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JELLYFISH BLOOMS

# Influence of decomposing jellyfish on the sediment oxygen demand and nutrient dynamics

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**Abstract** Jellyfish populations can grow rapidly to attain large biomasses and therefore can represent significant stocks of carbon and nitrogen in the ecosystem. Blooms are also generally short-lived, lasting for just weeks or months, after which time the population can decline rapidly, sink to the bottom and decompose. The influence of decomposing jellyfish (*Catostylus mosaicus*, Scyphozoa) on benthic dissolved oxygen and nutrient fluxes was examined in a mesocosm experiment at Smiths Lake, a coastal lagoon in New South Wales, Australia. Sediment (10 l) was placed in each of 10 mesocosms (50 × 40 cm, 30 cm deep and ~60 l volume) which were supplied a continuous flow of fresh lagoon water. One jellyfish (1.6 kg wet weight or ~25 g C $m^{-2}$) was added to each of five mesocosms, with the remaining five mesocosms serving as controls. Exchanges of dissolved oxygen, organic and inorganic nutrients between the benthos and water column were measured 14 times over a period of nine days. The addition of dead jellyfish tissue to the mesocosm sediments initially resulted in an efflux of phosphate, dissolved organic nitrogen and dissolved organic phosphorus to the water column. Dissolved organic nitrogen and dissolved organic phosphorus effluxed at rates more than 8 and 25 times greater than those measured in control mesocosms, respectively. This was probably due to the intracellular nutrients leaching from the jellyfish tissues. As decomposition proceeded, a large quantity of ammonium was released to the water column and sediment oxygen demand increased, indicating bacterial decomposition was dominant. Overall the addition of dead jellyfish caused a 454% increase in ammonium efflux and 209% increase in sediment oxygen demand over the 9-day experiment relative to the controls. The decomposition of large numbers of jellyfish after major bloom events could be a significant source of nutrients and, depending on the system, could have a major impact on primary production. Moreover, depending on the degree of mixing in the water column, decaying jellyfish may also contribute to bottom water hypoxia.

**Keywords** Decomposition · Decay · Organic matter · *Catostylus mosaicus* · Scyphozoa · Flux

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Jellyfish Blooms: Causes, Consequences, and Recent Advances

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## Introduction

The appearance and disappearance of large numbers of medusae is a common characteristic of jellyfish

populations (Graham, 2001; Mills, 2001). Blooms of jellyfish can attain very large biomasses and are generally short-lived, lasting for just weeks or months, after which time the population may crash rapidly (Mills, 2001). Jellyfish blooms rapidly assimilate carbon and nutrients from their planktonic prey and the nutrients assimilated in the large living biomass of jellyfish blooms can represent a significant stock of carbon and nutrients within the ecosystem (Pitt et al., this volume). Jellyfish tissue mainly consists of labile components, such as lipids, carbohydrates, and proteins, and has a low C:N ratio (Larson, 1986; Gorsky et al., 1988; Arai et al., 1989; Clarke et al., 1992). Therefore, microbial decomposition of jellyfish biomass could be rapid and result in a large and concentrated release of nutrients to the water column. Consequently, the collapse and decomposition of large jellyfish blooms could have significant impacts on ecosystem oxygen and nutrient dynamics (Hay, 2006).

In deep waters (e.g., fjords), a substantial proportion of decomposition may occur in the water column. For example, approximately 95% of the jellyfish, *Periphylla periphylla* (Péron & Lesuer, 1809), decomposed within five days when suspended in the water column in Raunefjorden, Norway (Titelman et al., 2006). During decomposition the jellyfish released large amounts of organic carbon to the water column, and while growth of some phylogenetic groups of bacteria was enhanced, growth of other groups was inhibited (Titelman et al., 2006). The rapid decay of jellyfish corpses and large release of nutrients in the water column represents an important trophic link in the ecosystem (Titelman et al., 2006). However, some moribund jellyfish would also accumulate on the surface of the sediment especially in shallow waters (Arai, 1997; Kingsford et al., 2000). For example, carcases of the giant jellyfish, *Nemopilema nomurai* (Kishinouye, 1922), sink to the seafloor upon death because the dead animals have a greater density than live animals and the surrounding seawater (Yamamoto et al., 2008). On the sediment surface, the decomposition of organic matter may enhance benthic microbial communities, causing a release of inorganic nutrients and increase in sediment oxygen demand, which then could influence nutrient and oxygen concentrations in the water column (Blackburn & Blackburn, 1993).

The presence of dead jellyfish on the seafloor was recorded as early as 1880 (Billett et al., 2006), and is evident in fossil records since the Cambrian (Hagadorn et al., 2002). Billett et al. (2006) reported a large decaying bloom of jellyfish on the seafloor off the coast of Oman, where jellyfish were observed tumbling down the continental shelf and accumulating over wide areas at depths between 350 and 3300 m. In the southwest Sea of Japan carcasses of *N. nomurai*, which can grow up to 2 m diameter and 200 kg, have been reported at densities of 0.2 to 5.1 individuals per $km^2$ (Yamamoto et al., 2008). Large numbers of jellyfish corpses are likely to be an important source of organic matter to the benthos and may play an important role in the transfer of organic matter from the pelagic zone to the seafloor and associated benthic communities (Billett et al., 2006; Yamamoto et al., 2008). There have been no previous studies that measure the influence of decomposing jellyfish on the sediment surface.

*Catostylus mosaicus* (Quoy & Gaimard, 1824) is a scyphozoan jellyfish that is very common in the estuaries of eastern Australia. Populations of *C. mosaicus* frequently form spectacular blooms that can exceed 500 ton/$km^2$ (Pitt & Kingsford, 2003a). Growth rates of *C. mosaicus* are extremely rapid and small medusae can grow up to 4.81 mm bell diameter per day (Pitt & Kingsford, 2003b). During rapid growth, *C. mosaicus* obtains nutrients from planktonic prey and a large proportion of the available nutrients in the system may potentially be incorporated into the jellyfish biomass. The entire life cycle of *C. mosaicus* may potentially be completed within 2 to 3 months, and abundances can fluctuate enormously over periods of weeks and months (Pitt & Kingsford, 2003b). When a population of *C. mosaicus* collapses, the large quantity of nutrients released during decomposition may have major effects on nutrient and oxygen dynamics. The aim of this study was to investigate the changes in sediment oxygen demand and nutrient dynamics associated with the benthic decomposition of the jellyfish, *C. mosaicus*.

## Materials and methods

### Experimental protocol

The influence of decomposing jellyfish on sediment and water column oxygen and nutrient fluxes was investigated in February and March 2006 at Smiths Lake (152°52′ E, 32°39′ S), a largely unmodified,

intermittently closed and open coastal lagoon on the east coast of Australia. Approximately 10 l of evenly-mixed sediment was collected from Smiths Lake at a depth of ~0.5 m and placed into each of 10 black plastic tubs, 50 × 40 cm, 30 cm deep and 60 l capacity, hereafter called mesocosms. The mesocosms were placed in Smiths Lake at 1.5 m depth from February 10 until March 3 to allow natural sediment chemistry and redox profiles to re-establish. They were then carefully removed from the lake and placed into a large pool (305 cm diameter and 75 cm deep) located on the shore. Natural water was continuously pumped (2800 RPM pump; ONGA, Australia) from ~20 m from the shoreline of Smiths Lake (~1.5 m water depth) into a 200 l overflowing drum. Water was gravity fed from the drum to 10 pipes with taps that flowed into individual mesocosms at a rate of ~3 l $min^{-1}$. Water overflowed from the mesocosms into the pool, which maintained a constant natural temperature in the mesocosms. The water level of the pool was lower than the rim of the mesocosms which prevented any mixing of water between mesocosms. Mesocosms were therefore considered independent. Physical parameters in the mesocosms remained relatively constant during the 9-day experiment, and similar to those of Smiths Lake (pH ~8; salinity ~20 ppt; temperature ~30°C; dissolved oxygen ~94% saturation). Five *C. mosaicus* (wet weight 1.6 ± 0.0 kg and ~5 g C each) that had previously been caught with a dip net from Smiths Lake and sacrificed by freezing, were thawed and placed on the sediment surface of five randomly selected mesocosms. No additions were made to the other five mesocosms, which served as controls. The mesocosms were maintained in the dark using black plastic sheeting so that the biogeochemical processes could be measured in the absence of photosynthetic production. Water in the mesocosms was continuously stirred either by the inflow of new water, or during incubations, using small electronic water pumps placed inside each mesocosm.

## Determination of sediment-water column oxygen and nutrient fluxes

In total, 14 flux incubations were done over the 9 days that the jellyfish took to visibly decompose. One flux incubation of all mesocosms was done before the addition of jellyfish to mesocosms and the timing of the other 13 was designed to ensure that both short-term and long-term changes in oxygen and nutrient fluxes would be measured. On the first 3 days of the experiment, 2 to 3 incubations were done per day; from day 4 onward, 1 incubation was done each day. During each incubation, water flow was simultaneously stopped in all mesocosms and floating lids were placed over each mesocosm to isolate them from the atmosphere. Small electronic water pumps inside each mesocosm were switched on to mix the water at a rate that did not disturb the sediments. The incubation times were varied to ensure that the oxygen exceeded 80% saturation throughout the incubation. The approximate incubation times required were predicted based on measurements made in previous incubations. Exact incubation times were recorded and ranged between 2 and 4 h. Water samples taken from each mesocosm before and immediately after incubations were analyzed for dissolved oxygen (DO), ammonium ($NH_4^+$), nitrite and nitrate ($NO_x$), phosphate ($PO_4^{3-}$), dissolved organic nitrogen (DON), dissolved organic phosphorus (DOP), total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP) concentrations.

## Water analyses

To measure DO, one water sample (12 ml) was collected from each mesocosm (~10 cm water depth) with a 30 ml sterile syringe (Termo, USA). Syringes had 10 cm of tubing placed on their nozzle to minimize contact with the air. Samples were carefully transferred into gas-tight 12 ml borosilicate glass vials (Labco, UK) containing a small glass ball. Water samples were immediately fixed with Winkler reagents A and B (APHA, 1999), and secured with a lid with small rubber septum (Labco, UK) to ensure that the samples were airtight. Care was taken to ensure that no bubbles were present in the samples, which were mixed using the small glass balls. Samples were stored at 4°C and analyzed within 24 h. DO concentrations were measured by the Winkler method with azide modification (APHA, 1999).

For inorganic and organic nutrient analyses, two 10 ml water samples were collected from each mesocosm (~10 cm water depth) with a 30 ml sterile syringe (Termo, USA), filtered (0.45 μm) into sterile plastic vials (Sarstedt, Australia) and frozen (−20°C). For all laboratory and field analyses, gloves

were worn and glassware and plasticware were cleaned by soaking in 10% (v/v) HCl (>24 h) and rinsing with de-ionized water (Milli-Q; 18 MΩ cm) prior to use. The concentrations of inorganic nutrients, $NH_4^+$, $NO_x$, and $PO_4^{3-}$, were measured using an Easychem Plus colorimetric analyzer (Systea Analytical technologies S.r.l., Anagni, Italy). Low nutrient seawater (GF filtered) was used for the preparation of standards for an 8-point calibration and for quality controls. Certified reference materials (CRMs) from the Queensland Health Scientific Services were used to verify samples. Recovery rates between 90 and 102% were achieved.

TDN and TDP were determined following oxidation. Water samples, blanks, standards, and CRMs were autoclaved (first digestion 45 min at 121°C; second digestion 15 min at 121°C) with 2:1 ratio of sample to digestion solution (20 g $K_2S_2O_8$ and 5.5 g NaOH in 1 l Milli-Q water). This digestion oxidized all organic and inorganic nitrogen and phosphorus to $NO_x$ and $PO_4^{3-}$, respectively. TDN and TDP concentrations were measured as $NO_x$ and $PO_4^{3-}$, as described above. Concentrations of DON were calculated as the concentration of TDN minus the sum of $NH_4^+$ and $NO_x$. Similarly, concentrations of DOP were calculated as the concentration of TDP minus $PO_4^{3-}$.

### Flux calculations

For each measured compound, the net flux between the sediment and water column during each incubation was calculated as:

$$\text{Flux} = \frac{(DC \times V)}{(A \times T)}$$

where $DC$ is the difference in concentration (μmol) between the water samples taken before and after the incubation, $V$ is the mesocosm volume (l), $A$ is the sediment surface area ($m^2$), and $T$ is the incubation time (h). If the flux was positive, it indicated that the compound effluxed from the sediment (or sediment and jellyfish) to the water; if negative, it indicated the net consumption of the compound by the sediment (or sediment and jellyfish).

### Sediment profiles

At the end of the experiment, sediment samples were taken from each mesocosm to analyze depth profiles of sediment exchangeable $PO_4^{3-}$ and $NH_4^+$ pools. For these analyses, two arbitrarily positioned sediment cores were taken from each mesocosm using a 3-ml sterile syringe (0.9 mm diameter) (Termo, USA) that had the nozzle removed. From each core, six sediment aliquots (0.5 ml) at 8 mm depth intervals were placed in 10 ml sterile plastic vials (Sarstedt, Australia) containing 9 ml of either 1 M KCl or 1 M $MgCl_2$; samples were shaken vigorously to extract $NH_4^+$ and $PO_4^{3-}$, respectively, from the sediment into solution and frozen (−20°C). To measure the concentrations of exchangeable $PO_4^{3-}$ and $NH_4^+$, samples were defrosted and centrifuged; the supernatant liquid was filtered through a GF filter membrane (Whatman, Australia) and analyzed for $NH_4^+$ and $PO_4^{3-}$ as described above, except that standards and blanks were prepared with 1 M KCL or 1 M $MgCl_2$, as appropriate.

### Statistical analyses

One-way Analyses of Variance (ANOVAs) were used to test for differences in fluxes of each measured compound between jellyfish and control mesocosms separately for each of the 14 incubations. One-way ANOVAs were also used to test for differences in sediment exchangeable $PO_4^{3-}$ and $NH_4^+$ pools between control and jellyfish mesocosms, separately for each sediment depth, as depths were not independent. The assumption of homoscedasticity was tested with Levene's test and data were transformed using ln(x) transformations when Levene's test was significant. If the data had negative values, the smallest number was added to each value before transformation to make the values positive (Quinn & Keough, 2002). Levene's test showed that all data transformations removed heterogeneity; therefore, analyses were done on transformed data.

## Results

The decomposition of *C. mosaicus* medusae was rapid; after 9 days, the jellyfish mesocosms were visually similar to the controls. During decomposition, the jellyfish mesocosms contained black stained, sulfide-rich sediment around the jellyfish, had an obvious white layer of sulfur oxidizing bacteria, and had a pungent smell of hydrogen sulfide.

## Sediment oxygen demand

Before jellyfish were added to the mesocosms, the sediment oxygen demand (SOD) in the jellyfish and control mesocosms were similar with a mean (±SE) of 2177 ± 272 μmol $m^{-2}$ $h^{-1}$ (Fig. 1). The mean SOD in control mesocosm incubations remained low for the entire experiment, fluctuating between 1132 ± 788 and 2590 ± 718 μmol $m^{-2}$ $h^{-1}$ (Fig. 1). Conversely, SOD in the jellyfish treatment increased considerably and was significantly greater than the controls at 15 h ($F_{1,9} = 5.5$; $P = 0.04$), 30 h ($F_{1,9} = 15.8$; $P < 0.1$), 42 h ($F_{1,9} = 5.71$; $P = 0.04$), 73 h ($F_{1,9} = 5.8$; $P = 0.04$), 85 h ($F_{1,9} = 11.1$; $P = 0.01$), and 96 h ($F_{1,9} = 8.7$; $P = 0.02$). The average SOD in the jellyfish mesocosm reached a maximum of 6161 ± 3422 μmol $m^{-2}$ $h^{-1}$ at 85 h, which was nearly 9 times greater than the control at that time. SOD in the jellyfish treatment remained high over the following 5 days, with a mean of 4418 ± 737 μmol $m^{-2}$ $h^{-1}$. Variability in the jellyfish incubations during this time was large, however, and no significant differences between the jellyfish and control mesocosms were detected. Overall, the addition of the jellyfish represented an average 209% increase in SOD compared with the controls when integrated over 9 days.

## Nutrient fluxes

The mean $NH_4^+$ (±SE) fluxes in the jellyfish and control treatments were similar at Time 0, prior to the addition of the jellyfish (13 ± 48 μmol $m^{-2}$ $h^{-1}$; Fig. 2A). The control fluxes of $NH_4^+$ remained low throughout the experiment and ranged between −70 ± 32 and 588 ± 62 μmol $m^{-2}$ $h^{-1}$ (Fig. 2A). In the jellyfish mesocosms, the efflux of $NH_4^+$ increased and reached a maximum of 2044 ± 519 μmol $m^{-2}$ $h^{-1}$ at 73 h, which was nearly 9 times greater than the control mesocosms (Fig. 2A). Jellyfish mesocosm incubations showed significantly greater efflux than controls at 42 h ($F_{1,9} = 12.0$; $P = 0.01$), 60 h ($F_{1,9} = 7.8$; $P = 0.02$), 73 h ($F_{1,9} = 12.1$; $P = 0.01$), 114 h ($F_{1,9} = 8.34$; $P = 0.02$), and 141 h ($F_{1,9} = 6.0$; $P = 0.04$) after the jellyfish were added. Thereafter, fluxes slowed and were similar to the controls. Overall, efflux of $NH_4^+$ was 454% higher in the jellyfish mesocosms compared with the controls when integrated over the entire 9 days. Mean $NO_x$ fluxes were relatively low and variable for both the jellyfish and control mesocosms for all incubations, fluctuating between −235 ± 109 and 144 ±

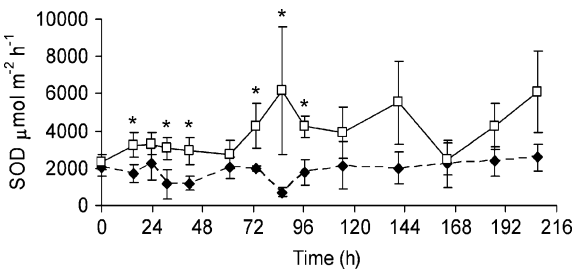


**Fig. 1** Sediment oxygen demand (SOD) during incubations of *Catostylus mosaicus* jellyfish (□) and control (◆) mesocosms before (Time 0) and after jellyfish were added. * indicates significant differences between jellyfish and control mesocosms ($P < 0.05$). Each point (mean ± SE) represents 5 replicates

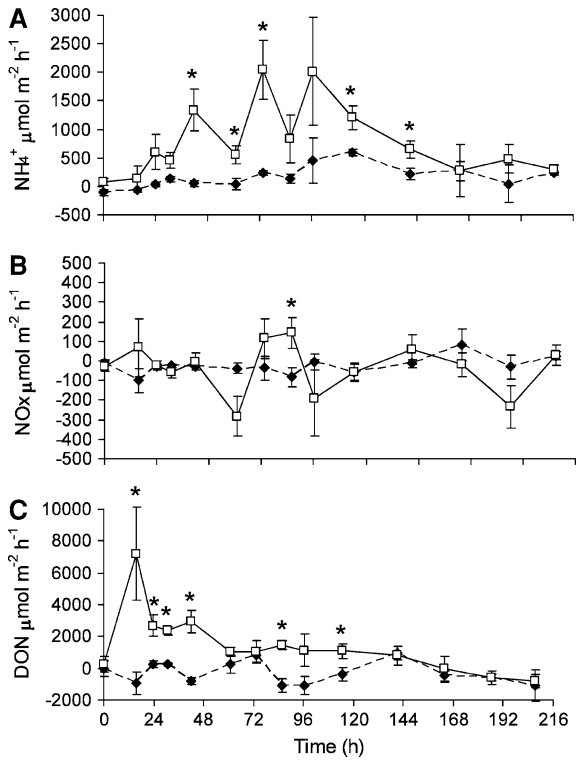


**Fig. 2** Water-column nutrient fluxes during incubations of *Catostylus mosaicus* jellyfish (□) and control (◆) mesocosms before (Time 0) and after jellyfish were added. (**A**) ammonium $NH_4^+$, (**B**) nitrite and nitrate $NO_x$ and (**C**) dissolved organic nitrogen DON. * indicates significant differences between jellyfish and control mesocosms ($P < 0.05$). Each point (mean ± SE) represents 5 replicates

78 μmol $m^{-2}$ $h^{-1}$ for the entire experiment (Fig. 2B); however, $NO_x$ efflux was significantly greater than the controls 85 h ($F_{1,9} = 6.1$; $P = 0.04$) after the jellyfish were added to the mesocosms.

Before the addition of the jellyfish, the mean fluxes of DON in the control and jellyfish mesocosms were similar, with an average of 125 ± 338 μmol $m^{-2}$ $h^{-1}$ (Fig. 2C). The flux of the control treatments remained low, averaging 403 ± 163 μmol $m^{-2}$ $h^{-1}$ during the 9 days (Fig. 2C). Following the addition of jellyfish to the mesocosms there was a rapid efflux of DON, which reached a maximum of 7182 ± 2934 μmol $m^{-2}$ $h^{-1}$, 8-fold higher than the controls (Fig. 2C). DON efflux was significantly different than the controls at 15 h ($F_{1,9} = 2.7$; $P = 0.03$), 24 h ($F_{1,9} = 11.65$; $P = 0.01$), 30 h ($F_{1,9} = 145.3$; $P < 0.1$), 42 h ($F_{1,9} = 27.1$; $P < 0.1$), 85 h ($F_{1,9} = 23.5$; $P < 0.1$), and 114 h ($F_{1,9} = 5.6$; $P = 0.04$) after the jellyfish were added to the mesocosms. Thereafter, DON effluxes in the jellyfish mesocosms gradually declined. When integrated over the entire experiment, DON effluxes were 316% greater in the jellyfish mesocosms compared with the controls. For the first 60 h of the experiment, the efflux of TDN in the jellyfish mesocosms was mainly DON (75–92%); for the remaining incubations, efflux was mostly DIN (84–100%), with the exception of the incubation at 73 h, in which TDN was comprised equally of organic and inorganic components.

Before the addition of jellyfish, mean fluxes of $PO_4^{3-}$ for the jellyfish and control mesocosms were very low and similar, with a mean of 2 ± 1 μmol $m^{-2}$ $h^{-1}$ (Fig. 3A). The $PO_4^{3-}$ flux in the jellyfish treatment was significantly greater than in the control treatment 15 h after addition of the jellyfish ($F_{1,9} = 37.6$; $P < 0.1$). During this incubation, the jellyfish mesocosm reached a maximum of 287 ± 47 μmol $m^{-2}$ $h^{-1}$ (Fig. 3A), which was 448 times greater than the controls. For the remainder of the experiment, the fluxes of $PO_4^{3-}$ in the jellyfish and control treatments were low and similar (Fig. 3A). DOP showed similar trends, with jellyfish mesocosms remaining low and similar to the controls (average −2 ± 2 μmol $m^{-2}$ $h^{-1}$), except for a rapid efflux in the jellyfish mesocosms at 15 h. This was significantly different than the control mesocosms ($F_{1,9} = 31.1$; $P < 0.1$). At 15 h, DOP in the jellyfish mesocosms reached a maximum of 725 ± 124 μmol $m^{-2}$ $h^{-1}$, which was more than 25 times higher than the mean

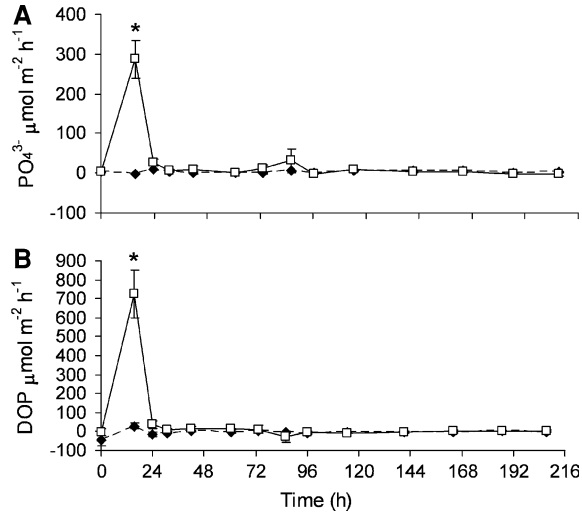


**Fig. 3** Water-column nutrient fluxes during incubations of *Catostylus mosaicus* jellyfish (□) and control (◆) mesocosms before (Time 0) and after jellyfish were added. (**A**) phosphate $PO_4^{3-}$ and (**B**) dissolved organic phosphorus (DOP). * indicates significant differences between jellyfish and control mesocosms ($P < 0.05$). Each point (mean ± SE) represents 5 replicates

control flux (Fig. 3B). TDP flux at 15 h in the jellyfish mesocosms was composed mainly of DOP (>70%).

### Sediment profiles

Depth profiles of exchangeable $NH_4^+$ were similar in the jellyfish and control treatments at all sediment depths (0.0–4.8 cm) at the end of the experiment. Exchangeable $PO_4^{3-}$ concentrations were significantly different ($F_{1,9} = 8.22$; $P = 0.02$) at sediment depth 4.0–4.8 cm, with the jellyfish mesocosms averaging 5 times greater than the controls (Fig. 4). All other sediment depths were not significantly different (Fig. 4).

## Discussion

Key factors regulating benthic nutrient regeneration are the quality, quantity, and spatial distribution of organic matter deposited on the sediment (Blackburn & Henriksen, 1983; Blackburn & Blackburn, 1993). Jellyfish tissue has a simple matrix, a high water content (>90%), and low carbon to nitrogen ratio (Shenker, 1985; Larson, 1986; Gorsky et al., 1988; Clarke et al., 1992; Shushkina et al., 2000), therefore

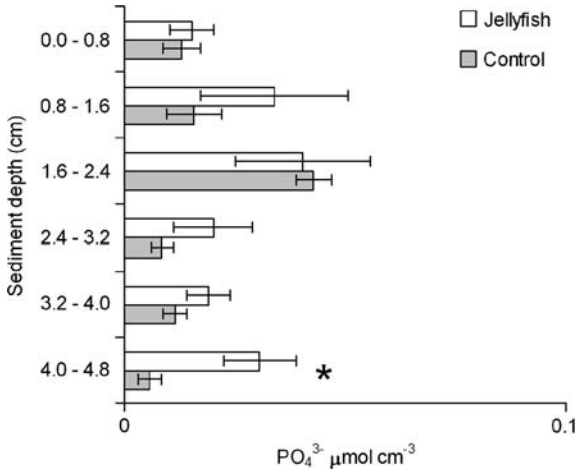


**Fig. 4** Concentration of exchangeable phosphate $PO_4^{3-}$ at different sediment depths (0.8 cm intervals) in *Catostylus mosaicus* jellyfish and control mesocosms at the end of the 9 day experiment. * indicates significant differences between jellyfish and control mesocosms ($P < 0.05$). Each point (mean ± SE) represents 5 replicates

it consists of high quality labile organic matter and is likely to rapidly decompose, causing large increases in oxygen demand and nutrient regeneration rates (Blackburn & Henriksen, 1983; Blackburn & Blackburn, 1993). In this study, the decomposition of dead, *C. mosaicus* jellyfish conformed to predictions for a high surface input of labile organic matter, because decay was rapid (9 days), organically bound nutrients were quickly recycled to the water column, and SOD increased, suggesting that microbial processes were enhanced.

The decomposition of dead jellyfish tissue initially showed a large efflux of organic nutrients. DOP was more than 25-times higher in the jellyfish mesocosms compared with the controls 15 h after the jellyfish was added. DON efflux during this time was 8-fold larger in the jellyfish mesocosms compared with the controls, and while the controls were a moderate sink for DON, the jellyfish mesocosms reversed the direction of fluxes and were a large source. From estimates of C:N ratio of *C. mosaicus* (West, unpublished data) and literature values of P (Schneider, 1990; Arai, 1997), we estimate that 5 g of C, 1.5 g of N and 0.1 g of P were in the jellyfish biomass that was added to the mesocosms. Therefore the initial efflux during the first 24 h represents ~18% of the total nitrogen and ~35% of the total phosphorus in the original jellyfish tissue. This is likely to be a result of soluble compounds rapidly leaching from dead jellyfish tissues. These results are consistent with the rapid leaching of dissolved organic carbon (DOC) observed from dead *P. periphylla* tissue in the water column (Titelman et al., 2006). Although freezing the jellyfish to kill them may have resulted in cell damage and an overestimation of the rate of leaching, these organic nutrients are likely to represent the intracellular pool that would diffuse from the cells, albeit at a slower rate than if they died naturally.

Following the initial leaching period, there was a gradual efflux of DIN from the jellyfish biomass. This efflux lasted for ~5 days and overall 455% more $NH_4^+$ effluxed from the jellyfish than the control mesocosms. The efflux of $NH_4^+$ is likely to be a result of microbial mineralization of the jellyfish tissue, which is further supported by the consumption of oxygen in the jellyfish mesocosms indicating the aerobic respiration by micro-organisms. SOD in the jellyfish mesocosms integrated over all incubations showed a 209% increase when compared with the controls. While DIP was not released to the water column after the first day of mineralization, the increased exchangeable $PO_4^{3-}$ in the sediments suggests that some of the phosphorus may have accumulated in the sediments. Exchangeable $PO_4^{3-}$ in the sediments is indirectly linked to rates of sulfide production and reoxidation (Azzoni et al., 2001). Thus, the black iron sulfide of the top sediment layers was reduced and $PO_4^{3-}$ diffused and accumulated in deeper sediments (4.0–4.8 cm), which were likely to have more iron hydroxides available. There was also no large change in the concentration of $NO_x$ in the jellyfish mesocosms compared with the controls. This is largely as expected because chemoautotrophic organisms, which are responsible for nitrification, tend to be out competed by heterotrophs for available oxygen (Herbert, 1999). Thus, whilst $NH_4^+$ was in excess in the jellyfish treatment it probably could not be extensively utilized by the nitrifiers due to the low availability of oxygen on the surface of the sediment.

Ecological stoichiometry considers the elemental composition in biological transformations, where an elemental imbalance or mismatch of consumers (e.g., microbes) and resources (e.g., organic matter) will determine ecological interactions (Sterner & Elser, 2002). For example, the decomposition of organic matter will be fastest when the elemental composition

(or C:N:P) of the organic matter is similar to that of the microbes because the consumer obtains elements from the resource in the same proportions required for their own growth and reproduction; however, as organic matter decomposes, the elemental stoichiometry changes (Frost et al., 2002). In this study, the C:N of jellyfish tissue when it was first introduced to the mesocosms was ~3.9 (West, unpublished data). This ratio is similar to that of heterotrophic bacteria (~4; Sterner & Elser, 2002), which, therefore, can easily utilize the jellyfish tissue as a resource. As labile components are utilized, the residual jellyfish biomass becomes more refractile and therefore the C:N ratio increases and differs from that of the heterotrophic bacteria. Thus the continual high SOD and low effluxes of N and P in the jellyfish mesocosms may be due to preferential microbial retention of these nutrients in their biomass, as the C:N:P of the residual jellyfish tissue increased during the decomposition process.

The extent to which decomposing jellyfish will influence nutrient recycling in an estuary will largely rely on the biomass of the population. Billett et al. (2006) observed large aggregations of dead jellyfish on the seabed off the coast of Oman that ranged from a few individual jellyfish to a continuous layer of rotting jellyfish slime. These jellyfish were estimated to have a standing stock of carbon that spatially varied between 1.5 and 78 g C per $m^2$. In some areas, the downward flux of organic carbon during this time exceeded the annual average estimates by more than an order of magnitude (Billett et al., 2006). In the present study, we report the large increase in SOD and release of organic and inorganic nutrients from a jellyfish that covered ~20% of the sediment surface and was equivalent to ~25 g C per $m^2$, which is well within the range reported by Billett et al. (2006). In some areas, Billett et al. (2006) reported patches that were several metres in diameter and covered 17–100% of the sediment surface. Decomposing blooms of this scale are likely to affect nutrient concentrations in the water column and oxygen demand, which could have cascading ecosystem effects.

The recycled inorganic nutrients, which can be a limiting factor in many marine systems (Fenchel et al., 1998), are likely to enhance primary production in the overlying water column. Apparent limited top–down control of jellyfish populations often leads to the erroneous assumption that they are dead ends or sinks in marine trophic food webs (Arai, 1988, 2005). However, jellyfish have recently been identified as an important component of pelagic food webs providing inorganic nutrients to primary producers during excretion (e.g., Pitt et al., 2005) and as a source of prey for many animals including fish, turtles, and birds (Arai, 2005). Further, the large release of nutrients during decomposition of jellyfish tissue, shown in the present study, may stimulate primary production and is also likely to represent an important trophic link to pelagic environments.

The large SOD of decomposing jellyfish may result in changes in the overall ecosystem function. Oxygen depletion as a result of the breakdown of labile organic matter in coastal areas is a global concern, particularly in enclosed or stratified water bodies (Keister et al., 2000). Oxygen depletion can affect community dynamics by causing direct mortality; reducing growth and reproduction rates; limiting abundances and distributions; and altering interactions among organisms (Keister et al., 2000). Flushing and mixing regimes are likely to determine the severity of oxygen depletion (Keister et al., 2000). Impacts of blooms are likely to be particularly severe in closed or intermittently-closed waterways with limited flushing with the ocean. For example, Smiths Lake, where this study was done, opens to the ocean every 1.5 years, on average, and therefore has a long water residence time. Additionally, stratification of water bodies can result from density differences in marine and fresh water or temperature differences, which prevent vertical mixing and can isolate the bottom waters and give rise to hypoxic or anoxic conditions. One example of an anoxic event from the aerobic decomposition of animal tissues was reported in Mariager Fjord, Denmark. There, the rapid decomposition of a large population of mussels, *Mytilus edulis* (Linnaeus, 1758), consumed oxygen, which subsequently caused anoxia in the water column (Lomstein et al., 2006).

In the present study, experiments were done in isolated tubs that did not incorporate the role of macro-fauna in decomposition. Benthic macroinfauna can alter sediment particle size and pore size, and can physically stir sediments, which may alter biogeochemical processes (Welsh, 2003). Predation of jellyfish corpses would also direct nutrients to predators rather than to the water column or

sediments. Yamamoto et al. (2008) caught four species of benthic scavengers in crab traps baited with dead jellyfish, *N. nomurai*, and measured an average 40% of the carcass mass was reduced after 23 h. Predation on dead jellyfish, however, is likely to be determined by factors, such as the number of corpses and types and abundances of scavengers. Further, sulfidic black sediments and reduced oxygen concentrations resulting from decaying jellyfish may kill some macro-fauna. Further studies on predation rates on jellyfish corpses and effects on benthic macro-faunal communities are required.

## Conclusion

Decomposition of *C. mosaicus* resulted in a rapid leaching of organic nutrients from the dead tissues. Following this, microbial mineralization dominated, which consumed oxygen and released dissolved inorganic nutrients. Although this release of nutrients may serve as a trophic link to the pelagic primary producers, it may also lead to environmental problems associated with low oxygen concentrations, depending on the size of the bloom and the degree of mixing in the system.

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