BG-2016-14 Response To Reviews

Reviewer 1 Major Comments:

We would like to thank the reviewer for their thorough review, and for their overall positive opinion.

Reviewer: Carbon processing categorization The discussion 4.5. based on many uncertainty and speculations, and need to remove from the manuscript. The authors proposed the categorization of C processing using data in this study and references. However, there is no mention on how and why authors selected specific time scale of the incubation duration. In Woulds et al. (2009), there were circle graphs of carbon fate for both _2 days and _5 days. However, in this paper, only one of them (I guess so) are shown. It is expected that the respired C increases with time (as mentioned in the line 563) while macrofaunal and bacterial 13C-label will be respired and decreased. Further, the faunal uptake and bacterial uptake also showed different patterns with time between taxa: for instance, macrofauna responded quicker than foraminifera (Witte et al. 2003, Nature), bacterial assimilation decreased after 1 or 2 days (Middelburg et al. 2000) whereas foraminiferal uptake showed increasing pattern during similar time scale (Moodley et al. 2000). It is thus obvious that the time scale selection is the most important factor to properly categorize the carbon processing. In this manuscript, data from different time scales (hours to 23 days) were combined without description what time scale of incubation was selected in the categorization from several different incubation periods (e.g. Moodley et al. 2002, Witte et al. 2003a, b, Bhuring et al. 2006). Also, there is no discussion on the effect of time scale (except line 563, which mentioned as to explain the irregular pattern of the categorization). I therefore recommend to remove discussion 4.5 from the manuscript and just discuss Loch Etive was macrofauna dominated C processing and Ythan sand flat was bacteria dominated. The manuscript itself can withstand as research paper without the chapter 4.5.

Answer: The reviewer is correct that in the medium and longer term the experiment duration will have an effect on biological C processing pattern, with respiration becoming more important with time (and in the end we might expect C which was incorporated into biomass to be respired as well, such is the nature of a pulse chase experiment). Our manuscript concerns the short-term biological processing of organic carbon, and therefore these longer term fates are not directly relevant to the categorisation. The wording of section 4.5 has been adapted to clarify this.

The reviewer is also correct that smaller variations in the relative importance of different pathways tend to be observed within the short term, however this does not lead to problems for our categorisation. The experiments presented in figure 5 range from 6 h to 23 days, with the majority falling in the 1-7 days range (i.e. the single 23 day experiment was the only one longer than 7 days). Therefore the only one which cannot truly be said to represent ‘short-term’ biological C processing is the 23 day experiment (Porcupine Abyssal Plain, Witte et al., 2003b). This has been excluded.

In a few cases experiments were conducted over multiple durations at the same sites. In the case of 5 sites across the Pakistan margin the difference in duration between 2 and 5 days never caused a shift in the category of short term biological C processing (Woulds et al., 2009). Similarly in the Sognefjord the C processing pattern remained in the same category in experiments lasting both 1.5 and 3 days (Witte et al., 2003a). In the German Bight, experiments lasting 0.5 to 1.5 days always showed a bacterial uptake dominated pattern, and bacterial uptake remained equally important as respiration after 5.5 days (Bhuring et al., 2006). Therefore, while we accept that experiment duration does play a role in determining the finer detail of the pattern of biological C processing observed in an experiment, it does not determine the category of C processing pattern within the range of experiment durations included here (and is certainly not the ‘most important factor’ as the reviewer suggests).

The Porcupine Abyssal Plain is the only example of a site where different short-term experiment durations led to different biological C processing categories (Witte et al., 2003b). At this site, where we would expect to see 'respiration dominated' biological C processing, the shortest experiment (60 h) actually showed 'active faunal uptake', with macrofaual uptake accounting for 26% of biological C processing. All longer experiments (8 d and 23 d) showed 'respiration dominated' biological C processing. This site has been removed from the standard categorisation and is instead discussed alongside the other exceptions.

Therefore we feel that the variation in experiment duration between the results does not cause sufficient changes to C processing patterns to invalidate the categorisation, and that therefore section 4.5 and figure 5 should be retained. We have added discussion of effect of experiment duration on categorisation as part of the discussion of the Porcupine Abyssal Plain experiments (detailed above), and have added a column to table 1 showing experiment duration, so that all details are clearly available.

Reviewer: Differences in light condition. The authors performed the 13C-labeled phytodetritus experiments with and without light (with light: Loch Etive, without light: Ythan sand flat). The authors validate the different conditions because natural environments are dark and light conditions, respectively. However, I believe that the incubation with light makes complicated pathways. Without light, the 13C-phytodetritus is ncorporated into heterotrophic microbes or eukaryotes, and either assimilated into their biomass or respired as 13CO2. With light, however, the respired 13CO2 can be assimilated into photoautotrophic microbial biomass via photosynthesis. This leads underestimation of respired carbon and overestimation of bacterial assimilation. Without light, chemolithoautotrophic microbes can also cause same process, but the contribution must be smaller than photosynthesis. How much proportion of CO2 was labeled with 13C? If the 13C concentrations in CO2 is almost negligible (few %), then the bacterial assimilation via photosynthesis may also be negligible. This can be calculated from the DIC-d13C data of the study. Or, if there are literature which investigated bacterial community at this area, then the authors may validate that photoautotrophic bacteria was minor.

Answer: Once again the reviewer is correct that the different light conditions led to a difference in the C flow pathways that were possible in the two experiments. However the different light levels were necessary in order to correctly re-create natural conditions. The labelling level of DIC in the Ythan experiment remained very low throughout (never 1.33> atom % ^{13}C), therefore the underestimation of respiration due to use of respired DIC by photoautotrophs is negligible, as the reviewer suggests. In addition, this will not have interfered with measurements of bacterial C uptake as the sub-set of PLFAs used are specific to bacteria (as opposed to benthic algae), and are regularly used for this purpose, including in intertidal incubations performed in the presence of light. A note has been added to section 4.1.

Reviewer: Uptake calculation The authors calculated the Carbon uptake by sample with the equation (3), line 253. However, the At% phytodetritus must be subtracted by At% background. I understand that the extent of 13C-label in this study (25% and 34%) are high and the re-calculated values using subtracted value may change only 2 or 3 % (considering 25 become 23.9 and 34 become 32.9). However, the it is necessary to indicate appropriate values as much as possible.

Answer: We do not agree that it is necessary to subtract the natural occurrence of ^{13}C from the labelling level of the phytodetritus when calculating C uptake into the different C pools. It is true that phytodetritus grown without any artificial ^{13}C enrichment would indeed have contained a natural amount of ^{13}C, but this does not change the fact that the phytodetritus actually added to our experiments had the labelling levels as measured and reported. Both the 'naturally' present and artificially enriched fractions of the ^{13}C in the phytodetritus serve as tracer, and the only thing that has to be subtracted out is naturally occurring ^{13}C in the sediment system to which the tracer was

added. We do not feel that it is necessary to add this explanation to the manuscript, unless the editor feels that it should go in.

Specific comments:

Reviewer: Line 32 Did the accessibility by bacteria to added C similar between two sites? Please show the vertical profiles of 13C if possible.

Answer: Accessibility by bacteria will have been similar in the sense that in both experiments phytodetritus was added to the sediment surface in the same way. Thereafter it may have been transported through the sediment differently due to differences between permeable and cohesive sediments. Unfortunately downcore ^{13}C profiles are not available.

Reviewer: Line 145. Figure 1 does not show any sills or geographical names. Please include these information to the figure or delete the citation (Fig.1) from the end of this sentence.

Answer: Figure reference removed.

Reviewer: Line 163. While the Loch Evive site has 70 m water depth, the Ythan estuary site exposed during low tide. This is a great difference between two sites, in addition to sediment grain size and OC concentrations. The authors need to discuss the potential impacts of these differences of OC cycling and validate why the authors did not perform the experiment at coarse grained, OC poor site having similar water depths (or vice versa).

Answer: This was driven by the coring technique and technology available for coarse grained sediment (required taking cores by hand). A note has been added to section 4.1.

Reviewer: Line 171. What exactly was the phytodetritus labeled with 13C? Was that degraded in some way? Or some sort of algal species? Was this same to the one which was added to Ythan sand flat? Please clarify these details.

Answer: Details have been added in the methods section.

Reviewer: Line 173. How much volume was the overlying water in the core?

Answer: Detail added.

Reviewer: Line 185 150 um sieve is not typical size separation for meiofauna. Why did the authors choose this size?

Answer: It was only practical to extract the larger meiofauna, as time did not permit sorting fauna all the way down to 63μm. Such small fauna would also have been very challenging to analyse. A note has been added.

Reviewer: Line 189 Why the authors used milliQ water instead filtered seawater of artificial seawater? MilliQ water may had elution of organic matters from fauna due to osmoticshock (although the results showed insignificant effect).

Answer: Filtered seawater was used, not milliQ. This has been corrected.

Reviewer: Line 196 Bubbling with air in this experiment while the Loch Etive site cores weremaintained with oxystat system. How did this affect to 13C-CO2 amounts?

Answer: There will not have been an effect from air bubbling in the Ythan experiment on measured respiration rates, as air bubbling did not occur during respiration measurement periods, and ^{13}C DIC data from outside of those periods was not used in respiration calculations. Potential effects of the oxystat system on respiration measurements in the Loch Etive experiment are already addressed in the manuscript as follows "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. "

Reviewer: Line 253 The equation is not presented in correct way (no under bar below "C Uptakesample". What the unit of "C Uptake sample"?

Answer: Equation has been corrected, and units added.

Reviewer: Line 263 It is not clear about the linear regression. Do the authors mean linear regressionof different incubation periods? It is also important to show the changes in d13C-DIC (or 13C-respiration rates) with time, because the changes in 13C-respiration with time should give crucial info regarding faunal or bacterial responses and C processing.

Answer: Respiration was calculated separately for each separate incubation period.

Reviewer: Line 267 It is necessary to show the respiration data of Ythan sand flat, too, as Tableor supplementary figure.

Answer: A supplementary figure has been added displaying the increase in labelled DIC over time for all chambers, and including regression lines and equations. This has been referred to in the text as appropriate.

Reviewer: Line 274 Please describe the centrifuge condition (x g, how long, and what temperatureetc). It will help to guess the potential effects of centrifuge on bacterial PLFA loss.

Answer: Detail has been added.

Reviewer: Line 279. Did the authors examine the d13C of bulk sediments? If so, please includeas Table etc.

Answer: These data are not available.

Reviewer: Line 282 Again, it is important to show temporal changes in d13C (or respired 13C).

Answer: A supplementary figure has been added.

Reviewer: Line 326. 0.00023 mgC per mgC corresponds _5 or 10 per mil of Dd13C, which isrelatively low labeling. What were the variation in d13C of natural PLFA and labeled

PLFA? Can you add as Table?

Answer: This is a large amount of data to tabulate (del13C values for several depths in the sediment, plus background values, for 4 PLFAs, for each of 4 incubation cores per site), and I am not convinced that it would provide much clarity for the reader. The background del13C values for the bacteria-specific PLFAs were similar at each site (-20 to -25 ‰). Δδ values were higher than the reviewer suggests in the surface sediment horizon (100's ‰), but this will have been balanced by them being lower (10's ‰ or less) in deeper horizons at Loch Etive. As expected, these Δδ values were at least an order of magnitude greater for the Ythan sand flat.

Reviewer: Lines 347 to 353. Whatever the C dose amounts were similar, the authors should think about the difference in natural phytodetritus supply rates at two sites. The same amount of 13C-phytodetritus input should have completely different effects on between originally eutrophic (in terms of OM) site and oligotrophic site. The authors should

discuss these point of view by referring the primary production rates at two sites.

Answer: 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 discussion). 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. This discussion has been added.

Reviewer: Line 368 Can you cite any paper which dealing different size screens?**Answer:** We are not aware of a paper dealing with the effect caused by this difference in screen sizes, and can only re-iterate that the sizes were standard for the sediment types in question, and were also most favourable in terms of practicality (using a 300μm screen in a sandy sediment would lead to very high retention of sediment, making extraction of fauna particularly difficult).

Reviewer: Lines 376 to 380. Due to the osmotic shock by milliQ water (according to M&M), the fauna may be dead and did not have a time to void the gut.

Answer: This step was not actually conducted in Milli-Q (corrected in response to an earlier comment), so osmotic shock will not have been a problem.

Reviewer: Line 431. Gooday et al. 2008 represent biomass-uptake relationships with different symbols for bacteria, fauna, foraminifera. Can you also make such kind of Figure 4 for better comparison?

Answer: Figure 4 would be unclear if taxonomic information was included where all the points are plotted together, therefore two panels have been added, one for each site, showing data for the different taxa.

Reviewer: Line 438. This may suggest that the macrofauna of Ythan sand flat has low background metabolism than Loch Etive.

Answer: Agreed, this comment has been added.

Reviewer: Line 459. I cannot follow why the authors said "macrofaunal biomass" in this sentence whereas the line 456 mentioned "biomass (faunal plus bacterial)". Please describe

more in detail if the authors actually intended to say "macrofaunal biomass".

Answer: Clarification has been added.

Reviewer: Chapter 4.4. can be combined to 4.3.

Answer: These two sections both consider points related to faunal C uptake. However, the main point made in section 4.4. is distinct from those in section 4.3, and therefore we feel that the additional sub-heading remains helpful.

Reviewer: Line 520. Both methods (Total respiration rate measurements and bacterial C assimilation rates) has considerable uncertainty. Thus the discussion here, dealing bacterial growth efficiency, is somewhat over-interpretation. Also, as mentioned earlier, because the incubation of Ythan sand flat sediment was carried out under light condition, it is possible that some 13C-bacterial lipids were originated from the photoautotrophic microbes, not by heterotrophic bacteria which incorporated 13C-labeled phytoplankton.

Answer: The sub-set of PLFAs used to quantify bacterial uptake are regularly used to indicate bacterial activity as separate from microphytobenthis production, including in incubations in which light was present. We agree however, and acknowledge in the text, that our measurements do not allow an accurate quantification of bacterial growth efficiency. The text has been shortened accordingly.

Reviewer: Line 571 Again, temporal changes in DIC-13C at both site may give better idea about these interpretations.

Answer: A supplementary figure has been added.

Reviewer: Line 673 Hunter et al. 2012b. There is no Hunter et al. 2012a, thus deleted "b".

Answer: Corrected.

Reviewer: Table 1 Please add a new column showing incubation periods.

Answer: Added.

Reviewer: Figure 2. Please add "n.d." for meiofauna and foraminifera of Ythan sand flat.

Answer: Note added to the caption.

Reviewer 2:

Once again we would like to thank the reviewer for their overall positive opinion, and for their attention to detail which will allow us to improve the manuscript.

Major comments:

The main comment from this reviewer is that the discussion is overly long. We agree, especially concerning the section about bacterial growth efficiency. The discussion has now been shortened significantly.

Specific comments:

Reveiwer: Line 73: It might be worth pointing out what does biological C processing not cover. Is there non-biological C processing in these systems? It might be worth pointing out the differences.

Answer: The term is used to distinguish between short term uptake and cycling and longer tern C burial. This has been clarified.

Reveiwer: Line 76: A quibble: Stable isotope tracer experiments are an excellent tool, but not ideal. For instance, radiotracer 14C incubations are far more sensitive and do not depend on sorting out mass of naturally occurring background tracer distribution.

Answer: Acknowledged, but working with stable isotopes has practical benefits which can allow increased numbers of experimental treatments/durations/replicates. Wording has been changed.

Reveiwer: Line 117 and following: Independent of the food-web tracer studies, it would be nice to have some information on the relative benthic biomasses for these two sediment types, e.g. muddy and sandy bottoms. I would be surprised if muddy bottoms actually supported more faunal biomass.

Answer: This section does not seem an appropriate place to review biomass data for different estuarine sediments, however such details can be found in Table 1 (biomass data are independent of the associated C tracing experiments)..

Reveiwer: With the exception of the respiration measurements, these are single endpoint experiments. Dynamics between the pools are not necessarily accessible.

Answer: We are not clear which part of the text the reviewer is referring to here.

Reveiwer: Line 124: "Recent findings" is relative; dynamic biogeochemical cycling in low OC permeable sediments has been extensively documented over the last two decades.

Answer: Agreed, wording has been amended.

Reveiwer: Line 171: Please describe more carefully the labeled phytodetritus in more detail. Was it composed of a single species and what? Was it prepared in the same fashion for both sites? What was it composed of? How fresh was it? Was it added as fresh or freeze-dried material.

Answer: Detail has neen added to the methods section.

Reveiwer: Does the difference between the labeling percentages (ca. 25% and 34%) for the two sites reflect different batch preparations, or differing compositions of pytodetritus?

Answer: Different phytodetritus batches and species. Detail has been added (see above)..

Reveiwer: Methods: It's not entirely clear to me that total bulk 13C of the sediment was determined (i.e. total Corg 13C). This must have been done in order to calculate the recoveries of tracers shown in Figure 2.

Answer: The totals shown in figure 2 are total biologically processed C, and therefore do not contain C remaining in the sediment. Data for 13C remaining in the sediment are not available.

Reveiwer: Is there a time zero sample, i.e. samples taken from one core immediately after the addition of the 13C-labeled phytodetritus?

Answer: This is only available for Loch Etive, and not on the Ythan sand flat, therefore data has not been included.

Reveiwer: Line 244 and following: It is not really clear to me why the authors work with the del (_) notation for these type of experiments. There is also no obvious connection from how they go from Equation 2 to Equation 3, the latter of which is the more relevant for this manuscript.

Answer: Data are reported using the del notation in the results section because many workers in the field use this notation, and $\Delta\delta$ is a clear way of displaying isotopic enrichments. However, our calculations for uptake used At% instead. There is not supposed to be a connection between equation 2 and equation 3.

Reveiwer: Calculations with exceedingly large enrichments, for instance as seen in the macrofaunal biomass (lines 290 and following), become inaccurate.

Answer: The reviewer's meaning is not quite clear, however if this is given as a reason for not using the del notation, then note that uptake calculations were made using At% instead.

Reveiwer: Line 280: . . ..or as dissolved organic carbon.

Answer: This has been added.

Reveiwer: Section 3.1: It might be helpful for the reader to plot the remineralization data over the time course of the experiment.

Answer: These plots have been added as supplementary information.

Reveiwer: Section 4.2: This whole discussion is rather contradictory. On one hand the authors claim that the temperature and organic C loading are similar (line 384), but then suggest that temperature plays a larger role than biomass or organic C (lare 395) does not make sense. Furthermore, there are no proper controls for assessing any of these factors. I would drop this whole discussion (see further discussion about curtailing discussion) and the conclusions regarding temperature (line 571). This was not the point of the study, it was not properly assessed, nor is it supported by the data.

Answer: The point made in this section is that despite many differences between the settings of the two experiments, the measured respiration rates were very similar, and this is attributed to the fact that the experiments were conducted at the same temperature. Supporting material from the literature is provided. This section has been shortened and clarified, and we do not feel that this point goes beyond the reach of the data.

Reveiwer: Line 494: “This hypothesis. . ..” Which hypothesis? From this paper or Woulds et al. 2009? Actually I find the whole discussion of hypotheses, both here and earlier in the manuscript (line 134 and following) a bit specious. I think that it is enough for the authors to state that they are comparing two types of sites that are thus far lacking from the overall range of sites on which such experiments have been performed.

Answer: The sentence in question has been changed to clarify which hypothesis is being referred to. It is not clear why the reviewer finds the earlier statement of our hypotheses to be specious, as the reflect our expectations before the experiments were conducted. We have retained these hypotheses, as we feel they are the best way of providing the appropriate focus to the manuscript.

Reveiwer: Figure 2: I assume that “Total” stand for the sum of respiration, bacterial uptake, etc. in that case, there is also no Total for the % of Biologically Processed C. It might also be interesting to add a third panel to include total initial pool size of each of the separate pools (i.e. how much C is in each pool originally).

Answer: This is an interesting suggestion, but we do not feel that it would work well in graph form. The information on macrofaunal and bacterial biomass is already given in the results text. It is not so helpful to quantify the amount of C in the DIC pool, as the absolute amount depends on the height of the water column in the experimental chamber. This varied for each chamber. Of course it could be given for a standard height of water column, but the choice of height would be entirely arbitrary, and so it would not make a meaningful comparison with the macrofaunal and bacterial pools.

Reveiwer: Figures 5 and 6: These figures are quite compelling, although I think that they could be combined. It is not entirely obvious why there are two separate figures.

Answer: The figures have been combined.

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~~ideal~~ 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., 201222b), 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 ~~recent~~ 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 ~~(Fig. 1)~~. 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 21□m with 78 % fines (<63 □m) 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 $\delta^{13}C$- 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 sea~~Milli-Q~~ water for several hours before freezing.

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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 $\delta^{13}C$ 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%.

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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 $\delta^{13}C$.

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 $\delta^{13}C$.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).

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

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).

$$\Delta\delta = \delta^{13}C\ sample - \ \delta^{13}Cbackground \quad (2)$$

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):

$$\frac{C\ Uptake_{sample} = \left(At\ \%_{sample} - At\ \%_{background}\right) X\ C\ Contents_{sample}}{At\ \%_{phytodetritus}} X100$$

$$C\ Uptake_{sample}\ (\mu g) = \frac{(At\ \%_{sample} - At\ \%_{background}) \times\ C\ Contents_{sample}}{At\ \%_{phytodetritus}} \times 100 \quad (3)$$

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 $\delta^{13}C$-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 $\delta^{13}C$ 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 ~~of sediment core incubations under natural conditions~~, nevertheless had slightly different experimental setups. The water depth, ~~temperature,~~ core size, stirring regime, light availability and C dose added all differed between the two study sites. The differences in stirring regime~~, temperature~~, and light availability were enforced to properly replicate natural conditions in each experiment, thus any contrasts ~~between experiments~~ caused by these conditions ~~are simply reflections of actual~~reflect differences in functioning of the two ~~benthic~~ 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 ~~relatively~~ minor differences in C dose (Woulds et al., 2009). ~~In cases w~~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 ~~and ecologically meaningful~~.

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 ~~with respect to their biomass~~ in the present study but, despite wide variations in the importance of meiofaunal uptake ~~for the immediate fate of deposited organic C~~ (Nomaki et al., 2005; Sweetman et al., 2009; Evrard et al., 2010), ~~meiofaunal C uptake~~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 ~~more~~ practical in coarser grained sediments~~, such as those of the Ythan sand flat~~. The larger mesh used on the Ythan sand flat is likely to have reduced the macrofaunal biomass ~~recovered, and thus the macrofaunal~~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 ~~prior to analysis~~, and were therefore analysed with their gut contents in place. The exception to this was two ~~(out of four)~~ of the Loch Etive ~~replicate~~ cores, ~~the fauna from which were placed in clean water and~~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 ~~(which would have been simulated by being placed in water without sediment present)~~ by retaining their gut contents for days or weeks. Therefore it is possible that ~~many~~ 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~~so its exclusion from the analysis of fauna from two replicate cores did not produce a difference that was measurable above the comparatively large variation in faunal C uptake between cores caused by faunal patchiness~~. Thus ~~it should be noted that~~ the values reported here as faunal C uptake include ~~both~~ C ~~residing~~ in both gut contents ~~and that which was assimilated into~~ faunal tissue.

4.2 Respiration rates

The respiration rates observed in Loch Etive and on the Ythan sand flat were very similar (Fig. 2). ~~In one sense t~~This is unsurprising, as the two experiments were conducted at the same temperature, and similar C loadings

were applied. Temperature is known to ~~be a major~~ control ~~on~~ 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). ~~Increased temperatures accelerate the diffusion of reactants and metabolites through the sediment, and also increase microbial process rates.~~ 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. ~~Thus, they showed that temperature can be the dominant control on sediment community respiration rate.~~ Our finding of similar rates of respiration ~~in response to added phytodetritus in Loch Etive and on the Ythan sand flat~~, despite marked differences in influential factors ~~which can influence respiration rates~~ 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. ~~This is in line with findings of a much wider study of ecosystem respiration rates, in which their dependence on temperature was found to be remarkably similar across both terrestrial and aquatic habitats, despite marked contrasts in taxa, biomass, and abiotic factors (Yvon-Durochet et al., 2015).~~

4.3 Faunal uptake

In ~~the case of~~ 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~~b~~), the distribution of C uptake amongst ~~macrofauna, metazoan meiofauna and foraminifera~~faunal classes was largely determined by the relative biomass of each group. The dominance of faunal C uptake by macrofauna ~~(as opposed to meiofauna and forminifera)~~ 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~~r C in some situations~~ (e.g. Moodley et al., 2000). Where macrofauna are absent, or where conditions ~~do not favour their functioning~~are unfavourable, smaller taxa can ~~come to~~ 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 ~~such as low oxygen~~. This was the case at 2170 m water depth in the NE Atlantic, in Sagami Bay and at a subtidal Wadden Sea site, ~~where~~ foraminifera and meiofauna have been observed to consume more C than macrofauna, sometimes despite having lower biomass ~~dominated the initial uptake of added ^{13}C~~ (Moodley et al., 2002; Nomaki et al. 2005; Evrard et al., 2010)~~., and also in Sagami Bay, where Nomaki et al. (2005) observed foraminifera to take up more C than metazoan fauna. At a sandy subtidal site in the Wadden Sea, meiofauna was found to consume more C than macrofauna, despite the former having a lower overall biomass (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 ~~total~~ macrofaunal C uptake than they accounted for macrofaunal biomass (Fig. 3),and thus were disproportionately responsible for macrofaunal C uptake ~~the large amount of added C that was routed into macrofaunal biomass and gut contents~~. On the Ythan sand flat, the contribution to C uptake by the dominant oligochaetes was in line with and ~~therefore presumably controlled by their contribution to the~~their biomass (both ~50%, Fig. 3). However, ~~the~~ other faunal groups ~~present~~ contributed differently to biomass and C uptake. Nematodes were responsible for less C uptake than ~~might be~~ expected ~~from their biomass~~, while the ~~rarer~~ polychaetes, amphipods and molluscs fed comparatively efficiently on the added C~~OM~~. 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 ~~total~~ 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 ~~necessarily~~ fully explain the lower faunal C uptake observed there, as biomass specific C uptake was also considerably lower than in Loch Etive. ~~Therefore, the inter-site difference in faunal C uptake requires an additional explanatory factor.~~ We suggest that the low OC standing stock in the permeable sediment of the Ythan sand flat~~,~~ supports a lower biomass and ~~also~~ 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~~contrary to those arising from others~~, and the reasons for this variation ~~within the literature~~ 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~~b~~).

4.4 Total biological C processing rates

~~Of our two study sites,~~ Loch Etive showed the largest~~a greater~~ amount of total biologically processed C (Fig. 2). As both sites showed very similar respiration rates ~~of added C~~, the difference in total biological C processing was driven by greater faunal uptake in Loch Etive (Fig. 2), and ~~. T~~this~~e greater faunal uptake in Loch Etive~~ was a result of greater faunal biomass~~, as shown by the relationship between biomass and C uptake for the specimens analysed in this study (Fig. 4).~~.

The~~Such a~~ relationship between biomass and total biological C processing is also shown by data gathered from previously published isotope tracing experiment~~s results, where biomass data are also available~~ (Table 1)~~.~~ ~~,~~

which show~~Data from the experiments shown in Table 1 shows~~ 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 ~~macrofaunal~~ 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 ~~B~~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, ~~similar proportions of biologically processed C having been subjected to respiration,~~ the dominant fate of biologically processed~~such~~ 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 ~~actually~~ observed in Loch Etive was most similar to the category labelled 'macrofaunal uptake dominated' (Fig. 5), in which~~. In this category,~~ 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 ~~comparatively~~ unusual pattern, previously only observed in the lower margin~~transition zone~~ 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 ~~of such magnitude~~ was due to the presence of particularly high OC concentrations in the sediment, coupled with sufficient oxygen for larger organisms ~~(as opposed to at lower oxygen concentrations within the oxygen minimum zone)~~. This explanation also applies to ~~the site studied here in~~ Loch Etive, where the sediment OC concentration was nearly 5 %. In contrast to the Arabian Sea site however, ~~our~~ Loch Etive ~~site~~ 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 ~~and the resultant faunal community~~, rather than by low oxygen conditions. Experiments conducted in Pearl Harbour sites impacted by invasive mangroves also show OC availability controlling ~~A further indication of the control by OC availability on~~ the relative importance of faunal C uptake ~~is shown in isotope tracing experiments conducted at sites in Pearl Harbour impacted by invasive mangroves~~ (Sweetman et al., 2010). A control site was OC poor (0.5% wt % OC) and ~~correspondingly~~ showed respiration dominated biological C processing (Fig. 56), while~~. In contrast,~~ a nearby site from which invasive mangroves had been removed showed active (macro)faunal uptake (Fig. 56), in line with higher~~increased~~ sediment OC content (3.1%

wt % OC) and an elevated macrofaunal biomass. ~~A third site at which the invasive mangroves were still present however showed respiration dominated C processing despite very high OC concentration (8.2% wt % OC). However, in that case the unusual properties of mangrove detritus (being tannin rich, with fibrous root mats binding the sediment) made the sediment inhospitable for many macrofauna taxa, therefore bacterial C uptake and respiration was favoured over macrofaunal uptake (Sweetman et al., 2010).~~

We hypothesised that the Ythan sand flat would show a short term biological C processing pattern that did not fit with the categories suggested~~those laid out~~ by Woulds et al. (2009). Our~~This~~ 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 ~~use them to~~ propose a new biological C processing category labelled 'bacterial uptake dominated' (Fig. 5). In the new category, bacterial uptake~~, rather than respiration,~~ 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 ~~over faunal uptake and total community respiration~~. 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)~~, and~~ thus ~~both the~~ substrate and electron acceptors for bacterial respiration are supplied. ~~This efficient introduction of fresh OC is consistent with the fact that Loch Etive and the Ythan sand flat showed similar bacterial biomass despite considerable difference in OC concentration, thus OC supply rather than standing stock appears to be important in determining bacterial biomass and activity.~~

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~~In a year-round study of permeability on the Ythan sand flat,~~ (Zetsche et al.~~,~~ ~~(~~2011)~~.~~ ~~observed clogging of pore spaces during the summer, which was then removed. Therefore one possible explanation for the lack of accumulation of bacterial biomass in permeable sediments is regular removal of bacterial biomass during sediment reworking~~.

T~~It is worth noting that t~~he domination of short term biological C processing by bacterial uptake~~, to the extent that it is equal to or greater than total community respiration,~~ implies a high value for bacterial growth efficiency (BGE). This ~~parameter~~ is calculated as bacterial secondary production divided by the sum of bacterial secondary production and bacterial respiration~~, and thus represents the proportion of assimilated C that is routed into~~

anabolism rather than catabolism. Bacterial respiration is not quantified here, challenging to quantify, and is not quantified during isotope tracing experiments. Hhowever, it is likely that a large proportion of total community respiration is attributable to bacteria (Schwinghamer et al., 1986; Hubas et al., 2006). FThus, 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 mean value of 0.51±0.18 (this will be a conservative estimate). This value is indeed 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)es in that same review. Bacterial growth efficiency is widely variable, both spatially and temporally, and the factors that control it are not well understood. and the factors which control it are not well understood. In the case of several potential controlling factors, such as temperature and inorganic nutrient limitation, evidence is conflicting. HHowever 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). In particular increased supply of amino acids tends to increase BGE, and, amongst broad types of OC, only that excreted by phytoplankton showed a high (>50%) mean BGE (Del Giorgio and Cole, 1998) Bacterial growth efficiency also tends to increase from oligotrophic to eutrophic environments, and thus it often correlates with primary productivity (Del Giorgio and Cole, 1998). This is consistent with high BGE in ese trends mean it is perhaps relatively unsurprising that permeable sediments, which have aith their potentially high input of fresh OC through from filtering during advective porewater flow have high BGE (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). In addition, it may be that BGE is maximised if there is a shift in the relative proportions of bacterial cells that are highly active, versus those which are dormant, inactive or dead (Del Giorgio and Cole, 1998). Furthermore, the proportion of highly active cells has been found to increase with productivity. Thus, the high BGE observed on the Ythan sand flat (and in the German Bight by Buhring et al., 2006) may be due to the fact that bacterial communities in permeable sediments tend to be particularly active compared to those in cohesive sediments (Huettel et al., 2014)..

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 that might be expected based on permeable sediment from the Ythan sand flat and the German Bight. Instead it shows respiration dominated biological C processing, with bacterial uptake, although greater than faunal uptake, responsible for only 16% (Fig. 56). Further, an OC rich site with invasive mangroves in Hawaii shows respiration dominated biological C processing, instead of the expected 'active faunal uptake'

pattern (Fig. 56, Sweetman et al., 2010), due to mangrove roots and detritus making the sediment ~~however in this case the impact of mangrove roots on the sediment make it~~ 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 ~~in question~~ contained a muddy fraction, although also featuring~~ed~~ 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, ~~more~~ in line with expectations ~~for the site~~. 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 Proce Rate (mg C
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

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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).

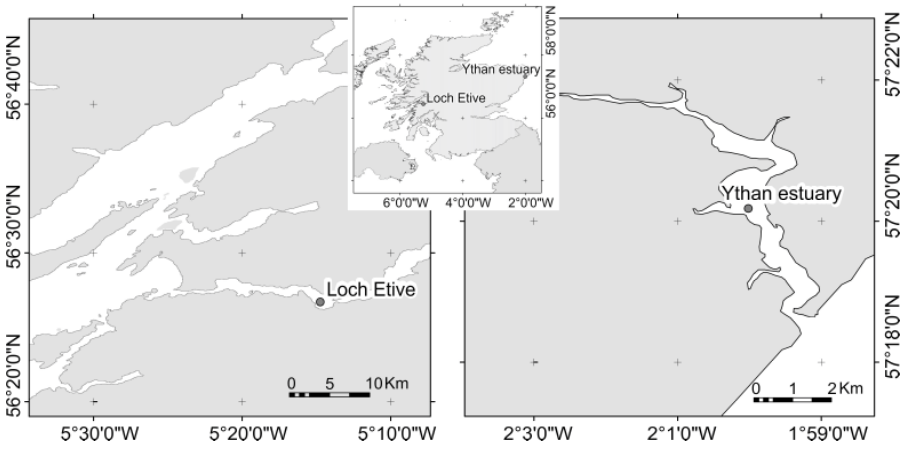
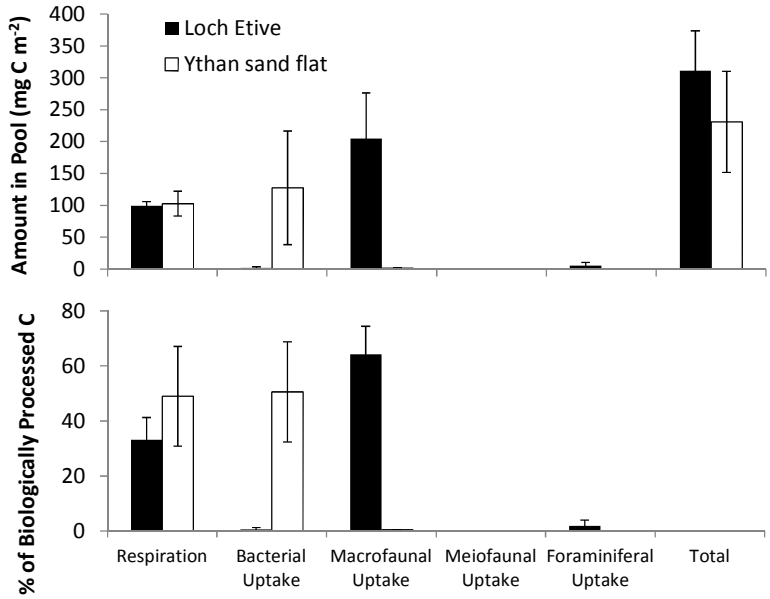


Figure 1. Map showing site locations.



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1164 Figure 2.The distribution of initially added C between different biological pools at the end of the experiments in
1165 absolute terms (upper panel), and as percentages of total biological C processing (lower panel). Note there are
1166 no data for meiofaunal or foraminiferal uptake on the Ythan sand flat.

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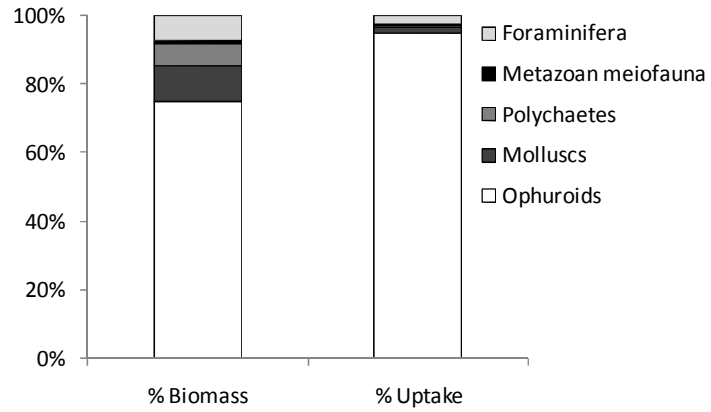

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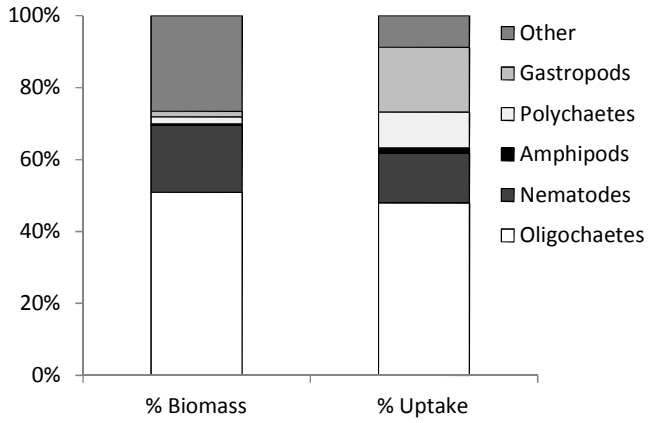
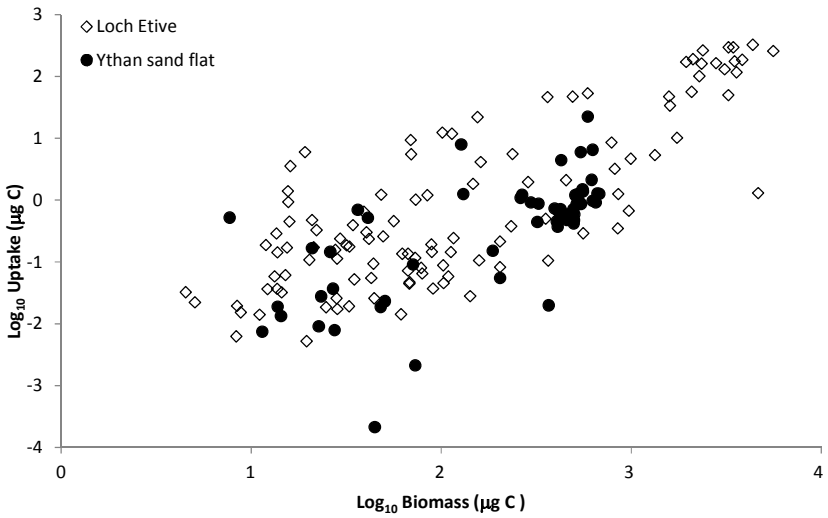
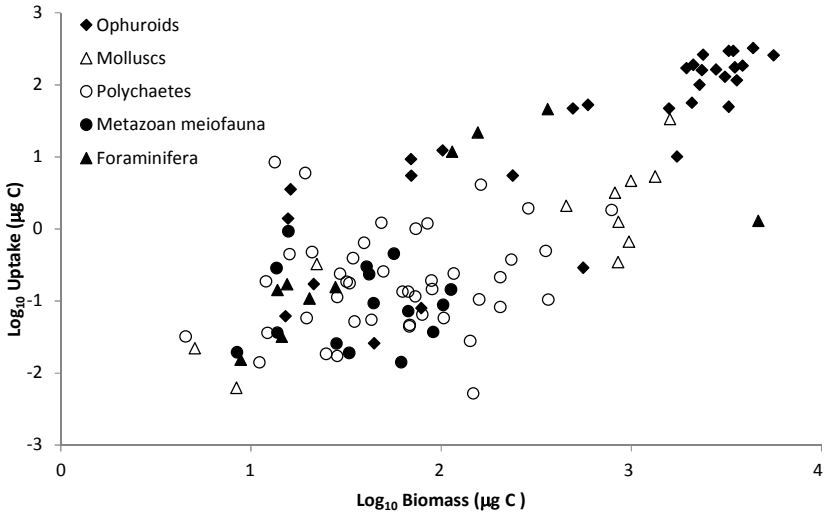


B

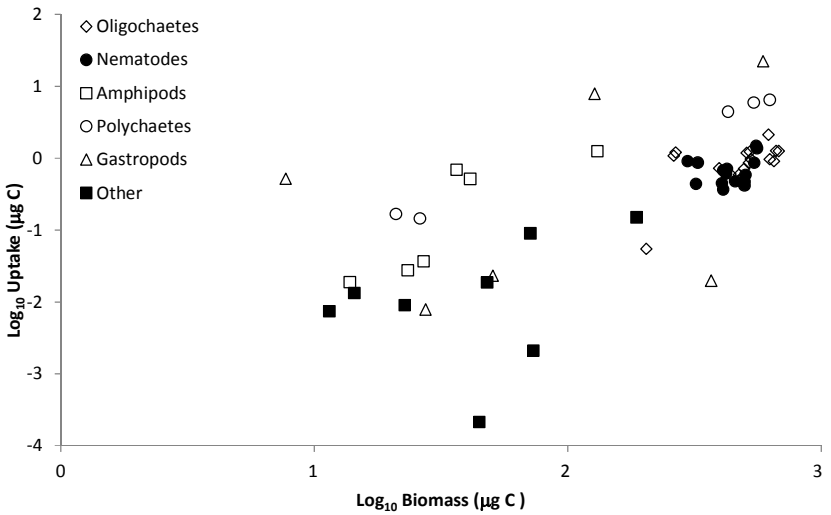
Figure 3.Taxa responsible for biomass and C uptake in a) Loch Etive, and b) the Ythan sand flat.


Loch Etive
Ythan sand flat
Log10 Uptake (µg C)
Log10 Biomass (µg C)

A


Ophuroids
Molluscs
Polychaetes
Metazoan meiofauna
Foraminifera
Log10 Uptake (µg C)
Log10 Biomass (µg C)

B



C

Figure 4. Log_{10} uptake against Log_{10} C biomass for: a) all specimens analysed in Loch Etive and on the Ythan sand flat, b) Loch Etive with taxonomic detail, and c) the Ythan sand flat with taxonomic detail.

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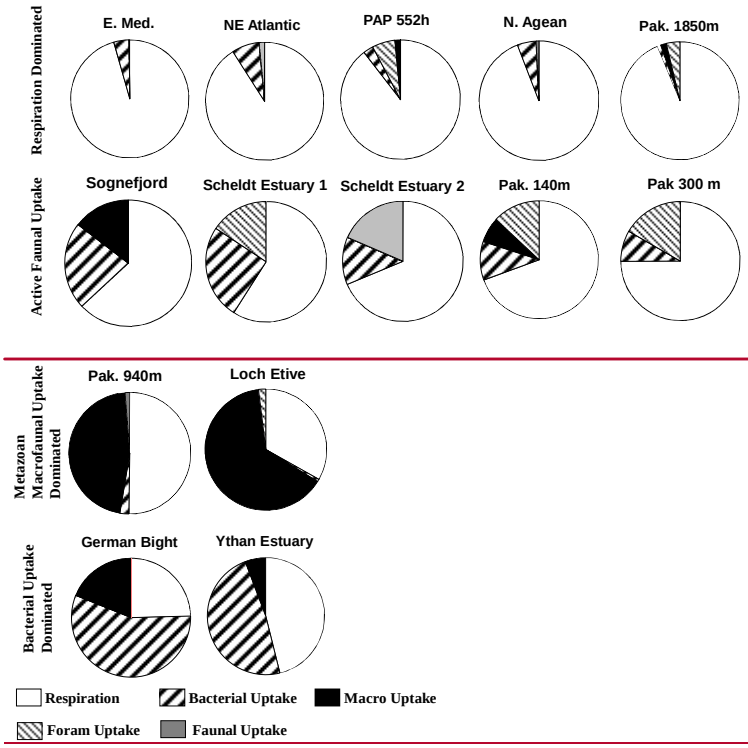
Respiration Dominated
E. Med.
NE Atlantic
PAP 552h
N. Agean
Pak. 1850m
Active Faunal Uptake
Sognefjord
Scheldt Estuary 1
Scheldt Estuary 2
Pak. 140m
Pak 300 m
Metazoan Macrofaunal Uptake Dominated
Pak. 940m
Loch Etive
Bacterial Uptake Dominated
German Bight
Ythan Estuary
Respiration
Bacterial Uptake
Macro Uptake
Foram Uptake
Faunal Uptake

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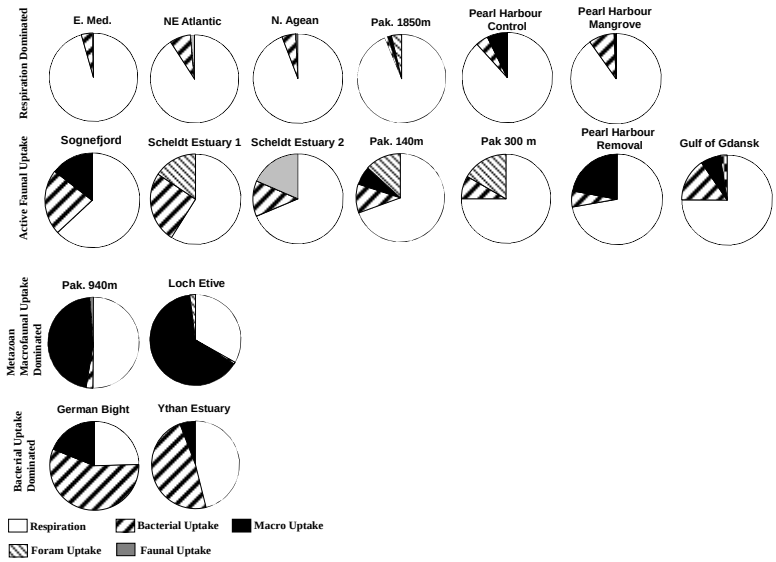


Figure 5. Biological C processing pattern categories adapted from Woulds et al. (2009), with the experiments from this study and the new category 'bacterial uptake dominated' added. Data sources are as follows; Eastern Mediterranean (E. Med.), NE Atlantic, North Aegean (N. Aegean) and Scheldt Estuary 2: Moodley et al. (2005); ~~Porcupine Abyssal Plain (PAP 552 h): Witte et al. (2003 b);~~ 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).

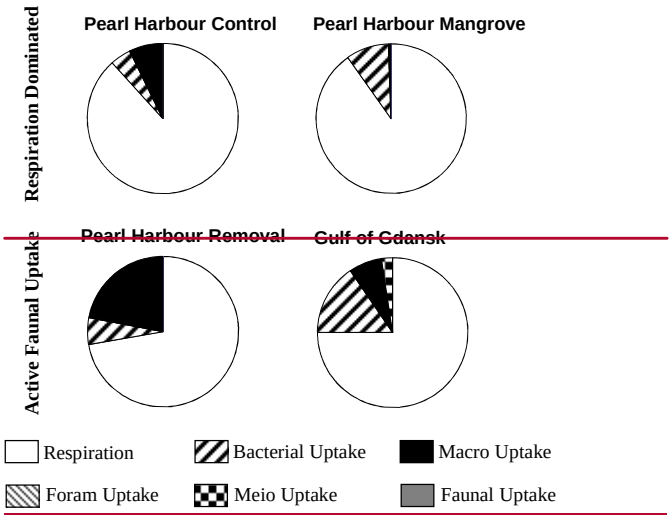
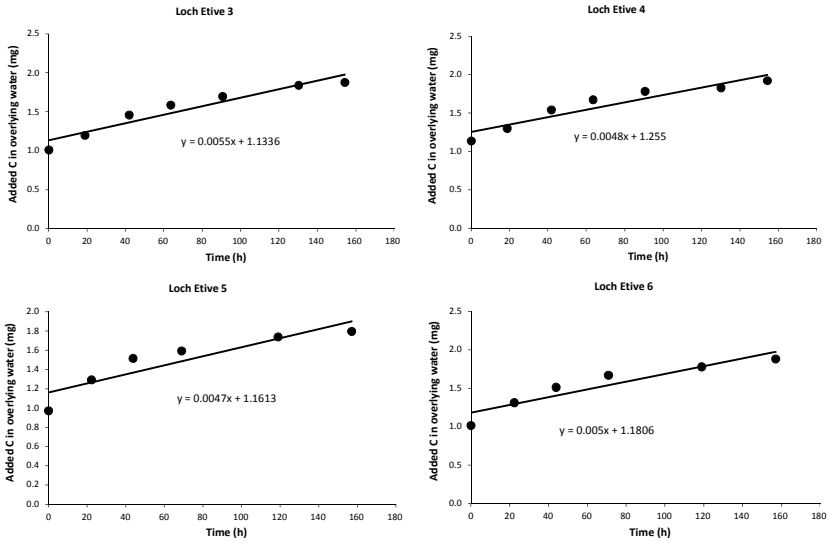


Figure 6.Biological C processing categories in two recent studies. Pearl Harbour data are from Sweetman et al. (2010), Gulf of Gdansk data are from Evrard et al. (2012).

Supplementary Information



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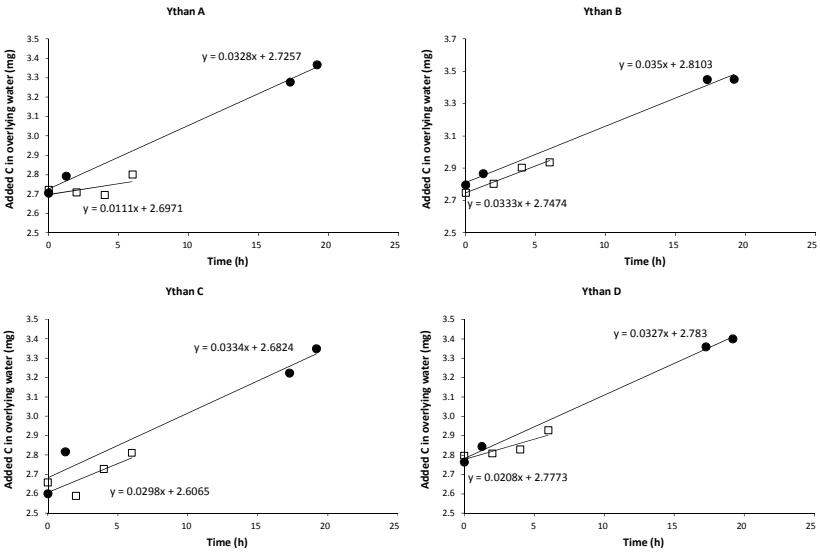

B

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).

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BG-2016-14 Response To Reviews

Reviewer 1 Major Comments:

We would like to thank the reviewer for their thorough review, and for their overall positive opinion.

Reviewer: Carbon processing categorization The discussion 4.5. based on many uncertainty and speculations, and need to remove from the manuscript. The authors proposed the categorization of C processing using data in this study and references. However, there is no mention on how and why authors selected specific time scale of the incubation duration. In Woulds et al. (2009), there were circle graphs of carbon fate for both _2 days and _5 days. However, in this paper, only one of them (I guess so) are shown. It is expected that the respired C increases with time (as mentioned in the line 563) while macrofaunal and bacterial 13C-label will be respired and decreased. Further, the faunal uptake and bacterial uptake also showed different patterns with time between taxa: for instance, macrofauna responded quicker than foraminifera (Witte et al. 2003, Nature), bacterial assimilation decreased after 1 or 2 days (Middelburg et al. 2000) whereas foraminiferal uptake showed increasing pattern during similar time scale (Moodley et al. 2000). It is thus obvious that the time scale selection is the most important factor to properly categorize the carbon processing. In this manuscript, data from different time scales (hours to 23 days) were combined without description what time scale of incubation was selected in the categorization from several different incubation periods (e.g. Moodley et al. 2002, Witte et al. 2003a, b, Bhuring et al. 2006). Also, there is no discussion on the effect of time scale (except line 563, which mentioned as to explain the irregular pattern of the categorization). I therefore recommend to remove discussion 4.5 from the manuscript and just discuss Loch Etive was macrofauna dominated C processing and Ythan sand flat was bacteria dominated. The manuscript itself can withstand as research paper without the chapter 4.5.

Answer: The reviewer is correct that in the medium and longer term the experiment duration will have an effect on biological C processing pattern, with respiration becoming more important with time (and in the end we might expect C which was incorporated into biomass to be respired as well, such is the nature of a pulse chase experiment). Our manuscript concerns the short-term biological processing of organic carbon, and therefore these longer term fates are not directly relevant to the categorisation. The wording of section 4.5 has been adapted to clarify this.

The reviewer is also correct that smaller variations in the relative importance of different pathways tend to be observed within the short term, however this does not lead to problems for our categorisation. The experiments presented in figure 5 range from 6 h to 23 days, with the majority falling in the 1-7 days range (i.e. the single 23 day experiment was the only one longer than 7 days). Therefore the only one which cannot truly be said to represent ‘short-term’ biological C processing is the 23 day experiment (Porcupine Abyssal Plain, Witte et al., 2003b). This has been excluded.

In a few cases experiments were conducted over multiple durations at the same sites. In the case of 5 sites across the Pakistan margin the difference in duration between 2 and 5 days never caused a shift in the category of short term biological C processing (Woulds et al., 2009). Similarly in the Sognefjord the C processing pattern remained in the same category in experiments lasting both 1.5 and 3 days (Witte et al., 2003a). In the German Bight, experiments lasting 0.5 to 1.5 days always showed a bacterial uptake dominated pattern, and bacterial uptake remained equally important as respiration after 5.5 days (Bhuring et al., 2006). Therefore, while we accept that experiment duration does play a role in determining the finer detail of the pattern of biological C processing observed in an experiment, it does not determine the category of C processing pattern within the range of experiment durations included here (and is certainly not the ‘most important factor’ as the reviewer suggests).

The Porcupine Abyssal Plain is the only example of a site where different short-term experiment durations led to different biological C processing categories (Witte et al., 2003b). At this site, where we would expect to see 'respiration dominated' biological C processing, the shortest experiment (60 h) actually showed 'active faunal uptake', with macrofaual uptake accounting for 26% of biological C processing. All longer experiments (8 d and 23 d) showed 'respiration dominated' biological C processing. This site has been removed from the standard categorisation and is instead discussed alongside the other exceptions.

Therefore we feel that the variation in experiment duration between the results does not cause sufficient changes to C processing patterns to invalidate the categorisation, and that therefore section 4.5 and figure 5 should be retained. We have added discussion of effect of experiment duration on categorisation as part of the discussion of the Porcupine Abyssal Plain experiments (detailed above), and have added a column to table 1 showing experiment duration, so that all details are clearly available.

Reviewer: Differences in light condition. The authors performed the 13C-labeled phytodetritus experiments with and without light (with light: Loch Etive, without light: Ythan sand flat). The authors validate the different conditions because natural environments are dark and light conditions, respectively. However, I believe that the incubation with light makes complicated pathways. Without light, the 13C-phytodetritus is ncorporated into heterotrophic microbes or eukaryotes, and either assimilated into their biomass or respired as 13CO2. With light, however, the respired 13CO2 can be assimilated into photoautotrophic microbial biomass via photosynthesis. This leads underestimation of respired carbon and overestimation of bacterial assimilation. Without light, chemolithoautotrophic microbes can also cause same process, but the contribution must be smaller than photosynthesis. How much proportion of CO2 was labeled with 13C? If the 13C concentrations in CO2 is almost negligible (few %), then the bacterial assimilation via photosynthesis may also be negligible. This can be calculated from the DIC-d13C data of the study. Or, if there are literature which investigated bacterial community at this area, then the authors may validate that photoautotrophic bacteria was minor.

Answer: Once again the reviewer is correct that the different light conditions led to a difference in the C flow pathways that were possible in the two experiments. However the different light levels were necessary in order to correctly re-create natural conditions. The labelling level of DIC in the Ythan experiment remained very low throughout (never 1.33> atom % ^{13}C), therefore the underestimation of respiration due to use of respired DIC by photoautotrophs is negligible, as the reviewer suggests. In addition, this will not have interfered with measurements of bacterial C uptake as the sub-set of PLFAs used are specific to bacteria (as opposed to benthic algae), and are regularly used for this purpose, including in intertidal incubations performed in the presence of light. A note has been added to section 4.1.

Reviewer: Uptake calculation The authors calculated the Carbon uptake by sample with the equation (3), line 253. However, the At% phytodetritus must be subtracted by At% background. I understand that the extent of 13C-label in this study (25% and 34%) are high and the re-calculated values using subtracted value may change only 2 or 3 % (considering 25 become 23.9 and 34 become 32.9). However, the it is necessary to indicate appropriate values as much as possible.

Answer: We do not agree that it is necessary to subtract the natural occurrence of ^{13}C from the labelling level of the phytodetritus when calculating C uptake into the different C pools. It is true that phytodetritus grown without any artificial ^{13}C enrichment would indeed have contained a natural amount of ^{13}C, but this does not change the fact that the phytodetritus actually added to our experiments had the labelling levels as measured and reported. Both the 'naturally' present and artificially enriched fractions of the ^{13}C in the phytodetritus serve as tracer, and the only thing that has to be subtracted out is naturally occurring ^{13}C in the sediment system to which the tracer was

added. We do not feel that it is necessary to add this explanation to the manuscript, unless the editor feels that it should go in.

Specific comments:

Reviewer: Line 32 Did the accessibility by bacteria to added C similar between two sites? Please show the vertical profiles of 13C if possible.

Answer: Accessibility by bacteria will have been similar in the sense that in both experiments phytodetritus was added to the sediment surface in the same way. Thereafter it may have been transported through the sediment differently due to differences between permeable and cohesive sediments. Unfortunately downcore ^{13}C profiles are not available.

Reviewer: Line 145. Figure 1 does not show any sills or geographical names. Please include these information to the figure or delete the citation (Fig.1) from the end of this sentence.

Answer: Figure reference removed.

Reviewer: Line 163. While the Loch Evive site has 70 m water depth, the Ythan estuary site exposed during low tide. This is a great difference between two sites, in addition to sediment grain size and OC concentrations. The authors need to discuss the potential impacts of these differences of OC cycling and validate why the authors did not perform the experiment at coarse grained, OC poor site having similar water depths (or vice versa).

Answer: This was driven by the coring technique and technology available for coarse grained sediment (required taking cores by hand). A note has been added to section 4.1.

Reviewer: Line 171. What exactly was the phytodetritus labeled with 13C? Was that degraded in some way? Or some sort of algal species? Was this same to the one which was added to Ythan sand flat? Please clarify these details.

Answer: Details have been added in the methods section.

Reviewer: Line 173. How much volume was the overlying water in the core?

Answer: Detail added.

Reviewer: Line 185 150 um sieve is not typical size separation for meiofauna. Why did the authors choose this size?

Answer: It was only practical to extract the larger meiofauna, as time did not permit sorting fauna all the way down to 63μm. Such small fauna would also have been very challenging to analyse. A note has been added.

Reviewer: Line 189 Why the authors used milliQ water instead filtered seawater of artificial seawater? MilliQ water may had elution of organic matters from fauna due to osmoticshock (although the results showed insignificant effect).

Answer: Filtered seawater was used, not milliQ. This has been corrected.

Reviewer: Line 196 Bubbling with air in this experiment while the Loch Etive site cores weremaintained with oxystat system. How did this affect to 13C-CO2 amounts?

Answer: There will not have been an effect from air bubbling in the Ythan experiment on measured respiration rates, as air bubbling did not occur during respiration measurement periods, and ^{13}C DIC data from outside of those periods was not used in respiration calculations. Potential effects of the oxystat system on respiration measurements in the Loch Etive experiment are already addressed in the manuscript as follows "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. "

Reviewer: Line 253 The equation is not presented in correct way (no under bar below "C Uptakesample". What the unit of "C Uptake sample"?

Answer: Equation has been corrected, and units added.

Reviewer: Line 263 It is not clear about the linear regression. Do the authors mean linear regressionof different incubation periods? It is also important to show the changes in d13C-DIC (or 13C-respiration rates) with time, because the changes in 13C-respiration with time should give crucial info regarding faunal or bacterial responses and C processing.

Answer: Respiration was calculated separately for each separate incubation period.

Reviewer: Line 267 It is necessary to show the respiration data of Ythan sand flat, too, as Tableor supplementary figure.

Answer: A supplementary figure has been added displaying the increase in labelled DIC over time for all chambers, and including regression lines and equations. This has been referred to in the text as appropriate.

Reviewer: Line 274 Please describe the centrifuge condition (x g, how long, and what temperatureetc). It will help to guess the potential effects of centrifuge on bacterial PLFA loss.

Answer: Detail has been added.

Reviewer: Line 279. Did the authors examine the d13C of bulk sediments? If so, please includeas Table etc.

Answer: These data are not available.

Reviewer: Line 282 Again, it is important to show temporal changes in d13C (or respired 13C).

Answer: A supplementary figure has been added.

Reviewer: Line 326. 0.00023 mgC per mgC corresponds _5 or 10 per mil of Dd13C, which isrelatively low labeling. What were the variation in d13C of natural PLFA and labeled

PLFA? Can you add as Table?

Answer: This is a large amount of data to tabulate (del13C values for several depths in the sediment, plus background values, for 4 PLFAs, for each of 4 incubation cores per site), and I am not convinced that it would provide much clarity for the reader. The background del13C values for the bacteria-specific PLFAs were similar at each site (-20 to -25 ‰). Δδ values were higher than the reviewer suggests in the surface sediment horizon (100's ‰), but this will have been balanced by them being lower (10's ‰ or less) in deeper horizons at Loch Etive. As expected, these Δδ values were at least an order of magnitude greater for the Ythan sand flat.

Reviewer: Lines 347 to 353. Whatever the C dose amounts were similar, the authors should think about the difference in natural phytodetritus supply rates at two sites. The same amount of 13C-phytodetritus input should have completely different effects on between originally eutrophic (in terms of OM) site and oligotrophic site. The authors should

discuss these point of view by referring the primary production rates at two sites.

Answer: 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 discussion). 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. This discussion has been added.

Reviewer: Line 368 Can you cite any paper which dealing different size screens?**Answer:** We are not aware of a paper dealing with the effect caused by this difference in screen sizes, and can only re-iterate that the sizes were standard for the sediment types in question, and were also most favourable in terms of practicality (using a 300μm screen in a sandy sediment would lead to very high retention of sediment, making extraction of fauna particularly difficult).

Reviewer: Lines 376 to 380. Due to the osmotic shock by milliQ water (according to M&M), the fauna may be dead and did not have a time to void the gut.

Answer: This step was not actually conducted in Milli-Q (corrected in response to an earlier comment), so osmotic shock will not have been a problem.

Reviewer: Line 431. Gooday et al. 2008 represent biomass-uptake relationships with different symbols for bacteria, fauna, foraminifera. Can you also make such kind of Figure 4 for better comparison?

Answer: Figure 4 would be unclear if taxonomic information was included where all the points are plotted together, therefore two panels have been added, one for each site, showing data for the different taxa.

Reviewer: Line 438. This may suggest that the macrofauna of Ythan sand flat has low background metabolism than Loch Etive.

Answer: Agreed, this comment has been added.

Reviewer: Line 459. I cannot follow why the authors said "macrofaunal biomass" in this sentence whereas the line 456 mentioned "biomass (faunal plus bacterial)". Please describe

more in detail if the authors actually intended to say "macrofaunal biomass".

Answer: Clarification has been added.

Reviewer: Chapter 4.4. can be combined to 4.3.

Answer: These two sections both consider points related to faunal C uptake. However, the main point made in section 4.4. is distinct from those in section 4.3, and therefore we feel that the additional sub-heading remains helpful.

Reviewer: Line 520. Both methods (Total respiration rate measurements and bacterial C assimilation rates) has considerable uncertainty. Thus the discussion here, dealing bacterial growth efficiency, is somewhat over-interpretation. Also, as mentioned earlier, because the incubation of Ythan sand flat sediment was carried out under light condition, it is possible that some 13C-bacterial lipids were originated from the photoautotrophic microbes, not by heterotrophic bacteria which incorporated 13C-labeled phytoplankton.

Answer: The sub-set of PLFAs used to quantify bacterial uptake are regularly used to indicate bacterial activity as separate from microphytobenthis production, including in incubations in which light was present. We agree however, and acknowledge in the text, that our measurements do not allow an accurate quantification of bacterial growth efficiency. The text has been shortened accordingly.

Reviewer: Line 571 Again, temporal changes in DIC-13C at both site may give better idea about these interpretations.

Answer: A supplementary figure has been added.

Reviewer: Line 673 Hunter et al. 2012b. There is no Hunter et al. 2012a, thus deleted "b".

Answer: Corrected.

Reviewer: Table 1 Please add a new column showing incubation periods.

Answer: Added.

Reviewer: Figure 2. Please add "n.d." for meiofauna and foraminifera of Ythan sand flat.

Answer: Note added to the caption.

Reviewer 2:

Once again we would like to thank the reviewer for their overall positive opinion, and for their attention to detail which will allow us to improve the manuscript.

Major comments:

The main comment from this reviewer is that the discussion is overly long. We agree, especially concerning the section about bacterial growth efficiency. The discussion has now been shortened significantly.

Specific comments:

Reveiwer: Line 73: It might be worth pointing out what does biological C processing not cover. Is there non-biological C processing in these systems? It might be worth pointing out the differences.

Answer: The term is used to distinguish between short term uptake and cycling and longer tern C burial. This has been clarified.

Reveiwer: Line 76: A quibble: Stable isotope tracer experiments are an excellent tool, but not ideal. For instance, radiotracer 14C incubations are far more sensitive and do not depend on sorting out mass of naturally occurring background tracer distribution.

Answer: Acknowledged, but working with stable isotopes has practical benefits which can allow increased numbers of experimental treatments/durations/replicates. Wording has been changed.

Reveiwer: Line 117 and following: Independent of the food-web tracer studies, it would be nice to have some information on the relative benthic biomasses for these two sediment types, e.g. muddy and sandy bottoms. I would be surprised if muddy bottoms actually supported more faunal biomass.

Answer: This section does not seem an appropriate place to review biomass data for different estuarine sediments, however such details can be found in Table 1 (biomass data are independent of the associated C tracing experiments)..

Reveiwer: With the exception of the respiration measurements, these are single endpoint experiments. Dynamics between the pools are not necessarily accessible.

Answer: We are not clear which part of the text the reviewer is referring to here.

Reveiwer: Line 124: "Recent findings" is relative; dynamic biogeochemical cycling in low OC permeable sediments has been extensively documented over the last two decades.

Answer: Agreed, wording has been amended.

Reveiwer: Line 171: Please describe more carefully the labeled phytodetritus in more detail. Was it composed of a single species and what? Was it prepared in the same fashion for both sites? What was it composed of? How fresh was it? Was it added as fresh or freeze-dried material.

Answer: Detail has neen added to the methods section.

Reveiwer: Does the difference between the labeling percentages (ca. 25% and 34%) for the two sites reflect different batch preparations, or differing compositions of pytodetritus?

Answer: Different phytodetritus batches and species. Detail has been added (see above)..

Reveiwer: Methods: It's not entirely clear to me that total bulk 13C of the sediment was determined (i.e. total Corg 13C). This must have been done in order to calculate the recoveries of tracers shown in Figure 2.

Answer: The totals shown in figure 2 are total biologically processed C, and therefore do not contain C remaining in the sediment. Data for 13C remaining in the sediment are not available.

Reveiwer: Is there a time zero sample, i.e. samples taken from one core immediately after the addition of the 13C-labeled phytodetritus?

Answer: This is only available for Loch Etive, and not on the Ythan sand flat, therefore data has not been included.

Reveiwer: Line 244 and following: It is not really clear to me why the authors work with the del (_) notation for these type of experiments. There is also no obvious connection from how they go from Equation 2 to Equation 3, the latter of which is the more relevant for this manuscript.

Answer: Data are reported using the del notation in the results section because many workers in the field use this notation, and $\Delta\delta$ is a clear way of displaying isotopic enrichments. However, our calculations for uptake used At% instead. There is not supposed to be a connection between equation 2 and equation 3.

Reveiwer: Calculations with exceedingly large enrichments, for instance as seen in the macrofaunal biomass (lines 290 and following), become inaccurate.

Answer: The reviewer's meaning is not quite clear, however if this is given as a reason for not using the del notation, then note that uptake calculations were made using At% instead.

Reveiwer: Line 280: . . ..or as dissolved organic carbon.

Answer: This has been added.

Reveiwer: Section 3.1: It might be helpful for the reader to plot the remineralization data over the time course of the experiment.

Answer: These plots have been added as supplementary information.

Reveiwer: Section 4.2: This whole discussion is rather contradictory. On one hand the authors claim that the temperature and organic C loading are similar (line 384), but then suggest that temperature plays a larger role than biomass or organic C (lare 395) does not make sense. Furthermore, there are no proper controls for assessing any of these factors. I would drop this whole discussion (see further discussion about curtailing discussion) and the conclusions regarding temperature (line 571). This was not the point of the study, it was not properly assessed, nor is it supported by the data.

Answer: The point made in this section is that despite many differences between the settings of the two experiments, the measured respiration rates were very similar, and this is attributed to the fact that the experiments were conducted at the same temperature. Supporting material from the literature is provided. This section has been shortened and clarified, and we do not feel that this point goes beyond the reach of the data.

Reveiwer: Line 494: “This hypothesis. . ..” Which hypothesis? From this paper or Woulds et al. 2009? Actually I find the whole discussion of hypotheses, both here and earlier in the manuscript (line 134 and following) a bit specious. I think that it is enough for the authors to state that they are comparing two types of sites that are thus far lacking from the overall range of sites on which such experiments have been performed.

Answer: The sentence in question has been changed to clarify which hypothesis is being referred to. It is not clear why the reviewer finds the earlier statement of our hypotheses to be specious, as the reflect our expectations before the experiments were conducted. We have retained these hypotheses, as we feel they are the best way of providing the appropriate focus to the manuscript.

Reveiwer: Figure 2: I assume that “Total” stand for the sum of respiration, bacterial uptake, etc. in that case, there is also no Total for the % of Biologically Processed C. It might also be interesting to add a third panel to include total initial pool size of each of the separate pools (i.e. how much C is in each pool originally).

Answer: This is an interesting suggestion, but we do not feel that it would work well in graph form. The information on macrofaunal and bacterial biomass is already given in the results text. It is not so helpful to quantify the amount of C in the DIC pool, as the absolute amount depends on the height of the water column in the experimental chamber. This varied for each chamber. Of course it could be given for a standard height of water column, but the choice of height would be entirely arbitrary, and so it would not make a meaningful comparison with the macrofaunal and bacterial pools.

Reveiwer: Figures 5 and 6: These figures are quite compelling, although I think that they could be combined. It is not entirely obvious why there are two separate figures.

Answer: The figures have been combined.

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~~ideal~~ 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., 201222b), 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 ~~recent~~ 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 ~~(Fig. 1)~~. 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 21□m with 78 % fines (<63 □m) 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 $\delta^{13}C$- 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 sea~~Milli-Q~~ water for several hours before freezing.

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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 $\delta^{13}C$ 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%.

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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 $\delta^{13}C$.

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 $\delta^{13}C$.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).

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

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).

$$\Delta\delta = \delta^{13}C\ sample - \ \delta^{13}Cbackground \quad (2)$$

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):

$$\frac{C\ Uptake_{sample} = \left(At\ \%_{sample} - At\ \%_{background}\right) X\ C\ Contents_{sample}}{At\ \%_{phytodetritus}} X100$$

$$C\ Uptake_{sample}\ (\mu g) = \frac{(At\ \%_{sample} - At\ \%_{background}) \times\ C\ Contents_{sample}}{At\ \%_{phytodetritus}} \times 100 \quad (3)$$

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 $\delta^{13}C$-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 $\delta^{13}C$ 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 ~~of sediment core incubations under natural conditions~~, nevertheless had slightly different experimental setups. The water depth, ~~temperature,~~ core size, stirring regime, light availability and C dose added all differed between the two study sites. The differences in stirring regime~~, temperature~~, and light availability were enforced to properly replicate natural conditions in each experiment, thus any contrasts ~~between experiments~~ caused by these conditions ~~are simply reflections of actual~~reflect differences in functioning of the two ~~benthic~~ 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 ~~relatively~~ minor differences in C dose (Woulds et al., 2009). ~~In cases w~~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 ~~and ecologically meaningful~~.

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 ~~with respect to their biomass~~ in the present study but, despite wide variations in the importance of meiofaunal uptake ~~for the immediate fate of deposited organic C~~ (Nomaki et al., 2005; Sweetman et al., 2009; Evrard et al., 2010), ~~meiofaunal C uptake~~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 ~~more~~ practical in coarser grained sediments~~, such as those of the Ythan sand flat~~. The larger mesh used on the Ythan sand flat is likely to have reduced the macrofaunal biomass ~~recovered, and thus the macrofaunal~~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 ~~prior to analysis~~, and were therefore analysed with their gut contents in place. The exception to this was two ~~(out of four)~~ of the Loch Etive ~~replicate~~ cores, ~~the fauna from which were placed in clean water and~~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 ~~(which would have been simulated by being placed in water without sediment present)~~ by retaining their gut contents for days or weeks. Therefore it is possible that ~~many~~ 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~~so its exclusion from the analysis of fauna from two replicate cores did not produce a difference that was measurable above the comparatively large variation in faunal C uptake between cores caused by faunal patchiness~~. Thus ~~it should be noted that~~ the values reported here as faunal C uptake include ~~both~~ C ~~residing~~ in both gut contents ~~and that which was assimilated into~~ faunal tissue.

4.2 Respiration rates

The respiration rates observed in Loch Etive and on the Ythan sand flat were very similar (Fig. 2). ~~In one sense t~~This is unsurprising, as the two experiments were conducted at the same temperature, and similar C loadings

were applied. Temperature is known to ~~be a major~~ control ~~on~~ 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). ~~Increased temperatures accelerate the diffusion of reactants and metabolites through the sediment, and also increase microbial process rates.~~ 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. ~~Thus, they showed that temperature can be the dominant control on sediment community respiration rate.~~ Our finding of similar rates of respiration ~~in response to added phytodetritus in Loch Etive and on the Ythan sand flat~~, despite marked differences in influential factors ~~which can influence respiration rates~~ 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. ~~This is in line with findings of a much wider study of ecosystem respiration rates, in which their dependence on temperature was found to be remarkably similar across both terrestrial and aquatic habitats, despite marked contrasts in taxa, biomass, and abiotic factors (Yvon-Durochet et al., 2015).~~

4.3 Faunal uptake

In ~~the case of~~ 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~~b~~), the distribution of C uptake amongst ~~macrofauna, metazoan meiofauna and foraminifera~~faunal classes was largely determined by the relative biomass of each group. The dominance of faunal C uptake by macrofauna ~~(as opposed to meiofauna and forminifera)~~ 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~~r C in some situations~~ (e.g. Moodley et al., 2000). Where macrofauna are absent, or where conditions ~~do not favour their functioning~~are unfavourable, smaller taxa can ~~come to~~ 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 ~~such as low oxygen~~. This was the case at 2170 m water depth in the NE Atlantic, in Sagami Bay and at a subtidal Wadden Sea site, ~~where~~ foraminifera and meiofauna have been observed to consume more C than macrofauna, sometimes despite having lower biomass ~~dominated the initial uptake of added ^{13}C~~ (Moodley et al., 2002; Nomaki et al. 2005; Evrard et al., 2010)~~., and also in Sagami Bay, where Nomaki et al. (2005) observed foraminifera to take up more C than metazoan fauna. At a sandy subtidal site in the Wadden Sea, meiofauna was found to consume more C than macrofauna, despite the former having a lower overall biomass (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 ~~total~~ macrofaunal C uptake than they accounted for macrofaunal biomass (Fig. 3),and thus were disproportionately responsible for macrofaunal C uptake ~~the large amount of added C that was routed into macrofaunal biomass and gut contents~~. On the Ythan sand flat, the contribution to C uptake by the dominant oligochaetes was in line with and ~~therefore presumably controlled by their contribution to the~~their biomass (both ~50%, Fig. 3). However, ~~the~~ other faunal groups ~~present~~ contributed differently to biomass and C uptake. Nematodes were responsible for less C uptake than ~~might be~~ expected ~~from their biomass~~, while the ~~rarer~~ polychaetes, amphipods and molluscs fed comparatively efficiently on the added C~~OM~~. 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 ~~total~~ 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 ~~necessarily~~ fully explain the lower faunal C uptake observed there, as biomass specific C uptake was also considerably lower than in Loch Etive. ~~Therefore, the inter-site difference in faunal C uptake requires an additional explanatory factor.~~ We suggest that the low OC standing stock in the permeable sediment of the Ythan sand flat~~,~~ supports a lower biomass and ~~also~~ 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~~contrary to those arising from others~~, and the reasons for this variation ~~within the literature~~ 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~~b~~).

4.4 Total biological C processing rates

~~Of our two study sites,~~ Loch Etive showed the largest~~a greater~~ amount of total biologically processed C (Fig. 2). As both sites showed very similar respiration rates ~~of added C~~, the difference in total biological C processing was driven by greater faunal uptake in Loch Etive (Fig. 2), and ~~. T~~this~~e greater faunal uptake in Loch Etive~~ was a result of greater faunal biomass~~, as shown by the relationship between biomass and C uptake for the specimens analysed in this study (Fig. 4).~~.

The~~Such a~~ relationship between biomass and total biological C processing is also shown by data gathered from previously published isotope tracing experiment~~s results, where biomass data are also available~~ (Table 1)~~.~~ ~~,~~

which show~~Data from the experiments shown in Table 1 shows~~ 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 ~~macrofaunal~~ 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 ~~B~~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, ~~similar proportions of biologically processed C having been subjected to respiration,~~ the dominant fate of biologically processed~~such~~ 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 ~~actually~~ observed in Loch Etive was most similar to the category labelled 'macrofaunal uptake dominated' (Fig. 5), in which~~. In this category,~~ 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 ~~comparatively~~ unusual pattern, previously only observed in the lower margin~~transition zone~~ 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 ~~of such magnitude~~ was due to the presence of particularly high OC concentrations in the sediment, coupled with sufficient oxygen for larger organisms ~~(as opposed to at lower oxygen concentrations within the oxygen minimum zone)~~. This explanation also applies to ~~the site studied here in~~ Loch Etive, where the sediment OC concentration was nearly 5 %. In contrast to the Arabian Sea site however, ~~our~~ Loch Etive ~~site~~ 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 ~~and the resultant faunal community~~, rather than by low oxygen conditions. Experiments conducted in Pearl Harbour sites impacted by invasive mangroves also show OC availability controlling ~~A further indication of the control by OC availability on~~ the relative importance of faunal C uptake ~~is shown in isotope tracing experiments conducted at sites in Pearl Harbour impacted by invasive mangroves~~ (Sweetman et al., 2010). A control site was OC poor (0.5% wt % OC) and ~~correspondingly~~ showed respiration dominated biological C processing (Fig. 56), while~~. In contrast,~~ a nearby site from which invasive mangroves had been removed showed active (macro)faunal uptake (Fig. 56), in line with higher~~increased~~ sediment OC content (3.1%

wt % OC) and an elevated macrofaunal biomass. ~~A third site at which the invasive mangroves were still present however showed respiration dominated C processing despite very high OC concentration (8.2% wt % OC). However, in that case the unusual properties of mangrove detritus (being tannin rich, with fibrous root mats binding the sediment) made the sediment inhospitable for many macrofauna taxa, therefore bacterial C uptake and respiration was favoured over macrofaunal uptake (Sweetman et al., 2010).~~

We hypothesised that the Ythan sand flat would show a short term biological C processing pattern that did not fit with the categories suggested~~those laid out~~ by Woulds et al. (2009). Our~~This~~ 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 ~~use them to~~ propose a new biological C processing category labelled 'bacterial uptake dominated' (Fig. 5). In the new category, bacterial uptake~~, rather than respiration,~~ 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 ~~over faunal uptake and total community respiration~~. 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)~~, and~~ thus ~~both the~~ substrate and electron acceptors for bacterial respiration are supplied. ~~This efficient introduction of fresh OC is consistent with the fact that Loch Etive and the Ythan sand flat showed similar bacterial biomass despite considerable difference in OC concentration, thus OC supply rather than standing stock appears to be important in determining bacterial biomass and activity.~~

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~~In a year-round study of permeability on the Ythan sand flat,~~ (Zetsche et al.~~,~~ ~~(~~2011)~~.~~ ~~observed clogging of pore spaces during the summer, which was then removed. Therefore one possible explanation for the lack of accumulation of bacterial biomass in permeable sediments is regular removal of bacterial biomass during sediment reworking~~.

T~~It is worth noting that t~~he domination of short term biological C processing by bacterial uptake~~, to the extent that it is equal to or greater than total community respiration,~~ implies a high value for bacterial growth efficiency (BGE). This ~~parameter~~ is calculated as bacterial secondary production divided by the sum of bacterial secondary production and bacterial respiration~~, and thus represents the proportion of assimilated C that is routed into~~

anabolism rather than catabolism. Bacterial respiration is not quantified here, challenging to quantify, and is not quantified during isotope tracing experiments. Hhowever, it is likely that a large proportion of total community respiration is attributable to bacteria (Schwinghamer et al., 1986; Hubas et al., 2006). FThus, 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 mean value of 0.51±0.18 (this will be a conservative estimate). This value is indeed 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)es in that same review. Bacterial growth efficiency is widely variable, both spatially and temporally, and the factors that control it are not well understood. and the factors which control it are not well understood. In the case of several potential controlling factors, such as temperature and inorganic nutrient limitation, evidence is conflicting. HHowever 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). In particular increased supply of amino acids tends to increase BGE, and, amongst broad types of OC, only that excreted by phytoplankton showed a high (>50%) mean BGE (Del Giorgio and Cole, 1998) Bacterial growth efficiency also tends to increase from oligotrophic to eutrophic environments, and thus it often correlates with primary productivity (Del Giorgio and Cole, 1998). This is consistent with high BGE in ese trends mean it is perhaps relatively unsurprising that permeable sediments, which have aith their potentially high input of fresh OC through from filtering during advective porewater flow have high BGE (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). In addition, it may be that BGE is maximised if there is a shift in the relative proportions of bacterial cells that are highly active, versus those which are dormant, inactive or dead (Del Giorgio and Cole, 1998). Furthermore, the proportion of highly active cells has been found to increase with productivity. Thus, the high BGE observed on the Ythan sand flat (and in the German Bight by Buhring et al., 2006) may be due to the fact that bacterial communities in permeable sediments tend to be particularly active compared to those in cohesive sediments (Huettel et al., 2014)..

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 that might be expected based on permeable sediment from the Ythan sand flat and the German Bight. Instead it shows respiration dominated biological C processing, with bacterial uptake, although greater than faunal uptake, responsible for only 16% (Fig. 56). Further, an OC rich site with invasive mangroves in Hawaii shows respiration dominated biological C processing, instead of the expected 'active faunal uptake'

pattern (Fig. 56, Sweetman et al., 2010), due to mangrove roots and detritus making the sediment ~~however in this case the impact of mangrove roots on the sediment make it~~ 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 ~~in question~~ contained a muddy fraction, although also featuring~~ed~~ 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, ~~more~~ in line with expectations ~~for the site~~. 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 Proce Rate (mg C
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

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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).

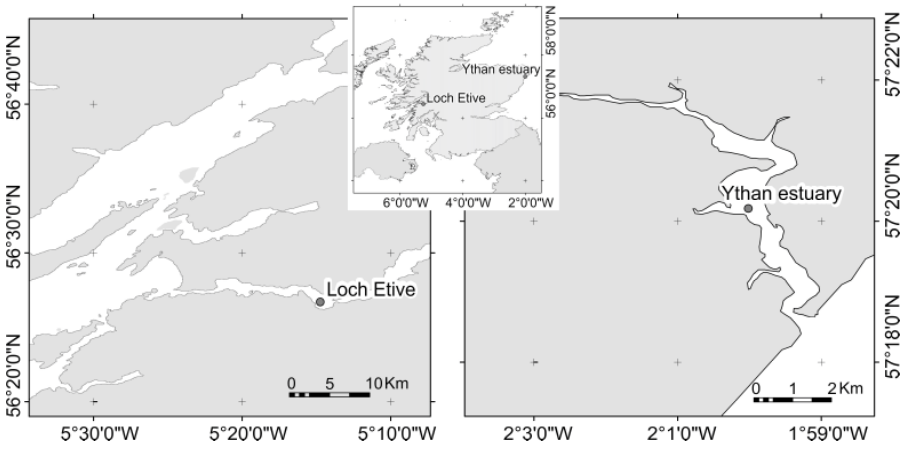
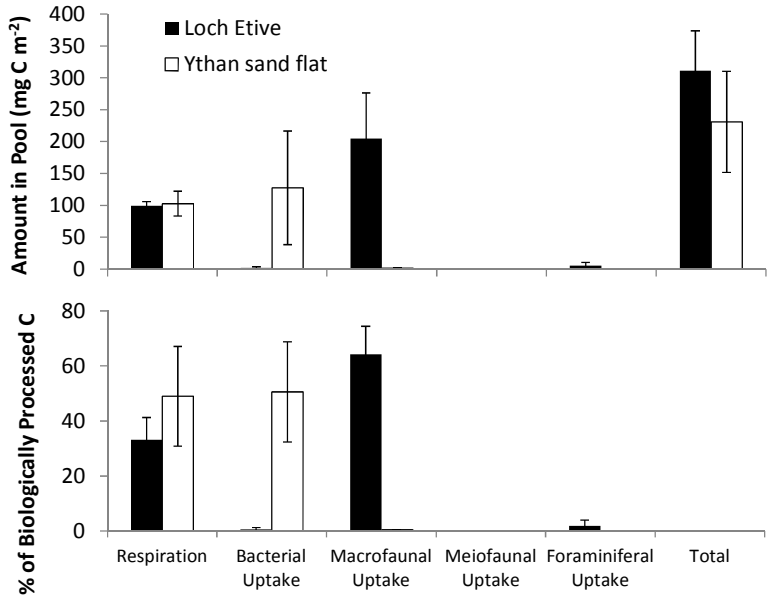


Figure 1. Map showing site locations.



1163

1164 Figure 2.The distribution of initially added C between different biological pools at the end of the experiments in
1165 absolute terms (upper panel), and as percentages of total biological C processing (lower panel). Note there are
1166 no data for meiofaunal or foraminiferal uptake on the Ythan sand flat.

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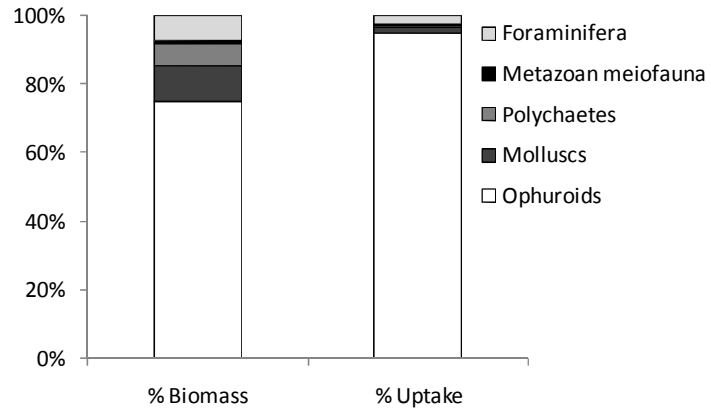

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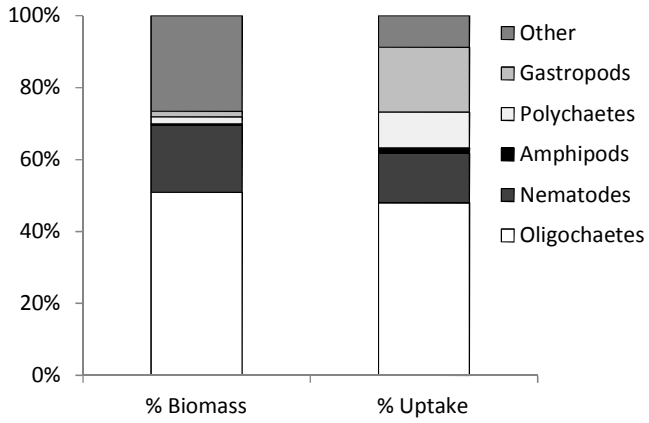
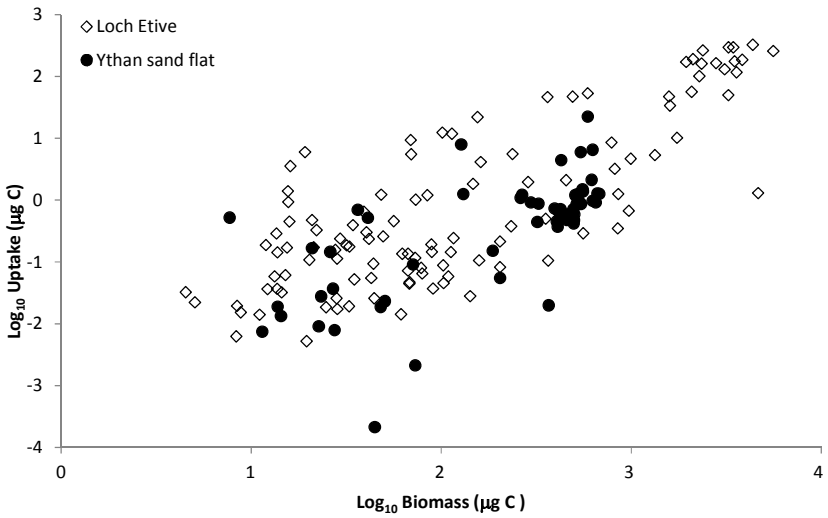
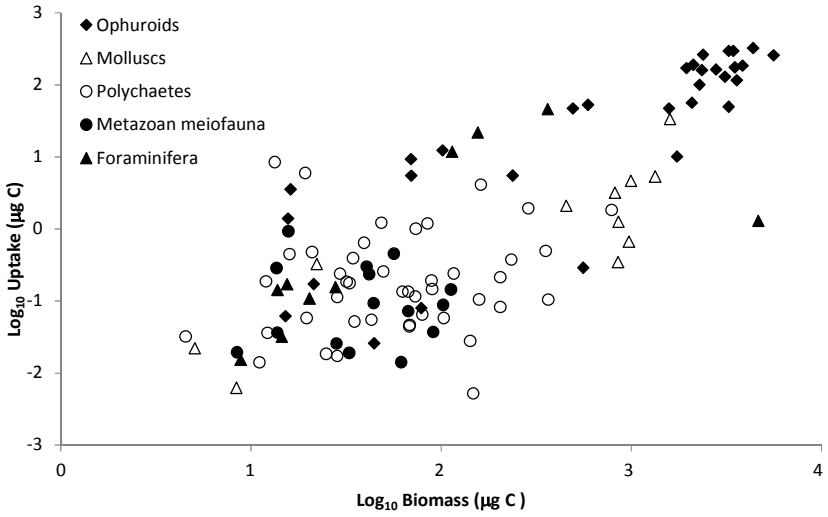


B

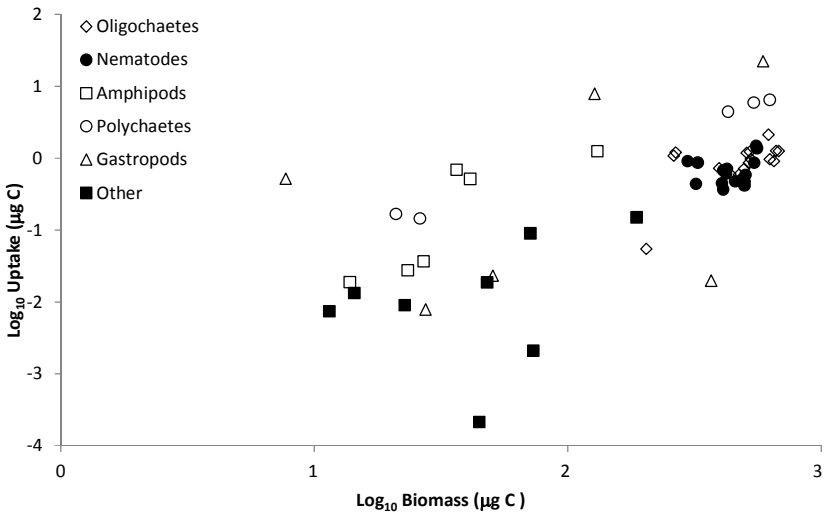
Figure 3.Taxa responsible for biomass and C uptake in a) Loch Etive, and b) the Ythan sand flat.


Loch Etive
Ythan sand flat
Log10 Uptake (µg C)
Log10 Biomass (µg C)

A


Ophuroids
Molluscs
Polychaetes
Metazoan meiofauna
Foraminifera
Log10 Uptake (µg C)
Log10 Biomass (µg C)

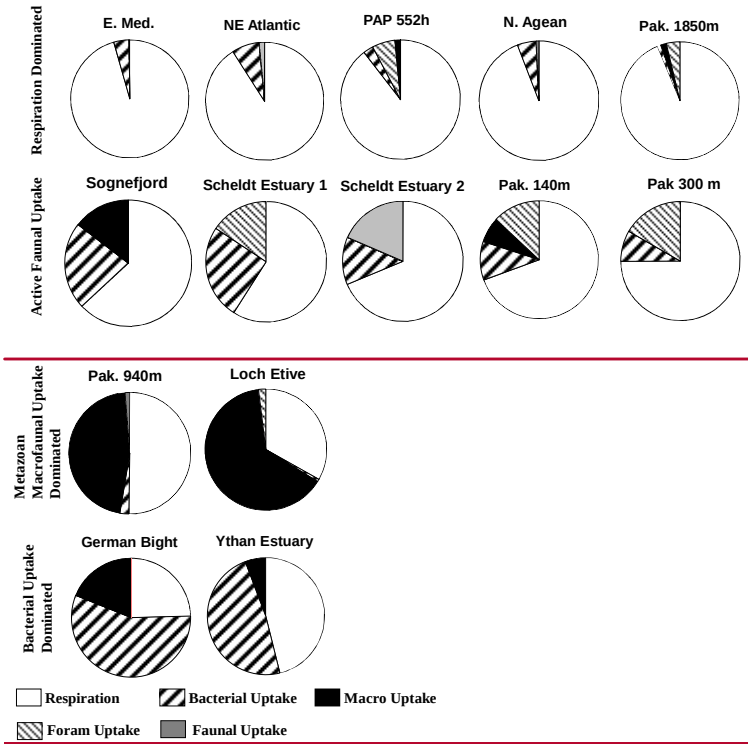
B



C

Figure 4. Log_{10} uptake against Log_{10} C biomass for: a) all specimens analysed in Loch Etive and on the Ythan sand flat, b) Loch Etive with taxonomic detail, and c) the Ythan sand flat with taxonomic detail.

1185


Respiration Dominated
E. Med.
NE Atlantic
PAP 552h
N. Agean
Pak. 1850m
Active Faunal Uptake
Sognefjord
Scheldt Estuary 1
Scheldt Estuary 2
Pak. 140m
Pak 300 m
Metazoan Macrofaunal Uptake Dominated
Pak. 940m
Loch Etive
Bacterial Uptake Dominated
German Bight
Ythan Estuary
Respiration
Bacterial Uptake
Macro Uptake
Foram Uptake
Faunal Uptake

1186

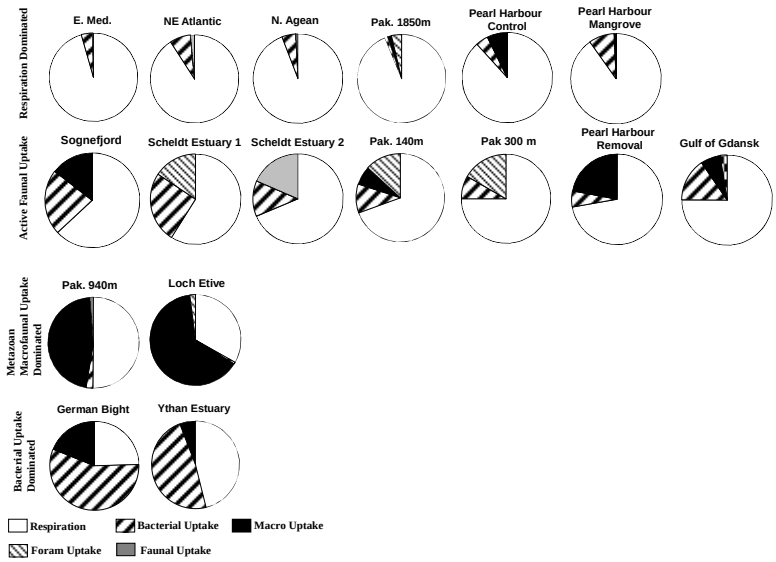


Figure 5. Biological C processing pattern categories adapted from Woulds et al. (2009), with the experiments from this study and the new category 'bacterial uptake dominated' added. Data sources are as follows; Eastern Mediterranean (E. Med.), NE Atlantic, North Aegean (N. Aegean) and Scheldt Estuary 2: Moodley et al. (2005); ~~Porcupine Abyssal Plain (PAP 552 h): Witte et al. (2003 b);~~ 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).

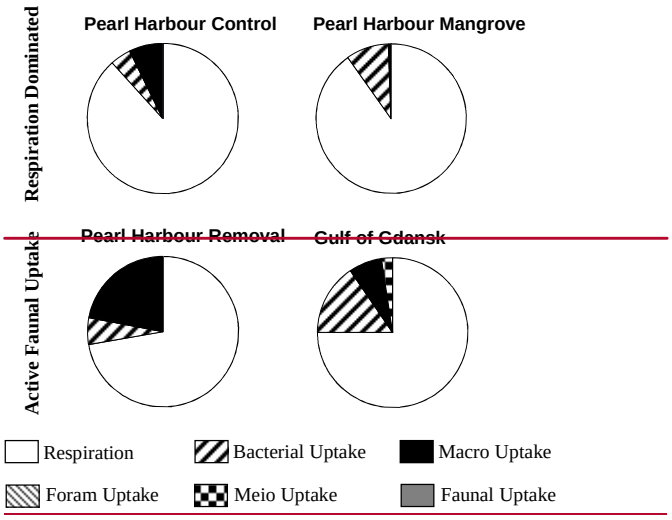
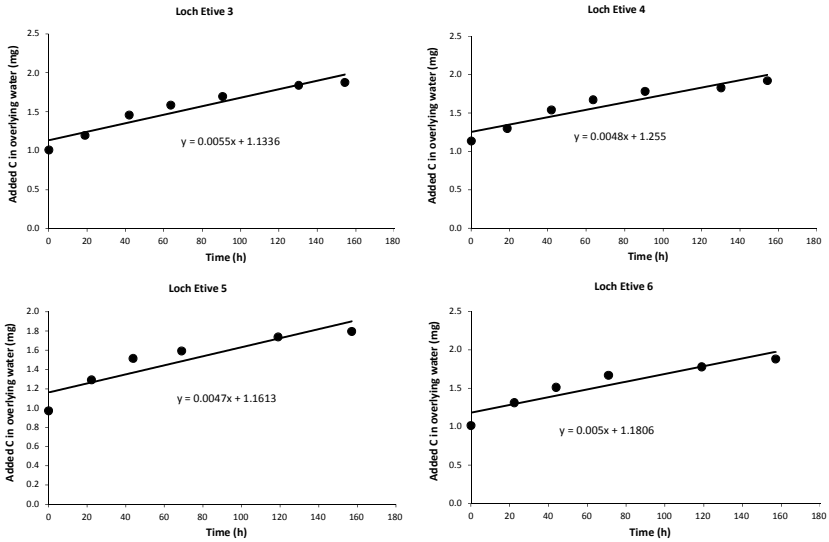
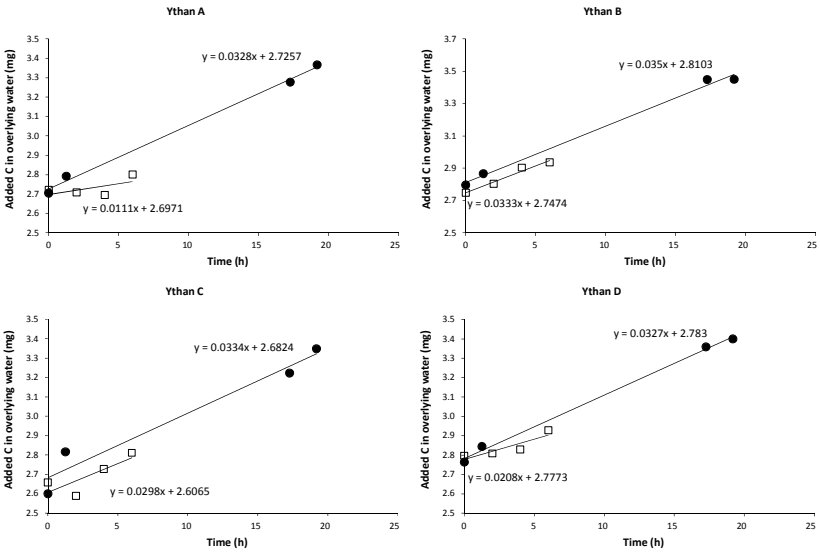


Figure 6.Biological C processing categories in two recent studies. Pearl Harbour data are from Sweetman et al. (2010), Gulf of Gdansk data are from Evrard et al. (2012).

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).

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