 | 1 | 43.5 | 8.19 | **0.010** |
| | 96 | 1 | 0.256 | 0.16 | 0.693 |
| | 120 | 1 | 2.01 | 0.23 | 0.635 |
| Ctenophore*Nutrients | 48 | 1 | 35.7 | 6.72 | **0.017** |
| | 96 | 1 | 1.73 | 1.08 | 0.311 |
| | 120 | 1 | 6.38 | 0.74 | 0.401 |

(b)

Table 2. Results of two-way ANOVA testing for differences in mesozooplankton abundance (with nutrients and ctenophores as fixed variables) among treatments at $T_{120}$ during M1 and M2.

| | Mesozooplankton | | | | |
|---|---|---|---|---|---|
| M1 | | *df* | *MS* | *F* | *p* |
| | Nutrients | 1 | 52100 | 0.741 | 0.407 |
| | Ctenophore | 1 | 23000 | 0.327 | **0.008** |
| | Ctenophore*Nutrients | 1 | 362 | 0.005 | 0.817 |
| M2 | | | | | |
| | Nutrients | 1 | 0.563 | 32.19 | **0.005** |
| | Ctenophore | 1 | 1.2 | 68.8 | **<0.001** |
| | Ctenophore*Nutrients | 1 | 0.003 | 0.19 | 0.674 |

Table 3. Results of repeated measures ANOVA testing for differences in microplankton abundance (a) and biomass (b) among treatments during M1 ($T_0$, $T_{48}$, $T_{96}$, and $T_{120}$). Homogeneity of variance was tested prior to ANOVAs using $F_{max}$, Scheffé-Box (log-anova) and Levene tests for homogeneity of variance (BIOMstat). Where necessary, data were log-transformed [ ln(x+1)] prior to the ANOVAs. Cten = ctenophore, Nuts = nutrients.

| Variable: | | Centric diatoms | | Pennate diatoms | | Dinoflagellates | | Flagellates | | Aloricate ciliates | | Loricate ciliates | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Transformation: | | (none) | | ln(x+1) | | (none) | | (none) | | (none) | | (none) | |
| | *df* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* |
| Nutrients | 1 | 1910 | 0.219 | 9.81 | **<0.001** | 2030 | 0.295 | 3006 | **0.003** | 60067 | **0.048** | 727 | 0.154 |
| Ctenophore | 1 | 865 | 0.396 | 0.486 | 0.126 | 4670 | 0.128 | 27.9 | 0.698 | 7480 | 0.435 | 15.2 | 0.825 |
| Cten*Nuts | 1 | 1120 | 0.337 | 0.005 | 0.869 | 149 | 0.770 | 4.39 | 0.877 | 600 | 0.822 | 1620 | **0.046** |
| Time | 2 | 10133 | **0.001** | 2.32 | **<0.001** | 5.6 | 0.995 | 896 | 0.198 | 27530 | **0.045** | 1492 | **0.008** |
| Time Nuts | 2 | 2570 | 0.095 | 0.035 | 0.567 | 1400 | 0.381 | 171 | 0.715 | 4850 | 0.528 | 54.3 | 0.786 |
| Time Ctenophore | 2 | 693 | 0.493 | 0.104 | 0.205 | 670 | 0.622 | 956 | 0.180 | 10240 | 0.274 | 159 | 0.504 |
| Time Cten*Nuts | 2 | 906 | 0.401 | 0.007 | 0.897 | 497 | 0.701 | 207 | 0.668 | 7902 | 0.362 | 1098 | **0.021** |

(a)

| Variable: | | Centric diatoms | | Pennate diatoms | | Dinoflagellates | | Flagellates | | Aloricate ciliates | | Loricate ciliates | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Transformation: | | ln(x+1) | | ln(x+1) | | (none) | | ln(x+1) | | (none) | | ln(x+1) | |
| | *df* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* |
| Nutrients | 1 | 2.78 | 0.069 | 6.37 | **<0.001** | 306 | 0.156 | 1.09 | 0.503 | 145000 | **0.014** | 17.8 | 0.341 |
| Ctenophore | 1 | 0.04 | 0.807 | 0.527 | 0.099 | 121 | 0.354 | 0.589 | 0.620 | 8670 | 0.464 | 6.26 | 0.565 |
| Cten*Nuts | 1 | 1.21 | 0.204 | 0.063 | 0.538 | 129 | 0.339 | 2.27 | 0.342 | 192 | 0.912 | 19.3 | 0.323 |
| Time | 2 | 3.36 | **0.007** | 2.25 | **0** | 169 | 0.410 | 2.17 | 0.286 | 9710 | 0.154 | 14.5 | 0.136 |
| Time Nuts | 2 | 0.71 | 0.263 | 0.018 | 0.703 | 82.1 | 0.640 | 1.83 | 0.343 | 677 | 0.865 | 0.524 | 0.922 |
| Time Ctenophore | 2 | 0.47 | 0.405 | 0.218 | **0.03** | 247 | 0.279 | 0.734 | 0.640 | 10800 | 0.128 | 29.1 | **0.028** |
| Time Cten*Nuts | 2 | 1.05 | 0.149 | 0.034 | 0.522 | 126 | 0.509 | 0.415 | 0.775 | 11100 | 0.123 | 4.02 | 0.548 |

(b)

Table 4. Results of repeated measures ANOVA testing for differences in microplankton abundance (a) and biomass (b) among treatments during M2 ($T_0$, $T_{48}$, $T_{96}$, and $T_{120}$). Homogeneity of variance was tested prior to ANOVAs using $F_{max}$, Scheffé-Box (log-anova) and Levene tests for homogeneity of variance (BIOMstat). Where necessary, data were log-transformed [ ln(x+1)] prior to the ANOVAs. Cten = ctenophore, Nuts = nutrients.

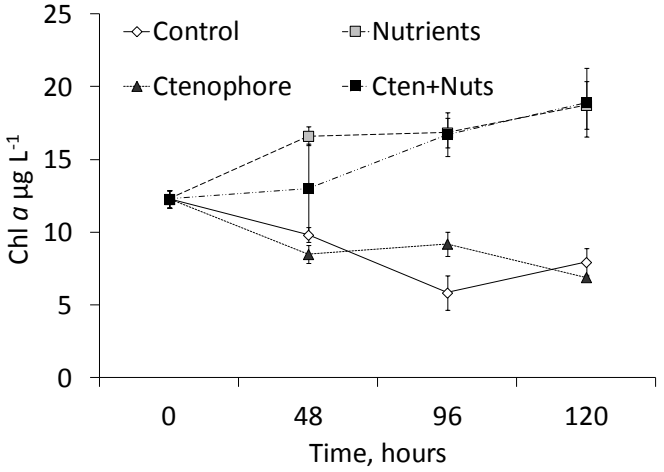
| Variable: | | Centric diatoms | | Pennate diatoms | | Dinoflagellates | | Flagellates | | Aloricate ciliates | | Loricate ciliates | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Transformation: | | ln(x+1) | | ln(x+1) | | ln(x+1) | | (none) | | ln(x+1) | | ln(x+1) | |
| | *df* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* |
| Nutrients | 1 | 49.7 | **0.005** | 41.1 | **<0.001** | 1.8 | **0.003** | 81500 | **0.035** | 9.19 | **0.003** | 22.4 | **<0.001** |
| Ctenophore | 1 | 0.566 | 0.697 | 0.175 | 0.390 | **0.003** | 0.877 | 62100 | 0.058 | 23.8 | **<0.001** | 22.2 | **<0.001** |
| Cten*Nuts | 1 | 0.101 | 0.868 | 1.2 | **0.045** | 0.237 | 0.170 | 51000 | 0.08 | 3.52 | **0.033** | 6.86 | **0.006** |
| Time | 2 | 24.9 | **<0.001** | 0.14 | 0.443 | 1.91 | **0.002** | 73200 | **0.002** | 3.98 | **0.004** | 9.28 | **0** |
| Time Nuts | 2 | 2.48 | 0.305 | 6.87 | **<0.001** | 1.09 | **0.014** | 61200 | **0.004** | 3.43 | **0.007** | 6.07 | **<0.001** |
| Time Ctenophore | 2 | 0.714 | 0.697 | 0.247 | 0.252 | 0.378 | 0.175 | 61000 | **0.004** | 10.4 | **<0.001** | 5.58 | **<0.001** |
| Time Cten*Nuts | 2 | 0.25 | 0.880 | 0.372 | 0.136 | 0.284 | 0.261 | 40800 | **0.016** | 0.624 | 0.306 | 3.08 | **<0.001** |

(a)

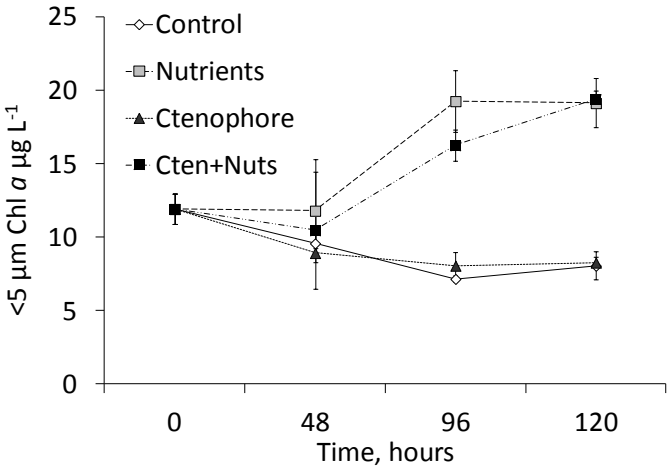
| Variable: | | Centric diatoms | | Pennate diatoms | | Dinoflagellates | | Flagellates | | Aloricate ciliates | | Loricate ciliates | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Transformation: | | (none) | | ln(x+1) | | ln(x+1) | | ln(x+1) | | ln(x+1) | | ln(x+1) | |
| | *df* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* | *MS* | *p* |
| Nutrients | 1 | 51400 | **0.002** | 36.5 | **<0.001** | 2.08 | **0.003** | 2.76 | 0.263 | 9.68 | **<0.001** | 31.9 | **<0.001** |
| Ctenophore | 1 | 3261 | 0.292 | 0.706 | 0.178 | 0.004 | 0.868 | 2.3 | 0.303 | 18.7 | **<0.001** | 16.3 | **0.005** |
| Cten*Nuts | 1 | 2160 | 0.386 | 1.8 | **0.046** | 0.235 | 0.206 | 0.079 | 0.844 | 1.89 | **0.045** | 3.77 | 0.106 |
| Time | 2 | 7910 | **0.011** | 1.3 | **0.023** | 2.45 | **0.001** | 3.39 | 0.471 | 5.7 | **0.002** | 8.79 | **0.012** |
| Time Nuts | 2 | 1350 | 0.375 | 6.88 | **<0.001** | 1.49 | **0.007** | 8.49 | 0.171 | 3.23 | **0.015** | 7.32 | **0.022** |
| Time Ctenophore | 2 | 599 | 0.637 | 0.347 | 0.305 | 0.421 | 0.175 | 0.439 | 0.903 | 8.49 | **<0.001** | 4.13 | 0.095 |
| Time Cten*Nuts | 2 | 1450 | 0.350 | 0.295 | 0.361 | 0.208 | 0.403 | 2.48 | 0.573 | 0.505 | 0.439 | 4.62 | 0.075 |

(b)

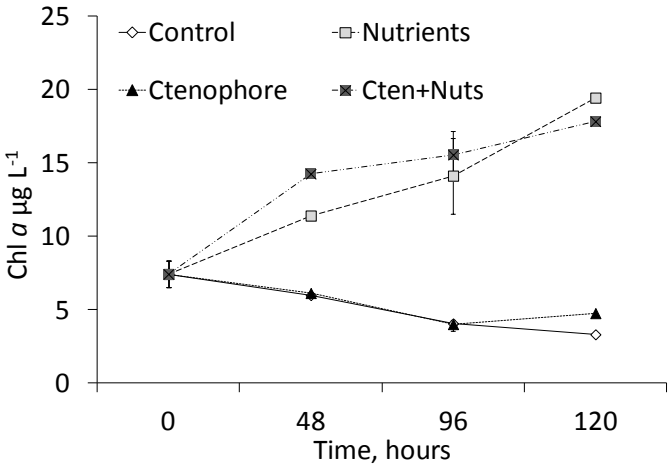
Figure 1. Whole and size-fractionated chl *a* content (µg $L^{-1}$) by treatment and time interval during M1 (a, b) and M2 (c, d). Cten+Nuts = ctenophores and nutrients.



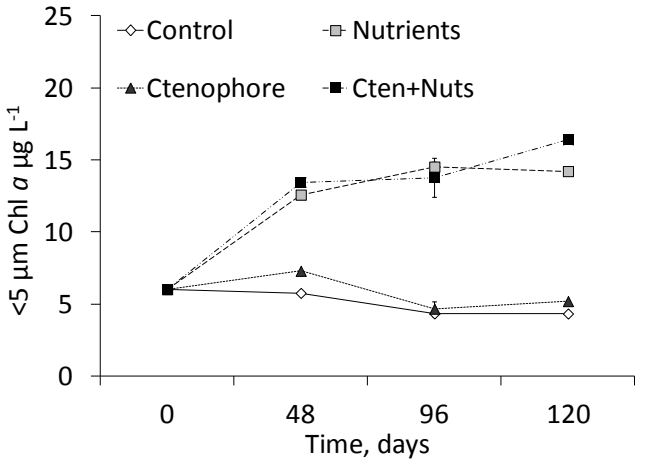

(a)




(b)




(c)




(d)

Figure 2. Mean mesozooplankton (+/- s.d.) densities at $T_{120}$ in each treatment during M1 and M2. Cten+Nuts = ctenophores and nutrients.

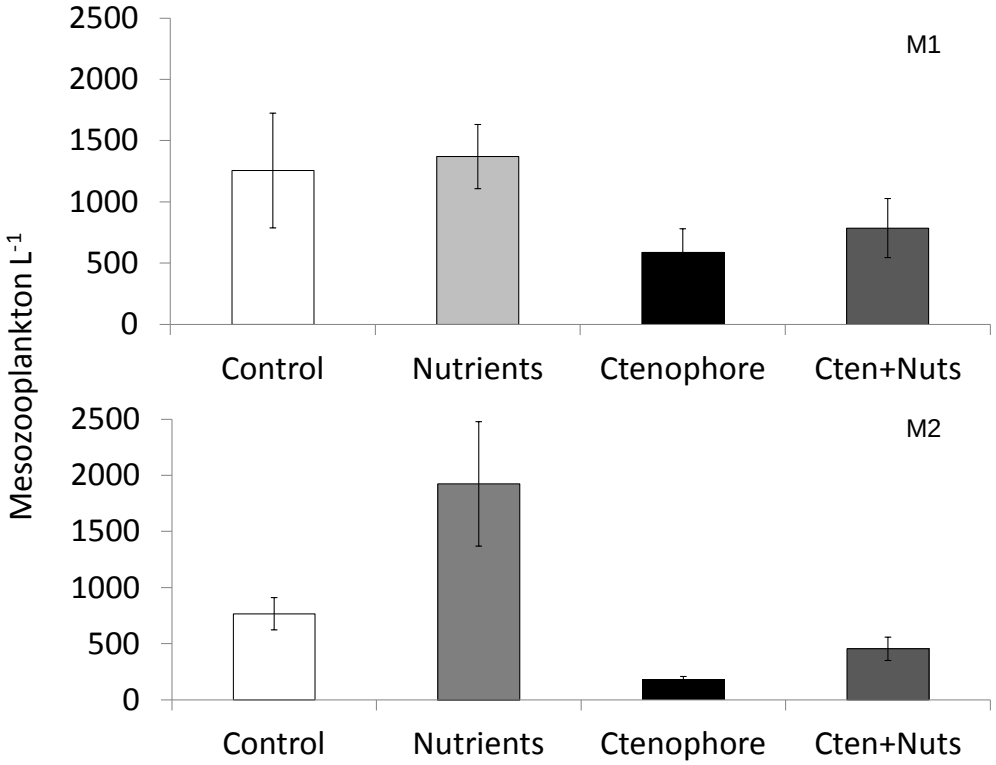
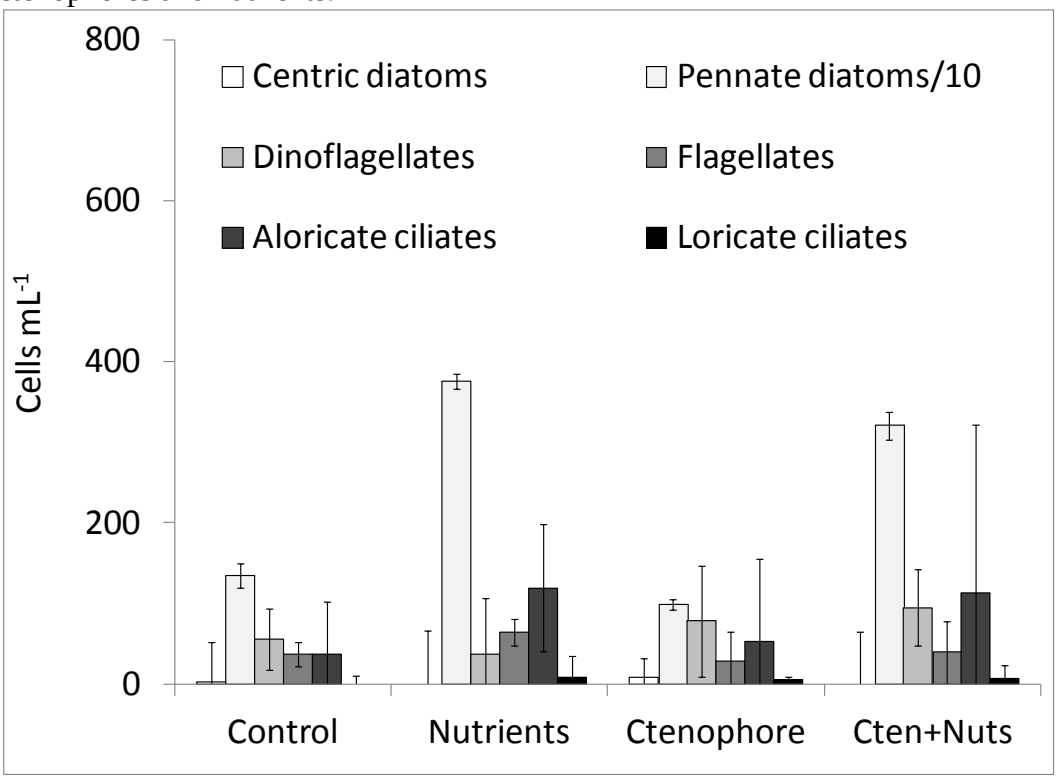
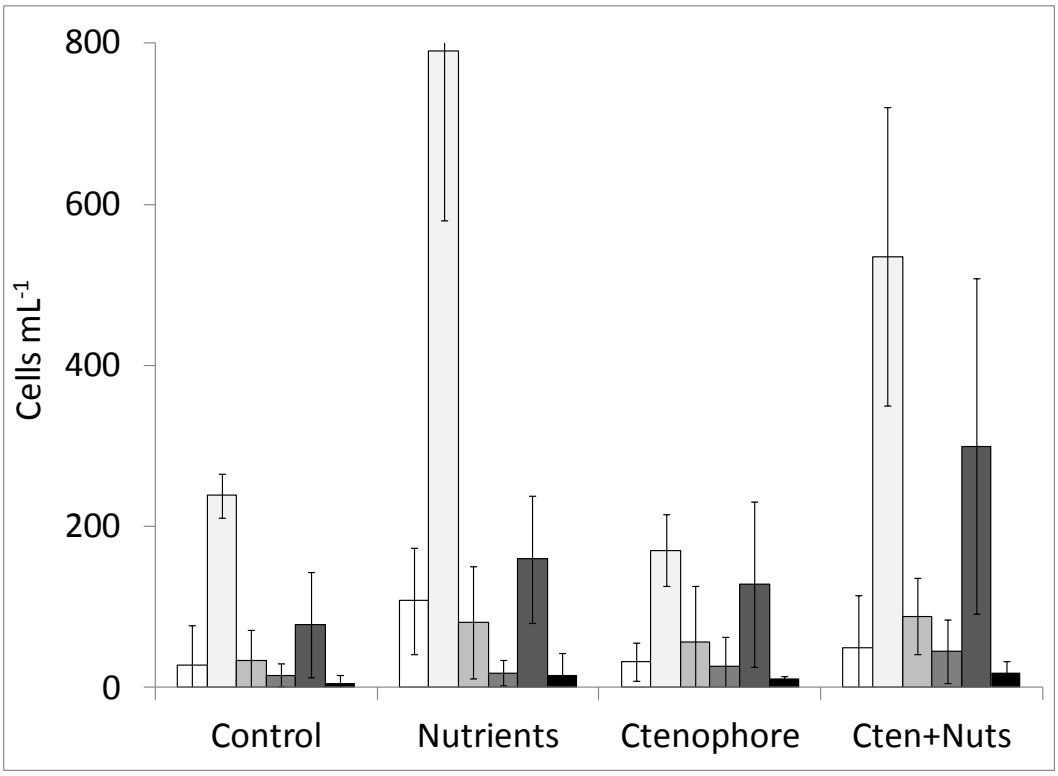


Figure 3. Abundance (cells $mL^{-1}$) of centric and pennate* diatoms, dinoflagellates, flagellates, and aloricate and loricate ciliates at $T_{96}$ (a) and $T_{120}$ (b) during M1. *Note that abundances of pennate diatoms have been divided by ten to appropriately fit on the graph. Cten+Nuts = ctenophores and nutrients.

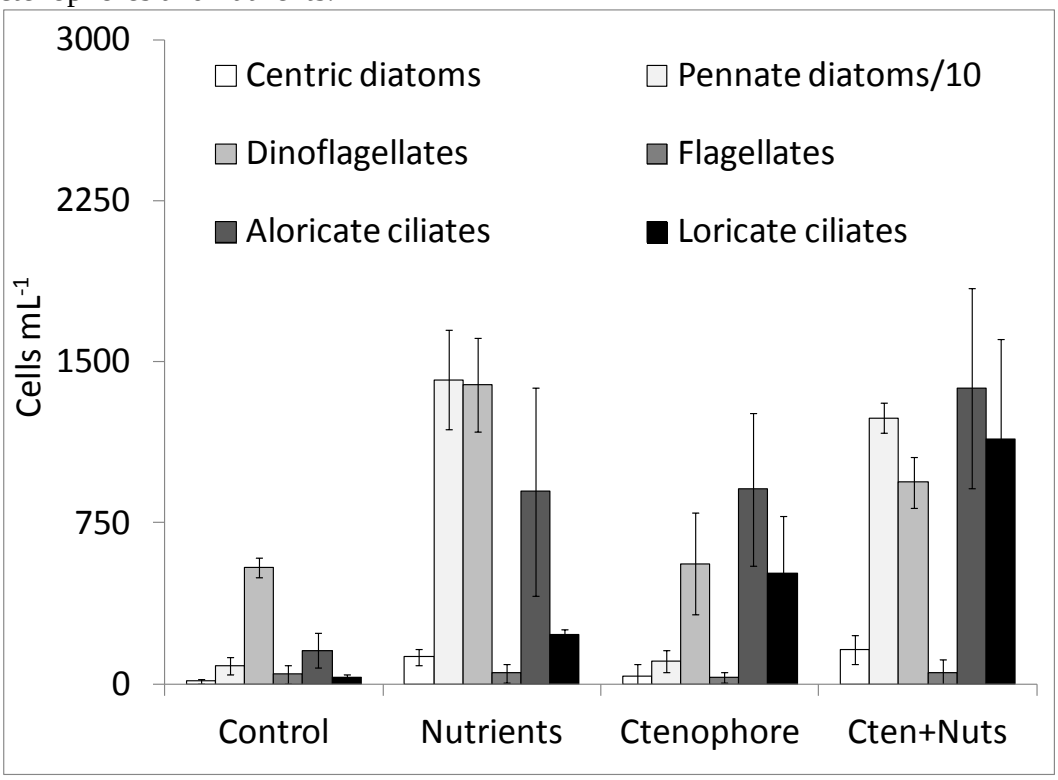



(a)

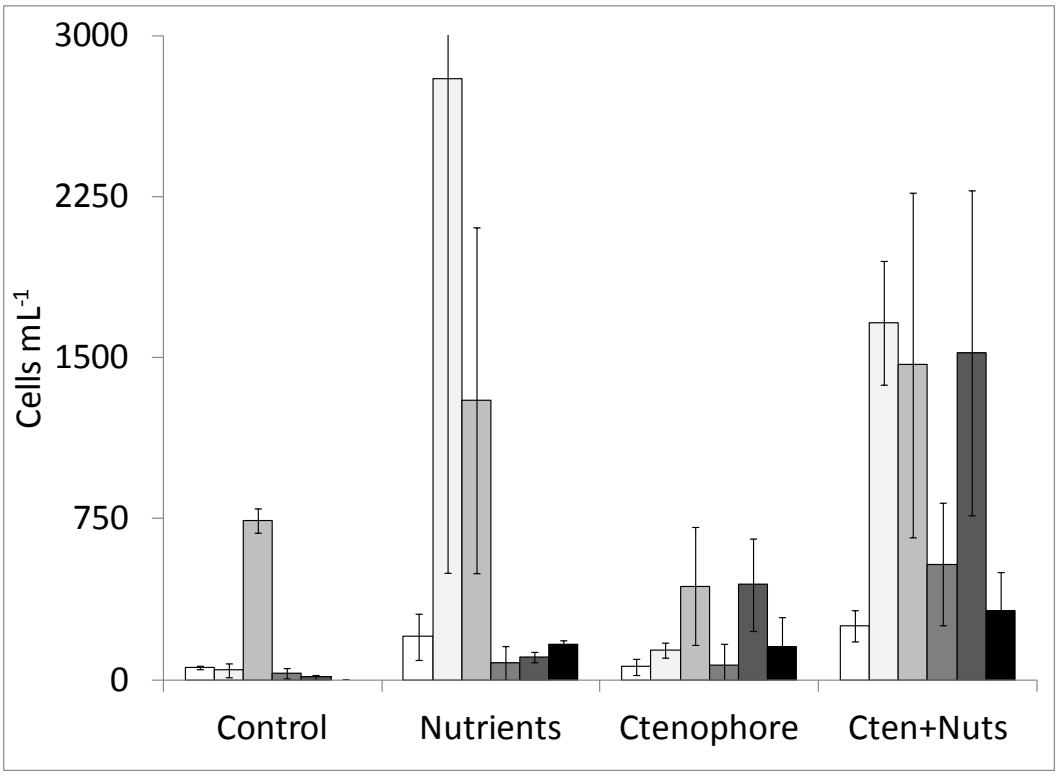



(b)

Figure 4. Abundance (cells $mL^{-1}$) of centric and pennate* diatoms, dinoflagellates, flagellates, and aloricate and loricate ciliates at $T_{96}$ (a) and $T_{120}$ (b) during M2. *Note that abundances of pennate diatoms have been divided by ten to appropriately fit on the graph. Cten+Nuts = ctenophores and nutrients.

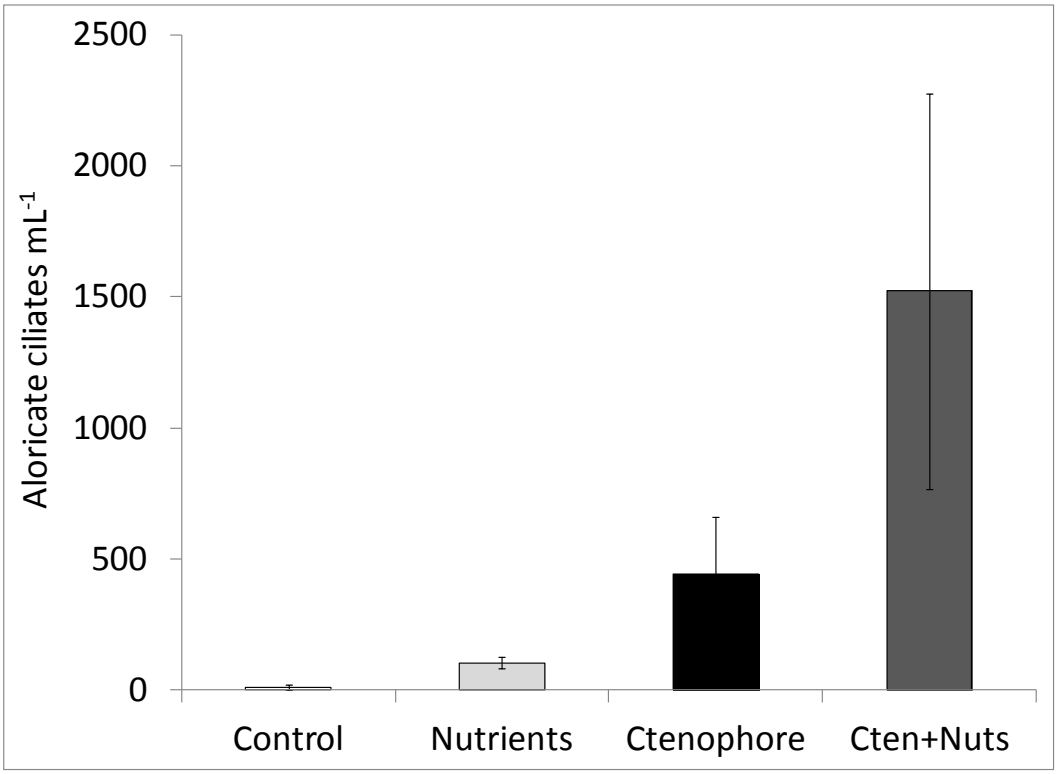



(a)

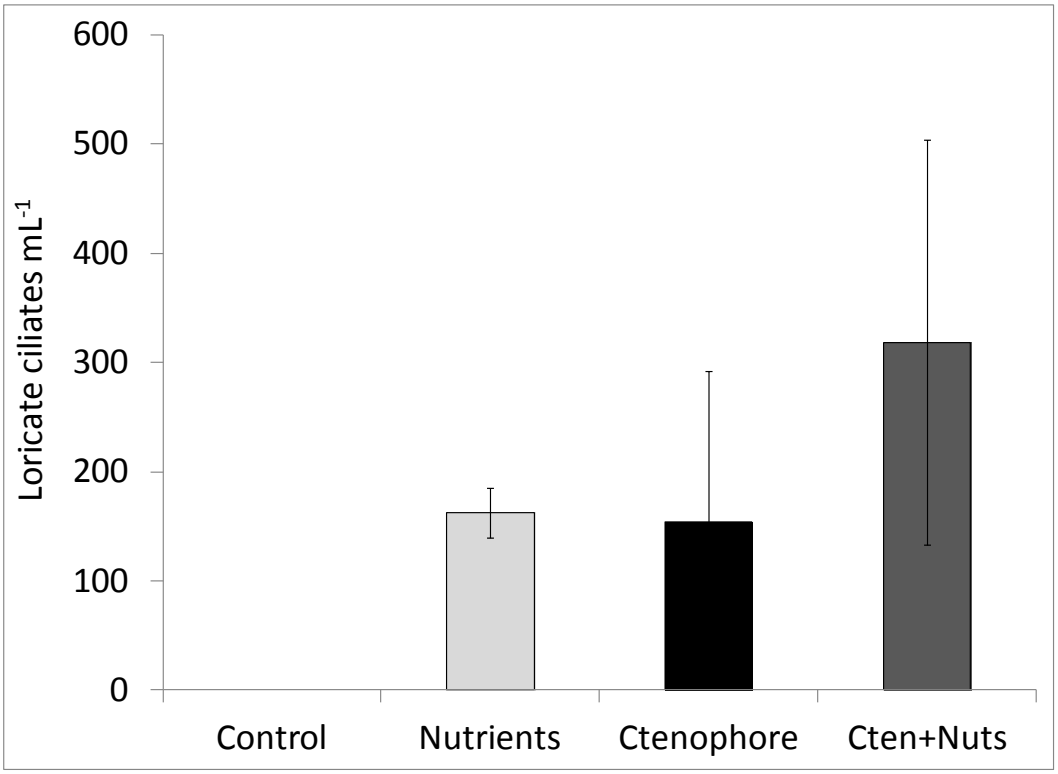



(b)

Figure 5. Abundance (cells $mL^{-1}$) of aloricate (a) and loricate ciliates (b) at $T_{120}$ for mesocosm experiment M2. Note the differences in y-axes. Cten+Nuts = ctenophores and nutrients.




(a)




(b)

# CHAPTER FOUR

Elemental composition of *Mnemiopsis leidyi* A. Agassiz 1865 and its implications for nutrient recycling in a Long Island estuary

## Abstract

The ctenophore *Mnemiopsis leidyi* is an ecologically-important predator in temperate coastal environments. Their populations fluctuate seasonally, serving as sinks of nutrients during periodic blooms, but as sources *via* excretion and during population collapse. Ctenophores were analyzed for elemental composition (C, N, and P) during 2008 and 2009 in Great South Bay, New York. Salt-free weight percent C, N and P correlated positively with ctenophore sizes and zooplankton prey abundances. Nitrogen and P were higher at the onset of blooms than during collapse when prey were substantially fewer. Ctenophores collected during average to high zooplankton densities had atomic ratios averaging C/N ~ 6:1 and C/P ~ 66:1, but became C- and P-depleted (C/N ~ 5:1 C/P ~ 128:1) with decreasing zooplankton. Incubations demonstrated rapid remineralization of ctenophore biomass (as $NH_4^+$, $HPO_4^{2-}$), following first order kinetics (e.g., $k \sim 0.1 – 0.4\ d^{-1}$) with enriched stoichiometric N and P fractionation relative to biomass under both oxic and anoxic conditions. Based on reported excretion rates, nutrient regeneration from excretion by active populations greatly exceeds nutrients remineralized during population crashes. To my knowledge, this is the first study documenting natural seasonal patterns in ctenophore elemental stoichiometry as a function of ctenophore size and prey availability.

## Introduction

Ctenophore populations are typically characterized by considerable seasonal fluctuations in abundance, potentially influencing nutrient cycles (e.g., carbon, nitrogen, and phosphorus). Because of their boom and bust population dynamics, ctenophores may act as sinks of nutrients during bloom formation, but are sources of nutrients from excretion and the decomposition of collapsing populations (Pitt et al. 2009). Previous investigations into the contribution of nutrients by ctenophores have focused on respiration, excretion, and "sloppy feeding". Kremer (1975; 1976; 1977), Nemazie et al. (1993), and Condon et al. (2010) have provided much of the documentation on elemental composition and nutrient regeneration of the lobate ctenophore *Mnemiopsis leidyi* A. Agassiz 1865. Ctenophores, like most zooplankton, excrete nitrogen and phosphorus primarily as ammonium and phosphate, but also as dissolved organic compounds (~20% N, ~30% P; Kremer 1976; Condon et al. 2010). Ammonium and phosphate excretion, in particular, can have important implications for phytoplankton and bacterioplankton dynamics, since these are the preferred forms taken up by many planktonic species (MacIsaac and Dugdale 1972; Condon et al. 2010). Moreover, the release of carbon, nitrogen and phosphorus (C, N, and P) *via* decomposition following seasonal population collapses of gelatinous zooplankton may contribute a significant and as yet unconstrained contribution of organic matter to the planktonic ecosystem (Pitt et al. 2009; West et al. 2009b).

As *M. leidyi* populations are characterized by significant seasonal variation in abundance, the contribution to C, N, and P dynamics by *M. leidyi* is likely to change over time, and may vary according to ctenophore size-structure and nutritional status (Condon et al. 2010). Carbon to dry weight ratios have been shown to change with morphology and life stage; for example, newly-hatched cyddipid larvae possess greater than five-times the carbon ratio of lobate adults (Kremer et al. 1986; Reeve et al. 1989). Further, carbon to dry weight ratios of *M. leidyi* generally increase with zooplankton abundance, likely the result of consumption of carbon-rich prey. In laboratory studies, starved *Mnemiopsis* shrank, and C and N decreased, both in content and in proportion to dry weight (Kremer 1982; Kremer and Reeve 1989). Thus, the nutritional and resulting compositional status of natural populations with varying food sources cannot be assumed to be the same as those reared in the laboratory, and will likely vary temporally

alongside changes in ctenophore size and nutritional status (e.g., Kremer 1975; Reeve et al. 1989).

In the present study, I evaluated the relative roles of *M. leidyi* as a source or sink of nutrients in a coastal system using natural population dynamics, seasonal elemental analyses, and experimentally-determined remineralization kinetics of decomposing biomass. In order to specifically evaluate possible temporal changes in composition, individual *M. leidyi* of varying size were collected for elemental composition (C, N, and P) seasonally over two years (2008 and 2009) in Great South Bay, Long Island, New York. Bulk C, N, and P values were used together with *in situ* abundances to estimate the amount of C, N, and P released by *M. leidyi* by excretion (using literature values) and during biomass remineralization. To my knowledge, this is the first study documenting seasonal patterns in the elemental stoichiometry of an *in situ* population of *M. leidyi* as a function of size and prey availability.

## Methods

*Temporal and spatial distribution of Mnemiopsis leidyi and mesozooplankton*

Collections for *Mnemiopsis leidyi* were made weekly from May through October in 2008 and 2009 in Great South Bay, Long Island, New York (Figure 1). *Mnemiopsis* is largely absent from the bay during other periods of the year. Sampling was conducted by boat and occurred weekly at site M and biweekly at site A (except during high *M. leidyi* abundance when weekly collections were made) using a 1.0-m diameter, 1000-μm mesh net and a 0.5-m diameter, 250-μm mesh net equipped with flow meters. Two replicate tows (per net) were conducted obliquely to sample the entire water column (~1.5 m and 3 m at sites A and M, respectively). Ctenophores were counted and measured (length, including lobes) to the nearest 0.5 cm (when smaller individuals dominated) or 1.0 cm (when larger individuals dominated) and divided into length-based size classes. Depending upon abundance, either the entire sample or only a subsample was enumerated. Other species of ctenophores (*i.e.*, *Pleurobrachia pileus* Müller 1776, *Beroe ovata* Mayer 1912) were also counted and their total biovolume determined.

Collections for mesozooplankton were made using a 0.5-m diameter, 64-μm mesh net (n=2 replicates) also equipped with a flow meter. Samples were preserved immediately in 5% buffered formalin. In the laboratory, all mesozooplankton and micrometazoa (e.g., copepod eggs and nauplii, tintinnids) were identified to the lowest possible taxonomic group (usually species) using a dissecting microscope.

*Elemental composition of C, N, and P of M. leidyi*

*Mnemiopsis leidyi* of varying size were analyzed for elemental composition in both years at both sites. Collections were made only when ctenophores were sufficiently abundant because all specimens were gently and individually recovered by dip net, making collections difficult during low (<1 $m^{-3}$) densities. Ctenophores were kept in ambient seawater and returned to the laboratory within 2-4 hr where they were placed in 0.45μm-filtered seawater for 1-2 hr to be purged of all digested materials. Length (to the nearest millimeter) and wet weight (to the nearest tenth of a milligram) of each ctenophore were measured. Very small ctenophores (<1 cm) were grouped together to ensure sufficient quantity for elemental analyses. Ctenophores were then transferred into pre-weighed, acid-washed (10% HCl) beakers and placed in a drying oven for up to 36 hr at 60°C (to constant weight). Each sample was finely homogenized using a mortar and pestle, and a portion (<10 mg measured using a Mettler Toledo MX5 microbalance) was

transferred into pure tin cups. Total organic carbon and nitrogen of each specimen was determined in duplicate or triplicate using a Flash 1112 Series elemental analyzer (Thermo Finnigan).

Total chloride and phosphate ($HPO_4^{-2}$; total phosphate = ΣP) analyses were conducted when sufficient quantities of dried ctenophore remained following C and N analyses. Total phosphate content was determined using the method of Aspila et al. (1976; sample ashed at 450°C; leached 24 hr with 1N HCl; phosphate analysis of leachate in triplicate using molybdate blue method on Polarstar Omega plate reader). Chloride content was determined by rehydrating dried ctenophore in 1-10 mL of distilled water to dissolve halite (NaCl), and subsamples were analyzed in triplicate using a Radiometer CMT10 Chloride Titrator. The salt content of each sample was then determined from the $Cl^-$ concentration assuming the total salt/ $Cl^-$ mass ratio in seawater (0.5517 mg salt/mg $Cl^-$). Extreme outliers were removed following a Q test. A mean weight percent salt content of 91% (0.7% standard error, n=35) was found and used to calculate salt-free weights of all samples from total dry weights. CNS and $Cl^-$ analysis of a set of subsamples demonstrated that, within analytical error, all detectable S was from salt (as gypsum). Water column salinity values were determined on all sampling dates using a YSI Model 85 at 0.5-m and 1.0-m beneath the surface, and 0.5-m above the bottom. Salinity during elemental sampling dates ranged from 25 to 28 in 2008 and from 22 to 25 in 2009. Salinity varied by only ~2 within a single sampling date, and differences between and within sampling years were assumed to be negligible in making salt-free weight corrections.

Percent C, N and P of salt-free dry weights of *M. leidyi* were compared to mean mesozooplankton densities in Great South Bay. Molecular ratios (C/N/P) of *M. leidyi* were determined (without salt correction to minimize total analytical uncertainty) and also compared to mesozooplankton densities. Possible differences in the percent and molecular ratio values of C, N, and P of *M. leidyi* with ctenophore size were also evaluated.

*Remineralization rates and stoichiometries*

Experimental batch incubations were carried out to directly determine ctenophore remineralization kinetics and the stoichiometries of net remineralization under both oxic and anoxic conditions (McNamara et al. 2013b). *Mnemiopsis leidyi* were collected in Long Island Sound, NY for oxic incubations on Jul 25, 2007 (*Mnemiopsis* 1), for anoxic incubations on Sep 20, 2007 (*Mnemiopsis* 2), and for simultaneous oxic and anoxic incubations on Sep 12, 2008 (*Mnemiopsis* 3). In each case, *M. leidyi* were killed (confirmed using microscopic examination of ctene activity) by rapid cold–warm temperature cycling (ΔT ~20° C) over ~24 hr before introduction as whole individuals into glass jars containing 1 to 4 L of 0.4-um filtered seawater. The number of ctenophores introduced into 1 L of seawater varied between ~18–40, with total initial salt free dry weights of ~0.5–1.0 g in *Mnemiopsis* 1 and 2. The number of ctenophores in experimental incubation series 3 (4 L seawater) were 194 and 118 for oxic and anoxic conditions, respectively, and were dominated by size classes 0.5–1.0 cm (~90%). All incubations were carried out in the dark at 22°C. Oxic incubations were continuously and vigorously aerated; anoxic incubations were first purged with $N_2$, sealed, and then stirred continuously with a magnetic bar. Ctenophores quickly (~1 d) disintegrated into shards of tissue. Seawater samples for $\Sigma CO_2$, $NH_4^+$, $NO_2^-$ + $NO_3^-$, and $HPO_4^{2-}$ were taken serially at ~0.5–1.0 d intervals over 10–21 days depending on the incubation series. Total bacteria counts on unfiltered samples using DAPI staining and general microscopic examinations were also made on oxic and anoxic incubations for *Mnemiopsis* 3. Nutrient samples were filtered through 0.2-μm polysulfone membranes. Only

anoxic incubation samples were analyzed for $\Sigma CO_2$. Analytical methods used were: $NH_4^+$ (indophenol blue; Solorzano 1969); $NO_2^- + NO_3^-$ (Greiss reaction; Strickland and Parsons 1968); $HPO_4^{-2}$ (molybdate blue reactive phosphate; Presley 1971); and $\Sigma CO_2$ (flow injection conductivity; Hall and Aller 1992). The N and P methods were modified for use with a 96-well microplate reader (Polarstar Omega). Analytical precisions were ~2% for $\Sigma CO_2$ and ~2-3% for nutrient analyses.

*Statistical analyses*

Statistical analyses (multiple and linear regressions, one-way ANOVA) were conducted using BIOMstat: Statistical Software for Biologists, Version 3.30 by Applied Biostatistics, Inc., 10 Inwood Road, Port Jefferson, NY 11777.

**Results**

*Temporal and spatial distribution of Mnemiopsis leidyi and mesozooplankton*

The densities of *Mnemiopsis leidyi* varied both within and between the two years (McNamara et al. 2013a; Chapter One). In 2008, the highest abundance of *M. leidyi* occurred on Jul 17 with 8.7 ctenophores $m^{-3}$ at site M (Figure 2a), and 13.5 $m^{-3}$ at site A (Figure 2b). The appearance of the predatory ctenophore *Beroe ovata* coincided with the decline of *M. leidyi* at both sites (Figures 2a; b). *Mnemiopsis* was undetectable at site M on the last day of sampling (Oct 09). In 2009, peak abundance of *M. leidyi* occurred on Jul 29 at site M and Aug 05 at site A with 43.8 and 65.5 individuals $m^{-3}$, respectively (Figures 3a; b). Coincident with substantially-reduced mesozooplankton densities, *M. leidyi* declined to 0.5 individuals $m^{-3}$ on Aug 20 at site M, and 1.0 individuals $m^{-3}$ on Aug 12 at site A (no sampling occurred on Aug 20 at site A). In the absence of *B. ovata*, *M. leidyi* exhibited a second (but reduced) population peak on Oct 9 with 19.6 $m^{-3}$ at site M, and to a lesser extent at site A with 8.3 $m^{-3}$ on Sep 18.

In both sampling years, *M. leidyi* abundance varied inversely with mesozooplankton abundance (Figures 2 and 3). Highest densities of *M. leidyi* coincided with an immediate and precipitous decline in mesozooplankton, which in 2008 plunged from 344.4 individuals $L^{-1}$ to 7.2 individuals $L^{-1}$ and from 859.6 individuals $L^{-1}$ to 2.8 individuals $L^{-1}$ in 2009 (site M). Recovery of mesozooplankton occurred following the appearance of *B. ovata* and subsequent decline of *M. leidyi* in 2008 (Figure 2).

Mean body size of *M. leidyi* continuously decreased with declining zooplankton density in both years. In 2008, the average size of *M. leidyi* decreased from 2.8 to 2.1 cm and from 2.5 to 1.2 cm in 2009 (data not shown). The average size of ctenophores collected for elemental analysis were in good agreement with these values, ranging from 2.8 to 2.1 cm in 2008 and from 2.5 to 1.3 cm in 2009 (Table 1).

*Elemental composition of C, N, and P of M. leidyi*

Total dry weight-based percentage of carbon for *M. leidyi* ranged from 1.2% to 2.0% while percent nitrogen ranged from 0.3% to 0.5% over both sampling years (Table 1). Mean percentage values of carbon, nitrogen and phosphorus based on salt-free dry weight of *M. leidyi* (referred to as salt-free percent C, N, and P) varied substantially over the sampling period in both years. During the two years, mean salt-free percent C ranged from 12.9% to 22.1%; salt-free percent N ranged from 3.1% to 5.5%; and salt-free percent P ranged from 0.2% to 0.8% (Table 2).

Salt-free percent C, N, and P of *M. leidyi* were compared to mean zooplankton abundance. In both years, individual *M. leidyi* collected at the onset of the ctenophore bloom contained significantly higher percentages of C, N, and P than individuals sampled during their collapse, when zooplankton abundance was substantially lower (Table 2). Salt-free percent C, N, and P values of *M. leidyi* correlated positively with zooplankton abundance in 2008 and 2009 (Table 3). During both years, higher C and N percentages co-occurred with high (>300 $L^{-1}$) zooplankton abundances (Figures 4a, b; 5a, b), but dropped by ~30-40% during low (<10 $L^{-1}$) abundances. Salt-free percent phosphorus followed similar trends as carbon and nitrogen, but more dramatically (Figures 4c; 5c). Salt-free percent P of *M. leidyi* experienced a >60% decline in 2008 and 2009 alongside low zooplankton densities. In 2009, percent C, N, and P showed slight increases in October when zooplankton abundances increased slightly from 2.8 individuals $L^{-1}$ to 34.3 individuals $L^{-1}$ (Figures 5a-c).

Elemental analyses of *M. leidyi* revealed seasonal changes in C, N, and P values of *M. leidyi* in both an absolute (percent) and relative (stoichiometric) sense. In both sampling years, C, N, and P ratios of *M. leidyi* correlated with mean zooplankton densities. Carbon to phosphorus (C/P) ratios of *M. leidyi* ranged from 66.2 to 127.8 (Table 2) and correlated significantly with zooplankton densities for the two years (Linear regression, $df = 1, 8$; $FS = 11.1$; $p = 0.01$). Nitrogen to phosphorus (N/P) ratios of *M. leidyi* ranged from 12.3 to 27.8 (Table 2) and also correlated significantly with zooplankton densities ($df = 1, 8$; $FS = 5.7$; $p = 0.04$). Both C/P and N/P increased significantly with decreasing zooplankton densities in 2008 (Figure 6) and 2009 (Figure 7). In 2009, C/P and N/P values nearly doubled from 66.2 to 126.2 and from 12.3 to 22.2, respectively, when zooplankton densities plummeted. Carbon to nitrogen (C/N) ratios of *M. leidyi* varied from 4.6 to 4.8 in 2008, and from 5.0 to 6.1 in 2009 (Table 2) and exhibited a general decline with decreasing zooplankton densities, although not statistically significant ($df = 1, 9$; $FS = 0.006$; $p = 0.98$). No trends were identified at site A, likely because of the limited sampling conducted at this site.

Salt-free percent C, N, and P correlated with ctenophore size, although differently among the two years. In 2008, salt-free percent C, N and P correlated positively and significantly with ctenophore length (Table 3; Figure 8). In 2009, salt-free percent C correlated marginally with ctenophore size at site M, but not at site A; and salt-free percent N correlated significantly and positively with size in 2009 at site M, but not A (Table 3). However, salt-free percent P did not correlate significantly with ctenophore size at either site in 2009 (Table 3).

*Remineralization rates and stoichiometries*

The net release patterns of remineralized C, N, and P (McNamara et al. 2013b) were consistent with first order decomposition kinetics under both oxic and anoxic conditions (e.g., Skopintsev 1981; Burdige 2006). Dissolved C, N, and P followed time-dependent functions of the form: $C_i(t) = C_{1i}(1\text{-}\exp(-kt)) + C_{2i}$; where $k$ = first order rate constant and $C_{1i}$ and $C_{2i}$ are constants reflecting initial and asymptotic concentrations for solute $C_i$ (Figure 9). Generation of dissolved or colloidal organic intermediates (transients), synthesis of new biomass (bacteria), and relatively long-term behavior (for example: progressive dominance of nitrification under oxic conditions >1–2 wk) are not considered (Von Brand et al. 1937; Grill and Richards 1964; Skopintsev 1981). $NO_2^- + NO_3^-$ were either depleted with time (anoxic incubations) or increased slightly (oxic), but were usually relatively small fractions of the $NH_4^+$ concentrations during the modeled incubation period (e.g., less than ~2% in *Mnemiopsis* 1 and 2). The saturated $O_2$

conditions (220–250 μM $O_2$; oxic) and lack of additional oxidants capable of generating $NO_2^-$ +$NO_3^-$ (anoxic) preclude significant denitrification over the course of the incubations.

The observed values of *k* for all solutes were ~0.42–0.45 $d^{-1}$ for *Mnemiopsis* incubation sets 1 (oxic) and 3 ($\Sigma CO_2$, (anoxic)), and 0.13–0.16 $d^{-1}$ in *Mnemiopsis* 2 (anoxic). The functional fit to $NH_4^+$ in *Mnemiopsis* 1 did not include t >5 d because of $NO_3^-$ formation (Figure 9a). Rate constants of 0.45 $d^{-1}$ indicate an average decomposition lifetime of ~2.2 days, or a half-life for complete remineralization of *M. leidyi* biomass of approximately 1.5 days following death. A rate constant of 0.15 $d^{-1}$ corresponds to an average remineralization lifetime of ~6.8 days. The net release of dissolved inorganic C, N, and P were coherent with time in *Mnemiopsis* 1 and 2 (Figure 9), consistent with similar rate constants. The net stoichiometric C/N release ratio was 2.1 in *Mnemiopsis* 2 (anoxic) and 4.3 in *Mnemiopsis* 3 (anoxic). The C/P net release ratio was ~42 in *Mnemiopsis* 2 (anoxic), and in *Mnemiopsis* 1 (oxic) the N/P was ~14 for t ≤ 5d (N/P = 12 including all points). There was no measureable net release of P in the *Mnemiopsis* 3 incubation under either oxic or anoxic conditions. Although the C/N stoichiometric release ratios are lower than bulk elemental analyses of biomass, the patterns in *Mnemiopsis* 1 and 2 are in good overall agreement with expectations of N and P enrichment relative to C. Bacterial growth and grazing by protists (oxic) were not controlled in these end-member batch experiments. In the *Mnemiopsis* 3 incubation, bacteria numbers (data not shown) peaked at 1 day (~7 x $10^7$ $mL^{-1}$; otherwise ~$10^4$ $mL^{-1}$) and 2 days (~5 x $10^7$ $mL^{-1}$; otherwise ~$10^4$ $mL^{-1}$) in oxic and anoxic incubations respectively, and large numbers of protists were subsequently observed in the oxic series (McNamara et al. 2013b).

*Estimating the contribution of C, N, and P from M. leidyi populations in Great South Bay*

Mean elemental composition (C, N, and P) values of *M. leidyi* were applied to their abundance data to track temporal changes in C, N, and P contained in the *M. leidyi* population. Carbon, N, and P values of *M. leidyi* (μmol ctenophore$^{-1}$) were averaged by 1.0-cm size classes and multiplied by mean abundance (per size class) to determine total μmol C, N, and P in ctenophores $m^{-3}$ and to estimate the amount of C, N, and P potentially released by *M. leidyi* during remineralization. Carbon, N and P (μmol) in *M. leidyi* $m^{-3}$ varied by one and two orders of magnitude over the sampling period in 2008 and 2009, respectively (Table 4). Population pools of C and N (μmol $m^{-3}$) ranged from 2170 to 11, and 371 to 2.1, respectively, with declining *M. leidyi* and mesozooplankton abundance. In 2009, the collapse of *M. leidyi* potentially returned 150, 26 and 18 μmol C, N and P $m^{-3}$ $d^{-1}$, respectively, to other components of the ecosystem between Jul 29 and Aug 12, and 4.4 and 0.8 μmol C and N $m^{-3}$ $d^{-1}$ upon further population declines between Aug 12 and Aug 26 (no sample remained for phosphate analyses on Aug 26). Conversely, since the decline of *M. leidyi* coincided with the arrival of *B. ovata* in 2008 and the contribution of C, N, and P to the ecosystem *via* decomposition was likely minimal, no such estimates were calculated for 2008.

## Discussion

*Elemental composition of M. leidyi changes with ctenophore size and prey availability*

My data demonstrated seasonal changes in salt-free based percentages of C, N and P of natural populations of *M. leidyi* as a function of ctenophore size and prey availability. Previous studies of C, N, and P contents were based exclusively on total dry weight and may not be representative of the true elemental constitution of *M. leidyi* nor may they be accurately

compared across habitats with different salinities (e.g., Nemazie et al. 1993). In this study, *in situ* C, N, and P of *M. leidyi* correlated with temporal changes in zooplankton prey abundances. The mean C, N, and P content of *M. leidyi* decreased significantly as zooplankton densities declined. These results are consistent with previous, laboratory-based investigations (e.g., Kremer 1982; Reeve et al. 1989). For example, *Mnemiopsis* experimentally-starved over five days shrank in size and contained only 1.6% C dry weight$^{-1}$ in contrast to well-fed ctenophores which grew slightly and contained 3.7% C (Kremer and Reeve 1989). Although abundances of *M. leidyi* differed markedly between 2008 and 2009, their apparent impact on zooplankton abundance was similar. During blooms of *M. leidyi* (here defined as abundances >1 m$^{-3}$) in both years, mesozooplankton declined >98% (site M), which in turn led to declines in the abundance of *M. leidyi*. These patterns demonstrate similar predator-prey interactions between *M. leidyi* and mesozooplankton as have been documented for Chesapeake and Narragansett Bays (Purcell and Decker 2005; Sullivan et al. 2007; Condon and Steinberg 2008).

Salt-free percent C, N, and P values of *M. leidyi* also correlated positively with ctenophore size in Great South Bay. C/N and C/P ratios tended to decrease with size, although the high variability precluded a statistically significant relationship ($p = 0.87$ (C/P); $p = 0.94$ (C/N)). Such correlations presumably reflect the association of growth and increased average size with the availability of zooplankton food and a favorable nutritional status. During both years, ctenophore size declined with decreasing zooplankton densities. Thus it may be said that percent C, N and P of *M. leidyi* declined alongside, but not necessarily because of, decreasing ctenophore size in Great South Bay. My study documented elemental ratios (C/N/P) ranging from 66:12:1 to 128:28:1. C/N of *M. leidyi* was highest during high zooplankton densities and decreased with decreasing zooplankton densities. When zooplankton abundances were high, N/P ratios of *M. leidyi* ranged between 12:1 and 18:1 but increased to between 22:1 and 28:1 during low zooplankton abundances. C/P ratios of *M. leidyi* ranged from 66:1 to 128:1, with low and high molecular ratios being obtained during high and low zooplankton densities, respectively. As ctenophores became depleted in C and P, they first became more P-depleted than C-depleted.

Unlike C, N, and P weight percentages, elemental ratios are not affected by salt contributions and may be compared directly between studies. Kremer (1975) reported atomic ratios of C/N/P for *M. leidyi* from Narragansett Bay of 122:31:1, which agrees very well with my values obtained for ctenophores collected during low zooplankton densities, but not with those obtained during high prey densities. C/N ratios of 4.0 for *Mnemiopsis* in Narragansett Bay and 4.6 for Biscayne Bay (Kremer 1982) show a moderate deviation from those obtained in this study (4.6 to 6.1), and may reflect differences in elemental composition within the species, physiological states, and/or food resources. While percent C, N, and P values indicate that *M. leidyi* become depleted in C, N, and P during periods of starvation, elemental ratios indicate that *M. leidyi* are N-enriched during periods of reduced prey availability relative to C and P.

Previous studies investigating P and N content in wild-caught ctenophores have focused on respiration and excretion (e.g., Kremer 1975; Kremer 1977; Park and Carpenter 1987; Nemazie et al. 1993; Condon et al. 2010). Kremer (1977) found *M. leidyi* excretion to be P-rich (total dissolved N/total dissolved P = 9.8; $NH_4^+/PO_4^{3-}$ = 7.4 mol mol$^{-1}$) relative to its bulk C/N/P ratio (110:28:1), and suggested that *M. leidyi* secretes excess P to maintain a nutrient balance of C, N and P since their zooplankton prey were N-poor relative to *M. leidyi*. Condon et al (2010) measured similar P-enriched excretion of both organic and inorganic solutes relative to typically-reported body compositions of N and P. Kremer (1977) calculated elemental turnover rates of 5% to 19% d$^{-1}$ for C and N, respectively, and 20% to 48% d$^{-1}$ for phosphorus. Weight-specific

excretion, and thus C/N/P turnover, has been found to be largely independent of ctenophore size and to vary with temperature (Kremer 1977; Condon et al. 2010). These data were derived from individuals collected either at a single time or over a relatively restricted period. My data indicate that the stoichiometry of excretion of organic and inorganic components, and the turnover of biomass N and P from excretion likely varies substantially seasonally as a function of prey availability and ctenophore size composition. These results agree well with Kremer (1982) who found that food availability had a marked effect on the metabolic rate and C and N composition of *M. leidyi* during laboratory investigations.

I do not know why *M. leidyi* becomes P-depleted during periods of lower food availability. The reduction in P (total and percent) during periods of decreased zooplankton densities may be associated with body shrinkage or differential loss of tissues. Schoo et al. (2010) suggested that the loss of whole cells (including DNA and RNA) occurring during ctenophore shrinkage may have explained the loss of P during experimental starvation in the cydippid ctenophore *Pleurobrachia pileus*. Previous studies have found non-starved *M. leidyi* to contain fewer energy reserves, but proportionately high amounts of protein relative to carbohydrates and lipids (Kremer 1975; Anninsky et al. 2005). A physiological explanation for the compositional and stoichiometric variability of *M. leidyi* coincident with declining prey abundance is as yet unknown, and warrants further study.

*Remineralization rates and regeneration stoichiometries*

The decomposition experiments (McNamara et al. 2013b) demonstrate that net remineralization of *M. leidyi* biomass is characterized by first order decomposition kinetics and is stoichiometrically-coherent with respect to inorganic components (Figure 9). Dissolved organic matter and colloidal intermediates were not measured, so total decomposition rates of biomass are underestimated. In two of the three experimental series (oxic, anoxic), rate constants correspond to characteristic complete remineralization times of $1/k$ ~2.2 days ($k$ = 0.45 $d^{-1}$; $t_{1/2}$ = Ln(2)/$k$ ~1.4 d), and in one of the incubation series (anoxic), $1/k$ ~6.8 days ($k$ = 0.15 $d^{-1}$; $t_{1/2}$ ~4.7 d). These remineralization timescales are consistent with previous studies of decomposition, where fragmentation of gelatinous planktonic biomass took place with rate constants of 0.67–1.1 $d^{-1}$ (Titleman et al. 2006) and, following an initial transient delay of 1–2 days, $NH_4^+$ net remineralization rates were in the range of $k$ ~0.1–0.28 $d^{-1}$ (modeled data from Tinta et al. 2010). Decomposition of gelatinous biomass deposited on the surface of sediment microcosms degrades over similar timescales (days), and supports significant increases in $O_2$ uptake and nutrient fluxes (West et al. 2009b); however, the complex transport–reaction conditions in this latter study preclude straightforward kinetic modeling of remineralization. Although there are indications that inhibitory compounds can be present in gelatinous biomass (Tinta et al. 2010), the net kinetic rate constants obtained here for remineralization of ctenophore biomass are in the range of the most labile natural organic substrates (e.g., Skopintsev 1981; Westrich and Berner 1984; Middelburg et al. 1993). Decomposition of labile substrates is generally independent of specific redox conditions (Lee 1992; Kristensen and Holmer 2001).

The stoichiometries of net remineralization are consistent with the relative enrichment of N, and sometimes P, relative to C in ctenophore biomass compared to phytoplankton, as measured in the bulk elemental analyses. However, the absolute estimated values of C/N and C/P released during initial net decomposition and periods of high prey availability tend to be smaller than those measured directly in biomass (except in *Mnemiopsis* 3). These differences may reflect preferential remineralization of N and P relative to C, experimental variability (*i.e.*, ctenophore

population variations), or analytical errors. Bacterial growth and grazing were not controlled and it is therefore also possible that differences in these factors account for at least some of the variability in rates and net release ratios between experiments. The lack of measureable P release in the *Mnemiopsis* 3 experiment, for example, may reflect a combination of bacterial growth and P uptake during incubation and a relatively-depleted P in ctenophore biomass at the time of collection (late September 2008). It seems likely that in all cases the experimental rate constants are minimal relative to field conditions where grazing is maximal under oxic conditions and dissolved and colloidal intermediates are generated (Titelman et al. 2006; Tinta et al. 2010). The primary conclusions for the present study are that complete remineralization is rapid, and the nutrient elements composing ctenophore biomass are virtually immediately available to microbes and phytoplankton following ctenophore mortality.

*Estimating the contribution of C, N, and P from M. leidyi populations in Great South Bay*

The potential for ctenophores to serve as nutrient sources to plankton *via* excretion by active populations, and from net remineralization during population collapse is widely recognized, but the latter role, in particular, is not well understood. Using maximum values reported by Condon et al. (2010) for dissolved organic C, N, and P, $NH_4^+$, and $PO_4^{-3}$ released by *M. leidyi* in Chesapeake Bay, estimates were made for the amount of C, N and P released $m^{-3}$ $d^{-1}$ *via* excretion during high and low ctenophore abundance in 2009 in Great South Bay. During peak ctenophore abundance (Jul 29), populations of *M. leidyi* potentially released as much as 9400, 850, and 75 μmol DOC, DON and DOP $m^{-3}$ $d^{-1}$, respectively, and approximately 300, 30, and 2 μmol DOC, DON and DOP $m^{-3}$ $d^{-1}$, respectively, during reduced abundance on Aug 26. At their maximum abundance, *M. leidyi* potentially excreted ~3000 and 100 μmol $NH_4^+$ and $PO_4^{-3}$ $m^{-3}$ $d^{-1}$ in contrast to 96 and 3 μmol $NH_4^+$ and $PO_4^{-3}$ $m^{-3}$ $d^{-1}$ on Aug 26. The calculated daily excretion contributions of C, N, and P during low ctenophore abundance are *higher* than those potentially released by rapid decomposition of the standing stock of ctenophore biomass in Great South Bay (Table 4), suggesting that nutrient regeneration *via* excretion by active populations greatly exceeds nutrients remineralized during population crashes.

The amount of C, N and P locked up in populations of *M. leidyi* during seasonal peaks in abundance can be substantial, but decreases as prey abundances become reduced. Since starving ctenophores contain less C, N, and P than well-fed individuals, reports on the influence of a pulsed release of C, N, and P during population collapses of some gelatinous zooplankton (see Pitt et al. 2009 for a summary) may be inflated. Well-fed ctenophores contribute substantially larger quantities of C, N and P $d^{-1}$ during steady inputs from excretion than do starving ctenophores *via* catastrophic population demise. Therefore, in general, the contribution of C, N, and P during population collapse is much less important than the sustained release of nutrients by live animals during normal to high *M. leidyi* abundance. Future studies investigating the release of nutrients during population collapses of gelatinous zooplankton are cautioned to employ *in situ* C, N, and P values to accurately determine the contribution of these nutrients to the marine ecosystem upon their deaths.

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J. Aller, A. Kaushik, Y. Liu, M. Murray, L. Schnal, C. Wall, S. Waugh, and K. Zamborsky for their assistance in the field and laboratory.

Table 1. Sampling size (n), mean size (length) and total dry weight-based percent C and N (+/- s.d.) and C/N of *M. leidyi* at both sampling stations in 2008 and 2009.

| Date | Site | n | Size, cm | %C | %N | C/N |
|---|---|---|---|---|---|---|
| 10-Jul-08 | M | 32 | 2.8 (1.3) | 2.0 (0.10) | 0.5 (0.02) | 4.3 |
| 24-Jul-08 | M | 28 | 2.6 (1.2) | 1.3 (0.05) | 0.3 (0.02) | 4.3 |
| 14-Aug-08 | M | 16 | 2.1 (1.0) | 1.2 (0.06) | 0.3 (0.02) | 4.1 |
| 22-Jul-09 | M | 10 | 2.3 (1.7) | 1.8 (0.16) | 0.4 (0.24) | 4.8 |
| 29-Jul-09 | M | 9 | 2.5 (1.0) | 1.9 (0.07) | 0.4 (0.04) | 5.8 |
| 5-Aug-09 | A | 15 | 2.2 (0.9) | 1.8 (0.10) | 0.4 (0.02) | 4.9 |
| 12-Aug-09 | M | 7 | 1.9 (0.8) | 1.3 (0.08) | 0.3 (0.02) | 4.9 |
| 12-Aug-09 | A | 7 | 1.5 (0.7) | 1.3 (0.09) | 0.3 (0.02) | 4.8 |
| 26-Aug-09 | M | 9 | 1.6 (0.6) | 1.3 (0.06) | 0.3 (0.01) | 4.4 |
| 26-Aug-09 | A | 10 | 1.3 (0.7) | 1.3 (0.09) | 0.3 (0.02) | 4.4 |
| 23-Oct-09 | M | 7 | 2.6 (1.2) | 1.6 (0.08) | 0.4 (0.02) | 4.3 |

Table 2. Mean mesozooplankton abundances (+/- range), salt-free dry weight percentages of C, N, and P (+/- s.d.) and atomic ratios of *M. leidyi* at both sampling stations during 2008 and 2009.

| Date | Site | Zooplankton $L^{-1}$ | n | %C | %N | %P | C/N | C/P | N/P |
|---|---|---|---|---|---|---|---|---|---|
| 10-Jul-08 | M | 344.40 (91.8) | 32 | 22.1 (4.9) | 5.5 (1.4) | 0.6 (0.18) | 4.8 | 86.8 | 18.3 |
| 24-Jul-08 | M | 88.27 (12.9) | 28 | 14.2 (3.1) | 3.5 (0.9) | 0.3 (0.05) | 4.7 | 122 | 25.8 |
| 14-Aug-08 | M | 7.23 (2.3) | 16 | 12.9 (2.4) | 3.3 (0.8) | 0.2 (0.08) | 4.6 | 127.8 | 27.8 |
| 22-Jul-09 | M | 859.6 (348.7) | 10 | 20.2 (5.8) | 4.4 (1.6) | 0.8 (0.34) | 5.4 | 66.2 | 12.3 |
| 29-Jul-09 | M | 72.5 (31.0) | 9 | 20.9 (2.5) | 4.0 (1.3) | 0.5 (0.03) | 6.1 | 104.4 | 17.0 |
| 5-Aug-09 | A | 7.7 (2.0) | 15 | 19.5 (4.2) | 4.0 (0.9) | 0.4 (0.11) | 5.6 | 126.2 | 22.5 |
| 12-Aug-09 | M | 15.4 (3.7) | 7 | 15.0 (2.3) | 3.1 (0.5) | 0.3 (0.04) | 5.7 | 126.2 | 22.2 |
| 12-Aug-09 | A | 3.6 (1.3) | 7 | 14.7 (2.7) | 3.1 (0.7) | 0.4 (0.03) | 5.5 | 84.7 | 15.4 |
| 26-Aug-09 | M | 2.8 (1.1) | 9 | 14.8 (2.0) | 3.3 (0.5) | n/a | 5.2 | n/a | n/a |
| 26-Aug-09 | A | 5.9 (2.3) | 10 | 15.0 (3.3) | 3.4 (0.8) | 0.3 (0.16) | 5.1 | 125.0 | 24.4 |
| 23-Oct-09 | M | 34.3 (4.7) | 7 | 17.7 (2.4) | 4.1 (0.7) | 0.4 (0.13) | 5.0 | 103.7 | 20.6 |

Table 3. Dependence of salt-free percent C, N, and P on zooplankton density ($L^{-1}$) and ctenophore size (length) determined from multiple regression analysis.

| Dependent Variable | Year | Station | Independent Variable | *df* | *F* | *p* |
|---|---|---|---|---|---|---|
| **%Carbon** | 2008 | M | Zooplankton density | 1,70 | 55.6 | <0.01 |
| | | | Ctenophore size | 1,70 | 8.9 | <0.01 |
| **%Carbon** | 2008 | M & A | Zooplankton density | 1,78 | 66.1 | <0.01 |
| | | | Ctenophore size | 1,78 | 10.9 | <0.01 |
| **%Carbon** | 2009 | M | Zooplankton density | 1,39 | 5.8 | 0.02 |
| | | | Ctenophore size | 1,39 | 3.6 | 0.07 |
| **%Carbon** | 2009 | A | Zooplankton density | 1,29 | 9.6 | <0.01 |
| | | | Ctenophore size | 1,29 | 0.7 | 0.4 |
| **%Carbon** | 2009 | M & A | Zooplankton density | 1,71 | 6.7 | 0.01 |
| | | | Ctenophore size | 1,71 | 2.4 | 0.12 |
| **%Nitrogen** | 2008 | M | Zooplankton density | 1,66 | 23.9 | <0.01 |
| | | | Ctenophore size | 1,66 | 12.8 | <0.01 |
| **%Nitrogen** | 2008 | M & A | Zooplankton density | 1,68 | 24.5 | <0.01 |
| | | | Ctenophore size | 1,68 | 13.5 | <0.01 |
| **%Nitrogen** | 2009 | M | Zooplankton density | 1,39 | 3.9 | 0.06 |
| | | | Ctenophore size | 1,39 | 5.8 | 0.02 |
| **%Nitrogen** | 2009 | A | Zooplankton density | 1,29 | 4.2 | 0.05 |
| | | | Ctenophore size | 1,29 | 0.8 | 0.4 |
| **%Nitrogen** | 2009 | M & A | Zooplankton density | 1,61 | 5.6 | 0.02 |
| | | | Ctenophore size | 1,61 | 11.8 | <0.01 |
| **%Phosphorus** | 2008 | M | Zooplankton density | 1,61 | 39.5 | <0.01 |
| | | | Ctenophore size | 1,61 | 10.6 | <0.01 |
| **%Phosphorus** | 2008 | M & A | Zooplankton density | 1,63 | 44.5 | <0.01 |
| | | | Ctenophore size | 1,63 | 10.8 | <0.01 |
| **%Phosphorus** | 2009 | M | Zooplankton density | 1,15 | 6.7 | 0.02 |
| | | | Ctenophore size | 1,15 | 1.7 | 0.2 |
| **%Phosphorus** | 2009 | A | Zooplankton density | 1,16 | 0.03 | 0.9 |
| | | | Ctenophore size | 1,16 | 0.2 | 0.7 |
| **%Phosphorus** | 2009 | M & A | Zooplankton density | 1,34 | 13.3 | <0.01 |
| | | | Ctenophore size | 1,34 | 0.6 | 0.5 |

Table 4. Mean *M. leidyi* abundance (+/- s.d.), zooplankton abundance (+/- range) and estimated total µmol C, N, and P contained within *M. leidyi* populations (+/- s.d.) at site M in 2008 and 2009.

| Date | *M. leidyi* $m^{-3}$ | Zooplankton $L^{-1}$ | µmol C $m^{-3}$ | µmol N $m^{-3}$ | µmol P $m^{-3}$ |
|---|---|---|---|---|---|
| 7/10/2008 | 1.8 (1.3) | 344.4 (91.8) | 229.9 (78.8) | 15.7 (6.8) | 0.5 (0.3) |
| 7/24/2008 | 3.8 (0.6) | 88.3 (12.9) | 316.4 (46.4) | 73.3 (14.0) | 1.7 (0.3) |
| 8/14/2008 | 0.7 (0.6) | 7.2 (2.3) | 29.8 (16.4) | 6.4 (3.5) | 1.2 (0.7) |
| 7/22/2009 | 0.3 (0.2) | 859.6 (348.7) | 52.5 (15.4) | 10.5 (3.1) | 3.7 (1.0) |
| 7/29/2009 | 43.8 (27.2) | 72.5 (31.0) | 2174.0 (1309) | 371.4 (230.8) | 261.0 (179.2) |
| 8/12/2009 | 2.0 (0.6) | 15.4 (3.7) | 72.3 (13.3) | 12.8 (2.4) | 8.1 (1.5) |
| 8/26/2009 | 1.4 (0.6) | 2.8 (1.1) | 11.3 (3.5) | 2.1 (0.6) | n/a |
| 10/23/2009 | 13.0 (12.5) | 34.3 (4.7) | 1631.7 (1161.1) | 320.5 (227.4) | 15.2 (10.6) |

Figure 1. Sampling locations (sites M and A) in Great South Bay, Long Island, N.Y.

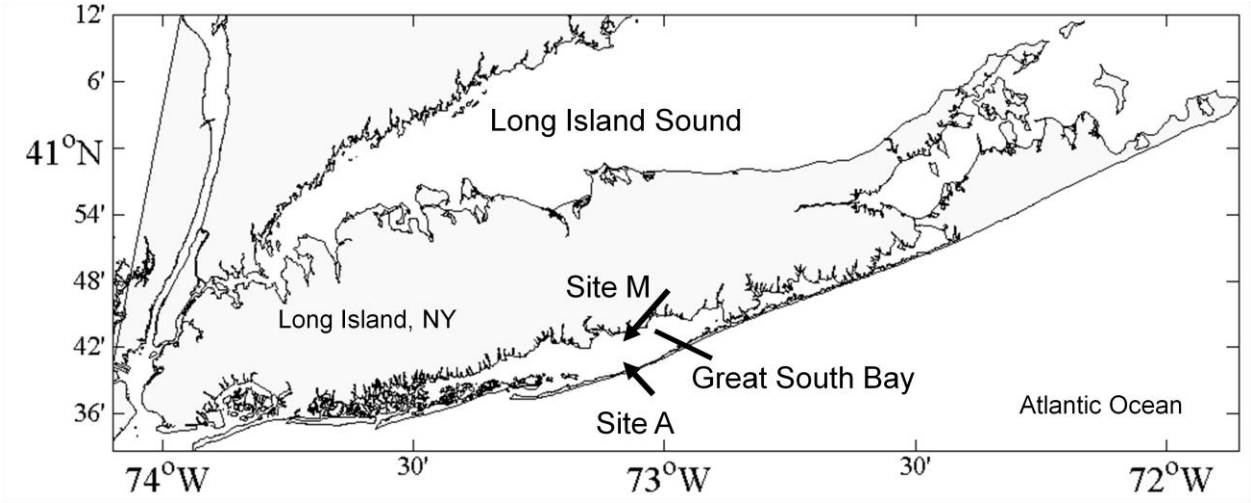
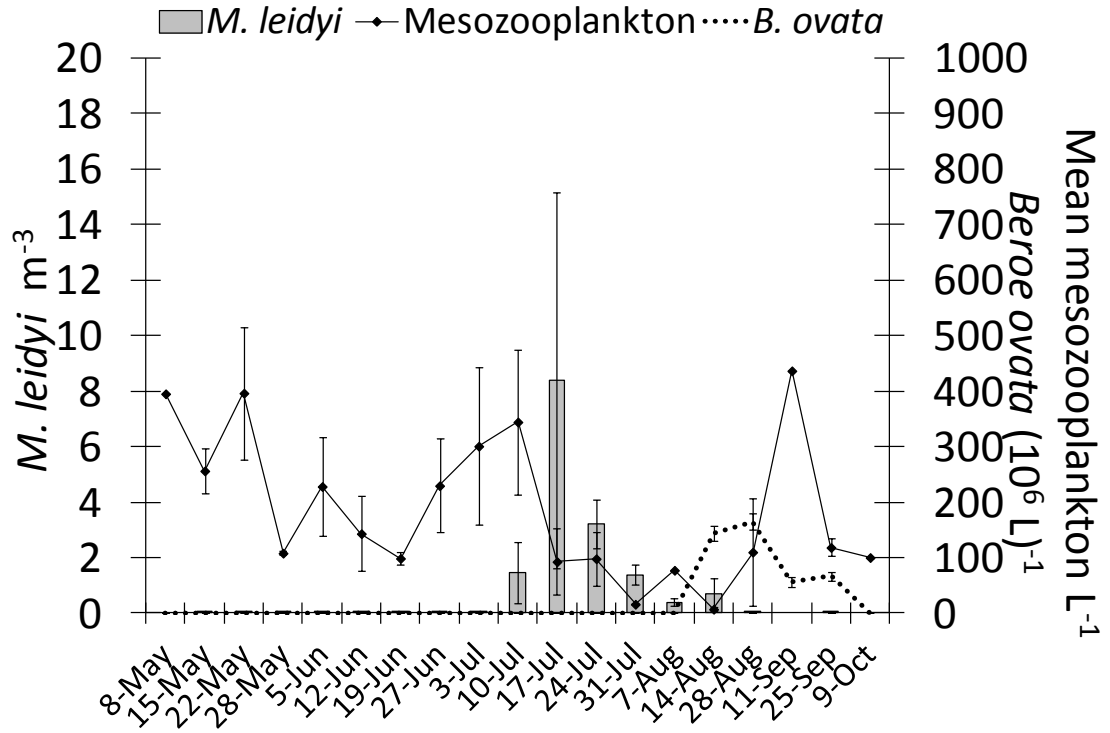
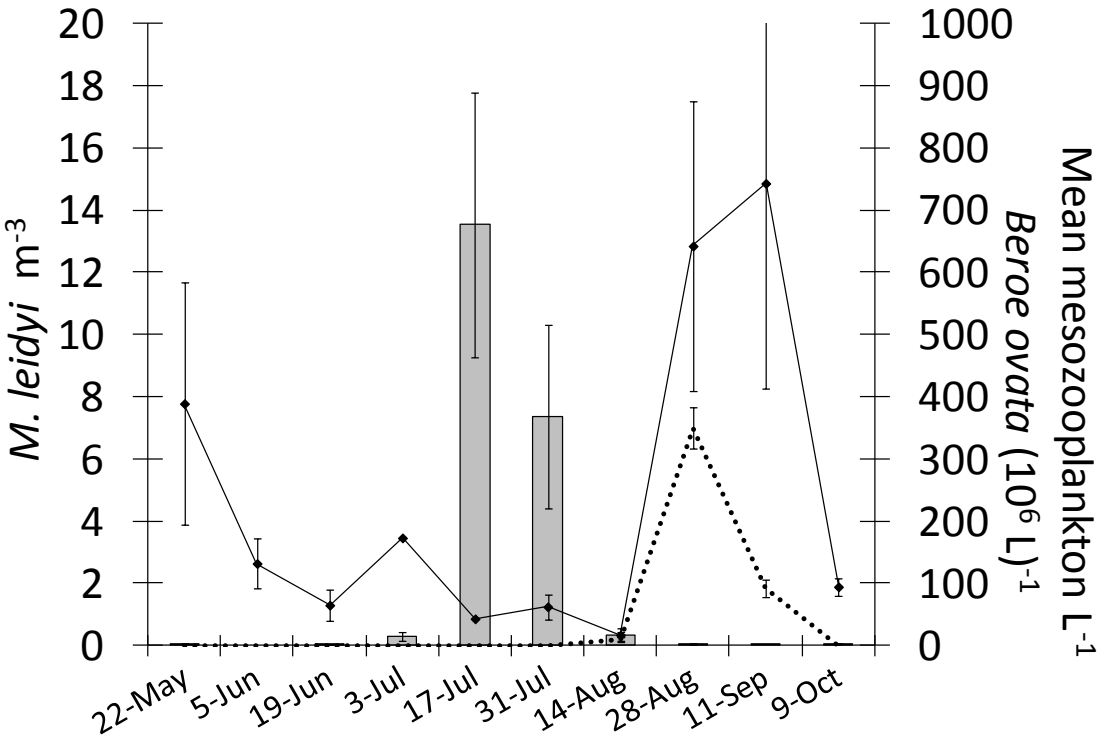


Figure 2. Mean mesozooplankton (+/- range), *Beroe ovata* (+/- s.d.) and *M. leidyi* (+/- s.d.) abundance in Great South Bay at sampling sites M (a) and A (b), during 2008.

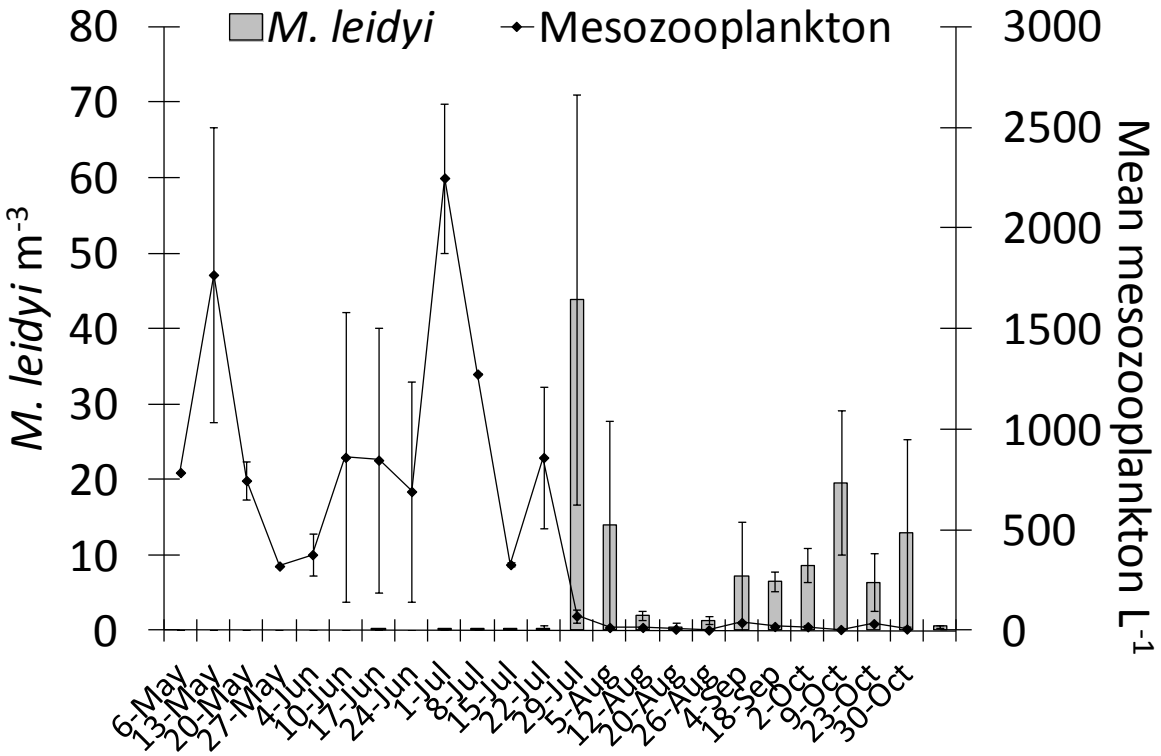



(a)

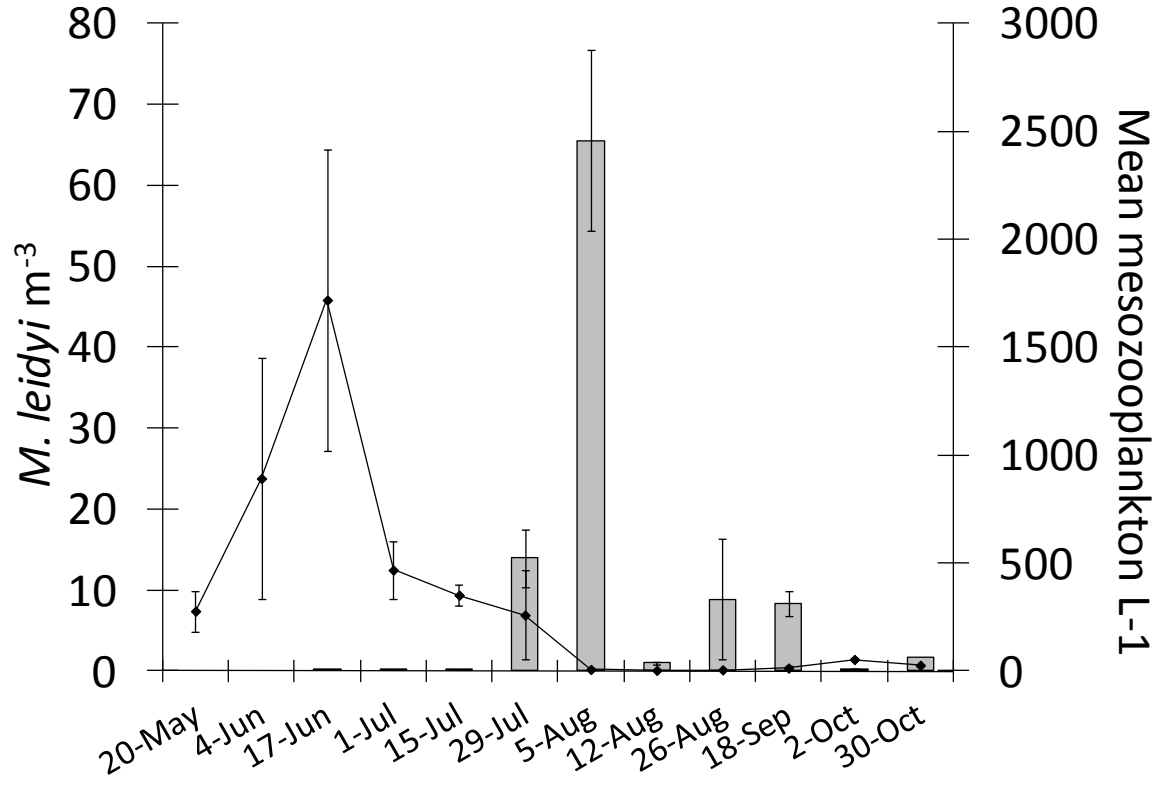



(b)

Figure 3. Mean mesozooplankton (+/- range) and *M. leidyi* (+/- s.d.) abundance in Great South Bay at sampling sites M (a) and A (b), during 2009.

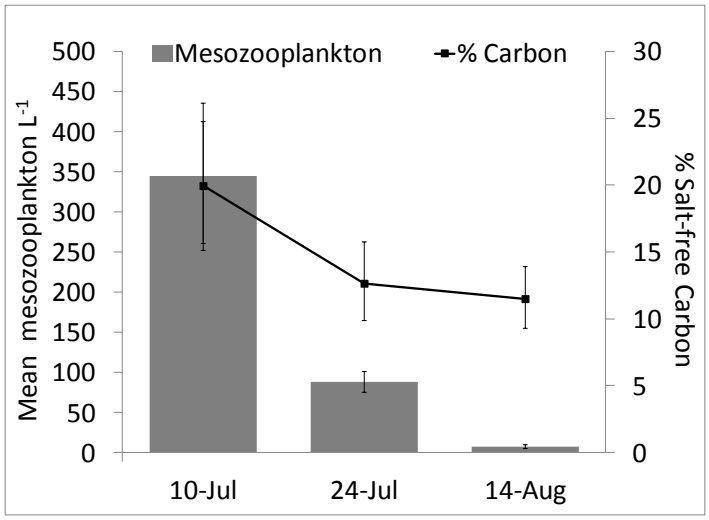



(a)

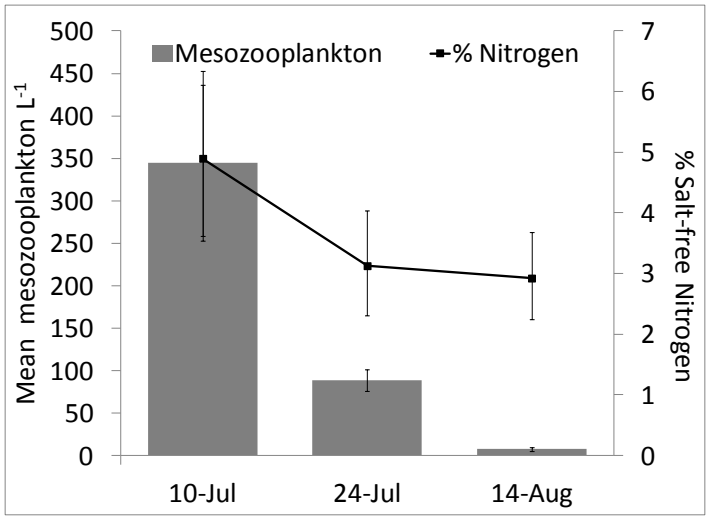



(b)

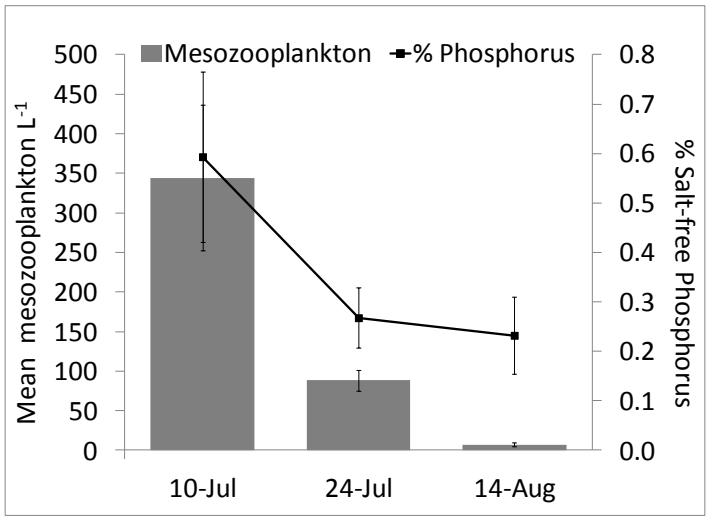
Figure 4. Mean percent (+/- s.d.) carbon (a), nitrogen (b), and phosphorus (c) based on salt-free dry weights of *M. leidyi* (all size classes) and mean mesozooplankton abundance (+/- range) at site M in 2008.




(a)

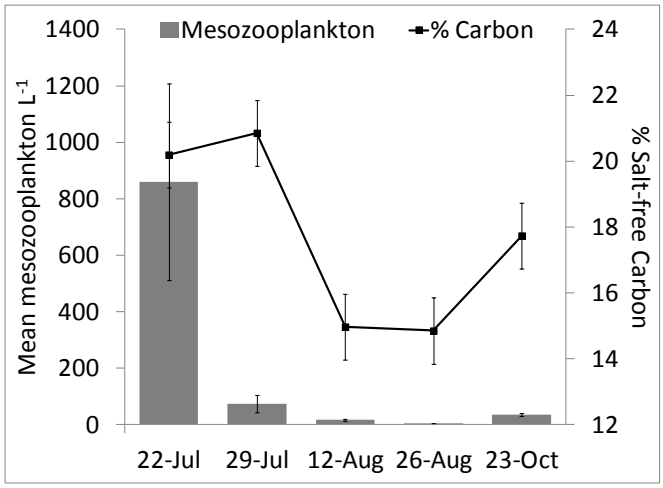



(b)

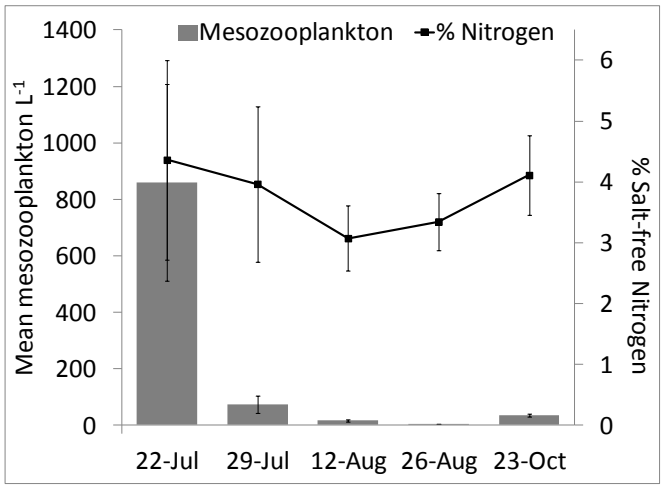



(c)

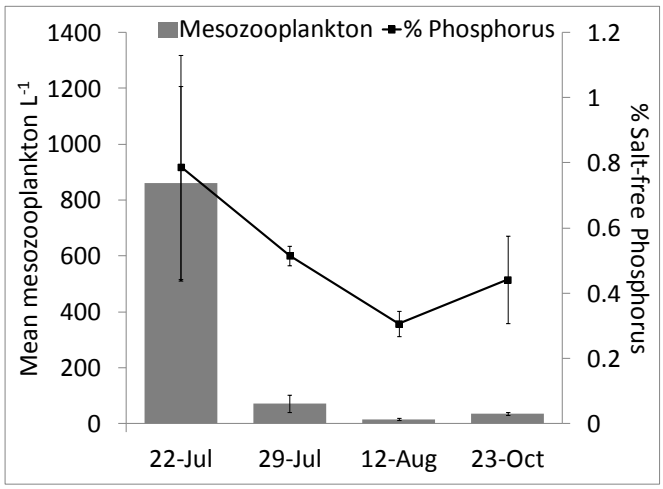
Figure 5. Mean percent (+/- s.d.) carbon (a), nitrogen (b), and phosphorus (c) based on salt-free dry weights of *M. leidyi* (all size classes) and mean mesozooplankton abundance (+/- range) at site M in 2009.




(a)




(b)




(c)

Figure 6. Mean molecular ratios of C/N, C/P, and N/P (+/- s.d.) of *M. leidyi* (all size classes) and mean mesozooplankton abundance (+/- range) at site M in 2008. Note that the error bars of C/N ratios do not appear due to the scale of the graph.

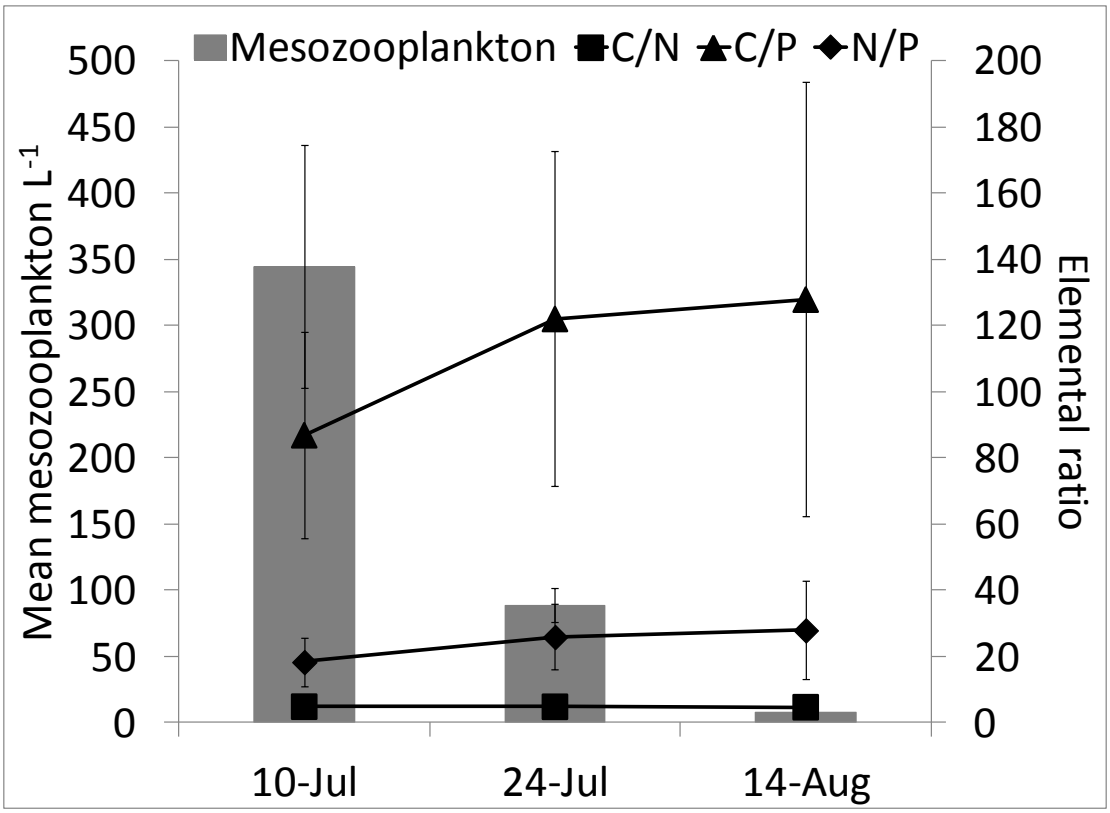


Figure 7. Mean molecular ratios of C/N, C/P, and N/P (+/- s.d.) of *M. leidyi* (all size classes) and mean mesozooplankton abundances (+/- range; n=2) at site M in 2009. Note that the error bars of C/N ratios do not appear due to the scale of the graph.

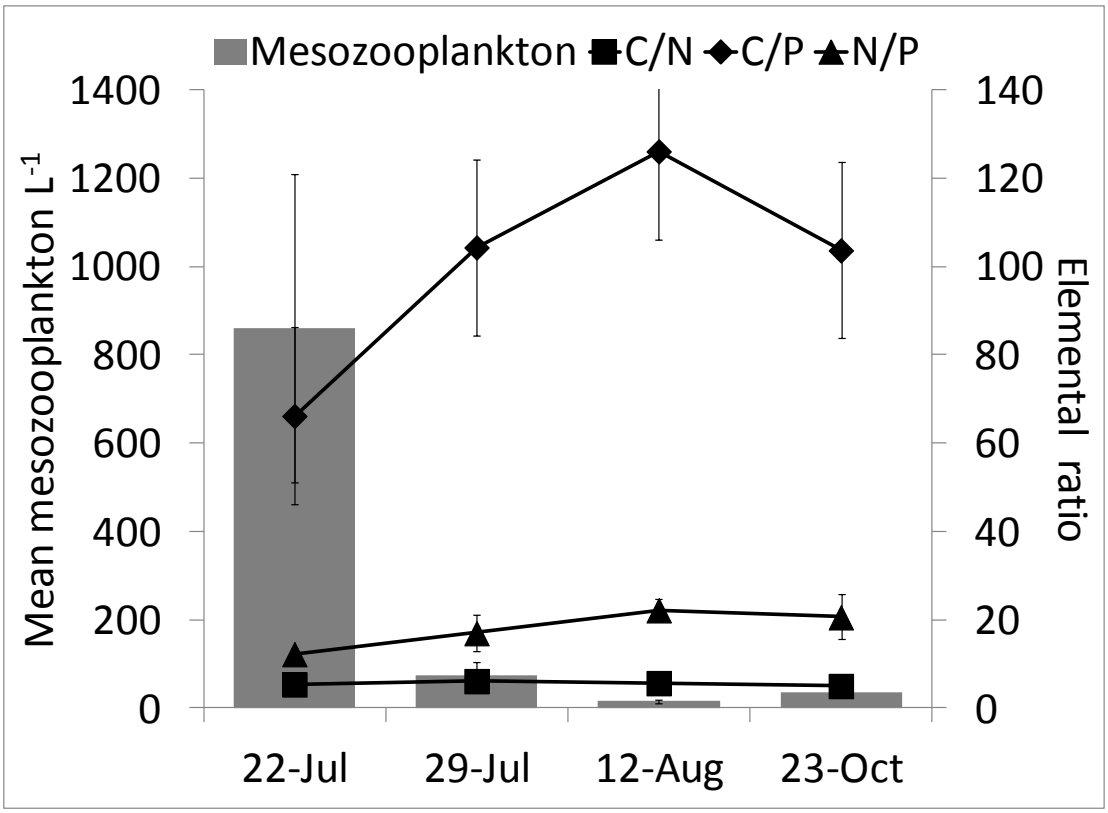
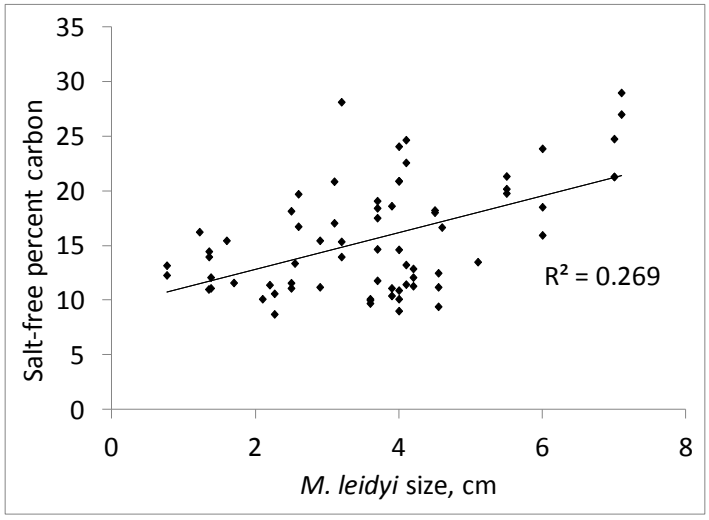
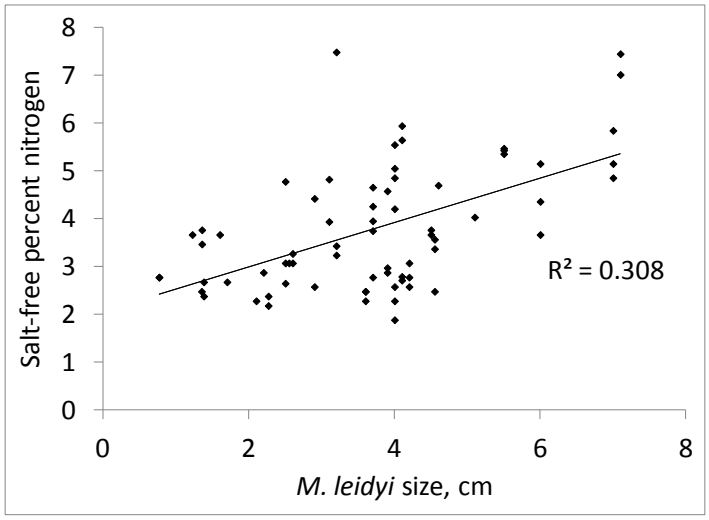


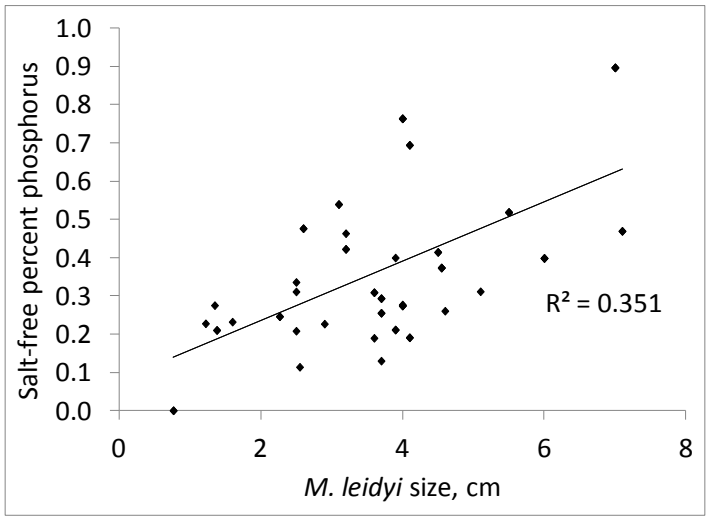
Figure 8. Percent carbon (a), nitrogen (b), and phosphorus (c) based on salt-free dry weights *versus* length of *M. leidyi* at sites M and A (combined) in 2008.




(a)

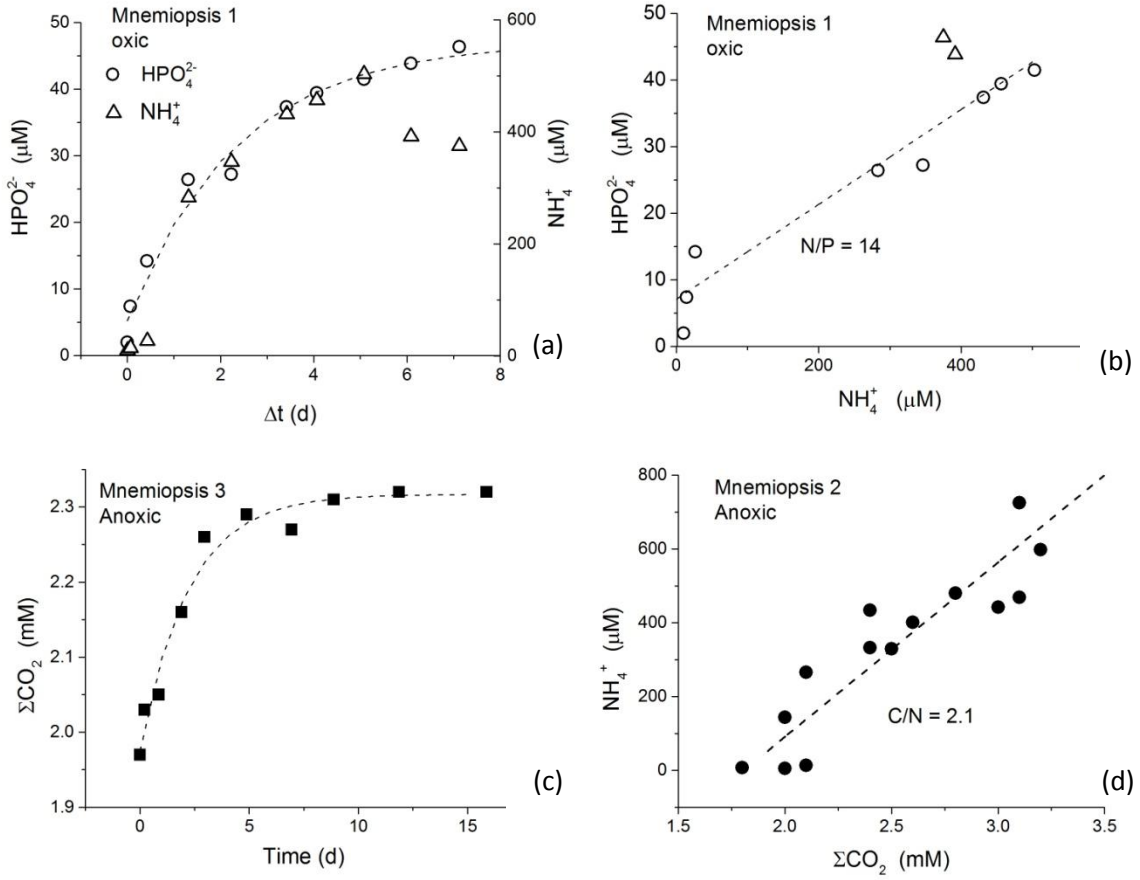



(b)




(c)

Figure 9 (McNamara et al. 2013b). (a) Time-dependent release of $NH_4^+$ and $HPO_4^{2-}$ during decomposition of *M. leidyi* under oxic conditions (*Mnemiopsis* 1). The model fit (dashed curve) for $HPO_4^{2-}$ shown is $HPO_4^{2-}$ = 41.9(1-exp(-0.424t)) + 47.1 µM; (b) $HPO_4^{2-}$ versus $NH_4$ during oxic decomposition (Δt < 6 d; M*nemiopsis* 1, circles; Δt > 6 d, triangles). Geometric mean (type II) regression shown for Δt < 6 d: P = 0.0712 N + 7.11 µM ($r^2$ = 0.95); (c) Time-dependent release of $\Sigma CO_2$ during decomposition of *M. leidyi* under anoxic conditions (*Mnemiopsis* 3). The model fit (dashed curve) shown is $\Sigma CO_2$ = 0.34(1-exp(-0.449t)) + 2.32 mM; (d) $NH_4$+ *vs.* $\Sigma CO_2$ during anoxic decomposition (Δt < 6 d; M*nemiopsis* 2). Geometric mean (type II) regression shown: N = 473 ($\Sigma CO_2$) - 855 µM ($r^2$ = 0.82)



## SYNTHESIS

Previous field studies of the gelatinous predator *Mnemiopsis leidyi* have generally focused on the top-down (predatory) role of the ctenophore in native and exotic habitats. Populations of adult *M. leidyi* populations exhibit seasonal increases in abundance, exerting significant predation pressure on the surrounding mesozooplankton community (e.g., Kremer 1979; Deason and Smayda 1982; Purcell et al. 2001; Purcell and Decker 2005; McNamara et al. 2010). However, little attention has been paid to the predatory influence of larval *M. leidyi*, which frequently dominate during high numerical abundances (e.g., Costello et al. 2006; Condon and Steinberg 2008). Blooms of *M. leidyi* are made up of both lobate adults and cydippid larvae, the latter of which must pass through distinct physiological and feeding-mode stages. Larval *M. leidyi* possess two tentacles which are used to seize and capture microplanktonic prey (Sullivan and Gifford 2007); as the larva grows, it develops lobes and the tentacles are resorbed (Reeve et al. 1978). Since larval *M. leidyi* depend on microplankton for prey, the abundance and composition of the microplankton community may regulate the timing and magnitude of ctenophore blooms and their subsequent recruitment into mesozooplankton-feeding adults (Sullivan and Gifford 2004; Rapoza et al. 2005).

This dissertation examined the hypotheses that certain microplanktonic taxa (*i.e.*, ciliates and dinoflagellates) are important prey for larval *M. leidyi* and that predation by larval *M. leidyi* can significantly influence the abundance of these microplanktonic taxa in coastal ecosystems. Further, this dissertation explored the possibility that blooms of *M. leidyi* are involved in a feedback system, wherein intense feeding activity by adults on mesozooplankton releases microplankton from grazing pressure, increasing prey for their larvae. These hypotheses were tested by implementing weekly sampling (May-October) of *M. leidyi*, mesozooplankton and microplankton over two sampling years (2008 and 2009) in Great South Bay, a shallow, lagoonal embayment located on the south shore of Long Island, New York.

Field studies, outlined in Chapter One (McNamara et al. 2013a) documented predatory control of microplanktonic dinoflagellates and ciliates by larval *M. leidyi* in Great South Bay. Previous studies investigating the predatory impact of larval *M. leidyi* on microplankton have done so experimentally (e.g., Reeve et al. 1978; Stanlaw et al. 1981; Stoecker et al. 1987; Sullivan and Gifford 2004; 2007; Waggett and Sullivan 2006) and results from this study agree well with these laboratory-based investigations. In Great South Bay, high abundances of adult and larval *M. leidyi* coincided with significant declines in mesozooplankton and microzooplankton, respectively. Also identified was a positive relationship between adult *M. leidyi* and microplankton (*i.e.*, dinoflagellates and ciliates) abundance, which preceded an increase in *M. leidyi* larvae, demonstrating the dependence of larval *M. leidyi* on microplanktonic prey and supporting the hypothesis that intense feeding by adult *M. leidyi* enhances prey conditions for their larvae.

In 2009, the reduction of dinoflagellates and ciliates during high larval *M. leidyi* densities further resulted in a cascading influence on nanoplankton. These field data agree with previous mesocosm experiments by Granéli and Turner (2002) who suggested that ciliates serve as a "trophic link" between their mesozooplankton predators and flagellate prey. Their experiments documented increased ciliate abundance and subsequent declines in phytoflagellates in treatments containing the cydippid ctenophore *Pleurobrachia pileus*. The predatory influence of adult *M. leidyi* did not extend to nanoplankton in this study, suggesting that the cascading influence of ctenophore predation is limited to three trophic levels in Great South Bay; adult *M. leidyi*-mesozooplankton-microplankton and larval *M. leidyi*-microplankton-nanoplankton. To my

knowledge, this is the first study to compare temporal changes in mesozooplankton, microplankton and nanoplankton to *M. leidyi* abundance and size composition *in situ*.

A plankton community that supports developing larval ctenophores must also promote fecund, reproducing adults to ensure proliferation of the population; only when prey conditions are ideal for both larval and adult *M. leidyi* are population blooms likely to occur (e.g., Rapoza et al. 2005). This dissertation also examined the hypothesis that mismatches between abundant mesozooplanktonic prey for adults and microplanktonic prey for larvae would limit the overall production of *M. leidyi.* In Chapter Two, I examined ctenophore egg production rates and gut contents alongside plankton abundance and composition to identify the biotic factors influencing fecundity and recruitment of *M. leidyi* in Great South Bay.

Significant interannual differences in *M. leidyi* abundance, fecundity and recruitment were identified. Firstly, ctenophores produced twice as many eggs and contained nearly three times as many gut contents in 2008 than in 2009. Egg production by *M. leidyi* is dependent on ctenophore size and prey density (Baker and Reeve 1974; Kremer 1976; Reeve et al. 1989; Grove and Breitburg 2005), however no significant difference in *M. leidyi* size or mesozooplankton abundance was detected between the two years. To investigate why *M. leidyi* fecundity was enhanced in 2008 relative to 2009, I examined the potential influence of brown tide (*Aureococcus anophagefferens*), which occurred in 2008, but was relatively absent from the bay during 2009. The number of gut contents identified in *M. leidyi* correlated positively and significantly with *A. anophagefferens*, suggesting that brown tide enhances feeding success in *M. leidyi*. To understand how brown tide may improve *M. leidyi* feeding dynamics, I further considered the feeding mechanisms of the lobate ctenophore.

To successfully capture prey, *M. leidyi* relies upon ciliary flow fields for small and slowly-swimming zooplankton, but on direct encounters for more actively-swimming prey such as *Acartia tonsa* (Costello et al. 1999). In fact, the percentage of *A. tonsa* adults identified in *M. leidyi* gut contents was two times greater in 2008 than in 2009. *Acartia tonsa* are known to switch feeding and subsequent swimming behavior based on prey availability, relying on suspension-feeding when diatoms and flagellates are present, but switching to an ambush strategy when ciliates are plentiful (Jonsson and Tiselius 1990; Kiørboe et al. 1996). Microplankton field data demonstrated significantly higher densities of microflagellates in 2008, and a positive correlation between microflagellate and *A. anophagefferens* abundance was identified. These data suggest that *A. anophagefferens* indirectly enhances ctenophore fecundity by altering the feeding behavior of the latter's prey. Chapter Two further demonstrates the influence that a lower trophic level organism (*A. anophagefferens*; picoplankton) can exert over a higher order predator (*M. leidyi*; macroplankton) through step-wise regulatory impacts on subsequently higher (flagellates; microplankton) and higher (*A. tonsa*; mesozooplankton) trophic levels, implying that trophic cascades are not limited to top-down influences as have traditionally been investigated.

However, despite its improved fecundity, *M. leidyi* abundance was five-times lower in 2008 than in 2009. Field data identified a mismatch between maximum ctenophore egg production rates and high microplankton abundance in 2008, in contrast to 2009 when the two coincided. Increases in larval *M. leidyi* did not coincide with elevated egg production in 2008 but rather followed high (>2000 μg C $L^{-1}$) densities of dinoflagellates and ciliates. These data further support the hypotheses that ciliates and dinoflagellates are important prey for developing *M. leidyi*, and their abundance regulates, in part, the timing and magnitude of *M. leidyi* population blooms.

Over the past few decades, populations of *M. leidyi* have increased in abundance and expanded their seasonal range in Chesapeake Bay (Condon and Steinberg 2008), Narragansett Bay (Sullivan et al. 2001, Costello et al. 2006), and Long Island estuaries (McNamara et al. 2010; McNamara et al. 2013a, Chapter One). Localized changes in ctenophore abundance and distribution may be the result of shifts in plankton community structure via eutrophication, overfishing and/or localized climate change (Purcell et al. 2007). Experimental mesocosms have demonstrated substantial increases in microplankton exposed to simultaneous predation by a gelatinous predator and nutrient enhancement, compared to treatments receiving nutrient or predator amendments alone (Stibor et al. 2004; Pitt 2007). Increases in microplankton, whether by top-down or bottom-up processes, can significantly influence *M. leidyi* population dynamics. To examine the individual and interactive influence of nutrients and *M. leidyi* predation on microplankton community structure, I conducted field-based mesocosms over two years in Great South Bay, using historic ("low") and recent ("high") abundances of the ctenophore in Long Island estuaries (Chapter Three).

Predation by high (recent) densities of *M. leidyi* during periods of nutrient enrichment altered the plankton community in a way that was distinctly different from when the predatory and nutrient processes occurred independently of one another. Ciliates (aloricate and loricate) increased by an order of magnitude in cylinders receiving daily nutrient additions and in cylinders containing high densities of *M. leidyi*, however, they increased by two orders of magnitude in cylinders receiving both nutrient and ctenophore amendments. Since ciliates are important prey for developing *M. leidyi*, eutrophication may enhance *M. leidyi* recruitment by increasing prey availability for their larvae. Further, *M. leidyi* recovered from 'ctenophore and nutrient' treatments produced three times as many eggs as *M. leidyi* removed from 'ctenophore only' treatments. The addition of nutrients significantly increased the abundance of mesozooplankton, suggesting that eutrophication enhances the fecundity of *M. leidyi* by increasing prey for reproducing ctenophores. These data may help explain recently documented shifts in the population dynamics of *M. leidyi* in mid-Atlantic and other coastal estuaries.

Finally, Chapter Four examined the elemental composition (carbon, nitrogen, and phosphorus) of *M. leidyi* and its implications for nutrient cycling in Great South Bay. Because of their boom and bust population dynamics, ctenophores act as sinks of nutrients during bloom formation, but become sources of nutrients when the population collapses (Pitt et al. 2009). The contribution of C, N, and P by *M. leidyi* is likely to change over time, and vary with ctenophore size and nutritional status (e.g., Kremer 1975). Elemental ratios of starved *M. leidyi in situ* are of particular relevance, since population collapse is most likely to occur following a prolonged period of insufficient prey density, and cannot be inferred from examination of well-fed, laboratory-reared adults as previously described. This dissertation established salt-free based percentages of C, N, and P in *M. leidyi* and examined how elemental composition varied seasonally in Great South Bay.

Carbon, N, and P values of *M. leidyi* correlated positively with mesozooplankton abundance in 2008 and 2009, changing seasonally in both an absolute and relative (stoichiometric) sense. Ctenophores collected when zooplankton were plentiful had atomic ratios averaging C/N ~6:1 and C/P ~66:1, but became C- and P-depleted (C/N ~5:1 C/P ~128:1) with decreasing zooplankton and ctenophore size. The amount of C, N and P contained within populations of *M. leidyi* during seasonal blooms in abundance can be substantial, but decreases as prey abundances become reduced. To my knowledge, this is the first study documenting seasonal patterns in the elemental stoichiometry of an *in situ* population of *M. leidyi* as a function

of size and prey availability. Chapter Four (McNamara et al. 2013b) further confirmed that the sustained release of nutrients *via* excretion by active populations greatly exceeds the amount of nutrients remineralized during population collapse, suggesting that the bottom-up influence of *M. leidyi* on microbial and phytoplankton communities is greatest when thriving, rather than crashing, as has been previously suggested.

*Concluding Remarks*

This dissertation investigated the top-down and bottom-up control of the plankton community by the ctenophore *Mnemiopsis leidyi* in Great South Bay, New York *via* field and laboratory studies. Field results confirmed the existence of trophic cascades within the plankton community caused by top-down control of mesozooplankton and microplankton, by adult and larval *M. leidyi*, respectively, and documented the predatory influence (and dependence) of larval *M. leidyi* on microplanktonic ciliates and dinoflagellates. These data suggest that blooms of adult *M. leidyi* are involved in a direct feedback system, which enhances prey conditions for their larvae (Chapter One; McNamara et al. 2013a). Future studies focusing on the predatory impact of *M. leidyi* in coastal ecosystems are encouraged to distinguish between larval and adult abundances of *M. leidyi* and to include microplankton abundance and composition in their examinations. Comparisons between Great South Bay and other coastal embayments (e.g., Naraggansett Bay, Chesapeake Bay, etc.) are also necessary to determine whether the trophic cascades documented in this study are typical of a five-chain trophic system (ctenophore-mesozooplankton-microplankton-nanoplankton-picoplankton) and whether these cascading influences differ with plankton food web structure (and length). Future studies are also encouraged to include nano- and picoplankton in their analyses.

Intra- and interannual differences in *M. leidyi* fecundity and recruitment were also identified (Chapter Two). The presence of a brown tide bloom in 2008 appeared to enhance *M. leidyi* feeding and fecundity, however, recruitment and overall abundance of the ctenophore was ultimately limited by a mismatch between optimal egg production and microplankton abundance. Establishment of microplankton abundance (and composition) before and during *M. leidyi* population blooms across regions may help determine correlations between microzooplankton (dinoflagellate and ciliate) abundance and larval *M. leidyi* recruitment. Long-term monitoring of *M. leidyi*, mesozooplankton and microplankton abundance in Great South Bay is especially lacking. Previous (pre-2006) studies of *M. leidyi* in Long Island estuaries were limited to the late 1970s (Peconic Bay; Turner et al. 1983) and 1980s (Great South Bay; Quaglietta 1987) and do not provide the resolution necessary to determine trends in ctenophore abundance and predatory impact in local estuaries. The influence of brown tide on the microplankton community and subsequent feeding behavior of *A. tonsa* (and *M. leidyi* encounter rates with the copepod) also demands further examination. Furthermore, suggestions that *M. leidyi* is increasing in Long Island estuaries are based on 'historic' abundance estimates from 1985 and 1986 (Quaglietta 1987), yet it is interesting to note that an extensive *A. anophagefferens* bloom occurred during both years of her sampling. A five-fold increase in *M. leidyi* abundance reported by McNamara et al. (2010) was also identified in 2009 relative to 2008, the latter a brown tide year (this study), and may be reflective of comparisons between non-bloom and bloom years rather than continuing increases in ctenophore abundance within the bay. A long-term, consistent monitoring project of *M. leidyi* in Great South Bay is needed.

Experimental mesocosms substantiated the cascading influence of adult *M. leidyi* on ciliates and demonstrated the interactive influence of *M. leidyi* predation and nutrient enrichment

on ciliate abundance in Great South Bay (Chapter Three). Ctenophores reared in nutrient-amended tanks produced nearly three times as many eggs as those in tanks not receiving nutrient additions. These data suggest that anthropogenic eutrophication may enhance fecundity and recruitment of *M. leidyi* and may help explain recently-documented increases in coastal ecosystems. The increase in ciliates in ctenophore treatments during recent, but not 'historic' abundances of *M. leidyi* further suggest that there may be a 'threshold' of ctenophore abundance that results in cascading influences on the microplankton community and subsequent enhancement of larval *M. leidyi.* Examination of microplankton abundance prior to and during *M. leidyi* blooms *in situ* is, again, strongly encouraged. It may also be beneficial to repeat these experiments with varying abundances of larval *M. leidyi* to examine their predatory and cascading impacts on microplankton and nanoplankton, respectively.

Finally, *M. leidyi* were analyzed for elemental composition over two years in Great South Bay (Chapter Four; McNamara et al. 2013b). Ctenophores collected towards the start of their population bloom contained significantly more C, N and P than those collected towards their collapse, when zooplankton abundances were fewer. Future studies are strongly encouraged to employ salt-free weight based percentages of C, N, and P to allow comparisons of gelatinous zooplankton across regions. The extreme loss of P by starving *M. leidyi* also warrants further examination to determine the underlying cause and its implications for the ctenophore (e.g., survival, recovery, etc). Investigation into the remaining elemental composition of the ctenophore (hydrogen, oxygen, silica, sulfur, etc) is also encouraged. Finally, future studies estimating the release of nutrients by moribund populations of *M. leidyi* and other gelatinous zooplankton are encouraged to employ caution and base their estimates only on *in situ* values of elemental composition.

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