NYSG Completion Report Instructions & Required Format

Report Written By: Darcy J. Lonsdale, Christopher J. Gobler, David Rawitz, and Laura M. Treible Date: May 12, 2014

Portions of this report have been modified from the M.S. thesis by L.M. Treible (2013) or from a manuscript currently in review (Treible, Lonsdale, and Gobler) (see C6). Additional information is from the M.S. thesis in preparation by D. Rawitz (see D2 for each research focus).

A. Project Number and Title:R/CE-31-NYCT The Influence of Gelatinous Zooplankton on Nutrient Cycles, Hypoxia, and Food webs across Long Island Sound

B. Project Personnel: Darcy J. Lonsdale and Christopher J. Gobler, Project Investigators; Laura M. Treible and David Rawitz, NYSG Scholars; Lee Holt, technician.

C. Project Results:

C1. Meeting the Objectives:

Objective 1: Conduct field studies on the pelagic population cycles of gelatinous zooplankton

Field sampling began in May and continued through October in both 2011 and 2012. 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). To determine abundances of gelatinous zooplankton, oblique net tows were performed at each station with 202-μm and 1000-μm mesh nets fitted with a flowmeter (n=2 for each). Tows were conducted for 2-4 minutes to minimize net clogging or damage to gelatinous zooplankton. Even though other gelatinous zooplankton species occur in Long Island Sound, only the ctenophore *Mnemiopsis leidyi* was collected during the sampling period. All ctenophores were placed into a graduated cylinder to measure the total biovolume (ml) for each tow. Each ctenophore in the sample was measured for length with a graduated petri dish to the nearest tenth of a cm. If the total biovolume greatly exceeded 500 ml, a subsample (400-500ml) was taken from the well-mixed sample to perform the counts and measurements. Abundance (ind. m^{-3}) and biovolume (mL m^{-3}) were calculated by combining the individual gelatinous zooplankton counts (individuals) and biovolumes (mL) with the calculated volume of seawater sampled (m^{-3}).

In 2011, ctenophore biovolume was below 1.0 mL m^{-3} in May and early June (Figure 1). 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 remained low for the rest of the sampling season. Biovolumes of *M. leidyi* were markedly lower in 2012, remaining below 1 mL m^{-3} at WLIS throughout the sampling season (Figure 2). Minor increases in biovolume occurred at MLIS and CLIS in early July and again at CLIS in late August (7.49 ± 1.69 mL m^{-3}), but biovolumes remained below 3 mL m^{-3} at MLIS and CLIS for the rest of the sampling dates.

Objective 2: Quantify ingestion rates and mortality impacts of gelatinous zooplanktivores on mesozooplankton and micrometazoa

In order to determine ingestion and mortality rates of ctenophores on zooplankton additional oblique tows were performed at each site to determine mesozooplankton and micrometazoan composition and abundance. In 2011, net tows were performed with a 0.5-m diameter, 64-μm mesh net (n=2) and in 2012 additional tows were performed using a 202-μm mesh net (n = 2) for comparison with previous studies of zooplankton in LIS (e.g., Capriulo et al. 2002). Upon completion of each tow, contents of the cod end were rinsed onto a 64-μm sieve and preserved. Zooplankton samples were identified and enumerated to the lowest taxonomic level.

In 2011, coincident with increases in adult ctenophores, copepod abundance decreased, which in turn may have released microplankton from predation pressure as the latter’s numbers increased indicating a trophic cascade

(Figures 3a-c). Such population relationships have been previously documented in Great South Bay (McNamara et al., 2013). Preliminary results from cross-correlation analysis indicated a positive correlation between adult *M. leidyi* and microplankton at the three sites. In contrast to 2011, there was no correlation between the above-described abundances in 2012 (Fig. 3d-f). In 2012, ctenophore predation on copepods was significantly lower than in 2011 (see below), hence ctenophore adult and microplankton populations did not demonstrate any correlations.

Estimates of ctenophore consumption rates (based on gut-contents and estimates of digestion time) of copepods highlight the interannual variation of the impact that ctenophores on zooplankton in LIS. In 2011 the consumption rate of copepods by the ctenophore population averaged ~ 3,117 m^{-3} d^{-1} in the WLIS and 5,308 m^{-3} d^{-1} in the CLIS, while in 2012, the average rates were only 8.0 m^{-3} d^{-1} and 35.5 m^{-3} d^{-1}, respectively. The predatory impacts of ctenophores on the net growth rate of prey populations were also variable between stations and prey species. For example, the daily predation rates on the copepods *Acartia tonsa* and *Oithona similis*. were compared to estimates of their daily population growth (the latter data obtained from Huntley and Lopez, 1992). In CLIS in 2011, *M. leidyi* may have consumed up to 67.2% of the daily growth of adults and copepodites of *A. tonsa,* 13.5% of their nauplii but only 2.6% of *O. similis* adults and copepodites. In the WLIS, the highest estimated ctenophore consumption was 13.2% of the daily growth of *A. tonsa*, 5.6% of nauplii, and 6.8 % of *O. similis*.

Objective 3: Estimate the oxygen consumption rates of gelatinous zooplankton

Given the substantial lack of ctenophore consumers in LIS, the probable fate of the dead ctenophores is bacterial decomposition, and thus the collapse of a ctenophore bloom could potentially promote localized hypoxic events. Using the carbon decomposition rates for dead ctenophores (see below), and assuming an elemental ratio of 138 O_2: 106 C, when ctenophores died, bacteria could have depleted 270.1 μmol O_2 m^{-3} day^{-1} in WLIS and 28.4 μmol O_2 m^{-3} day^{-1} in CLIS. In LIS, total bacterial respiration ranges from 0.3 to 1.5 mmol O_2 m^{-3} $hour^{-1}$ (Goebel and Kremer 2006). Thus, in the Western Sound, bacterial respiration from decaying ctenophore biomass would represent less than 5% of total bacterial respiration, and in the Central Sound this contribution would be even less. Although these numbers are relatively small percentages in relation to overall bacterial respiration, any additional oxygen depletion from decaying ctenophores could contribute to the summer hypoxia that occurs annually in LIS.

Ctenophores may also contribute to oxygen depletion in the LIS *via* their metabolism and respiration. The data on carbon content of ctenophores is being utilized to estimate their individual respiration rates (ml O_2 d^{-1}). The conversion of carbon content to respiration rate (RR) according to Purcell (2009) is as follows: $\mathrm{Log_{10}RR}$ (ml O_2 d^{-1}) = 0.871 * $\mathrm{Log_{10}}$ (g C) + 1.686. Total oxygen consumption by larval (< 0.5 cm) and adult ctenophores (mL O_2 m^{-3} d^{-1}) will then be determined based on total abundance. At the present time, the data are still being worked up.

Objective 4: Quantify the reservoir of nutrients held in gelatinous zooplankton and nutrient-release rates of living and decomposing animals

Reservoir of nutrients held by ctenophores

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. (Due to the low field abundances of adult organisms throughout 2012, no sampling dates provided sufficient numbers to collect ctenophores for elemental analysis or nutrient-release experiments). Individual ctenophores were measured and weighed (wet-weight). Dry-weights were determined after drying for 24 hours at 60°C. Each dried sample was then 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. The elemental content of individuals (mg ind^{-1}) was normalized to dry weight (mg gDW^{-1}). A relationship was determined ($DW = 0.0074(length)^{2.13}$) between length and dry weight which allowed for estimation of total field population dry weight (gDW m^{-3}) from 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.

The elemental composition of ctenophores averaged 19.4 ± 5.4 mgC gDW^{-1} and 4.0 ± 1.1 mgN gDW^{-1} in WLIS and 17.4 ± 4.3 mgC gDW^{-1} and 3.7 ± 0.9 mgN gDW^{-1} in CLIS (Fig. 4). Carbon:nitrogen ratios of ctenophores 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 ctenophore size.

After combining elemental analysis results with biomass estimates, at the highest biovolume of ctenophores in WLIS in 2011 (August 3), the population sequestered about 2913 μmol C m^{-3} and 580 μmol N m^{-3}. The CLIS had the largest biovolume in mid-July, and contained 1291 μmol C m^{-3} and 239 μmol N m^{-3}. The ctenophore post-bloom occurred in mid-August and September at WLIS and CLIS, respectively. At this time, in WLIS, ctenophores held only ~8 μmol C m^{-3} and 1.6 μmol N m^{-3}. The population decline at WLIS was abrupt (14 d) indicating an average biomass loss of 207 μmol C m^{-3} day^{-1} and 41 μmol N m^{-3} day^{-1}. In CLIS, post-bloom populations held 69 μmol C m^{-3} and 14 μmol N m^{-3}. The decline in the population from peak biovolumes at CLIS occurred gradually over 56 days. Although rates of biomass loss and decomposition would generally slow as the ctenophore population declined, average rates of biomass loss would be about 22 μmol C m^{-3} day^{-1} and 4 μmol N m^{-3} day^{-1}.

Nutrient-release impacts

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. 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. Dissolved nutrient samples (10ml, n=2) were obtained from each container every three hours for a total of 12 hours. After the 12-h 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.

In 2011, ctenophores in WLIS released ammonium at rates from about 0.006 to 0.62 μmol ind^{-1} h^{-1}, and phosphate at rates from about 0.004 to 0.13 μmol ind^{-1} h^{-1}. 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 and their relationship to release rates were also investigated. The combined effect of temperature and ctenophore weight more accurately described the nutrient-release rates than the combined effect of weight, temperature, and food concentration or weight alone.

In WLIS, the maximum turnover of both ammonium and phosphate by the ctenophore population likely occurred on August 3, when its biovolume was at a maximum. Using a rate to body weight relationship where $Rate = a\ DW^{b}$ and $Rate$ is the nutrient release rate in μmol ind^{-1} h^{-1}, DW the dry weight of the individual in grams, and *a*, and *b* are constants used to fit the relationship to the data, the total population of *M. leidyi* at peak abundance could have released ammonium and phosphate of up to 49 μmol m^{-3} day^{-1} and 13 μmol m^{-3} day^{-1}, respectively. Comparing these rates to nutrient pools in WLIS (data not presented), the total population could have turned over up to 3.20% day^{-1} of ammonium and 0.57% day^{-1} of phosphate.

In CLIS, maximum daily population release of ammonium and phosphate by ctenophores would have occurred on July 6 when the total *M. leidyi* population could have released ammonium and phosphate of up to 37.17 μmol m^{-3} day^{-1} and 15.55 μmol m^{-3} day^{-1}, respectively. 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. In LIS in the summer, nitrogen pools are turned over several times daily by phytoplankton. It would take peak abundances of *M. leidyi* in WLIS over 31 days to turn over the ammonium pool at that site. Due to lower stocks of nitrogen in the CLIS, it would take about 7 days for the maximum abundance of CLIS ctenophores to turn over the ammonium pool. 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.

Estimating an average rate of primary production in the summer from oxygen evolution (430 mmol O_2 m^{-2} d^{-1}; Goebel et al. 2006), an oxygen to carbon ratio of 138 O_2:106 C, and assuming that the elemental composition of phytoplankton conformed to the Redfield ratio of 106 C:16 N:1 P, the amounts of ammonium and phosphate released by peak *M. leidyi* populations could support <1% of daily primary production in LIS (Schneider 1989).

Objective 5: Model the ecosystem-wide impacts of gelatinous zooplankton on nutrient cycles, hypoxia, and food webs across LIS.

Portions of this objective have been addressed (see the above regarding evidence for a trophic cascade and nutrient turnover rates) while the contribution of ctenophores to hypoxia has yet to be thoroughly addressed.

C2. Scientific Abstract: In most marine environments, gelatinous zooplankton play a significant role in the food web dynamics of the water column. The “top-down” influences of gelatinous zooplankton have been the primary focus of many studies, but there is increasing evidence they may also have important “bottom-up” impacts on primary productivity through nutrient sequestration and/or excretion. We studied both these aspects of the ctenophore *Mnemiopsis leidyi*, the most abundant gelatinous zooplankton in Long Island Sound (LIS) at three stations from the central basin to the western basin during 2011-2012. One striking aspect of this study was the large interannual variation in ctenophore abundance with 2011 experiencing relatively high abundances while in 2012 the peak abundances were on the order of a magnitude lower. In 2011, ctenophore and microplankton abundances were positively correlated, suggesting a trophic cascade brought about by the reduction of mesozooplankton from ctenophore predation. The predatory impacts of ctenophores on their prey, such as copepods, were also variable between stations and among prey. For example, the daily predation rates by the ctenophore population were compared to estimates of daily population growth for the copepods *Acartia tonsa* and *Oithona similis* (the latter rates obtained from Huntley and Lopez, 1992). In 2011 in the central basin at peak ctenophore abundance, *M. leidyi* may have consumed up to 67.2% of the daily production of adults and copepodites of *A. tonsa*, 13.5% of their nauplii but only between 0% to 2.6% of *O. similis* adults and copepodites. In the WLIS, the highest estimated rate of ctenophore consumption was lower for *A. tonsa* (13.2%) and nauplii (5.6%) but 6.8 % for *O. similis.*

In 2011, to address the “bottom-up” role of ctenophores, the chemical content and nutrient remineralization rates (i.e., NH_4^+, PO_4^{3-}) of *M. leidyi* were quantified. Ctenophores remineralized NH_4^+ and PO_4^{3-} at rates up to 0.62 μmol ind^{-1} h^{-1} and 0.13 μmol ind^{-1} h^{-1}, respectively, and were capable of large releases of nutrients upon the demise of the bloom (48.59 μmol m^{-3} $day^{-1}$of NH_4^+ and 13.41 μmol m^{-3} day^{-1} of PO_4^{3-}). However in both cases, these rates were not in quantities sufficient to support a sizeable fraction of primary production (< 1 % d^{-1}) when compared to the background concentrations of the nutrients. Collectively, this study suggests that gelatinous zooplankton may make only a minor contribution to nutrient pools in highly eutrophic, urban estuaries.

Given the substantial lack of ctenophore consumers in LIS, the likely fate of the dead ctenophores is bacterial decomposition, and thus the collapse of a ctenophore bloom could potentially exacerbate localized hypoxic

events. Using the carbon decomposition rates for dead ctenophores (207.5 μmol C m^{-3} day^{-1} in WLIS and 21.8 μmol C m^{-3} day^{-1} in CLIS), and the elemental ratio of 138 O_2: 106 C, when ctenophores died, bacteria could deplete 270.1 μmol O_2 m^{-3} day^{-1} in WLIS and 28.4 μmol O_2 m^{-3} day^{-1} in CLIS. In LIS, total bacterial respiration ranges from 0.3 to 1.5 mmol O_2 m^{-3} $hour^{-1}$ (Goebel and Kremer 2006). Thus, in the Western Sound, bacterial respiration from decaying ctenophore biomass would represent less than 5% of total bacterial respiration, and in the Central Sound this contribution would be even less. Although these numbers are relatively small percentages in relation to overall bacterial respiration, any additional oxygen depletion from decaying ctenophores could contribute to the summer hypoxia that occurs annually in LIS.

References

Capriulo, G.M., G. Smith et al. (2002) The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. Hydrobiologia 475/476: 263-333.

Goebel N.L., J.N. Kremer, C.A. Edwards (2006) Primary production in Long Island sound. Estuaries and Coasts 29: 232-245.

Huntley, M.E., M.D.G. Lopez (1992) Temperature-dependent production of marine copepods: A global synthesis. American Naturalist 140: 201-242.

McNamara, M.E., D.J. Lonsdale, R.M. Cerrato (2013) Top-down control of mesozooplankton by adult *Mnemiopsis leidyi* influences microplankton abundance and composition enhancing prey conditions for larval ctenophores. Estuarine, Coastal and Shelf Science 133: 2-10

C3. Problems Encountered: None

C4. New Research Directions: The research project remained essentially the same as proposed.

C5. Interactions:

1. Dr. James P. Browne, Conservation Biologist for the Town of Hempstead, Department of Conservation and Waterways contacted us regarding this study as he has been looking into the correlations between nutrients and various marine species, including ctenophores, on the south shore and north shores of Long Island, including Long Island Sound. He was sent a PDF of Ms. Treible's thesis.

2. Dr. Thomas F. Ihde, Fisheries/Ecosystem Modeler with the National Marine Fisheries Service, NOAA Chesapeake Bay Office also requested information on our project and was interested in the estimates of nutrient regeneration by ctenophores. He also was sent Ms. Treible's thesis.

C6. Presentations and Publications:

Presentations:

1. Treible, L.M., D.J. Lonsdale, and C.J. Gobler, Long Island Sound Research Conference, "The role of ctenophores in nutrient regeneration in Long Island Sound", Port Jefferson, NY, 2013.
Abstract: 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 significant rates of nutrient regeneration. During 2011, the population biomass of *M. leidyi* was monitored and nutrient regeneration rates (i.e., NO_3^-, PO_4^{3-}) were calculated based on laboratory experiments.

Preliminary results from 2011 indicate that ctenophores in LIS have the potential, at times, to overturn substantial amounts of these nutrients daily. However, in 2012, the ctenophore bloom never occurred suggesting that rates of nutrient regeneration by gelatinous zooplankton also can vary widely on an interannual basis, complicating the assessment of the nutrient budget for LIS.

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2. Treible, L.M., D.J. Lonsdale, and C.J. Gobler, Aquatic Sciences Meeting, "The role of ctenophores in nutrient regeneration in Long Island Sound", New Orleans, LA, 2013 Abstract: 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 significant rates of nutrient regeneration. During 2011, the population biomass of *M. leidyi* was monitored and nutrient regeneration rates (i.e., NO_3^-, PO_4^{3-}) were calculated based on laboratory experiments. Preliminary results from 2011 indicate that ctenophores in LIS have the potential, at times, to overturn substantial amounts of these nutrients daily. However, in 2012, the ctenophore bloom never occurred suggesting that rates of nutrient regeneration by gelatinous zooplankton also can vary widely on an interannual basis, complicating the assessment of the nutrient budget for LIS.

3. Treible, L.M., D.J. Lonsdale, and C.J. Gobler. The Role of Ctenophores in Nutrient Regeneration in Long Island Sound, Long Island Marine Habitat (MAR 303-S) Graduate Student Presentations, Southampton, NY

Other Outreach:

Treible, L.M. Center for Talented Youth (CTY) Science and Technology Series; led the students in plankton tows and showed them various species under the microscope, 2012

Treible, L.M., D.J. Lonsdale, D. Rawitz. "VIP" Cruise on the R/V Seawolf Stony Brook University President, members of the President's council, and News 12 Network owner; performed plankton tows and showed them organisms under a microscope

Manuscript Submitted:

Treible, L.M., D.J. Lonsdale, and C.J. Gobler. The role of ctenophores in nutrient regeneration in Long Island Sound. Mar. Ecol. Prog. Ser. (in revision)

D. Accomplishments:

D1. Impacts & Effects: This study has addressed some fundamental data gaps on the role of ctenophores in the planktonic food web in LIS, including the predatory impact of ctenophores on zooplankton and nutrient cycling, including nitrogen. Nitrogen has been the focus of numerous experimental and modeling efforts as it relates to hypoxia in the Long Island Sound. The data generated by our research may also be of interest to others studying the ecology of this ubiquitous group of marine planktonic predators. Numerous published studies have indicated that gelatinous zooplankton may have a substantial impact on rates of primary productivity via nutrient regeneration. Our study, albeit based on limited interannual sampling, concluded differently, in that in LIS gelatinous zooplankton make only a minor contribution to nutrient pools in this eutrophic estuary. We anticipate that the results of this study will also useful for resource managers and ecosystem modelers in that it will provide information on the potential contribution of ctenophores to community oxygen demand generated by the living ctenophores and bacterial decomposition of decaying ctenophore biomass. As described above, we have already received requests for our data from a resource manager and an ecosystem modeler.

D2. Scholar(s) & Student(s) Status:

1. Laura M. Treible, M.S. degree May 2013
   "The Role of the Ctenophore *Mnemiopsis leidyi* on Nutrient Cycling in Long Island Sound, NY", Stony Brook University, 40 p.

   Current employment: Instructor, University of North Carolina Wilmington, undergraduate biology laboratory (BIO105), and laboratory technician for Rob Condon, a gelatinous zooplankton ecologist. Laura will also be pursuing her Ph.D. this fall at UNC in this area of study.

2. David Rawitz, M.S. degree expected August 2014
   "On the Impacts of the Lobate Ctenophore *Mnemiopsis leidyi* to Zooplankton Community Dynamics in the Long Island Sound"

D3. Volunteers:

Lauren VanSicklin, undergraduate from Delaware Valley College, assisted in the field and laboratory between May and Nov 2012.

D4. Patents: None

E. Stakeholder Summary:

In most marine environments, gelatinous zooplankton play a significant role in the food web dynamics of the water column. Large population increases and subsequent crashes of these animals are common in coastal waters. Gelatinous zooplankton, including ctenophores, are effective top predators and their voracious feeding has consequences that can cascade through the planktonic food web. And although this "top-down" impact of gelatinous zooplankton has been the primary focus of many studies, there is increasing evidence they may also have an important "bottom-up" impact on primary productivity through nutrient sequestration and/or excretion. We studied both these aspects of the ctenophore *Mnemiopsis leidyi*, the most abundant gelatinous zooplankton in Long Island Sound (LIS) during 2011-2012. One striking aspect of this study was the large interannual variation in ctenophore abundance with 2011 experiencing relatively high abundances while in 2012 the peak abundances were an order of a magnitude lower than the previous year. In turn, the predatory impacts on their prey, such as copepods, were also highly variable between the two years.

In 2011, to address the "bottom-up" role of ctenophores in LIS we quantified the chemical content of the ctenophore population and their excretion rates of nutrients required by phytoplankton (i.e., nitrogen and phosphate). The chemical content of the ctenophores indicates how much of various nutrients can be released back into the environment upon population demise while excretion rates measures ctenophore effects on nutrient cycles while the population is thriving. Our findings indicated that neither process provided nutrients in sufficient quantities to support a significant fraction of primary production in LIS ($< 1\% \ d^{-1}$) when compared to the background concentrations of nutrients. Collectively, this study suggests that gelatinous zooplankton may make only a minor contribution to nutrient pools in highly eutrophic estuaries such as LIS.

F. Pictorial: Previously provided to the New York Sea Grant Institute.

Figures

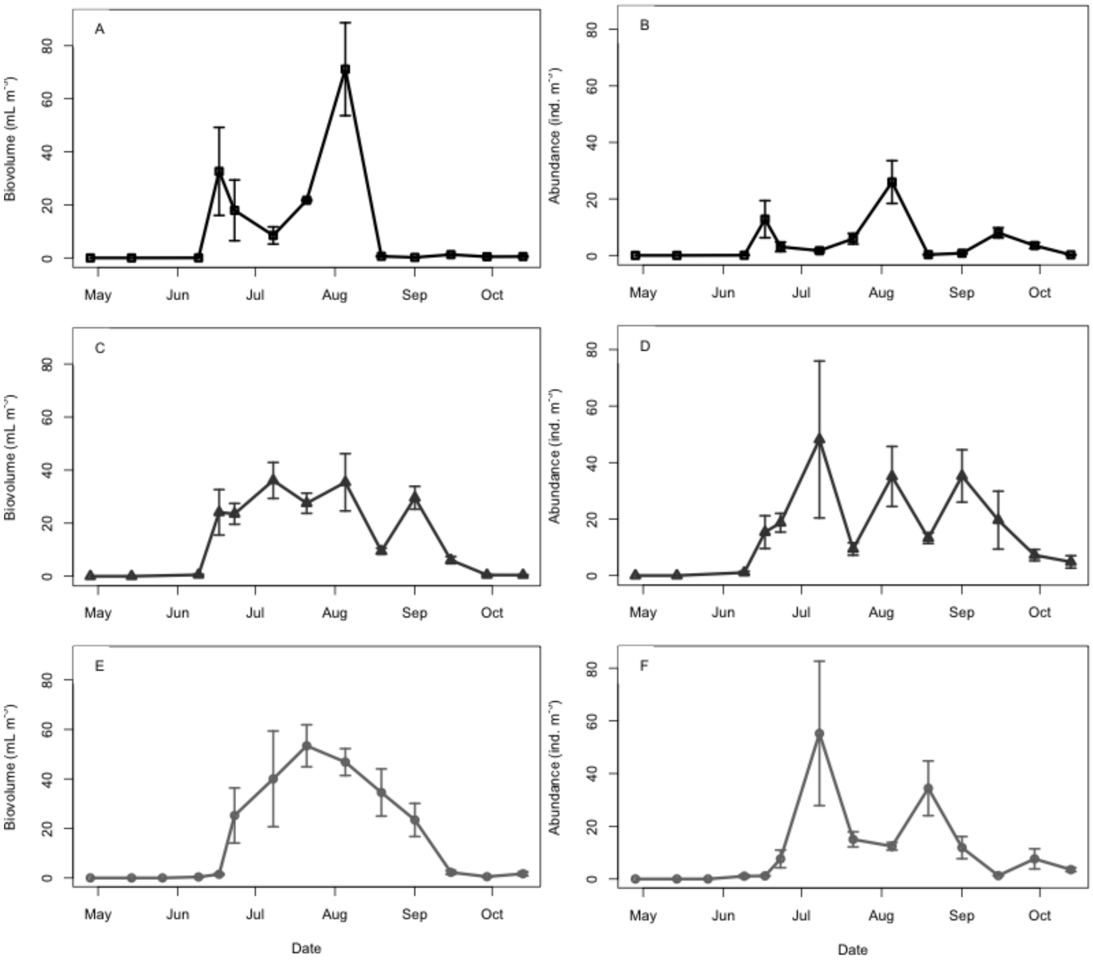


Figure 1**.** Ctenophore biovolumes (±1 s.e.; mL m^{-3}; A, C, E) and abundances (±1 s.e.; ind. m^{-3}; B, D, F) at WLIS (A, B), MLIS (C, D), and CLIS (E, F) during 2011.

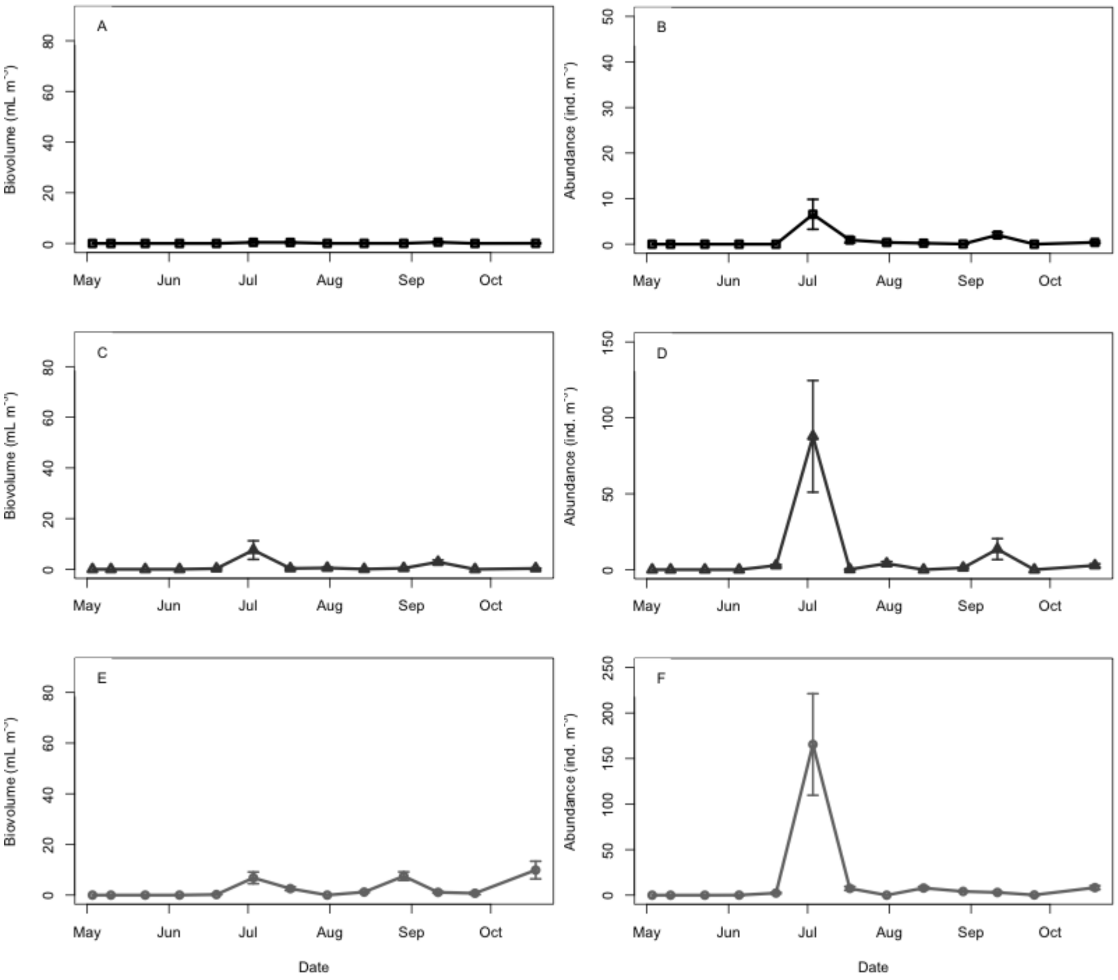
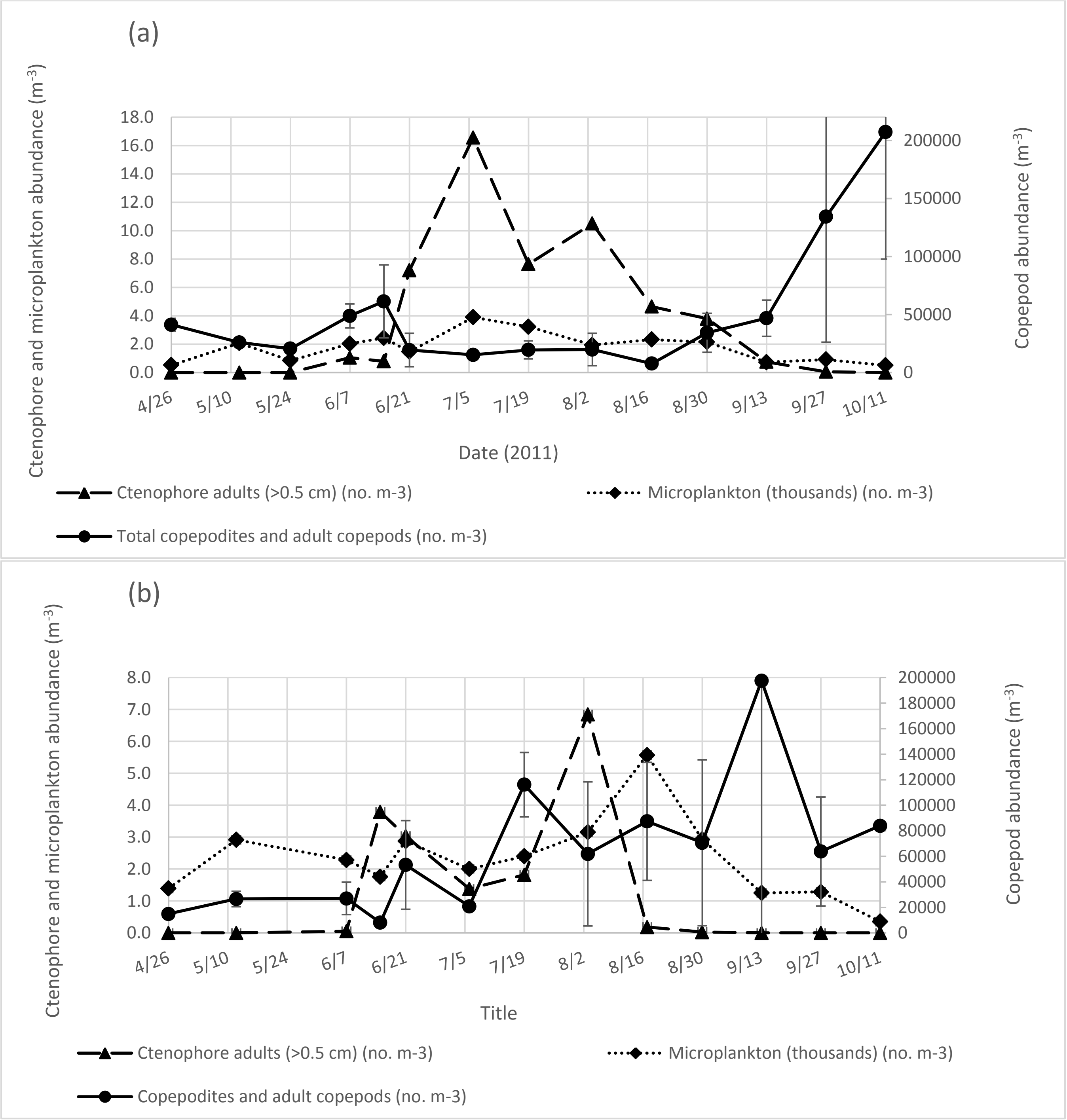
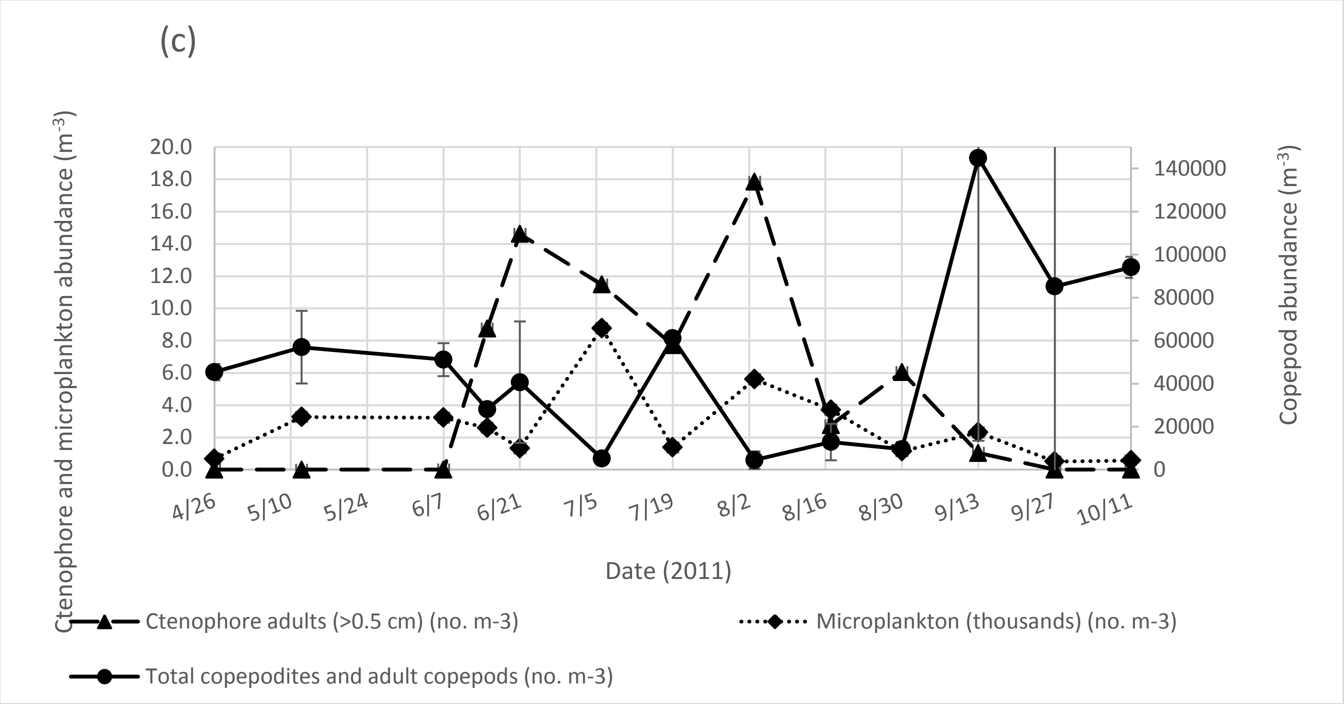
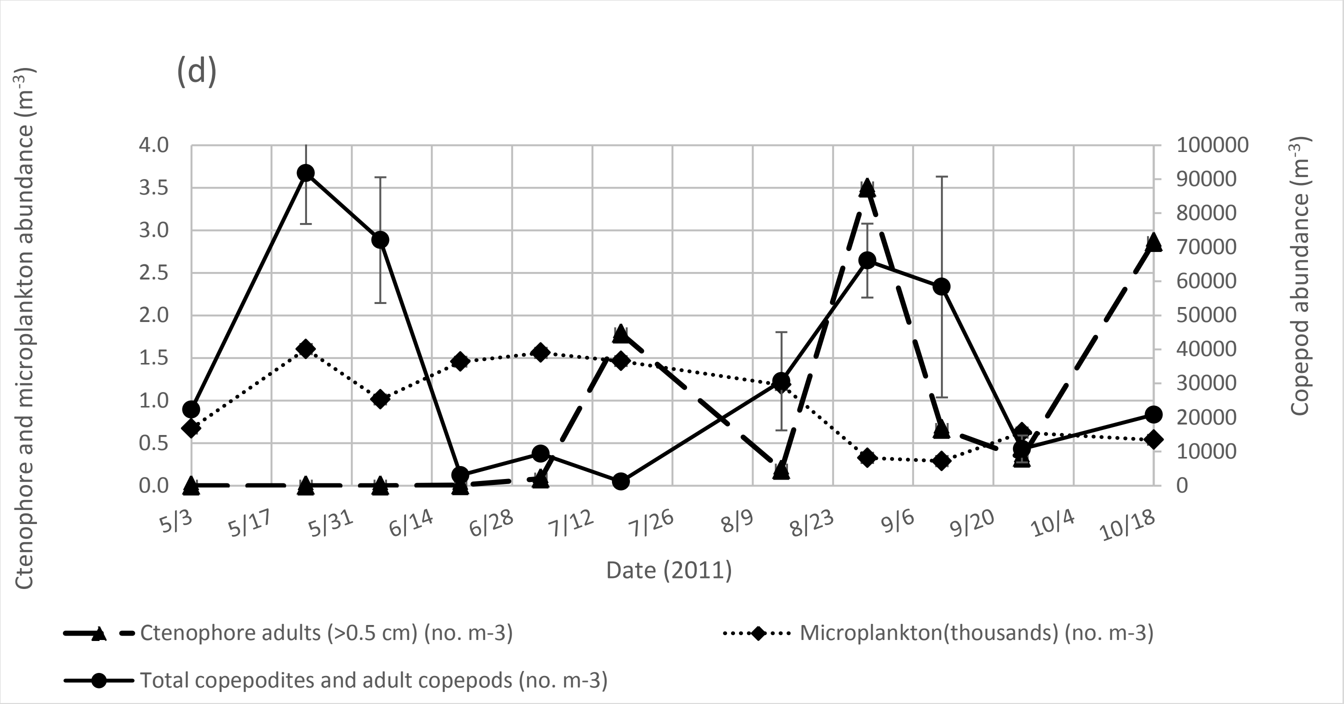


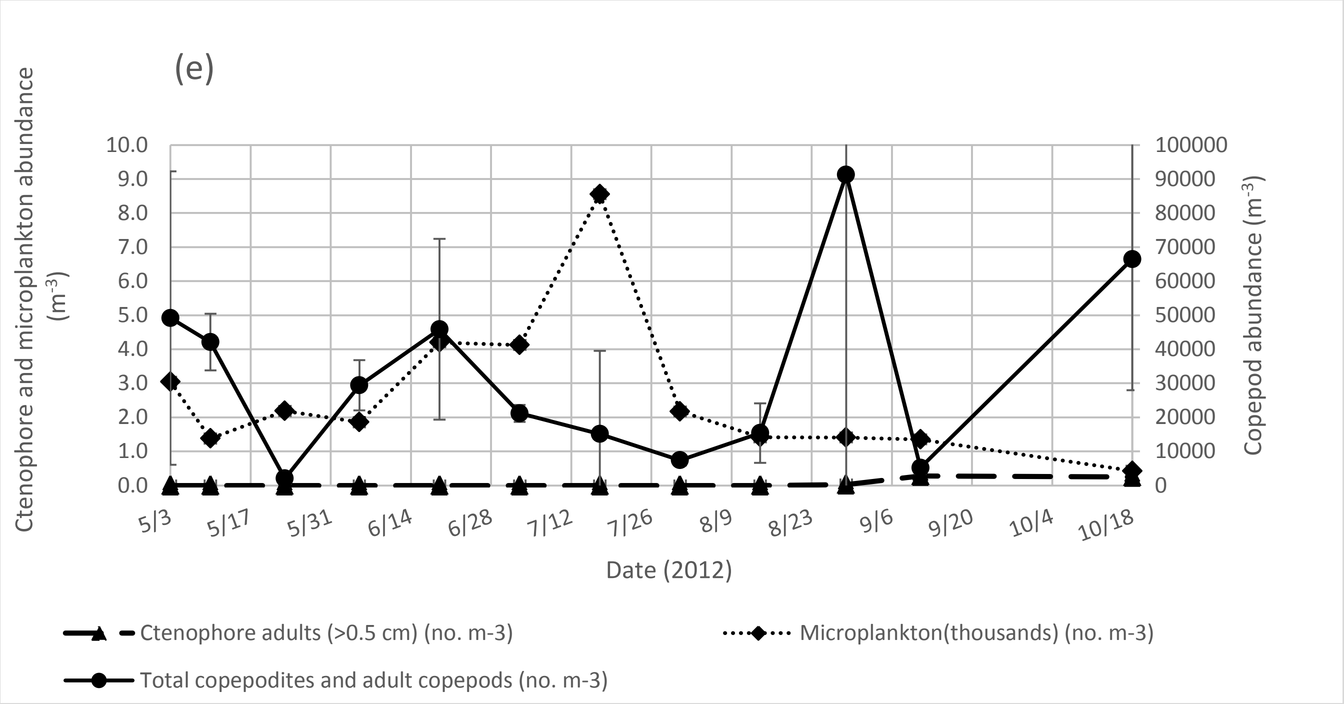
Figure 2. 2012 Ctenophore biovolumes (±1 s.e.; mL m^{-3}; A, C, E) and abundances (±1 s.e.; ind. m^{-3}; B, D, F) at WLIS (A, B), MLIS (C, D), and CLIS (E, F) during 2012.

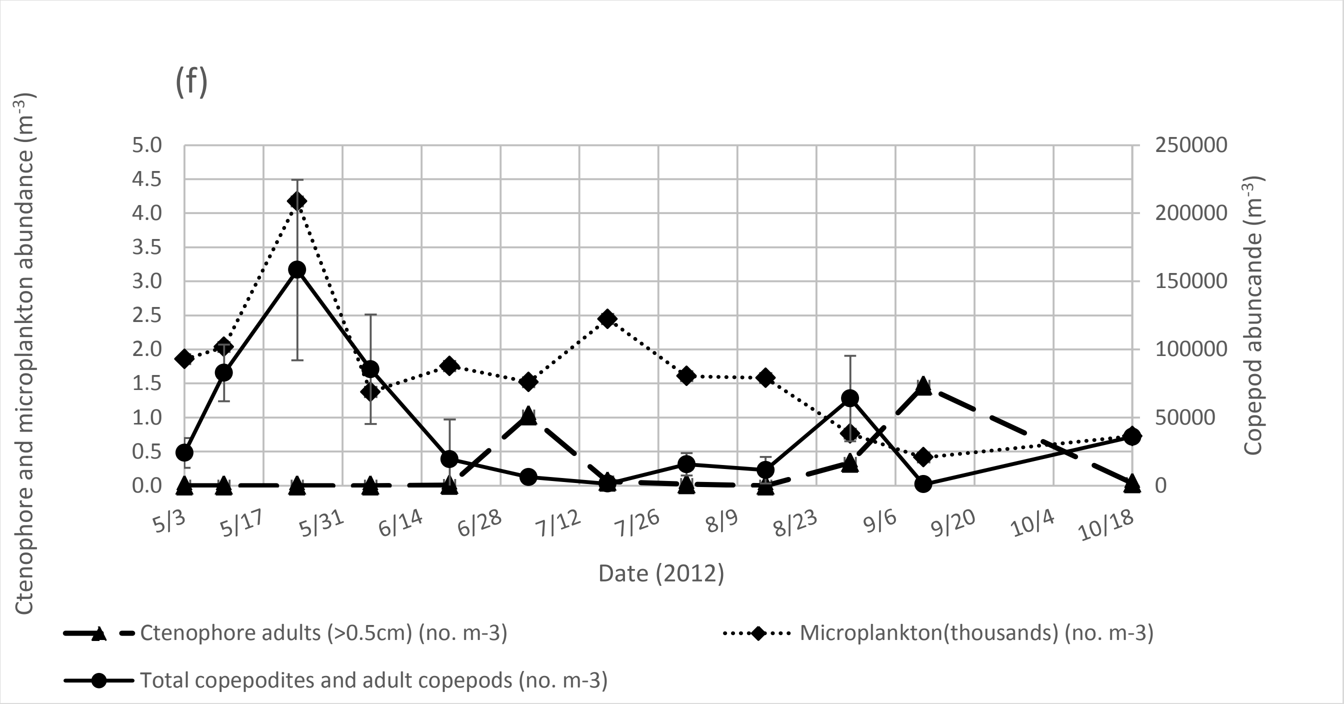
Figure 3. Seasonal abundances of adult ctenophores, microplankton, and total copepodites and adult copepods (no. m^{-3}) in (a) CLIS-2011, (b) WLIS-2011, (c) MLIS-2011, (d) CLIS-2012 (e) WLIS-2012, (f) MLIS-2012.




(c)
Ctenophore and microplankton abundance (m-3)
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
Copepod abundance (m-3)
140000
120000
100000
80000
60000
40000
20000
0
4/26
5/10
5/24
6/7
6/21
7/5
7/19
8/2
8/16
8/30
9/13
9/27
10/11
Date (2011)
Ctenophore adults (>0.5 cm) (no. m-3)
Microplankton (thousands) (no. m-3)
Total copepodites and adult copepods (no. m-3)


(d)
Ctenophore and microplankton abundance (m-3)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Copepod abundance (m-3)
100000
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
5/3
5/17
5/31
6/14
6/28
7/12
7/26
8/9
8/23
9/6
9/20
10/4
10/18
Date (2011)
Ctenophore adults (>0.5 cm) (no. m-3)
Microplankton(thousands) (no. m-3)
Total copepodites and adult copepods (no. m-3)


(e)
Ctenophore and microplankton abundance (m-3)
Copepod abundance (m-3)
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
100000
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
5/3
5/17
5/31
6/14
6/28
7/12
7/26
8/9
8/23
9/6
9/20
10/4
10/18
Date (2012)
Ctenophore adults (>0.5 cm) (no. m-3)
Microplankton(thousands) (no. m-3)
Total copepodites and adult copepods (no. m-3)


(f)
Ctenophore and microplankton abundance (m-3)
Copepod abuncande (m-3)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
250000
200000
150000
100000
50000
0
5/3
5/17
5/31
6/14
6/28
7/12
7/26
8/9
8/23
9/6
9/20
10/4
10/18
Date (2012)
Ctenophore adults (>0.5cm) (no. m-3)
Microplankton(thousands) (no. m-3)
Total copepodites and adult copepods (no. m-3)

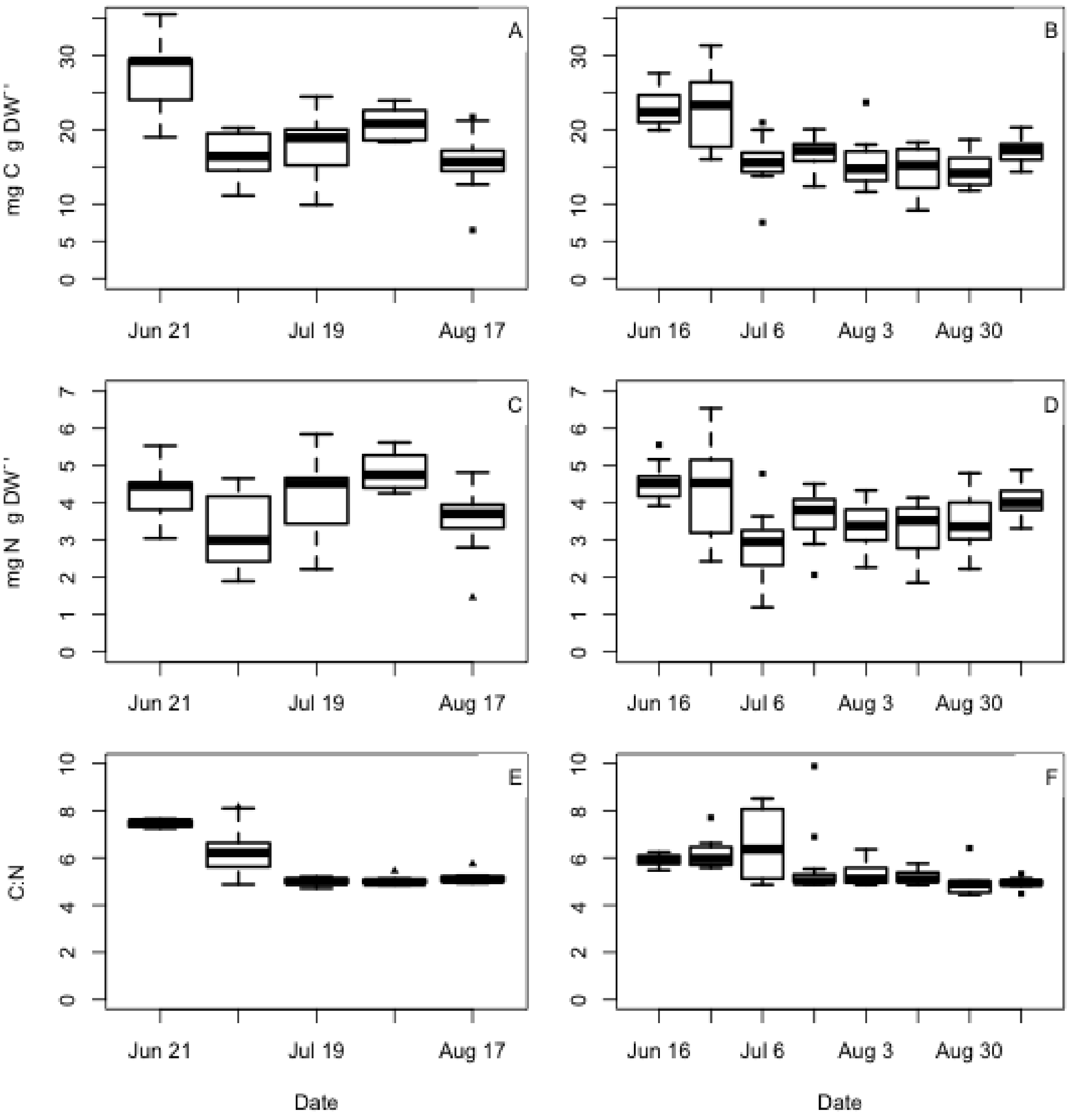


Figure 4. Ctenophore body composition (mgC gDW^{-1} A, B; mgN gDW^{-1}, C, D) and body composition ratios (C:N; E, F) at WLIS (A, C, E) and CLIS (B, D, F) for the 2011 sampling season.