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Role of the ctenophore *Mnemiopsis leidyi* in nutrient cycling in Long Island Sound, New York, USA

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ABSTRACT: The population dynamics of the ctenophore *Mnemiopsis leidyi* are often characterized by a substantial build-up and demise in abundance in coastal and estuarine waters, a pattern that may have a significant impact on nutrient cycling. Since many coastal ecosystems are experiencing negative impacts of eutrophication, there is great interest in quantifying nutrient loading sources. Still, the ability to calculate robust nutrient budgets in many coastal systems has been hampered by a poor understanding of the contribution of gelatinous zooplankton to nutrient pools. Long Island Sound is a highly productive, urban estuary within which *M. leidyi* occurs, but the role of this species in nutrient cycling was unknown. In 2011, the population biomass and nutrient remineralization rates (i.e. NH_4^+, PO_4^{3-}) of *M. leidyi* in the estuary were evaluated. Ctenophores remineralized NH_4^+ and PO_4^{3-} at rates up to 0.62 and 0.13 µmol ind.$^{-1}$ h^{-1}, respectively, and were capable of substantial release of nutrients upon population demise (39.32 µmol m^{-3} d^{-1} of NH_4^+ and 20.02 µmol m^{-3} d^{-1} of PO_4^{3-}). However, in both cases, these rates were not in quantities sufficient to support a major fraction of primary production (<1% d^{-1}). This study suggests that ctenophores may contribute only in a minor way to nutrient pools in highly eutrophic ecosystems.

KEY WORDS: Gelatinous zooplankton · Nitrogen cycling · Nutrient remineralization · Phosphate cycling

INTRODUCTION

The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 inhabits coastal regions and estuaries along the Atlantic coastlines of the USA, including Long Island embayments, where it is the most abundant gelatinous zooplankton species (Turner 1982, McNamara et al. 2010). The current extent of the species in the USA is north to Cape Cod and south to the Gulf of Mexico (Kremer 1977, Sullivan et al. 2001). Studies suggest that in New York embayments (e.g. Great South Bay and Peconic Bay; McNamara et al. 2010) as well as nearby Narragansett Bay, Rhode Island (Sullivan et al. 2001), this species has been increasing in biomass, possibly due to climate change.

Gelatinous zooplankton populations are dynamic and often characterized by cycles of blooms and crashes (Pitt et al. 2014). Blooms of *M. leidyi* can be controlled by both biotic (changes in prey abundance; Kremer 1994) and abiotic factors (temperature and salinity; Kremer 1994, Costello et al. 2006, Jaspers et al. 2011, Lehtiniemi et al. 2012), but in coastal areas, blooms are most often triggered by seawater temperature increase (Kremer 1994, Costello et al. 2006). Reproductive output increases with increasing temperatures, and during favorable conditions (19–23°C for *M. leidyi*) egg production can exceed 8000 eggs d^{-1} (Kideys 1994). At 23°C, fertilized eggs develop into the larval stage quickly, leading to dramatic increases in abundance in just a few

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days (Kideys 1994, GESAMP 1997, Graham et al. 2001). Such blooms can cover widespread areas and achieve high biomasses (i.e. over 400 ind. m^{-3}, and greater than 100 ml biovolume m^{-3}) (Sullivan et al. 2001, McNamara et al. 2010).

During blooms, gelatinous zooplankton are often the dominant water-column predators of zooplankton. These predators may exert a top-down control that can initiate changes that influence lower trophic levels (Oguz et al. 2001, Graneli & Turner 2002, Purcell & Decker 2005, Pitt et al. 2007, West et al. 2009a, McNamara et al. 2013b). For example, intense predation on mesozooplankton by ctenophores can indirectly enhance phytoplankton abundances by reducing grazing pressure from zooplankton (Deason & Smayda 1982, Purcell & Decker 2005). Alternatively, gelatinous zooplankton including ctenophores (*M. leidyi*; Deason & Smayda 1982, Nasrollahzadeh et al. 2008) and medusae (*Catostylus mosaicus*; Pitt et al. 2007, West et al. 2009a) may exert bottom-up influences by excretion of dissolved nutrients, which may stimulate primary production. Specifically in coastal systems, excreted nutrients may be a major source of recycled nutrients for primary producers (Pitt et al. 2005). *Mnemiopsis leidyi* and other lobate ctenophores capture prey using their lobes, which are lined with mucus (Condon et al. 2010). This mucus is thought to contribute to both organic and inorganic nutrient releases (Nasrollahzadeh et al. 2008, Pitt et al. 2009, Condon et al. 2010, Niggl et al. 2010, Condon et al. 2011).

Nitrogen release by gelatinous zooplankton species is primarily in inorganic forms (Steinberg & Saba 2008). Many species, including *M. leidyi*, are ammonotelic, excreting ammonium (NH_4^+) as the main nitrogenous waste, while phosphorus excretion is primarily in the form of inorganic phosphate (PO_4^{3-}) (Shimauchi & Uye 2007, Condon et al. 2010). Ctenophores are likely to be major contributors of recycled nutrients in coastal areas, but little is known about the rates of excretion and their overall ecological role in nutrient cycling (Pitt et al. 2009, Condon et al. 2010). There is great interest in controlling nitrogen loading rates to many estuaries in order to relieve the symptoms of eutrophication (Nixon 1995). In most estuaries, a paucity of information regarding nutrient cycling by gelatinous zooplankton prohibits their contribution to ecosystem nutrient loads from being estimated.

This study examined the role of *M. leidyi* in nutrient cycling in Long Island Sound (NY-CT), the third largest estuary in the USA. The contribution of the live population to dissolved inorganic nutrient pools was examined experimentally through nutrient-release experiments. The temporal dynamics (changes in parameters over time) of the physical environment, nutrients, and mesozooplankton densities were investigated to determine the influence of each factor on the rates of dissolved nutrient release by ctenophores. In addition, the elemental composition of *M. leidyi* was examined to determine the magnitude of removal of these elements from the system during ctenophore blooms, and release rates back to the system upon population demise. Rates of bacterial oxygen consumption that would occur during degradation of the ctenophore population were calculated to determine this contribution to hypoxia. Few studies have directly determined nutrient-release rates as well as elemental composition of *M. leidyi*, and to our knowledge nothing was known regarding their role in nutrient cycling in the estuary despite a multi-billion dollar effort to restrict nutrient loads to this system (US EPA 1994). We hypothesized that blooms of *M. leidyi* would have a substantial impact on nutrient cycling in Long Island Sound through both live nutrient release as well as degradation during population crashes.

MATERIALS AND METHODS

Field sampling

Field sampling began in May and continued through October 2011 (n = 14 sampling occasions) to ensure that we captured the duration of a typical bloom found in other local estuaries (Kremer & Nixon 1976, McNamara et al. 2010, McNamara et al. 2013a,b). Biweekly sampling occurred at 2 stations in Long Island Sound (LIS): Western Long Island Sound (WLIS; 40° 52.320′ N, 73° 44.040′ W; bottom depth 32.6 m) and Central Long Island Sound (CLIS; 41° 3.572′ N, 73° 8.674′ W; bottom depth 40.9 m) (Fig. 1). These stations were selected as representative of 2 of the major basins (Western Basin and Central Basin) within LIS (Riley 1952, Buck et al. 2005), and although there are no published studies of ctenophore populations in LIS, the western end of the basin was chosen due to speculation about higher abundances in the west following higher copepod concentrations (Capriulo et al. 2002).

Seawater properties

At each station, temperature (°C), salinity, and dissolved oxygen (% saturation and mg l^{-1}) were meas-

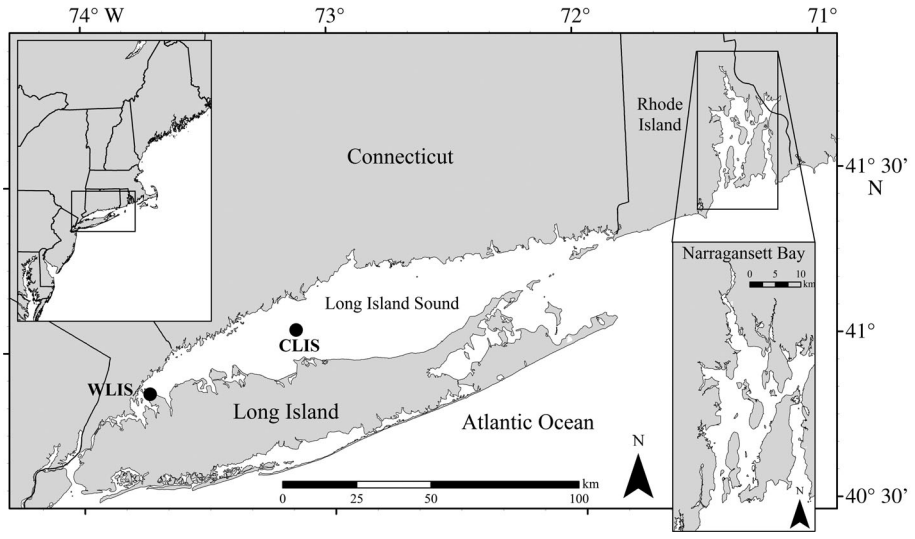

Fig. 1. Field sampling sites in Long Island Sound. Bi-weekly sampling occurred in 2011 at 2 stations: Western Long Island Sound (WLIS) and Central Long Island Sound (CLIS)

ured using a handheld YSI 85 CTD probe. For dissolved nutrient analyses, seawater samples were collected using a Niskin bottle from each site at 1 m depth. Seawater was filtered through a pre-combusted (2 h at 450°C) 0.2 µm glass-fiber filter and stored frozen for later analyses, which were performed for NH_4^+ and PO_4^{-3} using standard wet chemistry and colorimetric methods (Parsons et al. 1984) adapted to a 96-well spectrophotometric microplate reader. Seawater was also collected from the surface mixed layer for use in nutrient-release experiments.

Gelatinous zooplankton abundance

To determine abundances of gelatinous zooplankton, on each sampling date, 2 tows were performed at each station with a 0.5 m diameter, 202 µm mesh plankton net, and 2 tows were performed with a 1 m diameter, 1000 µm mesh plankton net, both equipped with a flexible plastic cod end and General Oceanics or Sea-Gear mechanical flowmeter (Smith et al. 1968, Tranter & Smoith 1968, Sameoto et al. 2000). Tows were performed obliquely in the top 15–20 m of the water column, and were confined to 2–4 min in length to minimize net clogging or damage to organisms (Smith et al. 1968). Average volumes of seawater sampled per tow ranged from 16 to 72 m^3, depending on net size and tow duration.

Upon completion of each tow, contents of the cod end were gently rinsed with 20-µm-filtered seawater onto a 202 µm sieve so that gelatinous zooplankton were free of 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 (only *Mnemiopsis leidyi* appeared in the samples with the exception of one individual of *Cyanea capillata*) was measured for total length (aboral to bottom of lobes) with a graduated Petri dish to the nearest 0.5 cm. If the total biovolume greatly exceeded 500 ml, a subsample (400–500 ml) was taken from the gently well-mixed sample to perform the counts and measurements. To subsample, the samples were gently transferred to a large bucket with seawater. A gentle mixing with seawater (in a figure-eight motion, such that the animals did not concentrate in the center) allowed for a homogeneous mixture from which a subsample could then be taken out with another small bucket. Abundance (ind. m^{-3}) and biovolume (ml m^{-3}) were calculated by dividing the individual ctenophore counts (individuals) and measured biovolumes (ml) by the calculated volume of seawater sampled (m^3) determined from a calibrated flowmeter (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 using a 0.5 m diameter, 64 µm mesh plankton net (n = 2 at each site) (Smith et al. 1968, Tranter & Smoith 1968, Sameoto et al. 2000), equipped with a plastic cod end and mechanical flowmeter. Upon completion of each tow, contents of the cod end were rinsed with 20-µm-filtered seawater onto a 64 µm sieve and preserved in 10% buffered formalin (final concentration 5%), and

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

For laboratory experiments, live *M. leidyi* were collected via dip net from the surface layer (Raskoff et al. 2003) at the WLIS and CLIS stations. Live organisms were transported back to the laboratory in ambient seawater for elemental analysis and nutrient-release experiments. All animals were held for a minimum of 1 h in 0.2-µm-filtered seawater to rinse off debris (e.g. other zooplankton) and allow time for the animals to depurate (Condon et al. 2010).

Elemental analysis

Elemental analysis of carbon and nitrogen was performed in triplicate on 4 size classes (small: 1–2.5 cm length; medium: 3–3.5 cm; large: 4–4.5 cm; extra large: ≥5 cm) of *M. leidyi*. Ctenophores were collected from WLIS from 21 June to 17 August (n = 5 dates), and from CLIS from 16 June to 13 September (n = 8 dates). Individual ctenophores were measured and weighed (wet weight). Dry weights (DW) were determined after drying for 24 h at 60°C (Lovegrove 1966). Each dried sample was then individually stored in aluminum foil packages for elemental analysis at a later date. Samples were homogenized using a mortar and pestle, and then 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 g^{-1} DW). Dry weight data were pooled from both sites to determine a relationship between dry weight and organism length for analyses. This relationship (DW = 0.0074 × length$^{2.13}$) allowed for estimation of total field population dry weight (g DW m^{-3}) from the ctenophore size distribution and abundance. The elemental analysis results (mg g^{-1} DW) were combined with the field population data (g DW m^{-3}) to determine the total pool of carbon and nitrogen held in the LIS population (mg m^{-3}). These values from the peak of the bloom (3 August in WLIS and 19 July in CLIS) were also used to determine quantities of nitrogen and carbon returned back into LIS upon demise of the bloom. Rates of bacterial oxygen consumption that would occur during degradation of dead ctenophores were also calculated using calculated carbon decomposition rates for dead ctenophores, and assuming an elemental ratio of 138:106 O_2:C.

Nutrient-release experiments

For the nutrient-release experiments, ctenophores were collected from WLIS from 6 July to 17 August (n = 3 dates), and from CLIS from 6 July to 8 August (n = 4 dates). The experiments were performed on live organisms, in triplicate, on 3 size classes (small: 2–2.5 cm length; medium: 3–4 cm; and large: 5–6 cm). Individual organisms were placed in 1.2 l glass containers (acid-washed) containing 0.2-µm-filtered seawater collected from the sampling stations. Initial dissolved nutrient samples were obtained prior to starting each experiment. Containers were incubated in the dark at ambient seawater temperature (Condon et al. 2010). Dissolved nutrient samples (10 ml, n = 2) were obtained from each container every 3 h for a total of 12 h. After the incubation period, the wet weights of each individual ctenophore were recorded, and then dry weights were determined as previously described. Dissolved nutrient analyses were performed for NH_4^+ and PO_4^{3-} concentrations for all experimental samples using methods previously described (Parsons et al. 1984).

Ecosystem-wide nutrient remineralization by ctenophores

Hypothetical release rates of each nutrient by ctenophores in LIS were determined by performing robust, linear regression analyses of experimental nutrient concentration as a function of time for each experiment, with the resulting slope of the line representing the release rate in µmol ind.$^{-1}$ h^{-1}. Since nutrient concentrations were determined at multiple time points over the course of an experiment, robust regressions were used to down-weight the influence of outliers. Release rates less than zero were not included in the analysis (Condon et al. 2010). Individual release rates were compared with dry weight of individuals to fit the equation:

$$R = aW^b \quad (1)$$

where R is the release rate of ammonium or phosphate (µmol ind.$^{-1}$ h^{-1}), W is the dry weight of the

individual (g), and a and b are constants used to fit the relationship to the data in accordance with Matsakis (1992). Seawater temperature and mesozooplankton data from the sampling occasions were used to determine the impacts of each factor on the rates of dissolved nutrient release by ctenophores. Assuming ctenophore weight and seawater temperature to be 2 independent variables, the simultaneous effect of temperature and weight can be described by the equation:

$$R = aW^b c^T \quad (2)$$

where T is the temperature (°C) and c is a constant, in accordance with Matsakis (1992). Excretion rates may also be affected by prey concentration. The combined effect of weight, temperature, and food concentration can be expressed as:

$$R = aW^b c^T d^F \quad (3)$$

where F is the mesozooplankton concentration (ind. m^{-3}) and d is a constant, in accordance with Matsakis (1992).

Estimation of total field population dry weight (g DW m^{-3}) from measured ctenophore size distribution was determined with a relationship between all experimental organismal lengths and their respective dry weights. Population biomass (g DW m^{-3}) and temperature (°C) were used to determine the total nutrient release per day for each site using the fitted equation (Eq. 2). These values were then compared with ambient nutrient concentrations (µmol m^{-3}) to determine the relative percentage of each nutrient turned over by the ctenophore population per day. All analyses were performed using the statistical computing software R. Models were fit using nonlinear least squares with the 'nls2' R package. Akaike's information criteria (AIC) was used to determine which model equation most accurately describes the data.

RESULTS

Physical measurements

Surface water temperatures were lowest (7.6–8.8°C) at the beginning of the sampling season and gradually increased to 18–20°C (favorable temperatures for *Mnemiopsis leidyi* reproduction) by 21 June. Temperatures at both sites rose above 20°C in early July and remained above this level through mid-October. Salinities ranged from 21 to 26 and were highly variable over the sampling season. The western site showed the lowest salinity values (0.1–2.6 ppt lower than CLIS) due to its proximity to the East River. Surface dissolved oxygen levels decreased over the sampling season, and hit minimums from mid-July to mid-August (3.0–6.5 mg l^{-1}; Table 1).

Both dissolved phosphate (PO_4^{3-}) and ammonium (NH_4^+) concentrations were higher in WLIS than in CLIS, and levels generally increased during our sampling period (Fig. 2). Phosphate concentration increased most noticeably in WLIS (400–500% of initial concentration) over the course of the study, but also increased in CLIS by 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 (Fig. 2).

Table 1. Surface temperature, salinity, and dissolved oxygen (DO) data for all sampling sites and dates (m/dd) in 2011. WLIS: Western Long Island Sound; CLIS: Central Long Island Sound; ND: not determined; Temp.: Temperature

Date	Site	Temp. (°C)	Salinity	DO (mg l^{-1})
4/18	CLIS	6.7	24.8	13.13
4/26	CLIS	7.6	24.0	13.62
	WLIS	8.8	23.0	9.34
5/12	CLIS	8.9	24.7	ND
	WLIS	11.4	23.8	11.60
5/24	CLIS	11.3	24.6	12.58
6/07	CLIS	16.0	24.1	8.55
	WLIS	16.3	23.1	9.95
6/15	CLIS	16.7	24.4	9.75
	WLIS	17.7	23.6	9.50
6/21	CLIS	18.5	23.6	8.95
	WLIS	19.6	23.0	10.38
7/06	CLIS	22.3	24.1	4.47
	WLIS	20.1	23.4	7.38
7/19	CLIS	23.5	24.8	5.88
	WLIS	21.4	24.1	4.22
8/03	CLIS	23.1	25.7	3.17
	WLIS	22.7	24.4	4.88
8/17	CLIS	22.6	25.6	5.55
	WLIS	22.6	24.0	4.23
8/30	CLIS	22.6	24.7	6.89
	WLIS	22.4	23.7	5.54
9/13	CLIS	22.7	23.9	7.02
	WLIS	22.3	21.3	5.58
9/27	CLIS	22.0	24.4	7.29
	WLIS	21.7	23.3	5.80
10/11	CLIS	20.2	24.5	6.72
	WLIS	19.8	23.0	5.56

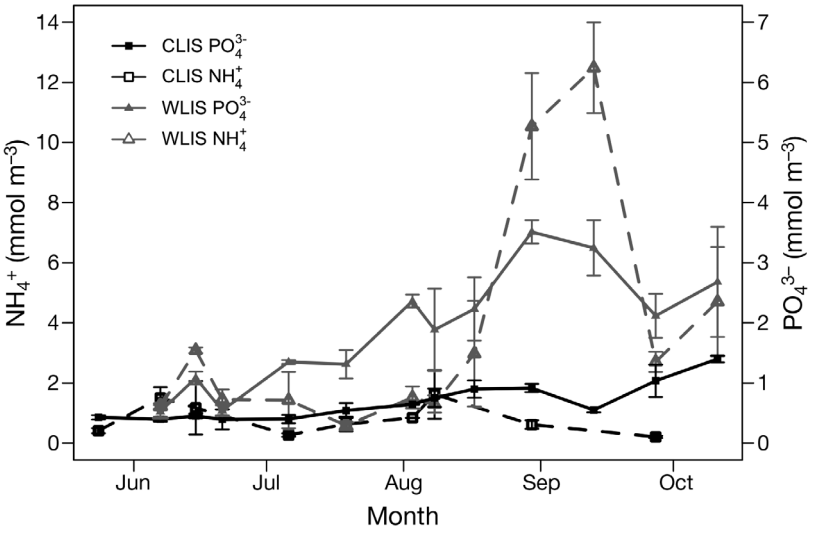

Fig. 2. Dissolved surface ammonium (NH_4^+, dashed lines) and phosphate (PO_4^{3-}, solid lines) concentrations (mmol m^{-3}) at Western Long Island Sound (WLIS; gray) and Central Long Island Sound (CLIS; black)

Zooplankton abundance

Mesoplankton and micrometazoan abundances are presented as total number of organisms (collectively referred to as 'zooplankton') available for ctenophore consumption, excluding polychaetes, which *M. leidyi* does not appear to consume in NY estuaries (M. E. McNamara, pers. comm.). The total abundance of mesozooplankton and micrometazoans (>64 µm) averaged (mean ± SE) 3.55 ± 0.20 × 10^5 organisms m^{-3} in WLIS and 2.22 ± 0.20 × 10^5 organisms m^{-3} in CLIS throughout the sampling period. At both sites, abundances were lowest throughout a majority of the summer and increased towards the end of the sampling season.

In WLIS, there was no obvious relationship between ctenophore abundance and mesozooplankton abundance during the ctenophore bloom. At CLIS, an inverse relationship was seen most prominently during the ctenophore bloom. Maximum ctenophore densities on 6 July coincided with a decline in mesozooplankton abundance. By mid-July to early August, ctenophore populations declined while mesozooplankton abundances increased. A secondary ctenophore density peak occurred on 17 August, which also corresponded to a decrease in mesozooplankton. Both sites exhibited the most dramatic increases in mesozooplankton abundance after the collapse of the ctenophore population, beginning on 8 August in WLIS and 30 August in CLIS (Fig. 3).

Elemental analysis of ctenophore biomass

Ctenophore body composition averaged (mean ± SD) 19.4 ± 5.38 mg C g^{-1} DW and 4.01 ± 1.06 mg N g^{-1} DW in WLIS and 17.4 ± 4.34 mg C g^{-1} DW and 3.71 ± 0.92 mg N g^{-1} DW in CLIS (Fig. 4). C:N ratios of individuals were significantly different between WLIS (range 4.71–8.15) and CLIS (range 4.43–9.88; nested ANOVA, date within site, $F_{2,136} = 3.84$, $p < 0.05$), and at both sites, the C:N ratio decreased significantly over the sampling season ($F_{4,136} = 5.65$, $p < 0.001$). There was no relationship between individual size and C:N ratios.

Inventories of the total mass of nutrients (C and N) and *M. leidyi* biomass suggested that the population sequestered about 2910 µmol C m^{-3} and 580 µmol N m^{-3} during peak biomass (3 August) at WLIS. The central site had the largest ctenophore biovolume on 19 July, and contained 1290 µmol C m^{-3} and 239 µmol N m^{-3} (Table 2). By 17 August, at WLIS, the ctenophores held only 8.29 µmol C m^{-3} and 1.60 µmol N m^{-3}. The population decline at WLIS was abrupt (Fig. 3) and went from peak biovolumes to post-bloom densities (<5 ind. m^{-3}) in only 14 d, resulting in an average biomass loss of 207 µmol C m^{-3} d^{-1} and 41.3 µmol N m^{-3} d^{-1} (Table 2). In CLIS, post-bloom populations (by 13 September) held 69.3 µmol C m^{-3} and 14.0 µmol N m^{-3}. The decline in the population from peak biovolumes at CLIS occurred more gradually, over ~56 d (Fig. 3), resulting in average biomass loss rates of about 21.8 µmol C m^{-3} d^{-1} and 4.01 µmol N m^{-3} d^{-1} (Table 2).

Nutrient-release rates of ctenophores

Individual ctenophores were found to release 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} (Fig. 5). Release rates of both ammonium and phosphate were significantly dependent on ctenophore dry weight, with larger ctenophores exhibiting higher individual release rates ($F_{1,50}$ = 42.712, $p < 0.001$; $F_{1,45} = 8.4021$, $p < 0.01$, respectively). The influences of seawater temperature and zooplankton density on these rates were also investigated (Table 3). The combined effect of temperature and

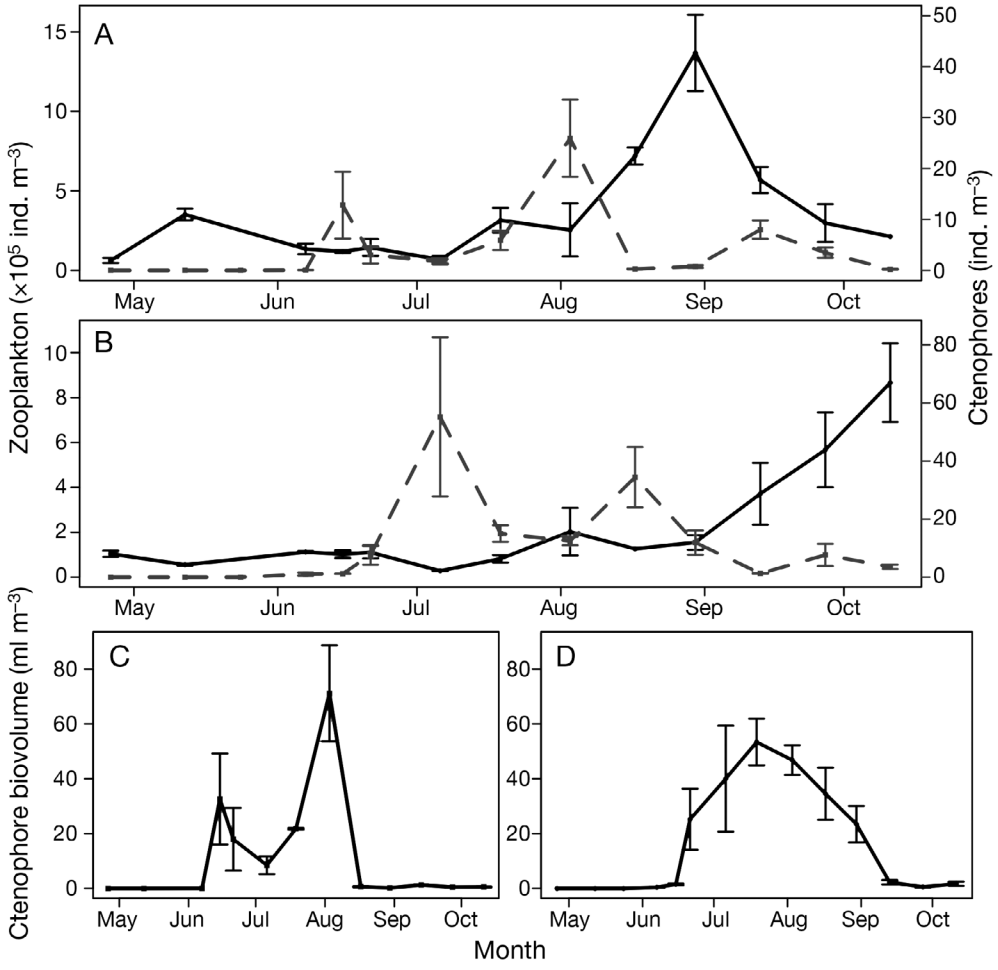

Fig. 3. Mean abundance (ind. m^{-3}) of zooplankton (i.e. total mesozooplankton and micrometazoans except polychaetes; $\times 10^5$; solid black lines) and *Mnemiopsis leidyi* (dashed gray lines) for (A) Western Long Island Sound (WLIS) and (B) Central Long Island Sound (CLIS), and (C) *M. leidyi* biovolume (ml m^{-3}) at WLIS and (D) CLIS. Error bars are ±range for zooplankton (n = 2) and ± SE (n = 4) for ctenophores

ctenophore dry weight (Eq. 2) more accurately described the nutrient-release rates than the combined effect of weight, temperature, and food concentration (Eq. 3), or dry weight alone (Eq. 1; Table 3).

In WLIS, the maximum turnover of ammonium likely occurred on 3 August, when *M. leidyi* biovolume was at a maximum, while the maximum turnover of phosphate would have occurred earlier in the season on 15 June, when ambient standing stocks of phosphate were lower. Using the relationship of rate to dry weight and temperature (Eq. 2), the total population of *M. leidyi* on these dates could have released ammonium and phosphate of up to 39.31 and 20.01 µmol m^{-3} d^{-1}, respectively (Table 4). Comparing these rates with nutrient pools at these dates in WLIS (Fig. 2), the total population could have contributed 2.59 % d^{-1} of the ammonium pool and 1.85 % d^{-1} of the orthophosphate pool (Table 4). In CLIS, maximum daily release of ammonium by the ctenophores would have occurred on 6 July, and maximum daily release of phosphate would have occurred on 21 June. By these dates, the total *M. leidyi* population could have regenerated 29.54 µmol ammonium m^{-3} d^{-1} and up to and 12.06 orthophosphate µmol m^{-3} d^{-1} (Table 4). The ctenophores in CLIS at these dates could have contributed 10.93 % d^{-1} of the ammonium pool and 3.06 % d^{-1} of orthophosphate (Table 4). At these rates, it would take peak abundances of *M. leidyi* more than a week to turn over the ammonium pools in LIS (Table 4). Over the course of the season, averaged abundances would take longer to turn over inorganic nutrient pools, with average ammonium release rates of 10.41 µmol m^{-3} d^{-1} at WLIS and 11.68 µmol m^{-3} d^{-1} at CLIS, and average phosphate release rates of 3.46 µmol m^{-3} d^{-1} at WLIS and 3.20 µmol m^{-3} d^{-1} at CLIS (Table 4).

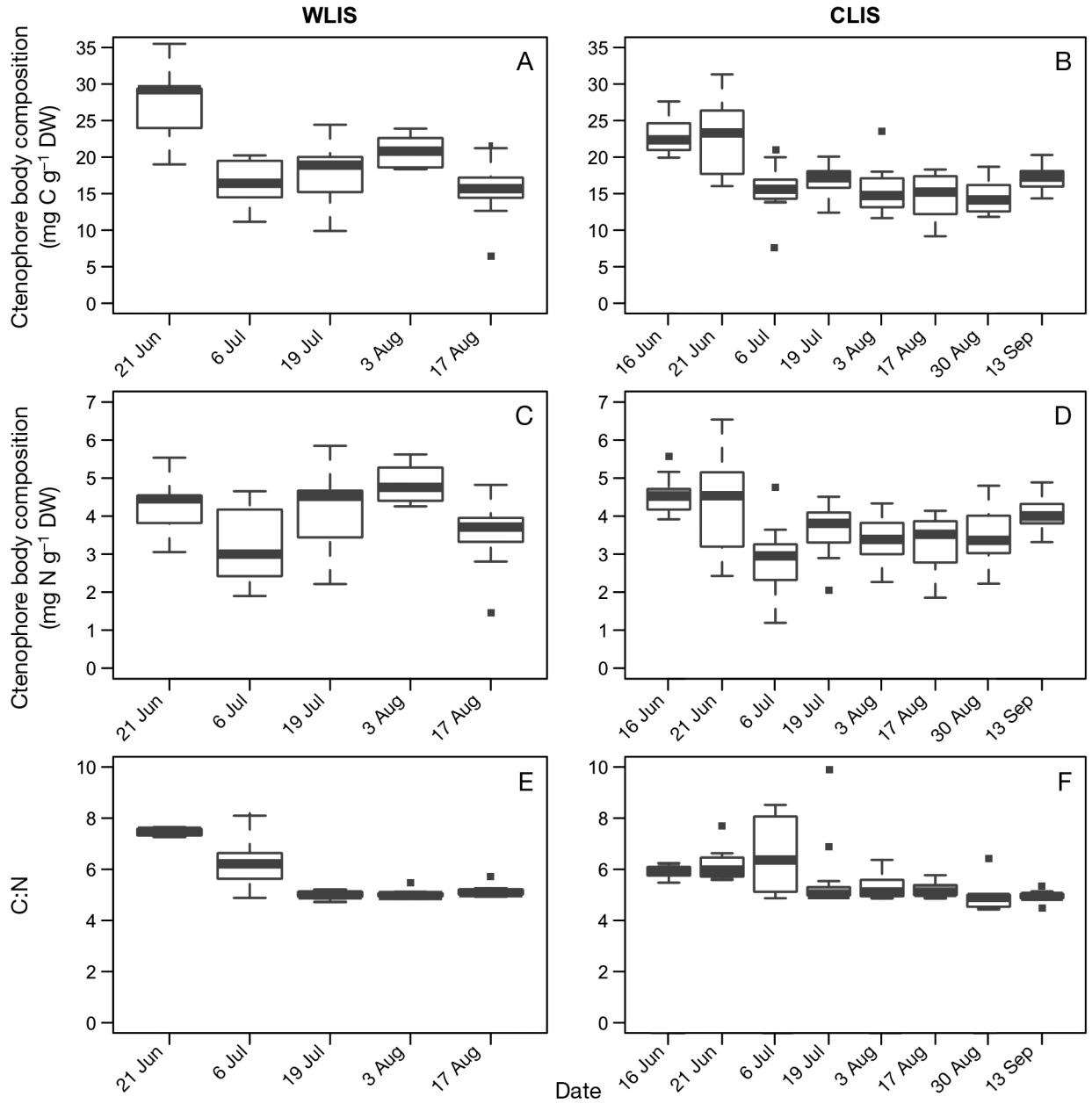

Fig. 4. Ctenophore body composition (A,B) mg C g^{-1} DW, (C,D) mg N g^{-1} DW and (E,F) body composition ratios (C:N) at (A,C,E) WLIS and (B,D,F) CLIS. Data are presented as modified box plots, where the box comprises the median and first and third quartiles. Outliers are denoted as any points greater than the third quartile plus 1.5 times the interquartile range, and less than the first quartile minus 1.5 times the interquartile range, or roughly ±2 standard deviations (Crawley 2012)

Table 2. Nutrient content of the *Mnemiopsis leidyi* population (means ± SE) and rates of carbon and nitrogen released to the ecosystem between maximum *M. leidyi* biovolume and post-bloom stocks at both Western Long Island Sound (WLIS) and Central Long Island Sound (CLIS)

Site	Element	Bloom peak (µmol m^{-3})	Post-bloom (µmol m^{-3})	Time (d)	Release (µmol m^{-3} d^{-1})
WLIS	C	2912.76 ± 849.26	8.29 ± 3.01	14	207.46
	N	579.89 ± 169.08	1.60 ± 0.58		41.31
CLIS	C	1290.84 ± 245.86	69.25 ± 6.82	56	21.81
	N	238.63 ± 45.45	14.02 ± 1.38		4.01

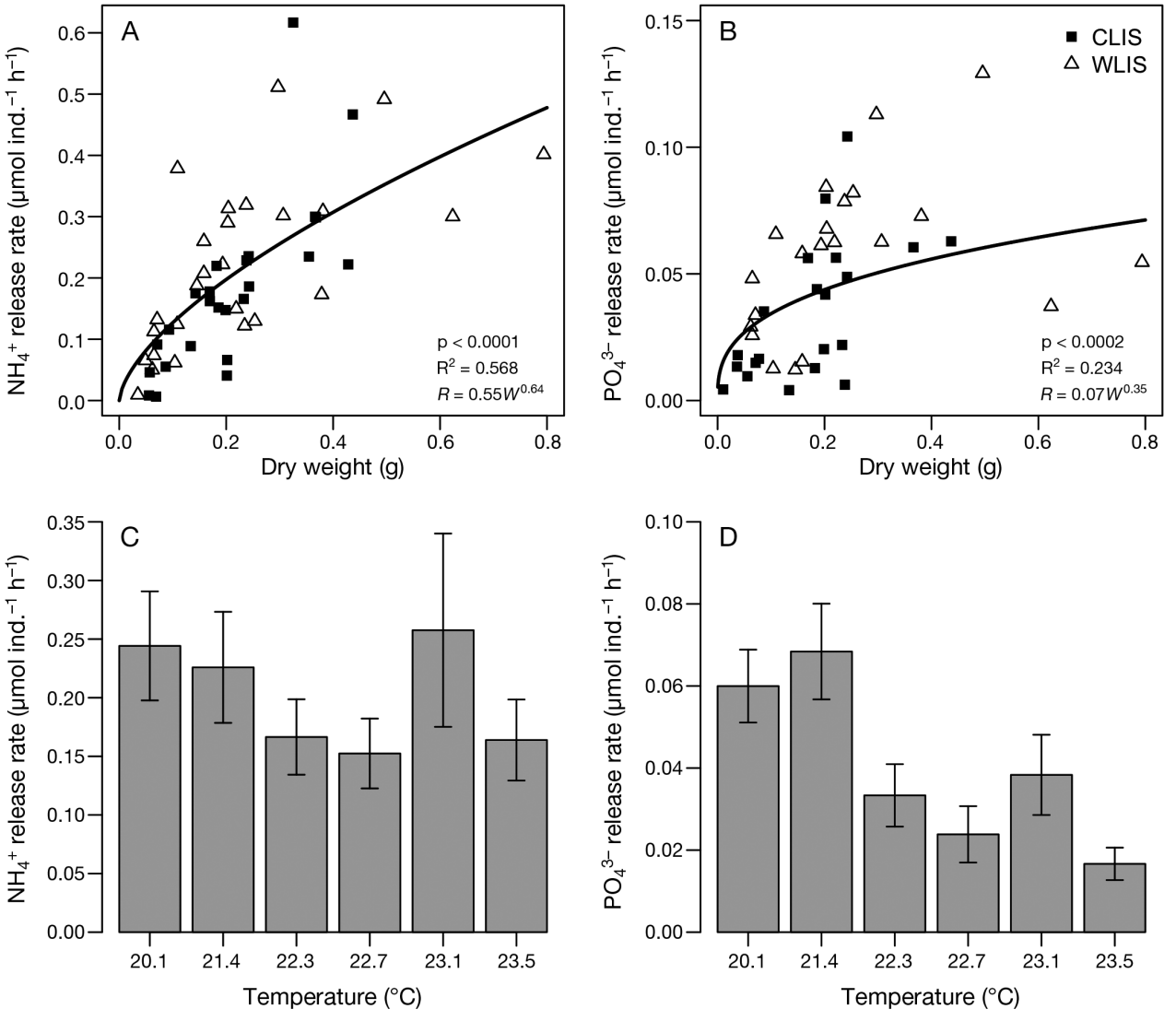

Fig. 5. Release rates of (A,C) NH_4^+ and (B,D) PO_4^{-3} for individual *Mnemiopsis leidyi* (µmol ind.$^{-1}$ h^{-1}) versus (A,B) dry weight and (C,D) temperature in Western Long Island Sound (WLIS) and Central Long Island Sound (CLIS). Error bars are ±SE. *R*: release rate of ammonium or phosphate; *W*: dry weight of the individual

Table 3. Parameter estimates, Akaike's information criterion (AIC), the difference between each model and the 'best' model (ΔAIC), and Akaike weights (W_i; the ratio of ΔAIC values for each model relative to the whole set of candidate models) for all nutrient-release models (Eqs. 1, 2, 3). *R* is the release rate of ammonium or phosphate (µmol ind.$^{-1}$ h^{-1}), *W* is the dry weight (g) of the individual ctenophore, *T* is the temperature (°C), *F* is the zooplankton concentration (ind. m^{-3}), and *a*, *b*, *c*, and *d* are constants

Nutrient	Model	*a*	*b*	*c*	*d*	AIC	ΔAIC	W_i
NH_4^+	Eq. (2): $R = aW^bc^T$	47.94	0.726	0.821		−95.654	0.000	0.686
	Eq. (3): $R = aW^bc^Td^F$	51.77	0.752	0.822	1.000	−94.036	1.618	0.306
	Eq. (1): $R = aW^b$	0.551	0.638			−86.801	8.853	0.008
PO_4^{3-}	Eq. (2): $R = aW^bc^T$	389.3	0.618	0.689		−222.749	0.000	0.609
	Eq. (3): $R = aW^bc^Td^F$	535.8	0.579	0.674	1.000	−221.859	0.890	0.391
	Eq. (1): $R = aW^b$	0.077	0.352			−196.243	26.506	0.000

Table 4. Maximum daily inorganic nutrient release, maximum daily contribution to inorganic nutrient pools, and minimum turnover time estimates for NH_4^+ and PO_4^{3-} in Western Long Island Sound (WLIS; maximum nutrient release dates 2011: NH_4^+ 3 August, PO_4^{3-} 15 June) and Central Long Island Sound (CLIS; NH_4^+ 6 July, PO_4^{3-} 21 June), and average daily nutrient release, average daily contribution to inorganic nutrient pools, and average turnover time estimates for the entire course of the sampling season

Site	Nutrient	Max. release (µmol m^{-3} d^{-1})	Max. contribution (% d^{-1})	Min. turnover time (d)	Avg. release (µmol d^{-1})	Avg. turnover (% d^{-1})	Avg. turnover time (d)
WLIS	NH_4^+	39.31	2.59	38.61	10.41	0.67	21560.65
	PO_4^{3-}	20.01	1.85	54.16	3.46	0.32	26272.22
CLIS	NH_4^+	29.54	10.93	9.15	11.68	2.67	250.85
	PO_4^{3-}	12.06	3.06	32.63	3.20	0.67	951.92

DISCUSSION

Nutrient uptake and release, and environmental influences on nutrient cycling by ctenophores

During blooms, some gelatinous zooplankton can contribute to significant nutrient sequestration and subsequent release back to seawater (Titelman et al. 2006, Tinta et al. 2010). In contrast, *Mnemiopsis leidyi*, in LIS, contributed minimally to the standing stock of nutrients. Here, we highlight the factors driving these trends.

During this study, ctenophore body composition ranged from 1.45 to 2.69% C dry weight and from 0.29 to 0.48% N dry weight across study sites in LIS. These percentages are similar to historic values for ctenophores in Narragansett Bay, RI, USA (Kremer 1977), which physically exchanges seawater with the eastern extreme of LIS. This similarity in body composition between our sites in LIS and Narragansett Bay suggests that the ctenophore population is typically homogeneous throughout the area, and values determined in this study can be used as representative of the entire ecosystem. The C:N ratio of *M. leidyi* ranged from 4.71 to 8.15 in WLIS, and from 4.43 to 9.88 in CLIS, although for the majority of the sampling season the body composition of *M. leidyi* was below the Redfield ratio of 6.6 C:N (Redfield 1934). Enrichment of nitrogen relative to carbon in ctenophores is expected, as nitrogen enrichment relative to their food source is common in zooplankton (Kremer & 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 in LIS (Gobler et al. 2006), suggesting that ctenophores could represent an important nitrogen sink when population abundances are high and perhaps an important source upon their demise.

Gelatinous zooplankton contribute to nutrient pools through nutrient excretion (Matsakis 1992, Shimauchi & Uye 2007). While rates of dissolved inorganic nitrogen and phosphorus release by *M. leidyi* in LIS were as high as 0.62 µmol ammonium $ind.^{-1}$ h^{-1} and 0.13 µmol phosphate $ind.^{-1}$ h^{-1}, the rates were highly dependent on size and allometric relationships between size and rates of nutrient release were identified (Eq. 1; Table 3). Weight-specific release rates for LIS ctenophores were similar to published release rates for *M. leidyi* in Narragansett Bay and the Chesapeake Bay (Kremer 1977, Nemazie et al. 1993, Condon et al. 2010).

Cycles of *M. leidyi* abundance and their nutrient dynamics have been related to the abundance of their prey (McNamara et al. 2013a). Food availability can control the initiation and magnitude of a ctenophore bloom (Deason & Smayda 1982, Oguz et al. 2001), and in 2011 in LIS, *M. leidyi* and zooplankton abundances were inversely related, suggesting a significant predator–prey interaction (Fig. 3). Hence, many of the ecological and physiological characteristics of *M. leidyi* (including nutrient release from live animals) may be related to zooplankton abundance.

Beyond food, rates of nutrient release by live ctenophores can also be affected by ctenophore size and water temperature. Beginning with the basic model of nutrient-release rate as a function of individual dry weight (Eq. 1), coefficients were determined that were similar to those of other published studies (Matsakis 1992, Nemazie et al. 1993, Condon et al. 2010). The addition of temperature significantly increased the fit of the model (Table 3), while addition of food did not. However, ctenophores were not freshly fed prior to the nutrient excretion experiments, an approach that could have obscured the effects of food. McNamara et al. (2013a) reported that the elemental content of *M. leidyi* (i.e. C:N and C:P) was a function

of both individual size and prey availability. In our study, however, there was no significant relationship between elemental content ratios (C:N) and ctenophore size or prey availability. A lack of response to prey availability may be driven by homogeneity of field zooplankton densities, so in the future, manipulation of experimental prey concentrations may further refine these models.

Scaled to population abundance in LIS (using Eq. 2), the contribution of nutrients remineralized by ctenophores to the total inorganic nutrient pool was estimated to range between 3.06 and 10.93% d^{-1} of ammonium and 1.84 and 2.59% d^{-1} of phosphate. While the present study focused on inorganic nutrient release and remineralization by these organisms, total nutrient release (including organic forms) would be higher, particularly considering the large amount of mucus generated by *M. leidyi* (Nasrollahzadeh et al. 2008, Pitt et al. 2009, Condon et al. 2010, 2011, Niggl et al. 2010). *Mnemiopsis* release on average 21% of their total dissolved nitrogen as dissolved organic nitrogen (DON), and 34% of total dissolved phosphorus as dissolved organic phosphorus (DOP) (Condon et al. 2010). Using these values, *M. leidyi* in LIS could potentially excrete up to 10.45 and 10.31 µmol m^{-3} d^{-1} of DON and DOP, respectively.

Remineralization of nutrients by ctenophores and phytoplankton demand

Some studies have suggested that a variety of gelatinous zooplankton taxa (Biggs 1977, Pitt et al. 2009), including jellyfish (*Catostylus mosaicus*; Pitt et al. 2005, West et al. 2009a; *Aurelia aurita*; Shimauchi & Uye 2007) and ctenophores (*M. leidyi*; Nasrollahzadeh et al. 2008, Condon et al. 2010), can regenerate limiting nutrients and consequently stimulate primary production. Reported estimates indicate that excretion by a variety of gelatinous zooplankton taxa could supply 39–63% of the nitrogen required to sustain phytoplankton production in the North Atlantic (Biggs 1977). Excretion of NH_4^+ by various jellyfish taxa in Australia has been estimated to supply 8–11% of the inorganic nitrogen requirements of phytoplankton (Pitt et al. 2005).

In areas in which nutrients are limiting, remineralization by gelatinous zooplankton can have a substantial impact on primary production (Nasrollahzadeh et al. 2008, Pitt et al. 2009). Despite this potential for stimulation of primary production, *M. leidyi* was seemingly not a significant nutrient source in LIS, at least during the 2011 study period. Assuming 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 138:106, and that the elemental composition of phytoplankton conformed to the Redfield ratio of 106:16:1 C:N:P (Redfield 1934), the amounts of ammonium and phosphate remineralized during peak abundance of *M. leidyi* would support <1% of daily primary production in LIS (Schneider 1989). Due to its geographic location near the largest urban population center in the USA, the western sound (WLIS) is highly eutrophic (Buck et al. 2005), with more than one billion gallons of sewage discharged daily into this estuary (US EPA 1994). Hence, relative to these large nutrient delivery processes, the impacts of ctenophores on nutrient pools appear to be minor.

Ctenophores and hypoxia in Long Island Sound

Overall, the growth and demise of gelatinous zooplankton can influence the nutrient dynamics in some coastal ecosystems (Titelman et al. 2006, West et al. 2009b, Tinta et al. 2010). At high biovolumes, ctenophores in LIS sequestered up to 2913 µmol C m^{-3} and 580 µmol N m^{-3} (Table 2). However, because these peaks in population are transient, C and N were only temporarily sequestered from surrounding waters. When the ctenophore population collapsed, nutrient releases were calculated to be as high as 200 µmol C m^{-3} d^{-1} and 40 µmol N m^{-3} d^{-1}. Given the very low presence of ctenophore consumers (e.g. one 'lion's mane', *Cyanea capillata*, and no *Beroe* sp. were collected during the entire study), the population crash was most likely not due to predation mortality. The probable fate of the dead ctenophores was bacterial decomposition, a process that consumes oxygen and may contribute toward hypoxia (Titelman et al. 2006, West et al. 2009b, Tinta et al. 2010). Using the carbon loss rates based on declining ctenophore biomass (207.46 µmol C m^{-3} d^{-1} in WLIS and 21.81 µmol C m^{-3} d^{-1} in CLIS), and the ratio of 138:106 O_2:C, when ctenophores died, bacteria could deplete 270 µmol O_2 m^{-3} d^{-1} in WLIS and 28.4 µmol O_2 m^{-3} d^{-1} in CLIS. In LIS, bacterial respiration rates range from 0.3 to 1.5 mmol O_2 m^{-3} h^{-1} (Goebel & Kremer 2006). Thus, in the Western Sound, bacterial respiration of decaying ctenophore biomass would represent less than 5% of total bacterial respiration, and in the Central Sound this contribution would be even less. While the turnover rates of ctenophore biomass during blooms are unknown, sustained bacterial respiration supported by ctenophore biomass over the

course of blooms would result in additional oxygen depletion that would contribute to the summer hypoxia that occurs annually in LIS.

CONCLUSIONS

On an ecosystem scale, nutrient release from live ctenophores in Long Island Sound in 2011 was found not to be an important process supporting primary production, most likely due to the already very high anthropogenic nutrient input into the system. Upon demise of the ctenophore bloom, there was a considerable input of organic matter and nutrients, but only as a brief pulse into the system. When the ctenophore population crashed, however, the dead biomass was likely colonized rapidly by bacteria and could have contributed toward localized hypoxia. Since abundances of gelatinous zooplankton can vary widely on an interannual basis (e.g. in LIS in 2012 ctenophore biovolume remained below 3 ml m^{-3}; L. Treible, D. Lonsdale and G. Gobler unpubl.), it is possible that in some years, the contribution of these animals to nutrient supply and oxygen demand would be larger. Even so, our collective findings indicate that ctenophores are likely minor sources of nutrients and organic matter in estuaries such as LIS that experience large external loads of nutrients.

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