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JELLYFISH BLOOMS

Pulse perturbations from bacterial decomposition of *Chrysaora quinquecirrha* (Scyphozoa: Pelagiidae)

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Abstract Bacteria decomposed damaged and moribund *Chrysaora quinquecirrha* Desor, 1848 releasing a pulse of carbon and nutrients. Tissue decomposed in 5–8 days, with 14 g of wet biomass exhibiting a half-life of 3 days at 22°C, which is 3× longer than previous reports. Decomposition raised mean concentrations of organic carbon and nutrients above controls by 1–2 orders of magnitude. An increase in nitrogen (16,117 μg l^{-1}) occurred 24 h after increases in phosphorus (1,365 μg l^{-1}) and organic carbon (25 mg l^{-1}). Cocci dominated control incubations, with no significant increase in numbers. In incubations of tissue, bacilli increased exponentially after 6 h to become dominant, and cocci reproduced at a rate that was 30% slower. These results, and those from previous studies, suggested that natural assemblages may include bacteria that decompose medusae, as well as bacteria that benefit from the subsequent release of carbon and nutrients. This experiment also indicated that proteins and other nitrogenous compounds are less labile in damaged medusae than in dead or homogenized individuals. Overall, dense patches of decomposing medusae represent an important, but poorly documented, component of the trophic shunt that diverts carbon and nutrients incorporated by gelatinous zooplankton into microbial trophic webs.

Keywords Jellyfish · Scyphomedusae · Bacterial decomposition · Carbon · Nitrogen · Phosphorus

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Introduction

Medusae raise interesting questions for ecologists seeking to understand carbon and nutrient cycles in marine systems. Individual medusae do not sequester large quantities of carbon and macronutrients because their bodies typically comprise 97% water and 3% organic matter consisting of 72 ± 14% protein (mean ± standard deviation), 22 ± 12% lipids, and 7 ± 5% carbohydrates (Larson, 1986; Schneider, 1988; Arai et al., 1989; Clarke et al., 1992; Lucas, 1994, 2009; Doyle et al., 2007; Pitt et al., 2009). Nevertheless, dense aggregations and blooms of medusae have been recorded (Graham et al., 2001; Mills, 2001; Richardson et al., 2009), and in such numbers, medusae irrefutably perturb the flow of energy and cycles of elements in an ecosystem.

Mass occurrences of medusae generally last for weeks to months (Mills, 2001; Sexton et al., 2010), and during this time, they assimilate and release carbon and nutrients creating a relatively protracted, press perturbation (sensu Glasby & Underwood, 1996). For example, medusae can consume significant numbers of zooplankton and larval fish and assimilate up to 88% of the carbon in their prey (Mills, 1995; Arai, 1997; Purcell, 1997; Purcell & Arai, 2001; Pitt et al., 2009). In turn, medusae excrete and secrete carbon, nitrogen, and phosphorus, primarily as mucus, ammonium, and phosphate (Pitt et al., 2009; Condon et al., 2011). Excretion rates vary among species, as well as with temperature and feeding history, but releases of 1,114 µmol g dry weight (DW)$^{-1}$ d^{-1} of dissolved organic carbon, 187 µmol g DW^{-1} d^{-1} of ammonium, 137 µmol g DW^{-1} d^{-1} of dissolved organic nitrogen, 36 µmol g DW^{-1} d^{-1} of phosphate, and 12 µmol g DW^{-1} d^{-1} of dissolved organic phosphorus have been recorded (Morand et al., 1987; Malej, 1989, 1991; Schneider, 1989; Nemazie et al., 1993; Hansson & Norrman, 1995; Shimauchi & Uye, 2007; Pitt et al., 2009; Condon et al., 2010, 2011). Rapidly accumulating evidence suggests that when medusae reach sufficient densities, these releases create a press response (sensu Glasby & Underwood, 1996) by supporting phytoplanktonic and bacterial production, although the magnitude of their influence depends heavily on the availability of carbon and nutrients from other sources and rates of flushing (Pitt et al., 2005; Malej et al., 2007; Condon et al., 2010, 2011). Yet, what happens when the medusae in an aggregation or bloom are damaged or die?

Damaged, moribund, or dead medusae should begin to decompose as they sink or drift, in part because the continuous release of organic matter while they were alive insures they are surrounded by a thriving bacterial assemblage (Doores & Cook, 1976; Heeger et al., 1992; Hansson & Norrman, 1995; Riemann et al., 2006). In some cases, decomposition is not completed in the water column, and carcasses of medusae carry hundreds of grams of carbon to the seafloor (Miyake et al., 2002, 2005; Billett et al., 2006; Koppelmann & Frost, 2008; Yamamoto et al., 2008; Murty et al., 2009). Observations of a carrion fall of *Pyrosoma atlanticum* Peron, 1804 (Lebrato & Jones, 2009) suggest that benthic scavengers will feed on accumulations of dead and moribund medusae. In addition, one set of field observations in deep water and one set of mesocosm experiments in shallow water indicate that medusae will decompose (Billett et al., 2006; West et al., 2009). Over a period of days, bacterial decomposition and respiration created pulse perturbations (sensu Glasby & Underwood, 1996) consisting of increased nutrients and reduced oxygen concentrations as evidenced by the production of hydrogen sulfide (Billett et al., 2006; West et al., 2009). Depending on the system's response, these two perturbations could yield discrete or protracted responses (sensu Glasby & Underwood, 1996). For example, nutrients could stimulate a discrete increase in primary productivity if there is sufficient light, and hypoxia/anoxia could create a protracted decrease in the abundance of infauna that persists through multiple cycles of recruitment. Thus, an understanding of impacts from carrion falls of medusae requires an understanding of their decomposition.

The three previous studies that examined decomposition of Scyphomedusae used suffocated, frozen or homogenized medusae, without controls for the effects of these treatments (Titelman et al., 2006; West et al., 2009; Tinta et al., 2010). Nevertheless, all three studies indicate that the carcasses of scyphomedusae contain few refractory, structural compounds, so they decay readily as bacteria digest their tissue, thereby releasing carbon, nitrogen, and phosphorus (Titelman et al., 2006; West et al., 2009; Tinta et al., 2010). Bacteria typically increased in abundance by one or more orders of magnitude over a period of days in incubations of suffocated or homogenized medusae (Titelman et al., 2006; Tinta et al., 2010). Measurements of half-lives for carcasses depended on ambient temperatures and ranged from 0.6 to 1.0 d, but these measurements potentially included unquantified loss

of tissue and consumption by scavengers (Titelman et al., 2006). In all cases, concentrations of carbon, nitrogen, and phosphorus in incubations of suffocated, frozen, or homogenized Scyphomedusae were significantly higher than those measured in controls (Titelman et al., 2006; West et al., 2009; Tinta et al., 2010).

This study tests hypotheses arising from the results of the three previous investigations. It employs a laboratory experiment to test the overall hypothesis that a pulse perturbation will be created by decomposing *Chrysaora quinquecirrha* Desor, 1848, a scyphomedusa with a circumglobal distribution and tendency to form aggregations and blooms (Graham, 2001; Graham et al., 2001; Mills, 2001; Purcell, 2005; Purcell & Decker, 2005; Hamner & Dawson, 2009; Sexton et al., 2010). In particular, the experiment addresses three related subhypotheses: (i) the half-life of tissue from damaged medusae will be longer than 24 h, (ii) the abundance and composition of bacterial assemblages will differ between incubations with and without tissue from damaged medusae, and (iii) concentrations of total organic carbon, total nitrogen, and total phosphorus will increase in incubations with tissue.

Materials and methods

Collection and handling

Individual Scyphomedusae, *Chrysaora quinquecirrha*, and ambient seawater were collected in 2–3 m of water near the mouth of the Steinhatchee River along Florida's west coast (N 29.6°; W 83.4°). Snorkelers allowed each medusa to swim into a stationary, handheld, 3-l polypropylene beaker (Kartell) that previously had been washed with a 10% hydrochloric acid solution to minimize contamination from beyond the sampling site. Onboard a boat, bell diameters and any visible signs of damage were recorded before each individual was placed in a new, labeled, 12-l plastic bag containing ambient seawater (Table 1). Each bag with its single medusa, was placed in a covered, 190-l bin containing ambient seawater. To alleviate heat stress, the water in the bin was replaced every 2–3 h. A total of 13 medusae was collected. At the same time, ambient seawater for use in experimental and control incubations was collected in an acid-washed 75-l carboy.

Table 1 Results of analysis of variance for $\log_{10}$-transformed concentrations of various elements and ratios of total organic carbon to total nitrogen during decomposition of quarters of *Chrysaora quinquecirrha* medusae

Parameter	Anderson–Darling *P*	Cochran's *P*	Source	*df*	SS	MS	*F*	*P*
$\log_{10}$(TOC)	<0.01	<0.01	Tr	1	7.538	7.538	126.82	<0.001
			Dur	8	1.698	0.212	3.57	0.002
			Tr * Dur	8	1.052	0.131	2.21	0.041
			Error	54	3.209	0.059		
$\log_{10}$(TN)	>0.01	>0.05	Tr	1	37.375	37.375	1989.21	<0.001
			Dur	8	2.120	0.265	14.10	<0.001
			Tr * Dur	8	2.671	0.334	17.77	<0.001
			Error	54	1.015	0.019		
$\log_{10}$(TP)	>0.05	>0.05	Tr	1	70.307	70.307	1451.52	<0.001
			Dur	8	2.574	0.322	6.64	<0.001
			Tr * Dur	8	1.968	0.246	5.08	<0.001
			Error	54	2.616	0.048		
$\log_{10}$(TOC:TN)	<0.01	<0.01	Tr	1	11.344	11.344	317.60	<0.001
			Dur	8	0.663	0.083	2.32	0.032
			Tr * Dur	8	0.854	0.107	2.99	0.008
			Error	54	1.929	0.036		

TOC total organic carbon (mg l^{-1}); *TN* total nitrogen (μg l^{-1}); *TP* total phosphorus (μg l^{-1}); *TOC:TN* ratio of total organic carbon to total nitrogen; *Tr* treatment, either with or without medusae; *Dur* duration of incubation

Experimental design

In the laboratory, medusae and water were held for less than 10 h in a climate-controlled room at 22°C (similar to conditions at the collection site) under a 12:12 light:dark cycle. Before processing, individual *Chrysaora quinquecirrha* were examined to ensure they were pulsing, swimming, and free from trapped air bubbles or visible damage to their bells in an effort to establish an unbiased starting point for decomposition. Three of the 13 medusae were classified as unhealthy, and they were held as whole specimens during the experiment. The remaining 10 healthy medusae were treated to simulate damage.

Individual medusae were removed from their plastic bags with acid-washed forceps, placed on a tared foil pan, blotted gently with a paper towel to remove excess water, and weighed to the nearest 0.1 g using an analytical balance. The balance and tared foil pan were cleaned prior to each measurement. With gloved hands, a scalpel was used to section each healthy individual into four, nearly equal pieces that were weighed separately. The 40 quarters created from these 10 medusae varied in weight from 9.6 to 19.6 g because all medusae had oral arms that differed in length and bell diameters that differed by 1–3 cm. According to previously determined random numbers, four replicate quarters were allocated to each of 10 durations, i.e., 0, 2, 6, 10, 24, 48, 72, 96, 120, and 200 h. In addition, previously selected random numbers were used to allocate four replicate controls to each duration.

Individual quarters and each of the three whole *Chrysaora quinquecirrha* medusae were incubated in an acid-washed, 1-l Nalgene plastic bottle that was loosely capped and contained 200 ml of ambient seawater drawn from the well-mixed carboy and 800 ml of air-filled headspace. The controls consisted of 200 ml of ambient seawater in similar, acid-washed, 1-l Nalgene plastic bottles. The water in experimental replicates and controls was devoid of visible zooplankters. Bottles were incubated at 22°C under a 12:12 light:dark cycle.

Sampling and analysis

The progress of decomposition was tracked by recording the state of tissue samples and associated water at least once each day. At each of the selected durations, any remaining tissue in each experimental replicate was removed and weighed as described above.

w?>Water for counts of bacteria was removed from the appropriate control and experimental bottles, preserved with buffered formalin (final concentrations 2%), and stored at −4°C until analysis. Bacteria in 1-ml aliquots were stained with acridine orange and filtered onto 0.22-mm, black, polycarbonate, membrane filters (Osmonics). Subsequently, filters were mounted onto microscope slides and bacteria enumerated at 1,000× magnification using immersion oil and a Nikon Labophot epifluorescence microscope. Numbers of bacteria per milliliter were estimated from counts of morphotypes in haphazardly chosen sets of five grids, until at least 100 specimens of a single morphotype were counted. Raw counts were scaled to account for dilution, number of grids examined, and the area of each grid.

Samples for carbon and nutrient analyses were preserved with 2 N sulfuric acid to pH <1 and stored at −4°C. Concentrations of total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP) were measured in aliquots of the appropriate water samples; if the initial value was beyond the relevant detection range, a second aliquot was analyzed after being diluted with pre-filtered, distilled water. Samples for analysis of TOC concentrations (mg l^{-1}) were sparged with carbon dioxide free air for 2 min to remove inorganic carbon prior to high temperature catalytic oxidation using a Shimadzu TOC-5000 analyzer with infra-red carbon dioxide detection. Each sample was analyzed twice, and each analytical run comprised 3–5, 60 µl injections, with injections ceasing when the coefficients of variation among replicates were <5%. Potassium hydrogen phthalate was used as a standard. Samples yielding total nitrogen concentrations (µg l^{-1}) were oxidized with persulfate, and the resulting nitrate was measured with second derivative spectroscopy (Bachmann & Canfield, 1996). Concentrations of TP (µg l^{-1}) were determined using an acidified solution of ammonium molybdate and antimony following a persulfate digestion (Murphy & Riley, 1962; Menzel & Corwin, 1965).

Statistical analyses

An exponential decay model was fitted to mean changes in wet weights of tissue over time. A half-life was calculated using the resulting decay coefficient. The relationship between degradation rates and initial

wet weights of quarters was evaluated by correlating proportional losses of wet weight with initial wet weights.

Linear regressions were used to compare temporal changes in counts of each bacterial morphotype between control and experimental treatments. Residuals were tested for normality with Anderson–Darling tests and equality of variance with Cochran's tests. Data were $\log_{10}$-transformed to improve normality and homoscedasticity. For each bacterial morphotype, an exponential growth curve was fitted to back-transformed mean counts and a doubling time calculated.

Differences in concentrations of TOC, TN, and TP, as well as ratios of TOC to TN, were tested with ANOVAs. Data were $\log_{10}$-transformed to improve normality and homoscedasticity, which were evaluated as described above. In ANOVAs, treatment (either control or experimental) and duration of incubation were treated as fixed factors. Data are presented as mean ± standard error.

Results

Evidence of decomposition began with a smell of rotting tissue that was noted in some incubations at 48 h, but one quarter was still pulsing at 72 h, which highlighted variation in responses to sectioning. The release of hydrogen sulfide was noted at 120 h in some incubations, which indicated the onset of anaerobic decomposition. Through time, wet weights decreased, with no tissue remaining in any sample at 200 h. An exponential decay curve fit to mean weight losses for 0–120 h yielded a half-life of 3 days or 72 h (wet weight $= 13.3 \times e^{-0.229 \times \text{days}}$; $r^2 = 0.883$). Proportional rates of tissue loss were not correlated with initial wet weights ($r = 0.272$, $P = 0.089$). In addition, three whole animals weighing 39.6–47.0 g were 92–100% decomposed by 120–200 h.

Samples from four controls spanning 120 h of incubation contained coccoid bacteria ($2.7 \times 10^5 \pm 4.8 \times 10^4$ cells ml^{-1}). Numbers of cocci did not vary significantly throughout the incubation period according to a linear regression (Fig. 1A; $F_{1,2} = 1.67$, $P = 0.326$, $r^2 = 0.45$).

The bacterial assemblage in experimental replicates containing quarters of *Chrysaora quinquecirrha* medusae diverged from that in controls. In analyses of abundance, one anomalously low value from 6 h was excluded from the regressions to improve normality and homoscedasticity; the degrees of freedom were reduced accordingly. Cocci were the only bacteria observed through the second hour ($5.5 \times 10^5 \pm 5.0 \times 10^4$ cells ml^{-1}), and their numbers increased significantly throughout the incubation period (Fig. 1A; $F_{1,31} = 67.1$, $P < 0.001$, $r^2 = 0.68$). From the sixth hour, bacilli were visible, and their numbers also increased significantly (Fig. 1B; $F_{1,31} = 21.6$, $P < 0.001$, $r^2 = 0.41$). In fact, the slopes of regression lines for cocci (0.02) and for bacilli (0.03) were similar if the initial samples that did not contain bacilli were excluded (Fig. 1E; $F_{1,24} = 58.6$, $P < 0.001$, $r^2 = 0.70$). Near the end of the experiment, bacterial films formed in some replicates with quarters of *C. quinquecirrha*.

Furthermore, both forms of bacteria exhibited exponential growth through 200 h (Fig. 1C, D; r^2 for cocci = 0.83; r^2 for bacilli = 0.93), with bacilli predominating by an order of magnitude (raw counts at 200 h = $1.2 \times 10^8 \pm 8.8 \times 10^7$ bacilli ml^{-1} and $1.5 \times 10^7 \pm 1.2 \times 10^7$ cocci ml^{-1}). As expected given their predominance, bacilli had a shorter doubling time (24.8 h) than cocci (33.6 h).

As indicated by significant interactions in ANOVAs and comparisons of back-transformed means (Table 1; Fig. 2), the introduction and incubation of tissue from *Chrysaora quinquecirrha* medusae led to increased concentrations of TOC, TN, and TP in the seawater. Concentrations of all elements were elevated immediately, and increases in concentrations of TOC, TN, and TP followed different time courses to eventually become 1–2 orders of magnitude higher than the relatively stable concentrations measured in controls (Fig. 2). As tissue decomposed, TOC and TP concentrations exhibited a three-fold increase between 24 and 48 h, whereas, a similar increase in TN occurred 24 h later (Fig. 2).

The time courses followed by ratios of TOC to TN also differed significantly between control and experimental replicates (Table 1), with ratios in controls always being higher (Fig. 2; 16.9 ± 1.1 for control incubations and 3.1 ± 0.5 for experimental incubations). In experimental replicates, TN concentrations lagged TOC concentrations by 24 h, which led to a maximum ratio of 5.3 at 48 h (Fig. 2B–D). In control replicates, the maximum ratio of 31.1 at 72 h was due to a relatively low mean concentration of TN (193 μg l^{-1} versus mean of all other values = 325 μg l^{-1}) and a

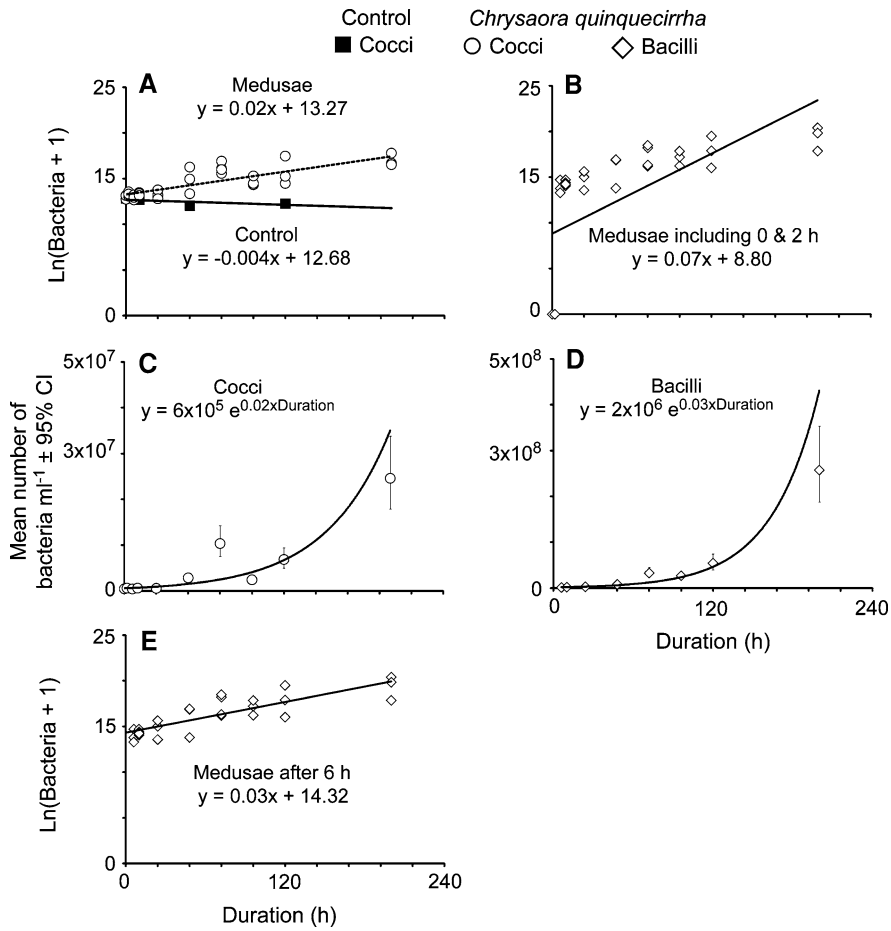

Fig. 1 Linear regressions based on natural log transformed counts of bacteria versus duration of the experiment and exponential growth curves fitted to back-transformed mean counts of bacilli and cocci in incubations of quarters of *Chrysaora quinquecirrha* medusae. **A** regressions for counts of cocci in seawater controls and experimental incubations with medusae; **B** regression for counts of bacilli in experimental incubations; **C** exponential growth curve fit to counts of cocci in experimental incubations; **D** exponential growth curve fit to counts of bacilli in experimental incubations; **E** regression for counts of bacilli in experimental incubations after they become established at 6 h. *CI* confidence interval

slightly higher mean concentration of TOC (6 mg l^{-1} versus mean of all other values = 5 mg l^{-1}).

Mean TOC, TN, and TP concentrations in experimental replicates yielded an elemental ratio of 23:8:1 (TOC:TN:TP by weight) immediately after the introduction of *C. quinquecirrha* tissue. At 96–120 h, a ratio of 14:8:1 was calculated from the relatively stable mean concentrations of TOC, TN, and TP (Fig. 2). In comparison to the Redfield ratio of 40:7:1, nitrogen and phosphorus concentrations remained near the theoretical balance, whereas carbon was limiting throughout the incubations.

Discussion

Quarters of *Chrysaora quinquecirrha* medusae lost weight exponentially and at rates that were statistically similar for pieces of tissue weighing 9.6–19.6 g. As hypothesized, these rates of tissue loss were slower than those reported for whole specimens of *Periphylla periphylla* Péron & Lesueur, 1810 (Titelman et al., 2006). In fact, the rate of tissue loss for quarters of *C. quinquecirrha* was 6.7–11.2× slower after using a Q_{10} of 2.3 to adjust the rates for *P. periphylla* from 10.1 or 12.5 to 22°C (Bidle et al., 2002; Titelman et al., 2006). Further evidence that tissue was lost over 8 days comes from observations that whole, unhealthy *C. quinquecirrha* decomposed in the same period of time as quarters of healthy individuals. In addition, previously frozen, whole *Catostylus mosaicus* Quoy & Gaimard, 1824 decomposed completely in approximately 9 days when resting on the bottom at 30°C (West et al., 2009). Although oxygen concentrations probably remained higher during the in situ incubations of *P. periphylla* in mesh bags, the most likely explanations for the more rapid change in wet weights would be the observed, but unquantified, loss of tissue during sample recovery and consumption by zooplankton that colonized the samples (Titelman et al., 2006).

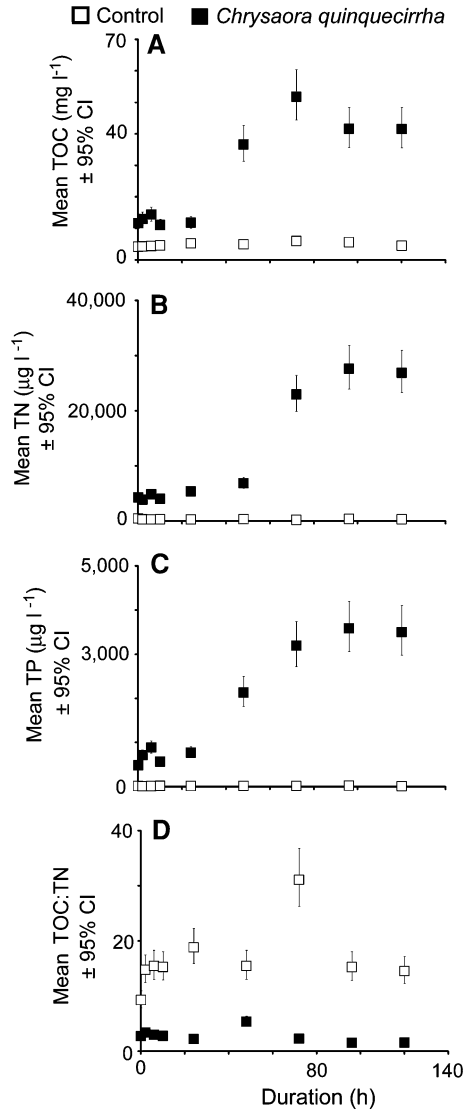

Fig. 2 Back-transformed mean concentrations of **A** total organic carbon (TOC in mg l^{-1}), **B** total nitrogen (TN in µg l^{-1}), and **C** total phosphorus (TP in µg l^{-1}), as well as **D** ratios of total organic carbon to total nitrogen in incubations containing quarters of *Chrysaora quinquecirrha* medusae and seawater controls. *CI* confidence interval

Tissue was not lost during *C. quinquecirrha* incubations, which did not contain visible zooplanktonic scavengers. Identifying the degree of consistency in decomposition rates and separating the consequences of scavenging and decomposition will be important for modeling of carbon and nutrient cycles.

Incubations with tissue from *Chrysaora quinquecirrha* exhibited changes in the abundance of bacteria as hypothesized. As the wet weight of tissue declined, numbers of two bacterial morphotypes increased exponentially, a bacterial film formed in some experimental replicates, and hydrogen sulfide was produced. The presence of a bacterial film resembled observations of "slime" on a massive carrion fall of *Crambionella orsini* Vanhöffen, 1888 in the Arabian Sea (Billett et al., 2006). Evidence of decreased oxygen concentrations in the experiment with *C. quinquecirrha* matched observations of anoxic sediments associated with the *C. orsini* fall (Billett et al., 2006) and other experiments on decomposition (West et al., 2009; Tinta et al., 2010). Overall, the experiment with *C. quinquecirrha* appeared to simulate conditions associated with carrion falls of Scyphomedusae, which makes the data on the release of carbon and nutrients valuable for predicting the magnitude and duration of these pulse perturbations. In fact, the results will have direct application for the Gulf of Mexico and Chesapeake Bay where *C. quinquecirrha* and several congeners are known to form blooms (Graham, 2001; Graham et al., 2001; Mills, 2001; Purcell, 2005; Purcell & Decker, 2005; Hamner & Dawson, 2009; Sexton et al., 2010).

The hypothesis that incubations with tissue will contain a different bacterial assemblage also was supported. Initially, control and experimental samples contained cocci, with bacilli observed in experimental bottles from 6 h onward. Growth coefficients and doubling times indicated that bacilli grew 1.4-times faster than cocci, and bacilli abundances became an order of magnitude greater. Naturally occurring bacteria from two locations in the Adriatic Sea, with temperatures from 10 to 19°C, grew rapidly on homogenates of *Aurelia* sp., with bacterial abundances typically increasing 100-fold in 1–3 days and only one experiment exhibiting a 6-day lag to maximum densities (Tinta et al., 2010). Bacilli also predominated when homogenized *Periphylla periphylla* medusae were incubated with natural bacterial assemblages (Titelman et al., 2006) and on moribund *Chrysaora quinquecirrha* medusae in Chesapeake Bay (Doores & Cook, 1976). In addition, analyses of bacterial DNA indicated that assemblages differed between seawater controls and incubations with homogenized tissue (Titelman et al., 2006; Tinta et al., 2010). Incubations of medusa tissue with naturally occurring microbial assemblages and specific bacterial isolates showed that numbers of some bacteria decreased or remained static, with the strongest inhibitory effect on bacteria

attributed to the umbrella of *P. periphylla* (Titelman et al., 2006). Nevertheless, numerous bacteria decompose medusae because nine bacterial isolates increased in numbers over 10 h in other experiments (Titelman et al., 2006). In summary, available data indicate that certain bacteria may be primarily responsible for decomposition of medusae and grow more rapidly than other forms that may benefit from the ensuing release of carbon and nutrients. This interpretation receives further support from field observations of higher abundances of certain bacteria in depth zones where *P. periphylla* were abundant (Riemann et al., 2006) and a laboratory experiment demonstrating that *Brevibacterium* sp. JCM 6894, but not *Escherichia coli* ATCC 9637, decomposed tissue of an unspecified medusa (Mimura & Nagata, 2001). In our experiments with *C. quinquecirrha*, coccoid bacteria may have utilized carbon and nutrients released during decomposition driven by bacilli.

Incubations with tissue of damaged medusae yielded the hypothesized increases in carbon and macronutrients. In fact, the introduction of *Chrysaora quinquecirrha* tissue raised concentrations of TOC, TN, and TP by 3-, 9-, and 35-fold, respectively, within $\sim$1 h, suggesting that damaged medusae leak carbon and nutrients. Concentrations of carbon and nutrients were elevated by approximately 1–2 orders of magnitude after 24–48 h in incubations containing tissue being decomposed by bacteria. A 16,117 $\mu g\ l^{-1}$ increase in TN lagged a 1,365 $\mu g\ l^{-1}$ increase in TP and a 25 $mg\ l^{-1}$ increase in TOC by 24 h, which resulted in a maximum TOC:TN ratio at 72 h. Thus, it appeared that nitrogen-rich proteins were not degraded faster than polysaccharides and other carbon-rich compounds, as previously hypothesized (Titelman et al., 2006). Perhaps, the proteins in pieces of tissue were less labile than those in homogenized tissue (Titelman et al., 2006), and the observation that one quarter continued to pulse for 72 h suggests that resistance to decomposition varied among individual *C. quinquecirrha*. Ultimately, the overall TOC:TN ratio in the water from experimental replicates was 2.7 ± 0.4, which was slightly lower than ratios of 3.4–4.1 previously reported for tissue of other medusae (Larson, 1986; Schneider, 1988; Clarke et al., 1992; Doyle et al., 2007). This discrepancy may have been due to mineralization of carbon during production of bacterial biomass, which would yield inorganic carbon that was not measured in our analyses. In fact, carbon appeared to be the limiting element throughout the incubations, and changes in TOC:TN:TP ratios between 0 h and 96–120 h indicated that it became increasingly limiting. In combination with increases in bacteria, this relatively large decrease compared to changes in concentrations of nitrogen and phosphorus signified a conversion of "pelagic" TOC to "benthic" bacterial biomass.

In combination with previous reports, our data demonstrate that damaged medusae decompose readily, with carbon, nitrogen, and phosphorus released from relatively labile compounds. Certain bacteria appear to drive decomposition, and the resulting dissolved carbon and nutrients support the growth of other bacteria and phytoplankton as shown here and in other studies (Pitt et al., 2005; Riemann et al., 2006; Malej et al., 2007; Shimauchi & Uye, 2007; Pitt et al., 2009; Condon et al., 2010, 2011). Although they decompose rapidly, carcasses of medusae may reach the sea floor as carrion falls that should provide food for benthic scavengers, will create hot spots with elevated concentrations of key elements in the sediment and adjacent water column, and will contribute to low oxygen concentrations in bottom waters and sediments (Billett et al., 2006; Yamamoto et al., 2008; West et al., 2009; this study). In addition, the results of this and previous studies suggest that pulse perturbations generated by carrion falls of Scyphomedusae should be integrated into the conceptual model of a trophic shunt that diverts carbon, nitrogen, and phosphorus through living gelatinous zooplankton and into microbial trophic webs (Condon et al., 2011). Further work determining rates of decomposition in diverse and realistic situations will yield an improved understanding of differences among species; the influence of temperature, water movement, and other environmental conditions; and differences between dead and living yet damaged medusae.

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