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**The Role of the Ctenophore *Mnemiopsis leidyi* in
Nutrient Cycling in Long Island Sound, NY**

A Thesis Presented

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Abstract of the Thesis

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Gelatinous zooplankton blooms have been increasing in magnitude and frequency globally. Seasonal variations in food availability and temperature can trigger a population bloom and subsequent crash in coastal and estuarine waters. Long Island Sound (LIS) is a highly-productive urban estuary. Due to its proximity to New York City and annual summer hypoxia, there has been substantial focus on anthropogenic nutrient inputs and reductions to LIS. When determining nutrient budgets, an important process is the recycling of nutrients within a system. Gelatinous zooplankton, including the most common species in LIS, the ctenophore *Mnemiopsis leidyi*, are capable of high rates of nutrient regeneration. During 2011 and 2012, the population biomass of *M. leidyi* was monitored and nutrient regeneration rates (i.e., NH_4^+ , PO_4^{3-}) were calculated based on laboratory experiments. Blooms of *M. leidyi* in Long Island Sound were moderate in 2011 and absent in 2012, despite an anomalously warm

spring during the latter. Ctenophores in LIS have the potential, at times, to release substantial amounts of these nutrients daily, but not in quantities sufficient to support a significant amount of primary production. Upon demise of the bloom, there is also a considerable input of nutrients, but such population demise is transient and represents only a brief pulse of nutrients into the system and may be colonized rapidly by bacteria and contribute toward hypoxia. Rates of live nutrient regeneration as well as overall gelatinous zooplankton biomass can vary widely on an interannual basis, complicating the assessment of the nutrient budget for LIS.

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INTRODUCTION

Gelatinous zooplankton populations have been increasing globally, especially in estuarine and coastal systems (Titelman et al. 2006, Condon et al. 2010, Condon et al. 2011). In some locations, populations have increased temporally and spatially, leading to increases in peak abundance and/or range expansion (Sullivan et al. 2001, Pitt et al. 2005, Pitt et al. 2007, Shimauchi and Uye 2007, West et al. 2009a, Condon et al. 2010, Condon et al. 2011). Changes in population structure have been linked to climactic variability, suggesting that long-term climate change may be driving these shifts (Titelman et al. 2006, Attrill et al. 2007, Purcell 2012). In Narragansett Bay, Rhode Island, earlier seasonal maxima of ctenophores were correlated with average seawater temperature increases over the same time period (Sullivan et al. 2001). Likewise, in the Black Sea and Bering Sea, colder winter temperatures were associated with lower gelatinous zooplankton densities (Brodeur et al. 1999, Shiganova et al. 2003). With projections of future climate conditions expected to result in increases in gelatinous zooplankton populations (Brodeur et al. 1999, Mills 2001, Attrill et al. 2007, Kolesar et al. 2010, Purcell 2012), it becomes increasingly important to assess the overall ecological role of these organisms.

In Long Island waters, the ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 is the most abundant gelatinous zooplankton species (Turner 1982, McNamara et al. 2010). *M. leidyi* inhabits coastal regions and estuaries along the Atlantic coastlines of the United States. The current extent of the species in the U.S. reaches north to Cape Cod and south to the Gulf of Mexico (Sullivan et al. 2001, Nasrollahzadeh et al. 2008, Colin et al. 2010). Studies suggest that populations in the Long Island bays (i.e., Great South Bay and Peconic Bay, McNamara et al. 2010) as well as nearby Narragansett Bay, RI have been increasing, possibly due to climate

change (Sullivan et al. 2001). However, no surveys have been performed in Long Island Sound.

Gelatinous zooplankton populations are dynamic and often characterized by cycles of blooms and subsequent crashes (Graham et al. 2001, Pitt et al. 2005, Pitt et al. 2007, Pitt et al. 2009). Blooms can be true or apparent, with true defined as “normal and/or abnormal seasonal abundance”, directly due to population increase and growth, and apparent as aggregation/dispersal of stable populations (Graham et al. 2001, Condon et al. 2012). In coastal areas, blooms are most often triggered by temperature increases (Kremer 1994, Costello et al. 2006a), including for *M. leidyi* (Sullivan et al. 2001). When temperatures become warm enough (19-23 °C for *M. leidyi*), the organisms are able to reproduce by releasing about 8000 eggs per event (Kideys 1994). At 23°C, embryos can develop in as little as 20 hours, leading to dramatic increases in abundance in relatively short time periods (Kideys 1994, GESAMP 1997, Graham et al. 2001). These dense blooms can cover widespread areas and achieve extremely high biomass (Sullivan et al. 2001, Pitt et al. 2009, West et al. 2009a, Condon et al. 2010).

During population blooms, gelatinous zooplankton are often the dominant water-column predators, possibly representing the largest proportion of pelagic consumers (Pitt et al. 2005, Pitt et al. 2007, Pitt et al. 2009, McNamara et al. 2010). These species often apply heavy predation pressure on mesozooplankton, exerting a top-down control that can initiate changes that influence lower trophic levels (Oguz et al. 2001, Graneli and Turner 2002, Pitt et al. 2005, Pitt et al. 2007, Condon et al. 2010). *M. leidyi* has been implicated in strong consumption pressure on a number of zooplankton taxa, including copepods, barnacle nauplii, bivalve and annelid larvae, and fish eggs (Burrell and Vanengel 1976, Deason and Smayda 1982, Govoni and Olney 1991, Colin et al. 2010, McNamara et al. 2010). At times, intense predation on

mesozooplankton can indirectly enhance phytoplankton abundances, because it reduces grazing pressure (Deason and Smayda 1982, Pitt et al. 2005, Pitt et al. 2007, West et al. 2009a). Increased numbers of gelatinous zooplankton could also follow this pattern, leading to relaxed grazing pressure by copepods, and subsequent increases in phytoplankton biomass (Sullivan et al. 2001).

Alternatively, gelatinous zooplankton may exert bottom-up influences by excretion of dissolved nutrients, which may have the ability to stimulate primary production (Deason and Smayda 1982, Pitt et al. 2007, Nasrollahzadeh et al. 2008, West et al. 2009a). Specifically in coastal systems, excreted nutrients may be a major source of recycled nutrients for primary producers (Pitt et al. 2005). *M. leidy*, and other lobate ctenophores capture and digest prey using their lobes, which are lined with mucus (Condon et al. 2010). This mucus is thought to be one of the primary mechanisms of both organic and inorganic nutrient release (Nasrollahzadeh et al. 2008, Pitt et al. 2009, Condon et al. 2010, Niggel et al. 2010, Condon et al. 2011).

Nitrogen is primarily released in inorganic forms by gelatinous zooplankton species. Many jellyfish species are ammonotelic, that is, they excrete ammonium (NH_4^+) as the main nitrogenous waste, while phosphorus excretion is also in the form of inorganic phosphate (PO_4^{3-}) (Shimauchi and Uye 2007, Condon et al. 2010). Excretion of inorganic N and P by *M. leidy* can support up to 39% of primary production in Great South Bay, Long Island (Park et al. 1986). Ctenophores are likely to be major contributors of recycled nutrients in coastal areas, but little is known about the rates of excretion and overall ecological role in nutrient cycling (Pitt et al. 2005, Condon et al. 2010), especially in Long Island Sound.

This study examined the role of the lobate ctenophore *Mnemiopsis leidy* in oxygen and

nutrient cycling in Long Island Sound (NY-CT, USA) during 2011 and 2012. The contribution of live ctenophore populations to dissolved inorganic nutrient pools was examined experimentally through nutrient-release experiments. The temporal dynamics of the physical environment, field nutrients, and mesozooplankton densities were investigated to determine the relationship of each factor on the rates of dissolved nutrient release by ctenophores. In addition, the elemental composition of *M. leidy* was examined to determine the magnitude of removal of these elements from the system during ctenophore blooms, and release of these nutrient stocks back to the system upon population demise. Rates of bacterial oxygen consumption that would occur during degradation of dead ctenophores were calculated to determine other impacts of declining ctenophore populations.

METHODS

Field Sampling

Field observations and sampling began in May and continued through October in both 2011 (n=14 sampling trips) and 2012 (n=13 sampling trips). Bi-weekly sampling occurred at three stations in Long Island Sound: Western Long Island Sound (WLIS; 40° 52.320N, 73° 44.040W), Central Long Island Sound (CLIS; 41° 3.572 N, 73° 8.674 W), and a site in-between the two, the “middle” site (MLIS; 40° 59.085N, 73° 27.038W) (Figure 1). Field sampling was performed on the *R/V Privateer* and *R/V Mako II* of Stony Brook University.

Seawater properties

At each station, temperature (°C), salinity, and dissolved oxygen (% and mg L⁻¹) were taken at the surface using a handheld YSI 85 CTD probe. Seawater samples were collected

using a Niskin bottle from each site at 1-m depth. Seawater was filtered through a pre-combusted (2h at 450 °C) 0.2- μm glass-fiber filter (GFF) and stored frozen for dissolved nutrient analysis. Dissolved nutrient analyses were performed for NH_4^+ , and PO_4^{3-} for all samples using standard wet chemistry and colorimetric methods (Parsons et al. 1984) adapted to a 96-well spectrophotometric microplate reader. Whole seawater was also collected from the surface mixed layer for use in nutrient-release experiments, and to determine particulate organic carbon and nitrogen content (POC and PON). POC and PON samples were filtered onto pre-combusted (2h at 450 °C) 0.2- μm glass-fiber filters (GFF) and stored frozen (Sharp 1974). POC/PON samples were then dried at 60 °C (Lovegrove 1962, 1966) before analysis on a Carlo Erba NA 1500 NCS system (Cutter et al. 1991).

Gelatinous Zooplankton Abundance

To determine abundances of gelatinous zooplankton, oblique net tows were performed at each station with a 0.5-m diameter, 202 μm mesh plankton net (n=2), and with a 1-m diameter, 1000 μm mesh plankton net (n=2), both equipped with a flexible plastic cod end and flow meter (Smith et al. 1968, Tranter and Smoith 1968, Sameoto et al. 2000). Tows were confined to 2-4 minutes in length to minimize net clogging or damage to organisms (Smith et al. 1968).

Upon completion of each tow, contents of the cod end were rinsed with 20 μm -filtered seawater onto a sieve so that only gelatinous zooplankton remained and were free of all other organisms and debris (Sameoto et al. 2000, Raskoff et al. 2003). All gelatinous zooplankton collected were gently placed into a graduated cylinder to measure the total biovolume (ml) for each tow (Postel et al. 2000). Each individual collected was separated by species, enumerated,

and measured for length with a graduated petri dish to the nearest tenth of a cm (Table 1). If the total biovolume greatly exceeded 500ml, a subsample (400-500ml) was taken from the well-mixed sample to perform the counts and measurements. Organisms were discarded overboard after completion of counts and measurements. Abundance (ind. m^{-3}) and biovolumes ($mL m^{-3}$) were calculated by combining the individual gelatinous zooplankton counts (individuals) and measured biovolumes (mL) with the calculated volume of seawater sampled (m^{-3}) (McNamara et al. 2010).

Mesozooplankton Community

Separate oblique net tows were also performed at each site to determine mesozooplankton and micrometazoan species composition and abundance. In 2011, net tows were performed with a 0.5-m diameter, 64 μ m mesh plankton net (n=2) (Smith et al. 1968, Tranter and Smoith 1968, Sameoto et al. 2000), and in 2012 additional tows were also performed (202 μ m mesh, n = 2) for comparison with previous studies of zooplankton in LIS (e.g. Capriulo et al. 2002, George 2012). Both nets were equipped with a flexible plastic cod end and flow meter, and tows were confined to 2-4 minutes in length (Smith et al. 1968). Upon completion of each tow, contents of the cod end were rinsed with 20 μ m-filtered seawater onto a 64- μ m sieve and preserved in 10% buffered formalin (final concentration 5%), then stored for later enumeration (Sameoto et al. 2000).

Zooplankton samples were identified and enumerated to the lowest taxonomic level using an Olympus SZX12 dissecting microscope. Samples were analyzed for nauplii, megalopae, larvae, copepods, and other mesozooplankton to characterize the zooplankton community in LIS.

Laboratory Experiments

In the field, *Mnemiopsis leidyi* were collected via dip net from the surface layer at the WLIS and CLIS stations (Raskoff et al. 2003). Live organisms were transported back to the lab in ambient seawater for elemental analysis and nutrient-release experiments. In the lab, all animals were held for a minimum of one hour in 0.2 µm-filtered seawater to rinse of debris (e.g. other zooplankton) and allow time for the animals to depurate (Condon et al. 2010).

Elemental Analysis

Elemental analysis was performed in triplicate on a variety of size classes of *M. leidyi*. In 2011, ctenophores were collected from WLIS from June 21 – August 17 (n=5 dates), and from CLIS from June 16 – September 13 (n=8 dates) for elemental analysis. Individual animals were measured (see Table 1) and weighed (wet-weight). Dry-weights were determined after drying for 24 hours at 60°C (Lovegrove 1962, 1966). Each dried sample was then individually stored in tin foil packages for elemental analysis at a later date. Subsequently, each sample was homogenized using a mortar and pestle. Samples were analyzed for particulate carbon and nitrogen content on a Carlo Erba NA 1500 NCS system (Sharp 1974). The elemental content of individuals (mg ind⁻¹) was normalized to dry weight (mg gDW⁻¹). A relationship was determined ($DW = 0.0074(\text{length})^{2.13}$) between all experimental organismal lengths and their respective dry weights, which allowed for estimation of total field population dry weight (gDW m⁻³) from the measured ctenophore size distribution. The elemental analysis results (mg gDW⁻¹) were combined with the field population data (gDW m⁻³) to determine the total pool of carbon and nitrogen held in the LIS populations (mg m⁻³).

These values from the peak of the bloom (Aug. 3 in WLIS and Jul. 19 in CLIS) were also used to determine quantities of nitrogen and carbon released back into the system upon demise of the bloom.

Nutrient-release Experiments

In 2011, ctenophores were collected from WLIS from July 6 – August 17 (n=3 dates), and from CLIS from July 6 – August 8 (n=4 dates) for nutrient-release experiments. Nutrient-release experiments were performed on live organisms, in triplicate, on a variety of size classes (Table 1). Individual organisms were placed in 1.2-L containers containing 0.2- μm filtered seawater collected from the sampling stations. Initial dissolved nutrient samples were obtained as previously described, prior to starting each experiment. Containers were incubated in the dark at ambient seawater temperature for 12 hours (Condon et al. 2010). Dissolved nutrient samples (10ml, n=2) were obtained from each container every three hours for a total of 12 hours. After the 12 hour incubation, the wet-weights of each individual ctenophore were recorded. Dry-weights were determined after drying for 24 hours at 60°C. Dissolved nutrient analyses were performed for NH_4^+ and PO_4^{-3} concentration for all experimental samples using methods previously described (Valderrama 1981, Jones 1984, Parsons et al. 1984).

Calculations and Ecosystem Modeling

To assess the role of live nutrient regeneration by ctenophores in the LIS ecosystem, nutrient-release rates were determined. Release rates of each nutrient were determined by running robust linear regressions of experimental nutrient concentration as a response to time, with the resulting slope of the line representing the release rate in $\mu\text{mol ind}^{-1} \text{h}^{-1}$. Since concentrations were determined at multiple time points over the course of the experiments,

robust regressions were used to down-weight the influence of outliers. Release rates less than zero were removed from the analysis (Condon et al. 2010). Individual release rates were compared to dry weight of individuals to fit the equation:

$$Rate = a DW^b \quad (1)$$

where *Rate* is the release rate of ammonium or phosphate in $\mu\text{mol ind}^{-1} \text{h}^{-1}$, *DW* is the dry weight of the individual in grams, and *a*, and *b* are constants used to fit the relationship to the data (Matsakis 1992, Nemazie et al. 1993, Condon et al. 2010). As previously stated, estimation of total field population dry weight (gDW m^{-3}) from measured ctenophore size distribution was determined with a relationship between all experimental organismal lengths and their respective dry weights. Population biomass (gDW m^{-3}) was converted to an overall population release per day for each site using the fitted equation (Eq. 1). These values were then compared to ambient nutrient concentrations to determine the relative percentage of each nutrient that is being turned over by the ctenophore population per day.

Temporal dynamics of seawater temperature and mesozooplankton densities were also investigated to determine the impacts of each factor on the rates of dissolved nutrient release by ctenophores. Assuming weight and seawater temperature to be independent, the simultaneous effect of temperature and weight can be described by the equation:

$$Rate = a DW^b c^T \quad (2)$$

Excretion rates may also be affected by food concentrations. The combined effect of weight, temperature, and food concentration can be expressed as:

$$Rate = a DW^b c^T d^F \quad (3)$$

where *Rate* is the release rate of ammonium or phosphate in $\mu\text{mol ind}^{-1} \text{h}^{-1}$, *DW* is the dry weight of the individual in grams, *T* is the temperature in degrees Celsius, *F* is the

mesozooplankton concentration in ind. m⁻³, and *a*, *b*, *c* and *d* are constants (Matsakis 1992, Nemazie et al. 1993, Condon et al. 2010). Akaike Information Criteria (AIC) was used to determine which model equation most accurately fit the data. These budgets and turnover rates allowed for assessment of ecosystem-wide impacts of ctenophore populations on LIS nutrient cycling.

RESULTS

Physical properties

2011 Surface Waters

Surface water temperatures were lowest (7.6-8.8 °C) at the beginning of the 2011 sampling season and gradually increased to 18-20 °C (favorable temperatures for *M. leidyi* reproduction) by June 21. Temperatures at all three sites rose above 20°C in early July and remained above this level through mid-October. Salinities ranged from 21-26 and were highly variable over the sampling season. The western site showed the lowest salinity values (0.1-2.6ppt lower than MLIS or CLIS) due to its proximity to the freshwater source, even though all sites appeared to fluctuate similarly. Surface dissolved oxygen levels decreased over the sampling season, and hit minimums from mid-July to mid-August, where dissolved oxygen levels reached the lowest values of the sampling season (3-6.5 mg L⁻¹) (Table 2).

2012 Surface Waters

At the beginning of the 2012 sampling season (early May through mid-June), surface water temperatures were on average 2.5 °C warmer than corresponding sampling dates in 2011.

However, temperatures reached values of 18-20 °C on June 19, similar to 2011. Temperatures again remained >20 °C from early July through September, but were on average about 1 °C warmer than 2011 (Table 2, Figure 3). Salinities ranged from 24.5-27.8 and generally increased over the sampling period at all stations. Similar to 2011, the western site showed the lowest salinity values (0.5-1.9 lower than CLIS) (Table 3). Surface dissolved oxygen levels decreased over the sampling season for all sites. The lowest dissolved value of 2012 occurred at the end of July in WLIS (July 31, 5.3 mg L⁻¹), whereas in 2011 the lowest dissolved oxygen concentrations were borderline hypoxic (3.2 mg L⁻¹ on August 3) (Table 3).

2011 Dissolved Nutrients

Both dissolved phosphate (PO₄³⁻) and ammonium (NH₄⁺) concentrations were greater in WLIS than CLIS. Phosphate concentration increased most noticeably in WLIS (400-500% of initial concentration) over the course of the sampling period, but also increased in CLIS about 220% over the same time period. Ammonium concentrations were more variable at both sites. A dramatic increase in ammonium (800-900% of initial concentration) was seen at WLIS from mid-August through mid-September. In CLIS, concentrations ranged from a tripling of initial concentration to a decrease to about 50% of initial concentration (Figure 3).

Gelatinous Zooplankton Populations

2011 Gelatinous Zooplankton

Even though other gelatinous zooplankton species have been present in Long Island Sound, only the ctenophore *Mnemiopsis leidyi* was collected during the sampling period. Population biovolume averaged 0.3 mL m⁻³ in May and early June, and then ctenophores began

appearing in slightly higher densities in mid-June. The population peak biomass occurred mid-July to early August, reaching 71.2 ± 17.5 , 35.4 ± 10.4 , and 53.4 ± 8.5 mL m⁻³ for WLIS, MLIS, and CLIS, respectively. Ctenophore biovolume began to decline mid-September, and then averaged 1.3 mL m⁻³ for the rest of the sampling season (Figure 4).

Biovolume estimates of *M. leidyi* varied noticeably between the three sampling sites. The western site had the greatest peak mean biovolume occurring on August 3 (71.2 ± 17.5 ml m⁻³), but also had a smaller peak earlier in the season on June 16 (32.6 ± 16.6 ml m⁻³). The middle site did not have a distinct peak in biovolume, but rather a series of increases on July 6, August 3, and August 30 (36.1 ± 6.8 ml m⁻³, 35.4 ± 10.4 ml m⁻³, 29.6 ± 4.3 ml m⁻³ respectively). At the central site, there was one distinct peak in biovolume in the middle of the sampling season on July 19 (53.4 ± 8.5 ml m⁻³) (Figure 4).

Abundances remained consistently lower at WLIS than the other two sites, with peak numbers occurring on June 16 (29.3 ± 17.1 ind. m⁻³) and August 3 (26.0 ± 7.6 ind. m⁻³). The highest mean abundances of *M. leidyi* occurred in CLIS and MLIS on July 6 (55.2 ± 27.4 , ind. m⁻³ and 48.2 ± 27.8 ind. m⁻³, respectively), with secondary peaks occurring on August 17 (34.4 ± 10.4 ind. m⁻³) in CLIS and August 3 (35.1 ± 10.6 ind. m⁻³) and August 30 (35.3 ± 9.3 ind. m⁻³) in MLIS (Figure 4).

Differences in temporal pattern between total biovolume and abundance are partly due to differences in the size distribution of ctenophores at each site. At the western site, large (5-7cm, and >7cm) ctenophores were present early June through early July. During this same period, the majority of the population in MLIS and CLIS consisted of small (<1cm, 1-3cm) individuals. Towards the end of the sampling season at all sites, the population was dominated by the smallest size class of individuals (<1cm). This shift towards the smallest size class first

occurred at WLIS on August 30, then MLIS on September 13, then CLIS on September 27 (Figure 6).

In both WLIS and MLIS, the highest biovolume of *M. leidy* coincided with the highest abundance. However, because of the size distribution in CLIS, the biovolume peak did not coincide with the highest abundance. The biovolume maxima occurred on July 19, which coincided with a relatively low mean abundance and was due to the majority of ctenophores occurring in the 1-3 cm and 3-5 cm size-classes. At peak abundances on July 6 and August 17, the contribution of larger ctenophores decreased and ctenophores <1cm increased in abundance, leading to lower biovolumes relative to abundances (Figure 4, Figure 6).

2012 Gelatinous Zooplankton

In 2012, biovolumes remained below 1 mL m^{-3} at WLIS for the entirety of the sampling season. Minor increases in biovolume occurred at MLIS and CLIS on July 3 ($7.57 \pm 3.68 \text{ mL m}^{-3}$ and $6.81 \pm 2.30 \text{ mL m}^{-3}$) and again at CLIS on August 29 ($7.49 \pm 1.69 \text{ mL m}^{-3}$), but biovolumes remained below 3 mL m^{-3} at MLIS and CLIS for the rest of the sampling dates (Figure 5). On these dates of biovolume peaks, ctenophores were composed of at least 20% >1cm individuals, as compared to the majority of the sampling season, which was composed almost entirely of the smallest size class (<1cm) individuals (Figure 5, Figure 6).

Although biovolumes were low the entire season, there was one noticeable increase in abundance at both MLIS and CLIS. This dramatic increase in abundance coincided with small biovolume peaks in MLIS and CLIS and occurred on July 3 ($87.80 \pm 36.80 \text{ ind. m}^{-3}$, and $165.43 \pm 55.76 \text{ ind. m}^{-3}$, respectively). Although these abundances were two to three times higher than peak abundances in 2011, the 2012 population was composed almost entirely of the

smallest size class (<1cm) individuals (Figure 4, Figure 5, Figure 6). These <1cm individuals are larvae, and not reproductively mature adults. While an overwhelmingly large number of these larvae were present, they only constituted a small biovolume, and never matured to produce the bloom of adult organisms as seen in LIS in 2011.

Due to the low field abundances of adult organisms throughout 2012, no sampling dates provided sufficient numbers to collect ctenophores for elemental analysis and nutrient-release experiments.

Mesozooplankton and Micrometazoa Abundances

Mesoplankton and micrometazoa abundances are presented as total number of organisms excluding polychaetes, which represents the total number of organisms available for ctenophore consumption. While *M. leidy* has been shown to consume many different zooplankton taxa including copepods, barnacle nauplii, bivalve larvae, and fish eggs (Burrell and Vanengel 1976, Deason and Smayda 1982, Govoni and Olney 1991, Colin et al. 2010, McNamara et al. 2010), in Long Island waters they tend to select against polychaetes (McNamara, *pers. comm.*). In 2011, the total abundance of mesozooplankton and micrometazoa (>64um, excluding polychaetes) averaged $3.55(\pm 0.20, \text{ s.e.}) \times 10^5$ organisms m^{-3} in WLIS, $2.60(\pm 0.26) \times 10^5$ organisms m^{-3} in MLIS, and $2.22(\pm 0.20) \times 10^5$ organisms m^{-3} in CLIS throughout the sampling period.

In WLIS, mean zooplankton densities were generally higher than the other two sites (on average, almost double the other sites), ranging from $6.24(\pm 1.61) \times 10^4$ organisms m^{-3} to $1.37(\pm 0.24) \times 10^6$ organisms m^{-3} . Mean zooplankton densities in MLIS and CLIS ranged from $2.35(\pm 0.21) \times 10^4$ organisms m^{-3} to $8.88(\pm 1.07) \times 10^5$ organisms m^{-3} , and $2.81(\pm 0.14) \times 10^4$

organisms m^{-3} to $8.67(\pm 1.75) \times 10^5$ organisms m^{-3} , respectively. At all sites, abundances were lowest throughout a majority of the summer and increased towards the end of the sampling season. Peak abundances occurred at WLIS on August 30, and both CLIS and MLIS on October 11 (Figure 7).

In WLIS, there was no strong relationship between ctenophore abundance and mesozooplankton abundance during the ctenophore bloom. In MLIS and CLIS, an inverse relationship was seen most prominently during the ctenophore bloom. In MLIS, a series of ctenophore density peaks (July 6, August 3, and August 30) coincided with decreases in mesozooplankton abundance. Similarly, ctenophore population decreases on July 19 and August 17, were paired with mesozooplankton increases. In CLIS, maximum ctenophore densities on July 6 coincided with a decline in mesozooplankton abundance. Mid-July to early August, ctenophore populations declined while mesozooplankton abundances increased. A secondary ctenophore density peak occurred August 17, which also corresponded to a decrease in mesozooplankton. All sites exhibited the most dramatic increases in mesozooplankton abundance after the collapse of ctenophore populations, beginning on August 8 in WLIS, and August 30 in MLIS and CLIS (Figure 8). Combining data from all three sites, mesozooplankton and ctenophore abundance showed a weak but present negative correlation (Pearson's Product Moment Correlation, $r=-0.33$).

Laboratory Experiments

Elemental Analysis of Ctenophore Biomass

In 2011, ctenophores were collected from WLIS from June 21 – August 17 (n=5 dates), and from CLIS from June 16 – September 13 (n=8 dates) for elemental analysis. Data is

presented as modified box plots, where outliers are denoted as any points greater than the third quartile plus 1.5 times the interquartile range, or less than the first quartile minus 1.5 times the interquartile range, or roughly ± 2 standard deviations (Crawley 2012). Body composition averaged 19.39 ± 5.38 mgC gDW⁻¹ and 4.01 ± 1.06 mgN gDW⁻¹ in WLIS and 17.44 ± 4.34 mgC gDW⁻¹ and 3.71 ± 0.92 mgN gDW⁻¹ in CLIS (Figure 9). C:N ratios of individuals were significantly different between WLIS and CLIS (nested ANOVA, date within site; Df=2,136, F=3.84, p<0.05), and at both sites, C:N ratio significantly decreased over the sampling season (Df=4,136, F=5.65, p<0.001). There was no relationship between C:N ratios and individual size.

After combining elemental analysis results with biomass estimates, at the highest biovolume of ctenophores at WLIS (August 3), the population sequestered about 2912.76 $\mu\text{mol C m}^{-3}$ and 579.89 $\mu\text{mol N m}^{-3}$. The central site had the largest biovolume on July 19, and contained 1290.84 $\mu\text{mol C m}^{-3}$ and 238.63 $\mu\text{mol N m}^{-3}$ (Table 4). The post-bloom ctenophore densities occurred on August 17 and September 13 at WLIS and CLIS, respectively. At this time, in WLIS, ctenophores held only 8.29 $\mu\text{mol C m}^{-3}$ and 1.60 $\mu\text{mol N m}^{-3}$. The population decline at WLIS was abrupt (see Figure 4) and went from peak biovolumes to post-bloom densities in only 14 days, resulting in an average biomass loss of 207.46 $\mu\text{mol C m}^{-3} \text{ day}^{-1}$ and 41.31 $\mu\text{mol N m}^{-3} \text{ day}^{-1}$ (Table 4). In CLIS, post-bloom populations held 69.25 $\mu\text{mol C m}^{-3}$ and 14.02 $\mu\text{mol N m}^{-3}$. The decline in the population from peak biovolumes at CLIS occurred gradually over 56 days (see Figure 4). Although rates of biomass loss and decomposition would generally slow as the bloom crashes, averaged rates of biomass loss would be about 21.81 $\mu\text{mol C m}^{-3} \text{ day}^{-1}$ and 4.01 $\mu\text{mol N m}^{-3} \text{ day}^{-1}$ (Table 4).

Nutrient-Release Rates of Ctenophores

In 2011, ctenophores were collected from WLIS from July 6 – August 17 (n=3 dates), and from CLIS from July 6 – August 8 (n=4 dates) for nutrient-release experiments. Individuals were found to release ammonium at rates from about 0.006 to 0.62 $\mu\text{mol ind}^{-1} \text{h}^{-1}$, and phosphate at rates from about 0.004 to 0.13 $\mu\text{mol ind}^{-1} \text{h}^{-1}$ (Figure 10). Release rates of both ammonium and phosphate were significantly dependent on size (Df=1,50, F=42.712, $p<0.001$; Df=1,45, F=8.4021, $p<0.01$). Temporal dynamics of seawater temperature and mesozooplankton densities were also investigated (Table 5, Table 6). The combined effect of temperature and weight (Eq. 2) more accurately described the nutrient-release rates than the combined effect of weight, temperature, and food concentration (Eq. 2), and just weight alone (Eq. 1) (Table 6).

In WLIS, the maximum turnover of both ammonium and phosphate likely occurred on August 3, when *M. leidy* biovolume was at a maximum. Using the rate to body weight relationship (Eq. 1), the total population of *M. leidy* at this date could have released ammonium and phosphate of up to 48.59 $\mu\text{mol m}^{-3} \text{day}^{-1}$ and 13.41 $\mu\text{mol m}^{-3} \text{day}^{-1}$, respectively (Table 6). Comparing these rates to nutrient pools at this date in WLIS, the total population could have turned over up to 3.20% day^{-1} of ammonium and 0.57% day^{-1} of phosphate (Table 6). In CLIS, maximum daily population release of ammonium and phosphate by ctenophores would have occurred on July 6. At this date, the total *M. leidy* population could have released ammonium and phosphate of up to 37.17 $\mu\text{mol m}^{-3} \text{day}^{-1}$ and 15.55 $\mu\text{mol m}^{-3} \text{day}^{-1}$, respectively (Table 6). The total population in CLIS at this date could potentially turnover up to 13.75% day^{-1} of ammonium and 3.88% day^{-1} of phosphate (Table 6). In LIS in the summer, nitrogen pools are turned over several times daily by phytoplankton (Carpenter and Dunham

1985, Goebel et al. 2006). It would take peak abundances of *M. leidy* in WLIS over 31 days to turnover the ammonium pool at that site. Due to lower stocks of nitrogen in the Central Sound, it would take about 7 days for the maximum abundance of CLIS ctenophores to turnover the ammonium pool (Table 6).

Assuming primary production average summer estimates of $430 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Goebel et al. 2006), an oxygen to carbon ratio of 138 O_2 :106 C, and that the elemental composition of phytoplankton conforms to the Redfield ratio of 106 C:16 N:1 P (Redfield 1934), the amounts of ammonium and phosphate release by peak *M. leidy* populations could support <1% of daily primary production in LIS (Schneider 1989).

DISCUSSION

Abundances of *Mnemiopsis leidy* in Long Island Sound

The current paradigm regarding gelatinous zooplankton is that they have been significantly increasing due to anthropogenic impacts such as eutrophication and climate change. Gelatinous zooplankton in Long Island Sound have not been examined previously, preventing direct comparisons to historical abundances or bloom timing. However, studies conducted historically and more recently in close proximity to Long Island Sound (LIS) support the idea that populations within this region are increasing. For the specific study organism, *Mnemiopsis leidy*, studies spanning decades suggest that populations of the ctenophore have increased in Long Island embayments and Rhode Island waters (Sullivan et al. 2001, Costello et al. 2006b, McNamara et al. 2010).

In Narragansett Bay, Rhode Island, populations of *M. leidy* have eclipsed 1000 individuals ($\text{ind.}) \text{ m}^{-3}$ in both 2002 and 2003 (Costello et al. 2006b), which has been a

significant increase over densities in 1983 (80 ind. m⁻³) and as recently as 1999 (350 ind. m⁻³; (Sullivan et al. 2001). In Great South Bay, Long Island, studies by McNamara et al. (2010) show populations of *M. leidy* in the mid-2000s (up to 142.1 mL m⁻³) were 3-5 times more abundant by volume than those in the mid-1980s (42 mL m⁻³ in 1986; (Quaglietta 1987)). Similar trends were seen in the Peconic Bay estuary where populations in the mid-2000s were up to 90 mL m⁻³ (McNamara et al. 2010), approximately 3-4 times greater than previous values in 1978 and 1979 (Turner 1982).

Peak biovolume and abundance estimates for this study in Long Island Sound reveal ctenophore abundance values much lower than the recent studies within the region. In 2011, peak biovolume estimates in LIS ranged from 35.4 to 71.2 mL m⁻³ being highest at the westernmost site. These values are within the range of values reported in the Peconic Bay estuary, but approximately half of recent biovolumes for Great South Bay (McNamara et al. 2010). The highest peak density estimates recorded in 2011 were 55.2 ind. m⁻³, recorded in central LIS, two orders of magnitude less than the peak *M. leidy* abundances reported for Narragansett Bay (Costello et al. 2006b).

The sampling methods for this study, however, used oblique net tows that only sampled the top 15m of the water column. In LIS, average water depths are around 25m, but can become much deeper (40-50m) in the center (between Long Island and Connecticut; Buck et al. 2005, where this sampling occurred). In GSB, depths average < 2m, and maximum depths only reach about 6m. Similarly in Peconic Bay and Narragansett Bay, depths average 4.5m and 8m, respectively. Since LIS is a much deeper body of water than previously studied embayments, there is the possibility that the net tows performed in this study did not adequately sample the entire vertical range of the ctenophore populations (Costello and

Mianzan 2003). Also, lack of long-term data for ctenophore abundances in LIS makes it difficult to conclude whether 2011 or 2012 *M. leidyi* densities were indicative of typical abundances, or how these populations may change in the future.

Despite differences in population size, the timing of peak *M. leidyi* abundances in LIS in 2011 were relatively consistent with studies performed by McNamara et al. (2010) in both Great South Bay and Peconic Bay. In the summer of 2006, the highest abundances of ctenophores in Great South Bay occurred in mid-June and late June to early July in Peconic Bay. In this study, peak densities occurred in WLIS in mid-June, and CLIS and MLIS in early July. These bloom dates occurred much earlier than blooms in the late 1970s and mid 1980s in Long Island embayments, which tended to be in September (Quaglietta 1987), and October (Turner 1982).

Warming temperatures may be the driving factor for earlier seasonal maxima in ctenophore abundance. Over 50 years in Narragansett Bay, *M. leidyi* seasonal maxima have shifted from late summer (1950 to 1985), to early summer (in the late 1980s), and more recently, to spring in 1999 and 2000, which corresponded with seawater temperature increases over the same period (Sullivan et al. 2001). Likewise, colder temperatures have been linked to lower gelatinous zooplankton populations (Brodeur et al. 1999, Shiganova et al. 2003). Data from LIS in 2012 complicates this trend. NOAA Northeast Fisheries Science Center (NEFSC) data show that the Northeast Shelf experienced warmer-than-average sea surface temperature (SST) during the winter and spring of 2012 (Friedland 2012), which should have led to an earlier and more intense bloom. Brodeur et al. (1999) suggests that spring temperatures may be the most influential in controlling blooms, and in LIS waters in 2012, the greatest temperature anomaly was seen in the spring months (Figure 2; Friedland 2012). Yet, the

bloom did not occur in LIS in 2012, and thus the lack of a ctenophore bloom following an anomalously warm spring in 2012 suggests that these population cycles may be less temperature-dependent than previously believed.

Two recent reviews by Condon et al. (2012, 2013) challenge the current paradigm that gelatinous species are increasing globally. In fact, gelatinous zooplankton populations may fluctuate on the order of 18-20 year time scales, and the majority of datasets examined (from 1970-2010) have most likely occurred during positive oscillations (Condon et al. 2012, 2013). Climate change and anthropogenic impacts may favor an increase or expansion of gelatinous species, but these may not be driving factors (Condon et al. 2012, Purcell 2012). These recent publications along with the findings of this study strongly call to attention the need for longer-term data sets when sampling gelatinous zooplankton.

Nutrient Uptake and Release

When in bloom, ctenophores can significantly contribute to nutrient sequestration and subsequent release (Titelman et al. 2006, Tinta et al. 2010). Ctenophore body composition ranged from 1.45-2.69% C and 0.29-0.48% N, across study sites and years in LIS. These values are similar to historic values for ctenophores in Narragansett Bay, RI (Kremer 1977). The C:N ratio ranged from 4.71-8.15 in WLIS, and 4.43-9.88 in WLIS. For the majority of the sampling season, the body composition of *M. leidyi* was below the Redfield ratio of 6.625 C:N (Redfield 1934). Enrichment of nitrogen relative to carbon in ctenophores is expected, as N enrichment is common in zooplankton relative to their food source (Kremer and Nixon 1976, Kremer 1977). This ratio also indicates a high protein composition, often seen in both ctenophore and jellyfish species (Kremer 1977, 1982, Larson 1986, Schneider 1989, Schoo et

al. 2010). In addition, the ratios observed for *M. leidyi* in this study were significantly below the published ratios for particulate organic matter (POM) in LIS (Gobler et al. 2006), and thus ctenophores may represent a significant N sink when population abundances are high (Pitt et al. 2009, West et al. 2009b).

At high biovolumes, ctenophores in LIS might sequester up to 2,913 $\mu\text{mol C m}^{-3}$ and 580 $\mu\text{mol N m}^{-3}$ (Table 4). However, these peaks in population are only transient, so C and N are only briefly removed from the system. When nutrients are released back into the environment upon death, biomass loss rates were as high as 207.46 $\mu\text{mol C m}^{-3} \text{ day}^{-1}$ and 41.31 $\mu\text{mol N m}^{-3} \text{ day}^{-1}$. Overall, the growth and decline of ctenophores suggest they are able to remove significant amounts of C and N, and then re-release these elements back into the water column upon death, making them available for use, and significantly altering nutrient dynamics (Titelman et al. 2006, West et al. 2009b, Tinta et al. 2010). The C:N ratios of *M. leidyi* are similar to that of heterotrophic bacteria, making gelatinous biomass an ideal bacterial substrate, and thus could promote localized hypoxic events (Titelman et al. 2006, West et al. 2009b, Tinta et al. 2010). Using the dead biomass carbon decomposition rates of 207.46 $\mu\text{mol C m}^{-3} \text{ day}^{-1}$ in WLIS and 21.81 $\mu\text{mol C m}^{-3} \text{ day}^{-1}$ in CLIS, and the ratio of 138 O_2 : 106 C, when ctenophore populations crash, bacteria could deplete 270.1 $\mu\text{mol O}_2 \text{ m}^{-3} \text{ day}^{-1}$ in WLIS and 28.4 $\mu\text{mol O}_2 \text{ m}^{-3} \text{ day}^{-1}$ in CLIS.

Ctenophores may also contribute significantly to the nutrient pool when they are alive. It has been well documented that gelatinous zooplankton are capable of releasing large amounts of ammonium, the main nitrogenous waste product of most zooplankton (Matsakis 1992, Shimauchi and Uye 2007). In the Caspian Sea, ammonium concentrations appeared positively correlated with *M. leidyi* abundance, with the maximum ammonium concentration

occurring during maximum *M. leidy* biomass (Nasrollahzadeh et al. 2008). In laboratory experiments, ammonium concentrations also increased with time after the addition of gelatinous zooplankton (Nasrollahzadeh et al. 2008, Tinta et al. 2010).

Ctenophores also contribute significantly to dissolved inorganic phosphorus (DIP) concentrations. Laboratory studies have documented rapid increases in DIP in bottles after the introduction of ctenophores (Nasrollahzadeh et al. 2008), while showing no similar increase in dissolved organic phosphorus (DOP; (Tinta et al. 2010). Similarly, concentrations of PO_4^{-3} were higher in all of the jellyfish treatments relative to controls. In field surveys of Chesapeake Bay, gelatinous zooplankton are a major source of nutrients to overall DIP pools (Condon et al. 2010).

Mnemiopsis leidy in Long Island Sound were found to release both ammonium and phosphate over the course of the 12-hour incubations. While rates of DIN and DIP release were as high as $0.62 \mu\text{mol ammonium ind}^{-1} \text{h}^{-1}$ and phosphate at rates up to $0.13 \mu\text{mol phosphate ind}^{-1} \text{h}^{-1}$, the rates were highly dependent on size, which was expected (Peters 1983). Many previous studies of *M. leidy* excretion however, presented excretion rates per gram dry weight of the organism, by assuming a linear correlation of nutrient release and size (Kremer 1977, Park et al. 1986, Nemazie et al. 1993, Condon et al. 2010). In this study, allometric relationships between size and rates of nutrient release were identified (Eq. 1, see Table 5). Standardized release rates in Long Island Sound are similar to published release rates in Narragansett Bay, Great South Bay, and the Chesapeake Bay (Kremer 1977, Park et al. 1986, Nemazie et al. 1993, Condon et al. 2010).

Ammonium release rates ranged between 0.10 and $3.47 \mu\text{mol gDW}^{-1} \text{h}^{-1}$ during this study. The low end of the range was similar to historical values in Great South Bay (Park et al.

1986) and Narragansett Bay (Kremer 1977), while the high end of the range was similar to historical rates in Chesapeake Bay (Nemazie et al. 1993). However, a study by Condon et al. (2010) found rates of ammonium excretion in *M. leidy* to approach $23.2 \mu\text{mol gDW}^{-1} \text{h}^{-1}$, which is over six times greater than this study, possibly due to using more recently fed organisms in the experimental incubations. Phosphate release rates standardized to dry weight for Long Island Sound were greater than estimates in Narragansett Bay (Kremer 1977), but similar to rates of phosphate release in Chesapeake Bay (Condon et al. 2010).

Scaled to population abundance, the contribution of ctenophores to the total pool of inorganic nutrients in LIS was estimated to range between 3.20-13.76% day^{-1} of ammonium and 0.57-3.88% day^{-1} of phosphate, depending on site. These turnover rates were significantly lower than rates in Chesapeake Bay and Narragansett Bay (Condon et al. 2010), possibly due to differences in bloom biomass and other nutrient inputs. Overall, live ctenophore populations do contribute to the remineralization of N and P in LIS, albeit at relatively low percentages. Although the overall percentages of nutrient turnover due to *M. leidy* are low, the individual rates are similar to published ammonium and phosphate release rates from other local estuaries (Kremer 1977, Park et al. 1986, Nemazie et al. 1993, Condon et al. 2010), and differences in turnover percentages may be due to differences in ctenophore abundance as well as higher standing stocks of nutrients in LIS (Buck et al. 2005).

Nutrient Cycling and LIS

It is possible that *Mnemiopsis leidy* population cycles are related to their prey resources. Food availability may control the initiation and magnitude of ctenophore blooms, by having a direct effect on egg production rates (Deason and Smayda 1982, Oguz et al. 2001),

and at all sites in 2011, mesozooplankton abundance was relatively high before the appearance of ctenophores (Figure 8). After the appearance of ctenophores, there was a general negative relationship between mesozooplankton abundance and *M. leidyi* abundance. Numerous studies conducted in other coastal embayments have found that populations of *M. leidyi* removed up to 60% of the zooplankton by exerting strong consumption pressure on a number of zooplankton taxa, including copepods, barnacle nauplii, bivalve and annelid larvae, and fish eggs (Burrell and Vanengel 1976, Deason and Smayda 1982, Govoni and Olney 1991, Colin et al. 2010, McNamara et al. 2010). Although this study did not specifically examine trophic relationships between *M. leidyi* and their prey resource, many of their ecological and physiological characteristics (including live nutrient release) may be related to mesozooplankton abundance.

Rates of live nutrient-release could be affected by food availability, as well as size and temperature. Beginning with the basic model of nutrient release rate as a function of size (Eq. 1), coefficients were determined that were similar to other published studies. The addition of temperature significantly increased the fit of the model as expected (see Table 6), but the addition of food actually slightly decreased the model fit. McNamara et al. (2013) presents significant findings for *M. leidyi* elemental content as a function of both individual size and prey availability. In this study, no relationship between elemental content and size or prey availability was found to be significant. Mesozooplankton concentrations did not significantly affect live nutrient-release or elemental composition of ctenophores in this study, but it is important to note that these organisms were not freshly fed prior to these laboratory experiments, which may obscure the effects of food.

Some studies suggest that gelatinous zooplankton, including ctenophores, can regenerate potentially limiting nutrients to stimulate phytoplankton primary production (Biggs

1977, Pitt et al. 2005, Shimauchi and Uye 2007, Nasrollahzadeh et al. 2008, Pitt et al. 2009, West et al. 2009a, Condon et al. 2010). Some estimates indicate excretion by gelatinous zooplankton could potentially supply 39–63% of the nitrogen required to sustain phytoplankton production in the North Atlantic (Biggs 1977). Excretion of NH_4^+ by jellyfish blooms in Australia has been estimated to supply 8-11% of the inorganic nitrogen requirements of phytoplankton (Pitt et al. 2005, Pitt et al. 2009). In Great South Bay, excretion of inorganic N and P by *M. leidyi* was estimated to support up to 39% of primary production (Park et al. 1986).

Despite the potential stimulation of primary production, this may not be the case in Long Island Sound, at least during the study period. At peak ctenophore abundances, recycled N and P would only satisfy <1% of the phytoplankton demand. Due to its geographic location near the largest urban population center in the United States, the western sound is highly eutrophic (Buck et al. 2005). Even in the Central Sound, at times nutrients might not be limiting (but see George 2012). It is in areas where nutrients are limiting that regenerated inorganic nutrients from gelatinous zooplankton could supply a significant amount of nutrients required for phytoplankton (Pitt et al. 2005, Nasrollahzadeh et al. 2008, Pitt et al. 2009, West et al. 2009a). In Long Island Sound, nitrogen pools are turning over multiple times per day (Carpenter and Dunham 1985, Goebel et al. 2006), so regenerated nutrients by ctenophores may be taken up and turned over as quickly as they are excreted.

A 2000 “Daily load analysis to achieve water quality standards for dissolved oxygen in LIS” determined the tons of nitrogen discharged annually to LIS through various sources (2000 TMDL). Total in-basin nitrogen loading was estimated to be about 53,271 tons of nitrogen per year in LIS. If *M. leidyi* populations remained at 2011 peak densities in LIS for an average

bloom time of 78 days, their total N input would produce about 7.5% of the total in-basin nitrogen sources.

Conclusion

Blooms of *M. leidyi* in Long Island Sound were moderate in 2011 and absent in 2012, despite an anomalously warm winter and spring during the latter. On an ecosystem scale, nutrient release from live ctenophores in Long Island Sound is relatively substantial, but not in quantities sufficient to support a significant amount of primary production. Upon demise of the bloom, there is also a considerable input, but such population demise is transient and represents only a brief pulse of nutrients into the system. When the ctenophore population crashes, it is also likely that the abundance of dead biomass may be colonized rapidly by bacteria and contribute toward hypoxia. Rates of live nutrient regeneration as well as overall gelatinous zooplankton biomass can vary widely on an interannual basis, complicating the assessment of the nutrient budget for LIS.

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FIGURES

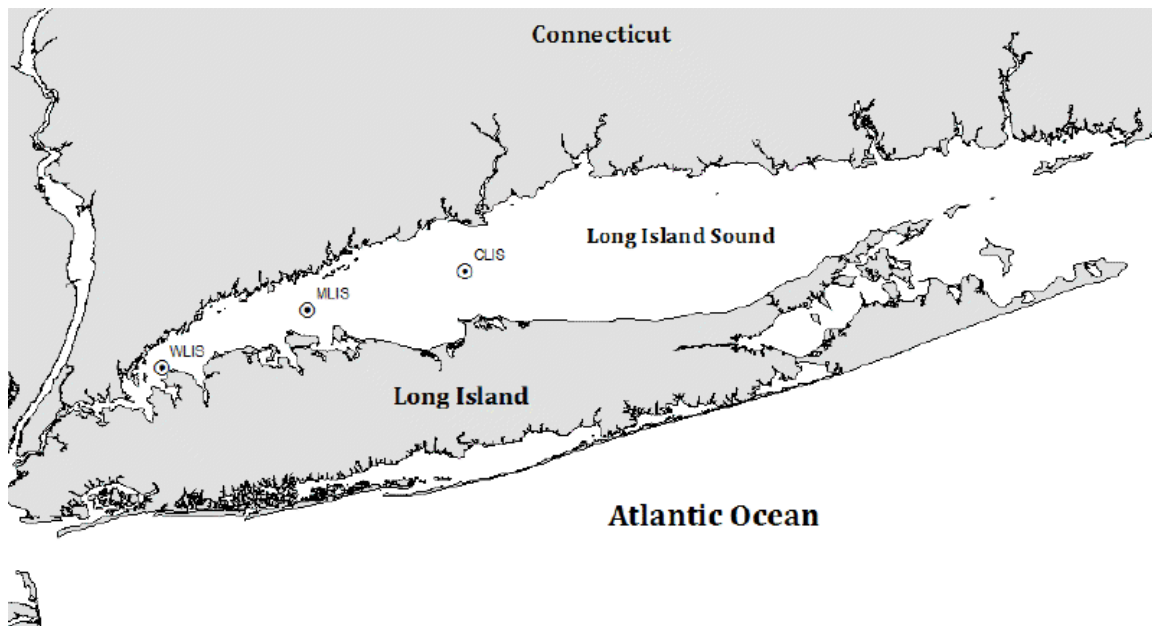


Figure 1. Field sampling sites in Long Island Sound. Bi-weekly sampling occurred in both 2011 and 2012 at all three stations: Western Long Island Sound (WLIS; $40^{\circ} 52.320\text{N}$, $73^{\circ} 44.040\text{W}$), Central Long Island Sound (CLIS; $41^{\circ} 3.572\text{ N}$, $73^{\circ} 8.674\text{ W}$), and a site in-between the two, the “middle” site (MLIS; $40^{\circ} 59.085\text{N}$, $73^{\circ} 27.038\text{W}$).

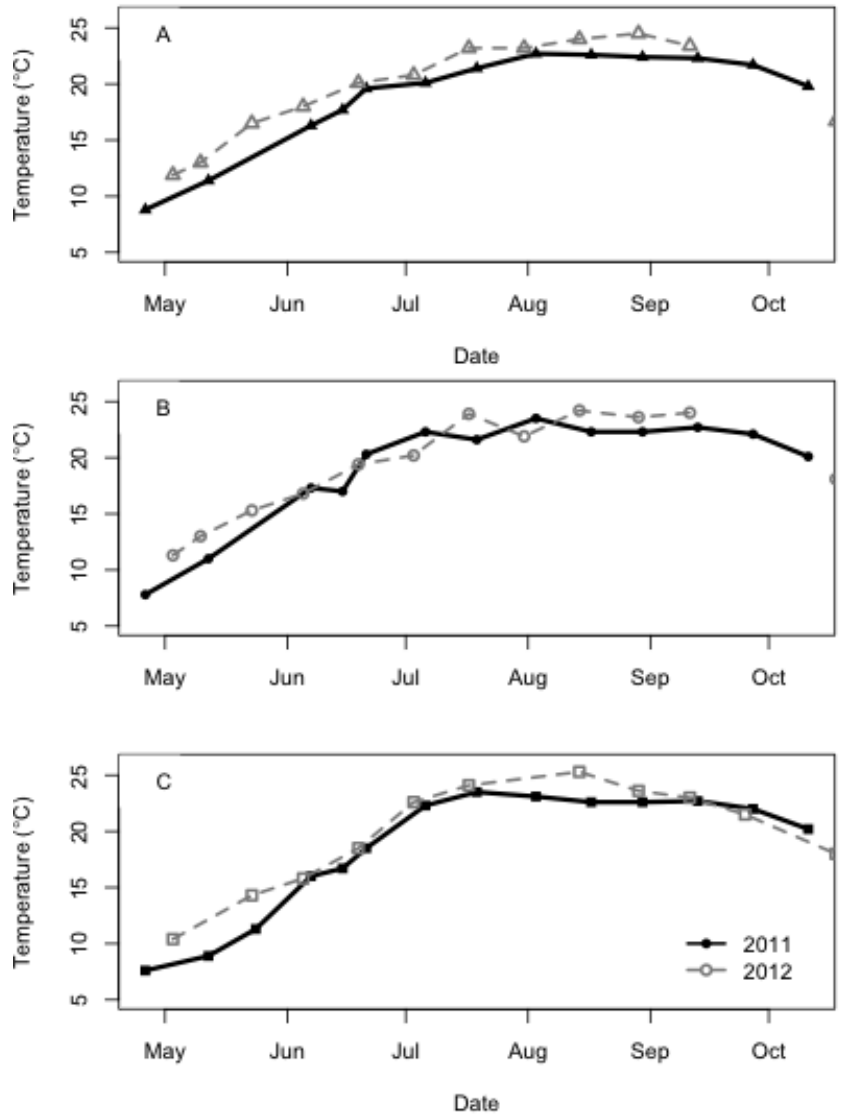


Figure 2. Surface seawater temperature (°C) for WLIS (A), MLIS (B), and CLIS (C) in 2011 (solid black lines) and 2012 (dashed gray lines).

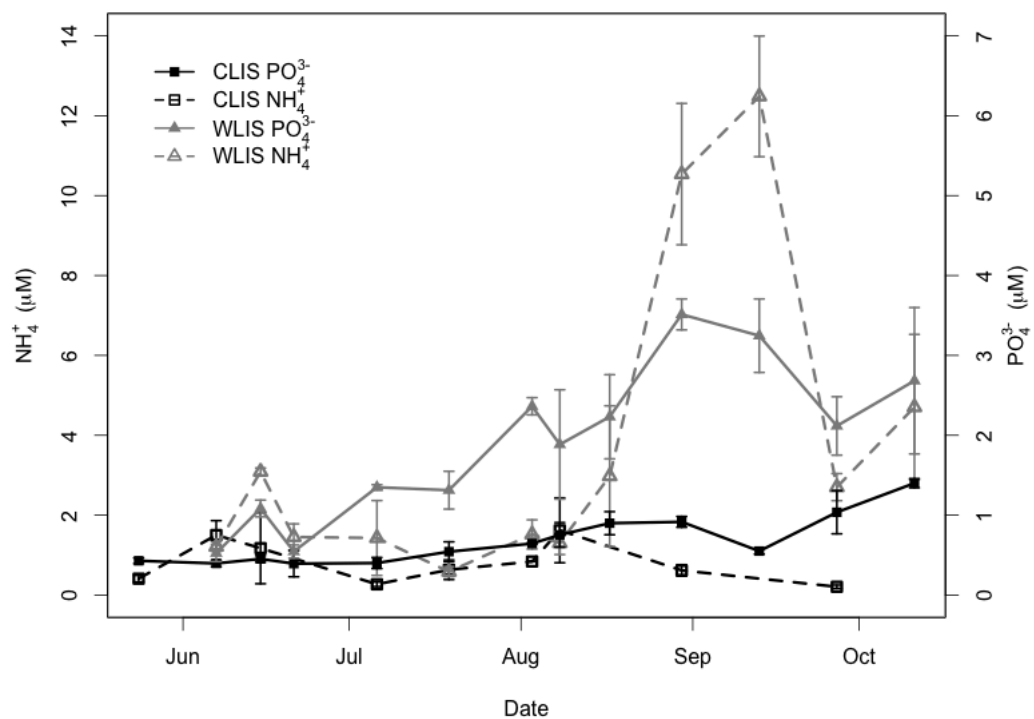


Figure 3. Dissolved surface ammonium (NH_4^+ , dashed lines) and phosphate (PO_4^{3-} , solid lines) concentrations (μM) at WLIS (gray) and CLIS (black) for the 2011 season.

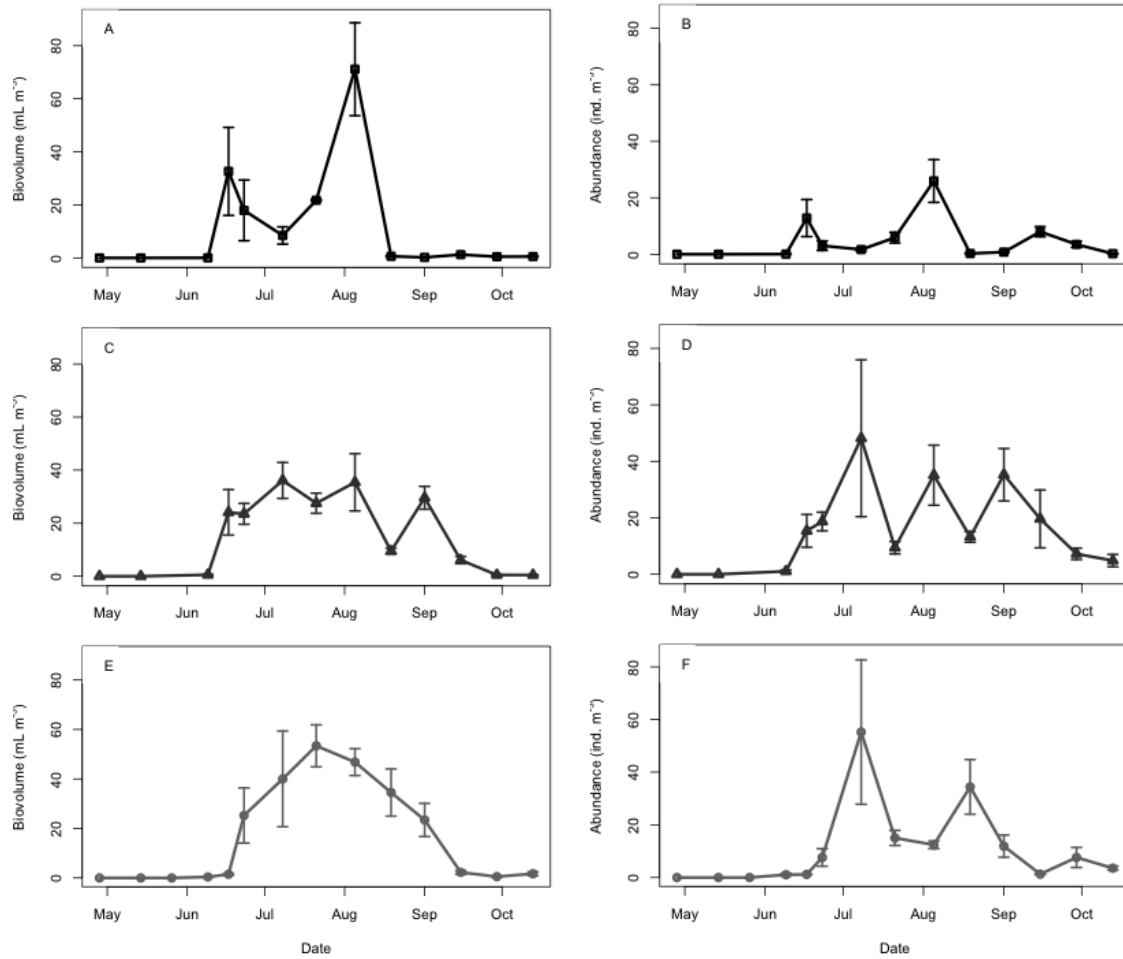


Figure 4. Ctenophore biovolumes (± 1 s.e.; mL m⁻³; A, C, E) and abundances (± 1 s.e.; ind. m⁻³; B, D, F) at WLIS (A, B), MLIS (C, D), and CLIS (E, F) for the 2011 sampling season.

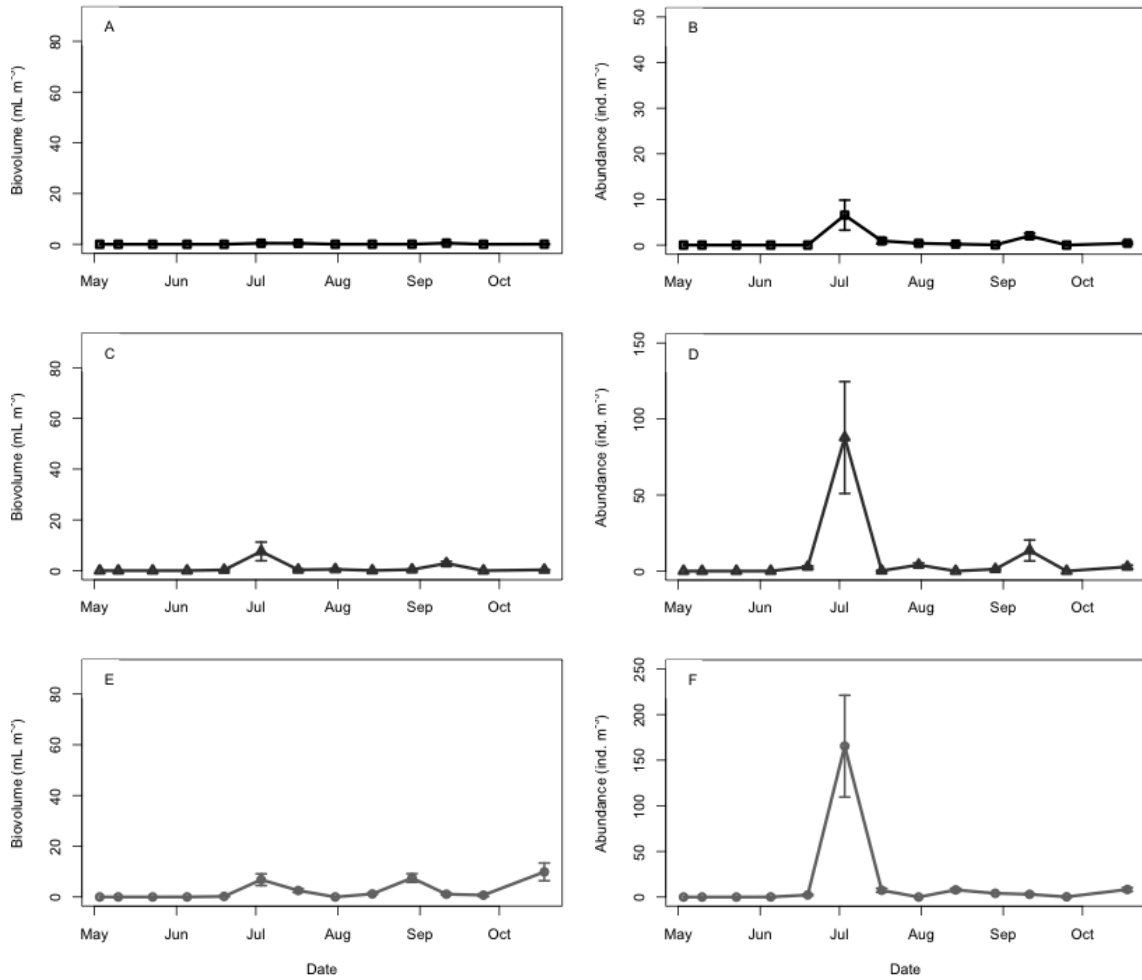


Figure 5. Ctenophore biovolumes (± 1 s.e.; mL m⁻³; A, C, E) and abundances (± 1 s.e.; ind. m⁻³; B, D, F) at WLIS (A, B), MLIS (C, D), and CLIS (E, F) for the 2012 sampling season.

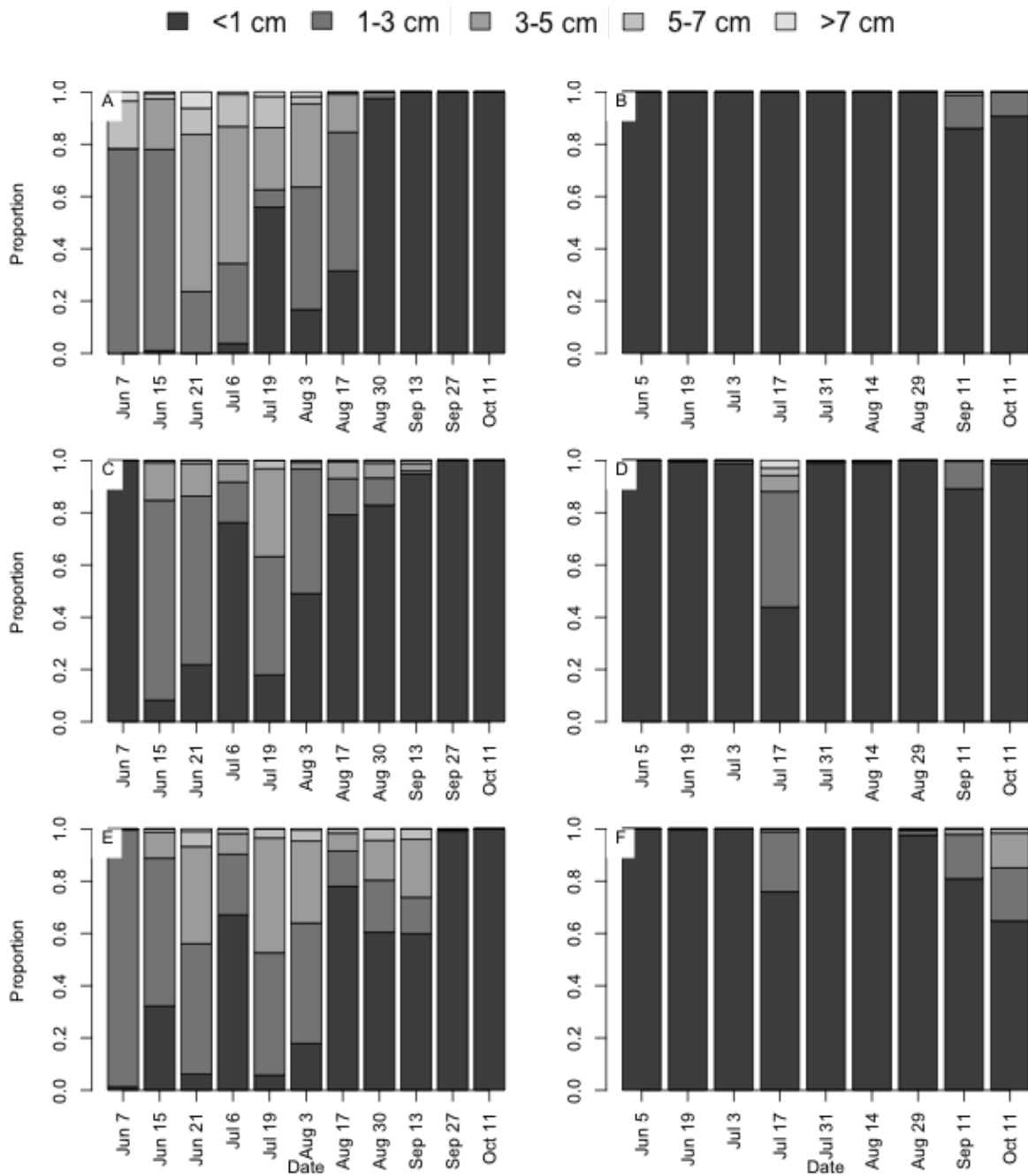


Figure 6. Ctenophore size composition at WLIS (A, B), MLIS (C, D), and CLIS (E, F) for the 2011 (A, C, E) and 2012 (B, D, F) sampling seasons.

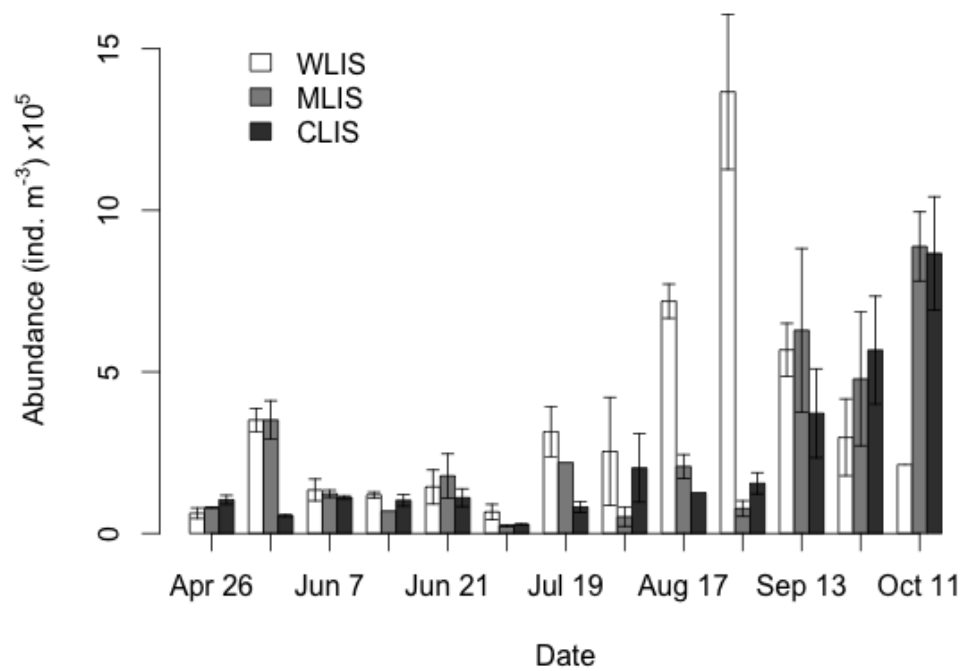


Figure 7. Mean (\pm range) abundance of mesozooplankton and micrometazoa (except polychaetes) (ind. m⁻³) for all sites and sampling dates during 2011.

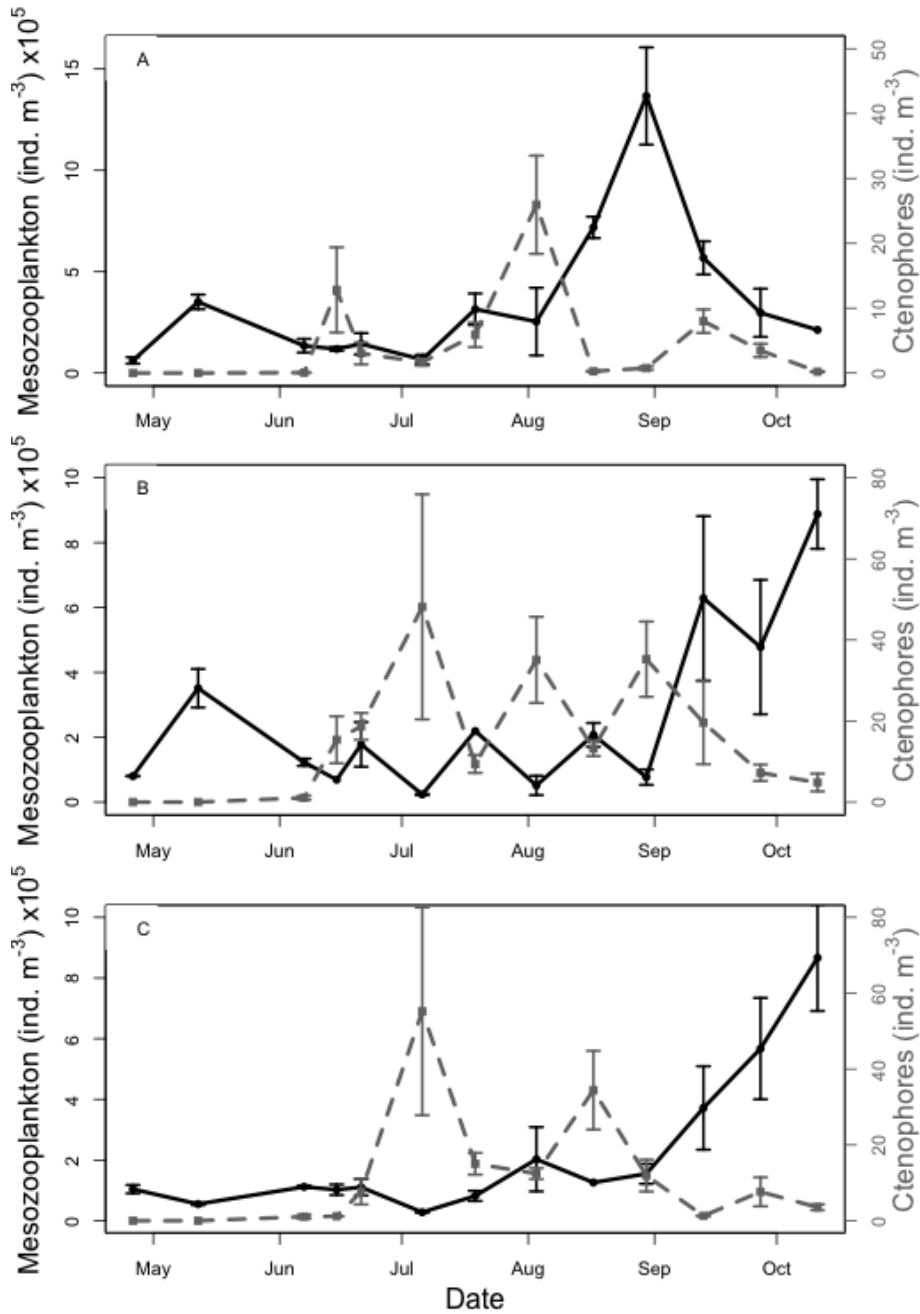


Figure 8. Mean abundance (ind. m^{-3}) of mesozooplankton and micrometazoa (except polychaetes; $\times 10^5$; solid black lines) and *M. leidy*i (dashed gray lines) for all WLIS (A), MLIS (B), and CLIS (C) for all sampling dates during 2011. Error bars are \pm range for mesozooplankton and \pm s.e. for ctenophores.

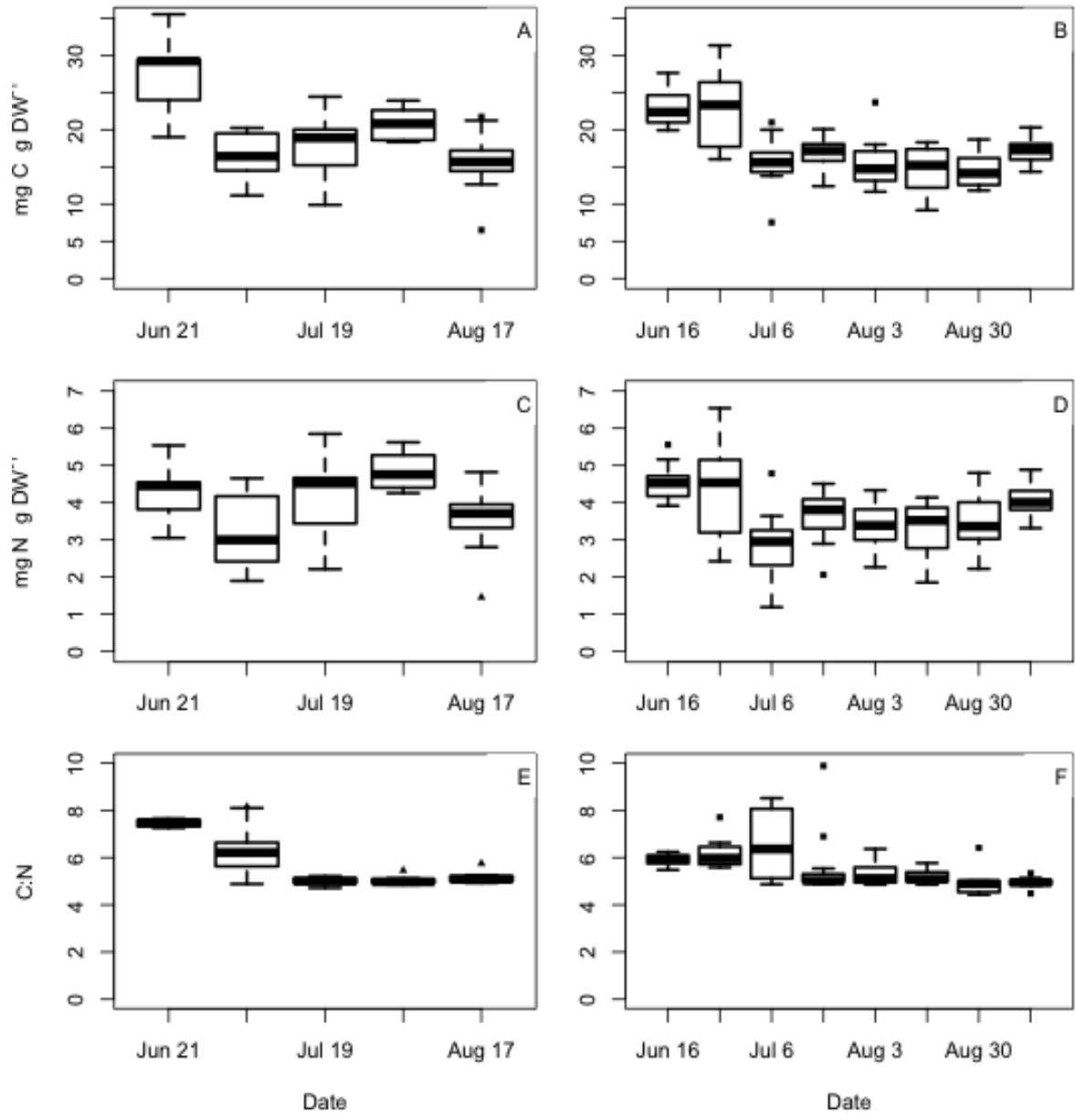


Figure 9. Ctenophore body composition (mgC gDW⁻¹ A, B; mgN gDW⁻¹, C, D) and body composition ratios (C:N; E, F) at WLIS (A, C, E) and CLIS (B, D, F) for the 2011 sampling season.

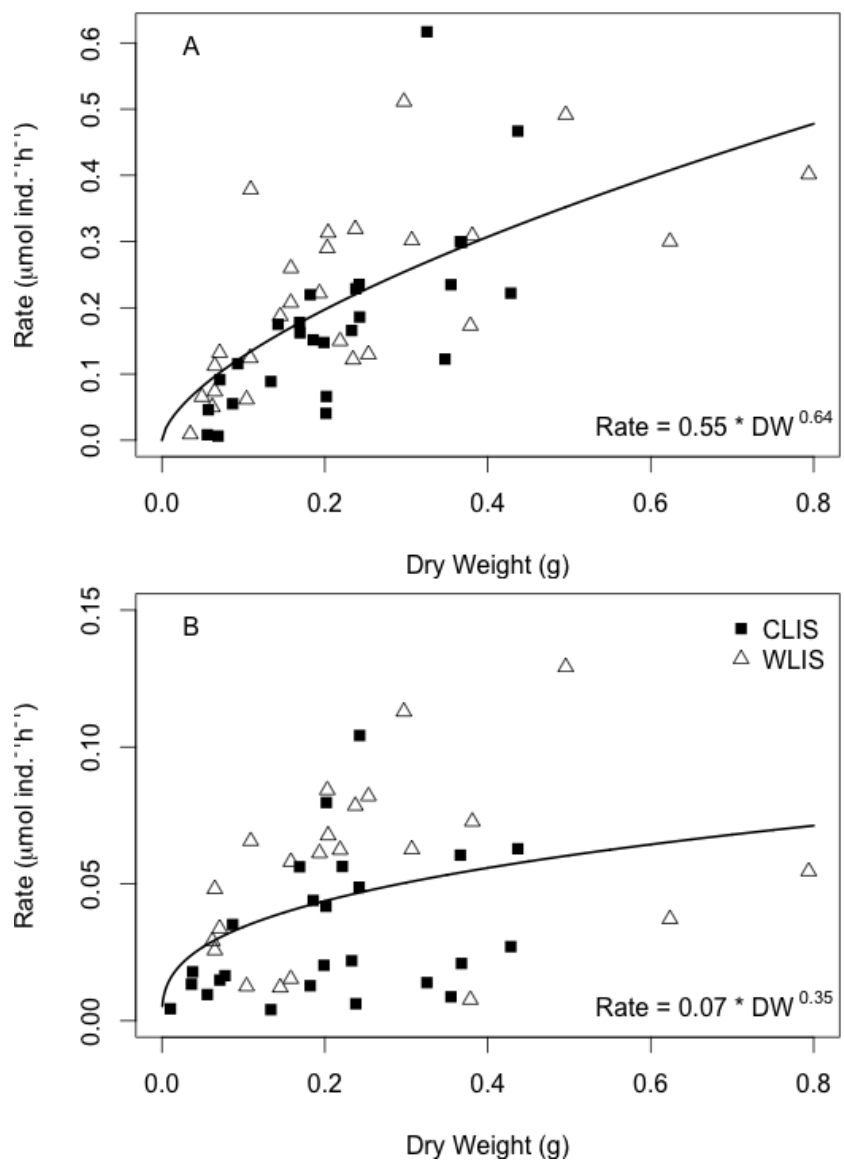


Figure 10. Release rates of NH_4^+ (A) and PO_4^{-3} (B) for individual *M. leidyi* plotted versus dry weight. $\text{Rate} = a \text{DW}^b$ (Eq. 1) was fit to each data set.

TABLES

Table 1. Size-class assignments for *M. leidy*. All ctenophores were measured to the nearest tenth of a centimeter in the field, and nearest half-centimeter for laboratory methods.

Field	Laboratory
< 1.0 cm	0.5 cm
1-1.9 cm	1, 1.5 cm
2-2.9 cm	2, 2.5 cm
3-3.9 cm	3, 3.5 cm
4-4.9 cm	4, 4.5 cm
5-5.9 cm	5, 5.5 cm
6-6.9 cm	6, 6.5 cm
7-7.9 cm	7, 7.5 cm
8-8.9 cm	8, 8.5 cm
> 9.0 cm	> 9.0 cm

Table 2. Surface temperature (°C), salinity, and dissolved oxygen (mg L⁻¹) data for all sampling sites and dates in 2011 (ND = no data).

Date	Site	Temp. (°C)	Salinity	DO (mg L ⁻¹)
4/18/11	CLIS	6.7	42.8	13.13
4/26/11	CLIS	7.6	24.0	13.62
	MLIS	7.8	24.6	14.50
	WLIS	8.8	23.0	9.34
5/12/11	CLIS	8.9	24.7	ND
	MLIS	11.0	24.4	11.80
	WLIS	11.4	23.8	11.60
5/24/11	CLIS	11.3	24.6	12.58
6/7/11	CLIS	16.0	24.1	8.55
	MLIS	17.3	23.9	9.60
	WLIS	16.3	23.1	9.95
6/15/11	CLIS	16.7	24.4	9.75
	MLIS	17.0	24.2	9.15
	WLIS	17.7	23.6	9.50
6/21/11	CLIS	18.5	23.6	8.95
	MLIS	20.3	23.8	10.58
	WLIS	19.6	23.0	10.38
7/6/11	CLIS	22.3	24.1	4.47
	MLIS	22.3	23.7	7.88
	WLIS	20.1	23.4	7.38
7/19/11	CLIS	23.5	24.8	5.88
	MLIS	21.6	24.2	5.37
	WLIS	21.4	24.1	4.22
8/3/11	CLIS	23.1	25.7	3.17
	MLIS	23.5	24.5	6.50
	WLIS	22.7	24.4	4.88
8/17/11	CLIS	22.6	25.6	5.55
	MLIS	22.3	25.6	5.53
	WLIS	22.6	24.0	4.23
8/30/11	CLIS	22.6	24.7	6.89
	MLIS	22.3	25.9	7.85
	WLIS	22.4	23.7	5.54
9/13/11	CLIS	22.7	23.9	7.02
	MLIS	22.7	23.4	7.33
	WLIS	22.3	21.3	5.58
9/27/11	CLIS	22.0	24.4	7.29

	MLIS	22.1	24.4	6.33
	WLIS	21.7	23.3	5.80
10/11/11	CLIS	20.2	24.5	6.72
	MLIS	20.1	24.7	6.04
	WLIS	19.8	23.0	5.56

Table 3. Surface temperature ($^{\circ}\text{C}$), salinity, and dissolved oxygen (mg L^{-1}) data for all sampling sites and dates in 2012 (ND = no data).

Date	Site	Temp. ($^{\circ}\text{C}$)	Salinity	DO (mg L^{-1})
5/3/12	CLIS	10.4	26.4	9.16
	MLIS	11.3	25.9	8.36
	WLIS	11.9	25	9.2
5/10/12	MLIS	13	25.6	10.44
	WLIS	13	25.1	8.71
5/23/12	CLIS	14.3	26.1	8.23
	MLIS	15.3	25.8	8.1
	WLIS	16.5	24.7	8.18
6/5/12	CLIS	15.8	26.1	13.22
	MLIS	16.8	25.8	7.23
	WLIS	18	24.8	7.52
6/19/12	CLIS	18.5	26.2	6.82
	MLIS	19.4	25.7	8.18
	WLIS	20.1	24.5	6.28
7/3/12	CLIS	22.6	26.1	5.92
	MLIS	20.2	25.9	6.03
	WLIS	20.8	25.4	5.52
7/17/12	CLIS	24.1	26	6.68
	MLIS	23.9	24.5	6.37
	WLIS	23.2	25.5	7.1
7/31/12	MLIS	21.9	26.5	5.69
	WLIS	23.2	25.7	5.3
8/14/12	CLIS	25.3	26.8	6.46
	MLIS	24.2	26.3	6.57
	WLIS	24	26.2	5.29
8/29/12	CLIS	23.6	27.5	6.97
	MLIS	23.6	27.2	5.89
	WLIS	24.5	26.5	5.55
9/11/12	CLIS	23	27.6	7.02
	MLIS	24	27.5	7.15
	WLIS	23.4	26.6	5.93
9/25/12	CLIS	21.5	27.7	6.7
10/18/12	CLIS	18	27.8	ND
	MLIS	18.1	27.7	ND
	WLIS	16.7	25.9	4.86

Table 4. Rates of carbon ($\mu\text{mol C m}^{-3} \text{ day}^{-1}$) and nitrogen ($\mu\text{mol N m}^{-3} \text{ day}^{-1}$) released to the ecosystem between maximum *M. leidyi* biovolume and post-bloom stocks at both WLIS and CLIS in 2011.

Site	Element	Bloom Peak ($\mu\text{mol m}^{-3}$)	Post-bloom ($\mu\text{mol m}^{-3}$)	Time	Release ($\mu\text{mol m}^{-3} \text{ day}^{-1}$)
<i>WLIS</i>	C	2912.76	8.29	14 days	207.46
	N	579.89	1.60		41.31
<i>CLIS</i>	C	1290.84	69.25	56 days	21.81
	N	238.63	14.02		4.01

Table 5. Parameter estimates for all nutrient-release models (Eq. 1, 2, 3), where *Rate* is the release rate of ammonium or phosphate in $\mu\text{mol ind}^{-1} \text{h}^{-1}$, *DW* is the dry weight of the individual in grams, *T* is the temperature in degrees Celsius, *F* is the mesozooplankton concentration in ind. m^{-3} , and *a*, *b*, *c* and *d* are constants.

Nutrient	Eq.1: $\text{Rate} = a DW^b$		Eq.2: $\text{Rate} = a DW^b c^T$			Eq.3: $\text{Rate} = a DW^b c^T d^F$			
	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>
NH_4^+	0.551	0.638	47.94	0.726	0.821	51.77	0.752	0.822	1.000
PO_4^{3-}	0.077	0.352	389.3	0.618	0.689	535.8	0.579	0.674	1.000

Table 6. AIC criteria for all fitted nutrient-release models (Eq. 1, 2, 3), where *Rate* is the release rate of ammonium or phosphate in $\mu\text{mol ind}^{-1} \text{h}^{-1}$, *DW* is the dry weight of the individual in grams, *T* is the temperature in degrees Celsius, *F* is the mesozooplankton concentration in ind. m^{-3} , and *a*, *b*, *c* and *d* are constants.

Nutrient	Model	AIC	Δ AIC	W_i
NH_4^+	$\text{Rate} = a DW^b c^T$	-95.654	0.000	0.686
	$\text{Rate} = a DW^b c^T d^F$	-94.036	1.618	0.306
	$\text{Rate} = a DW^b$	-86.801	8.853	0.008
PO_4^{3-}	$\text{Rate} = a DW^b c^T$	-222.749	0.000	0.609
	$\text{Rate} = a DW^b c^T d^F$	-221.859	0.890	0.391
	$\text{Rate} = a DW^b$	-196.243	26.506	0.000

Table 7. Maximum daily nutrient release ($\mu\text{mol day}^{-1}$), daily turnover ($\% \text{ day}^{-1}$), and turnover time (days) estimates for NH_4^+ and PO_4^{3-} in WLIS and CLIS in 2011.

Site	Nutrient	Release ($\mu\text{mol m}^{-3} \text{ day}^{-1}$)	Turnover ($\% \text{ day}^{-1}$)	Time to Turnover (days)
<i>WLIS</i>	NH_4^+	48.59	3.20	31.24
	PO_4^{3-}	13.41	0.57	176.29
<i>CLIS</i>	NH_4^+	37.17	13.76	7.27
	PO_4^{3-}	15.55	3.88	25.79