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Jellyfish decomposition at the seafloor rapidly alters biogeochemical cycling and carbon flow through benthic food-webs

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Abstract

Jellyfish blooms have increased in magnitude in several locations around the world, including in fjords. While the factors that promote jellyfish blooms and the impacts of live blooms on marine ecosystems are often investigated, the post-bloom effects from the sinking and accumulation of dead jellyfish at the seafloor remain poorly known. Here, we quantified the effect of jellyfish deposition on short-term benthic carbon cycling dynamics in benthic cores taken from a cold and deep fjord environment. Respiration was measured and ^{13}C-labeled algae were used as a tracer to quantify how C-flow through the benthic food web was affected over 5 d in the presence and absence of jellyfish carcasses. Benthic respiration rates increased rapidly (within 2 h) in the jellyfish-amended cores, and were significantly higher than cores that were supplied with only labeled phytodetritus between 17 h and 117 h. In the cores that were supplied with only labeled phytodetritus, macrofauna dominated algal-C uptake over the 5 d study. The addition of jellyfish caused a rapid and significant shift in C-uptake dynamics: macrofaunal C-uptake decreased while bacterial C-uptake increased relative to the cores supplied with only phytodetritus. Our results suggest that the addition of jellyfish detritus to the seafloor can rapidly alter benthic biogeochemical cycling, and substantially modify C-flow through benthic communities. If our results are representative for other areas, they suggest that jellyfish blooms may have cascading effects for benthic ecosystem functions and services when blooms senesce, such as enhanced bacterial metabolism and reduced energy transfer to upper trophic levels.

Organic material from the pelagic environment that sinks to the seafloor is one of the most important sources of carbon for the benthos, especially in systems beyond the euphotic zone (Graf 1992; Smith et al. 2008). This input of particulate organic material to the benthos is an important driver of sediment biogeochemical processes (Fenchel et al. 1998), and strongly impacts benthic community structure and ecosystem functioning (Smith et al. 2008). While many studies have assessed the seafloor response to inputs of phytodetritus (Woulds et al. 2009; Jeffreys et al. 2013; Sweetman et al. 2014a), the response of seafloor communities to other organic sources has received much less attention.

Jellyfish blooms are common in many areas, and while it is thought that jellyfish blooms are not increasing globally (Condon et al. 2013), blooms have become more common in some regions in recent decades (Aksnes et al. 2009; Haraldsson et al. 2012; Condon et al. 2013). The life histories of many gelatinous zooplankton species (e.g., their boom and bust population dynamics) can result in short periods during which large quantities of jellyfish sink to the seafloor following senescence of gelatinous zooplankton blooms (Lebrato et al. 2012). In recent years, a number of studies have described accumulations of dead jellyfish at the deep seafloor off Oman (Billett et al. 2006), the Ivory Coast (Lebrato and Jones 2009), in the Sea of Japan (Yamamoto et al. 2008), off

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the New Zealand margin (Henschke et al. 2013), the abyssal Pacific (A.K. Sweetman pers. obs.) and deep-sea fjords in Norway (Sweetman and Chapman 2011, 2015). These collective observations suggest that gelatinous zooplankton carcasses (hereafter referred to as jelly-falls) may provide an important transport vector for organic carbon and nitrogen to the seafloor (Sweetman and Chapman 2015).

Little is known about the fate of jellyfish detritus once it reaches the seafloor. In some circumstances, jelly-falls may be rapidly scavenged by demersal and benthic scavengers (Sweetman et al. 2014b). However, in situations where necrophagy is minimal, as has been found off the Oman margin and the Ivory Coast (Billett et al. 2006; Lebrato and Jones 2009), the sedimentation of jellyfish detritus may smother seafloor sediments and reduce oxygen diffusion into sediments. The accumulation of jellyfish material at the seafloor may also led to greater microbial metabolism since the C: N ratio of bacteria (~5–7: 1, Goldman and Dennett 2000) and jellyfish (~4–5, Pitt et al. 2009) are similar leading to easier bacterial degradation of gelatinous detritus. In situations where metazoan decomposition of organic matter is a keystone process in marine sediments (e.g., high latitude systems above 1000 m, Clough et al. 2005, including many Norwegian fjords, Sweetman et al. 2014a), a shift to microbial decomposition could have profound impacts on ecosystem function, including reduced energy flow to upper trophic levels and lower levels of C-storage in sediments. However, although some studies have assessed the impact of gelatinous detritus on benthic ecosystems in shallow environments at warm temperatures (West et al. 2009; Chelsky 2015; Chelsky et al. 2015), no studies have addressed these processes in cold, deep-water environments.

Periphylla periphylla (Scyphozoa, Coronatae) is a common inhabitant in many deep-sea fjords along the Norwegian coast (Gorsky et al. 2000; Youngbluth and Båmstedt 2001). Populations of *P. periphylla* appear to have increased in Norwegian fjords over the last few decades (Sørnes et al. 2007), perhaps as a result of water-column darkening favouring tactile predators over visual ones (Aksnes et al. 2009; Haraldsson et al. 2012). After death, *P. periphylla* sinks to the seafloor where it may be scavenged (Sweetman et al. 2014b) or, if deposited in large numbers, may undergo microbial remineralisation (Sweetman and Chapman 2011). In this study, we used isotope-labeled algae as a tracer to compare benthic ecosystem functioning (e.g., benthic oxygen demand, C-uptake by macrofauna and bacteria) in sediments with and without simulated *P. periphylla* deposition. While this approach involved manipulating an already manipulated system by the extra addition of jellyfish organic material, it was designed to specifically test how key benthic ecosystem functions (e.g., organic matter cycling) are modified by the addition of gelatinous detritus. Isotope-labelling studies are highly effective in measuring benthic ecosystem processes (Middelburg et al. 2000; van Oevelen et al. 2006), and can also be used to detect how specific stressors modify food-web processes (Sweetman et al. 2010, 2014b). In short, an isotope-labeled substrate (e.g., ^{13}C-labeled algae) is deposited over an enclosed area of seafloor in the presence/absence of a potential stressor. The uptake of labeled elements is tracked into sediment dwelling organisms and inorganic components, making it possible to quantify decomposition processes. We tested the following hypothesis: "*Short-term macrofaunal uptake of phytodetritus is significantly reduced in the presence of jellyfish detritus, whereas bacterial uptake of phytodetritus is significantly enhanced.*"

Materials and methods

Experimental design

A laboratory experiment was carried out on sediment cores collected in Fanafjorden, Norway in September 2012. Eight replicate box-cores were collected from randomly selected stations at a depth of 100 m using a 0.1 m^2 box corer (KC-Denmark®). Single, 15 cm deep sediment cores were then extracted from each box-core and extruded into clear, acrylic benthic chambers (10 cm Ø). Immediately after collection, all cored sediments were gently covered with 25 cm of 0.2 μm-filtered, oxygenated seawater previously pumped from 40 m depth near Espegrend marine station, Bergen. During this procedure, sediment disturbance was minimal. The cores were then transported to Espegrend Marine Station where they were placed in the dark in a temperature-controlled room that was maintained at in situ temperature (8°C). The cores were kept in a flow-through system for 1 week prior to the start of the experiments, which is a sufficient amount of time for sediments to settle and stabilize geochemically based on previous studies (e.g., Sweetman et al. 2010, 2014a).

An axenic clone of the diatom *Skeletonema costatum* was used as a labeled food source in our experiment. This diatom is a major component of the spring bloom in temperate Norwegian fjords (Erga and Heimdal 1984). This algal addition therefore allowed us to realistically trace the fate of labile carbon in the presence/absence of jellyfish detritus. Diatoms were cultured in artificial seawater modified with F/2 algal culture medium (Grasshoff et al. 1999), and labeled by replacing 25% of ^{12}C bicarbonate in the culture medium with $NaH^{13}CO_3$. To harvest the algae, the cultures were concentrated by filtration over a 0.45 μm filter (cellulose acetate), washed five times by centrifugation in un-labeled F/2 medium to remove excess labeled bicarbonate, and freeze dried. The absence of microbes was verified by microscopic observations after staining some inocula with Sybr Gold. The produced algae had a ^{13}C atom content of 20.4 ± 2.2 atom% (standard error (SE), $n = 8$) and a C: N ratio of 9.7 ± 1.9 (SE, $n = 8$).

To start the experiment, 142.4 ± 0.1 mg (SE, $n = 8$) of hydrated ^{13}C-labeled *S. costatum* (equivalent to a C addition of 3.6 g C m^{-2}) was injected into the eight chambers, and stirrers mounted 5 cm beneath the chamber lids were activated to homogeneously distribute the algae over the

enclosed sediment surface. Based on sediment density and C-content measured from nearby fjords (Sweetman et al. 2014a), this algal addition was equivalent to 2% of the C-stock in the top-most (0–1 cm) sediment layer. Ten minutes after the algae was injected, stirrers were switched off for 1 h to allow the labeled algae to sink to the sediment surface. One hour later, a 8.6 ± 0.1g (SE, $n = 4$) piece of thawed *Periphylla periphylla* jellyfish (C: N = 5.6, A. Sweetman, unpubl. data) was added to the sediment surface in four chambers (termed *+Phyto+Jellyfish* treatments), which covered approximately half of the sediment area in each core. A plastic coated metal ring was placed over the surface of each jellyfish piece to make the jellyfish negatively buoyant. This was repeated in the cores without jellyfish to standardise the procedure. The jellyfish addition represented an additional C-input of 27.4 g jelly-C m^{-2}. While this jellyfish detritus input was significantly greater than previously documented for Norwegian fjords (0–13.4 mg C m^{-2}, Sweetman and Chapman 2011, 2015), it was comparatively similar to jellyfish C-inputs documented in other areas around the world (Gulf of Oman: 1.5–75 g C m^{-2}, Billett et al. 2006; Ivory Coast: 1–20 g C m^{-2}, Lebrato and Jones 2009) and therefore allowed us to relatistically measure the seafloor impact from a large pulse of gelatinous detritus. The jellyfish that were used had been collected by a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) in Lurefjorden, western Norway, in September 2010 and immediately frozen. The remaining four cores were unamended with jellyfish (termed + *Phyto* treatments). Immediately after the jellyfish addition, stirrers in all cores were turned on and the chamber waters gently mixed (without resuspending sediments) at approximately 3 revolutions per minute for the remainder of the 5 d experiment. The experiment was carried out in the dark.

Chamber sampling

Cores were incubated to measure sediment community oxygen consumption (SCOC) at 0 h, 2 h, 17 h, 26 h, 37 h, 47 h, 64 h, 90 h, 117 h. To do this, chambers were sealed and oxygen concentrations were immediately measured by PreSens© oxygen probes. Oxygen concentrations were measured again at the end of each incubation, which lasted an average of 3.6 ± 0.1 h (SE, $n = 72$). Flux rates of O_2 (hence SCOC) were calculated from linear changes in the concentration of O_2 through time. To prevent anoxia in the chambers, chamber lids were removed after sampling for O_2 at the end of each incubation, and the overlying water in each chamber was carefully, and continuously exchanged (using a flow through system) with fresh, oxygenated filtered (0.45 μm) seawater to remove toxic metabolites (e.g., ammonium, sulphides) produced during the preceding incubation. The slow rate of water exchange ($\sim$0.5 L h^{-1}) prevented algal/jellyfish material/sediment from being resuspended during this procedure. After re-oxygenation and immediately prior to the next SCOC measurement, all visible bubbles were removed from beneath each chamber lid, the lids were replaced, and initial O_2 measurements taken again for the next SCOC measurement.

At the end of the 5 d experiment, the cores were processed for macrofauna and bacterial phospholipid-derived fatty-acid (PLFA) samples. While a large number of studies have demonstrated the key role of meiofauna and protozoa in benthic C-cycling dynamics (Woulds et al. 2007, 2009; Evrard et al. 2010), we decided to primarily focus our analyses on macrofauna and bacteria because C-uptake data on macrofauna and bacteria exist from other nearby fjords (e.g., Sweetman and Witte 2008; Sweetman et al. 2009, 2014a), and the small diameter of each core limited extra samples for other organism groups/size classes from being collected. To sample bacteria and macrofauna, sediment was extruded and sectioned into 0–2, 2–5, and 5–10 cm depth layers. During this procedure, some macrofauna were observed burrowing to deeper sediment layers. Thus, changes in ecosystem parameters as a function of sediment depth were not addressed in this study. Approximately one quarter of the core was sampled for bacterial PLFA analysis, and then frozen at −20°C until analysis. The remaining sediment from each layer was sieved on a 500-micron (μm) mesh with cool (8°C), filtered seawater to isolate macrofauna. The fauna were then transferred to plastic bottles and fixed with 4% buffered formaldehyde in seawater.

Sample analysis

Frozen sediment samples for bacterial analysis were freeze-dried (with no oil used for sealing) and subsequently ground with a mortar and pestle. Lipids were extracted from approximately 3 g of dried sediment by a Bligh and Dyer extraction procedure (Middelburg et al. 2000), during which lipids were sequentially isolated by rinsing on a silicic acid column with chloroform, acetone and methanol. The lipid extract was then derivatized to volatile fatty-acid methylesters (FAME) and measured by gas-chromatography isotopic ratio mass spectrometry (GC-IRMS) for PLFA concentration and δ^{13}C-signatures (Middelburg et al. 2000). The C-isotope ratios were corrected for the single methyl group inserted during derivatization. Bacterial biomass (mg C m^{-2}) was measured by GC-IRMS, and calculated as PLFA (*i*$C_{14:0}$, *i*$C_{15:0}$, *ai*$C_{15:0}$, cyclo $C_{19:0}$, 10 Methyl-$C_{16:0}$, Boschker and Middelburg 2002) concentration (μmol) mL^{-1} sediment/(a x b), where a is the average PLFA concentration in bacteria of 0.056 g C PLFA g^{-1} biomass (Brinch-Iversen and King 1990), and b is the average fraction-specific bacterial PLFA encountered in sediment dominated by bacteria (0.23; calculated after Rajendran et al. 1993, 1994). The prefixes "*i*" and "*ai*" refer to "*iso*" and "*antiso*", respectively.

Macrofauna fixed in formaldehyde were sorted and identified under a dissecting microscope. Polychaetes were identified to family, while crustaceans and other taxa were

identified to order or major taxa. Individual organisms were washed with filtered seawater to remove attached organic debris, placed in tin cups and dried at 40°C for 1 week. Calcareous shelled organisms were decalcified in silver cups using 2M HCl. To obtain sufficient biomass for isotope measurements, some individual organisms were combined.

The $\delta^{13}C$ isotopic ratios and C-content of macrofauna and bacteria were measured on an isotope ratio mass spectrometer at Griffith University, Australia, and the Royal Netherlands Institute of Sea Research (NIOZ), respectively. Uptake of ^{13}C by macrofauna (mg ^{13}C m^{-2}) was calculated as the product of the excess ^{13}C (E) and C-content in the animal (expressed as unit weight). E is the difference between the labeled fraction (F) of a PLFA/animal sample and a background PLFA/animal sample: $E = F_{sample} - F_{background}$ where $F = {}^{13}C/({}^{13}C + {}^{12}C) = R/(R+1)$, where $R = (\delta^{13}C/1000 + 1) \times R_{VPDB}$, and $R_{VPDB} = 0.0112372$. Background isotope information for bacteria and macrofauna were taken from samples collected in a nearby fjord by Sweetman et al. (2014a). Because of high enrichment (e.g., $\delta^{13}C$: 100‰) in the bacteria PLFA and fauna samples in our experiments, small differences (e.g., $\delta^{13}C$: 1–2‰) in background isotope signatures between our study site and that of Sweetman et al. (2014a) were considered negligible. If isotope signatures of certain macrofauna taxa were unavailable, E was calculated using background F values from closely related organisms as in Sweetman et al. (2014a). As a result of the labeled and background samples both being preserved in 4% formaldehyde seawater solution, preservation artefacts on isotope signatures were also considered negligible. For bacteria, total uptake (mg ^{13}C m^{-2}) of ^{13}C (Uptake (U)) was calculated according to Sweetman et al. (2010, 2014a) from label incorporation into bacterial fatty acids (iC$_{14:0}$, iC$_{15:0}$, aiC$_{15:0}$, cyclo C$_{19:0}$, 10 Methyl-C$_{16:0}$, Boschker and Middelburg 2002) as: $U_{bact} = \Sigma_{bact\ fatty\ acids}/(a \times b)$. To calculate the daily phytodetritus C-uptake rate (mg C m^{-2} d^{-1}), the amount of ^{13}C incorporated into macrofauna and bacteria (mg ^{13}C m^{-2}) was adjusted to account for the fractional abundance of ^{13}C in the added algae as: macrofaunal/bacterial C-uptake = ^{13}C incorporated (mg ^{13}C m^{-2})/fractional abundance of ^{13}C in algae, and divided by 5.

Data analysis

Changes in SCOC were analysed using a repeated measures two-way ANOVA, with time and treatment (*+Phyto+Jellyfish* and *+Phyto*) as the main effects, and each core as the subject being repeatedly sampled. Differences in macrofaunal and bacterial biomass, and differences in C-uptake between treatments, were assessed using a two-way ANOVA with organism group (macrofauna and bacteria) and treatment as factors. Significant differences were explored further using Holm-Sidak post-hoc tests. Prior to statistical analysis, data were checked for normality and heteroscedasticity. Data were square root/natural logarithm transformed when necessary to meet parametric assumptions. An α-level of 0.05 was chosen as the criterion for statistical significance.

Results

Sediment community oxygen consumption

SCOC rates measured at 0 h were 9.0 ± 1.9 mmol O_2 m^{-2} d^{-1} (SE, $n = 4$) and 11.7 ± 2.5 mmol O_2 m^{-2} d^{-1} (SE, $n = 4$) in the *+Phyto+Jellyfish* and *+Phyto* treatments, respectively (Fig. 1). SCOC varied between treatments, but the pattern of variation was not consistent through time (Repeated Measures ANOVA, $p < 0.001$). Two hours after the addition of the phytodetritus and jellyfish material SCOC increased to 29.0 ± 2.6 mmol O_2 m^{-2} d^{-1} (SE, $n = 4$) and 24.1 ± 2.1 mmol O_2 m^{-2} d^{-1} (SE, $n = 4$) in the *+Phyto+Jellyfish* and *+Phyto* treatments, respectively (Fig. 1). In the *+Phyto+Jellyfish* experiments, SCOC measured between 2 h and 117 h was significantly higher (Repeated Measures ANOVA, $p < 0.001$) than the SCOC at 0 h. SCOC rates measured between 17 h and 64 h were also significantly higher (Repeated Measures ANOVA, $p < 0.003$) than rates at 2 h in the *+Phyto+Jellyfish* treatment, although SCOC at 90 h and 117 h was not. The only significant difference in SCOC in the *+Phyto* treatments was that the SCOC rates at 2 h, 17 h, 26 h, 37 h, and 90 h were significantly higher than at 0 h (Repeated Measures ANOVA, $p < 0.001$). There was no significant difference in SCOC between the *+Phyto+Jellyfish* and *+Phyto* treatments at 0 h and 2 h. However, a significant increase in SCOC was detected in the *+Phyto+Jellyfish* treatment (Repeated Measures ANOVA, $p < 0.001$) compared with the *+Phyto* experiments after 17 h and significant differences between treatments remained until the end of the experiment (Repeated Measures ANOVA, $p < 0.001$, Fig. 1). The rate of oxygen consumption averaged between 17 h and 117 h in the *+Phyto+Jellyfish* treatment was 2.9 times that of the *+Phyto* experiments (Fig. 1).

Benthic biomass

Mean macrofaunal biomasses in the *+Phyto* and *+Phyto+Jellyfish* treatments were 798.7 ± 145.1 mg C m^{-2} (SE, $n = 4$) and 757.8 ± 111.2 mg C m^{-2} (SE, $n = 4$), respectively (Fig. 2). Polychaetes contributed the most to macrofaunal biomass in both the *+Phyto* (71–88%) and *+Phyto+Jellyfish* (74–92%) treatments. Of the polychaetes, surface-feeding spionid polychaetes contributed the most to total macrofaunal biomass in both the *+Phyto* (22–56%) and *+Phyto+Jellyfish* treatments (24–45%) (Fig. 3; Table 1). Please see Table 1 for a complete description of the contribution of different macrofauna taxa to benthic biomass. Bacterial biomasses (calculated from sediment PLFA concentrations at the end of the 5 d study) within the *+Phyto* (3558.4 ± 132.9 mg C m^{-2}, SE, $n = 4$) and *+Phyto+Jellyfish* treatments (4165.5 ± 374.1 mg C m^{-2}, SE, $n = 4$) were on average 4.5–5.5 times higher than macrofaunal biomass (Fig. 2). The PLFA iC$_{15:0}$, aiC$_{15:0}$ and 10 Methyl-C$_{16:0}$ contributed most to bacterial

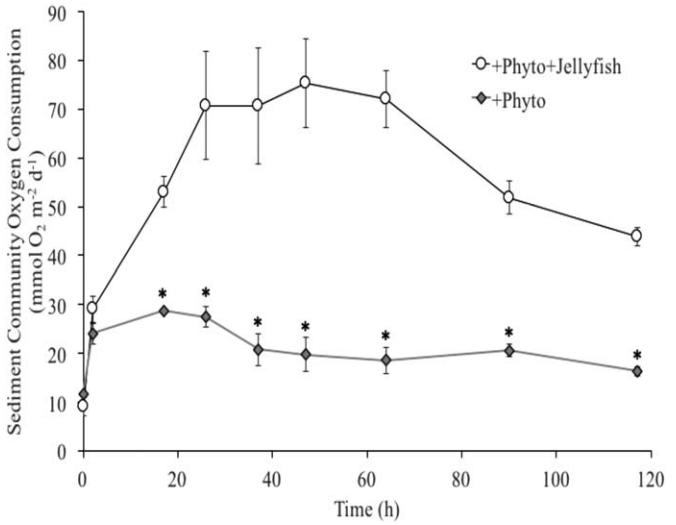

Fig. 1. Mean sediment community oxygen consumption (SCOC) through time in the two treatments analysed. SCOC was significantly different ($p < 0.05$) between treatments at the times indicated by stars (*). Error bars denote ± standard error ($n = 4$).

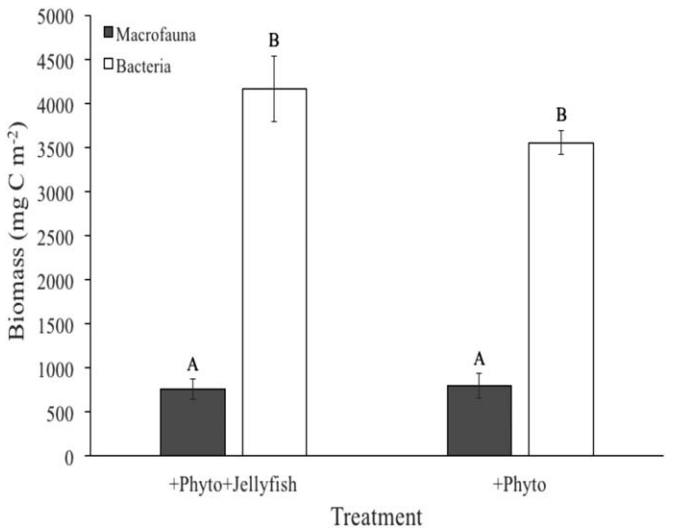

Fig. 2. Mean bacteria and macrofauna biomass (mg C m^{-2}) in the *+Phyto+Jellyfish* and *+Phyto* experimental cores. Significant differences ($p < 0.05$) are designated by different letters. Error bars denote ± 1 standard error ($n = 4$).

biomass in both treatments (Fig. 4). There was no significant treatment effect on biomass detected (2-Way ANOVA, $p = 0.394$), although there was a significant organism effect (2-Way ANOVA, $p < 0.001$), with mean bacterial biomass being significantly higher than macrofaunal biomass in both the *+Phyto* and *+Phyto+Jellyfish* treatments (Fig. 4).

Short-term phytodetritus C-uptake between treatments

The mean total amount of phytodetrital C taken up by bacteria and macrofauna over the 5 d study was 12.7 ± 0.9 mg C m^{-2} d^{-1} (SE, $n = 4$) and 11.6 ± 1.8 mg C m^{-2} d^{-1} (SE, $n = 4$) in the *+Phyto* and *+Phyto+Jellyfish* treatments, respectively. No significant organism or treatment effect was detected among C-uptake rates, but a significant interaction effect was (2-way ANOVA, $p = 0.002$). Mean macrofauna C-uptake was significantly higher (by a factor of 1.9 x) in the *+Phyto* treatment relative to bacteria (Fig. 5). In the *+Phyto+Jellyfish* experiment, however, mean short-term C-uptake by bacteria was significantly higher (by a factor of 2.6 x) than macrofauna C-uptake (Fig. 5).

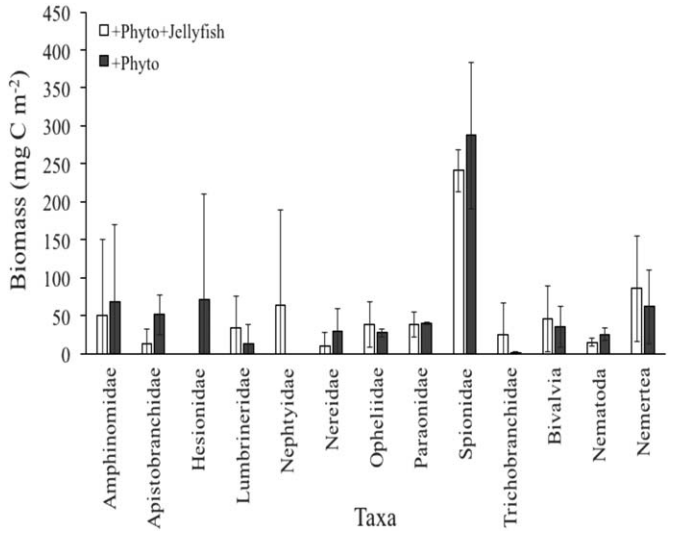

Fig. 3. Mean biomass (mg C m^{-2}) of the different macrofaunal organisms in the two treatments analysed. Only taxa whose biomass exceeded a threshold of > 25 mg C m^{-2} are shown. For a complete description of the contribution of all macrofauna taxa to benthic biomass, please see Table 1. Error bars denote ± 95% confidence intervals ($n = 4$), so significant differences between PLFA and treatments are designated by the lack of overlap between error bars.

Of the total amount of C taken up by macrofauna in the different treatments, polychaetes were responsible for the majority of C-uptake in the *+Phyto* (97–99%) and *+Phyto+Jellyfish* (88–98%) treatments (Fig. 6; Table 2). Within the Polychaeta, significantly more C was taken up by surface-feeding spionid polychaetes in both treatments relative to any other taxon (*+Phyto*: 36–84% of total faunal C-uptake; *+Phyto+Jellyfish*: 61–81% of total faunal C-uptake), as designated by the lack of overlap between the 95% confidence intervals between taxa (Fig. 6; Table 2). C-uptake and biomass specific uptake rates of spionids were significantly higher in the *+Phyto* compared with the *+Phyto+Jellyfish* experiments (Fig. 6; Table 2). In the *+Phyto* treatments, amphinomid (0–16% of total faunal C-uptake) and nereid (0–7% of total faunal C-uptake) polychaetes ingested moderate quantities of C, along with surface feeding apistobranchids (2–16% of total faunal C-uptake) and Sub-surface deposit feeding opheliid (4–7% of total faunal C-uptake)

Table 1. Mean macrofaunal biomass (mg C m^{-2}) in sediments from the two different treatments (± 95% confidence intervals, CI), and their average percentage contribution (%) to total biomass. Sample size (n) = 4 for all treatments.

Taxa	+*Phyto*+*Jellyfish*	95% CI	%	+*Phyto*	95% CI	%
Polychaeta						
Ampharetidae	0.4	0.9	0.0	0.6	1.1	0.1
Amphinomidae	50.8	99.5	5.6	68.2	101.6	6.3
Apistobranchidae	12.4	19.7	1.5	51.2	26.3	6.6
Capitellidae	21.3	17.8	3.4	8.5	12.1	1.3
Cirratulidae	8.5	4.7	1.1	3.2	2.3	0.4
Flabelligeridae	17.8	34.9	2.8	0.0	0.0	0.0
Glyceridae	1.8	2.1	0.2	4.4	1.2	0.6
Hesionidae	0.0	0.0	0.0	71.1	139.3	7.4
Lumbrineridae	33.4	42.7	6.1	13.0	25.6	1.2
Maldanidae	0.0	0.0	0.0	0.4	0.8	0.0
Nephtyidae	63.8	125.1	6.5	0.0	0.0	0.0
Nereidae	9.6	18.9	1.1	29.0	29.5	4.1
Opheliidae	38.5	30.0	5.7	27.4	5.4	4.0
Opistobranchia	0.0	0.0	0.0	7.5	10.6	0.8
Oweniidae	0.0	0.0	0.0	1.1	2.2	0.1
Paraonidae	38.2	16.8	5.2	39.4	1.4	5.5
Pholoidae	7.8	5.3	1.0	4.7	7.5	0.8
Phyllodocidae	1.2	2.4	0.1	0.0	0.0	0.0
Polynoidae	3.9	7.5	0.8	0.0	0.0	0.0
Sabellidae	0.6	1.2	0.1	2.6	5.2	0.2
Scalibregmidae	5.1	5.9	0.9	22.8	43.2	2.1
Sphaerodoridae	1.6	3.2	0.2	0.8	1.6	0.1
Spionidae	240.9	28.0	33.5	287.7	96.5	38.4
Syllidae	12.9	14.7	1.6	10.4	6.1	1.4
Terebellidae	2.6	5.1	0.4	0.0	0.0	0.0
Trichobranchidae	25.4	41.5	2.7	1.1	2.1	0.1
Crustacea						
Amphipoda	1.4	2.8	0.3	0.7	1.4	0.1
Cumacea	0.0	0.0	0.0	6.5	11.4	0.6
Tanaidacea	0.0	0.0	0.0	0.5	1.0	0.0
Other taxa						
Bivalvia	45.6	43.0	5.3	35.2	27.5	4.2
Nematoda	14.9	5.1	2.0	25.5	8.6	3.6
Nemertea	85.7	69.8	10.3	61.6	48.5	8.2
Oligochaeta	1.2	1.3	0.2	0.9	1.7	0.2
Ophiuroidea	4.1	3.9	0.5	3.2	2.2	0.5
Scaphopoda	5.3	7.8	0.7	6.6	4.7	0.7
Sipunculida	1.1	2.1	0.2	2.9	2.6	0.3

(Fig. 6; Table 2). Biomass specific uptake rates of nereids and ophellids in the +*Phyto* experiments were significantly higher relative to +*Phyto*+*Jellyfish* study (Table 2). Hesinoids ingested significant quantities of C in 1 +*Phyto* core (23% of total faunal C-uptake). C-uptake and biomass specific uptakes rates of apistobranchid polychaetes were significantly less in the +*Phyto*+*Jellyfish* experiments compared with the +*Phyto* study (Fig. 6; Table 2). Sub-surface opheliid polychaetes were important phytodetrital C-consumers in the +*Phyto*+*Jellyfish* treatment (5–23% of total faunal C-uptake) (Fig. 6; Table 2). Please see Table 2 for a complete description of the contribution of different taxa to macrofauna C-uptake.

Most of the C-uptake into bacterial PLFA was into the fatty acids $i\mathrm{C}_{15:0}$, $ai\mathrm{C}_{15:0}$, and 10 Methyl-$\mathrm{C}_{16:0}$. Significantly more C (per unit area per unit time) was assimilated into the PLFA 10 Methyl-$\mathrm{C}_{16:0}$ in the +*Phyto*+*Jellyfish* treatment relative to the +*Phyto* experiment, as indicated by the lack of

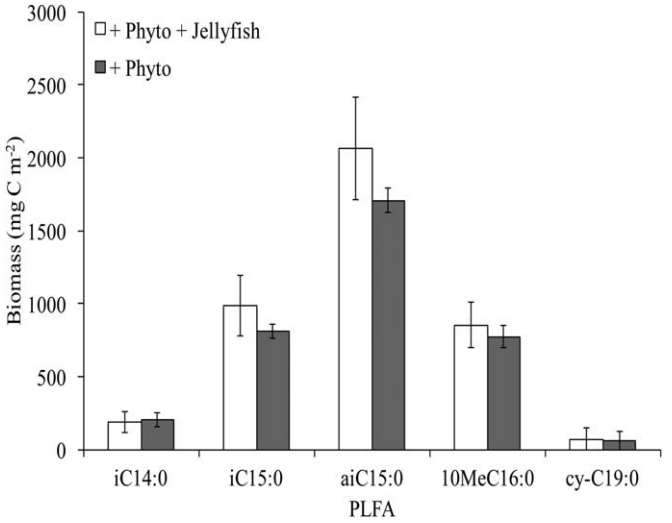

Fig. 4. Mean biomass (mg C m^{-2}) of individual bacterial PLFA in the two treatments analysed. Error bars denote ± 95% confidence intervals ($n = 4$), so significant differences between taxa and treatments are designated by the lack of overlap between error bars.

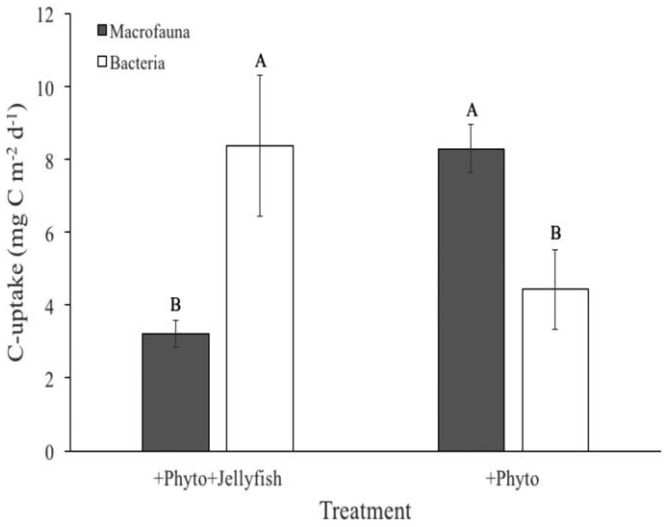

Fig. 5. Mean uptake of phytodetritus C (mg C m^{-2} d^{-1}) by the bacteria and macrofauna in the presence (*+Phyto+Jellyfish*) and absence (*+Phyto*) of jellyfish. Significant differences ($p < 0.05$) are designated by different letters. Error bars denote ± 1 standard error ($n = 4$).

overlap of the 95% confidence intervals between treatments (Fig. 7).

Discussion

In recent decades, many Norwegian fjords have become heavily populated by jellyfish (Aksnes et al. 2009). Studies suggest that the flux of dead jellyfish to the seafloor in these fjords can, at certain times of year, be comparable to phytodetrital fluxes (Sweetman and Chapman 2015). Mass jellyfish

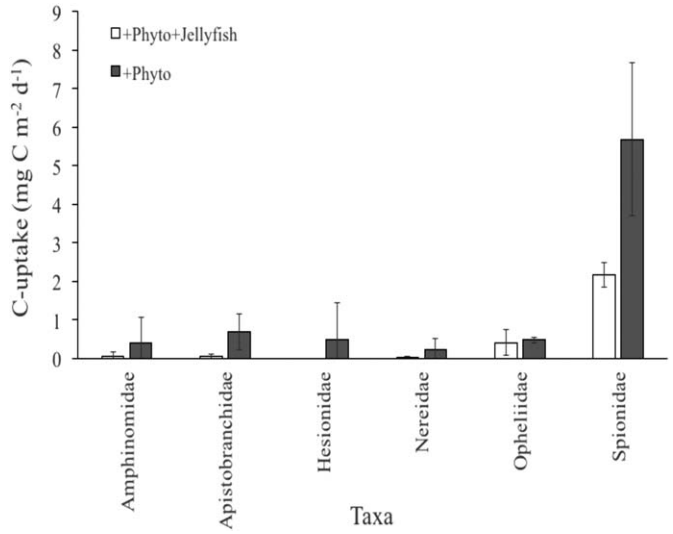

Fig. 6. Mean C-uptake (mg C m^{-2} d^{-1}) by different macrofaunal organisms in the two treatments analysed. Only taxa whose uptake exceeded a threshold of > 0.2 mg C m^{-2} d^{-1} are shown. For a complete description of the contribution of all macrofauna taxa to macrofauna C-uptake, please see Table 2. Error bars denote ± 95% confidence intervals ($n = 4$), so significant differences between taxa and treatments are designated by the lack of overlap between error bars.

deposition events also occur along the Norwegian coast and can result in jelly detritus layers of 10 cm or more at the seafloor (P. Renaud pers. obs.). However, whereas some studies have assessed the effect of dead jellyfish on benthic biogeochemical processes at warm temperatures (West et al. 2009), no studies have assessed the effects of large jelly-fall events on seafloor ecosystems in Norway. In this case study, we show that a large pulse of gelatinous organic matter to sediments at a cold, deep coastal site in Norway can lead to substantial changes in the cycling of organic matter in sediments, as evidenced by dramatic changes in respiration and C-uptake dynamics.

There were some limitations associated with this case study as a result of the short duration of each experiment, and the fact that algae were only added to the sediment surface, which allowed only short-term, near surface C-cycling processes to be quantified. In addition, benthic and demersal scavengers were excluded from the experimental design. Scavengers can play a key role in controlling the fate of jelly-falls at the seafloor (Sweetman et al. 2014b), and may significantly re-suspend sediments, modify nutrient concentrations and alter oxygen concentrations in the benthic boundary layer (Yahel et al. 2008). Their exclusion from our experimental design may have led to an artificially high standing stock of jelly detritus on the seafloor, so results from our study are most likely representative for large jelly-fall events where scavenging activities are limited (Billett et al. 2006; Lebrato and Jones 2009).

Table 2. Mean C uptake ($\times 10^{-3}$ mg C m^{-2} d^{-1}) ± 95% confident intervals (CI, $n = 4$), mean percent (%) contribution to macrofaunal C-uptake, and biomass specific uptake (x 10^{-6} d^{-1}) ± 95% CI ($n = 4$) of different macrofaunal taxa in sediments from each treatment.

	+Phyto+Jellyfish					+Phyto				
	C-uptake	95% CI	%	Biomass specific uptake	95% CI	C-uptake	95% CI	%	Biomass specific uptake	95% CI
Polychaeta										
Ampharetidae	4.09	8.03	0.13	2342.02	4590.27	20.04	39.28	0.30	9000.87	17641.37
Amphinomidae	56.63	110.99	1.65	278.86	546.55	397.54	660.14	4.60	6696.04	12559.81
Apistobranchidae	35.51	58.55	1.10	1327.26	1520.65	676.37	464.25	8.06	12393.91	6320.65
Capitellidae	1.61	1.16	0.05	61.07	42.48	0.65	0.85	0.01	41.86	48.65
Cirratulidae	86.68	58.58	2.51	10411.58	3276.13	46.80	48.72	0.53	10239.26	9221.21
Flabelligeridae	11.58	22.69	0.29	162.58	318.66	0.00	0.00	0.00	0.00	0.00
Glyceridae	0.65	1.00	0.02	162.50	231.42	2.89	1.67	0.03	675.19	332.02
Hesionidae	0.00	0.00	0.00	0.00	0.00	490.47	961.31	5.78	1724.91	3380.75
Lumbrineridae	17.81	23.90	0.72	643.81	739.13	37.83	74.14	0.38	725.40	1421.75
Maldanidae	0.00	0.00	0.00	0.00	0.00	0.48	0.94	0.01	305.19	598.16
Nephtyidae	2.72	5.34	0.09	10.67	20.91	0.00	0.00	0.00	0.00	0.00
Nereidae	13.79	27.03	0.40	357.95	701.57	235.53	266.38	2.97	6303.39	4576.06
Opheliidae	410.09	336.46	12.11	10359.03	1127.96	472.18	82.36	5.86	17317.62	723.05
Opistobranchia	0.00	0.00	0.00	0.00	0.00	30.78	49.74	0.32	1766.03	2185.29
Oweniidae	0.00	0.00	0.00	0.00	0.00	9.65	18.92	0.10	2145.23	4204.57
Paraonidae	16.95	10.52	0.61	446.74	248.16	14.98	14.14	0.20	374.81	342.94
Pholoidae	4.38	1.86	0.14	631.22	135.20	3.84	5.20	0.05	535.17	674.17
Phyllodocidae	1.05	2.05	0.03	210.89	413.33	0.00	0.00	0.00	0.00	0.00
Polynoidae	2.63	5.15	0.12	170.54	334.26	0.00	0.00	0.00	0.00	0.00
Sabellidae	0.42	0.82	0.01	166.62	326.57	10.64	20.86	0.11	1011.07	1981.65
Scalibregmidae	4.89	5.77	0.16	512.56	654.12	8.47	11.52	0.10	1075.75	1929.48
Sphaerodoridae	0.28	0.55	0.01	43.51	85.28	0.12	0.23	0.00	36.17	70.90
Spionidae	2173.94	314.68	69.08	9071.61	1408.92	5677.59	1983.97	68.83	19902.24	4914.24
Syllidae	3.07	4.14	0.09	152.68	114.20	9.32	12.42	0.11	678.81	522.89
Terebellidae	15.00	29.40	0.37	1454.67	2851.10	0.00	0.00	0.00	0.00	0.00
Trichobranchidae	98.80	152.26	3.10	3530.71	2428.65	3.16	6.19	0.03	748.05	1466.16
Crustacea										
Amphipoda	0.24	0.47	0.01	42.54	83.38	0.23	0.45	0.00	77.84	152.56
Cumacea	0.00	0.00	0.00	0.00	0.00	2.35	4.36	0.02	139.86	176.16
Tanaidacea	0.00	0.00	0.00	0.00	0.00	1.63	3.20	0.02	812.85	1593.17
Other taxa										
Bivalvia	121.05	168.06	3.78	2507.19	3972.61	37.49	44.31	0.43	690.26	661.98
Nematoda	5.61	4.79	0.17	346.56	181.95	8.68	8.41	0.12	370.69	406.85
Nemertea	98.68	117.16	2.66	1481.84	1336.88	42.93	68.99	0.44	1038.46	1010.63
Oligochaeta	0.16	0.22	0.01	69.15	92.57	0.08	0.15	0.00	21.65	42.42
Ophiuroidea	5.33	4.82	0.20	1512.30	2016.73	21.78	23.85	0.30	4669.90	4534.78
Scaphopoda	5.97	7.49	0.20	695.28	861.81	9.84	13.47	0.10	1017.47	1326.03
Sipunculida	7.10	13.92	0.18	1625.14	3185.22	18.14	21.91	0.20	4624.77	5266.87

Although the duration of this study was short, the addition of jellyfish detritus had a significant and rapid effect on benthic ecosystem processes. SCOC in the *+Phyto+Jellyfish* treatments was on average nearly three times higher than rates measured in the *+Phyto* experiments. This is consistent with the study of West et al. (2009) who showed > 2 times higher respiration rates in the presence of dead jellyfish relative to situations without jellyfish. Assuming the average

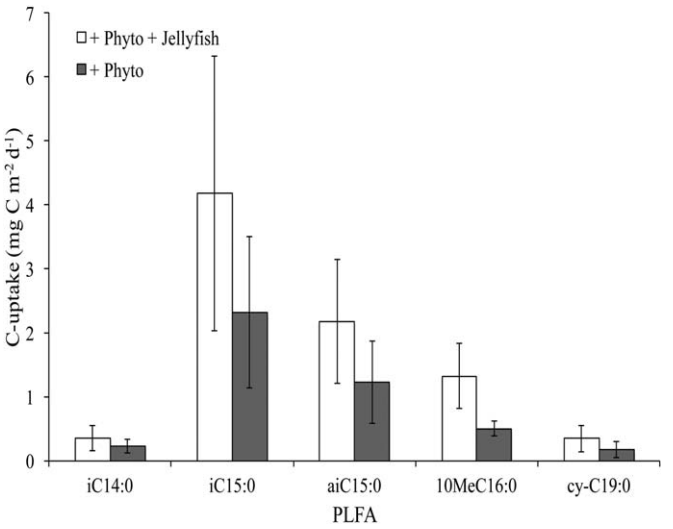

Fig. 7. Mean C-uptake (mg C m^{-2} d^{-1}) into individual bacterial PLFA in the two treatments analysed. Error bars denote ± 95% confidence intervals ($n = 4$), so significant differences between PLFA and treatments are designated by the lack of overlap between error bars.

SCOC rate measured at 0 h in both treatments (i.e., 10.3 ± 1.6 mmol O_2 m^{-2} d^{-1}, SE, $n = 8$) was equivalent to the degradation of background detrital C (C_{det}), the addition of phytodetritus and jellyfish in our experiments caused a ~2 to 6-fold increase in SCOC in the *+Phyto* and *+Phyto+Jellyfish* experiments, respectively. Much of this increase can be caused simply by the increase in particulate organic C (by approximately 2% and 14% of the ambient organic C) and its oxidation in the *+Phyto* and *+Phyto+ Jellyfish* experiments, respectively. Decaying gelatinous organic matter can enhance water-column nutrient and DOC concentrations (West et al. 2009; Chelsky et al. 2015), which can promote microbial respiration and growth (Titelman et al. 2006; West et al. 2009; Lebrato et al. 2012). Although not directly measured, the leaching of DOC from the jellyfish carcasses probably enhanced bacterial metabolism also, which was also partly responsible for the significantly elevated SCOC in the *+Phyto+Jellyfish* treatments relative to the *+Phyto* experiments. This is partly supported by the fact that algal C-uptake by bacteria, which can be used as an indicator of bacterial metabolism, was significantly elevated in the *+Phyto+Jellyfish* treatment relative to the *+Phyto* experiments (Fig. 5). The addition of the relatively small amount of phytodetritus material in the *+Phyto* experiments could have also led to the remineralization of old, less reactive terriegeneous organic matter that is abundant in fjord sediments (Nuwer and Keil 2005; Smith et al. 2015) through organic matter priming (van Nugteren et al. 2009; Guenet et al. 2010), leading to the elevated SCOC rates measured after 0 h in the *+Phyto* study. However, given that the relative importance of priming has been shown to decrease with increasing C loading (van Nugteren et al. 2009), we are doubtful that the elevated SCOC in the *+Phyto+Jellyfish* experiments was caused by priming. Nevertheless, similar benthic responses to added phytodetritus have been seen in other fjord studies (e.g., Witte et al. 2003), and the high SCOC rates observed in the *+Phyto+Jellyfish* experiments are also consistent with studies carried out in areas exposed to excessive organic matter input (Bannister et al. 2014; Sweetman et al. 2014a; Valdemarsen et al. 2015). The fact that our results are consistent with other organic addition studies, confirms that our findings may be generalizable to other areas. Further studies are needed to confirm this.

Assuming a respiratory quotient between O_2 and CO_2 of 1 (Middelburg et al. 2005), the mean C-degradation rate between 2 h and 117 h in the *+Phyto* experiments was 140.3 mg C m^{-2} d^{-1} (C_{phyto}) after correcting for C_{det} (expressed as mg C m^{-2} d^{-1}). Providing the C_{phyto} in the *+Phyto* experiments was exclusively due to the added phytodetritus (3.6 g C m^{-2}), the added tracer had a turnover rate of ~0.04 d^{-1}, which compares well to turnover rates for labile phytodetritus measured in other fjord environments (e.g., 0.05–0.1 d^{-1}, Sweetman et al. 2014a). After correcting for both C_{det} and C_{phyto}, the average C degradation rate of the jellyfish (C_{Jelly}) in the *+Phyto+Jellyfish* experiments between 2 h and 117 h was 435.2 mg C m^{-2} d^{-1}. Thus, the turnover rate of the added jellyfish C (27.4 g C m^{-2}) was 41% lower than for phytodetritus at 0.016 d^{-1} suggesting that the jellyfish material was being consumed at a slower rate, despite significantly elevating sediment oxygen demand relative to the *+Phyto* experiments. Dead jellyfish turnover rates measured in experimental mesocosms have been found to range between 0.02 d^{-1} and 0.05 d^{-1} (West et al. 2009), which compares well with our data. However, it must be kept in mind that the study by West et al. (2009) was undertaken at a much warmer temperature (30°C) compared with our study. This means that our jellyfish turnover rates may actually be high for cold-water environments, and indicates that the relative impact on degradation pathways may be more substantial in cold- relative to warm-water environments. Our results did, however, contrast with the results of Lebrato and Jones (2011) who modelled the decay of jellyfish and phytodetritus, and found that jellyfish material decayed faster (by ~4 times) over a range of temperatures (~5–17°C). The mean C: N ratio of the jellyfish used in the present study was 5.6 (A. Sweetman, unpubl. data), which was lower than for the added phytodetritus (9.7 ± 1.9, SE, $n = 8$). Therefore, if the turnover rates were exclusively controlled by substrate lability, jellyfish turnover rates should have been higher than for phytodetritus. Valdemarsen et al. (2009, 2012) documented that the C-input capacity for shallow and deep-water fjord sediment environments can range from 2520 mg C m^{-2} d^{-1} to 4884 mg C m^{-2} d^{-1} (experimental temperature: 8–15°C), and above these levels mineralization becomes hampered. If the sediments collected in this study

had a similar capacity to the sediments studied by Valdemarsen et al. (2009, 2012), it is conceivable that the lower jellyfish turnover rates relative to phytodetritus were due to the capacity of the sediment being exceeded by the large jellyfish C addition (27.4 g C m^{-2} that is equivalent to a C-addition of 5487 mg C m^{-2} d^{-1}), leading to hampered mineralization processes in the *+Phyto+Jellyfish* cores. Although further experiments using different quantities of jellyfish are needed to confirm this, it is conceivable that jelly- and other organic-falls exert a stronger impact on the seafloor in areas of high organic input (e.g., under fish farms) compared with less-organically stressed sites.

Total daily C-uptake rates from the added tracer in the experiments were similar to total daily C-uptake rates measured in nearby fjords (3–6 mg C m^{-2} d^{-1}, Witte et al. 2003; 22.2–28.3 mg C m^{-2} d^{-1}, Sweetman et al. 2014a), and were not significantly different between treatment types. The addition of phytodetritus to the *+Phyto* cores did, however, stimulate higher C-uptake by the macrofauna relative to bacteria, with surface feeding spionids taking up more C than any other taxon (Figs. 5, 6). These results are consistent with other fjord locations. For example, Sweetman et al. (2014a) documented 1.4 times greater phytodetritus C-uptake by macrofauna relative to bacteria in sediments collected at ~200 m depth in a western Norwegian fjord, and noted that surface feeding polychaetes (cirratulids) were the dominant metazoan involved in C-processing, which closely resemble the *+Phyto* experiment results. Clough et al. (2005) also showed macrofaunal C-cycling dominance relative to microbial processes at depths under 100 m at high latitudes. Thus, the SCOC and C-uptake data both appear to suggest that the benthic systems in the *+Phyto* cores were functioning in a similar way to other deep fjord sediment habitats. Because of the fact that ^{13}C-respiration was not measured in our study, it is not possible to precisely assign the *+Phyto* or *+Phyto+Jellyfish* experiments to any of the categories defined by Woulds et al. (2009). Nevertheless, it is most probable that the *+Phyto* sediments functioned in a manner similar to Woulds' et al. (2009) "active faunal uptake" category, as faunal C-uptake was greater than bacterial C-uptake. Moreover, "active faunal uptake" systems are typically found in estuarine and near-shore sites that have an abundant supply of organic matter, which support high macrofaunal biomasses (Woulds et al. 2009, 2016).

Under additional organic loading from jellyfish detritus, the benthic ecosystem changed in terms of C-cycling dynamics; mean macrofauna C-uptake was significantly reduced by approximately 2.6 times compared with the *+Phyto* treatments (Fig. 5), and was significantly less than bacterial C-uptake in the *+Phyto+Jellyfish* treatment after only 5 d (Fig. 5). Bacteria took up on average approximately 1.9 times more tracer C per day in the presence of dead jellyfish compared with when the labeled phytodetritus was added on its own (Fig. 5). Thus, the short-term C-uptake data showed that the deposition of gelatinous organic matter can initiate a rapid shift ($\leq$ 5 d) in an important benthic ecosystem function (i.e., organic matter processing), which supports our original hypothesis. The amount of gelatinous organic matter added to the four sediment cores amounted to 27.4 g Jelly-C m^{-2}, which is comparable to a jellyfish input of ~1.1 kg jellyfish m^{-2}. This addition is much larger than typical jelly-fall stocks measured in Norwegian fjords (Sweetman and Chapman 2011, 2015), but the input that was simulated was comparatively similar in terms of C-loading to that found in other jelly-fall events around the world. In December 2002, Billett et al. (2006) documented numerous jellyfish carcass deposits on the Oman Margin (1.5–75 g Jelly-C m^{-2}) and noted significant microbial degradation of the deposits. Similarly, Lebrato and Jones (2009) found significant microbial degradation at a large deposit of salp carcasses off the Ivory Coast (1–>20 g jelly C m^{-2}). Both of these observations are consistent with our findings from the *+Phyto+Jellyfish* experiments. Results from this present study may also be representative for processes occurring immediately beneath other types of organic falls such as squid, fish (Higgs et al. 2014) and pyrosome falls (Henschke et al. 2013) that accumulate at, but do not completely smother large expanses of seafloor.

The exact cause for the apparent shift in C-cycling dynamics was not tested in this study. Nevertheless, studies have shown that declining oxygen levels can initiate a switch in C-cycling processes similar to that seen in this study, from metazoan macrofauna being the main player in oxygenated settings to bacteria dominating C-uptake under low oxygen conditions (Diaz and Rosenberg 2008; Woulds et al. 2009). Woulds et al. (2009) attributed these types of shifts to a decline in metazoan macrofauna biomass with decreasing oxygen concentrations. In this study, bacterial biomass was significantly higher than macrofaunal biomass in both treatments, and neither macrofauna nor bacteria biomass changed as a function of the different treatments over the course of the 5 d study. The differences in macrofauna C-uptake between treatments could be partly caused by the higher contribution of the known diatom-ingesting amphinomid (Gontikaki et al. 2011; Jeffreys et al. 2013; Jumars et al. 2015) and apistobranchid (Jumars et al. 2015) polychaetes to faunal biomass in the *+Phyto* treatment relative to the *+Phyto+Jellyfish* experiments (Table 1). However, we are doubtful this was the main cause. Instead, the lower macrofauna C-uptake rates in the *+Phyto+Jellyfish* experiments appeared to be caused by the macrofauna reacting less to the added phytodetritus in the presence of jellyfish detritus as evidenced by the lower biomass specific uptake rates of many of the taxa (Table 2).

Using high-resolution in situ diffusive samplers, Chelsky (2015) showed that the presence of dead jellyfish at the sediment surface led to an increase in porewater Fe^{2+} and HS^- concentrations indicating elevated anaerobic metabolism and a reduction in the O_2 penetration depth. Although we did not measure sediment O_2 profiles in our study, the bacterial PLFA profiles suggested that anaerobic processes were significantly

up-regulated in the presence of dead jellyfish (Fig. 7). While the majority of algal tracer in both treatments was found in the bacterial PLFA $iC_{15:0}$ which is considered a biomarker for gram-positive bacteria (White et al. 1996; Bühring et al. 2006), significantly more C from the added phytodetritus went into the bacterial PLFA 10 Methyl-$C_{16:0}$ in the *+Phyto+Jellyfish* treatment compared with in the +Phyto study (Fig. 7). The PLFA 10 Methyl-$C_{16:0}$ is widely considered a biomarker for sulphate-reducing bacteria in the group Desulfobacteriaceae (Rutters et al. 2002; Bühring et al. 2006). The channeling of C into this group, therefore, supports the possibility that anaerobic bacteria were stimulated in the jellyfish treatments, possibly by a reduction in sediment O_2 conditions. If the jellyfish did in fact smother the sediment leading to an increase in anaerobic conditions, this could have been a major factor driving the reduction in biomass specific uptake and macrofauna C-uptake rates observed in the *+Phyto+Jellyfish* cores (Fig. 5). The more inhospitable conditions could have reduced macrofaunal activity (e.g., mobility, feeding) to the point where it was difficult for many macrofauna taxa (e.g., surface-feeding spionid polychaetes) to access and process the phytodetritus beneath the jellyfish, leading to lower macrofaunal C-uptake rates being measured. Regardless of the exact reason for the decrease in macrofaunal C-uptake rates recorded here, results from this case study provide clear evidence that shifts in benthic ecosystem functioning can occur rapidly following the deposition of jellyfish detritus without a need for changes in benthic biomass.

This case study provides a first description of the effects of jelly-falls on deep-water benthic ecosystems in boreal settings. It shows that the addition of jellyfish detritus to the seafloor can rapidly alter benthic biogeochemical cycling, and substantially modify short-term C-cycling dynamics at the seafloor. If our results are generalizable to other areas, they suggest that jellyfish blooms could have profound consequences on benthic ecosystems when blooms senesce (especially in areas where scavenging is limited), which may have cascading effects for other benthic ecosystem functions and services.

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