Patterns of carbon processing at the seafloor: the role of faunal and microbial communities in moderating carbon flows

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Abstract

Marine sediments, particularly those located in estuarine and coastal zones, are key locations for the burial of organic carbon (C). However, organic C delivered to the sediment is subjected to a range of biological C-cycling processes, the rates and relative importance of which vary markedly between sites, and which are thus difficult to predict.

In this study, stable isotope tracer experiments were used to quantify the processing of C by microbial and faunal communities in two contrasting Scottish estuarine sites: a subtidal, organic C rich site in Loch Etive with cohesive fine-grained sediment, and an intertidal, organic C poor site on an Ythan estuary sand flat with coarse-grained permeable sediments.

In both experiments, sediment cores were recovered and amended with ^{13}C labelled phytodetritus to quantify whole community respiration of the added C and to trace the isotope label into faunal and bacterial biomass. Similar respiration rates were found in Loch Etive and on the Ythan sand flat (0.64±0.04 and 0.63±0.12 mg C $m^{-2}h^{-1}$, respectively), which we attribute to the experiments being conducted at the same temperature. Faunal uptake of added C over the whole experiment was markedly greater in Loch Etive (204±72 mg C m^{-2}) than on the Ythan sand flat (0.96±0.3mg C m^{-2}), and this difference was driven by a difference in both faunal biomass and activity. Conversely, bacterial C uptake over the whole experiment in Loch Etive was much lower than that on the Ythan sand flat (1.80±1.66 and 127±89 mg C m^{-2} respectively). This was not driven by differences in biomass, indicating that the bacterial community in the permeable Ythan sediments was particularly active, being responsible for 48±18% of total biologically processed C. This type of biological C processing appears to be favoured in permeable sediments. The total amount of biologically processed C was greatest in Loch Etive, largely due to greater faunal C uptake, which was in turn a result of higher faunal biomass. When comparing results from this study with a wide range of previously published isotope tracing experiments, we found a strong correlation between total benthic biomass (fauna plus bacteria) and total biological C processing rates. Therefore, we suggest that the total C cycling capacity of benthic environments is primarily determined by total biomass.

1 Introduction

The burial of organic carbon in marine sediments is a key flux in the global carbon (C) cycle, linking the surface reactive C reservoirs to long term storage in the geological loop. In addition, organic detritus is the main food source for most benthic ecosystems, and its supply and cycling are thus important controlling factors for benthic ecology. Furthermore, the degradation of organic carbon (OC) in sediments usually drives their redox state, and together these determine nutrient regeneration rates and resupply to the water column. Estuarine sediments are particularly important locations for these functions. Of all marine benthic environments, estuarine (particularly fjordic) and shelf sediments host the largest proportion of marine sediment C burial (Berner, 1982; Duarte et al., 2005, Smith et al., 2015). The shallow water depths in estuaries result in the potential of benthic C burial and nutrient regeneration to control water column biogeochemistry and productivity (e.g. Middelburg and Levin, 2009). Therefore, there is a need to understand OC cycling and burial in marine sediments, and in estuarine sediments in particular.

Previous work has established that factors such as OC loading and degradation state, sediment grain size, and the time for which OC is exposed to oxygen before being buried below the oxycline combine to control the relative importance of remineralization and burial as a fate of C in marine sediments (Canfield et al., 1994; Mayer, 1994; Hedges and Keil, 1995; Hartnett et al., 1998). However, the pathways along which OC may travel towards burial or remineralisation must be elucidated in order to further our understanding of benthic C cycling and burial.

There are many processes to which OM arriving at the sediment surface, either of terrestrial origin delivered through riverine inputs or from surface phytoplankton production, may be subjected. First, a major fraction of fresh OC inputs may be fed upon by benthic fauna (Herman et al., 1999; Kristensen, 2001). Thus, C may be assimilated into faunal biomass, and may be transferred through benthic and/or pelagic food webs. Alternately, ingested sedimentary OC may survive gut transit and be egested back into the sediment, in which case it is likely to have been biochemically altered and physically re-packaged (e.g. Bradshaw et al., 1990 a, b; 1991 a, b; Woulds et al., 2012; 2014). In addition, at any trophic level of the food web, C may be metabolised and returned to the water column as CO_2. Further, during bioturbation many fauna transport OC through the sediment column, which may subject it to fluctuating redox conditions and accelerate decay, or sequester it at depth below the digenetically active zone (Aller, 1994; Sun et al., 2002). Secondly, deposited OC will be subject to microbial decay, and may thus be incorporated into microbial biomass, which itself may then progress through the foodweb, or may be returned to the water column as CO_2 through microbial respiration. In addition, it may be released as dissolved organic C (DOC) and re-incorporated into microbial and, subsequently, faunal biomass through the microbial loop (Pozzato et al., 2013 and references therein).

As the processes described above are all biologically driven, we will refer to them collectively as biological C processing (as opposed to long term C burial). The relative importance of the different processes, in turn, will be referred to as the biological C processing pattern.

Isotope tracer experiments, in which organic matter labelled with an enriched level of a naturally uncommon stable isotope (typically ^{13}C and/or ^{15}N) are an excellent tool to derive direct quantitative data on biological C processing patterns and rates (Middelburg, 2014). Such experiments have been conducted in a wide range of benthic environments, from estuarine sites (Moodley et al., 2000) to the deep abyssal plain (Witte et al., 2003 b), from OC rich sediments (Woulds et al., 2007) to oligotrophic sites (Buhring et al., 2006 b), and from polar regions (Gontikaki et al., 2011) to the tropics (Aspetsberger et al., 2007; Sweetman et al., 2010).

Many isotope tracer studies have found remineralisation by the entire benthic community (i.e. bacterial, meio-, and macrofauna combined) to form the dominant fate of the OC supplied (e.g., Woulds et al., 2009; Gontikaki et al., 2011c). It is reasonably well established that such benthic respiration rates are strongly controlled by temperature (Moodley et al., 2005), and also respond to OC input (Witte et al., 2003 b) and benthic community biomass (e.g. Sweetman et al., 2010)

However, considerable variations in carbon processing patterns and rates have been found between sites, with considerable differences in, for example, the biomass pools into which OC is dominantly routed. Thus, some studies have shown that OC uptake by foraminifera and/or bacteria can dominate in both the short and long term (Moodley et al., 2002; Nomaki et al., 2005; Aspetsberger et al., 2007), and others have shown a more prominent role for macrofauna (Witte et al., 2003 a). In some cases macrofaunal uptake can even be equal to total respiration (Woulds et al., 2009). Trends in faunal OC uptake are usually strongly determined by trends in the biomass of different faunal groups (e.g. Woulds et al., 2007; Hunter et al., 2012), although this is not always the case. For example, in sandy subtidal sediments, Evrard et al. (2010) found that more microphytobenthos C was consumed by meiofauna than by macrofauna, despite the lower biomass of the former. In cohesive sediments from a deep fjord, however, the opposite pattern was observed, when macrofaunal foraminifera ingested less OC than expected based on their importance in terms of biomass (Sweetman et al., 2009). This was thought to be due to their relatively deep dwelling lifestyle, suggesting they were not adapted for rapid feeding on freshly deposited OM. Thus, the ecology and community structure of any site is thought to exert significant control on its biological C processing pathways and rates. Furthermore, the examples given above illustrate how the extreme variability in the abundance and characteristics of organisms found at seafloor sites throughout the marine environment has resulted in the lack of a general understanding of how benthic communities impact seafloor C cycling patterns and rates.

In a review of isotope tracer experiments carried out in marine sediments, Woulds et al. (2009) proposed a categorisation of biological C processing patterns into three main types. ‘Respiration dominated’ sites were defined as systems in which >75% of biologically processed C was found as respired CO_2, and this tended to occur mostly in deep, cold, OM-poor sites with relatively low faunal biomass. ‘Active faunal uptake’ systems were described as sites in which respiration was still the major fate of biologically processed C, but where faunal uptake accounted for 10-25%. This pattern was found in shallower, more nearshore and estuarine sites, which were richer in OM, and which hosted correspondingly higher benthic faunal biomass. A third category labelled ‘metazoan macrofaunal dominated’ displayed an unusual pattern in which uptake by metazoan macrofauna accounted for >50% of biological C processing, and was chiefly exhibited in a lower oxygen minimum zone site on the Pakistan margin, where high OC concentrations and just sufficient oxygen supported an unusually high macrofaunal biomass (an ‘edge effect’, Mullins, 1985). This categorisation allowed predictions to be made regarding C processing patterns at a range of sites, but this ability was limited to the types of benthic environment in which isotope-tracing experiments had been conducted to that date.

The previously proposed categorisation was limited in the types of benthic environments covered, and was biased towards subtidal and deep-sea settings characterized by cohesive sediments. Therefore, a particular environment missing in previous syntheses was coarse-grained, permeable sediments, such as are typically found in coastal and shelf environments. One study in subtidal sandy sediments of the German Bight found unexpectedly rapid C processing rates, and suggested a C processing pattern that was dominated by bacterial uptake (Buhring et al., 2006 a). However, variation in results between different experiment durations implies that it could not be used to propose an additional category. The result was however consistent with findings that coarse-grained, permeable sediments are capable of more dynamic biogeochemical cycling than was previously assumed from their generally low OC contents (Huettel et al., 2014). The rapid biogeochemical cycling is driven by water flow over roughness on the sediment surface creating local pressure gradients, which lead to advective exchange of porewaters. This introduces fresh organic substrates and electron acceptors into the sediment, and removes metabolites, enhancing OC turnover (Huettel et al., 2014, and references therein). Therefore, further investigation of biological C processing in previously understudied permeable sediments is warranted.

Our study aimed broadly to investigate biological C processing rates and patterns in estuarine sediments. In particular, we aimed to compare biological C processing in cohesive, fine-grained sediments with that in permeable, coarse-grained sediments and to contrast the roles played by two communities with different compositions and structures. We hypothesised that, in keeping with previous subtidal/shelf/fjordic sites, the cohesive sediments would exhibit a C processing pattern dominated by respiration but with a marked role for faunal uptake, while permeable sediments would exhibit rapid OC turnover, and an OC processing pattern dominated by bacterial uptake. Further, we hypothesised that while faunal C uptake at the two sites would necessarily involve different taxa, the overall contribution of fauna to biological C processing would be related to their total biomass.

2 Methods

2.1 Study sites

Two sites were selected for study: one fine-grained, organic carbon-rich site in Loch Etive and a sandy site with low organic carbon content in the Ythan estuary.

Loch Etive lies on the west coast of Scotland (Fig. 1). It is a glacier carved feature, 30 km long, and is divided into three basins by two shallow sills at Bonawe and Connel. The loch exhibits positive estuarine circulation, with a strong outflow of freshwater in the surface 10m, and tidal exchange of seawater beneath (tidal range is 2 m, Wood et al. 1973). Phytoplankton standing stock has been found to be relatively high (Wood et al 1973). This, combined with input of substantial amounts of terrestrial OC and the tendency of fine sediment to be resuspended from the shallower areas and redeposited in the deeper areas (Ansell 1974) leads to relatively OC rich sediments in the deep basins. The site chosen for this study lies at the deepest point (Airds Bay, 70 m) of the middle basin of Loch Etive (Fig. 1). While the bottom water here is regularly renewed and is therefore well oxygenated, the sediment has a relatively high oxygen demand, and sulphate reduction occurs within 5 cm of the sediment-water interface (Overnell et al., 1996). The experiment was conducted during July 2004, at which point the bottom water dissolved oxygen saturation was close to 100%. The sediment had a median grain size of

21μm with 78 % fines (<63 μm) and contained ~4.9wt % organic C (Loh et al., 2008). The benthic community was dominated by ophuroids, with polychaetes and molluscs also being abundant (Gage 1972, C. Whitcraft unpubl. data).

The Ythan estuary is a well-mixed estuary on the East coast of Scotland (Fig. 1), 20 km north of Aberdeen. It is ~8 km long, with a mean width of 300 m. The Ythan sand flat study site was located around halfway along the estuary on an intertidal sand bar, and exhibited sandy, permeable and OC poor (~0.1 wt % organic C) sediments (Zetsche et al., 2011b) which were subject to semi-diurnal tides and seasonal storms. The median grain size was 336 μm with 11% fines (<63 μm, varying through the year), and the sand is described as well sorted (Zetsche et al., 2011 a). The study site was exposed at low tide, and covered by 1-2 m of water at high tide. The benthic community was dominated by oligochaetes, with polychaetes, molluscs, nematodes and crustaceans also present (Zetsche et al., 2012). The Ythan sand flat experiment was conducted during May 2008.

2.2 Isotope tracing experiments

The experimental setup varied slightly between sites, to account for the differences in their depth and sediment grain size.

2.2.1 Loch Etive

Four replicate sediment cores (up to 50 cm depth, 10 cm i.d.) were collected and placed in a controlled temperature laboratory set to the ambient temperature of11°C. Phytodetritus (*Thalassiosira*, a representative pelagic species) labelled with ^{13}C (~25%) was added to the sediment surface of intact cores to give a dose of 1050 ± 25 mg C m^{-2} (the standard deviation stated is due to variation between replicate cores). The cores were then sealed with water columns of 14-16.5 cm and incubated in the dark for 7 days (156 h). During the incubation, the oxygen concentration in core-top water was maintained by pumping the water through an ‘oxystat’ gill, composed of gas permeable tubing submerged in a reservoir of 100% oxygenated seawater (see Woulds et al., 2007), and monitored with Clark type electrodes. As the tubing used in the oxystat gill was permeable to all gases there was the potential for loss of some $^{13}CO_2$ generated during the experiment. However, the dissolved inorganic carbon (DIC) concentration difference between the incubation water and oxygenated reservoir will have remained small, thus this effect is thought to be minor. Samples of the overlying water were taken at 0, 24, 48, 72, 96, 120 and 144 hours after the introduction of the labelled phytodetritus. These were preserved in glass vials without a headspace and poisoned with $HgCl_2$ for DIC and δ^{13}C- DIC analysis.

At the end of the incubation period, cores were sectioned at intervals of 0.5 cm up to 2 cm depth, then in 1 cm sections up to 10 cm depth, and finally in 2 cm sections up to 20 cm depth. Half of each sediment slice was sieved, with >300 μm (macrofauna) and 150-300 μm (meiofauna) fractions retained. The other half of each slice was stored frozen in plastic bags. Sieve residues were examined under the microscope and all fauna were extracted. Organisms were sorted to the lowest taxonomic level possible and preserved frozen in pre-weighed tin boats and pre-combusted glass vials. Fauna from two of the four cores were allowed to void their guts before preservation. This was achieved by allowing them to remain in dishes of filtered seawater for several hours before freezing.

2.2.2 The Ythan sand flat

Four replicate sediment cores were collected by pushing 25 cm diameter acrylic core tubes into the sediment at low tide, and digging them out to obtain intact sediment cores 14-15 cm in length. These were returned to a controlled temperature laboratory set to 11°C at Oceanlab, University of Aberdeen. Filtered Ythan estuary water was added to each core to create a water column. A lid was placed on each core, leaving a headspace, with exhaust ports open. Fully oxygenated conditions were maintained by gentle bubbling with air, except during respiration measurements (see below). Lids were mounted with stirring disks, the rotation rates of which were calibrated to generate appropriate pressure gradients to prompt porewater advection (Erenhauss and Huettel, 2004). The overlying water was changed daily. Isotopically labelled (34 % ^{13}C) phytodetritus (freeze-dried *Navicula incerta*, a representative benthic species) was added to the water column and allowed to sink onto the sediment-water interface to give a dose of 753±9.4mg C m^{-2}. Twice during the subsequent 7 days (immediately after phytodetritus addition and 5 days later) the respiration rate in each core was measured. This involved filling the headspace in each core to exclude all air bubbles and sealing all lids. Time series water samples were taken over the subsequent 24 h and preserved for δ^{13}C DIC analysis as described above. At the end of each respiration measurement, lids were removed and dissolved oxygen was measured by Winkler titration to ensure it had not declined by more than 20%.

The experiment lasted 7 days (162 h), after which the overlying water was removed and a 5 cm diameter sub-core was taken from each core. This was sectioned at 1 cm intervals and frozen. The remaining sediment was sectioned at intervals of 0-1, 1-2, 2-3 and 3-5 cm, and sieved on a 500 μm mesh. Sediment and fauna remaining on the sieve was preserved in buffered 10% formaldehyde in seawater. Fauna were picked from sieve residues under a microscope, identified, and placed in glass vials or pre-weighed silver capsules.

2.3 Analysis

2.3.1 Bulk stable isotope analyses

Fauna samples were oven-dried at 45°C. Fauna with calcite skeletons (ophiuroids, molluscs and foraminifera) were de-carbonated by the addition of a few drops of 6 N HCl. For soft-bodied fauna, 1 N HCl was used to eliminate possible traces of carbonates. In all cases whole organisms were analysed. In the Loch Etive experiment fauna from two replicate cores were allowed time to void their guts, but it was not clear that they actually did so (see below). All samples were dried at ~50°C before analysis for OC content and δ^{13}C.

Loch Etive samples were analysed on a Europa Scientific (Crew, UK) Tracermass isotope ratio mass spectrometer (IRMS) with a Roboprep Dumas combustion sample converter. Appropriately sized samples of acetanilide were used for quantification, and all C abundance data were blank corrected. Replicate analyses revealed relative standard deviations of 4.6 % for C abundance and 0.7 ‰ for δ^{13}C.Ythan sand flat samples were analysed using a Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a Delta^{Plus} XP isotope ratio mass spectrometer (all ThermoFinnigan, Bremen, Germany). Carbon contents of the samples were calculated from the area output of the mass spectrometer calibrated against National Institute of Standards and Technology standard reference material 1547 (peach leaves), which was analysed with every batch of ten samples. The isotope ratios were traceable to International Atomic Energy Agency reference materials USGS40 and USGS41 (both L-glutamic acid); certified for $\delta^{13}C$ (‰). Long-term precisions for a quality control standard (milled flour) were: total carbon 40.3 ± 0.35 %, and $\delta^{13}C$ -25.4 ± 0.13 ‰.

Overlying water samples were analysed for concentration and $\delta^{13}C$ of DIC as described by Moodley et al. (2000). Briefly, a He headspace was created in sample vials, the CO_2 and $\delta^{13}C$ of which were quantified using a Carlo Erba MEGA 540 gas chromatograph, and a Finnigan Delta S isotope ratio mass spectrometer, respectively. The system was calibrated with acetanilide (Schimmelmann et al., 2009) and the IAEA-CH-6 standard. Repeat analyses of standard materials gave a relative standard deviation of 4.4% for DIC concentrations, and a standard deviation of ±0.09‰ for $\delta^{13}C$.

2.3.2 Bacterial phospholipid fatty acids(PLFA)

Aliquots of sediment were treated with a Bligh and Dyer extraction, involving shaking at room temperature in a 2:1:1 mix of methanol, chloroform and water. Lipids were recovered in the chloroform layer, and were loaded onto silica gel columns. Polar lipids were eluted in methanol, and methylated in the presence of methanolic NaOH. The C12:0 and C19:0 fatty acid methyl esters were used as internal standards. Fatty acids were separated by gas chromatography on a 30 m, 0.25mm i.d., 25 μm film thickness BPX70 column and combusted in a Thermo GC-combustion II interface. Isotope ratios were then determined using a Thermo Delta+ isotope ratio mass spectrometer (for further details see Woulds et al., 2014).

2.4 Data treatment

Uptake of added C by fauna is reported in absolute terms (see below), and as isotopic enrichments over the natural background faunal isotopic composition. Isotopic compositions were expressed as $\delta^{13}C$, derived using Eq. (1).

$$\delta ‰ = \left(\frac{Rs}{Rr} - 1\right) x\ 1000 \tag{1}$$

Where R_s and R_r are the $^{13}C/^{12}C$ ratio in the sample and the reference standard respectively. Isotopic enrichments ($\Delta\delta$) were then calculated using Eq. (2).

$$\Delta\delta = \delta^{13}C\ sample - \ \delta^{13}Cbackground \tag{2}$$

Carbon uptake by faunal groups was calculated by subtracting naturally occurring ^{13}C, multiplying by the sample C contents, and correcting for the fact that the added phytodetritus was not 100 % ^{13}C labelled, as shown in Eq. (3):

$$C\ Uptake_{sample}\ (\mu g) = \frac{\left(At\ \%_{sample} - At\ \%_{background}\right) \times \ C\ Contents_{sample}}{At\ \%_{phytodetritus}} \times 100$$

(3)

Where At % is the ^{13}C atoms present as a percentage of the total C atoms present. Data from individual specimens was summed to produce faunal C uptake by different groups of fauna. For Loch Etive, background ^{13}C was subtracted based on natural faunal isotopic data collected concurrently with the C tracing experiment. For the Ythan sand flat natural faunal isotopic data were not available, and instead the natural C isotopic signature of sedimentary organic C (-20.2 ‰) was used. Isotopic signatures of fauna at the end of the experiment had a maximum of 2460‰ and a mean of 175‰. Therefore the small inaccuracies introduced by the use of this natural background value will not have been significant.

The DIC concentrations and δ^{13}C-DIC were used to calculate the total amount of added ^{13}C present as DIC in experimental chambers at each sampling time. A linear regression was applied to these to yield a separate respiration rate for each core and for each period of respiration measurement (mean $R^2 = 0.909$, with the exception of one measurement showing poor linearity with $R^2 = 0.368$), and the rate was multiplied by experiment duration to calculate total respiration of added C during the experiment. In the case of the Ythan sand flat respiration was measured during two separate 24 h periods through the experiment. In this case average rates from the two measurements were used to calculate total respiration of added C throughout the experiment.

Bacterial C uptake was quantified using the compounds iC14:0, iC15:0, aiC15:0 and iC16:0 as bacterial markers. Bacterial uptake of added C was calculated from their concentrations and isotopic compositions (corrected for natural ^{13}C occurrence using data from unlabelled sediment), based on these compounds representing 14% of total bacterial PLFAs, and bacterial PLFA comprising 5.6% of total bacterial biomass (Boschker and Middelburg, 2002). In the case of Loch Etive, the sediments from which PLFAs were extracted had previously been centrifuged (10 mins, 3500 rpm, room temperature) for porewater extraction, which could have led to a slight reduction in the bacterial biomass and C uptake measured.

3. Results

The mean recovery of added C from the bacterial, faunal and respired pools together was 30±6% and 31±10% of that which was added for Loch Etive and the Ythan sand flat respectively. This is a good recovery rate compared to other similar experiments (e.g. Woulds et al., 2007). Most of the remaining C was likely left in the sediment as particulate organic C or as dissolved organic C.

3.1 Remineralisation

The average respiration rate of the added OC was similar in Loch Etive and the Ythan sand flat, and reached 0.64±0.4 and 0.63±0.12 mg C m-2h-1, respectively. Thus, the total amount of added C that was respired at each site (over 156 h in Loch Etive and 162 h on the Ythan sand flat) was 99.5±6.5 and 102.6±19.4 mg C m-2 for Loch Etive and the Ythan sand flat, respectively (Fig. 2). In both experiments, respiration rates measured in the first 48 h (1.41±0.14 and 0.74±0.02 mg C m-2h-1 for Etive and the Ythan sand flat, respectively) were higher than those measured in the last 48 h of the experiment (0.31±0.04 and 0.52±0.22 mg C m-2h-1 for Etive and the Ythan sand flat, respectively; this difference was significant only for Loch Etive, t-test, P<0.001). The increase in labelled DIC over time for each chamber is shown in Fig. S1.

3.2 Faunal biomass and C uptake

Macrofaunal biomass in the experimental cores was 4337±1202 mg C m^{-2} in Loch Etive and 455±167 mg C m^{-2} on the Ythan sand flat. Macrofaunal δ^{13}C signatures (for individual specimens) reached maximal values of 7647 ‰ and 2460 ‰ in Loch Etive and on the Ythan sand flat, respectively. Total faunal C uptake was orders of magnitude greater in Loch Etive (204±72 mg C m^{-2}) than on the Ythan sand flat (0.96±0.3 mg C m^{-2}) (Fig. 2). This difference was driven partly by a difference in biomass, but fauna on the Ythan sand flat were also comparatively less active, as reflected by biomass specific C uptake at the two sites (0.047±0.01 and 0.0022±0.0006 mg C uptake per mg C biomass for Loch Etive and the Ythan sand flat respectively).

In Loch Etive, both faunal biomass and carbon uptake were dominated by two ophuroids, *Amphiura fillaformis* and *A. chiajei*, which contributed 75 % and 95 %to the total biomass and to faunal C uptake, respectively (Fig. 3). The molluscs and polychaetes contributed 11 % and 6 % to biomass, but only 1.6 % and 1 % to faunal C uptake, respectively. Amongst the polychaetes, the *Flabelligeridae* and *Harmothoe* tended to show lower ^{13}C enrichment (i.e. a lower specific uptake of labelled C), while representatives of all other families (*Capitellidae*, *Syllidae*, *Cirratulidae*, *Cossura* and *Terebellidae*) showed much higher levels of labelling.

On the Ythan sand flat, the macrofaunal community was dominated by oligochaetes and nematodes (Fig. 3). The proportion of total faunal C uptake accounted for by oligochaetes (48%) approximately matched their contribution to faunal biomass (51%). However, nematodes contributed slightly less towards total faunal uptake (14%) than they did to total biomass (19%). Other minor groups included amphipods (0.3% of biomass), polychaetes (2% of biomass) and gastropods (1.5% of biomass). Of these groups, the polychaetes and gastropods made disproportionately large contributions to faunal C uptake, accounting for 10% and 18% respectively (Fig. 3).

In the Loch Etive experiment, metazoan meiofaunal and foraminiferal data were also collected. Metazoan meiofaunal and foraminiferal biomass in experimental cores were 47±14 mg C m^{-2} and 343±625 mg C m^{-2}, respectively. These two groups showed maximal $\Delta\delta^{13}$C values of 1360 ‰ and 3313 ‰, respectively. Metazoan meiofauna were not taxonomically sorted, but amongst the foraminifera the highest labelling was observed in *Crithionina sp*., while *Pelosina* did not show measurable label uptake. Compared to the macrofauna, meiofaunal C uptake was minor, at 0.18±0.20 and 5.21±5.15 mg C m^{-2} for metazoans and foraminifera, respectively (Fig. 2). Thus, metazoan meiofauna and foraminifera contributed 1 % and 7 % to the total faunal biomass, and 0.1 % and 2.5 % to faunal C uptake, respectively.

3.3 Bacterial biomass and C uptake

Bacterial biomass in the surface 5 cm of sediment in Loch Etive was 5515±3121 mg C m^{-2}, and on the Ythan sand flat was 7657±3315 mg C m^{-2}. The amount of added C incorporated into bacterial biomass was two orders of magnitude greater on the Ythan sand flat (127±89 mg C m^{-2}) than in Loch Etive (1.80±1.66 mg C m^{-2}, Fig. 2). In the majority of cores, >90% of bacterial uptake occurred in the top 3 cm of sediment. However in one core from Loch Etive, 28% of bacterial uptake occurred between 3 and 6 cm depth. In comparison, 52% of the bacterial biomass from the top 5 cm occurred shallower than 3 cm for Loch Etive, and this value was 66% on the Ythan sand flat. Biomass specific uptake for the bacteria was two orders of magnitude greater on the Ythan sand flat (0.016±0.004 mg C uptake per mg C biomass) than in Loch Etive (0.00023±.00013 mg C uptake per mg C biomass). Thus it appears that the rapid uptake of added C by bacteria at the sandy site was primarily driven by a more active bacterial community, rather than by a larger bacterial biomass.

3.4 Biological carbon processing patterns

The large differences in macrofaunal and bacterial C uptake rates between the two sites resulted in markedly different biological C processing patterns (Fig. 2). In both cases, respiration was an important, but usually not the dominant, fate of biologically processed C, accounting for 25-60 %. In the case of Loch Etive, the dominant fate of biologically processed C was macrofaunal uptake (64±10 %), and this also resulted in a greater amount of total biological C processing (Fig. 2) than on the Ythan sand flat. On the Ythan sand flat bacterial uptake (48±18 %) was the dominant fate of biologically processed C. In Loch Etive, uptake of C by bacterial, metazoan meiofaunal and foraminiferal communities made only minor contributions to total biological C processing (Fig. 2). On the Ythan sand flat, macrofaunal uptake made a relatively minor contribution (Fig.2). Unfortunately, uptake by meiofaunal organisms could not be quantified at the latter site.

4 Discussion

4.1 Experimental approach

This study compares data from two experiments which, while following the same principle, nevertheless had slightly different experimental setups. The water depth, core size, stirring regime, light availability and C dose added all differed between the two study sites. The differences in stirring regime, and light availability were enforced to properly replicate natural conditions in each experiment, thus any contrasts caused by these conditions reflect differences in functioning of the two habitats. The presence of light in the Ythan sand flat experiment means it is possible that some labelled DIC produced by respiration may have been utilised during photosynthesis, leading to an underestimation of respiration rate. However, as the isotopic labelling level of DIC always remained below 1.33 at % this is unlikely to have had a measurable effect. The difference in water depth and core diameters was driven by the practicality of collecting undisturbed sediment cores from the two contrasting sediment types. While the difference in depth means that photosynthesis and flux of CO_2 gas to the atmosphere during emergent periods would normally occur on the Ythan sand flat but not in Loch Etive, they remain comparable in their temperatures and estuarine locations. The difference in C dose added was minor (~25%) and also driven by practical constraints. Previous studies have found little impact of such minor differences in C dose (Woulds et al., 2009). Where the amount of added C has been observed to control biological processing patterns and rates, the difference in C dose has been much more pronounced (10-fold, Buhring et al., 2006 b). We acknowledge that the C dose represented a different proportion of naturally present OC at each site, and this could have led to an enhanced response at the Ythan sand flat. However, surface sediment OC concentrations are not necessarily a good reflection of actual C delivery to the seafloor, given the different transport mechanisms in permeable and cohesive sediments (see below). Further, there is a sparsity of data available on primary production rates, particularly for the Ythan sand flat. Therefore maintaining a uniform C addition was judged to yield the most comparable data. Thus, while experimental details varied between Loch

Etive and the Ythan sand flat, we are confident that direct comparisons between the results of the two experiments are valid.

Due to practical constraints, meiofauna were not included in the analysis of the Ythan sand flat experiment. Previous studies have found both that meiofauna consume disproportionate amounts of C relative to their biomass (Evrard et al., 2010), and that nematodes (a major meiofaunal group) made a negligible contribution to C cycling (Moens et al., 2007). We are unable to speculate how active the meiofauna were in C cycling in the present study but, despite wide variations in the importance of meiofaunal uptake (Nomaki et al., 2005; Sweetman et al., 2009; Evrard et al., 2010), it is usually similar to or less than macrofaunal C uptake (Nomaki et al., 2005; Evrard et al., 2010). Thus, we consider it unlikely that the meiofaunal community was involved in C processing on the same scale as observed for bacterial uptake and total respiration, and exclusion of meiofauna in the Ythan sand flat experiment is unlikely to have markedly altered the overall pattern of biological C processing that we observed.

There was a difference in the sieve mesh sizes used to collect macrofauna in the two experiments (300 μm in Loch Etive and 500 μm on the Ythan sand flat). The use of larger mesh sizes is more conventional and practical in coarser grained sediments. The larger mesh used on the Ythan sand flat is likely to have reduced the macrofaunal biomass and C uptake measured. However, the effect is likely to have been insufficient to explain the striking differences in macrofaunal C uptake and biomass specific uptake seen between the two sites.

Finally, the majority of fauna were too small for manual removal of gut contents, and were therefore analysed with their gut contents in place. The exception to this was two of the Loch Etive cores, which were allowed time to void their guts before freezing. However, this did not produce a significant difference in the mcarofaunal^{13}C pool between those cores and the other two in which fauna retained their gut contents (Mann-Whitney U, p =0.245). Some infauna respond to starvation by retaining their gut contents for days or weeks. Therefore it is possible that organisms either voided their guts incompletely, or not at all. It is also possible that the amount of added C residing in macrofaunal guts was comparatively small as shown by Herman et al. (2000), and thus not measurable above variation caused by faunal patchiness. Thus the values reported here as faunal C uptake include C in both gut contents faunal tissue.

4.2 Respiration rates

The respiration rates observed in Loch Etive and on the Ythan sand flat were very similar (Fig. 2). This is unsurprising, as the two experiments were conducted at the same temperature, and similar C loadings were applied. Temperature is known to control sediment respiration rates through impacts on diffusion and microbial process rates (Yvon-Durochet et al., 2015), and benthic respiration has been shown to respond to temperature changes with a Q_{10} of 2-3 (Kristensen 2000). Further, after manipulating the temperatures at which cores from both a deep-sea and an estuarine site were incubated, Moodley et al. (2005) found similar respiration rates of added phytodetritus at similar temperatures, despite differences in water depth and faunal community. Our finding of similar rates of respiration, despite marked differences in influential factors such as macrofaunal biomass, organic C concentration, and solute transport processes (Kristensen, 2000; Hubas et al., 2007; Huettel et al., 2014), supports the suggestion that temperature is the dominant control.

4.3 Faunal uptake

In Loch Etive, the macrofauna overwhelmingly dominated total faunal C uptake (accounting for 97 %), compared to metazoan meiofauna (0.1 %) and foraminifera (2.5 %,). These contributions were broadly similar to their contributions to total faunal biomass (92 %, 1 % and 7 % for macrofauna, metazoan meiofauna and foraminifera respectively). Thus, in line with previous findings (Middelburg et al., 2000; Woulds et al., 2007; Hunter et al., 2012), the distribution of C uptake amongst faunal classes was largely determined by the relative biomass of each group. The dominance of faunal C uptake by macrofauna has been observed previously. For example, in shorter experiments on the Porcupine Abyssal Plain (Witte et al., 2003b), in the deep Sognefjord (Witte et al., 2003 a) and at certain sites on the Pakistan margin (Woulds et al., 2007), macrofauna dominated faunal C uptake, and at an Antarctic site Moens et al. (2007) found that meiofaunal nematodes made a negligible contribution to C uptake. However, uptake into the macrofaunal pool can be most important during the initial response to an OC pulse, with bacterial uptake and respiration becoming more important over longer timescales (Moodley et al., 2002; Witte et al., 2003 b). Also in contrast to the findings above, metazoan meiofaunal and foraminiferal uptake have previously been shown to be more important pathways for C (e.g. Moodley et al., 2000). Where macrofauna are absent, or where conditions are unfavourable, smaller taxa can dominate C uptake, such as within the Arabian Sea oxygen minimum zone (Woulds et al., 2007). At other sites, meiofauna and foraminifera have been shown to take up more C than macrofauna without the presence of a stress factor. This was the case at 2170 m water depth in the NE Atlantic, in Sagami Bay and at a subtidal Wadden Sea site, foraminifera and meiofauna have been observed to consume more C than macrofauna, sometimes despite having lower biomass (Moodley et al., 2002; Nomaki et al. 2005; Evrard et al., 2010).

The marked uptake of C by macrofauna in Loch Etive was largely driven by two species of ophuroid, which also dominated the macrofaunal biomass (Fig. 3). However, the ophuroids accounted for a greater percentage of macrofaunal C uptake than they accounted for macrofaunal biomass (Fig. 3),and thus were disproportionately responsible for macrofaunal C uptake. On the Ythan sand flat, the contribution to C uptake by the dominant oligochaetes was in line with and their biomass (both ~50%, Fig. 3). However, other faunal groups contributed differently to biomass and C uptake. Nematodes were responsible for less C uptake than expected, while the polychaetes, amphipods and molluscs fed comparatively efficiently on the added C. This is in line with previous studies in which certain polychaete families have been found to be selective or rapid feeders on fresh algal detritus (e.g. Woulds et al., 2007).

When C uptake is plotted against biomass for each faunal specimen analysed across both study sites, a positive correlation is apparent (Fig. 4). This correlation has been reported previously (Moodley et al., 2005; Woulds et al., 2007), and suggests that faunal C uptake is largely driven by faunal biomass, despite the fact they are auto-correlations (uptake data are derived by multiplying C contents of a specimen by its isotopic signature). Within each site the distribution of C uptake amongst faunal groups was also dominantly driven by biomass. However, the lower faunal biomass on the Ythan sand flat does not fully explain the lower faunal C uptake observed there, as biomass specific C uptake was also considerably lower than in Loch Etive. We suggest that the low OC standing stock in the permeable sediment of the Ythan sand flat supports a lower biomass and less active faunal community with lower metabolic rates.

The identity of fauna responsible for C uptake was in line with expectations from some previous studies, but not with others, and the reasons for this variation are not clear. Therefore, while overall faunal uptake is dictated by biomass, it remains challenging to predict which faunal groups and taxa will dominate C uptake in a particular benthic setting. This appears to be determined by the complex interplay of factors that determine benthic community composition, such as the nature and timing of food supply (Witte et al., 2003 a, b), environmental stressors (Woulds et al., 2007), feeding strategies and competition (Hunter et al., 2012).

4.4 Total biological C processing rates

Loch Etive showed the largest amount of total biologically processed C (Fig. 2). As both sites showed very similar respiration rates, the difference in total biological C processing was driven by greater faunal uptake in Loch Etive (Fig. 2), and this was a result of greater faunal biomass. The relationship between biomass and total biological C processing is also shown by data gathered from previously published isotope tracing experiments (Table 1) , which show a correlation between total biomass (faunal plus bacterial) and total biological C processing rate (Pearson's correlation, r=0.499, p=0.002). We therefore suggest that benthic community structure impacts the total C processing capacity of benthic environments, through a relationship between biomass and total biological C processing rates, with an emphasis on the importance of macrofaunal biomass as indicated by the importance of macrofauna in Loch Etive, and the fact that the proportion of the bacterial biomass which is active can be rather variable (see below).

4.5 Short term biological C processing categories

The distribution of biologically processed C between different C pools (biological C processing pattern, Fig. 2) varied markedly between the two sites. While they both showed respiration to be an important process, the dominant fate of biologically processed C in Loch Etive was uptake by macrofauna, while on the Ythan sand flat it was uptake by bacteria (Fig. 2).

A review of previous isotope tracing experiments proposed a categorisation of short term biological C processing patterns (Woulds et al., 2009), which can be used as a framework to explain patterns observed in this study.

Loch Etive was expected to show a short term biological C processing pattern in line with the category labelled 'active faunal uptake'. In this category, biological C processing is dominated by respiration, but faunal uptake accounts for 10-25 % (Woulds et al., 2009). This category is found in estuarine and nearshore sites which are warmer than the deep sea, have slightly more abundant OM, and thus support higher biomass and more active faunal communities. However, the short term biological C processing pattern observed in Loch Etive was most similar to the category labelled 'macrofaunal uptake dominated' (Fig. 5), in which uptake of C by macrofauna accounts for a greater proportion of biologically processed C than total community respiration (Woulds et al., 2009). This is an unusual pattern, previously only observed in the lower margin of the Arabian Sea oxygen minimum zone. It was hypothesised in that case that the occurrence of a macrofaunal population capable of this magnitude of C uptake was due to the presence of particularly high OC concentrations in the sediment, coupled with sufficient oxygen for larger organisms. This explanation also applies to Loch Etive, where the sediment OC concentration was nearly 5 %. In contrast to the Arabian Sea site however, Loch Etive featured fully oxygenated bottom water. Thus, the occurrence of macrofaunal uptake dominated short term biological C processing appears to be facilitated by high OC availability, rather than by low oxygen conditions. Experiments conducted in Pearl Harbour sites impacted by invasive mangroves also show OC availability controlling the relative importance of faunal C uptake (Sweetman et al., 2010). A control site was OC poor (0.5% wt % OC) and showed respiration dominated biological C processing (Fig. 5), while a nearby site from which invasive mangroves had been removed showed active (macro)faunal uptake (Fig. 5), in line with higher sediment OC content (3.1% wt % OC) and an elevated macrofaunal biomass.

We hypothesised that the Ythan sand flat would show a short term biological C processing pattern that did not fit with the categories suggested by Woulds et al. (2009). Our hypothesis was supported, as biological C processing on the Ythan sand flat was dominated by bacterial C uptake (Fig. 2). There have been indications in previous isotope tracing experiments in sandy sediments of the German Bight that bacterial C uptake may be particularly important in sandy sediments (Buhring et al., 2006a). Thus we now combine the previous and current results and propose a new biological C processing category labelled ‘bacterial uptake dominated’ (Fig. 5). In the new category, bacterial uptake is the dominant short term fate of biologically processed C, accounting for ~35-70 %. Respiration remains important, accounting for 25-40% of biologically processed C, and faunal uptake tends to account for~5-20 %.

The new category of biological C processing so far has only been observed in two experiments targeting sandy, permeable sediments, and so the features of such sediments appear to favour bacterial C uptake. Advective porewater exchange in permeable sediments has been shown to enhance the rates of microbial processes such as remineralisation and nitrification (Huettel et al., 2014) through rapid supply of oxygen and flushing of respiratory metabolites. This is balanced by introduction of fresh OC as algal cells are filtered out of advecting porewater (Ehrenhauss and Huettel, 2004), thus substrate and electron acceptors for bacterial respiration are supplied.

While permeable sediments generally have similar or lower bacterial abundances than muddy sediments, their bacterial communities tend to be highly active, and it has been suggested that, because they are subjected to rapidly changing biogeochemical conditions, they are poised to respond rapidly to OC input (Huettel et al., 2014). Notably however, the rapid rates of bacterial activity observed in permeable sediments do not typically lead to build-up of bacterial biomass (Huettel et al., 2014). This may be due to regular removal of bacterial biomass during sediment reworking, in line with observations of seasonal changes in clogging of pore spaces in sandy sediment (Zetsche et al., 2011).

The domination of short term biological C processing by bacterial uptake implies a high value for bacterial growth efficiency (BGE). This is calculated as bacterial secondary production divided by the sum of bacterial secondary production and bacterial respiration. Bacterial respiration is not quantified here, however, it is likely that a large proportion of total community respiration is attributable to bacteria (Schwinghamer et al., 1986; Hubas et al., 2006). For the sake of discussion, BGE has been approximated for the Ythan sand flat experiments as bacterial C uptake divided by the sum of bacterial C uptake and total community respiration, giving a conservative estimate of 0.51±0.18. This is at the high end of the range of values (<0.05 to >0.5) reported in a review of growth efficiency for planktonic bacteria (Del Giorgio and Cole, 1998), but is in line with the modelled value of >0.5 for the most productive coastal and estuarine sites (Del Giorgio and Cole, 1998). Bacterial growth efficiency is widely variable, both spatially and temporally, and the factors that control it are not well understood. However both the rate of supply of organic substrate and its composition (bioavailable energy) seem to be positively correlated with BGE, and it tends to increase from oligotrophic to eutrophic environments (Del Giorgio and Cole, 1998). This is consistent with high BGE in permeable sediments, which have a high input of fresh OC from filtering during advective porewater flow (Ehrenhauss and Huettel, 2004), and where a high proportion of bacterial cells may be active (as indicated by higher biomass specific uptake on the Ythan sand flat).

Finally, faunal uptake was relatively minor in the Ythan sand flat experiment, and this suggests that bacterial C uptake may have been favoured by a lack of competition from or grazing by macrofauna. A negative relationship has previously been observed between macrofaunal biomass and bacterial C and N uptake in the Arabian Sea, and a similar effect has been observed in the Whittard canyon (Hunter et al., 2012; 2013).

The short term biological C processing patterns presented in Fig.5 can accommodate most observations in the literature, but some findings do not fit in this conceptual scheme. For example, an experiment conducted in permeable sediments of the Gulf of Gdansk does not show the expected bacterial dominated biological C processing pattern. Instead it shows respiration dominated biological C processing, with bacterial uptake responsible for only 16% (Fig. 5). Further, an OC rich site with invasive mangroves in Hawaii shows respiration dominated biological C processing, instead of ‘active faunal uptake’ pattern (Fig. 5, Sweetman et al., 2010), due to mangrove roots and detritus making the sediment inhospitable to macrofauna.

Finally, bacterial uptake dominated short term biological C processing has also been observed over 3 days in sediments from the Faero-Shetland channel at a depth of 1080 m (Gontikaki et al., 2011). This is considerably deeper than all other observations, and the sediments contained a muddy fraction, although also featuring grains up to gravel size. Thus this site does not fit the same general description as others showing bacterial uptake dominated biological C processing. In this case bacterial uptake dominated C processing was observed over the initial 3 days of the experiment, and after 6 days biological C processing was respiration dominated, in line with expectations. The authors explained the initial rapid uptake of C by bacteria as a reaction to the initially available reactive fraction of the added OM, before hydrolysis of the remaining OC began in earnest (Gontikaki et al., 2011). The Porcupine Abyssal plain also showed a change in short term biological C processing category between different experiment durations, showing an unexpected active faunal uptake pattern after 60 h, and the more expected ‘respiration dominated’ pattern after 192 h and 552 h (Table 1). This was explained as being due to the motility and selective feeding abilities of the macrofauna allowing them to initially outcompete bacteria. The majority of studies which have included experiments of multiple short term durations at the same site have showed consistency of short term biological C processing pattern (Table 1; Witte et al., 2003; Bhuring et al., 2006; Woulds et al., 2009), therefore, variation in experiment duration amongst the studies cited is not thought to be a major driver of short term biological C processing pattern.

In summary, the proposed categorisation of short term biological C processing patterns works well across many different sites, but variation in characteristics of individual sites can still lead to some unexpected results.

5 Conclusions

The rate of respiration of added phytodetritus was dominantly controlled by temperature, rather than other factors such as benthic community biomass, sediment OC concentration, or solute transport mechanism.

Faunal C uptake was related to faunal biomass. Further, total biological C processing rates in this and previous studies appear to be dominantly determined by benthic biomass. Therefore benthic community structure has a role in controlling the C processing capacity of benthic environments.

A new biological C processing pattern category was proposed titled ‘bacterial uptake dominated’, which seems usually to be observed in permeable sediments, where conditions are particularly conducive to active bacterial populations.

Author contributions

C. Woulds designed and conducted the experiments with input from G. Cowie, J. Middelburg and U. Witte. Sample analysis was completed by C. Woulds, S. Bouillon and E. Drake. C. Woulds prepared the manuscript with the assistance of all co-authors.

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Source	**Site/Experiment**	**Depth (m)**	**Temperature (°C)**	**Incubation Duration (h)**	**Macrofaunal Biomass (mg C m^{-2})**	**Bacterial Biomass (mg C m^{-2})**	**Respiration Rate (mg C m^{-2} h^{-1})**	**Total Processing Rate (mg C m^{-2} h^{-1})**
Moodley et al. 2000	Oosterschelde	Intertidal	10	6	nd	nd	7.758	13.150
Moodley et al. 2002	NW Spain	2170	3.6	35	39	2	0.083	0.290
Witte et al. 2003 b	PAP 60h	4800	nd	60	120	2500	0.167	0.225
Witte et al. 2003 b	PAP 192h	4800	nd	192	120	2500	0.167	0.188
Witte et al. 2003 b	PAP 552h	4800	nd	552	120	2500	0.236	0.263
Witte et al. 2003 a	Sognefjord 36h	1265	7	36	250	8500	0.539	0.781
Witte et al. 2003 a	Sognefjord 72h	1265	7	72	250	8500	0.451	0.715
Moodley et al. 2005	N. Sea (perturbed)	37	6	24	756	2688	0.600	0.735
Moodley et al. 2005	N. Agean	102	14	24	73	522	2.895	3.075
Moodley et al. 2005	N. Agean	698	14	24	37	366	3.110	3.290
Moodley et al. 2005	E. Med.	1552	14	24	6	254	2.750	2.830
Moodley et al. 2005	E. Med.	3859	14	24	4	312	2.495	2.610
Moodley et al. 2005	NE Atlantic 24h	2170	4	24	138	313	0.300	0.330
Moodley et al. 2005	N. Sea	37	16	24	732	2304	3.025	3.600
Moodley et al. 2005	Estuary	Intertidal	18	24	1356	1260	2.545	3.705
Bhuring et al. 2006	German Bight 12h	19	9	12	nd	nd	0.258	3.592
Bhuring et al. 2006	German Bight 30h	19	9	30	nd	nd	0.620	2.523
Bhuring et al. 2006	German Bight 132h	19	9	132	nd	nd	0.258	0.667
Bhuring et al. 2006	German Bight in situ	19	13	32	nd	nd	0.338	2.834
Woulds et al. 2009	PM pre 140 2d	140	22	68	110	1100	2.827	3.750
Woulds et al. 2009	PM post 140 2d	140	22	44	110	1100	2.066	2.977
Woulds et al. 2009	PM post 140 5d	140	22	118	110	1100	1.164	1.611
Woulds et al. 2009	PM post 140 in situ	140	22	60	110	1100	0.705	0.955
Woulds et al. 2009	PM pre 300 2d	300	15	61	0	1000	0.365	0.487
Woulds et al. 2009	PM pre 300 5d	300	15	127	0	1000	0.285	0.386
Woulds et al. 2009	PM post 300 2d	300	15	58	0	1000	0.527	0.931
Woulds et al. 2009	PM post 300 5d	300	15	155	0	1000	0.477	0.865
Woulds et al. 2009	PM post 300 in situ	300	15	60	0	1000	0.035	0.250
Woulds et al. 2009	PM pre 850 2d	850	10	46	nd	nd	1.064	1.934
Woulds et al. 2009	PM pre 940 5d	940	9	112	910	700	0.469	0.933
Woulds et al. 2009	PM post 940 5d	940	9	113	910	700	0.486	1.274
Woulds et al. 2009	PM post 940 in situ	940	9	48	910	700	0.155	0.986
Woulds et al. 2009	PM pre 1000 2d	1000	8	57	nd	nd	0.990	2.411
Woulds et al. 2009	PM pre 1200 5d	1200	7	114	60	nd	0.274	0.289
Woulds et al. 2009	PM pre 1850 2d	1850	3	48	110	300	0.065	0.235
Woulds et al. 2009	PM pre 1850 5d	1850	3	117	110	300	0.434	0.506
Woulds et al. 2009	PM post 1850 5d	1850	3	86	110	300	2.459	2.623
Sweetman et al. 2010	Pearl Harbour Control	Intertidal	24	48	337	5500	3.835	4.343
Sweetman et al. 2010	Pearl Harbour Removal	Intertidal	24	48	3391	4500	5.349	7.401
Sweetman et al. 2010	Pearl Harbour Mangrove	Intertidal	24	48	713	18154	5.456	6.048
Sweetman et al. 2010	Kaneohe Bay Control	Intertidal	24	48	882	3500	6.125	6.849
Sweetman et al. 2010	Kaneohe Bay Removal	Intertidal	24	48	1435	9000	5.295	7.475
Evrard et al. 2010	Wadden Sea	Photic Subtidal	15	96	nd	nd	0.031	0.034
Evrard et al. 2012	Gulf of Gdansk (sandy)	1.5	20	72	558	407	0.047	0.061
This study	Loch Etive	70	11	156	4337	5515	0.638	1.994
This study	Ythan sand flat	Intertidal	11	162	455	7657	0.633	1.421

Table 1. Sources and site details of previous isotope tracing experiment data. PAP = Porcupine Abyssal Plain. For Woulds et al. (2009) experiments PM = Pakistan Margin, ‘pre’ and ‘post’ indicate pre- or post-monsoon seasons, and 2d or 5d indicate approximate experiment durations in days. In some other cases experiment durations are indicated in hours (h).

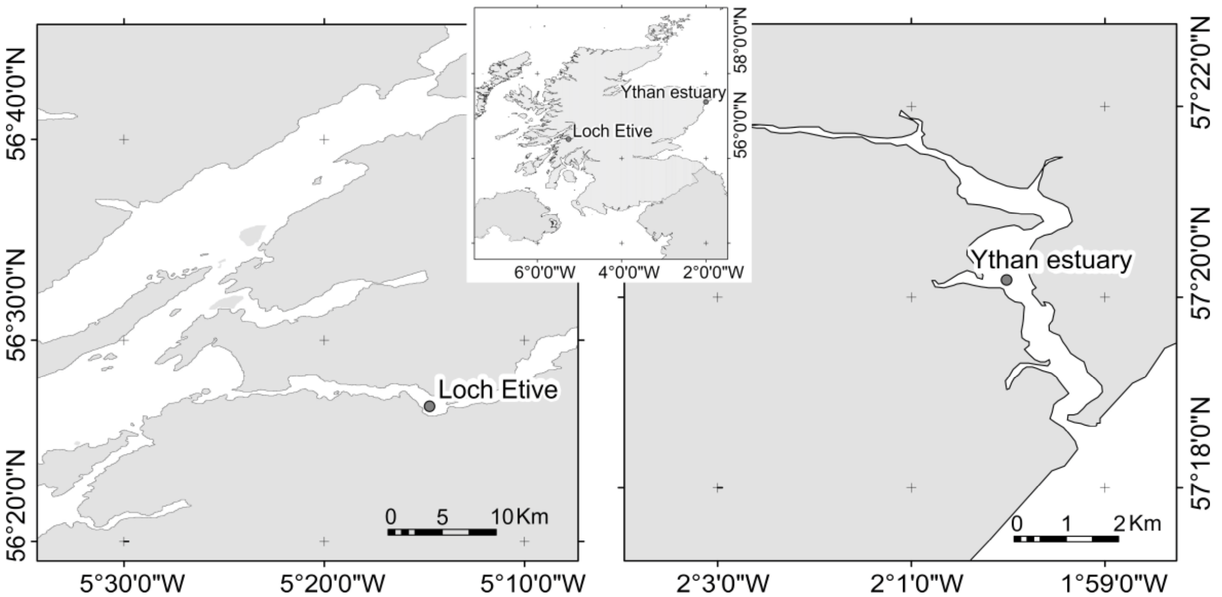


Figure 1. Map showing site locations.

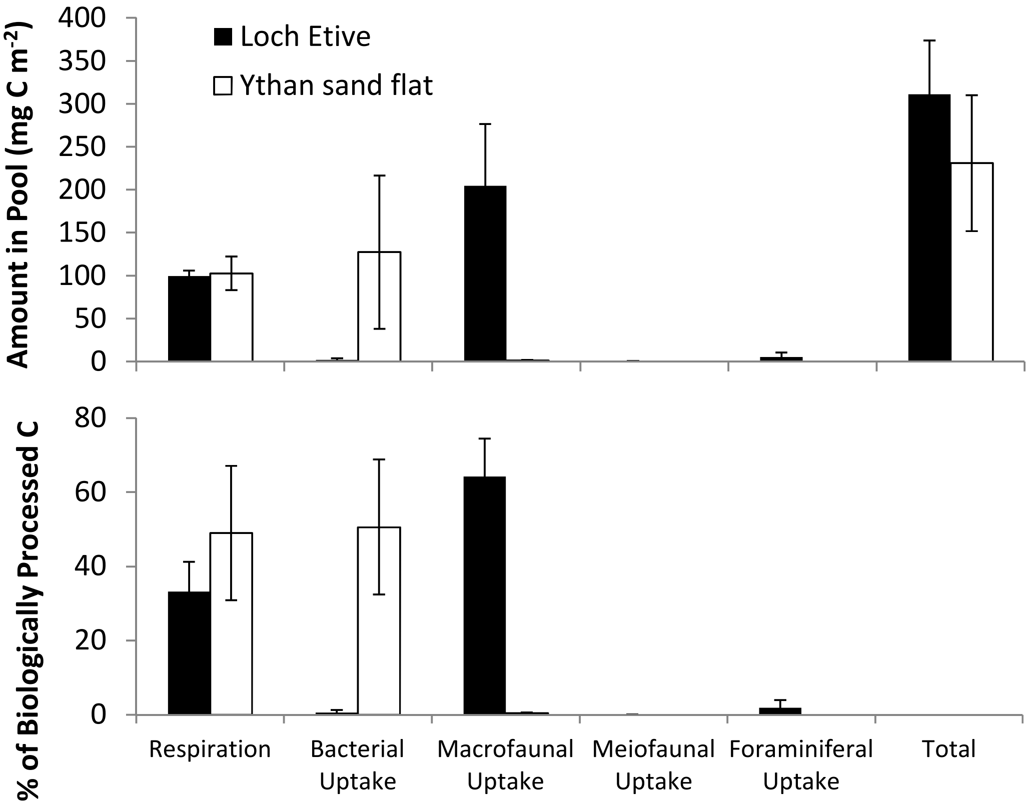


Figure 2.The distribution of initially added C between different biological pools at the end of the experiments in absolute terms (upper panel), and as percentages of total biological C processing (lower panel). Note there are no data for meiofaunal or foraminiferal uptake on the Ythan sand flat.

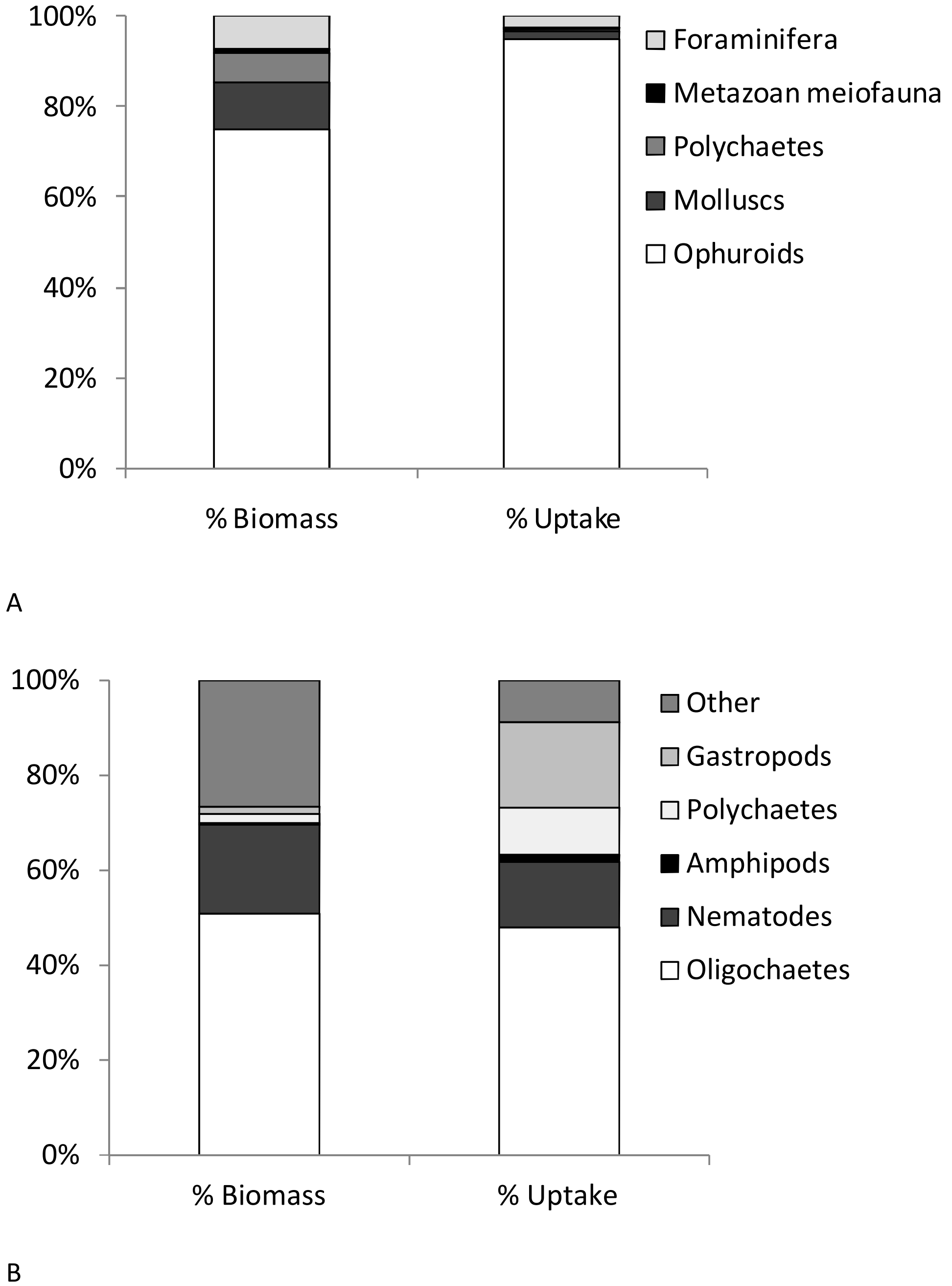
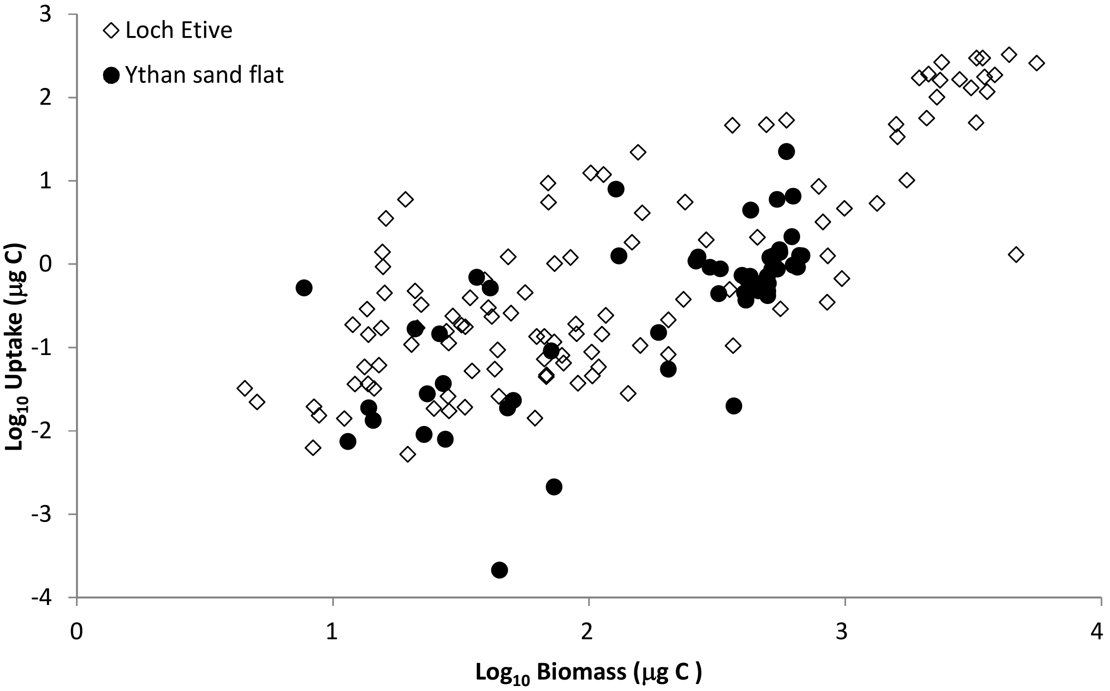
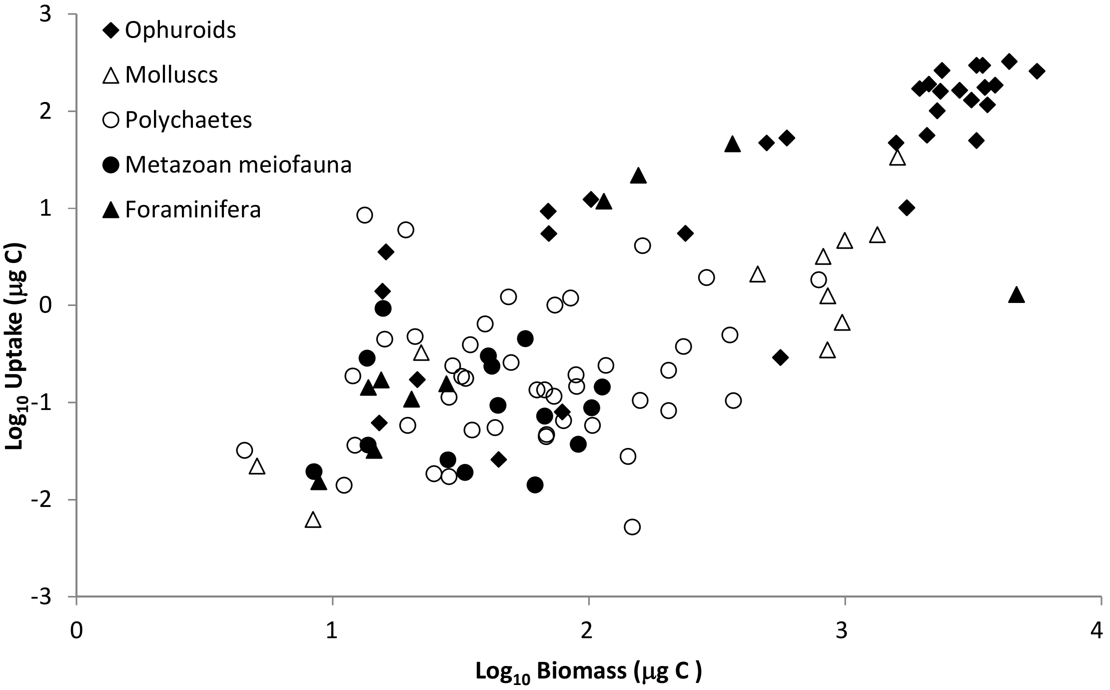


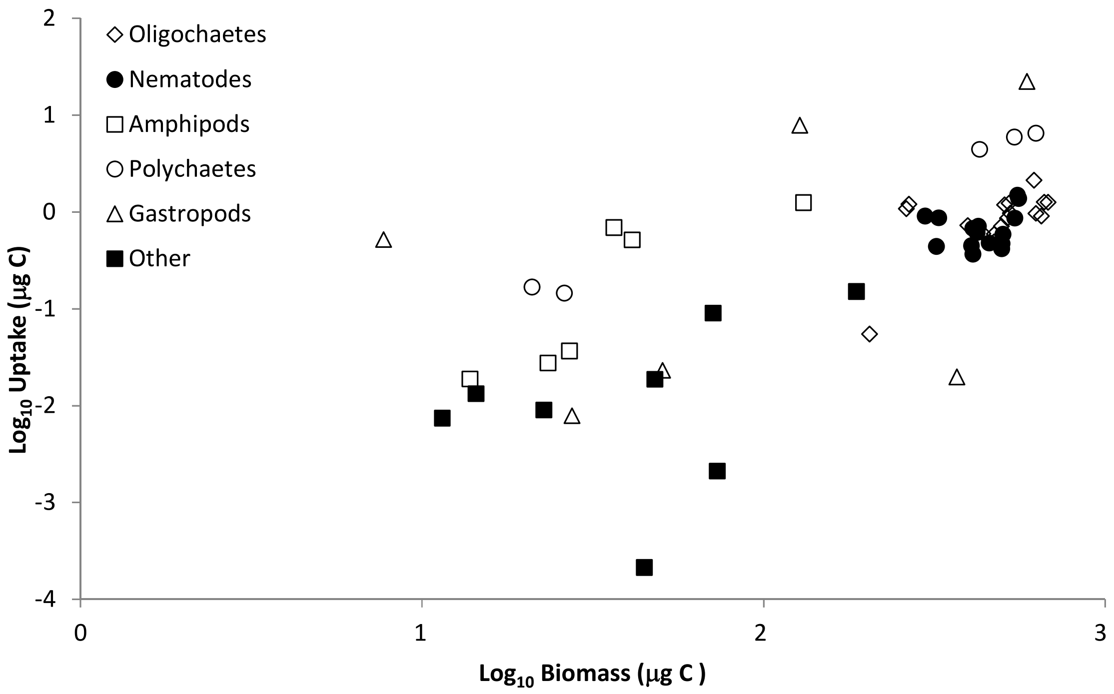
Figure 3.Taxa responsible for biomass and C uptake in a) Loch Etive, and b) the Ythan sand flat.


Loch Etive
Ythan sand flat
Log_{10} Uptake (µg C)
3
2
1
0
-1
-2
-3
-4
0
1
2
3
4
Log_{10} Biomass (µg C)

A


Ophuroids
Molluscs
Polychaetes
Metazoan meiofauna
Foraminifera
Log_{10} Uptake (µg C)
3
2
1
0
-1
-2
-3
0
1
2
3
4
Log_{10} Biomass (µg C)

B



776

777 C

778 Figure 4. Log$_{10}$ uptake against Log$_{10}$ C biomass for: a) all specimens analysed in Loch Etive and on the Ythan

779 sand flat, b) Loch Etive with taxonomic detail, and c) the Ythan sand flat with taxonomic detail.

780

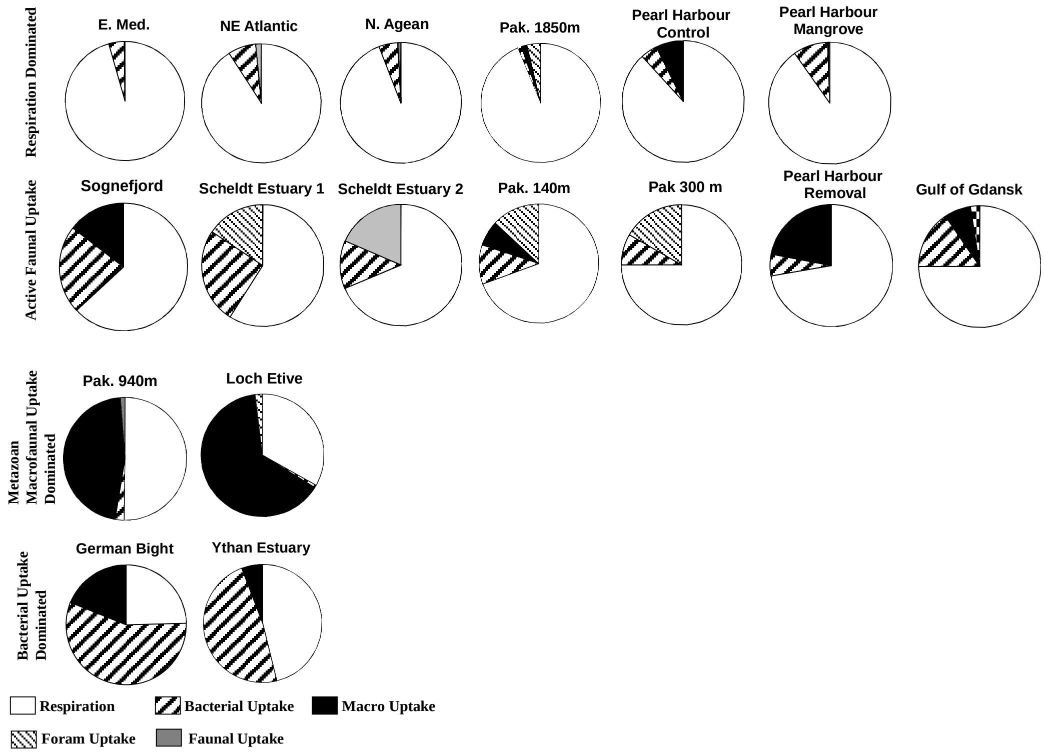
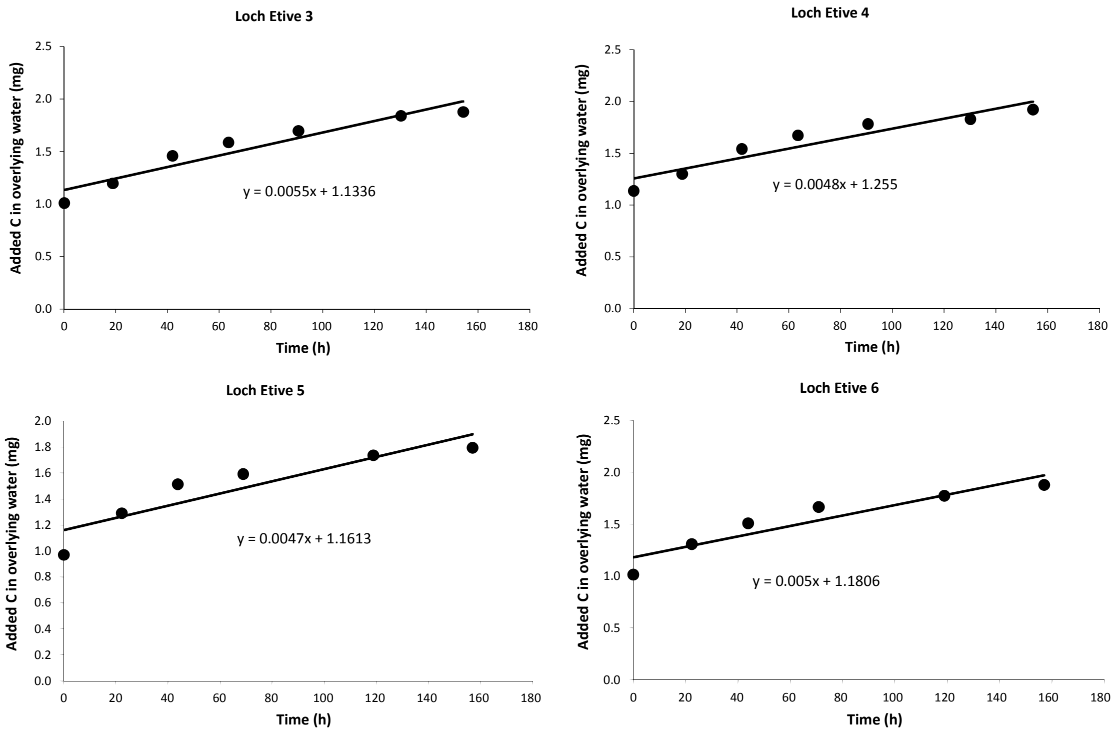
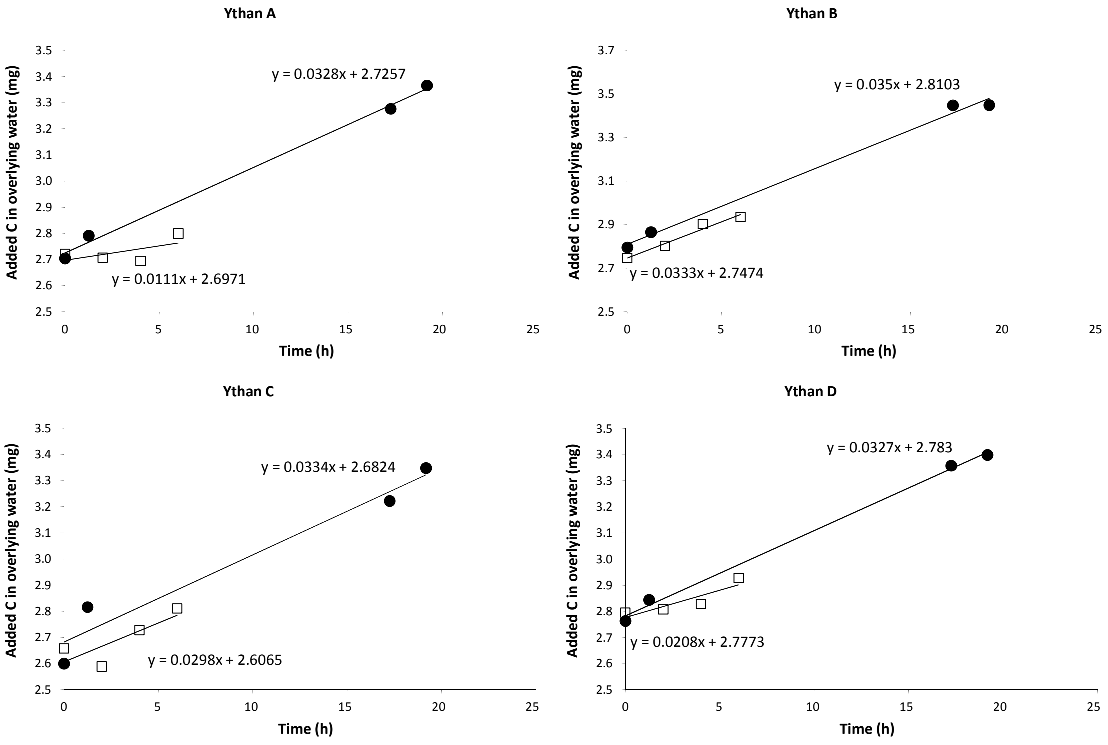


Figure 5. Biological C processing pattern categories adapted from Woulds et al. (2009), with the experiments from this study and the new category ‘bacterial uptake dominated’ added. Data sources are as follows; Eastern Mediterranean (E. Med.), NE Atlantic, North Aegean (N. Aegean) and Scheldt Estuary 2: Moodley et al. (2005); ; Pakistan Margin (Pak. 140 m, 300 m, 940 m, 1850 m): Woulds et al. (2009); Sognefjord: Witte et al. (2003 a); Scheldt Estuary 1: Moodley et al. (2000); Pearl Harbour: Sweetman et al. (2010); Gulf of Gdansk: Evrard et al. (2012); German Bight: Buhring et al., (2006).

Supplementary Information



A



B

Figure S1. Quantity of added C over time in experimental chamber water columns, with regression lines and equations used for calculating respiration rates, for a) Loch Etive and b) the Ythan sand flat. Note that the chamber surface area was different for the two study sites (see methods).