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Decomposition of jellyfish carrion *in situ*: Short-term impacts on infauna, benthic nutrient fluxes and sediment redox conditions

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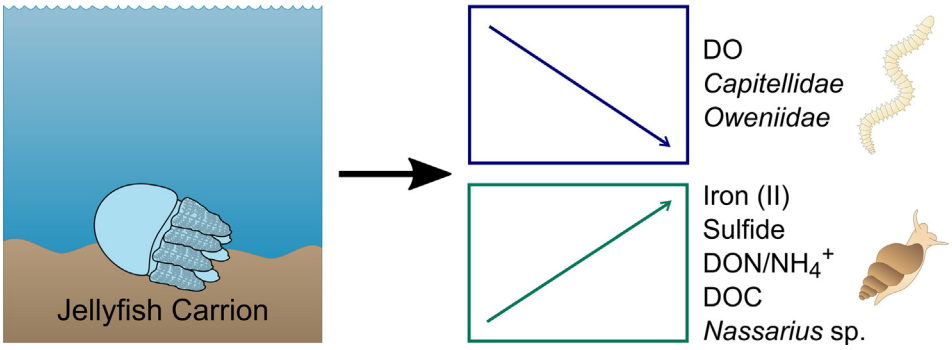
HIGHLIGHTS

- After jellyfish blooms collapse, carrion can sink and cover the benthos *en masse*.
- Studied effect of jellyfish decomposition on lithosphere, hydrosphere and biosphere.
- Measured nutrient fluxes, porewater Fe^{2+} and S^{2-}, and changes to infaunal community.
- Jellyfish carrion increased porewater S^{2-} and decreased abundance of some infauna.
- Collapse of blooms may have widespread effects on the benthic/pelagic environment.

GRAPHICAL ABSTRACT



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ABSTRACT

Jellyfish often form blooms that persist for weeks to months before they collapse *en masse*, resulting in the sudden release of large amounts of organic matter to the environment. This study investigated the biogeochemical and ecological effects of the decomposition of jellyfish in a shallow coastal lagoon in New South Wales, Australia. *Catostylus mosaicus* carrion was added to the surface of shallow sub-tidal sediments and biogeochemical parameters and macrofaunal abundance immediately below the jellyfish carrion were measured over three days. Sediment plots without jellyfish served as controls. Sediment oxygen demand and carbon and nitrogen efflux increased by up to 60-fold in the jellyfish plots, compared to control plots, and dissolved organic nutrient fluxes were more sustained than in previous studies due to the use of fresh rather than frozen biomass. The decomposing jellyfish progressively altered sediment redox conditions, indicated by an increase in porewater iron (II) and sulfide concentrations measured by high-resolution *in situ* diffusive samplers. Abundance of some macrofaunal taxa in the jellyfish plots decreased relative to controls, however, the abundance of a carnivorous gastropod, which was presumably feeding on the carrion, increased in the jellyfish plots. While jellyfish carrion may be a food source for some macrofauna, low oxygen conditions coupled with the accumulation of toxic dissolved sulfides in the near-surface sediments may explain the overall change in the macroinfaunal community.

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1. Introduction

The biomass of gelatinous zooplankton in the mixed layer of the ocean is estimated to be 38.3×10^{12} g carbon, of which 92% is comprised of cnidarian medusae (Lucas et al., 2014). Medusae can attain mean biomass densities of up to 50 kg wet weight 100 m^{-3} (Lilley et al., 2011) and entire blooms can reach biomasses of up to several million tonnes (e.g. Lynam et al., 2006). The nutrients assimilated within these blooms are often released back to the environment as one large pulse when the blooms collapse and decompose (Pitt et al., 2014). Decaying medusae often sink to the benthos in large quantities (Lebrato et al., 2012, 2013) but virtually nothing is known about how collapsed blooms affect benthic redox conditions and infaunal communities (Pitt et al., 2009).

Jellyfish carrion that reaches the benthos can be rapidly scavenged by a diverse range of taxa, including echinoderms, crustaceans and fish (see Lebrato et al., 2012; Sweetman et al., 2014). However, the biomass of carcasses that accumulates on the benthos after a bloom collapses can be so large that it exceeds the amount that can be scavenged. Indeed, carcasses can accumulate on the benthos in a layer up to 70 mm thick (Billett et al., 2006), and during such deposition events microbes are likely to play a major role in the remineralization of gelatinous tissue (Billett et al., 2006; Chelsky et al., 2015; West et al., 2009).

The microbial decomposition of gelatinous carrion on the benthos can elicit rapid changes to sediment biogeochemistry (Chelsky et al., 2015; West et al., 2009). Jellyfish tissue is very labile, as indicated by their low C:N ratio (Pitt et al., 2009), and can thus be rapidly remineralized (Chelsky et al., 2015; Titelman et al., 2006; West et al., 2009). The associated bacterial respiration can increase sediment oxygen demand (West et al., 2009) which, in turn, favors anaerobic metabolisms. The depletion of oxygen and the shift to the use of iron (III) and sulfate as terminal electron acceptors in the microbial respiration of organic matter may cause dissolved iron (II) and sulfide to accumulate in the sediment porewater (Canfield et al., 2005). The biomass of jellyfish carrion on the benthos can be so large that the oxygen demand associated with the decomposition of their tissue could lead to widespread hypoxia in the overlying water (Pitt et al., 2009). These effects may be exacerbated in areas of reduced water exchange, such as semi-enclosed coastal lagoons, which can support up to 500 tonnes km^{-2} of jellyfish biomass (e.g. Pitt and Kingsford, 2003). Although oxygen demand and nutrient regeneration rates associated with jellyfish decomposition have been quantified in several studies (Frost et al., 2012; Qu et al., 2015; Tinta et al., 2010, 2012; West et al., 2009), to date no study has investigated how the decomposition process could influence porewater solute concentrations and faunal communities in the sediment.

The biogeochemical changes associated with deposits of gelatinous carrion could impact benthic macrofaunal communities. Hypoxic or anoxic conditions created by microbial remineralization of large inputs of organic material can reduce faunal abundance and alter species composition (Gray et al., 2002). The low oxygen conditions can cause lateral migration, mortality, or emergence of sediment infauna that are intolerant of these conditions (Gray et al., 2002; Middelburg and Levin, 2009), with crustaceans typically the most sensitive and mollusks the most robust taxa (Vaquer-Sunyer and Duarte, 2008). The potential for sulfide accumulation in the sediment could also negatively impact benthic macroinfaunal communities (Vaquer-Sunyer and Duarte, 2010), as the presence of dissolved sulfides in the sediment porewater can impair respiratory function even at low micromolar concentrations (Bagarinao, 1992). Since carcasses often remain intact when they sink to the benthos and can cover patches of the sediment several meters in diameter (e.g. Billett et al., 2006; Lebrato and Jones, 2009), they may also create a diffusive barrier that inhibits reoxidation of sediments below their tissue (Lebrato et al., 2012). This could potentially exacerbate the adverse conditions for fauna below or in close proximity to the gelatinous carrion by favoring anaerobic microbial metabolism, sediment reduction and the accumulation of toxic sulfides in the sediment porewater.

The aim of this study was to evaluate the short-term effects of jellyfish carrion on sediment biogeochemistry and benthic macrofaunal communities. We hypothesized that jellyfish carrion would stimulate microbial decomposition processes (both aerobic and anaerobic) increasing benthic oxygen demand and nutrient regeneration rates, and that the increase in anaerobic metabolism would be evidenced by an accumulation of iron (II) and sulfide in the sediment porewater. We also hypothesized that macrofaunal abundance would decrease below the jellyfish carrion as taxa susceptible to low oxygen or sulfidic conditions died or migrated away.

2. Methods

The decomposition of the scyphozoan jellyfish, *Catostylus mosaicus* (Quoy and Gaimard, 1824), was studied in Smiths Lake (152°28′ E, 32°23′ S), a shallow semi-enclosed coastal lagoon in New South Wales, Australia, in October 2013. The experiment was done on shallow (~1 m depth), unvegetated, sub-tidal sandy sediments (salinity ~36, temperature ~ 23 °C). Smiths Lake was closed to the ocean at the time of the study so there was no tidal movement. There were two components to the study: (1) sediments were sampled to measure changes to macrofaunal assemblages and sediment porewater concentration profiles of iron (II) and sulfide, and (2) benthic chamber incubations were used to measure dissolved oxygen (DO), dissolved organic carbon (DOC), and dissolved organic and inorganic nitrogen (DON and DIN) fluxes between the benthos and water column. The destructive sampling of the sediments required for the first component prevented both components from being conducted on the same experimental plots, so they were run concurrently on adjacent plots. The experiment was concluded after three days when the majority of the carrion had disappeared and the sediment oxygen demand in the jellyfish treatment was less than twice the average control values.

Six *C. mosaicus* (all 30 cm bell diameter) were collected from Smiths Lake and transferred to small aquaria that were filled with lagoon water. The jellyfish were killed by sparging the aquaria with nitrogen gas for ~12 h. Jellyfish were then cut into quarters and each quarter was weighed (1.20 ± 0.05 kg wet weight) and assigned randomly to a plot. Jellyfish were sectioned because there were very few jellyfish in the lake at the time, making individuals of the same size difficult to find. It also enabled the addition of a consistent biomass to each plot.

2.1. Experimental setup and sampling

The experiment consisted of three treatments: jellyfish, controls and procedural controls. Jellyfish plots consisted of carrion enclosed in cages (steel with powder coat finish; mesh size: 3 cm; base: 40 cm × 50 cm; height: 24 cm). Cages allowed small benthic scavengers to access the carrion but prevented the entire carcasses from being removed by large opportunistic scavengers, such as large fish. The experiment thus represented a scenario of when the biomass of carrion would exceed that which could be consumed by large mobile scavengers. Within the cages jellyfish were anchored with nylon netting to limit their movement throughout the study. The netting was coarse (3 cm) to allow bacterial colonization and scavenging by benthic fauna and small fish, and was, therefore, considered to have a negligible effect on the decomposition process. Cages and netting over bare sediment were used as procedural controls to test for cage effects. All cages were anchored using 2–3 tent pegs. Areas of undisturbed sediment were used as controls. Plots were laid out as a grid in a 15 × 20 m area and 15 plots were randomly assigned to each of the 3 treatments. All plots were spaced >2 m apart to ensure independence. Five of the fifteen replicates in each treatment were sampled destructively on each of three consecutive days.

Combined diffusive gradients in thin films (DGT)/diffusive equilibrium in thin films (DET) probes were used to determine porewater sulfide and iron (II) co-distributions, respectively. These samplers can provide high resolution two-dimensional distributions of porewater

concentrations of sulfide and iron (II) (Robertson et al., 2008), and can measure changes in these distributions over relatively short time periods, such as diurnal cycles (Pagès et al., 2014, 2012). Probes were prepared, deployed, and analyzed according to Robertson et al. (2008), as modified by Bennett et al. (2012) for iron (II). The DGT/DET gel layers were contained within a plastic casing with a sampling window (18 × 150 mm), and comprised a sulfide-DGT binding layer (containing AgI) and a diffusive layer for iron (II) DET measurements, covered with a 0.45 μm cellulose nitrate filter membrane (Millipore, Billerica MA). One DGT/DET probe was inserted into the sediment in each plot the day before the plot was sampled. Probes were inserted adjacent to the jellyfish carrion in cages with a carcass and near the center of control and procedural control plots ($n = 5$ for each treatment). After ~20 h (exact time recorded) the DGT/DET samplers were removed from the sediment. The DET gels were immediately cut from the samplers, stained and scanned with a flatbed scanner (Canon CanoScan LiDE 200), as described by Bennett et al. (2012). DGT binding gels were removed from the probes, stored in deionized water, and scanned within 30 days. Pixel grey scale values were converted to concentrations according to Bennett et al. (2012) and Robertson et al. (2008) for iron (II) and sulfide, respectively. Calculated porewater solute concentrations for each square millimeter of the probes were laterally averaged across the probe width at 1 mm depth intervals to provide one-dimensional depth profiles. Two-dimensional, false-color distributions at 1 mm^2 resolution were generated using the filled-contour plot function in Matlab (R2014a).

Jellyfish carrion remaining in the plots was carefully removed, placed in a plastic bag and weighed within 1 h. Cores (15 cm Ø, 15 cm depth) of sediment were immediately taken from the center of the plot and the sediment was sieved for macrofauna (>500 μm). The sieved sample was preserved with 4% buffered formalin in seawater and stained with Rose Bengal. Macrofauna were sorted, identified and counted with a dissecting microscope. Nemerteans and foraminiferans were identified to phylum, polychaetes were identified to family, crustaceans were identified to order, and mollusks were identified to species. Nematodes were excluded from the analysis because they could not be accurately quantified, as many were smaller than the mesh size used.

2.2. In situ chamber incubations

To measure fluxes of DO, DOC, DON and DIN, four plots with carrion and four plots without carrion (i.e. controls), as above, were incubated within custom-made Perspex chambers. These plots were additional to those used to sample sediment biogeochemistry and macrofauna. Plots were incubated once before the cages and jellyfish carrion were added (time 0), and at 19, 44 and 64 h after the addition of carrion. Additional incubations were conducted on only the jellyfish plots after 5, 26, 50 and 72 h, as these were expected to be more variable over time. The chambers (volume 53.2 L, enclosed sediment area 0.174 m^2) consisted of a base that was inserted 15 cm into the sediment, onto which a dome was securely attached. This approach created a closed system that could be sampled via silicone tubing connected to a port in the chamber. The bases of the chambers were inserted at least 10 h before the start of the experiment to give the sediment time to settle and remained in place throughout the experiment. To initiate the flux incubations the domes were carefully attached to the chamber bases, the aquarium pumps within each chamber were started, and the water in the chambers was allowed to mix for approximately 15 min before the initial water samples were taken. Incubations were conducted under dark conditions (using black plastic covers) to avoid the potential confounding influences of photosynthesis by microphytobenthos on oxygen and nutrient fluxes. Incubation times ranged between 0.9 and 3.2 h depending on the day and treatment. The incubation times were shorter for the jellyfish plots when rates of remineralization and, therefore, oxygen demand, were high to ensure that the dissolved oxygen concentrations at the end of the incubations did not fall below 80% of the initial concentration (i.e. oxygen did not drop >20%). Water samples were collected at the start and end of the incubations via the sampling port. DO was measured with a Hach LDO optical dissolved oxygen probe, which was calibrated daily. Samples for nutrient analysis were filtered through Whatman glass fiber (GF/F) filters and frozen at −20 °C. DOC samples were similarly syringe filtered, immediately acidified with H_2SO_4 to pH 2, and frozen at −20 °C. Chamber domes were attached to their bases only during each incubation period and were otherwise removed.

2.3. Analysis of nutrients and dissolved organic carbon

Ammonium (NH_4^+) and NO_x ($NO_3^- + NO_2^-$) samples were analyzed using a Seal AA3 Segmented Flow Analyzer. All measurements were blank-corrected with 0.7 M NaCl and the limit of detection (LOD) was calculated as three times the standard deviation of the blanks. The LOD for both analytes was low (NH_4^+: 0.23 μmol L^{-1}; NO_x: 0.17 μmol L^{-1}). Total dissolved nitrogen (TDN) and DOC were analyzed with a Shimadzu Total Organic Carbon Analyzer (TOC-V series). Recoveries of quality controls were between 99 and 104%. Dissolved organic nitrogen (DON) was calculated as the difference between TDN and the inorganic nitrogen pools ($NH_4^+ + NO_x$). If NO_x or NH_4^+ values were below the LOD they were assumed to be zero when calculating DON, as they were considered negligible. The LOD for ammonium and NO_x were <3% and <2% of the lowest measured total dissolved nitrogen sample, respectively. Fluxes were calculated as described previously by Welsh et al. (2000):

$$F = (C_F - C_I)V/(A \times T)$$

where C_I and C_F are the initial and final concentrations of the analyte, respectively; V is the volume of the chamber; A is the surface area of the sediment and T is the incubation time. Fluxes of ammonium could not be determined on four occasions (for two controls and two jellyfish plots) because sample concentrations were below the LOD.

2.4. Sediment characteristics

The wet-bulk density, porosity, organic matter content and sediment grain size were characterized at the site of the experiment in five replicate cores that were taken haphazardly and frozen (−20 °C) until analysis. Wet-bulk density and porosity were measured and calculated according to Percival and Lindsay (1997). Organic matter content was determined as loss on ignition at 550 °C (LOI_{550}) according to Heiri et al. (2001). The size distribution of sediments was determined by dry sieving to quantify the proportion of grains in the following size categories: >1 mm, 1 mm–500 μm, 500–250 μm, 250–125 μm, 125–63 μm and <63 μm.

2.5. Data analysis

Variation in macrofaunal community structure was tested with a 2-way permutational analysis of variance (PERMANOVA), using modified Gower (log base 2) similarity measures (Anderson et al., 2006). The two factors were jellyfish treatment (jellyfish/control/procedural control) and day. Both factors were fixed. Significant results were visualized using canonical analysis of principal components (CAP). Vector overlays were used to visualize Pearson's product moment correlations between the data and CAP ordination axes (Anderson et al., 2008). Only taxa contributing most to the differences between levels within each factor were displayed as vectors (Pearson R value > 0.5). A 2-way analysis of variance (ANOVA) was used to compare abundances of these taxa of interest (Pearson R value > 0.5) between jellyfish treatment and day. Data were square root transformed to satisfy the assumptions of normality and homogeneity of variance. When significant differences were identified, LSD post hoc tests were used to identify which means differed.

Fluxes of nutrients and DO, and the depth profiles of iron and sulfide were analyzed using repeated measures linear mixed models. The analysis of flux data had two fixed factors: presence/absence of jellyfish and time (0, 5, 19, 26, 44, 50, 64, 72 h), which was the repeated measure. The incubations done only on the jellyfish plots were included in the analysis but the corresponding times for the control plots were treated as missing values. Sediment porewater profiles were analyzed using two fixed factors: treatment (jellyfish/control/procedural control) and depth (from 15 mm above to 120 mm below the sediment/water interface), which was the repeated measure. Comparisons between treatments and depth were only made within the same day and not between days. Data were tested for normality and homogeneity of variance and, when assumptions were not met, data were transformed using a square root transformation or log transformation for flux data and porewater concentrations, respectively. When significant interactions were identified, estimated marginal means were used to determine which means differed.

3. Results

3.1. Change in jellyfish biomass

The amount of gelatinous tissue remaining in the jellyfish plots rapidly declined from 68.7 ± 1.4% to 52.4 ± 3.5% and 33.7 ± 1.1% of the original biomass (wet weight) over the first, second, and third days, respectively. On the final day, one jellyfish carcass broke apart and was no longer contained within the experimental plot; it was, therefore, not included in the calculations of average biomass.

3.2. DET and DGT samplers

Porewater concentrations of iron (II) and sulfide changed over the three days of the experiment. On the first day, the patterns in iron (II) concentrations with depth were consistent across treatments ($p > 0.05$, Table S.1). The iron (II) concentrations were low, however, they gradually increased with depth and exceeded 40 μmol L^{-1} from 22 to 70 mm depth (Fig. 1A). On the second day porewater iron (II) concentrations were higher in the jellyfish treatment compared to the controls and procedural controls ($p = 0.018$, Table S.1) from the sediment surface (0 mm) to 15 mm depth, with average values exceeding 80 μmol L^{-1}, but were similar at deeper depths (Fig. 1B). On the final day the porewater iron (II) concentrations were often three times higher in the jellyfish plots than the controls ($p < 0.001$, Table S.1; Fig. 1C). Average values in the jellyfish plots exceeded 175 μmol L^{-1} and maximum concentrations occurred at 15 mm depth. Porewater iron (II) concentrations were greater in the jellyfish treatment relative to the controls from 6 mm above the sediment surface to 16 mm below, with the exception of 4, 2, and 1 mm above the sediment surface, when the jellyfish treatment only differed from the procedural control.

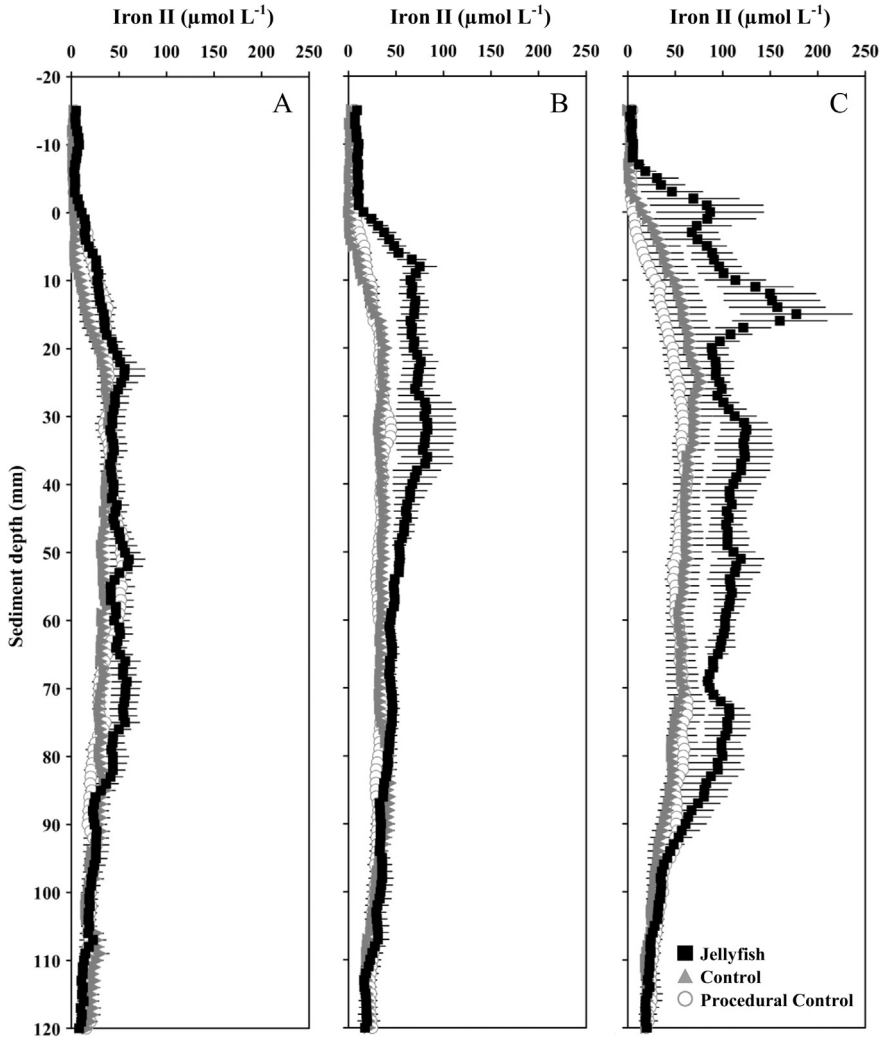

Fig. 1. Sediment porewater profiles of laterally averaged iron (II) concentrations with depth in jellyfish (black square), control (grey triangle), and procedural control (white circle) plots on day 1 (A), day 2 (B) and day 3 (C). Data are mean values of profiles ($n = 5$) for each individual probe and error bars represent standard error. Negative depths denote distance above the sediment surface.

Porewater sulfide concentrations did not differ among treatments or depths on the first day ($p > 0.05$, Table S.2). Although it appeared that mean concentrations of sulfide were higher in the jellyfish treatment (Fig. 2A), they did not differ from the control treatments due to the high variability in the data. On the second day concentrations were consistently low in all three treatments (Fig. 2B) but they changed with depth ($p = 0.029$, Table S.2), with a small increase in average concentrations to a maximum of 3.5 μmol L^{-1} at 9 mm depth. On the final day, porewater concentrations of sulfide were significantly higher in the jellyfish treatment than in both control treatments from 3 mm above the sediment surface to 83 mm below the sediment surface ($p = 0.023$, Table S.2; Fig. 2C). Concentrations were similar in all treatments below that point. The highest laterally averaged porewater sulfide concentration in the jellyfish plots was 45.6 μmol L^{-1} (16 mm depth), however, some concentration "hot spots" in the two-dimensional distributions of the individual probes approached 150 μmol L^{-1} (Fig. S.1). The two-dimensional distributions of porewater sulfide show concentrations were high in all jellyfish plots on the last day, however, the depth at which the highest sulfide concentrations occurred differed due to the heterogeneity within the sediment (Fig. S.1). Thus, the laterally averaged porewater profiles of sulfide in the jellyfish treatment had high variability (Fig. 2C) despite showing relatively consistent patterns.

3.3. Macrofauna

The addition of jellyfish to the sediment elicited changes to the macrofaunal community and patterns between treatments changed over time ($p = 0.011$, Table S.3; Fig. 3A). Macrofaunal communities in jellyfish plots differed to those in procedural control plots ($p = 0.016$) but not control plots after one day ($p > 0.05$, Table S.3). During Days 2 and 3, however, macrofaunal communities in the jellyfish plots differed from both controls ($p < 0.05$, Table S.3). Communities in control plots and procedural control plots remained similar throughout the experiment ($p > 0.05$, Table S.3). Eight taxa were correlated (Pearson R value > 0.5) to patterns observed in the macrofauna community data (Fig. 3B). Three taxa had patterns that were consistent with an effect of the jellyfish addition; one increased in abundance and two decreased. The taxon that contributed the most to differences between jellyfish treatments was the small whelk *Nassarius burchardi*. This whelk was often observed on the sediment surface underneath the jellyfish carrion. *N. burchardi* was more abundant in the jellyfish plots than both control treatments (Fig. 4A) and the effect of the jellyfish addition on *N. burchardi* abundance was rapid, as this pattern manifested on the first day and persisted throughout the experiment ($p < 0.001$, Table S.4). Abundances of *N. burchardi* did not differ between controls and procedural controls (Fig. 4A). The two taxa that decreased in abundance

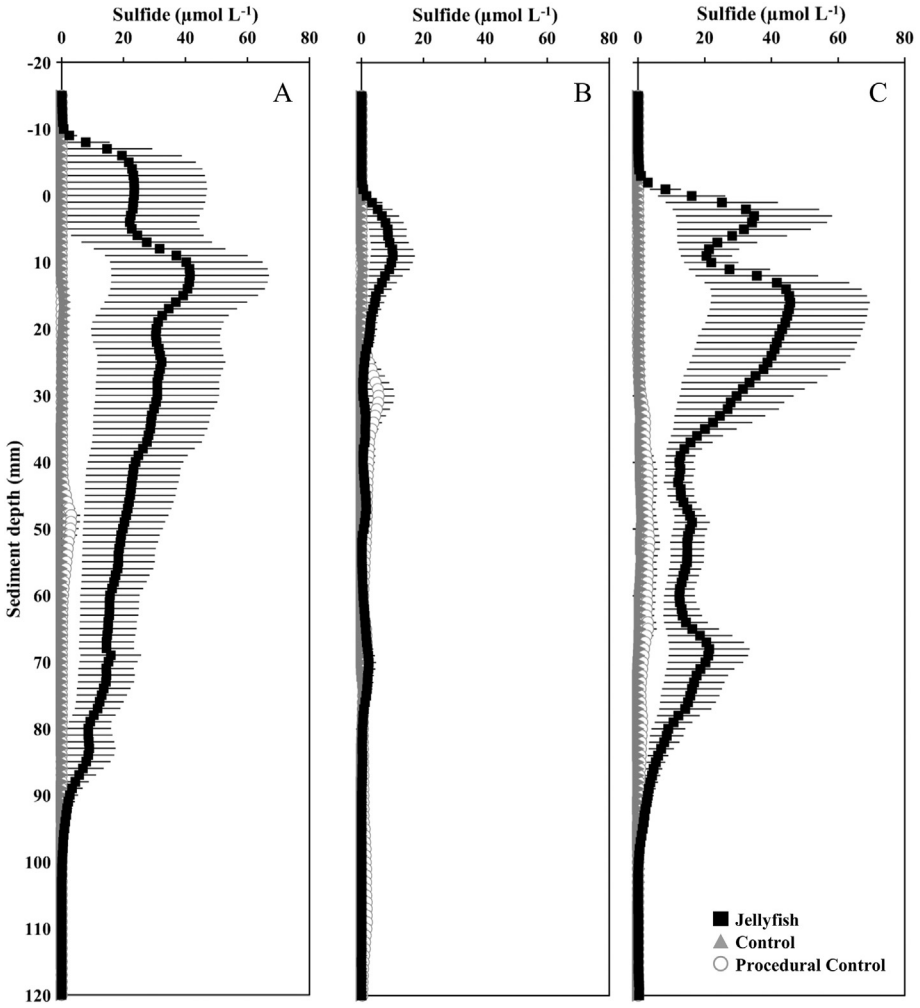

Fig. 2. Sediment porewater profiles of laterally averaged sulfide concentrations with depth in jellyfish (black square), control (grey triangle), and procedural control (white circle) plots on day 1 (A), day 2 (B) and day 3 (C). Data are mean values of profiles ($n = 5$) for each individual probe and error bars represent standard error. Negative depths denote distance above the sediment surface.

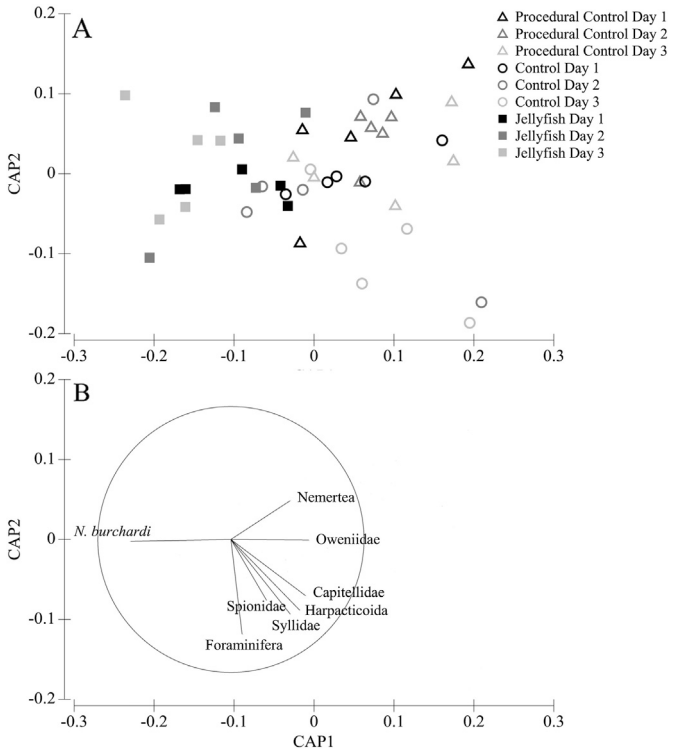

Fig. 3. Canonical analysis of principal coordinates (CAP) showing differences between the macrofaunal community in the jellyfish, control and procedural control plots over three days (A). Points that are closer together are more similar in community composition. Vector overlays (B) represent taxa correlations to the ordination axes with Pearson R values > 0.5. The length of the vector indicates the strength of the correlation.

with the addition of jellyfish were the polychaete families *Oweniidae* and *Capitellidae* (Fig. 4B, C, respectively). Both families were less abundant in the jellyfish plots than the controls, and the controls and procedural controls did not differ from each other for either taxa (Fig. 4B, C). Other taxa that were correlated with patterns in the community data had varied responses to the addition of jellyfish, often with a lower abundance in the jellyfish treatment relative to the controls or procedural controls, but not lower relative to both control treatments. These taxa included two polychaete families, *Syllidae* and *Spionidae*, as well as *Nemertea*, *Harpacticoida* and *Foraminifera*.

3.4. Benthic metabolism and nutrient fluxes

The fluxes of all analytes varied between jellyfish treatments but patterns changed through time ($p < 0.05$, Table S.5). Fluxes were the same in the jellyfish and control plots before the jellyfish were added at time 0 but then increased in the jellyfish treatment as the decomposition of the jellyfish progressed (Fig. 5). Sediment oxygen demand (SOD) in the jellyfish plots reached a maximum of 5654 ± 481 μmol m^{-2} h^{-1} at 50 h but then decreased and was less than twice the average control value of 1730 ± 199 μmol m^{-2} h^{-1} by 72 h (Fig. 5). SOD in the control chambers remained consistently low throughout the experiment. SOD was higher in the jellyfish treatment relative to the controls at 44 h and 64 h after the addition of carrion (Fig. 5). Fluxes of DOC showed similar patterns to those of SOD. They reached a maximum at 50 h, and the jellyfish treatment was higher than the control at 44 and 64 h (Fig. 5). DON production attained a maximum of 1907 ± 647 μmol m^{-2} h^{-1} at 44 h in the jellyfish plots and was higher than the control plots at 19 and 44 h (Fig. 5). Ammonium effluxes in the jellyfish plots were elevated for most of the experiment and reached a maximum at 50 h of 1899 ± 163 μmol m^{-2} h^{-1} (Fig. 5). Ammonium fluxes were higher in the jellyfish treatment than the controls

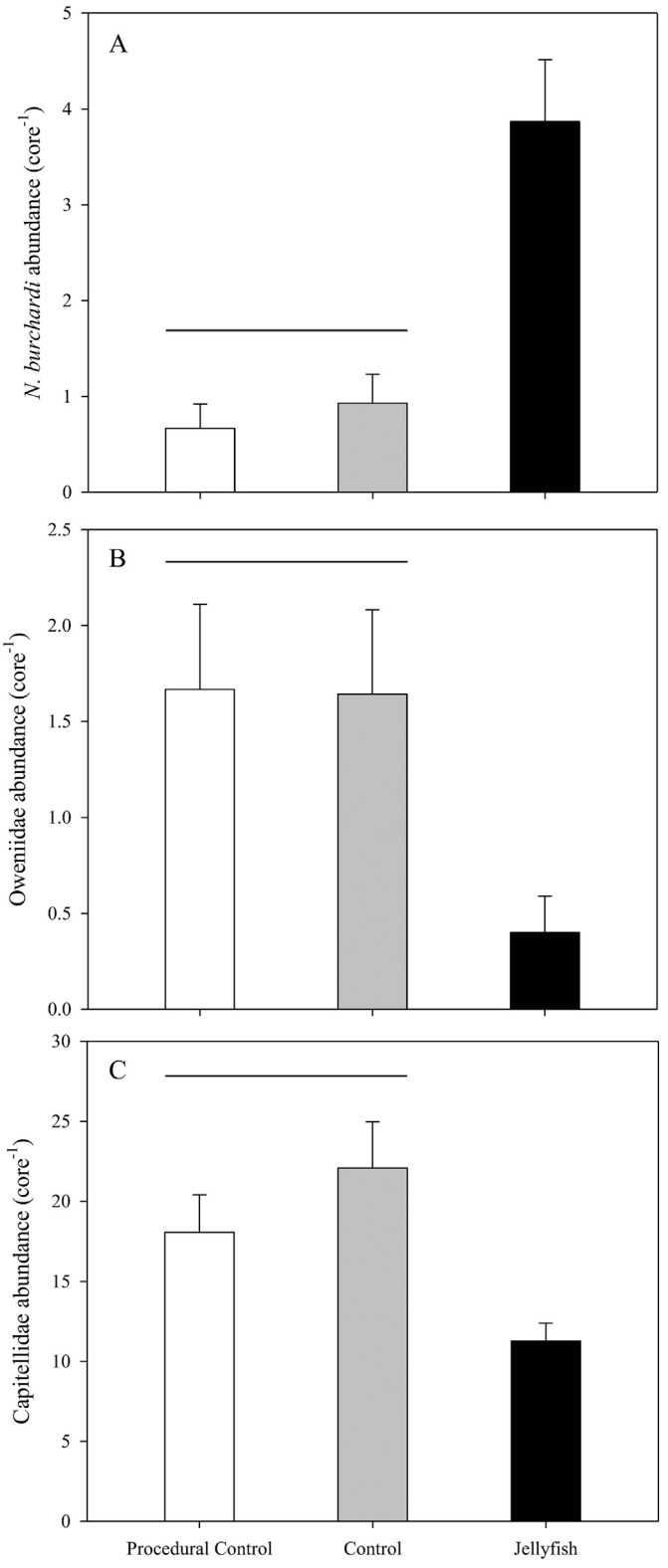

Fig. 4. Mean abundance (±standard error) averaged over three days of *Nassarius burchardi* (Gastropoda) (A), *Oweniidae* (Polychaeta) (B), and *Capitellidae* (Polychaeta) (C), in the jellyfish (black), control (grey) and procedural control (white) plots. Total volume of the cores was 2650 cm^3. Horizontal lines indicate no significant difference between treatments based on post-hoc tests.

at 19, 44 and 64 h (Fig. 5). By the final incubation at 72 h, fluxes of all analytes in the jellyfish treatment had decreased and did not differ from their original t = 0 values.

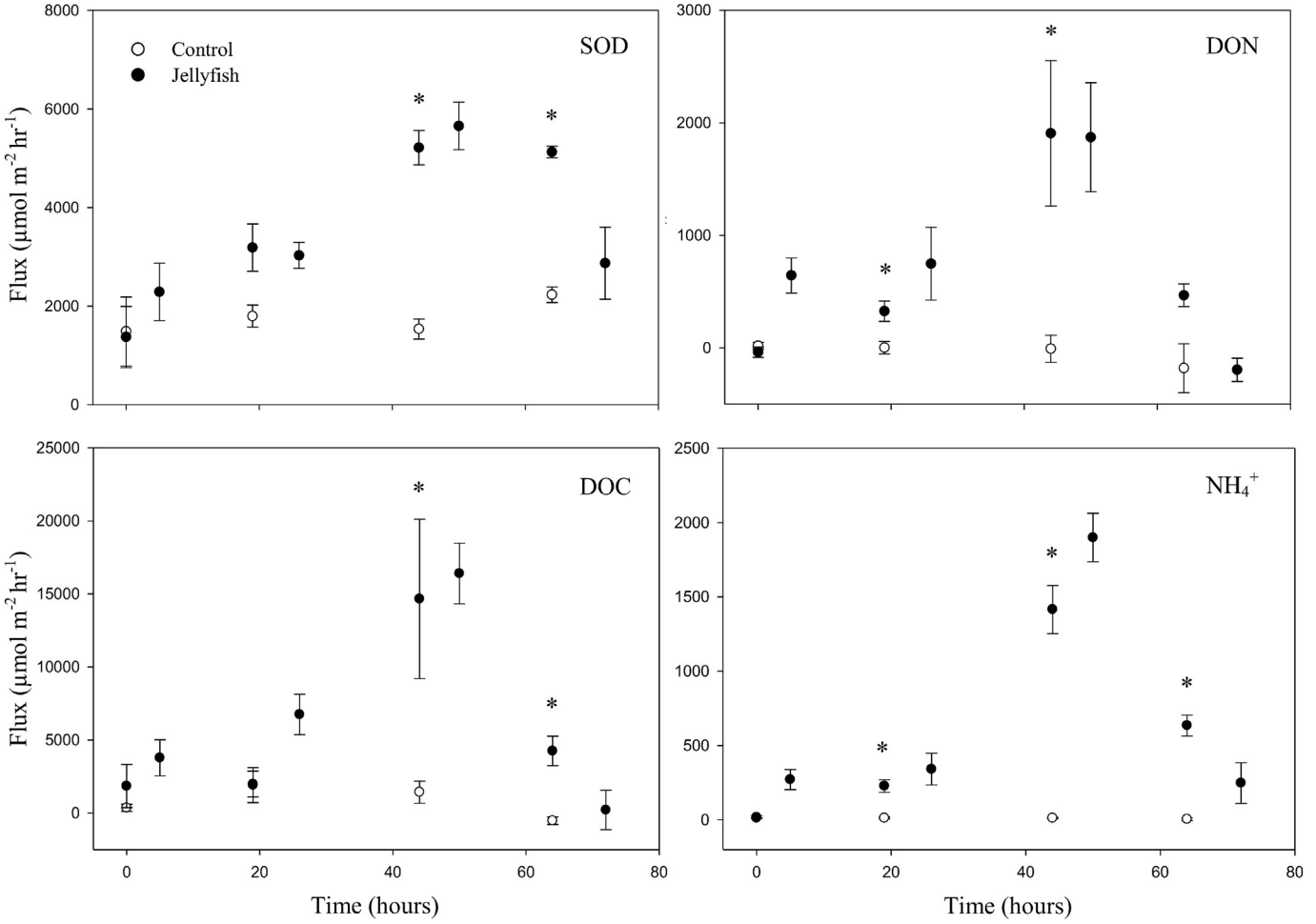

Fig. 5. Water-column fluxes in jellyfish (black circle) and control (white circle) chambers of dissolved oxygen, expressed as sediment oxygen demand (SOD), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), and ammonium (NH_4^+). Only jellyfish chambers were sampled at 5, 26, 50, and 72 h. Data are mean values and error bars represent standard error. Asterisks denote significant differences between treatments.

3.5. Sediment characteristics

The sediment was primarily composed of medium and fine sands, with 88.9% of sediment grains being 125–500 μm in size. The median grain size range was 250–500 μm. Bulk density was 1.97 ± 0.01 g cm^{-3} and porosity was 35.1 ± 0.9%. Organic matter content was low, with an LOI_{550} of 0.416 ± 0.026%.

4. Discussion

The input of gelatinous carrion to the benthos elicited rapid changes to all biological and biogeochemical parameters measured. Decomposition of *C. mosaicus* stimulated sediment oxygen demand, an efflux of carbon and nitrogen, and changed sediment redox conditions. The patterns in sediment biogeochemistry corresponded to changes observed in the macrofaunal assemblages, with some taxa decreasing in abundance. This highlights the advantages of using a multidisciplinary approach to elucidate potential underlying drivers of ecological patterns.

Jellyfish carrion had cascading effects on benthic biogeochemistry. The high demand for respiratory electron acceptors due to decomposition most likely created anoxic conditions in the surficial sediments below and around the jellyfish carcasses. This resulted in a shift towards anaerobic respiration as indicated by the accumulation of iron (II) and sulfide, the end-products of iron and sulfate reduction, in the sediment porewater when rates of SOD were elevated. Over time the porewater iron (II) increased in concentration and its concentration maximum migrated closer to the sediment surface. Although the sulfide profiles in the first two days were variable, the final day showed significant increases in porewater sulfide concentrations in jellyfish plots. The accumulation of these reduced analytes was likely also enhanced by the physical presence of the jellyfish, which formed a barrier and probably impeded the transfer of dissolved oxygen to the underlying sediment (Lebrato et al., 2012), limiting chemical and biological reoxidation of iron (II) and sulfide and allowing them to accumulate and diffuse towards the sediment surface (Middelburg and Levin, 2009). Furthermore, the physical barrier created by the jellyfish carrion may have limited the ability of burrowing fauna to ventilate their burrows, thus reducing the transport of oxygen into the deeper sediment strata and limiting the reoxidation of reduced respiratory electron acceptors (Welsh, 2003), favoring their accumulation beneath the jellyfish. This is the first study to investigate the effect of the decomposition of carrion on sediment biogeochemistry using DGT/DET probes and demonstrates that they are highly effective tools for this purpose.

The biogeochemical conditions created by the decomposing carcasses had implications for the benthic community because they created less hospitable conditions for metazoan assemblages. Low oxygen conditions can be detrimental to the macrobenthos (Gray et al., 2002), and sediment porewater sulfide concentrations, which attained 150 μmol L^{-1} beneath the carcass, were high enough to have potentially toxic effects on infauna (Bagarinao, 1992). The presence of sulfide in combination with hypoxic and anoxic conditions can be particularly harmful to benthic organisms, reducing survival times by ~30% (Vaquer-Sunyer and Duarte, 2010). Median lethal times in the presence

of sulfide (at concentrations <200 μmol L^{-1}) and low oxygen conditions can often be <72 h, and below 10 h for some sensitive species (Vaquer-Sunyer and Duarte, 2010). The rapid decrease in abundance of some taxa beneath the jellyfish carrion may, therefore, be due to the combined effects of low oxygen and the presence of sulfide in the sediment porewater.

The abundance of some taxa below the jellyfish carrion decreased, presumably because they died or migrated away from the changed sediment conditions. In particular, the decrease in *Capitellidae* abundance is noteworthy, as capitellid polychaetes can be abundant in areas with high organic enrichment (Pearson and Rosenberg, 1978), although this may be due in part to their ability to rapidly recolonize rather than a tolerance for low oxygen conditions (Tsutsumi, 1987). It is possible that if the experiment ran for longer, the initial decrease in capitellid abundance would be followed by an increase in the abundance of this taxon and other opportunistic species (Kelaher and Levinton, 2003). Only one taxon increased in abundance with the addition of the jellyfish; the carrion attracted the scavenging gastropod *Nassarius burchardi* (Britton and Morton, 1991). Nassariid gastropods are known to commonly consume carrion, using chemotaxis to find and rapidly move towards a food source (Britton and Morton, 1991). *N. burchardi* was, therefore, probably attracted to and migrating below the jellyfish to consume the gelatinous material.

The impacts of the decomposing material may persist over a period of days, as indicated by the increased SOD and the release of DOC, DON and NH_4^+ from the jellyfish, which reached maxima between 44 and 50 h and remained elevated for 64 h. The release of dissolved organic carbon and nitrogen was more prolonged than reported in the two other studies of jellyfish decomposition on the benthos, which used frozen gelatinous material (see West et al., 2009; Chelsky et al., 2015) rather than freshly killed jellyfish as the carrion. The rapid release of organic nutrients observed by West et al. (2009) and Chelsky et al. (2015) was probably an artifact of freezing the jellyfish, which enhanced the leaching of organic nutrients due to physical damage to the jellyfish tissues during freezing and thawing. The elevated fluxes of DO, DOC, DON and NH_4^+ associated with carrion decomposition have the potential to have longer lasting effects than the three days of this study. For example, the flux of DOC and DON to the water column could stimulate bacterioplankton production and respiration (Condon et al., 2011; Pitt et al., 2009), which could amplify the effects of the oxygen demand for benthic decomposition and potentially contribute to water column hypoxia. Whereas, the remineralization of organic nitrogenous compounds to inorganic nitrogen could support primary production (West et al., 2009).

The DGT/DET probes enabled fine scale measurements of changes to sediment porewater solutes as jellyfish detritus decomposed. Despite their efficacy, these passive samplers have rarely been used for ecological applications (Pagès et al., 2014, 2012). Many conventional sampling techniques for iron (II) and sulfide, such as core slicing and porewater extraction by centrifugation, do not provide sufficient spatial resolution for interpreting biogeochemical processes that can occur on the millimeter scale (Robertson et al., 2009; Stockdale et al., 2009). Fine scale variations in porewater solute concentrations were evident in the two-dimensional distributions of iron (II) and sulfide, as can be seen in the day 3 sulfide distributions (Fig. S.1). As with other studies (e.g. Robertson et al., 2009), our data show a high degree of spatial heterogeneity in the distributions of iron (II) and sulfide, and that shifts in these distributions are not uniform but result from changes in the intensity and size of the sediment zones dominated by iron (II) and sulfide. This further reinforces the need for two dimensional, high resolution, *in situ* measurements that avoid disturbing the spatial distribution of solutes and thereby allow their potential ecological impacts to be better assessed. For example, our data show that even on the final day, large zones of the sediment in the jellyfish treatment remained sulfide-free and could potentially act as refugia that would allow infauna to survive the short-term impacts of jellyfish bloom collapses.

The biogeochemical and biological effects of decomposing jellyfish could have impacts on an ecosystem level, especially when considered at the scale on which blooms can occur. *C. mosaicus*, in particular, often forms large blooms in semi-enclosed lagoons with limited mixing (Pitt and Kingsford, 2000). A bloom in another Australian coastal lagoon, for example, attained the fourth largest biomass of a jellyfish bloom ever recorded (>500 tonnes km^{-2}; Lilley et al., 2011; Pitt and Kingsford, 2003). The collapse of a bloom in a system like this could lead to generalized hypoxic conditions in the water column and the widespread occurrence of sulfidic conditions in the sediment with impacts on infaunal communities such as those observed in this study. If jellyfish carcasses were to aggregate in particular areas due to the effects of currents, these impacts could result in mass faunal mortality over large areas, as has been observed during the collapse and decomposition of macroalgal blooms (Castel et al., 1996; Cloern, 2001).

The decomposition of jellyfish carrion has major, albeit potentially short-term, implications for benthic biogeochemistry and faunal assemblages. Jellyfish carcasses have been observed at high densities on the benthos in several locations globally (Lebrato et al., 2012), however, the effect of this gelatinous material on benthic processes and communities has rarely been studied. The integrated approach used here, evaluating biogeochemistry and faunal assemblages, provides a more complete picture of decomposition effects than has been previously presented, and enables a better understanding of the ecosystem perturbations resulting from collapsed jellyfish blooms.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.05.011.

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