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Production of dissolved organic matter and inorganic nutrients by gelatinous zooplankton in the York River estuary, Chesapeake Bay

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Large "blooms" of ctenophores (*Mnemiopsis leidyi*) and scyphomedusae (*Chrysaora quinquecirrha*) occur throughout the York River, a sub-estuary of Chesapeake Bay. These gelatinous zooplankton blooms can influence carbon (C) and nutrient cycling through excretion of dissolved organic matter (DOM), and inorganic nitrogen (N) and phosphorus (P). We measured dissolved organic carbon, nitrogen and phosphorus (DOC, DON and DOP), ammonium (NH_4^+) and phosphate (PO_4^{3-}) released by *M. leidyi* and *C. quinquecirrha* in the laboratory, and estimated their contribution to *in situ* DOC and inorganic pools. Both species released high amounts of DOC compared with DON and DOP. DOM released by *Mnemiopsis* was C-rich with higher DOC:DON (29:1) compared with the Redfield ratio (6.6C:1N). Daily turnover of DOC and DON in ctenophores was high (25.2% of body C and 18.3% of body N), likely due to mucus production. In contrast, individual *Chrysaora* released DOC and DON similar to Redfield stoichiometry, but daily turnover of these compounds was low (<3% of body C and N). Both species released dissolved N and P in inorganic form but also released sizeable quantities of DON (21 and 35% of total dissolved nitrogen, TDN, for ctenophores and medusae, respectively) and DOP (34 and 46% of TDP). Most of the DOC in the York River came from *Mnemiopsis* populations during summer (May–July). While their contribution to bulk DOC pools was low (<1% day^{-1}), ctenophore populations released higher amounts of DOC to labile pools (18–29% day^{-1}). Contributions to NH_4^+ and PO_4^{3-} pools were highest at times when the York River was N-limited (5.8N:1P). Despite their potential to release phytoplankton from nutrient limitation, N excretion from gelatinous zooplankton supported <4% of primary production. Because net NH_4^+ released by *Mnemiopsis* populations exceeded standing concentrations, we hypothesize an alternative DIN sink whereby bacterioplankton supplement uptake of DOM released by gelatinous zooplankton with inorganic N and P to satisfy intracellular elemental requirements.

INTRODUCTION

Estuaries are dynamic ecosystems that sustain high productivity and large fluxes of organic and inorganic nutrients. Chesapeake Bay is a well-studied estuary that receives large inputs of inorganic nutrients but exports large amounts of organic nutrients on an annual basis

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(Kemp *et al.*, 2005). Quantifying nutrient source–sink dynamics of inorganic and organic pools, therefore, is critical to understanding carbon (C), nitrogen (N) and phosphorus (P) cycling in this highly productive ecosystem. Zooplankton play an important role in the cycling of nutrients in planktonic food webs via their excretion of inorganic nutrients, primarily in the form of ammonium (NH_4^+) and phosphate (PO_4^{3-}) (Steinberg and Saba, 2008), and by release of dissolved organic matter (DOM; Steinberg *et al.*, 2000, 2002; Carlson, 2002; Bronk and Steinberg, 2008). Most studies of zooplankton excretion have emphasized the role of crustacean zooplankton (e.g. copepods, euphausiids), whereas little is known about excretion by gelatinous zooplankton (Steinberg and Saba, 2008; Pitt *et al.*, 2009) and how these common organisms affect nutrient dynamics.

Over the past decade or more, large spatial and temporal increases in gelatinous zooplankton have occurred in coastal and estuarine systems worldwide. Gelatinous zooplankton are major predators of crustacean zooplankton and may play an equally important role in nutrient cycling (Kremer, 1977; Pitt *et al.*, 2009). Chesapeake Bay supports high biomass (blooms) of two native species: the ctenophore *Mnemiopsis leidyi* and the scyphomedusan *Chrysaora quinquecirrha* (Purcell and Decker, 2005; Condon and Steinberg, 2008). Because of their high biomass during blooms, gelatinous zooplankton can influence nutrient cycling (Condon and Steinberg, 2008; Pitt *et al.*, 2009).

To date, the relatively few studies examining gelatinous zooplankton excretion have focused on excretion of NH_4^+ and PO_4^{3-}, with little attention to DOM production. The excretion of inorganic N and P by *M. leidyi* ctenophores and *Aurelia* sp. medusae can support up to 39% and 23%, respectively, of primary production in Great South Bay, Long Island and Kiel Bight (Park and Carpenter, 1987; Schneider, 1989), but N is a minor contributor (3% of microplankton production) in Chesapeake Bay (Nemazie *et al.*, 1993). However, NH_4^+ and PO_4^{3-} excretion by coastal and estuarine scyphomedusae might be more important for supporting primary production during times of nutrient limitation (Schneider, 1989; Pitt *et al.*, 2005). Alternatively, the simultaneous release of DOM and inorganic nutrients by zooplankton may have greater influence on microbial communities in net heterotrophic Chesapeake Bay (Schultz and Ducklow, 2000), because microbial production is supported by organic matter pools (Raymond and Bauer, 2000). DOM excretion may also be augmented in gelatinous zooplankton by release of DOM through mucus production (Shanks and Graham, 1988; Hansson and Norrman, 1995).

The ctenophore *M. leidyi*, as well as *Aurelia* semaeostome medusae, are known to release significant quantities of their total excretia as dissolved organic carbon, nitrogen and phosphorus (DOC, DON and DOP) (Kremer, 1977; Hansson and Norrman, 1995). The response of bacterioplankton to crustacean zooplankton DOM excretia indicates that this material is labile and can support substantial bacterial production (Møller *et al.*, 2003; Nelson *et al.*, 2004; Steinberg *et al.*, 2004). Although DOC concentrations in Chesapeake Bay are high, only a small proportion is labile (Raymond and Bauer, 2000). Thus, blooms of gelatinous zooplankton could contribute to labile DOC pools that can support microbial production. This is in contrast to the current paradigm in which phytoplankton are viewed as the primary source of DOM in marine systems (Carlson, 2002, 2007).

Here, we report results from laboratory experiments measuring simultaneous release of DOM and inorganic nutrients by *M. leidyi* ctenophores and *C. quinquecirrha* medusae from the York River estuary, a southern tributary of Chesapeake Bay. The C:N:P ratios of released organic and inorganic excretia by both gelatinous zooplankton species are compared with the canonical Redfield ratio (106C:16N:1P) (Redfield *et al.*, 1963) in order to explore possible stoichiometric variations in the release of DOM and inorganic nutrients (Sterner and Elser, 2002). Furthermore, we evaluated the contributions made by gelatinous zooplankton blooms to DOC and dissolved inorganic N and P (DIN and DIP) pools by combining results from laboratory experiments with abundance and biometric measurements of ctenophore and medusae populations from field surveys in the York River estuary.

METHOD

Collection and preparation of zooplankton for experiments

Chrysaora quinquecirrha medusae were collected by dipnet or in 20 L buckets (for larger animals) from surface waters. *Mnemiopsis* ctenophores were collected during 30 s, gentle plankton tows using a 200 μm mesh net and a non-filtering cod end. Upon collection, medusae and ctenophores were immediately transported to the laboratory and incubated with field-collected copepod prey (20–100 copepods L^{-1}) at *in situ* temperature for 30 min. Damaged animals were discarded, but in general most animals appeared healthy and undamaged after collection. Prior to experimentation, gelatinous zooplankton were gently transferred individually to separate 20 L buckets filled with 0.2 μm filtered York River water where they remained for 15 min. This step rinsed the animals and provided them time to clear their guts (R. Condon, personal observation), reducing potential

Table I: Physical conditions and incubation times for laboratory experiments

Date	Sample size (*n*)		Temperature (°C)	Salinity (psu)	Incubation (h)
	Mnem	*Chry*			
17 July 2003	7	NA	26	20	10
29 July 2003	6	NA	25	20	10
24 Oct 2003	NA	6	14	20	6
15 Aug 2003	8	NA	25	17	12
4 Feb 2004	12	NA	5	20	12
18 March 2004	9	NA	10	21	7–8
24 Aug 2005	10	9	27	20	3–4
2 May 2007	10	NA	14	20	8
5 May 2007	12	NA	20	20	7

Mnem, *Mnemiopsis leidyi* ctenophores; *Chry*, *Chrysaora quinquecirrha* medusae; NA, not applicable.

confounding effects of sloppy feeding and leaching of DOM from fecal material during the experiments.

Gelatinous zooplankton DOM and inorganic release experiments

We conducted nine laboratory experiments between July and August 2003–2007 to determine the simultaneous release rates of DOM and inorganic nutrients by *M. leidyi* ctenophores and *C. quinquecirrha* scyphomedusae in the York River estuary (Table I). For each experiment, individual animals were incubated in the dark for 4–12 h in 1.2 L (for *M. leidyi*) or 4 L (for *C. quinquecirrha*) acid-cleaned, polycarbonate containers filled with 0.2 μm filtered (Nucleopore® polycarbonate filters), low-nutrient Sargasso Sea water diluted with Nanopure Diamond (Barnstead®) water to *in situ* York River salinity (17–21 psu). The low DOM content (e.g. 40–50 μM DOC) in the experimental media reduced methodological error and improved precision of DOM measurements. Container sizes were determined based on results from preliminary trials showing no significant difference in *Mnemiopsis* NH_4^+ excretion rates between 1.2 and 4 L containers [one-way analysis of variance (ANOVA), $P > 0.05$, $n = 10$]. At the start of the experiment, one animal was randomly added to each experimental container (treatment) and the release of DOM and inorganic N and P determined by measuring changes in DOC, DON, DOP and inorganic constituents (nitrite [NO_2^-], nitrate [NO_3^-], NH_4^+ and PO_4^{3-}) in the water every 3–4 h. Water without animals was transferred from holding buckets to control containers in order to account for the small addition of nutrients associated with transferring the animal into each chamber. At the completion of the experiment, medusae and ctenophores were removed and their wet and dry weights, and elemental composition determined according to Condon and Steinberg (Condon and Steinberg, 2008).

DOM and inorganic release rates were expressed as a function of body mass according to the allometric equation:

$$Y = a_1 W^b \quad (1)$$

and expressed as a dual function of body mass and temperature by the multiple regression equation:

$$\log Y = a + a_1 \log W + a_2 T \quad (2)$$

where Y is the release rate of organic or inorganic excretia (μmol ind.$^{-1}$ h^{-1}), W the dry weight (g DW), b the exponent relating excretion to body mass and a, a_1 and a_2 are constants (Ikeda, 1985; Nemazie *et al.*, 1993). Release rates were further characterized by comparing C, N and P ratios of released DOM and inorganic nutrients between the two gelatinous species and with the Redfield ratio.

DOM and inorganic release rates were normalized to gelatinous zooplankton dry weight (μmol g DW^{-1} h^{-1}), allowing comparison to rates reported for other gelatinous zooplankton species. Elemental turnover rates were also determined on individual medusae and ctenophores (% released day^{-1}) by dividing excretion rates (μmol ind.$^{-1}$ h^{-1}) by respective amounts of body C, N and P (μmol ind.$^{-1}$) then multiplying by 24 h.

The possible influence of bacterial uptake of gelatinous zooplankton DOM metabolites on measured excretion rates was investigated by measuring bacterial production in a subset of excretion chambers ($n = 10$). Using a bacterial growth efficiency of 30% (R. Condon, unpublished data), these measurements suggest that our DOM release rates were only slightly underestimated, with bacteria potentially utilizing between 1% and 13% of DOC released by *M. leidyi* ctenophores and *C. quinquecirrha* medusae during incubations, and thus we do not correct for bacterial uptake.

Field surveys

We combined data from laboratory experiments with field surveys to evaluate the contributions by *M. leidyi* and *C. quinquecirrha* populations to DOC, DIN and DIP pools in the York River. Field surveys were conducted during 2004–2006 along a salinity gradient in the lower York River, and measured species composition and biomass of gelatinous zooplankton, DOM (C, N and P) and inorganic nutrients. Gelatinous zooplankton were collected during 2 min, double-oblique plankton

tows in surface waters (0–2 m). Biomass of *M. leidyi* and *C. quinquecirrha* populations (g DW m^{-3}) was determined by converting individual ctenophore and medusae sizes to DW using empirically derived regressions (Condon and Steinberg, 2008). For DOM and inorganic nutrients, bulk concentrations were determined in the laboratory on water collected from the top 1 m in 2 L, dark, acid-washed polycarbonate bottles.

Daily population release (DPR) of DOC and inorganic nutrients (μmol m^{-3} day^{-1}) were determined as follows:

$$\mathrm{DPR} = \Upsilon \times \mathrm{DWP} \times 24 \quad (3)$$

where Υ is the temperature-corrected, weight-specific release rate from experiments [μmol g $(DW)^{-1}$ h^{-1}; equation (1)], DWP is population biomass for ctenophores and medusae (g DW m^{-3}) and 24 is a conversion factor for hourly into daily release rates. Daily contributions made to bulk and labile DOC, and DIN and DIP pools (% contributed day^{-1}) were determined by dividing daily population release rates by respective organic and inorganic nutrient concentrations (μmol m^{-3}). Labile DOC pools were estimated using a conversion factor of 2.8% of bulk DOC, which was based on net bacterial DOC uptake over the initial and 5-day timepoints of experimental incubations conducted by Raymond and Bauer (Raymond and Bauer, 2000) during summer in the lower York River estuary. The contribution of inorganic nutrients by gelatinous zooplankton to primary production was also assessed under conditions of phytoplankton nutrient limitation according to Sin *et al.* (Sin *et al.*, 1999). Prior studies of zooplankton in the York River demonstrated that upriver, mesohaline waters support significantly higher densities and biovolumes of gelatinous zooplankton when compared with downriver, polyhaline regions near the mouth of the river. Thus, the impacts of gelatinous zooplankton on DOC and inorganic nutrient pools were based on comparisons between upriver and downriver locations (stations 1 and 2 for upriver and stations 3 and 4 for downriver) (Condon and Steinberg, 2008). Although exposure to a wide salinity gradient could also affect DOM and inorganic excretion by gelatinous zooplankton populations, this effect was likely minor in this study because salinity differences between upriver and downriver locations were small (3.8 ± 2.6 psu; R. Condon, unpublished data).

Chemical analyses

Water subsampled from incubation bottles was filtered through pre-combusted (500°C for 4 h) Whatman GF/F filters, and dissolved nutrients determined in the filtrate. DOC concentrations were measured via high-temperature combustion on a Shimadzu 5000A Total Organic Carbon (TOC) analyzer using potassium hydrogen phthalate ($C_8H_5O_4K$) as standard (Peltzer *et al.*, 1996). Prior to combustion, 6 N HCl was added to 5 mL samples (pH <3) and sparged for 2 min with C ultra free air to ensure removal of dissolved inorganic C. DOC concentrations were based on the best three of a maximum of five column injections within an analytical detection error set to a peak area standard deviation of ± 120 or coefficient of variance of 0.8%. Samples with ± 1.5 μM error were reanalyzed. In addition, data precision, instrument accuracy and platinum catalyst efficiency were quality checked with low C (1–2 μM DOC) and deep Sargasso Sea water (44–46 μM DOC) reference standards provided by the C reference material program, University of Miami (http://www.rsmas.miami.edu/groups/biogeochem/CRM.html) (Sharp, 2002).

Total dissolved N (TDN) and P (TDP) were analyzed by persulfate oxidation (Bronk *et al.*, 2000; Sharp, 2002), NO_3^- by the spongy cadmium (Cd) method, and NO_2^- and PO_4^{3-} were measured on a Lachat™ QuikChem 8500 nutrient autoanalyzer (Koroleff, 1983). During analysis, the conversion of NO_3^- to NO_2^- by Cd catalyst was monitored and columns regenerated if reduction efficiency was $<97\%$. NH_4^+ was measured on a Shimadzu UV-1601 spectrophotometer by the manual hypochlorite method (Koroleff, 1983) using standard curves corrected for sample salinity. DON and DOP were determined by calculating the difference between total dissolved and inorganic fractions (Sharp, 2002).

Particulate organic C and N content of ctenophores used in experiments were measured on a Carlo Erba EA-1108 CHN Elemental Analyzer (Condon and Steinberg, 2008), and C and N content in medusae were determined following Nemazie *et al.* (Nemazie *et al.*, 1993). Particulate organic P content of jellyfish was estimated using a literature dry weight-specific conversion factor of 0.06% (Kremer, 1975).

Statistical analyses

Data describing gelatinous zooplankton release rates and ratios were analyzed using single and multiple linear regressions, ANOVA and *t*-tests using Minitab statistical software (level of significance of $\alpha < 0.05$). Regressions were checked for outliers using Cook's *D* statistic and, where applicable, removal of outliers in analyses are denoted in the text. Differences in weight-specific release and turnover rates between both gelatinous species were determined using two-sample *t*-tests.

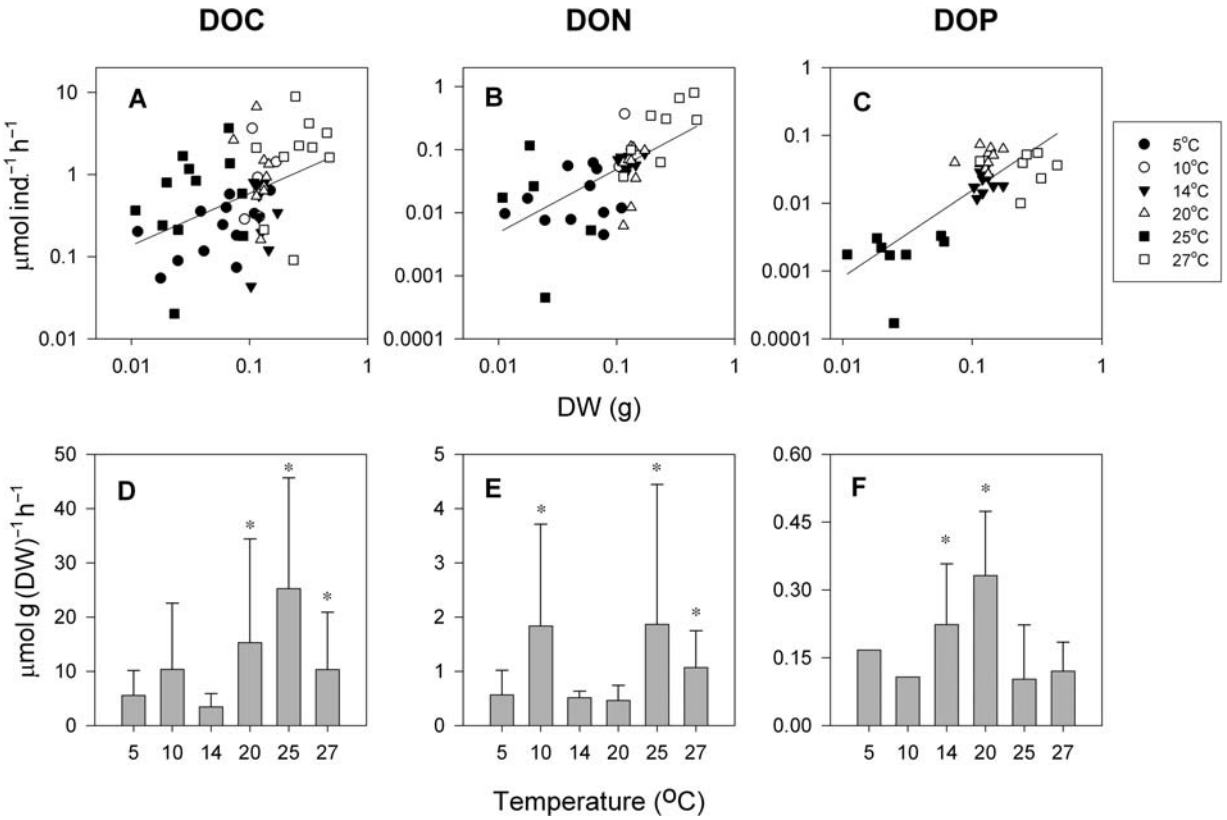

Fig. 1. Release rates of DOM by *M. leidyi* ctenophores (μmol ind.$^{-1}$ h^{-1}). **(A)** DOC, **(B)** DON and **(C)** DOP. Ctenophore weight-specific release (μmol g DW^{-1} h^{-1}) across temperatures of (**D**) DOC, (**E**) DON and (**F**) DOP. Error bars are ±1 SD. Sample size (*n*) for each temperature given in Table I. DW, dry weight. *denotes temperatures with significantly higher DOM release rates, $P < 0.05$.

Differences in York River DOM, DIN and DIP concentrations between upriver and downriver sites were determined using nested ANOVAs with date and species nested in location. If ANOVAs were significant, *post hoc* pairwise comparison of means using Tukey's HSD tests were performed (Quinn and Keough, 2002). Prior to analyses, data were checked for normality and homogeneity of variance using the Kolmogorov–Smirnov tests, and box plots and histograms of data and residuals. Non-conforming data were converted using $\log_{10}$ or fourth-root transformations (Quinn and Keough, 2002).

RESULTS

DOM release rates

Both species of gelatinous zooplankton released relatively high amounts of their total metabolites as DOC, DON and DOP, with higher release of DOC vs. DON and DOP (*M. leidyi*: $P < 0.001$, Fig. 1; *C. quinquecirrha*: $P < 0.05$, Fig. 2). Using data across all temperatures, weight-specific DOC release rates were similar between ctenophores and scyphomedusae (Table II). Release per individual animal ranged 0.02–8.86 μmol DOC ind.$^{-1}$ h^{-1} for *M. leidyi* (Fig. 1A) and 1.2–58.3 μmol DOC ind.$^{-1}$ h^{-1} for *C. quinquecirrha* (Fig. 2A), although data were highly variable (Table II). Similarly, at 14°C and temperatures >25°C, weight-specific DOC release was the same in both species ($P = 0.84$, Figs 1D and 2D). Release per individual animal ranged 0.001–0.8 μmol DON ind.$^{-1}$ h^{-1} and 0.0001–0.07 μmol DOP ind.$^{-1}$ h^{-1} for *M. leidyi* (Fig. 1B and C), and 0.7–5.0 μmol DON ind.$^{-1}$ h^{-1} and 0.1–1.3 μmol DOP ind.$^{-1}$ h^{-1} for *C. quinquecirrha* (Fig. 2B and C). Weight-specific DON release rates were higher than DOP rates for *M. leidyi* ctenophores ($P < 0.001$, Fig. 1E and F) and for *C. quinquecirrha* medusae ($P < 0.05$, Fig. 2E and F, Table II). Weight-specific excretion of DON by medusae was higher than for ctenophores ($P < 0.05$), whereas DOP excretion was the same between species ($P = 0.82$).

For *M. leidyi*, DOC, DON and DOP release increased with body mass, but only DOC release was significantly positively correlated with temperature ($P <$

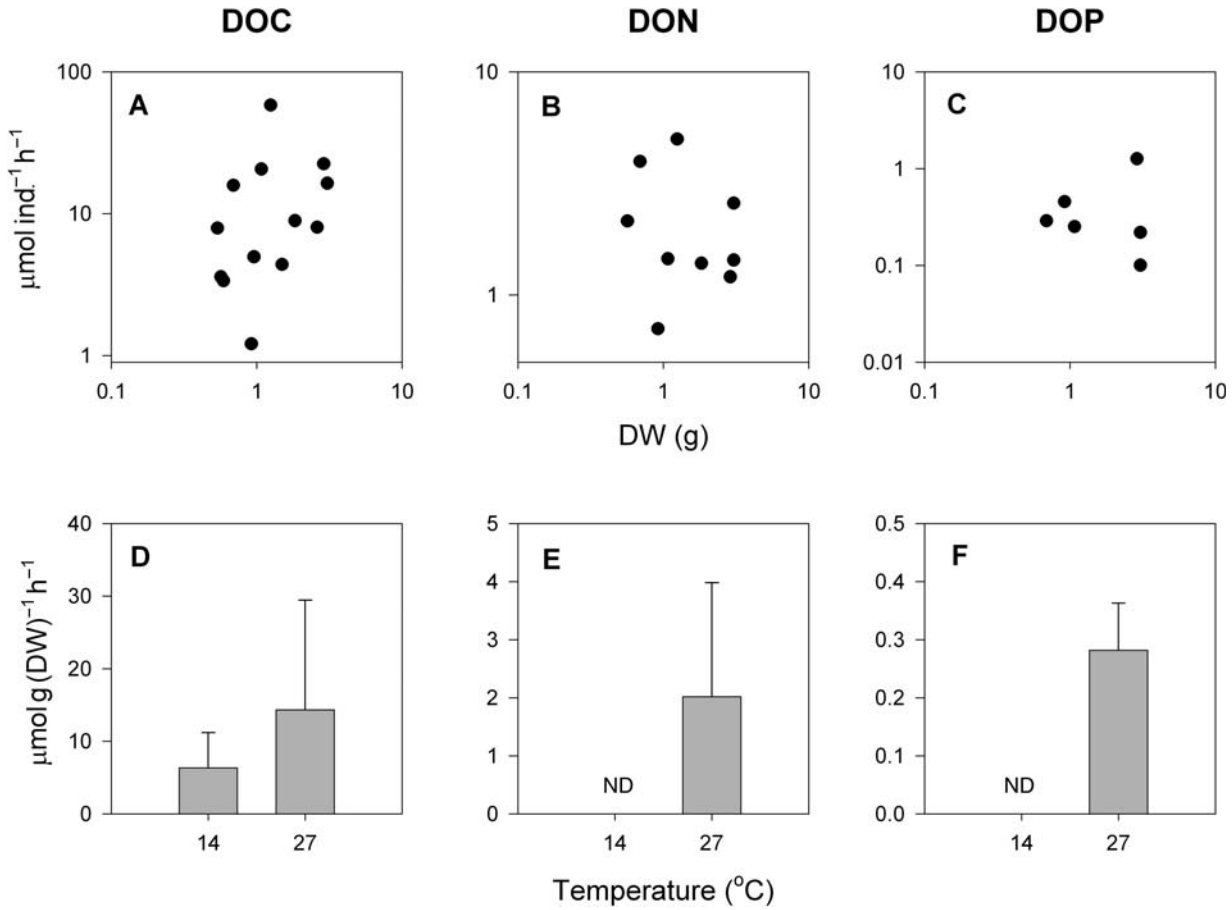

Fig. 2. Release rates of DOM at 27°C by individual *C. quinquecirrha* scyphomedusae (µmol ind.$^{-1}$ h^{-1}). **(A)** DOC, **(B)** DON and **(C)** DOP. Medusae weight-specific release (µmol g DW^{-1} h^{-1}) across temperatures of (**D**) DOC, (**E**) DON and (**F**) DOP. Error bars are ±1 SD. Sample size (*n*) for each temperature given in Table I. DW, dry weight. ND, no data.

Table II: Linear and multiple linear regressions of DOM and inorganic nutrient release rates by Mnemiopsis ctenophores and Chrysaora medusae

					$Y = a_1 W^b$			Log $Y = a_0 + a_1 \log W + a_2 T$			
	Var.	T (°C)	n	WS Rel. (µmol g DW^{-1} h^{-1})	a_1	b	r^2	a_0	a_1	a_2	r^2
ML	DOC	5–27	59	12.0 ± 15.0	2.54	0.63	0.18**	−0.09	0.53	0.023	0.29**
	DON	5–27	45	0.8 ± 1.0	0.49	1.00	0.39**	−0.53	0.93	0.010	0.40**
	DOP	14–27	35	0.2 ± 0.2	0.29	1.28	0.62**	−0.09	1.24	−0.023	0.66**
	NH_4^+	5–27	65	4.9 ± 5.5	1.48	0.79	0.23**	−0.08	0.65	0.045	0.60**
	PO_4^{3-}	5–27	58	0.3 ± 0.3	0.18	0.83	0.48**	−1.22	0.73	0.023	0.66**
CQ	DOC	14–27	13	11.3 ± 12.6	7.67	0.64	0.15^{NS}	0.44	0.54	0.021	0.24^{NS}
	DON	27	9	2.0 ± 1.4	1.99	−0.19	0.04^{NS}	ND			
	DOP	27	6	0.3 ± 0.2	0.32	−0.08	0.00^{NS}	ND			
	NH_4^+	14–27	11[c]	2.5 ± 2.5	0.74	0.91	0.08^{NS}	−1.81	0.91	0.079	0.89**
	PO_4^{3-}	14–27	12[c]	0.2 ± 0.1	0.18	0.94	0.60*	−1.18	0.89	0.021	0.81**

Errors are ±1 standard deviation. ML, *Mnemiopsis leidyi*; CQ, *Chrysaora quinquecirrha*; *Y*, gelatinous zooplankton release rate (µmol ind.$^{-1}$ h^{-1}); DOC, dissolved organic carbon; DON, dissolved organic nitrogen; DOP, dissolved organic phosphorus; NH_4^+, ammonium; PO_4^{3-}, phosphate; *W*, dry weight (g); *T*, temperature (°C); WS Rel., mean weight-specific release rate of DOM or inorganic nutrients; *a*, constants; *b*, slope of the regression lines relating organic or inorganic release to body mass; var., organic or inorganic variable; [c]outliers removed from analyses (Fig. 3); *n*, sample size; r^2, correlation coefficient; *$P < 0.05$; **$P < 0.001$; NS, non-significant; ND, no data.

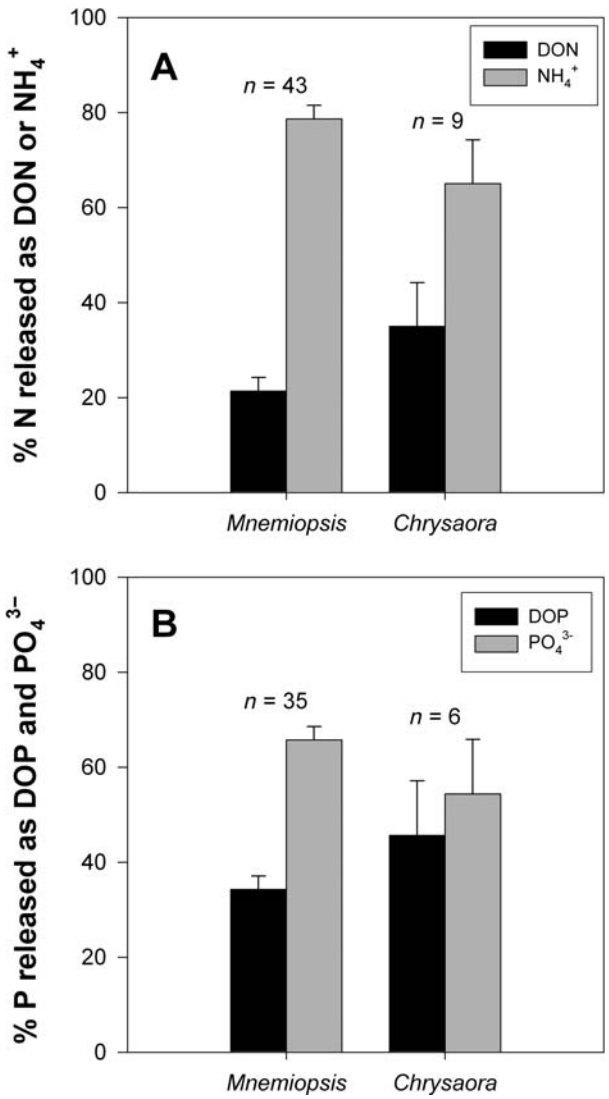

Fig. 3. Comparison of inorganic vs. organic nitrogen (N) and phosphorus (P) release by ctenophores and medusae. **(A)** Percent total dissolved N released as DON and ammonium (NH_4^+), and **(B)** percent total dissolved P released as DOP and phosphate (PO_4^{3-}), by *M. leidyi* ctenophores across all experimental temperatures and *C. quinquecirrha* scyphomedusae at 27°C. Error bars are ± 1 SE.

0.05, Table II, data not shown). Slopes of log-transformed data that regressed body mass against DOC, DON and DOP release rates indicated that weight-specific release rates decreased with body size for DOC ($b = 0.63$), were independent of body size for DON ($b = 1.00$) and increased with size for DOP ($b = 1.28$) (Table II). Multiple regressions of body mass and temperature slightly improved predictability of DOC release by ctenophores (Table II). In contrast, release rates of DOC, DON and DOP by *Chrysaora* medusae release were not related to body size, and DOC was not related to temperature (Table II; no temperature-dependent DON and DOP release rates were measured), although due to small sample sizes (Table I), the statistical power of the tests may have been too low to detect differences.

Mean daily DOC and DON turnover rates were higher in *M. leidyi* compared with *C. quinquecirrha* (Table III), and ranged 0.9–127% body C day^{-1} and 0.4–98.7% body N day^{-1} for ctenophores and 0.3–12.2% C day^{-1} and 0.5–6.9% N day^{-1} for medusae. There was no significant difference in mean body P turnover between species (*M. leidyi*: 0.8–79.4% P day^{-1}, *C. quinquecirrha*: 1.6–24.7% P day^{-1}; Table III, $P = 0.19$). Ctenophore C turnover was negatively correlated to body mass and positively correlated to temperature, although the relationship was weak (multiple $r^2 = 0.15$, Table III). Turnover of body N and P by ctenophores was not related to body mass or temperature (Table III). Similarly, C and P turnover by *C. quinquecirrha* was not related to body size or temperature, but medusa N turnover decreased with increasing body size (27°C only; Table III).

Most of the TDN and TDP excreted by medusae and ctenophores were NH_4^+ and PO_4^{3-}, although sizeable proportions of DON and DOP were released by both gelatinous zooplankton species (Fig. 3). DON comprised a higher proportion of TDN released by *C. quinquecirrha* medusae (mean = 35%) compared with *M. leidyi* ctenophores (mean = 21%) (Fig. 3A). Similarly, DOP comprised a higher proportion of TDP released by medusae (mean = 46%) when compared with ctenophores (mean = 34%). Proportions of DOP released by *Chrysaora* were similar to PO_4^{3-} released (Fig. 3B).

Excretion of inorganic nutrients

Excretion rates of NH_4^+ and PO_4^{3-} by individual *C. quinquecirrha* were typically higher than *M. leidyi*, ranging from 0.1 to 22.6 μmol NH_4^+ $ind.^{-1}\,h^{-1}$ and 0.1–0.9 μmol PO_4^{3-} $ind.^{-1}\,h^{-1}$ for medusae and 0.02–2.9 μmol NH_4^+ $ind.^{-1}\,h^{-1}$ and 0.003–0.1 μmol PO_4^{3-} $ind.^{-1}\,h^{-1}$ for ctenophores (Figs 4A, B and 5A, B). However, there was no significant difference in weight-specific excretion rates between both species (NH_4^+: $P = 0.096$, PO_4^{3-}: $P = 0.125$, Table II). NH_4^+ and PO_4^{3-} excretion rates increased significantly with dry body weight (g) and temperature (°C) for both species (Fig. 5, Table II), but there was no difference between ctenophore weight-specific excretion of inorganic nutrients at temperatures ≥20°C (Fig. 4). The slopes of log-transformed regressions relating body mass to inorganic N and P excretion rates were similar within each species, but slightly higher for *C. quinquecirrha* compared with *M. leidyi* (Table II), suggesting a decrease in

Table III: Linear and multiple regressions of daily DOM and inorganic nutrient turnover rates by Mnemiopsis ctenophores and Chrysaora medusae

					$DT = a_1 W^b$			$\log DT = a_0 + a_1 \log W + a_2 T$			
	Var.	Temp (°C)	*n*	DT (% released day^{-1})	a_1	b	r^2	a_0	a_1	a_2	r^2
ML	DOC	5–27	59	25.2 ± 30.4	6.7	−0.29	0.05^{NS}	0.39	−0.38	0.020	0.15*
	DON	5–27	45	18.3 ± 19.2	14.1	0.09	0.01^{NS}	1.01	0.05	0.006	0.02^{NS}
	DOP	14–27	35	26.1 ± 18.5	36.3	0.28	0.07^{NS}	2.00	0.24	−0.023	0.16^{NS}
	NH_4^+	5–27	49	53.0 ± 42.7	31.6	−0.07	0.004^{NS}	0.71	−0.31	0.035	0.54**
	PO_4^{3-}	5–27	58	42.6 ± 31.6	21.9	−0.17	0.04^{NS}	0.87	−0.27	0.023	0.36**
CQ	DOC	14–27	13	2.9 ± 3.3	1.99	−0.37	0.06^{NS}	−0.15	−0.46	0.021	0.16^{NS}
	DON	27	9	2.4 ± 2.4	2.39	−1.19	0.62*	ND			
	DOP	27	6	14.0 ± 9.9	16.2	−1.08	0.44^{NS}	ND			
	NH_4^+	14–27	14	3.0 ± 3.0	1.13	0.91	0.16^{NS}	−1.84	0.42	0.087	0.87**
	PO_4^{3-}	14–27	14	11.4 ± 5.5	9.64	0.21	0.08^{NS}	0.47	0.08	0.024	0.54*

Errors are ±1 SD. DT, daily turnover (% released day^{-1}); for remainder of abbreviations see Table II.

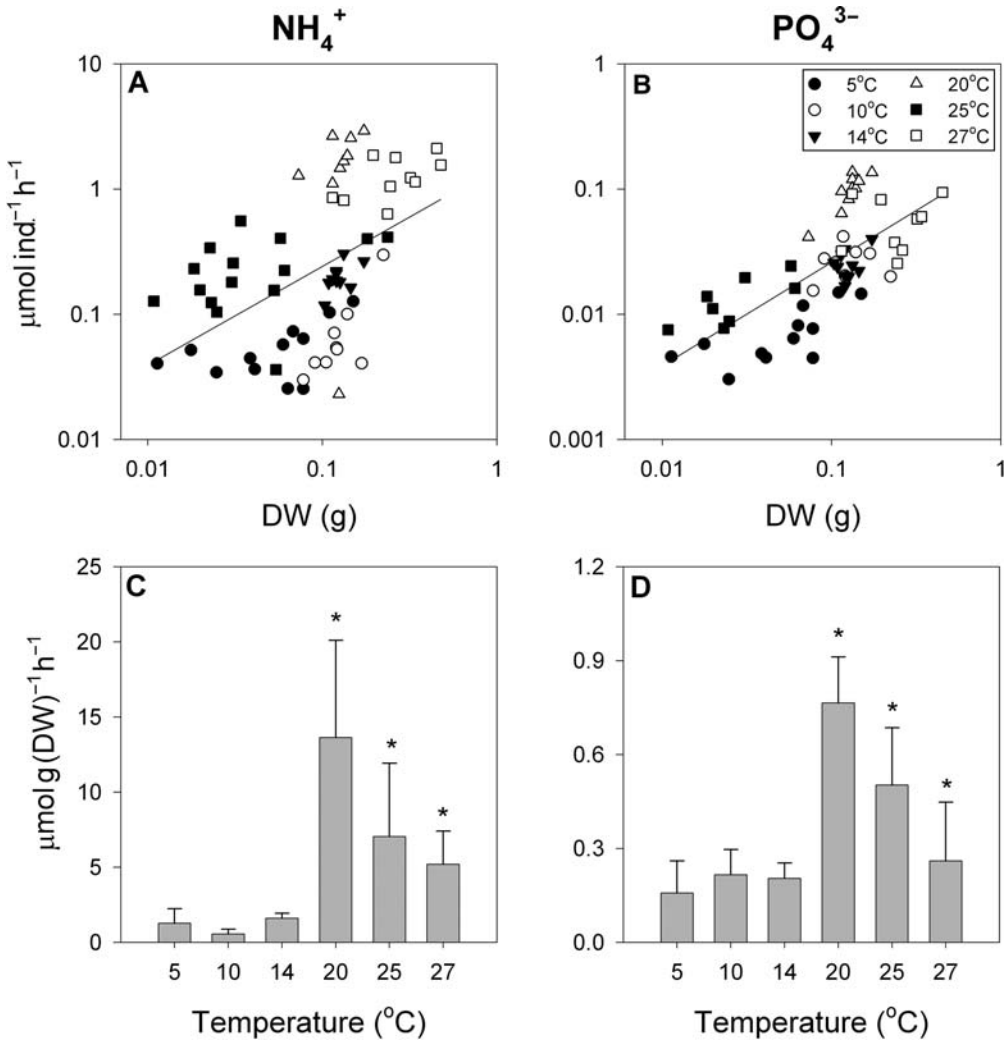

Fig. 4. Excretion rates of **(A)** ammonium (NH_4^+) and **(B)** phosphate (PO_4^{3-}) by *M. leidyi* ctenophores (µmol ind.$^{-1}$ h^{-1}). Ctenophore weight-specific excretion (µmol g DW^{-1} h^{-1}) of **(C)** NH_4^+ and **(D)** PO_4^{3-} across experimental temperatures. Sample size (*n*) for each temperature given in Table I. Error bars are ±1 SD. DW, dry weight. *$P < 0.05$.

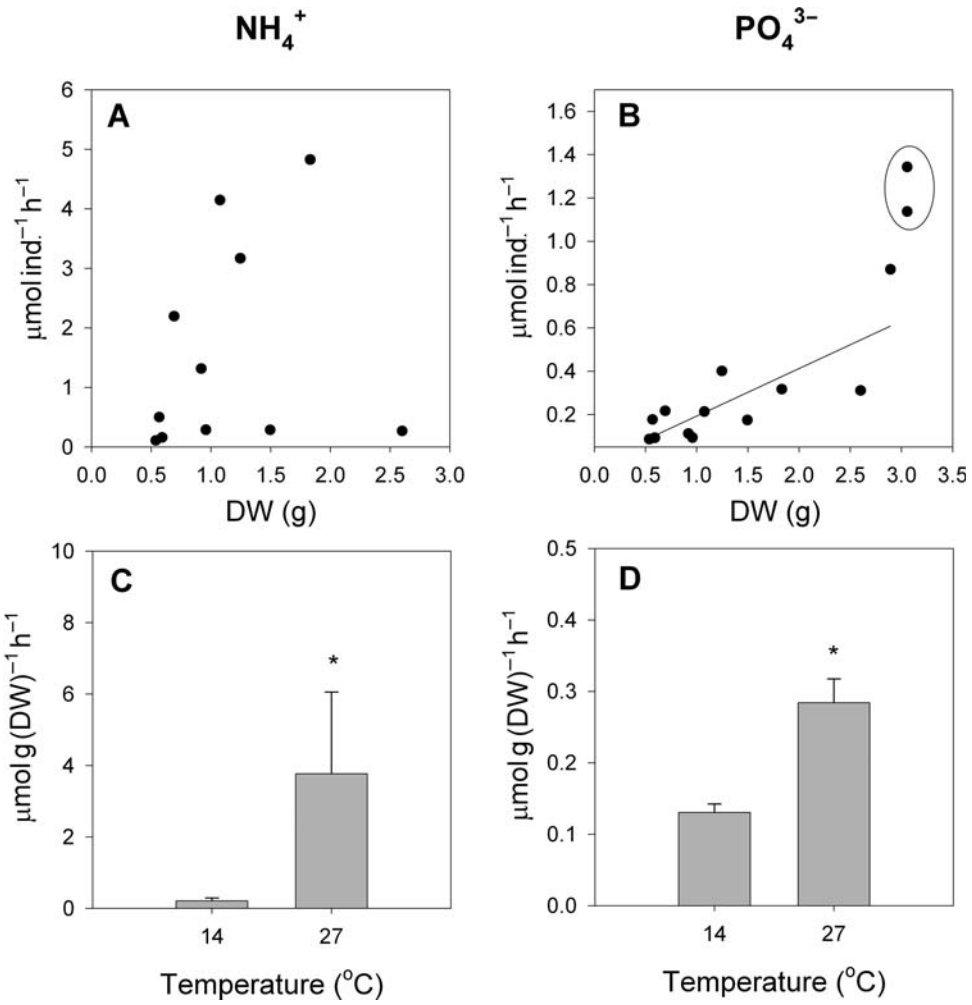

Fig. 5. Excretion rates of **(A)** ammonium (NH_4^+) and **(B)** phosphate (PO_4^{3-}) at 27°C by *C. quinquecirrha* medusae (µmol ind.$^{-1}$ h^{-1}). Medusae weight-specific excretion (µmol g DW^{-1} h^{-1}) of **(C)** NH_4^+ and **(D)** PO_4^{3-} across experimental temperatures. Sample size (*n*) for each temperature given in Table I. Error bars are ± 1 SD. DW, dry weight. *$P < 0.05$. Circled data indicate outliers removed from statistical analyses (Table II).

weight-specific excretion rate with an increase in body size.

Daily turnover of NH_4^+ and PO_4^{3-} by *M. leidyi* was greater than for *C. quinquecirrha* (NH_4^+: $P < 0.001$; PO_4^{3-}: $P < 0.001$). Inorganic nutrient turnover by ctenophores was high with similar turnover rates for NH_4^+ and PO_4^{3-} ($P = 0.47$, Table III). For *C. quinquecirrha*, inorganic N turnover was comparable to DON turnover, but significantly lower than inorganic P turnover ($P < 0.001$, Table III). Multiple regressions of dry weight and temperature showed that NH_4^+ and PO_4^{3-} turnover by *M. leidyi* were negatively correlated with body mass but positively correlated to temperature (Table III). In contrast, NH_4^+ and PO_4^{3-} turnover by medusae were positively correlated to both body size and temperature (Table III).

C, N, and P stoichiometry of DOM and inorganic nutrients

DOC:DON ratios of DOM released by *M. leidyi* averaged 29:1, higher than Redfield (6.6C:1N), but were highly variable, ranging 0.62–472:1 (Fig. 6A). In comparison, *Chrysaora* DOC:DON ratios were closer to Redfield C:N, averaging 8.1 (Fig. 6A). DOC:TDN ratios (mean = 2.8:1) were significantly lower than DOC:DON for *M. leidyi* ($P < 0.001$) but were similar for medusae (mean = 5.6; Fig. 6B). In addition, DOC:TDN release ratios by *M. leidyi* were negatively correlated to both increasing body size and increasing temperature ($P < 0.05$). For *M. leidyi*, DOC:DOP release ratios were variable but on average simultaneous release of DOC and DOP (118:1, Fig. 6C) was similar to C:P Redfield stoichiometry (106:1). Multiple

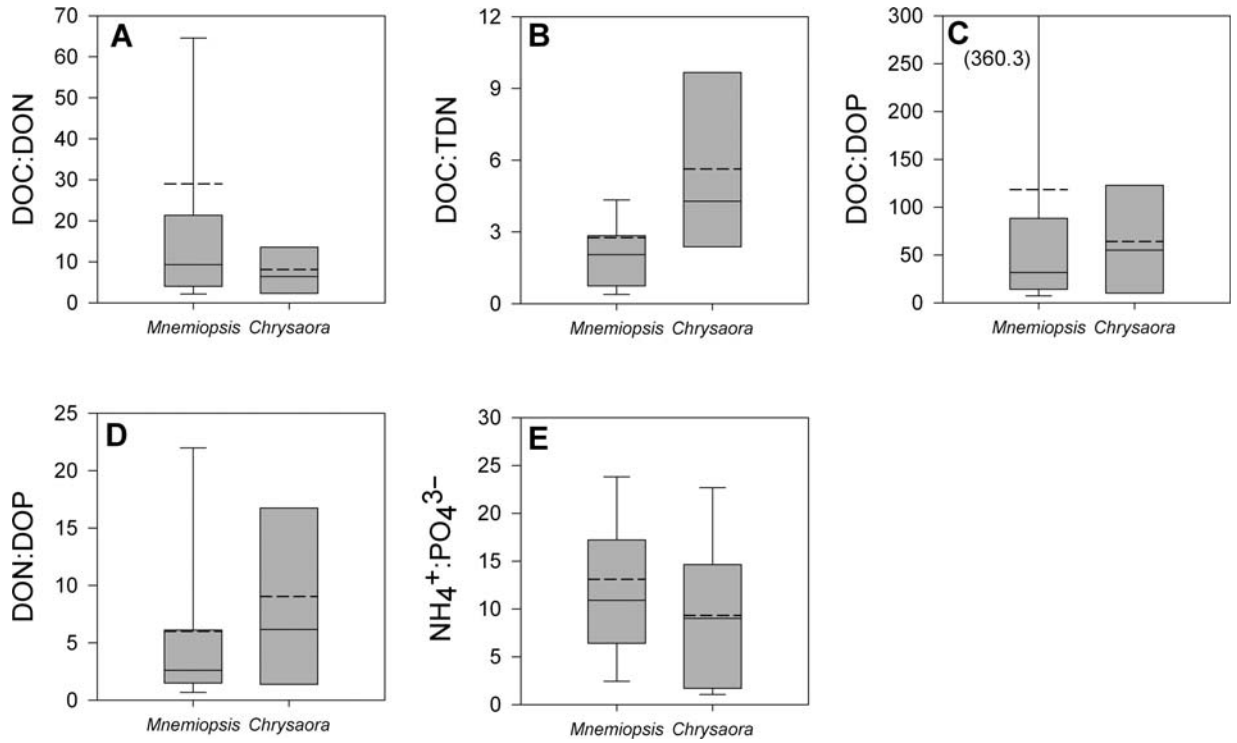

Fig. 6. Box plots comparing organic and inorganic release ratios by individual *M. leidyi* ctenophores and *C. quinquecirrha* medusae. (**A**) DOC to DON, (**B**) DOC to TDN, (**C**) DOC to DOP, (**D**) DON to DOP and (**E**) ammonium (NH_4^+) to phosphate (PO_4^{3-}) release ratios. Box and whiskers represent 10th, 25th, median, 75th and 90th percentiles. Outliers not shown. Out of range value in parentheses. Vertical dashed lines represent average release ratio.

regressions of DOC:DOP decreased with ctenophore dry weight ($P < 0.05$) and increased with temperature ($P < 0.05$), although correlations were weak ($r^2 = 0.43$). Mean release ratios of DON and DOP (6:1) were below Redfield N:P ratio (16:1) for *M. leidyi* ctenophores and *C. quinquecirrha* medusae (9:1, Fig. 6D). Linear regressions relating DOC:DON and DON:DOP release rates with body size and temperature were non-significant for both species.

In general, NH_4^+:PO_4^{3-} excretion ratios were similar or slightly below Redfield stoichiometry of 16N:1P for *M. leidyi* (mean = 13.1) and *C. quinquecirrha* (mean = 9.3), although data exhibited high variability (Fig. 6E). NH_4^+:PO_4^{3-} excretion ratios increased significantly with temperature for both species ($P < 0.001$), but were not related to body weight.

York River bulk DOC and inorganic nutrient concentrations

Bulk DOC concentrations were typically between 200 and 400 μM and were higher upriver compared with downriver (log-transformed, $P < 0.001$; Fig. 7A and B). In general, York River DOC (μM) followed a seasonal pattern at both locations with lowest DOC concentrations observed during summer (May–July), followed by an increase during autumn (August–December) before reaching a maximum during late winter and spring (January–April) (Fig. 6A and B); spring 2005 (March–April) with low DOC was an exception.

Inorganic N and P concentrations varied greatly with season (Fig. 7C–F). Within sample dates, there was no significant difference in concentrations of NH_4^+ (Fig. 7C and D) and NO_x ($NO_2^- + NO_3^-$) between upriver and downriver locations; however, there were significantly higher PO_4^{3-} concentrations upriver compared with downriver ($P < 0.05$; Fig. 7E and F). DIN concentrations were high during late winter–spring (January–April), but both NH_4^+ (Fig. 7C and D) and NO_x were low and often below detection during summer months (May–August). In contrast, PO_4^{3-} concentrations were low and often-below analytical detection limits during spring (January–April), and significantly higher during summer months (July–September; Fig. 7E and F). DIN:DIP on bulk inorganic N ($NO_x^- + NH_4^+$) and P pools were high during spring (>100N:P), resulting in phytoplankton P-limitation throughout the York River. During summer, DIN:DIP ratios were significantly lower upriver (5.8:1) compared with downriver (13.7:1, $P = 0.04$).

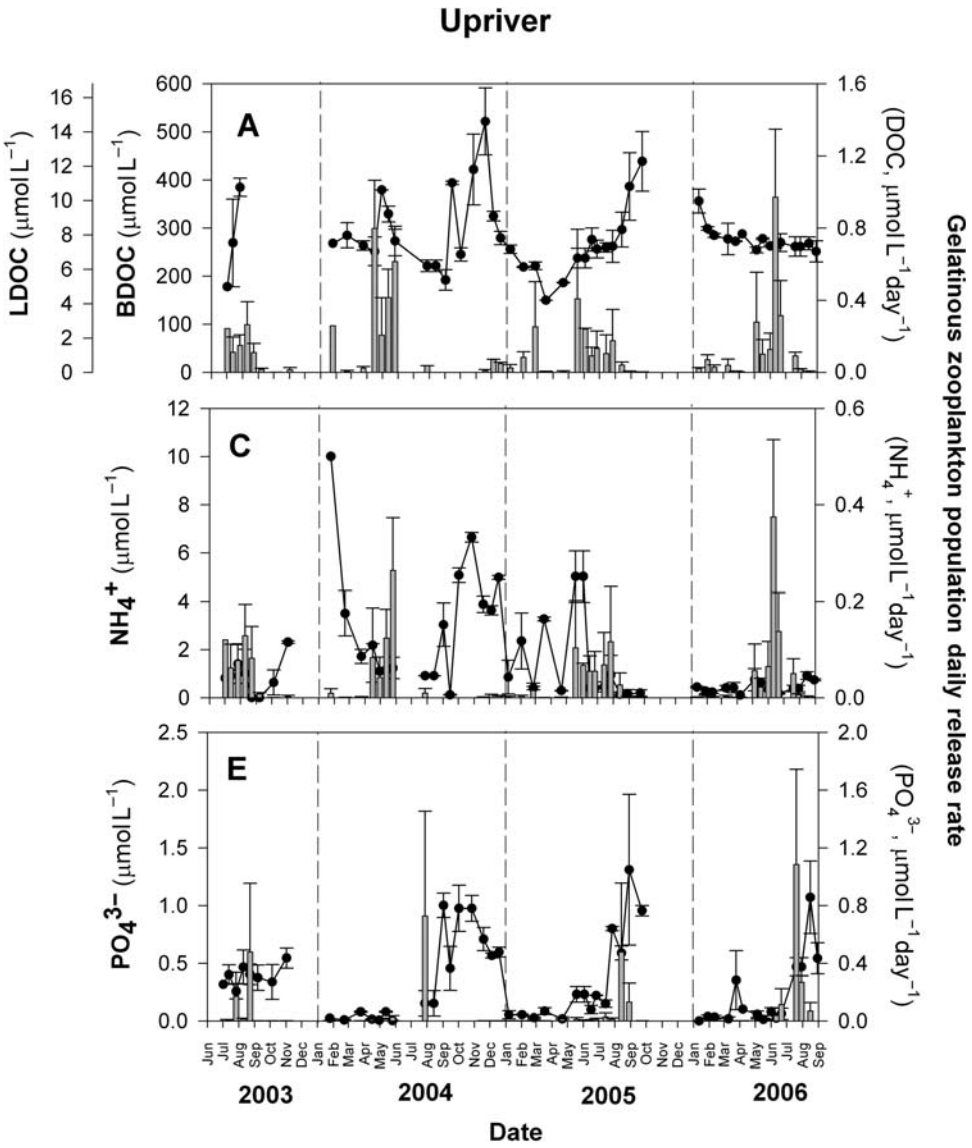

Fig. 7. Lines signify upriver and downriver concentrations of **(A** and **B)** DOC, **(C** and **D)** ammonium (NH_4^+) and **(E** and **F)** phosphate (PO_4^{3-}) (µmol L^{-1}). Bars show the contributions made by gelatinous zooplankton populations (µmol L^{-1} day^{-1}) to DOC, NH_4^+ and PO_4^{3-} pools in the York River. Upriver and downriver regions are located at stations 1 (37° 20.046′N, 076° 36.052′W) and 2 (37° 14.273′N, 076° 30.274′W) and stations 3 (37° 14.233′N, 076° 14.232′W) and 4 (37° 14.535′ N, 076° 20.633′W), respectively, according to Condon and Steinberg (Condon and Steinberg, 2008). BDOC, bulk DOC; LDOC, labile DOC. LDOC defined as 2.8% of BDOC following Raymond and Bauer (Raymond and Bauer, 2000). Error bars are ±1 SD.

Gelatinous zooplankton biomass and contributions to DOC, DIN and DIP pools

Biomass of gelatinous zooplankton in the York River was dominated by *Mnemiopsis* ctenophores. High biomass of *M. leidyi* (g DW m^{-3}) was observed during summer and winter months, with significantly higher ctenophore biomass occurring upriver ($P < 0.001$). During summer, peak ctenophore biomass consistently occurred during May (average range 0.4–1.2 g DW m^{-3}) and June (average range 0.3–1.5 g DW m^{-3}), although high biomass occurred at other times. Winter biomass peaks usually occurred during January and February and were comparable to summer peaks (average range 0.02–1.2 g DW m^{-3}). *Chrysaora* medusae were present in the York River during July and August and primarily occurred at the upriver station. *Chrysaora* biomass was about an order of magnitude lower than that of ctenophores, and ranged 0.01–0.23 g DW m^{-3} during July and 0.002–0.14 g DW m^{-3} during August.

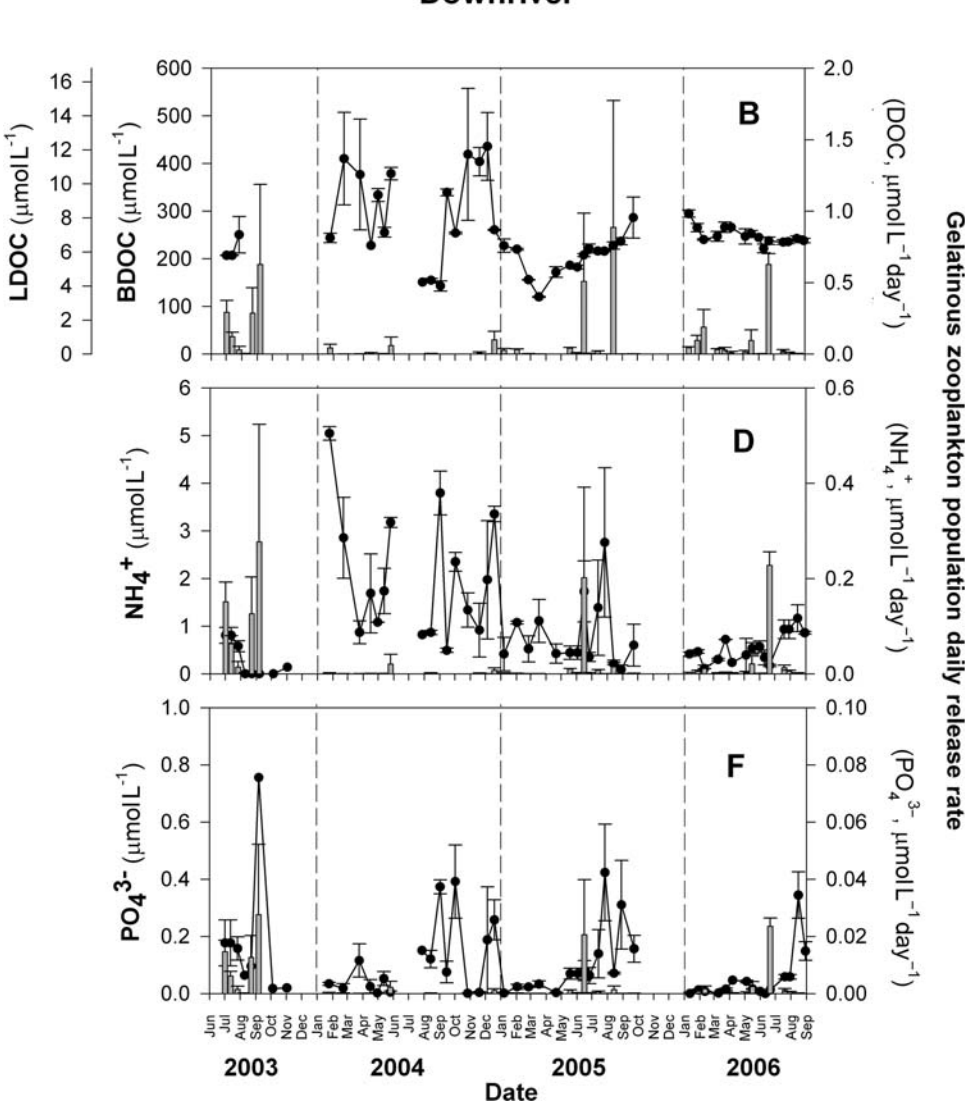

Fig. 7. (Continued).

Contributions by gelatinous zooplankton to DOC and dissolved inorganic N and P pools were greatest during *M. leidyi* blooms (Fig. 7A and B). In general, release of DOC by *Mnemiopsis* populations was higher upriver compared with downriver, with high release of DOC occurring during summer (May–July) and minor contributions during winter and spring (February–April) (Fig. 7A and B). Daily contributions by ctenophore populations to bulk DOC pools were low (<1%); however, when compared with labile DOC pools contributions were higher with maximum daily contributions ranging 18–29% (Fig. 7A). Daily contributions by *C. quinquecirrha* populations to bulk and labile DOC pools were low (<1%).

Maximum excretion of NH_4^+ by gelatinous zooplankton populations was highest upriver during summer (May–July) when annual bulk DIN concentrations were lowest (Fig. 7C and D). At these times, mean daily NH_4^+ production by *M. leidyi* populations represented 2–50% of York River NH_4^+ concentrations, and individual estimates often exceeded 100% (Fig. 7C and D). Net PO_4^{3-} excretion by gelatinous zooplankton was high upriver during late summer (July–August, Fig. 7E and F); however, during March–April, low release of PO_4^{3-} by ctenophore populations still represented a major daily source of DIP to bulk pools (57–119% of PO_4^{3-}; Fig. 7E and F).

Table IV: Comparison of weight-specific release rates of dissolved organic and inorganic nutrients for ctenophores and scyphomedusae species (adapted from Nemazie et al.*, 1993)*

Species	Temp (°C)	NH_4^+ WS Ex. (μmol g DW^{-1} h^{-1})	*b*	PO_4^{3-} WS Ex (μmol g DW^{-1} h^{-1})	*b*	DOC WS Rel. (μmol g DW^{-1} h^{-1})	*b*	DON WS Rel. (μmol g DW^{-1} h^{-1})	DOP WS Rel. (μmol g DW^{-1} h^{-1})	Ref.
Ctenophores										
Mnemiopsis leidyi	5–27	0.2–23.2	0.79	0.06–1.0	0.83	0.4–61.6	0.63	0.02–6.3	0.01–0.6	1
M. leidyi	18–27	3.0–4.8	0.74	ND						2
M. leidyi	10–24	0.4–1.5	0.89–1.16	0.08–0.20	0.53–1.11	0.18–0.86	ND	0.04–0.08	0.001–0.002	3
M. leidyi	17–24	0.06–0.11	ND	ND		ND		ND	ND	4
M. mccradyi	22	0.4–1.8	0.94	ND		ND		ND	ND	5
Ocyropsis sp.	25	0.7–0.9	0.76	ND		ND		ND	ND	6
Bolinopsis vitrea	25	0.25–1.1	1.06	ND		ND		ND	ND	6
Beroe ovata	25	2.3	0.93	ND		ND		ND	ND	6
Eurhamphaea vexillegera	25	0.5	0.93	ND		ND		ND	ND	6
Bathocyroe fosteri	9–13	0.1	1.20	ND		ND		ND	ND	7
Scyphomedusae										
Chrysaora quinquecirrha	14–27	0.1–7.8	0.91	0.12–0.44	0.89	1.3–46.4	0.64	0.4–5.7	0.03–0.5	1
C. quinquecirrha	18–28	3.5–5.0	1.00	ND		ND		ND	ND	2
Aurelia aurita	15	1.2–3.9	0.93	ND		ND		ND	ND	8
A. aurita						1.2–6.7	0.10			9
Pelagia noctiluca	21	1.9–4.1	0.90	ND		ND		ND	ND	10
P. noctiluca	12–23	0.3–7.2	0.65	0.8–1.5	1.06	ND		ND	ND	11

WS Ex., weight-specific excretion rate; WS Rel., weight-specific release rate; NH_4^+, ammonium; PO_4^{3-}, phosphate; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; DOP, dissolved organic phosphorus; *b*, slope of the regression lines relating organic or inorganic release to body mass; ND, no data; Ref. reference; 1, this study; 2, Nemazie *et al.* (1993); 3, Kremer (1977); 4, Park and Carpenter (1987); 5, Kremer (1982); 6, Kremer *et al.* (1986); 7, Youngbluth *et al.* (1988); 8, Schneider (1989); 9, Hansson and Norrman (1995); 10, Morand *et al.* (1987); 11, Malej (1989).

DISCUSSION

Comparison of excretion rates with previous studies

The general trends of higher NH_4^+ and PO_4^{3-} excretion rates with increased body size and temperature, and decreased ($b < 1.0$) or stable ($b = 1.0$) weight-specific inorganic excretion in larger animals are consistent with previous studies on gelatinous zooplankton excretion (Table IV). However, in our study, weight-specific release rates of DOM by both gelatinous species and NH_4^+ excretion by *M. leidyi* ctenophores are higher than in previous studies (Table IV). High inorganic excretion and nutrient turnover has been reported for gelatinous zooplankton fed on high prey concentrations (Kremer *et al.*, 1986), in short incubations (3 h), and at higher temperatures (>25°C) (Malej, 1989). In addition, measurements based on long incubations (>12 h) without correction for bacterial utilization of metabolites may underestimate DOM release rates (Hansson and Norrman, 1995). In this study, experimental incubations were short (4–12 h), bacterial uptake of DOM was low and release rates were measured on recently fed animals. Moreover, inorganic N and P excretion rates by *Chrysaora* and PO_4^{3-} excretion rates by ctenophores were similar to previous studies. We suggest that higher weight-specific excretion rates of inorganic N by ctenophores were primarily due to release of excess assimilated N as shown by high daily turnover rates of body N as NH_4^+.

Factors controlling DOM excretion by gelatinous zooplankton

Both *M. leidyi* ctenophores and *C. quinquecirrha* medusae released high quantities of DOC. Released DON and DOP also comprised a sizeable fraction of the total N and P released. Comparisons of DOP released on a per-individual and dry-weight basis were similar for ctenophores and medusae. However, daily turnover rates of DOC and DON were higher in ctenophores than in the medusae, and the ratios in which these organic compounds were released differed between the species. Ultimately, the turnover of assimilated C, N and P elements is linked to both the metabolic conditions (e.g. temperature) and the elemental stoichiometric requirements of the animal (Sterner and Elser, 2002). We suggest that differences in the release of DOC and DON observed between the two species were related to the production of mucus in ctenophores and retention of organic C and N for body structural components and nematocysts in scyphomedusae.

Mnemiopsis released DOM with high organic C content as indicated by significantly higher release of DOC compared with DON. High release of DOC by gelatinous zooplankton has been attributed to their "leaky" nature (Kremer, 1977), and to mucus production (Hansson and Norrman, 1995; Steinberg *et al.*, 2000), and these attributes may have driven the high variability in DOM release rates observed in this study. Lobate ctenophores, such as *M. leidyi*, primarily use mucus-lined lobes to capture and digest prey (Costello *et al.*, 1999). As a result, mucus production is key for maintaining daily elemental body requirements via assimilation of prey. The biochemical composition of *M. leidyi* mucus is unknown, but colloids released by corals and scyphomedusae are composed of glycoproteins that are C-rich relative to N due to their high carbohydrate content (Ducklow and Mitchell, 1979; Hansson and Norrman, 1995; Cohen and Forward, 2003). If mucus release is the primary pathway for DOC and DON production, then organic C and N release rates would be independent of the physical controls of metabolism, and related more to biometric parameters involved in ctenophore feeding (e.g. surface area on lobes) because the elemental composition and production of mucus are independent of intracellular physiology (Heeger and Möller, 1987). Our results indicate that both DOC and DON release by ctenophores were significantly positively correlated with body size; however, weight-specific DOC and DON release was either weakly or not correlated with temperature and remained the same with body size. Furthermore, DOC:DON release ratios were not related to body size and temperature, suggesting that ctenophores primarily release DOC and DON compounds of similar elemental proportions independent of intracellular metabolism. Collectively, these results support the hypothesis that mucus production is the principal mechanism of DOC and DON release in lobate ctenophores.

In contrast, turnover of C and N, as released DOC and DON, by individual *C. quinquecirrha* was low and on average <3% of body C and N per day. This is consistent with a prior study showing that DOC turnover in *Aurelia* medusae was a minor component of the C budget and equivalent to the C allocated to reproduction (Hansson and Norrman, 1995). Although weight-specific release rates between medusae and ctenophores were similar for DOC but higher for DON in medusae, individual medusae have a higher dry weight (>1 g) and a greater amount of organic C and N compared with individual ctenophores. Thus, similarities in organic release rates between individual ctenophores and medusae further emphasize the relatively low release rates of DOC and DON by *C. quinquecirrha*.

In contrast to ctenophores, there was no relationship between DOC and DON release and body size in medusae. And similar to ctenophores, there was no difference in weight-specific DOC release with a 10°C increase in temperature, suggesting that organic C and N release was not linked to C or N metabolism. Scyphomedusae are tentaculate predators that slough mucus and nematocysts as a defense strategy (Shanks and Graham, 1988), and DOC:DON release ratios were not indicative of C-rich mucus production as observed for *M. leidyi*. Rather, medusae DOC:DON release ratios were closer to the C:N elemental ratios of *Chrysaora* organic body content of about 4C:1N by atom (Nemazie *et al.*, 1993). *Chrysaora* are more robust than *M. leidyi* due to higher amounts of N-rich collagen fibers in the mesoglea per individual medusae (Arai, 1997). In addition, nematocyst capsules used in prey capture are made of C- and N-based chitin molecules (Hessinger and Lenhoff, 1988). Thus, compared with ctenophores, medusae have high organic C and N requirements related to body structure that potentially increase as the medusa grows. This is supported by medusae daily DON turnover rates that significantly decreased with increased body size, suggesting retention of organic N in larger animals. We suggest that low turnover of DOC and DON for *C. quinquecirrha* scyphomedusae is due to preferential retention of these compounds for use in structural components and that the release of DOC and DON is associated with the turnover of these structural components, rather than due to feeding or C and N metabolism.

Importance of gelatinous zooplankton for DOC cycling in the York River

The highest contributions by gelatinous zooplankton to DOC pools occurred during summer, with the majority of DOC contribution associated with *M. leidyi* ctenophore blooms. While ctenophore populations contributed $<1\%$ to bulk DOC pools, they contributed up to 18% and 28% day^{-1} to labile DOC pools in upriver and downriver locations. This ctenophore production of labile DOC could support bacterial production comparable to that supported by phytoplankton production of DOC (del Giorgio and Cole, 1998). In the spring, DOC contribution by *M. leidyi* blooms was minor; this is a time when DOC exudates released by spring phytoplankton blooms potentially contribute the majority of labile DOC (Raymond and Bauer, 2000). Therefore, the importance of *M. leidyi* blooms as a major source to labile DOC pools is likely restricted to summer months when ctenophore DOC release rates are high and allochthonous sources of DOC to the York River are low (Raymond and Bauer, 2000). At these times, ctenophore populations may further impact labile DOM pools because the high release of C-rich DOM would shift the stoichiometric balance toward organic ratios biased for DOC relative to DON and DOP. This is in contrast to phytoplankton-dominated systems which control the ratio of organic C, N and P in seawater close to canonical Redfield stoichiometry—106C:16N:1P by atoms (Redfield *et al.*, 1963; Steinberg *et al.*, 2000; Sterner and Elser, 2002).

The high contribution of labile DOC by *M. leidyi* blooms has implications for bacterioplankton communities in the York River estuary, which have high C metabolic demands and are utilizing DOC from large pools that are primarily refractory (Raymond and Bauer, 2000; Schultz and Ducklow, 2000). This process may be accentuated in the York River estuary because temporal shifts have occurred in *M. leidyi* blooms that have increased both C residence times in and potential release of DOC by gelatinous zooplankton populations (Condon and Steinberg, 2008). This potential utilization of ctenophore-derived DOC by bacteria may represent a primary C pathway in gelatinous zooplankton-dominated systems (Riemann *et al.*, 2006; Condon and Steinberg, 2008), whereby C (as well as N and P) can be assimilated by bacteria and reincorporated into planktonic food webs (Riemann *et al.*, 2006).

In contrast, *C. quinquecirrha* populations contributed minor amounts ($<1\%$) to labile DOC pools and thus direct release of DOC by medusae is likely not important in DOC cycling in the York River. Sloppy feeding or leaching of fecal material was not addressed in this study because medusae were not fed during experiments. Leaking of organic material via feeding may be a more important mechanism by which medusae contribute to labile DOC pools (Hansson and Norrman, 1995). Alternatively, *Chrysaora* medusae could be a "sink" for organic C through direct uptake and assimilation of DOC from bulk pools (Ferguson, 1988).

Importance of DON and DOP metabolites released by gelatinous zooplankton

To our knowledge, there are no previously published rates of DOP release for gelatinous zooplankton. However, high daily turnover of DOP, increased release of organic N and P with body size and high population biomass of *M. leidyi* compared with *C. quinquecirrha* suggest that ctenophore populations might be an important source of DON and DOP in the York River estuary. Using an average biomass of 1.5 g DW m^{-3} and daily weight-specific release rates of 48.0 μmol DON g DW^{-1} day^{-1} and 14.4 μmol DOP

g DW^{-1} day^{-1}, we estimate that during summer *M. leidyi* populations release 72.0 μmol DON m^{-3} day^{-1} and 21.6 μmol DOP m^{-3} day^{-1}. During summer, organic N and P concentrations in the York River typically range 10–15 μM for DON (R. Condon, unpublished data), and 0.2–0.6 μM for DOP, assuming similar concentrations to lower Chesapeake Bay (Conley *et al.*, 1995). Comparison of population release rates with bulk DON and DOP concentrations suggests that *M. leidyi* populations contribute more to DOP (3.6–11%) than DON pools (<1%). The release of DOP compounds by gelatinous zooplankton may thus have important implications for bacterioplankton and P cycling in coastal and estuarine systems (Karl and Bjorkman, 2002), particularly as DOP is preferentially remineralized by bacteria (Loh and Bauer, 2000).

Impacts of DIN and DIP excretion on inorganic nutrient cycling

Large seasonal variations in inorganic nutrients occurred throughout the York River, consistent with previous reports on nutrient cycling in this region (Sin *et al.*, 1999; Schultz *et al.*, 2003; Kemp *et al.*, 2005). Our calculations also suggest that gelatinous zooplankton are a major source of recycled nutrients to DIN and DIP pools in the York River estuary. The highest contributions of inorganic N and P occurred during summer in upriver locations that supported high gelatinous zooplankton biomass. For the York River, which sustains high phytoplankton biomass during summer (Sin *et al.*, 1999; Condon and Steinberg, 2008), the release of nutrients by gelatinous zooplankton may favor phytoplankton growth because their excretion of NH_4^+ and PO_4^{3-} occurs in ratios similar to Redfield N:P stoichiometry (Kemp *et al.*, 2005), and may release phytoplankton from N-limitation (Fig. 7).

During summer, daily primary production rates in lower Chesapeake Bay are ~83.3 mmol C m^{-2} day^{-1} (Chesapeake Bay Remote Sensing Program: http://www.cbrsp.org/). If we assume similar phytoplankton production rates for the York River and Redfield nutrient uptake kinetics, daily N and P production rates by phytoplankton are 12.6 mmol N m^{-2} day^{-1} and 0.78 mmol P m^{-2} day^{-1}. Comparison of these N and P production rates with daily inorganic N and P released by gelatinous zooplankton (rates taken from Fig. 7) indicates that recycled nutrients by ctenophores and medusae combined support <4% of daily primary production. This is similar to results from the mesohaline Chesapeake Bay, where ctenophores and medusae support up to 3% of microplankton production (Nemazie *et al.*, 1993), and within the range reported for other estuarine and coastal regions (Bronk and Steinberg, 2008). Gelatinous zooplankton excretion thus supports a small fraction of primary production in Chesapeake Bay, and phytoplankton must largely utilize other N and P sources for production. For the York River, additional sources might include the flux of NH_4^+ and PO_4^{3-} from sediments during hypoxia (Kemp *et al.*, 2005), river runoff, desorption of PO_4^{3-} from particles (Sin *et al.*, 1999) and regeneration of NH_4^+ by non-gelatinous zooplankton (Park and Carpenter, 1987; Miller and Glibert, 1998; Kirchman, 2000).

These results also imply an alternative sink to phytoplankton for rapid utilization of gelatinous zooplankton inorganic excretia because high inorganic excretion occurred at times when DIN and DIP pools were low or below detection. Advection may be responsible for the removal of some of these nutrients, but low river flow, summer water residence times greater than inorganic production rates and strong vertical stratification gradients would limit flushing and ensure retention of nutrients in surface waters (Hayward *et al.*, 1982; Shen and Haas, 2004; L. Haas, personal communication). We hypothesize that the release of inorganic N and P by ctenophores and medusae favors growth of bacterial communities because there may be a stoichiometric imbalance in labile organic pools created by the high release of C-rich DOM by *M. leidyi* populations that drives supplemental uptake of inorganic nutrients in order to satisfy relatively high bacterial N and P demands (Kirchman, 2000). Here, bacteria would have a competitive advantage over phytoplankton for inorganic resources because of their higher surface area: volume ratios. Low DOC:TDN and DOC:TDP release by gelatinous zooplankton that are similar to bacterial C:N and C:P elemental ratios and nutrient stoichiometric requirements (Goldman *et al.*, 1987; Kirchman, 2000) would also favor uptake of inorganic N and P released by bacteria over phytoplankton. In conclusion, we emphasize that understanding the nature of interactions of gelatinous zooplankton with bacteria is important if we are to fully understand the role gelatinous zooplankton play in DOM and inorganic nutrient cycling in regions where gelatinous zooplankton proliferate.

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