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Biogeochemical implications of decomposing jellyfish blooms in a changing climate

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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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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