Estuarine, Coastal and Shelf Science 154 (2015) 77–83

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Biogeochemical implications of decomposing jellyfish blooms in a changing climate

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ARTICLE INFO

Article history:
Received 27 July 2014
Accepted 22 December 2014
Available online 31 December 2014

Keywords:
bacterial degradation
pH
gelatinous zooplankton
nutrient flux
scyphozoa
remineralisation

ABSTRACT

Jellyfish often exhibit 'boom and bust' population dynamics whereby they proliferate rapidly and then die *en masse* and decompose. The few studies that have investigated post-bloom processes have not studied how changing ocean conditions will alter rates of decomposition. Climate change will result in warmer and more acidic waters, and studies therefore need to consider these factors in concert to determine their combined effect on decomposition processes. To quantify the effect, we measured oxygen consumption and nutrient regeneration rates during decomposition of *Catostylus mosaicus* in mesocosms at current average summer pH and temperature (pH 8.0 and 27 °C) as well as conditions projected for year 2100 (pH 7.8 and 30 °C) and compared these fluxes to control mesocosms without jellyfish over 12 days. We hypothesised that rates of jellyfish decomposition, as measured by oxygen demand and nutrient regeneration, would be accelerated in the end-of-century treatments, compared to present day treatments. Overall decomposition rates were only slightly elevated under end–of-century conditions, and the difference was only significant for ammonium fluxes from 19 h until 43 h after the experiment commenced. The difference between treatments was much smaller than would be expected due to the temperature increase, based on theoretical modelling of jellyfish decomposition which predicts a Q_{10} of 4.28, or a 1.5 fold increase in decomposition rates. This highlights the importance of investigating net effects on decomposition rates, as simultaneous shifts in temperature and pH may not follow patterns predicted due to one stressor alone. Ultimately, these results suggest that rates of oxygen consumption and nutrient regeneration resulting from collapsed jellyfish blooms may not change drastically over the next 100 years.

1. Introduction

Many marine organisms including phytoplankton, macroalgae, and gelatinous zooplankton exhibit boom and bust population dynamics (i.e. a rapid increase in biomass followed by mass mortality). These plants and animals play an important role in nutrient cycling because the large stocks of nutrients that accumulate in their biomass are released suddenly during mass decomposition. Jellyfish blooms in particular can attain huge biomasses, and the gelatinous carrion that sinks to the benthos can locally exceed annual downward fluxes of other organic carbon sources by more than tenfold in a single large pulse (Billett et al., 2006). The sudden input of labile organic material to the benthos from collapsed blooms can have major effects on fauna and biogeochemical processes (Pitt et al., 2009).

Gelatinous tissue that sinks to the benthos may be scavenged by animals and/or decomposed by heterotrophic microorganisms (Lebrato and Jones, 2009; Sweetman and Chapman, 2011). Sometimes, however, the biomass of moribund jellyfish is so large that it exceeds local rates of opportunistic scavenging, resulting in the accumulation of large quantities of carrion (Billett et al., 2006), which can induce hotspots of microbial activity (West et al., 2009). Bacterial remineralisation of jellyfish carrion can rapidly deplete oxygen in the surrounding water and release nutrients and organic carbon from the carcasses at rates which may be significant on an ecosystem scale (Titelman et al., 2006; Pitt et al., 2009; West et al., 2009).

Anthropogenic changes to ocean temperature and pH have the potential to significantly alter biogeochemical processes (Mora et al., 2013), including rates of decomposition (Piontek et al.,

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http://dx.doi.org/10.1016/j.ecss.2014.12.022
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2009, 2010). Models of jellyfish decomposition suggest it to be strongly temperature dependent (Lebrato et al., 2011), thus a changing climate may accelerate the associated rate of nutrient release and oxygen consumption in the future. The potential consequences of ocean acidification for bacterial degradation of organic matter, however, are more equivocal (Liu et al., 2010), with both increased and decreased rates of organic matter mineralisation predicted (e.g. Piontek et al., 2010; Yamada and Suzumura 2010). Most studies on microbial processes have only examined the effect of individual climate stressors (Liu et al., 2010). To our knowledge, no study has investigated how simultaneous changes in ocean temperature and pH may affect decomposition rates of organic matter, which makes it difficult to predict how decomposition dynamics of gelatinous zooplankton may respond to changing environmental conditions.

Jellyfish populations oscillate globally on approximately 20 year cycles and, although the claim that populations are increasing globally is unsubstantiated (Condon et al., 2013), there are regions that have experienced significant increases in gelatinous biomass (e.g. Uye, 2008; Kogovšek et al., 2010; Eriksen et al., 2012). Thus, for such areas, understanding how changing climate conditions will alter the decomposition of moribund jellyfish blooms has become increasingly important.

Our objective was to investigate the net effect of changing climate conditions on the degradation of jellyfish biomass. This study focused specifically on *Catostylus mosaicus* (Quoy and Gaimard, 1824), a scyphozoan jellyfish which has a widespread distribution along the east and north coasts of Australia (Kramp, 1965), and can form blooms where the biomass exceeds 500 ton/km^2 (Pitt and Kingsford, 2003). Our hypothesis was that decomposition of jellyfish carrion would be accelerated under end-of-century (increased temperature and lower pH) relative to present day conditions, which would be indicated by an earlier onset of oxygen consumption and elevated rates of oxygen demand and nutrient regeneration.

2. Methods

2.1. Experimental setup

Twenty cylindrical chambers (28 cm Ø; 40 cm height) were filled with sandy/muddy sediment, collected manually from the low intertidal zone of southern Moreton Bay (153° 24′E, 27°57′S, Queensland, Australia). The sediment was sieved to remove fauna (>2 mm) and chambers were placed in a temperature-controlled room (25 °C) in a flow-through seawater system. Each chamber contained on average (±SE) 18.5 (0.1) L mixed sediment (approx. 14 cm depth) and 22.3 (0.1) L overlying water. Minor differences in water volumes among chambers were accounted for in all calculations. Water collected from Moreton Bay was gravity fed from 200 L header tanks to the individual chambers at a rate of 1.3 L/hour. The water column within the chambers was mixed using small aquarium pumps attached to the chamber walls, with the rate of flow set to prevent any sediment resuspension. Chambers were individually sparged with air and pre-incubated under present day conditions for 5 months in the dark to re-establish sediment profiles. *Catostylus mosaicus* were collected from Moreton Bay and sacrificed by freezing. While there are artefacts associated with freezing a jellyfish carcass (West et al., 2009), jellyfish are robust animals, making them difficult to kill without affecting the quality of their tissues. Freezing was chosen, similar to West et al. (2009), as it had less disadvantages compared to refrigeration which can be ineffective (West, pers. comm.), freezing with liquid nitrogen which compromises the integrity of the carcass (pers. obs.), and homogenising the jellyfish (Tinta et al., 2010) which increases the surface area of the tissues available for colonisation by bacteria.

The experiment consisted of two orthogonal factors: presence/absence of jellyfish and current (8.0 and 27 °C) and projected end-of-century (7.8 and 30 °C) pH and temperature conditions, respectively (Fig. 1). Five replicate chambers were allocated randomly to each treatment. Present day conditions were based on average summer conditions in Moreton Bay, and end-of-century conditions were derived from IPCC climate change scenarios (Stocker et al., 2013). One jellyfish (378 ± 8 g wet weight, equivalent to ~2.7 g carbon, 43.2 g C m^{-2}; based on data from other rhizostomes (Lucas et al., 2011)) was placed on the surface of the sediment in the appropriate chambers. The temperature of individual chambers was manipulated by partially submerging the chambers in water baths that were heated to the target temperature using aquarium heaters. Air stones continuously mixed the water in each bath. Similarly, the temperature of the water in the header tanks was adjusted using aquarium heaters. Present day treatment chambers were sparged with compressed air and pCO_2 was manipulated in the end-of-century treatments by continuously bubbling the chamber water with a CO_2 (1000 ppm) enriched air mixture at a rate of 100 ml/min, thereby creating head spaces with current and end-of-century conditions. Water flowing from the header tanks into the chambers overflowed via a u-bend tube near the lid of the chamber, which created an air-tight set-up so that target pCO_2 conditions in the headspace could be maintained. By manipulating the pCO_2 of the headspace we were able to expose the chambers to future pH conditions while at the same time allowing the pH of the water to fluctuate as it would naturally during the decomposition process. Temperature and pCO_2 were modified in the end-of-century chambers three days prior to the start of the experiment to allow porewaters in the surface sediment to equilibrate with changed water-column conditions.

2.2. Flux incubations

The experiment ran for 12 days, until all visible jellyfish carrion had disappeared and the oxygen demand in the jellyfish treatments was less than twice of that in the controls. Over the 12 days, flux incubations were conducted to measure the rate of change in the concentrations of dissolved oxygen (DO), dissolved inorganic and organic carbon (DIC and DOC), and organic and inorganic nutrients, by sealing the chambers from the atmosphere and incubating the sediment and overlying water. Flux incubations were carried out once prior to jellyfish additions (time 0), and at 1, 19, 43, 67, 92, 140, 212, and 284 h after the addition of the jellyfish carrion to the chambers. The incubation at time 0 was completed immediately prior to the jellyfish being added to ensure that conditions were consistent between jellyfish and control chambers. The duration of the incubations varied throughout the experiment (determined via pilot studies) to ensure conditions did not become hypoxic in the jellyfish treatments during the incubations, and DO levels did not fall below 80% of air saturation in the control chambers. Incubation periods ranged from 0.5 to 5 h depending on the treatment and stage of jellyfish decomposition, with the shortest incubations corresponding to the peak of the bacterial mineralisation of the gelatinous tissue (19 h) in the jellyfish treatments. During flux incubations the flow of water to the chambers was interrupted, the lids of the chambers were removed, and the chambers were sealed with floating lids to prevent gaseous exchange with the atmosphere. Dark conditions were maintained during incubations by covering the chambers with opaque lids, to prevent potential interferences from photosynthetic activity. Water samples were collected at the start and end of incubations to determine concentrations of oxygen, DOC, DIC, and inorganic and organic

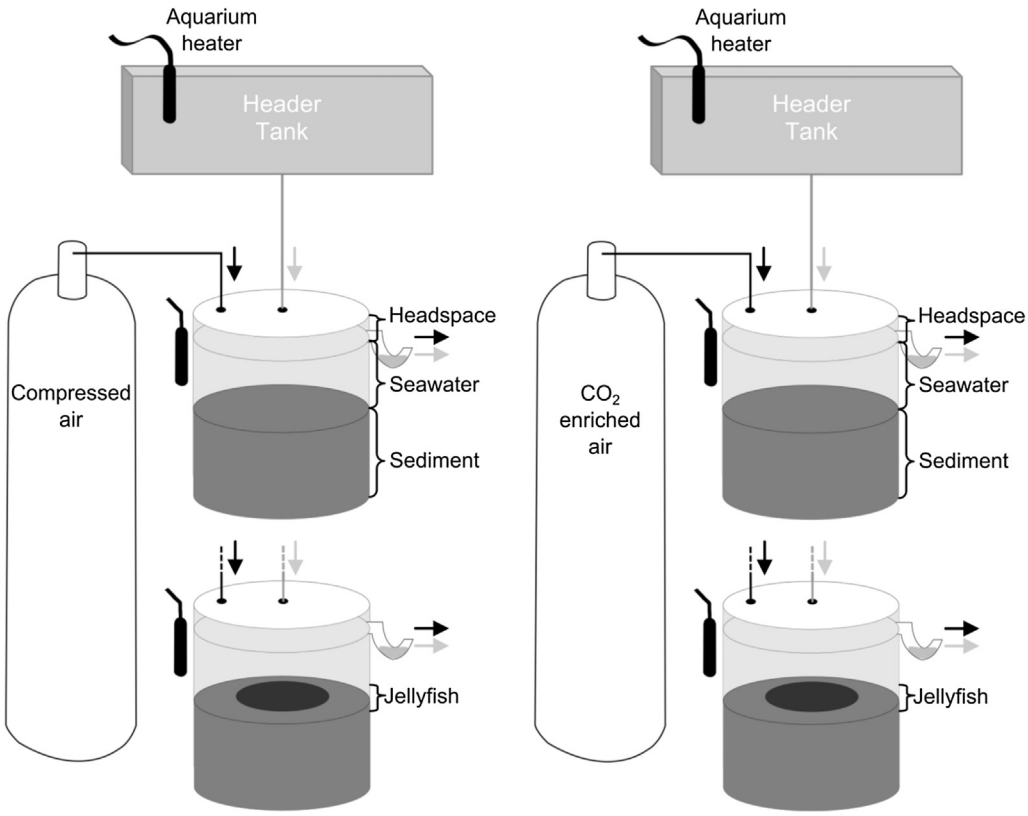

Fig. 1. Conceptual diagram of the experimental set-up. Movement of air and water are indicated with black and grey arrows, respectively. One example chamber is shown for each treatment, and each treatment had five replicate chambers. Water baths, which held the aquarium heaters, are not pictured.

nutrients. All water samples were collected using syringes and tubing that were washed with 10% HCl and rinsed with deionised water (Milli-Q Element, Millipore), and care was taken to avoid bubbles forming when samples were extracted. Samples for inorganic nutrients (NH_4^+, PO_4^{3-}, NO_x) and dissolved organic N and P (DON and DOP) analysis were passed through a Whatman GF/F glass microfiber filter into vials, and stored frozen until analysed. Samples for DIC and DOC were filtered into 100 ml airtight glass bottles, fixed with 20 μL of a 50% saturated mercuric chloride solution and stored at 4 °C. Dissolved oxygen was measured directly with a Mettler Toledo OptiOx DO sensor that was calibrated daily.

At the start of every incubation, pH, temperature, salinity and DIC concentration were measured and used to calculate dissolved pCO_2 using CO_2SYS software, which characterises the CO_2 system in seawater based on the input parameters (pH and DIC) and conditions (temperature, salinity etc.) (Lewis and Wallace, 1998), to ensure that target pCO_2 levels were maintained. pH was measured with a Mettler Toledo FG2 pH probe using the NIST scale. Temperature was measured with an Electronic Temperature Instruments Ltd. Thermapen digital thermometer calibrated with a mercury thermometer. Salinity was measured with a TPS MC-84 conductivity salinity meter.

2.3. Dissolved carbon and nutrient analyses

DIC and DOC concentrations were determined within 7 days of sample collection using a Shimadzu Total Organic Carbon analyser (TOC-V series). NH_4^+ was analysed spectrophotometrically using the salicylate-hypochlorite method described by Bower and Holm-Hansen (1980). PO_4^{3-} and NO_x were analysed on a Seal AA3 Segmented Flow Analyser and a Westco Smartchem SC200 Wet Chemistry Discrete Analyser, respectively. Total dissolved nitrogen (TDN) and phosphorus (TDP) were determined in the same manner as NO_x and PO_4^{3-}, respectively following UV/persulfate digestion, and the DON and DOP pools were calculated as the difference between the dissolved total and summed inorganic pools. Digestion efficiencies of organic N and P were between 91 and 106%. All measurements were blank-corrected (using artificial seawater) and the limit of detection (LOD) was calculated as three times the standard deviation of the blanks.

2.4. Calculation of solute fluxes

Fluxes of all analytes were calculated from the change in the water column concentration according to the following equation:

$$\text{Flux} = ((C_E - C_S) * V)/(A * T)$$

where C_E is the concentration at the end of the incubation, C_S the concentration at the start of incubation, V the volume of water in the chamber, A the area of the sediment surface, and T the duration of the incubation. All concentrations were in μmol l^{-1}, volume in litres, area in m^2, time in hours, and the fluxes were calculated as μmol m^{-2} $hour^{-1}$. Ambient concentrations of all nutrients were generally low, therefore the control samples were usually below the LOD for ammonium (0.096 μmol L^{-1} NH_4^+), NO_x (0.37 μmol L^{-1} NO_x), phosphate (0.050 μmol L^{-1} PO_4^{3-}), and total phosphorus (0.269 μmol L^{-1} TP). To avoid artificially enlarging the difference between the jellyfish treatments and their corresponding control, maximum fluxes (i.e. initial concentration was assumed to be zero and final concentration was assumed to be the LOD) were utilised for data analyses when this occurred.

2.5. Statistical analysis

Dissolved oxygen, DOC, and nutrient (NH_4^+, PO_4^{3-}, NO_x, DON, DOP) data were analysed using a repeated measures linear mixed model. The repeated covariance type was determined by comparing models of covariance structure, and auto-regressive 1 (AR1), a first-order autoregressive structure with homogeneous variances, was chosen, as this best explained the covariance structure of the residuals (IBMCorp. 2012). The analysis consisted of three fixed factors: jellyfish (presence/absence), climate scenario (present day/end-of-century) and time, which was the repeated measure. When significant interactions were identified, planned contrasts were used to determine which means differed. Data were tested for normality and homogeneity of variance and, when assumptions were not met, data were transformed using a square root transformation. All statistical analyses were carried out using SPSS version 22.0 software.

3. Results

3.1. Carbonate chemistry parameters

The pH and temperature conditions within the chambers were consistent with the end-of-century IPCC scenarios throughout the experiment. In the present day controls the pH was 8.03 ± 0.01 (mean ± SE) and in the end-of-century controls it was 7.82 ± 0.01 (Fig. 2). At the start of the experiment, before the addition of jellyfish, pH in the jellyfish treatments was consistent with the controls (present day 8.00 ± 0.02; end-of-century 7.80 ± 0.01). With the onset of biological activity, however, pH initially decreased in both jellyfish treatments to a minimum of 7.85 ± 0.02 in the present day treatment, and 7.48 ± 0.04 in the end-of-century treatment (Fig. 2). Temperature in the present day treatments was 27.2 ± 0.01 °C and 30.1 ± 0.05 °C in the end-of-century treatments.

3.2. Sediment oxygen demand and carbon fluxes

The sediment oxygen demand (SOD) for all chambers did not differ prior to the addition of jellyfish carcasses (t = 0, 784 ± 46 μmol m^{-2} h^{-1}). The addition of jellyfish resulted in an immediate increase in the SOD under both present day and end-of-century scenarios, resulting in a significant interaction

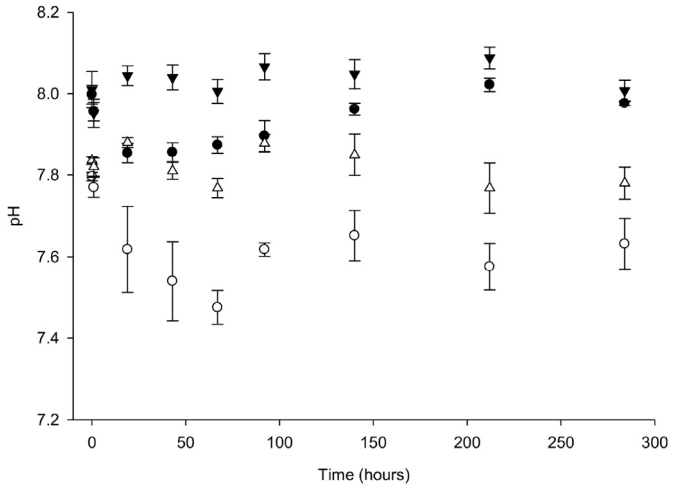

Fig. 2. Mean (±SE) pH of present day (●) and end-of-century (○) jellyfish treatments, and present day (▼) and end-of-century (△) controls for the duration of the experiment.

Table 1
Results of mixed model repeated measures of sediment oxygen demand (SOD), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), ammonium (NH_4^+), dissolved organic phosphorus (DOP) and phosphate (PO_4^{3-}) fluxes.

Source of variation	SOD			DOC			DON			NH_4^+			DOP			PO_4^{3-}		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Intercept	1	7978.22	<0.001	1	5426.60	<0.001	1	8786.18	<0.001	1	1108.26	<0.001	1	17270.43	<0.001	1	7586.73	<0.001
Jellyfish	1	487.37	<0.001	1	20.39	<0.001	1	24.45	<0.001	1	491.81	<0.001	1	26.82	<0.001	1	537.11	<0.001
Climate	1	4.04	0.051	1	3.10	0.084	1	0.26	0.613	1	4.59	0.038	1	0.99	0.324	1	0.05	0.829
Time	8	43.27	<0.001	8	27.87	<0.001	6	22.35	<0.001	8	71.60	<0.001	6	37.57	<0.001	6	337.48	<0.001
Jellyfish*Climate	1	3.94	0.053	1	0.231	0.633	1	0.68	0.412	1	4.25	0.046	1	0.05	0.831	1	1.27	0.265
Jellyfish*Time	8	30.23	<0.001	8	28.08	<0.001	6	20.82	<0.001	8	73.81	<0.001	6	53.06	<0.001	6	400.11	<0.001
Climate*Time	8	1.35	0.230	8	0.59	0.785	6	0.18	0.982	8	1.06	0.398	6	0.94	0.474	6	0.68	0.665
Jellyfish*Climate*Time	8	0.794	0.610	8	0.44	0.893	6	0.10	0.997	8	1.15	0.340	6	1.09	0.374	6	0.69	0.659

between presence/absence of jellyfish and time (Table 1; Fig. 3). Under both climate scenarios SOD in the jellyfish treatment remained significantly higher ($p < 0.05$) than in the corresponding control treatment for all time points (1–284 h) after the addition of the jellyfish. SOD peaked at 19 h after the addition of jellyfish for both climate scenarios at levels ~5 fold higher than the respective control treatment values. Thereafter, SOD in the jellyfish treatments slowly decreased for the remainder of the experiment, and at the conclusion of the experiment it was less than twice that of the controls. There was a strong tendency over the first 92 h after the addition of jellyfish for SOD values to be higher in the end-of-century compared to present day jellyfish treatments (Fig. 3), however, these differences were not statistically significant (Table 1; $p = 0.051$), and SOD values returned toward baseline values at the same time under both treatments. In the control treatments, SOD remained similarly and consistently low under both climate scenarios, with an overall mean of 942 ± 26 μmol m^{-2} h^{-1} (Fig. 3).

Release of DOC to the water column remained low in all treatments for most of the experiment, except for a large DOC efflux immediately after the addition of jellyfish (Fig. 4). The release of DOC in the jellyfish treatments peaked immediately after addition at $46{,}754 \pm 4282$ μmol m^{-2} h^{-1}. By 19 h the DOC fluxes had decreased and did not differ from those in the controls. There was no significant difference between the present day and end-of-century jellyfish treatments (Table 1). The jellyfish treatments were only significantly higher than the controls at $t = 1$ h ($p < 0.001$).

DIC fluxes could not be accurately calculated over the short incubation times as changes in DIC concentration were small (average increase <1%) relative to high initial background DIC concentrations.

3.3. Nutrient fluxes

Fluxes of DON (Fig. 5A) followed a very similar trend as those of DOC. At the start of the experiment, before the addition of jellyfish, all fluxes were very low and similar. Once the jellyfish were added, there was a large initial release of DON ($12{,}732 \pm 1177$ μmol m^{-2} h^{-1}) in the jellyfish treatments, which then decreased to initial levels by the incubation at 19 h (Fig. 5A).

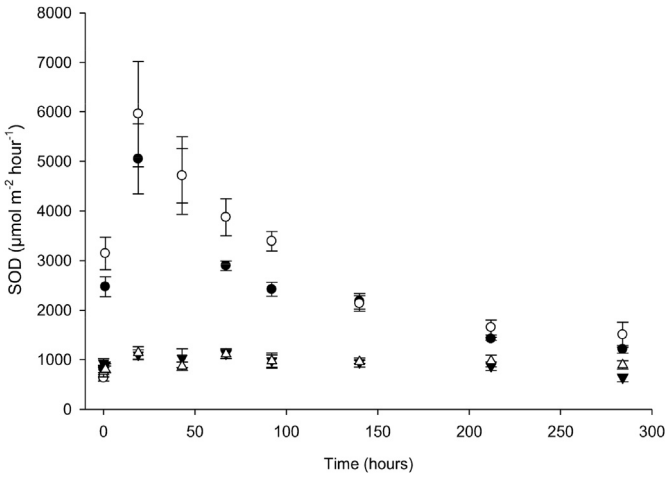

Fig. 3. Mean (±SE) sediment oxygen demand (SOD) of present day (●) and end-of-century (○) jellyfish treatments, and present day (▼) and end-of-century (△) controls throughout the experiment.

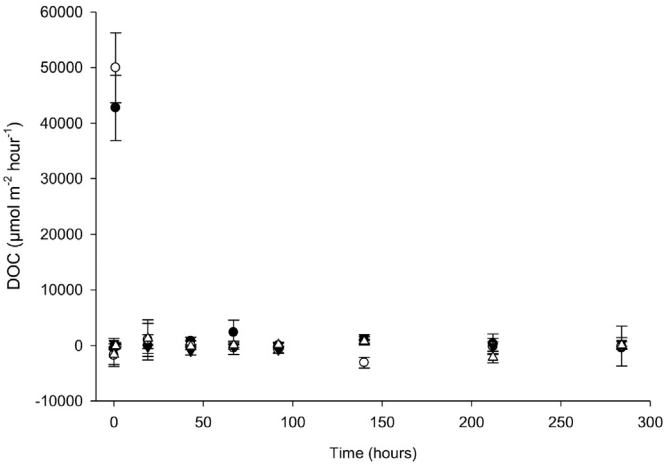

Fig. 4. Mean (±SE) dissolved organic carbon (DOC) fluxes of present day (●) and end-of-century (○) jellyfish treatments, and present day (▼) and end-of-century (△) controls throughout the experiment.

The only time point where there was a significant difference between treatments with and without jellyfish was at $t = 1$ h ($p < 0.001$). There was no significant difference between the present day and end-of-century jellyfish treatments (Table 1).

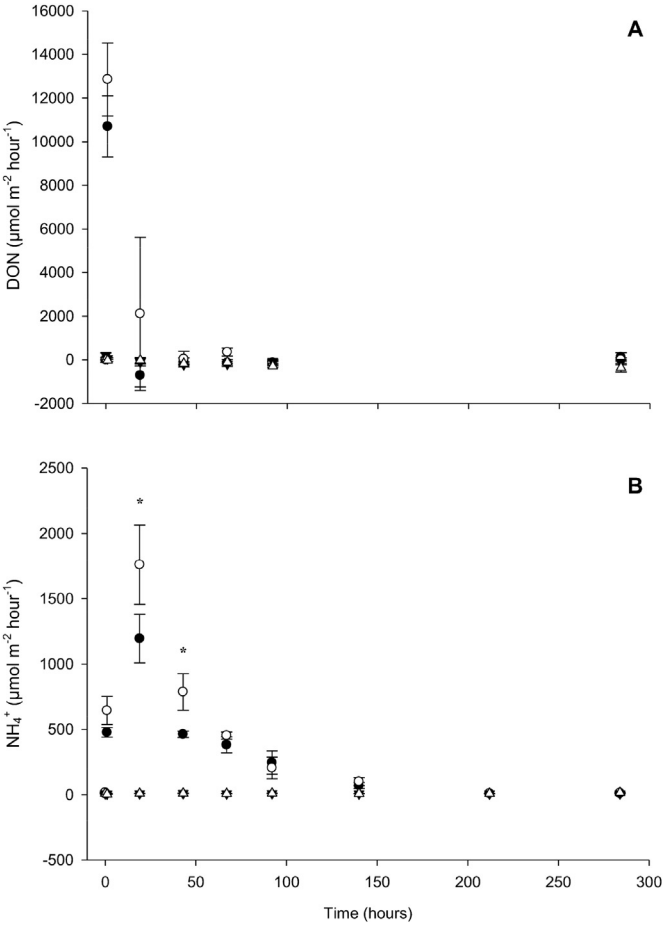

Fig. 5. Mean (±SE) fluxes of (A) dissolved organic nitrogen (DON) and (B) ammonium (NH_4^+) of present day (●) and end-of-century (○) jellyfish treatments, and present day (▼) and end-of-century (△) controls throughout the experiment. Significant differences between present day and end-of-century jellyfish treatments are represented with * ($p < 0.05$).

Ammonium fluxes were low and similar in all treatments before the addition of the jellyfish, with an overall average production of 11.2 ± 1.1 μmol m^{-2} h^{-1}. Once the jellyfish were added, ammonium effluxes increased in both treatments containing jellyfish and remained elevated relative to the controls from 1 to 140 h (Fig. 5B). Maximum ammonium regeneration rates were recorded in the present day (1194 ± 185 μmol m^{-2} h^{-1}) and end-of-century (1760 ± 304 μmol m^{-2} h^{-1}) jellyfish treatments during the incubation at 19 h. Ammonium regeneration was the only process to exhibit a significant interaction between presence/absence of jellyfish and climate scenario (Table 1). Planned contrasts showed a significant difference between present day and end-of-century jellyfish treatments at time 19 h ($p = 0.004$) and at time 43 h ($p = 0.047$). There was also a significant difference between presence/absence of jellyfish and time (Table 1). Fluxes of NO_X remained low (21.5 ± 3.5 μmol m^{-2} h^{-1}) in all treatments for the duration of the experiment.

Similar to the fluxes of DOC and DON, there was a large initial release of DOP and phosphate immediately after the addition of jellyfish, with a peak at t = 1 h of 345.9 ± 40.0 μmol m^{-2} h^{-1} (Table 1; Fig. 6A) and 323.7 ± 18.4 μmol m^{-2} h^{-1} (Table 1; Fig. 6B), for DOP and phosphate respectively. There was no significant difference between the present day and end-of-century jellyfish treatments. There was, however, a significant effect of presence/absence of jellyfish and time ($p < 0.001$) for both analytes.

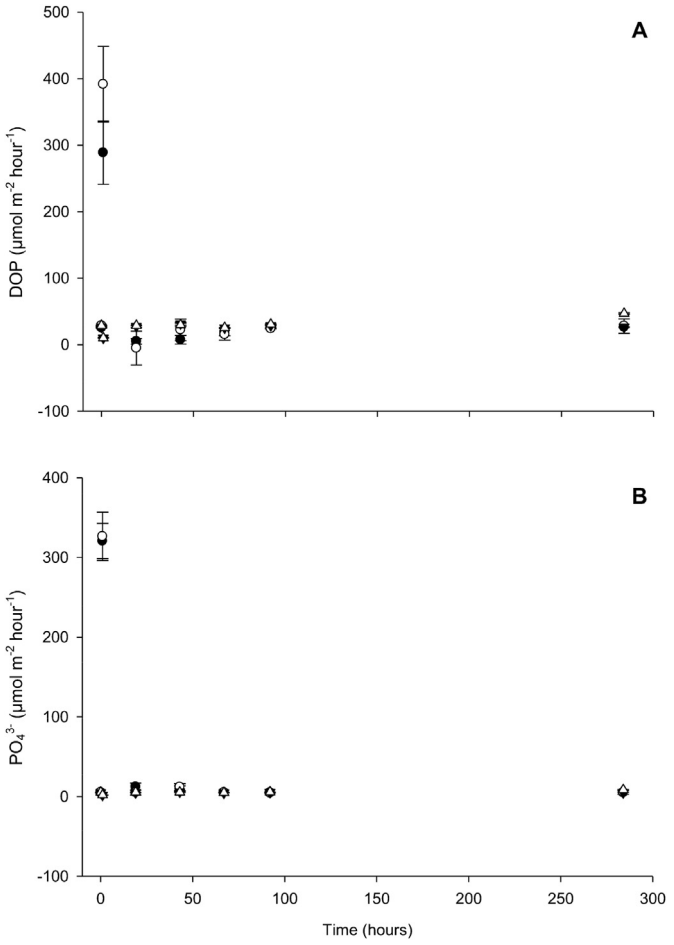

Fig. 6. Mean (±SE) fluxes of (A) dissolved organic phosphorus (DOP) and (B) phosphate (PO_4^{3-}) of present day (●) and end-of-century (○) jellyfish treatments, and present day (▼) and end-of-century (△) controls throughout the experiment.

4. Discussion

The consumption of oxygen and production of dissolved organic and inorganic nutrients, measures of microbial metabolic rates and overall decomposition rates, were very similar for the decomposition of *Catostylus mosaicus* under both climate scenarios tested. This finding was contrary to our hypothesis that decomposition would be accelerated under end-of-century conditions. A significant difference between climate scenarios was observed only for the production of ammonium, and then only for the incubations 19 and 43 h after the addition of jellyfish. All other nutrient fluxes, as well as oxygen consumption, were not significantly different between climate scenarios, although fluxes for all analytes were significantly higher than control chambers for at least part of the experiment.

While our study was not designed to determine the independent effects of temperature and pH, differences between present day and end-of-century jellyfish treatments were much smaller than would be expected due to the temperature difference alone based on known relationships between temperature and rates of bacterial metabolism. Bacterial metabolism is strongly temperature-dependent (White et al., 1991), as is the remineralisation of gelatinous tissue. The temperature dependence of jellyfish decomposition has been quantified with a Q_{10} value (the rate of increase that occurs with a 10 °C increase in temperature) of 4.28 (Lebrato et al., 2011), suggesting that with an increase of three degrees in temperature, the rate of decomposition would increase by a factor of 1.5. Rates of oxygen consumption, a direct proxy for microbial decomposition rates, did not significantly differ between climate scenarios, and were on average (±SE) only 1.1 (0.1) times greater in the end-of-century compared to present day jellyfish treatment. This lack of response is not only inconsistent with Q_{10} predictions based on jellyfish decomposition (i.e. a 1.5 fold increase), it is not consistent with a more general Q_{10} value of 3.3 for the growth of aquatic bacteria compiled from studies across a wide range of temperatures (0 to >35 °C) (White et al., 1991), which would predict a stimulation of 1.4 fold for a 3 °C temperature change. The observation that the system did not conform to robust theoretical predictions suggests that the lower pH may have counteracted the effects of higher temperature on the rate of decomposition in the end-of-century treatment. These factors would need to be investigated independently to confirm a counteractive effect of pH on decomposition.

Sediment oxygen demand also did not differ between the present day and end-of-century controls, indicating that there was little effect of temperature on the decomposition of other relatively recalcitrant organic matter sources present in the sediment. The only significant difference between the jellyfish treatments was for the production of ammonium. Ammonium fluxes may have increased in the end-of-century treatment because of the inverse relationship that exists between bacterial growth efficiency and temperature, whereby a lower proportion of the carbon mobilised during decomposition is assimilated into new biomass with increasing temperature (Fenchel et al., 1998; Rivkin and Legendre, 2001). This reduction in carbon assimilation efficiency would reduce the bacterial nitrogen demand for growth (Fenchel et al., 1998), which in turn would result in an increased proportion of the ammonium regenerated during the decomposition process fluxing to the water.

Decomposition causes several complex changes to sediment biogeochemistry, which can influence local sediment conditions. For example, the respiratory production of carbon dioxide can cause a decrease in pH (Wallace et al., 2014), while the production of alkaline compounds (e.g. NH_3, PO_4^{3-} etc.) generates alkalinity (Krumins et al., 2013). In this study, CO_2 concentrations were manipulated in the headspace (to mimic atmospheric changes)

which allowed the system to fluctuate as it normally would as the jellyfish decomposed. The pH decreased in both jellyfish treatments, most likely due to the respiratory production of carbon dioxide, however the decrease was more pronounced in the end-of-century treatment. Decomposition processes, therefore, reinforced the effect of climate change by further decreasing local pH. This feedback effect could be significant at an ecosystem level by pushing organisms or processes towards or beyond their pH tolerance limits (Feely et al., 2010) and may further explain why rates of decomposition were not as high as expected in this study, based on reported temperature effects.

Due to their short generation times and the potential for horizontal gene transfer, microorganisms have the potential to rapidly adapt to changing ocean conditions (Liu et al., 2010). Thus, if pH is indeed counteracting the effects of temperature on bacterial degradation, the degree to which this occurs may decrease in the future. Rates of decomposition in the future will also be influenced by whether changes to pH in coastal waters follow the same trajectory as projections for the open ocean. It has been suggested that coastal sediments will be able to buffer pH changes to a degree, however, high rates of organic material remineralisation may drive the pH even lower in heterotrophic coastal environments (Andersson et al., 2012). If this were the case, pH could exert an even stronger effect on rates of decomposition than simulated here.

Regardless of whether decomposition rates change, degradation of large amounts of gelatinous carrion may have detrimental consequences, particularly in areas with limited water exchange (West et al., 2009). Decomposing jellyfish carrion has the potential to create low oxygen conditions and locally decrease pH, reinforcing the decrease already caused by climate change, and facilitating the release of nutrients that could stimulate primary productivity and favour eutrophication. The collapse of blooms in areas that are experiencing regional increases in jellyfish abundance (Condon et al., 2013) could cause significant local perturbations to biogeochemical cycling in the future, even if rates of decomposition do not accelerate.

This study is an important first step in understanding how multiple climate stressors may influence the decomposition of organic matter, as no study to date has investigated the net effects of increasing temperature and decreasing pH on this process. Understanding how changing climate conditions will alter organic matter decomposition is imperative, as it plays a fundamental role in the cycling of carbon and nutrients (Piontek et al., 2010). The results here suggest that rates of decomposition may not change drastically by the end of the century, particularly for moribund gelatinous zooplankton blooms.

Acknowledgements

Funding for this project was provided by the Urban Fish Habitat Monitoring Program from the Queensland Government and Griffith University. We thank W Bennett, YT Ip, WY Fung, E Maron, G Wilkins and R Stewart for laboratory assistance and JM Arthur for statistical advice. Symbols in the graphical abstract are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

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