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Food web flows through a sub-arctic deep-sea benthic community

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ABSTRACT

The benthic food web of the deep Faroe–Shetland Channel (FSC) was modelled by using the linear inverse modelling methodology. The reconstruction of carbon pathways by inverse analysis was based on benthic oxygen uptake rates, biomass data and transfer of labile carbon through the food web as revealed by a pulse-chase experiment. Carbon deposition was estimated at 2.2 mmol C m^{-2} d^{-1}. Approximately 69% of the deposited carbon was respired by the benthic community with bacteria being responsible for 70% of the total respiration. The major fraction of the labile detritus flux was recycled within the microbial loop leaving merely 2% of the deposited labile phytodetritus available for metazoan consumption. Bacteria assimilated carbon at high efficiency (0.55) but only 24% of bacterial production was grazed by metazoans; the remaining returned to the dissolved organic matter pool due to viral lysis. Refractory detritus was the basal food resource for nematodes covering ~99% of their carbon requirements. On the contrary, macrofauna seemed to obtain the major part of their metabolic needs from bacteria (49% of macrofaunal consumption). Labile detritus transfer was well-constrained, based on the data from the pulse-chase experiment, but appeared to be of limited importance to the diet of the examined benthic organisms (<1% and 5% of carbon requirements of nematodes and macrofauna respectively). Predation on nematodes was generally low with the exception of sub-surface deposit-feeding polychaetes that obtained 35% of their energy requirements from nematode ingestion. Carnivorous polychaetes also covered 35% of their carbon demand through predation although the preferred prey, in this case, was other macrofaunal animals rather than nematodes. Bacteria and detritus contributed 53% and 12% to the total carbon ingestion of carnivorous polychaetes suggesting a high degree of omnivory among higher consumers in the FSC benthic food web. Overall, this study provided a unique insight into the functioning of a deep-sea benthic community and demonstrated how conventional data can be exploited further when combined with state-of-the-art modelling approaches.

1. Introduction

The deep-sea floor (below 200 m water depth) occupies approximately 65% of the Earth's surface, constituting the largest ecosystem on the planet (Thistle, 2003). Deep-sea sediments account for 50% of the global benthic mineralization (Middelburg et al., 1997) and host infaunal communities of high local and regional diversity (Levin et al., 2001). Despite the ecological significance of this ecosystem, the remoteness and the difficulties encountered in its exploration have resulted in the deep-sea being one of the least understood environments on earth (Tyler, 2003). As a result, the functional interactions within deep-sea benthic communities remain largely unknown. The processing of organic matter (OM) by benthic communities has significant consequences for the global carbon and nutrient cycles. Knowledge of the functional interactions between biological components in food webs is thus necessary if we are to understand and predict the response of deep-sea ecosystems to global change phenomena (Soetaert and van Oevelen, 2009b).

The quantification of energy flows between food web components is, in most instances, hampered by the lack of sufficient empirical data (Brown and Gillooly, 2003). This is especially true for deep-sea datasets that normally consist of biomass estimates of large taxonomic groups and occasional measurements of a single flux (Soetaert and van Oevelen, 2009b). Furthermore, direct observations on the feeding mode of deep-sea fauna are lacking and most inferences on the feeding habits of deep-sea animals rely largely on observations of shallow-water analogues (Jumars et al., 1990; Thistle, 2003). In recent years, stable isotope tracer experiments have provided direct observations of the transfer of fresh phytodetritus through food webs (e.g. Witte et al., 2003b; Moodley et al., 2005). Tracer experiments involve the introduction of an artificial stable isotope-labelled food pulse to the sediment and the subsequent "chase" of the tracer in various components of the food web (pulse-chase experiments). The pulse-chase methodology enabled the quantification of the contribution of particular taxonomic groups/species to the processing of fresh OM and revealed

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various benthic response patterns to OM enrichment depending on the environmental setting and the quality and quantity of the added material (Moodley et al., 2002; Witte et al., 2003a; Bühring et al., 2006; Aspetsberger et al., 2007; Woulds et al., 2007).

Despite the significant progress in unravelling trophic interactions using contemporary techniques, it is impossible to measure directly the full range of flows that exist in complex food webs. The linear inverse modelling (LIM) methodology was developed in order to overcome these data limitations and quantify biological interactions in complex food webs from incomplete and uncertain datasets (van Oevelen et al., 2010). Vezina and Platt (1988) pioneered inverse analysis in biological systems and since then this methodology has been used extensively to describe marine food webs (e.g. Richardson et al., 2004; Marquis et al., 2007). An issue of concern regarding this approach is the choice of the "best" solution from an infinite number of possible solutions based on an optimization criterion which has no ecological base (Kones et al., 2006). An alternative approach is the generation of a large number of solutions using the Monte Carlo sampling technique and taking the average values of the randomly generated solutions as the "best" estimation of food web flows (Kones et al., 2006; van Oevelen et al., 2010). Additional progress to the LIM methodology has been achieved by the combination of Monte Carlo sampling and tracer flow data from stable isotope pulse-chase experiments. In this advanced approach, tracer flow data are contrasted against modelled tracer dynamics for each food web generated by the Monte Carlo simulation thus providing a measure of the "best" food web solution based entirely on field data. The combination of the LIM methodology with tracer incorporation data (mentioned as combined LIM methodology from this point forward) has been implemented previously to model an intertidal benthic food web (van Oevelen et al., 2006a).

In this study, we use the combined LIM methodology to quantify carbon flows in a sub-arctic deep-sea benthic community. This is the first study to combine a high quality dataset consisting of flux measurements, biomass and isotope tracer data with the LIM methodology in deep-sea ecosystems. The data derived from sampling and experimental work in the Faroe–Shetland Channel (FSC). The FSC is a major pathway through which Arctic bottom waters escape to the south. Benthic communities below 600 m in the FSC are thus constantly subjected to sub-zero temperatures. A detailed description of the benthic community and the labelling experiment conducted in the FSC is presented in Gontikaki et al. (2010a and b). The taxonomic resolution of the food web compartments in the model was as detailed as allowed by the abundance, biomass and tracer uptake of the benthic fauna, as well as knowledge on the feeding mode of taxa. The main objective of this study was to use the combined LIM methodology to: (a) identify the major energy flows in the benthic food web of the deep FSC and (b) assess the feeding preferences of consumers based on the relative contribution of detrital, bacterial or faunal compartments to their diet.

2. Materials and methods

2.1. Study site and sampling

The data used in this study derived from sampling and experimental work conducted in May 2007 on FRV *Scotia* (Marine Scotland). The sampling station (61°13′88″N, 2°40′62″W) was located at 1080 m in the FSC. Bottom water temperature and salinity at the time of sampling was −0.7 °C and 34.9 respectively. Organic carbon (OC) content in the top cm was 0.2 wt.% and bottom water oxygen concentration averaged 306 ± 6.5 μmol L^{-1} (n = 9, ±*SD*). A Bowers and Connelly maxicorer was used for sediment core (i.d. 10 cm) retrieval. Six undisturbed sediment cores were sliced immediately after retrieval and were used for measuring the background (natural abundance) isotopic signatures of fauna, bulk sediment and bacterial lipids (background cores). Fifteen additional sediment cores were used in the tracer experiment (experimental cores).

2.2. Tracer experiment

The fate of phytodetritus on the seafloor of the FSC was quantified by means of a pulse-chase experiment. In order to simulate a sedimentation event, 60 mg of ^{13}C-enriched (46 atom% ^{13}C) freeze-dried diatoms (*Chaetoceros radicans*, CCMP, Bigelow Marine Laboratories) equivalent to 0.5 g C m^{-2}, was carefully added to each experimental core. The cores were sealed with lids to prevent gas exchange with air and were incubated in the dark at bottom water temperature. Three control cores (without labelled diatom addition) were also incubated together with the experimental cores. Water samples were taken at regular intervals (at time 0 and then after 24, 48, 72, 96 and 144 h) from all cores for oxygen and dissolved inorganic ^{13}C ($DI^{13}C$) concentration measurements. Oxygen concentration was measured onboard using Winkler titration and did not drop below 80% of the initial value during the experiment. The samples intended for $DI^{13}C$ analysis were filtered through a 0.2 μm syringe filter into 12 ml gas-tight glass vials and were poisoned with 100 μl of a saturated solution of $HgCl_2$ to stop bacterial activity. Six replicate cores were sectioned after 3 and 6 days of incubation (three cores for bacterial analysis and three cores for meio- and macrofaunal analysis). All control cores were sectioned on day 6. Sediment samples used for bacterial analysis [phospholipid fatty acid (PLFA) extraction] were taken from 0–0.5, 0.5–1, 1–2, 2–3, 3–5 and >5 cm horizons. The samples were placed in glass vials and stored at −20 °C until analysis. Faunal samples were taken from 0–2, 2–5 and 5–10 cm. Part of the slice was kept for meiofaunal analysis with the aid of a subcore (i.d. 2.5 cm) and the rest was sieved through a 250 μm mesh sieve. The sieved macrofauna was stored in 10% formalin until animals were picked and identified under a binocular microscope.

2.3. Sample analysis

Total lipids were extracted from sediment samples following the Bligh and Dyer (1959) extraction procedure as modified by White et al. (1979), using a single phase extractant consisting of chloroform, methanol and citrate buffer (1:2:0.8 v/v/v). The total lipid extract was fractionated into polarity classes on silicic acid columns (6 ml ISOLUTE SIS PE columns, International Sorbent Technology Ltd., UK) by sequential elution with chloroform (neutral lipids), acetone (glycolipids) and methanol (phospholipids). The phospholipids were transmethylated under alkaline methanolysis to yield fatty acid methyl esters (FAME). Details on the identification, quantification and measurement of isotopic composition of individual FAME are provided in Gontikaki et al., 2010b).

Specimens of the most abundant macrofaunal taxon (Polychaeta) were identified to genus or species level. The rest of macrofaunal organisms were identified to phylum, subphylum or order level. Nematodes that were recovered from the macrofaunal-size fraction (>250 μm) were also picked. Specimens were placed in preweighed tin cups and left to dry overnight in an evacuated desiccator. Each cup was weighed after drying in order to determine the dry weight of the specimen(s) within. The majority of specimens were analysed individually, but due to the extremely small size of some animals, some specimens of the same taxon had to be pooled together for isotopic analysis. In the case of meiofauna (retained on a 32 μm mesh sieve), only nematodes were in sufficient abundance for isotopic measurement. A minimum of 100

meiofaunal-sized nematodes per sample were picked to ensure sufficient biomass for reliable isotopic analysis. Faunal biomass (OC content) was calculated from the dry weight of each specimen (or specimens in each tin cup) and the % w/w C derived from the standard output of the isotope ratio mass spectrometer.

Carbon isotope ratios are expressed as per mil deviation (‰) from the isotope ratio of a reference material: $\delta^{13}C$ (‰) = $[(R_{sample}/R_{reference}) - 1)] \times 1000$, where R_{sample} is the ^{13}C:^{12}C ratio of the sample and $R_{reference}$ is the ^{13}C:^{12}C ratio of the international reference material for carbon Vienna Pee Dee Belemnite (R_{VPDB} = 0.0112372). Total ^{13}C uptake was calculated as the product of excess ^{13}C and the biomass of consumers or concentration of dissolved inorganic carbon (DIC) in the overlying water. Excess ^{13}C was given by the difference in the fraction ^{13}C in the sample (F_{sample}) and the background ($F_{background}$): $E = F_{sample} - F_{background}$, where $F = {}^{13}C/({}^{13}C + {}^{12}C) = R/(R + 1)$ and $R = (\delta^{13}C/1000 + 1) \times R_{VPDB}$ (Moodley et al., 2005). Bacterial uptake was based on ^{13}C incorporation into bacteria-specific PLFA according to Boschker and Middelburg (2002). Bacterial uptake calculations were based on the bacterial PLFA i15:0, a15:0 and i16:0 assuming that the average fraction of these particular PLFA is 0.11 (Gontikaki et al., 2010b) and that the average PLFA concentration in bacteria is 0.056 g C PLFA/g C biomass (Brinch-Iversen and King, 1990). The total algal carbon uptake (^{12}C + ^{13}C) recovered from bacteria, fauna and the DIC pool was calculated as the quotient of the total ^{13}C uptake and the fractional abundance of ^{13}C in the algae (0.46).

2.4. Linear inverse model formulation

The structure of the benthic food web in the FSC was described by means of a linear inverse model (Table ESM 1). The inverse modelling methodology is described extensively in Soetaert and van Oevelen (2009b) and van Oevelen et al. (2010). Briefly, this type of model is expressed as a set of linear equality equations and a set of inequality equations. The equality equations contain the mass balance of each compartment and the data on flow rates, whereas the inequality equations are used to place upper or lower boundaries on single flows or combinations of flows. The empirical data that were implemented as equalities in the FSC food web model were the whole community respiration and the stock value of each food web compartment (Table 1). The assignment of biologically realistic boundaries on unmeasured fluxes (implemented as inequality equations) was based on literature data (Table 2). Empirical data regarding physiological processes of deep-sea benthic species are lacking and thus the ranges used here derived from studies on shallow-water animals.

Inverse food web models typically have more unknown flows than equality equations (under-determinacy state). This means that an infinite number of solutions obey the equality and inequality equations (van Oevelen et al., 2006a). This set of feasible solutions is called solution space and from that we can (a) select the simplest or parsimonious food web (i.e. the solution with the minimal sum of squared flows $\Sigma_i x_i^2$), (b) quantify the range of each flow in the food web (van Oevelen et al., 2006a) or (c) perform the Monte Carlo sampling method (Kones et al., 2006; Soetaert and van Oevelen, 2009b; van Oevelen et al., 2010). In this study, we used the Monte Carlo method to sample 50,000 different food web solutions from the solution space using the R function *xsample* (van den Meersche et al., 2009). The flow values in each inverse solution are different but all combinations of flows satisfied the conventional and tracer uptake data. The complete model formulation and solution routines were performed in R 2.9.2 (R Development Core Team, 2009) using the R-package *LIM* (Soetaert and van Oevelen, 2009a) and *limSolve* (Soetaert et al., 2009).

Table 1
Field data used in the linear inverse model. Abbreviations regarding the polychaetes are: Pol_ff = filter-feeders, Pol_sdf = surface deposit-feeders, Pol_ssdf = sub-surface deposit-feeders, Pol_omn = omnivores, Pol_carn = carnivores.

Compartment name	Stock (mmol C m^{-2})
Labile detritus (det_l)	515
Non-labile detritus (det)	6450
DOC	13
Bacteria (Bac)	162
Small nematodes (Nem_s)	1.6
Large nematodes (Nem)	1.2
Polychaetes	
Pol_ff	3.4
Pol_sdf	14.5
Pol_ssdf	5.3
Pol_omn	7.6
Pol_carn	2.7
Porifera (Por)	0.9
Sipuncula (Sip)	1.6
Other macrofauna (OthMac)	16.9
Process name	Process rate (mmol C m^{-2} d^{-1})
Community respiration	1.12–3.5

2.5. Mass balances

A detailed description of the macrofaunal community structure can be found in Gontikaki et al. (2010a). Briefly, the macrofaunal community in the deep FSC was characterised by a shallow vertical distribution, in terms of both abundance and biomass. Approximately 90% of the animals were recovered from the top 2 cm. Polychaetes were the major taxon in the community and hence were identified to genus or species level. For the purposes of the food web modelling, polychaetes were grouped into feeding types according to Fauchald and Jumars (1979). An exception to this classification was the species *Paramphinome jeffreysii* (family Amphinomidae), which was considered as sub-surface deposit-feeder based on previous observations (Gontikaki et al., 2010a). Nematodes were not analysed further taxonomically, but were divided into two size groups: large nematodes (retained in the macrofaunal fraction) and small nematodes (retained on a 32 μm sieve).

Based on the taxonomic analysis, we considered the following biotic compartments for the food web model: small nematodes (meiofaunal-size), large nematodes (macrofaunal-size), filter-feeding polychaetes, surface deposit-feeding polychaetes, sub-surface deposit-feeding polychaetes, carnivore polychaetes, omnivore polychaetes, Porifera, Sipuncula and "other macrofauna" (Fig. 1). The latter grouped all taxa that could not form a separate compartment due to low abundance and biomass and lack of information on feeding types, i.e. Crustacea, Mollusca, Nemertea, Echiura and Hydrozoa. Bacteria formed a separate food web compartment. Bacterial biomass was determined from the concentration of bacteria-specific PLFA (White et al., 1979; Middelburg et al., 2000; Gontikaki et al., 2010b). Additionally, three abiotic compartments were defined: sedimentary labile detritus, sedimentary refractory detritus and pore-water dissolved organic carbon (DOC) (Fig. 1).

The biotic and abiotic compartments of the food web exchange flows with a number of compartments that are not considered in the food web (external compartments). Five external compartments were defined: the labile and refractory detritus in the water column, the overlying water DOC, the DIC and an external compartment that combined losses from the food web such as migration and predation by megafauna (export compartment) (Fig. 1). Carbon inputs are the labile and refractory detritus deposition (fluxes from the water column detritus pools to the sedimentary detritus pools). Filter-feeding polychaetes and Porifera ingest labile and refractory detritus from the water column. The particulate organic carbon (POC) in the sediment (labile and refractory sedimentary detritus) is hydrolysed by bacteria to DOC, which is either

Table 2
Physiological constraints used in the linear inverse model. References are (1) del Giorgio and Cole, 1998; (2) Kroer, 1993; (3) Danovaro et al., 2008; (4) Herman and Vranken, 1988; (5) Marchant and Nicholas, 1974; (6) Heip et al., 1985; (7) Schiemer, 1982; (8) Soetaert and van Oevelen, 2009b; (9) Buhr, 1976; (10) Loo and Rosenberg, 1996; (11) Jordana et al., 2001; (12) Vedel and Riisgard, 1993; (13) Stead et al., 2003; (14) Navarro and Thompson, 1996; (15) Rice et al., 1986; (16) Whitlatch, 1974; (17) Shafir and Field, 1980; (18) Nielsen et al., 1995; (19) Banse, 1979; (20) Navarro et al., 1994; (21) Davis and Wilson, 1985; (22) Clausen and Riisgard, 1996; (23) Sprung, 1993; (24) Robertson, 1979; (25) Tenore, 1982; (26) Johnson, 1976; (27) Heip and Herman, 1979; (28) Chesney, 1985; (29) Thompson and Schaffner, 2001; (30) Cartes et al., 2009; (31) Honjo et al., 1988; (32) Sauter et al., 2001; (33) Francois et al., 2002. Abbreviations of macrofaunal compartments as in Table 1.

Process	Min.	Max.	Reference
Bacteria			
BGE[a] (–)	0.4	0.6	1, 2
Viral lysis[b] (–)	0.4	3	
Nematodes			
Maintenance respiration (mmol C m^{-2} d^{-1})	Tlim[f] · 0.01 · [stock]		8
AE[c] (–)	0.06	0.3	8
NGE[d] (–)	0.3	0.9	4–8
Growth rate[e] (d^{-1})	Tlim[f] · 0.05	Tlim[f] · 0.25	4, 6, 7
Macrofauna			
Maintenance respiration (mmol C m^{-2} d^{-1})	Tlim[f] · 0.005 · [stock]		10, 17, 23, 24, 27–30
AE[c] (–)			
Pol_ff	0.6	0.7	9–14, 20
Pol_sdf	0.85	0.95	10, 13
Pol_ssdf	0.2	0.3	15, 16
Pol_carn	0.85	0.95	17, 26
Pol_omn	0.85	0.95	10, 13, 17, 26
Sip, Por, OthMac	0.4	0.75	9–17, 20, 26
NGE[d] (–)			
Pol_ff	0.75	0.85	20–22
Pol_sdf	0.5	0.8	19, 21
Pol_ssdf	0.2	0.5	19
Pol_carn	0.4	0.6	17, 18
Pol_omn	0.25	0.55	19, 21
Sip, Por, OthMac	0.5	0.7	17–22
Growth rate[e] (d^{-1})	Tlim[f] · 0.005	Tlim[f] · 0.01	10, 17, 21, 23–25, 27–30
Organic carbon flux (mmol C m^{-2} d^{-1})	0.46	2.4	31–33

[a] Bacterial growth efficiency (BGE) = $\frac{\text{bacterial assimilation-bacterial respiration}}{\text{bacterial assimilation}}$.
[b] Lysis = flow from bacteria → DOC.
[c] Assimilation efficiency (AE) = $\frac{\sum \text{consumption} - \text{defecation}}{\sum \text{consumption}}$.
[d] Net growth efficiency (NGE) = $\frac{\sum \text{consumption} - \text{defecation} - \text{growth respiration}}{\sum \text{consumption} - \text{defecation}}$.
[e] Growth rate (d^{-1}) = $\frac{\sum \text{consumption} - \text{defecation} - \text{growth respiration}}{\text{biomass}}$.
[f] Tlim $= Q10 \times \exp\left(\frac{T-20}{10}\right) = 0.24$, where $Q10 = 2$ and $T = -0.7$ °C.

consumed by bacteria or escapes to the water column (Fig. 1). The flow from bacteria to DOC represents losses from the bacterial compartment due to viral lysis. We considered the extracellular hydrolysis of particulate compounds and viral lysis of bacterial cells to be the major contributors to the DOC compartment (Danovaro et al., 2008). Although DOC may derive from alternative sources, such as direct release by bacteria in the form of extracellular enzymes or excretion and faecal pellet production by fauna, these are not considered to be of primary importance (Carlson, 2002). We are thus confident that the non-inclusion of secondary sources of DOM in the food web did not introduce great error.

Small nematodes consume bacteria and detritus (if not specified, both labile and refractory detritus pools are assumed under the general term "detritus"), while large nematodes consume bacteria and detritus plus meiofaunal-size nematodes. Surface and sub-surface deposit-feeding polychates and Sipuncula feed on detritus, bacteria and nematodes (meio- and macrofaunal-size). Omnivorous polychaetes feed on detritus, bacteria and all faunal compartments apart from carnivore polychaetes. Carnivorous polychaetes consume animals from all faunal compartments apart from omnivore polychaetes. Although categorised as carnivores, the actual feeding type of these animals is relatively unknown. For this reason carnivorous polychaetes were also linked with the labile and refractory detritus and the bacterial compartments. Due to the large size of the omnivore polychaetes in our study site (>2.8 mg WW ind^{-1}), predation on this group by other macrofauna was excluded. The "other macrofauna" compartment obtains its carbon from the water column detritus, the sediment detritus, bacteria and all faunal compartments apart from omnivore and carnivore polychaetes. All faunal compartments produce refractory detritus through defecation (dashed arrows, Fig. 1). The respiration flows from the bacterial and faunal compartments end up in the DIC pool. For simplicity reasons all respiration flows are depicted as one export flow to DIC (thick arrow, Fig. 1). Losses from each faunal compartment (diamond-head arrows, Fig. 1) are due to processes such as predation from megafauna or migration and end up in an external compartment (export). We considered only the 0–2 cm horizon because of the shallow distribution of the community and the absence of isotope tracer below 2 cm (Gontikaki et al., 2010a and b). The detritus stock was calculated from the total OC in the sediment. The labile detritus stock was set to be equal to the mineralizable carbon calculated by Heip et al. (2001) for a bathyal station (1034 m) in the Goban Spur. The DOC stock was calculated based on literature DOC pore-water concentrations from NE Atlantic and Arctic bathyal sediments (Hulth et al., 1996; Otto and Balzer, 1998; Papadimitriou et al., 2002).

2.6. Dynamic isotope tracer model

Each mass-balanced food web solution from the Monte Carlo sampling was used to start up a dynamic isotope tracer model,

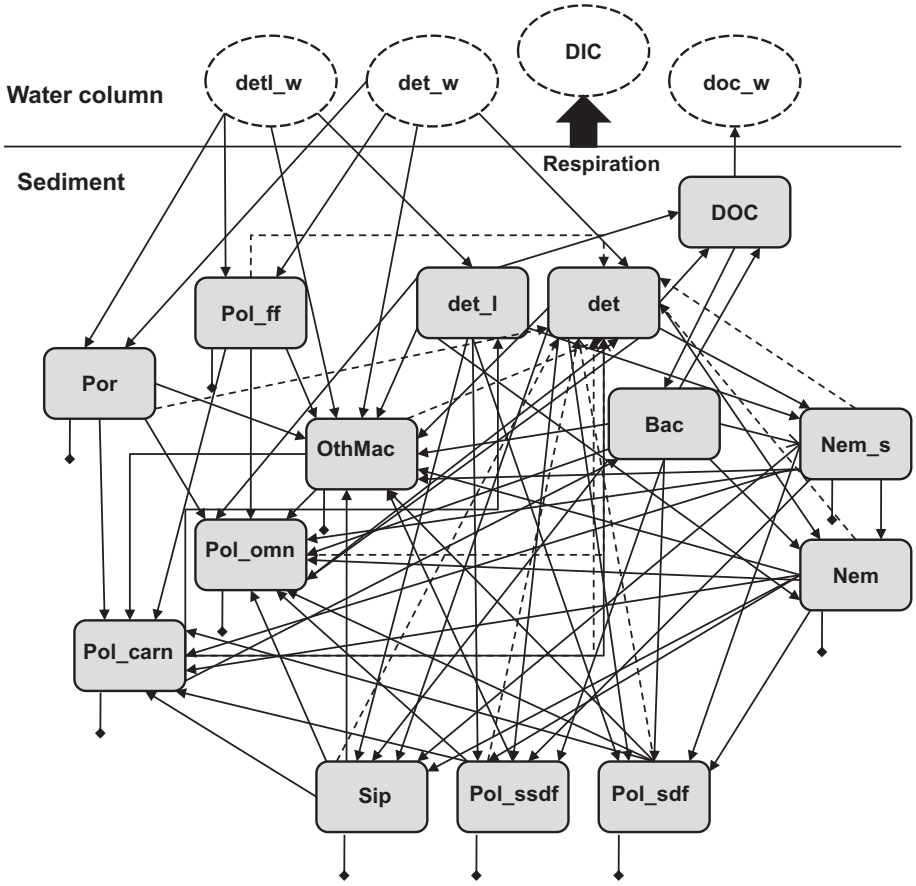

Fig. 1. The biotic, abiotic and external compartments considered in the food web model. Solid lines represent food web flows between compartments. Dashed lines illustrate defecation flows (flows from faunal compartments to the refractory detritus pool). The thick arrow is the combined respiration from the bacterial and faunal compartments and the diamond-head arrows represent losses that end up in the export compartment (not shown). detl_w: water column labile detritus, det_w: water column refractory detritus, DIC: dissolved inorganic carbon, doc_w: water column dissolved organic carbon, det_l: sedimentary labile detritus, det: sedimentary refractory detritus, DOC: pore-water dissolved organic carbon, Bac: bacteria, Nem_s: meiofaunal-size nematodes, Nem: macrofaunal-size nematodes, Pol_sdf: surface deposit-feeding polychaetes, Pol_ssdf: sub-surface deposit-feeding polychaetes, Pol_ff: filter-feeding polychaetes, Pol_omn: omnivore polychaetes, Pol_carn: carnivore polychaetes, Sip: Sipuncula, Por: Porifera, OthMac: other macrofauna.

which simulated the transfer of the ^{13}C tracer through the food web. The tracer was introduced in the labile detritus compartments (water column and sedimentary labile detritus pools) of the dynamic model to make the simulation comparable with the results from the ^{13}C-labelled phytodetritus deposition experiment. As such, the model-predicted tracer concentrations could be directly compared with the data from the tracer experiment. The purpose of the dynamic model was to find the solution from the set of 50,000 solutions (see Section 2.4) that best reproduced the experimental data.

The tracer model was set up under the assumption that the total carbon stock of each compartment remained in steady-state, but that the ^{13}C tracer concentration in each compartment was transient. In the following equations, the notation is as follows: $^{13}C_a$ is the excess ^{13}C in compartment a (mmol $^{13}C\,m^{-2}\,d^{-1}$), $f_{a\to b}$ is the carbon flow from compartment a to compartment b (mmol $C\,m^{-2}\,d^{-1}$), S_a is the standing stock of compartment a (mmol $C\,m^{-2}$) and F_a is the fraction of excess ^{13}C in compartment a ($^{13}C/^{12}C + {}^{13}C$). Further, AE_a is the assimilation efficiency of compartment a (–), NGE_a is the net growth efficiency of compartment a (–), BGE is the bacterial growth efficiency (–) and ρ_a is the biomass-specific maintenance respiration rate of compartment a (d^{-1}). For clarity, below each term in the following ordinary differential equations is a brief explanation.

The ordinary differential equations that describe the abiotic compartments of labile and refractory detritus are given by

$$\frac{d^{13}C_i}{dt} = \underbrace{f_{w\to i}\cdot F_w}_{\text{labile detritus deposition}} + \underbrace{\sum_{fau}\sum_k (1-AE_{fau})\cdot f_{k\to fau}\cdot F_k}_{\text{faeces production}} - \underbrace{\sum_j f_{i\to j}\cdot F_i}_{\text{detritus dissolution}}$$

in which *fau* represents an index for the faunal compartments and k their respective food sources. Note, that the term "labile detritus deposition" is included only in the mass balance of the labile detritus compartment and the "faeces production" term only in the mass balance of the refractory detritus compartment.

The DOC compartment is described by

$$\frac{d^{13}C_{doc}}{dt} = \underbrace{\sum_i f_{i\to doc}\cdot F_i}_{\text{detritus dissolution}} + \underbrace{f_{bac\to doc}\cdot F_{bac}}_{\text{bacterial mortality}} - \underbrace{f_{doc\to bac}\cdot F_{doc}}_{\text{bacterial uptake}} - \underbrace{f_{doc\to docw}\cdot F_{doc}}_{\text{doc efflux}}$$

where i is an index for the labile or the refractory detritus compartments. The bacterial compartment is given by

$$\frac{d^{13}C_{bac}}{dt} = \underbrace{f_{doc\to bac}\cdot F_{doc}}_{\text{uptake}} - \underbrace{(1-BGE)\cdot f_{doc\to bac}}_{\text{growth respiration}} - \underbrace{\sum_j f_{bac\to j}\cdot F_{bac}}_{\text{predation+mortality}}$$

where j is an index for the faunal compartments. The ^{13}C mass balance of the faunal compartments is given by

$$\frac{d^{13}C_{fau}}{dt} = \underbrace{\sum_k f_{k\to fau}\cdot F_k}_{ingestion} - \underbrace{(1-AE_{fau})\cdot\sum_k f_{k\to fau}\cdot F_k}_{faces\ production} - \underbrace{(1-NGE_{fau})\cdot AE_{fau}\cdot\sum_k f_{k\to fau}\cdot F_k}_{growth\ respiration} - \underbrace{\rho_{fau}\cdot S_{fau}\cdot F_{fau}}_{maintanance\ respiration} - \underbrace{\sum_j f_{fau\to j}\cdot F_{fau}}_{predation+export}$$

The flow values and the physiological parameters ρ, BGE, AE and NGE were calculated for each LIM solution. The dynamic tracer model was initialized by setting the Fdet_l and Fdetl_w (i.e. the $^{13}C/^{12}C + ^{13}C$ ratio of labile detritus in the sediment and water column respectively) to 0.46 (algal enrichment was 46 atom % ^{13}C). The ^{13}C and corresponding F values of the other compartments were initially set to zero. The tracer model was solved in the R environment with the *vode* integration routine (*deSolve* package; Soetaert et al., 2010).

The simulated tracer concentrations and respired ^{13}C in each compartment were compared to the total carbon uptake experimental data. The goodness-of-fit was evaluated by the following cost function:

$$J = \sum_{i=1}^{nv}\sum_{j=1}^{no}\left(\frac{Mod_{ij}-Obs_{ij}}{Obs_{ij}}\right)^2$$

where nv is the number of variables for which data are available, no is the number of observations for each variable, Mod_{ij} is the modelled value of the counterpart observation Obs_{ij}. For each model, data deviation is divided by the corresponding observational value to non-dimensionalize the cost function. The inverse solution that had the lowest cost function was accepted as the best food web solution. In order to assess the uncertainty of the flow values, we sampled the best 10% of all food webs that were tested by the dynamic model and defined the minimum and maximum value of each flow within this set of best solutions (see also van Oevelen et al., 2006a). Total computing time is ~2 days for the Monte Carlo sampling of the linear inverse model and another 2 days to evaluate the goodness-of-fit in the dynamic tracer model.

3. Results

3.1. Pulse-chase experiment

A detailed analysis of the pulse-chase experiment results can be found in Gontikaki et al. (2010a and b). In summary, 14.9 and 0.81 mg C m^{-2} of the algal carbon was recovered from bacterial and faunal biomass respectively after 3 days of incubation while only 3.8 mg C m^{-2} was respired. Respiration was the dominant tracer pathway after 6 days of incubation (44 mg C m^{-2}) while bacterial uptake did not increase significantly from day 3 to day 6. The tracer recovered from metazoan fauna at the end of the experiment constituted 3.2% (2 mg C m^{-2}) of the total processed carbon however, meiofauna contributed only ~1% to the total metazoan uptake. Approximately 70% of the macrofauna specimens had ingested the labelled substrate at the end of the experiment with surface deposit-feeding polychaetes, such as Ampharetidae and Cirratulidae, being among the most heavily labelled.

3.2. Dynamic tracer simulation

The best inverse model solution selected by the dynamic model overestimated the tracer flow in the small and large nematodes, and Sipuncula compartments (default model best solution, Fig. ESM1). The "problem" was that a simultaneous low contribution of labile detritus and bacteria (highly labelled food sources) to the diet of nematodes and Sipuncula was poorly sampled in the 50,000 set of solutions that were tested by the dynamic model. In order to obtain a better fit for the above compartments, we decided to "guide" the Monte Carlo sampling to produce a new set of solutions from the solution space that would be prone to give a better fit. For this purpose, a number of additional constraints were introduced as inequality equations in the LIM model (hereafter referred to as modified model) that posed limits on the contribution of the labelled food sources to the diet of both nematode compartments and Sipuncula (Table ESM 1). The correspondence between the ^{13}C uptake data and best solution of the modified model improved significantly for nematodes and Sipuncula, while the fit for the rest of the compartments remained satisfactory (Fig. 2, see also Fig. ESM1 for comparison with the default model). The residual errors in the small and large nematode compartments decreased by two and three orders of magnitude respectively. The improvement in the Sipuncula fit was even greater with the residual error dropping by five orders of magnitude. The flow values of the modified solution are presented in Table 3 and will be discussed throughout the remainder of the manuscript. For comparison, the flow values of the initial (default) solution are given in the Electronic Supplementary material (Table ESM 2).

3.3. Uncertainty analysis

The merging of tracer uptake data with the LIM model resulted in a significant decrease in the uncertainty associated with food web reconstructions. The range of possible values in 45% of the food web flows decreased by >20% while in 21% of the flows the range was reduced by >40% (Fig. 3, Table ESM 3). The uncertainty in the LIM model (before tracer data incorporation) was highest for the flows from refractory detritus to small and large nematodes and vice versa (det → Nem_s, Nem_sFeces, det → Nem, NemFeces) and for bacterial ingestion, with ranges >3.5 mmol C m^{-2} d^{-1} (Fig. 3, Table ESM 3). The tracer data constrained the uncertainty by ~80% for det → Nem_s and Nem_s → det, 35–38% for the large nematode compartment and 24% for bacterial ingestion. The largest uncertainty after the incorporation of tracer data among the highest magnitude flows was related to the fluxes from refractory detritus to DOC and from pore-water DOC to water column DOC (det → DOC and DOC → doc_w respectively; Fig. 3).

3.4. Benthic carbon flows

The bulk of the deposited OC (69%) was respired by the benthic community and 70% of total respiration was attributed to bacteria (Fig. 4). Macrofauna and meiofauna (including macrofaunal-size nematodes) were responsible for 14% and 16% of the total carbon respiration respectively (Fig. 4). Respiration among the assigned faunal groups from highest to lowest was: large nematodes > small nematodes > other macrofauna > omnivore polychaetes > sub-surface deposit-feeding polychaetes > surface deposit-feeding polychaetes > Sipuncula > carnivore polychaetes > filter-feeding polychaetes > Porifera (Table 3). Secondary production was estimated at 0.21 mmol m^{-2} d^{-1} and 72% of that was attributed to small and large nematode growth (Fig. 4).

Bacteria converted 2.03 mmol C m^{-2} d^{-1} of POC to the dissolved phase (sum of det_l → DOC and det → DOC). The DOC compartment was further complemented by viral-induced bacterial lysis (1.03 mmol C m^{-2} d^{-1}). DOC escaped from the sediment to the overlying bottom water at a rate of 0.61 mmol C m^{-2} d^{-1} (27% of OC flux and 39% of total respiration) but the uncertainty related to DOC efflux is high (range: 0–1.09 mmol C m^{-2} d^{-1}; Fig. 3). Bacterial uptake reached 2.45 mmol C m^{-2} d^{-1} and bacterial production (BP = BacIngestion – BacResp, Table 3) was estimated at 1.36 mmol C m^{-2} d^{-1} (range: 0.72–3.01 mmol m^{-2} d^{-1}) with a

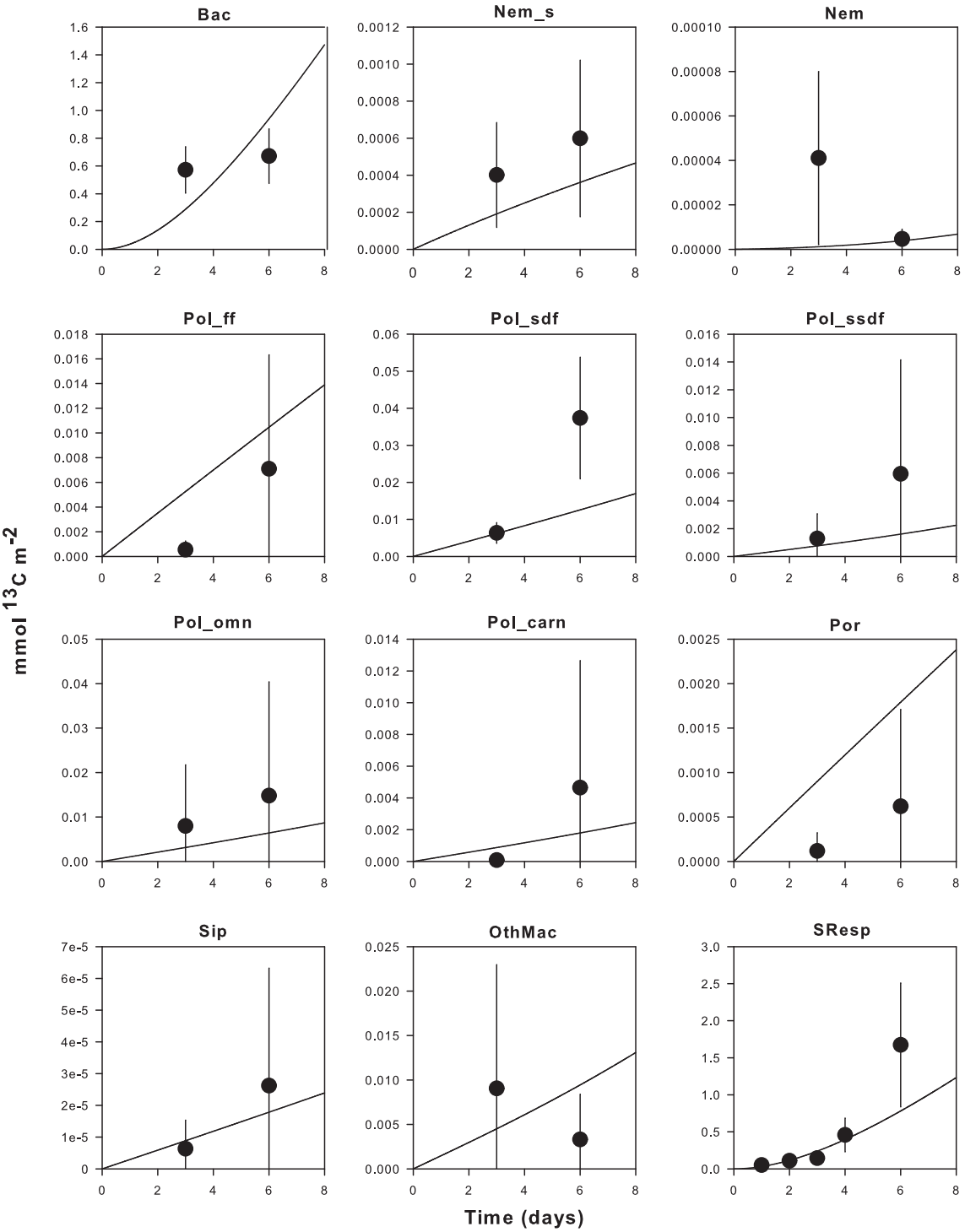

Fig. 2. Simulated tracer dynamics in the benthic food web compartments of the Faroe–Shetland Channel (solid lines) based on the best solution of the modified model. Filled symbols in the bacterial and faunal compartments correspond to the measured ^{13}C uptake values on days 3 and 6 after the initiation of the experiment (±SE, $n = 3$). The abbreviations for the faunal compartments are given in Fig. 1. SResp is the sum of respiration flows and filled symbols are the measured DI^{13}C concentration (± SE, $n = 6$) after 1, 2, 3, 4 and 6 days of incubation.

BGE $\left(=\frac{BP}{BP+BacResp}\right)$ of 0.55 (range: 0.55–0.59). Viral-induced bacterial lysis accounted for ~76% of BP (range: 67–96% of BP). The remaining fraction of BP (24%) was grazed by the metazoan community.

The main carbon source of metazoans was detritus (90%), followed by bacteria (7%) (Fig. 5). Approximately 90% of the ingested detritus derived from the refractory pool. Small and large nematodes were the major consumers of this refractory detritus among metazoan fauna accounting for 57% and 40% of the metazoan consumption of refractory detritus respectively (Fig. 5). Bacteria were grazed primarily by sub-surface deposit-feeding polychaetes and animals within the "other macrofauna" compartment (38% and 35% of metazoan bacterial consumption respectively) (Fig. 6) although these fluxes were not particularly well-constrained (Fig. 3). The diet of small and large nematodes de-

Table 3
Food web flow values (mmol C m^{-2} d^{-1}) derived from the best solution of the modified model. For meaning of abbreviations see Fig. 1.

Flow name	Flow value	Flow name	Flow value	Flow name	Flow value	Flow name	Flow value
detl_w → det_l	1.709	det → Pol_ssdf	0.036	Sip → Pol_omn	0.000	Pol_sdf → OthMac	0.006
det_w → det	0.503	Bac → Pol_ssdf	0.123	OthMac → Pol_omn	0.005	Pol_ssdf → OthMac	0.002
det_l → DOC	1.681	Nem_s → Pol_ssdf	0.062	Pol_omnResp	0.054	Pol_ff → OthMac	0.000
det → DOC	0.345	Nem → Pol_ssdf	0.025	Pol_omnFeces	0.007	Por → OthMac	0.000
DOC → doc_w	0.611	Pol_ssdfResp	0.048	Pol_omn → export	0.009	Sip → OthMac	0.000
BacIngestion	2.446	Pol_ssdf → export	0.004	detl_w → Pol_ff	0.005	OthMacResp	0.056
Lysis	1.031	Pol_ssdfFeces	0.198	det_w → Pol_ff	0.009	OthMacFeces	0.073
BacResp	1.089	det_l → Pol_carn	0.001	Pol_ffResp	0.006	OthMac → export	0.013
det_l → Nem_s	0.004	det → Pol_carn	0.001	Pol_ff Feces	0.005		
det → Nem_s	2.489	Bac → Pol_carn	0.008	Pol_ff → export	0.001		
Bac → Nem_s	0.019	Nem_s → Pol_carn	0.001	detl_w → Por	0.001		
Nem_sFeces	2.314	Nem → Pol_carn	0.001	det_w → Por	0.003		
Nem_sResp	0.106	Pol_sdf → Pol_carn	0.001	PorResp	0.002		
Nem_s → export	0.005	Pol_ssdf → Pol_carn	0.000	PorFeces	0.001		
det_l → Nem	0.000	Pol_ff → Pol_carn	0.000	Por → export	0.000		
det → Nem	1.740	Por → Pol_carn	0.000	det_l → Sip	0.000		
Bac → Nem	0.002	Sip → Pol_carn	0.000	det → Sip	0.064		
Nem_s → Nem	0.010	OthMac → Pol_carn	0.002	Bac → Sip	0.000		
NemFeces	1.554	Pol_carnResp	0.010	Nem_s → Sip	0.005		
NemResp	0.137	Pol_carnFeces	0.002	Nem → Sip	0.000		
Nem → export	0.031	Pol_carn → export	0.003	SipResp	0.015		
det_l → Pol_sdf	0.005	det_l → Pol_omn	0.006	SipFeces	0.053		
det → Pol_sdf	0.017	det → Pol_omn	0.014	Sip → export	0.001		
Bac → Pol_sdf	0.024	Bac → Pol_omn	0.037	detl_w → OthMac	0.003		
Nem_s → Pol_sdf	0.004	Nem_s → Pol_omn	0.003	det_w → OthMac	0.006		
Nem → Pol_sdf	0.001	Nem → Pol_omn	0.001	det_l → OthMac	0.005		
Pol_sdfResp	0.031	Pol_sdf → Pol_omn	0.000	det → OthMac	0.011		
Pol_sdf → export	0.007	Pol_ssdf → Pol_omn	0.000	Bac → OthMac	0.114		
Pol_sdfFeces	0.006	Pol_ff → Pol_omn	0.002	Nem_s → OthMac	0.001		
det_l → Pol_ssdf	0.007	Por → Pol_omn	0.001	Nem → OthMac	0.001		

pended heavily on refractory detritus (99% of total ingested carbon in both compartments). Refractory detritus was also the main source of energy for Sipuncula, Porifera and filter-feeding polychaetes accounting for 92% (0.005–0.077 mmol C m^{-2} d^{-1}), 79% (0–0.004 mmol C m^{-2} d^{-1}) and 67% (0–0.016 mmol C m^{-2} d^{-1}) of the total ingested carbon by each compartment respectively (Fig. 7). On the contrary, bacteria were the major contributor to the diet of "other macrofauna" (76%; 0–0.170 mmol C m^{-2} d^{-1}), carnivore polychaetes (53%; 0–0.011 mmol C m^{-2} d^{-1}), omnivore polychaetes (53%; 0–0.058 mmol C m^{-2} d^{-1}), sub-surface deposit-feeding polychaetes (49%; 0–0.178 mmol C m^{-2} d^{-1}) and surface deposit-feeding polychaetes (48%; 0–0.073 mmol C m^{-2} d^{-1}) (Fig. 7). Sub-surface deposit-feeding polychaetes were the only significant consumers of small nematodes (0–0.079 mmol C m^{-2} d^{-1}) obtaining 24% of their energy requirements from small nematode ingestion (Fig. 7). The rates of the calculated physiological processes for each faunal compartment in the food web are presented in Table 4.

4. Discussion

This study presents carbon flows through a cold-adapted deep-sea benthic food web, based on the integration of oxygen consumption, biomass and isotope tracer uptake of the organisms. The range and taxonomic resolution of the benthic organisms considered, as well as the replication of the experimental design are rare in deep-sea food web studies. The combination of such high quality data with the LIM methodology renders this food web reconstruction as one of the best constrained food webs in bathyal sediments so far. The food web formulation extended beyond a simple categorization of benthic organisms as a single "infaunal" group and allowed the study of niche differentiation between several faunal compartments (two meiofaunal and eight macrofaunal groups). The carbon budgets that will be discussed are based on total carbon flows in the food web and not ^{13}C only.

4.1. Benthic fluxes

Benthic secondary production in the deep-sea depends on the input of detrital OM produced in the euphotic zone. The biomass and abundance of benthic organisms is positively linked to the POC flux reaching the deep ocean floor which is largely reflected in the sediment community oxygen consumption (SCOC) (Smith et al., 2008, 2009). The SCOC calculated from the model output for the FSC (1.56 mmol C m^{-2} d^{-1}) is comparable to the compiled average oxygen uptake in the lower slope (1000–2000 m) of continental margins (1.23 mmol C m^{-2} d^{-1}; Canfield et al., 2005) and agrees well with previous measurements in Arctic slope sediments (1.57 mmol C m^{-2} d^{-1} at 1010 m; Hulth et al., 1994). The benthic DOC flux represented 39% of the total carbon oxidation rate, as calculated by the SCOC. This value is higher than the average % DOC flux to carbon oxidation in continental margin sediments (10% at 200–2000 m, Burdige et al., 1999), although similar or even higher fractions have been measured in certain abyssal stations in the NE Atlantic and in the Arabian Sea (Otto and Balzer, 1998; Papadimitriou et al., 2002; Lahajnar et al., 2005). It should be noted however that the uncertainty associated to this flux is considerable (the DOC efflux ranged between 0% and 40% of the total carbon oxidation rate) and thus no safe conclusions can be drawn from the modelled estimate.

4.2. Bacterial production and growth efficiency

BP in the FSC is among the highest values reported for deep-sea sediments (Danovaro et al., 2008). The high BP and turnover is supported by a strong viral shunt which is responsible for the release of readily available OC and stimulation of the metabolism of uninfected cells. The viral-induced bacterial lysis in the FSC sediments (76% of BP) fell between the global average estimate for mesopelagic (>160–1000 m) and >1000 m sediments (64% and 89% of BP respectively; Danovaro et al., 2008). The high percentage of

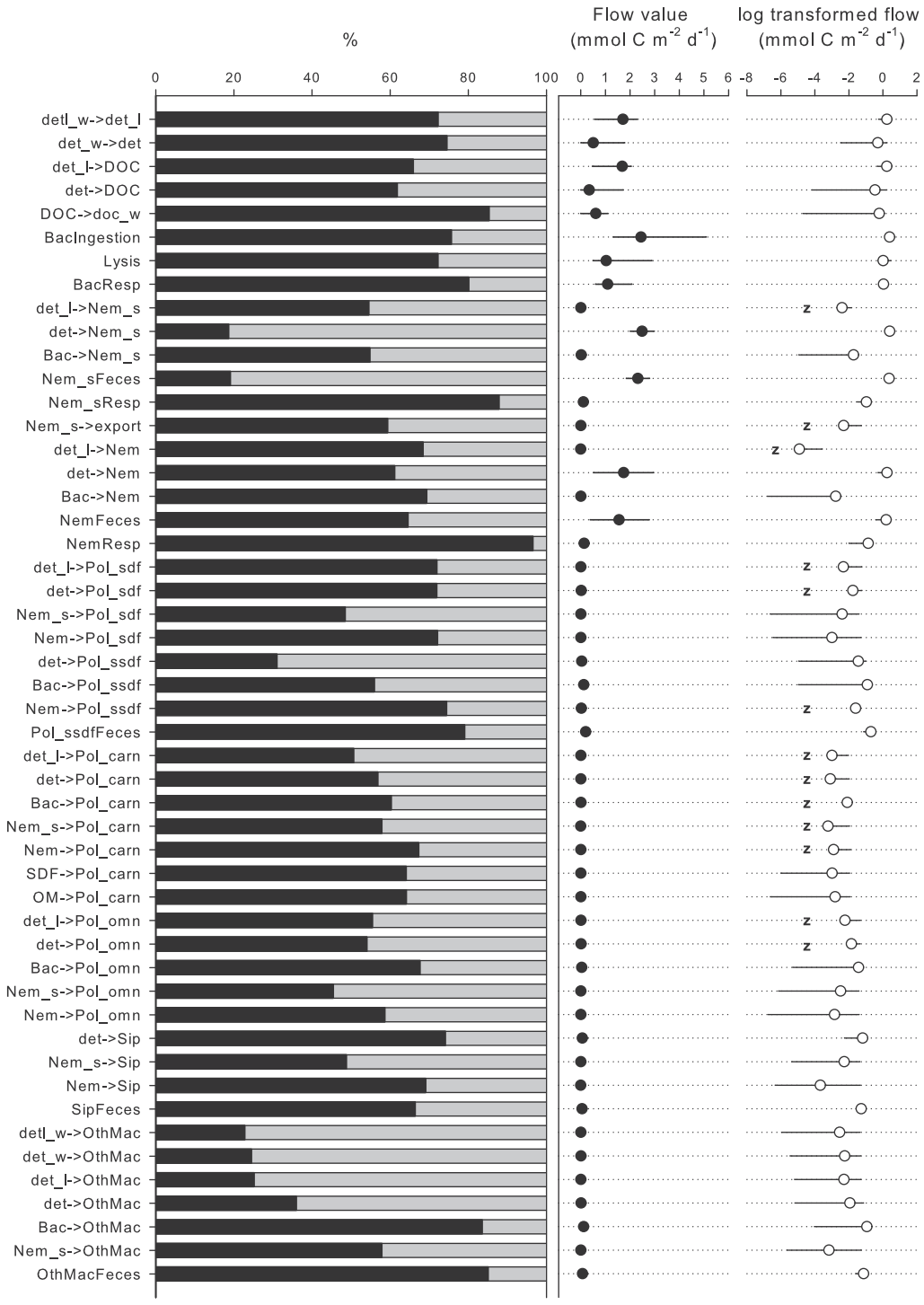

Fig. 3. Reduction in flow value uncertainty of 50 flows following the incorporation of tracer uptake data (grey area). Only flows of which the reduction in uncertainly was >15% were plotted. Small and large nematode respiration fluxes (Nem_sResp and NemResp respectively) were also plotted due to their importance in the food web (among the 20% highest fluxes) although the reduction in uncertainty was <15%. Absolute flow values (black circles) and log-transformed flow values (white circles) were based on the best model solution. The flow ranges that are shown were based on the best 10% of possible solutions derived from Monte Carlo sampling. The zero-bounded fluxes are indicated by "z" in the log-transformed flow axis.

prokaryote mortality in the FSC may result in the acceleration of biogeochemical processes in the sediment and could limit the transfer of bacterial carbon to higher trophic levels.

The high BGE of the FSC sedimentary bacteria implies that a relatively high percentage of bacterial carbon assimilation was channelled towards production rather than respiration. However, the modelled BGE is primarily constrained by the labile detritus fluxes (i.e. ^{13}C incorporation into bacterial biomass and ^{13}C-DIC production) and is thus expected to be slightly exaggerated compared to BGE values based on a mixture of labile and refractory substrates. Despite that, similar BGE values have been calculated for deep-sea sediments from the Greenland and Norwegian Basins (Deming and Yager, 1992), the Arabian Sea and the NW Mediterranean (Tholosan and Bianchi, 1998; Boetius et al., 2000). On the

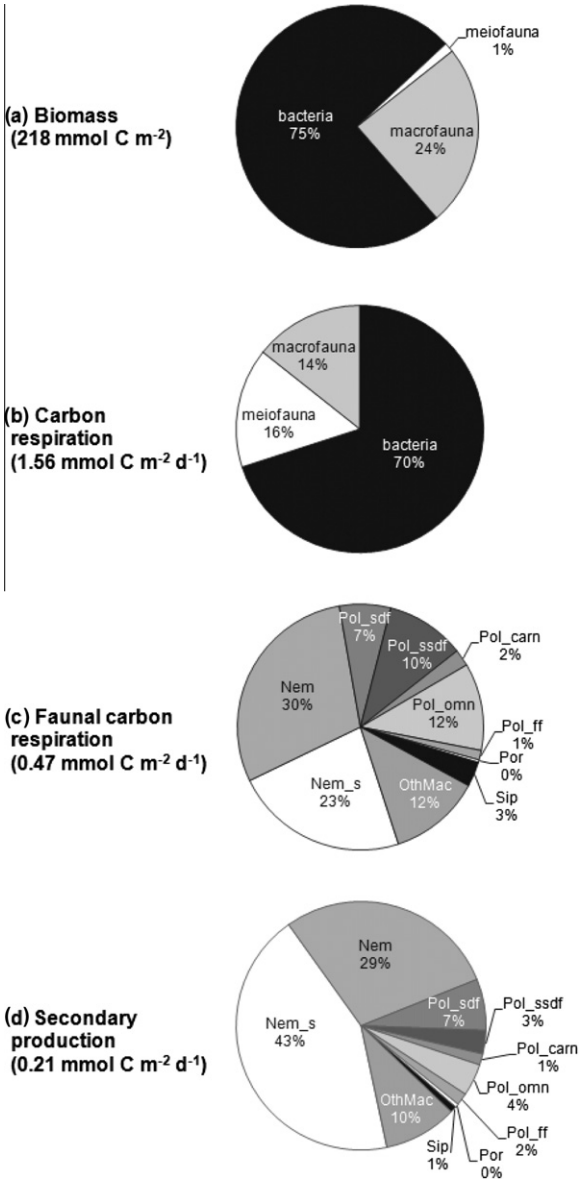

Fig. 4. Biomass distribution and partitioning of benthic respiration and secondary production among food web components. See Fig. 1 for meaning of abbreviations of the faunal compartments. In brackets is the total flux represented by each pie chart.

contrary, bacteria in abyssal sediments of the temperate NE Atlantic partitioned ~90% of the assimilated carbon towards respiration (low BGE) (Deming and Yager, 1992). It is apparent that much uncertainty surrounds the magnitude and variation of BGE in natural bacterial populations and several factors including temperature, OM availability and the particular energetic demands of each system, interact in producing the measured value (del Giorgio and Cole, 1998; Apple et al., 2006). Particularly high BGE values (0.5–0.8) have been measured when bacteria were supplied with OM excreted by phytoplankton (EOC) in comparison to lower values (0.1–0.3) when the energy source was particulate organic detritus derived from phytoplankton (del Giorgio and Cole, 1998). The addition of labelled diatoms into the experimental cores introduced both the above OM sources for sediment bacteria in the FSC. BGE was actually observed to change from initial high values to subsequent low values in the second half of the experiment, which probably indicated a change in the bacterial OM source from EOC to phytoplanktonic detritus (Gontikaki et al., 2010b). The misfit of the respiration data on day 6 (Fig. 2) can be explained adequately on the basis of a reduction in BGE with time. The initial high BGE was realised as high bacterial ^{13}C incorporation and low respiration, however the subsequent decrease of BGE and simultaneous enhancement of respiration was not accounted for in the model and resulted in a poorer fit of the data on day 6.

4.3. Respiration partitioning

Bacterial respiration accounted for ~70% of the sedimentary oxygen consumption in the FSC supporting the present view on heterotrophic bacteria as the major consumers and remineralizers of OM in the ocean (del Giorgio and Cole, 1998; Falkowski et al., 2008). Previously reported estimates of the contribution of bacterial respiration to the total oxygen consumption in the deep-sea ranged from 45% to 60% (Eldridge and Jackson, 1993; Rowe et al., 2008). Microfaunal respiration (bacteria and protozoa) in the Arctic (200–1000 m) accounted for 68% of SCOC (Piepenburg et al., 1995) and although the fraction of bacterial respiration was not specified, it is safe to assume that the major part of microfaunal respiration was attributed to bacteria. The respiration partitioning in the FSC (70% bacteria–30% metazoan respiration) was closer to the pattern reported for the lower slope (1460–4460 m) of the Goban Spur (~20% metazoan respiration and 80% microbial respiration) despite the fact that the macrofaunal community of the FSC resembled that of the upper slope (200–1000 m) in the Goban Spur (~50% metazoan respiration), in terms of abundance, biomass, vertical distribution and polychaete feeding type composition (Flach and Heip, 1996; Heip et al., 2001; Gontikaki et al., 2010a). The respiration rates of metazoans calculated by Heip et al. (2001) were based on allometric regressions with biomass (Mahaut et al., 1995) and the discrepancy with the FSC respiration partitioning could be explained on the basis of methodological differences. In order to verify the comparability between the two methods, we applied the allometric relation, developed by Mahaut et al. (1995), to assess macrofaunal respiration (macrofaunal-sized nematodes not included) in the FSC. The macrofaunal respiration rates calculated by both methods differed by <0.01 mmol C m^{-2} d^{-1} and suggested that allometric-based and modelled respiration rates are directly comparable. The difference in macrofaunal respiration rate between the upper slope of the Goban Spur and the FSC is thus more likely a result of the lower metabolic requirements of fauna at subzero temperatures (Clarke, 1993; Clarke and Fraser, 2004). On the other hand, the total SCOC of the two benthic communities (Goban Spur ~1000 m and FSC) is strikingly similar (1.8 mmol C m^{-2} d^{-1}, Heip et al., 2001; 1.56 mmol C m^{-2} d^{-1}, this study) suggesting that, unlike fauna, microbial respiration is not suppressed by low temperature and is more likely determined by POM flux and resulting trophic state of the sediment.

4.4. Metazoan carbon sources

Refractory detritus covered the major part of metazoan carbon requirements however, 96% of the total refractory detritus consumption was attributed to ingestion by nematodes. Ingestion and defecation by nematodes dominated carbon flows among metazoans (Fig. 5). However, due to their low AE, the dominance of nematodes vanished when considering respiration and/or secondary production (Table 4, Fig. 4). Macrofaunal organisms obtained their energy primarily from bacteria and, to a lesser extent, from refractory detritus. Labile detritus covered merely 5% of the energy requirements of macrofauna. However, only a minor proportion of the labile detritus flux was available for consumption by fauna since 98% was recycled within the DOC-bacteria loop (Fig. 5). Similarly to the respiration partitioning pattern, the dominance of bacteria in the labile detritus consumption could be attributed to an

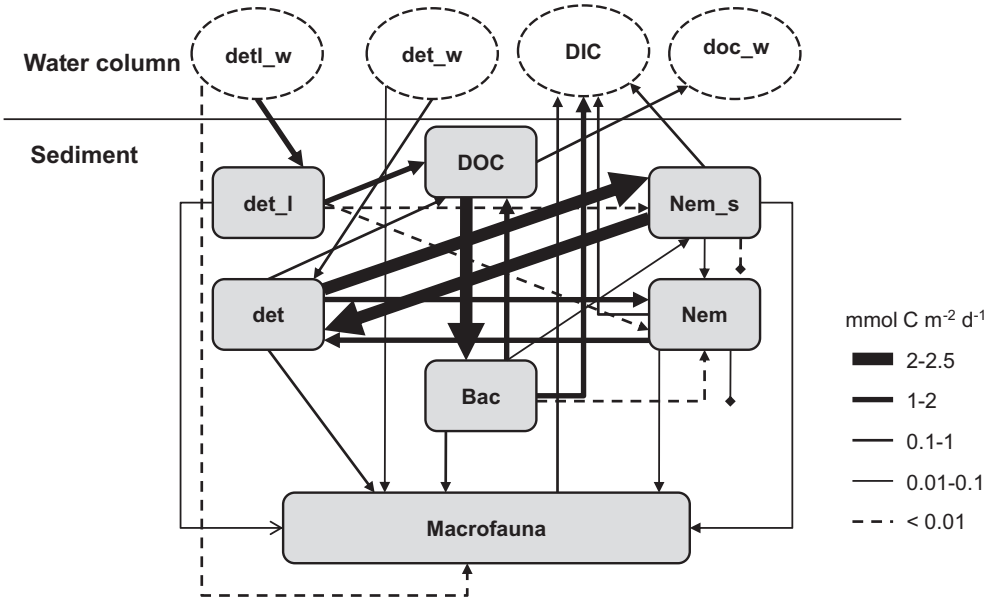

Fig. 5. Schematic representation of carbon flow magnitudes between food web compartments. All macrofauna are grouped under a single compartment for simplicity. See Fig. 6 for a detailed representation of macrofaunal fluxes. Diamond-head arrows represent losses to the export compartment.

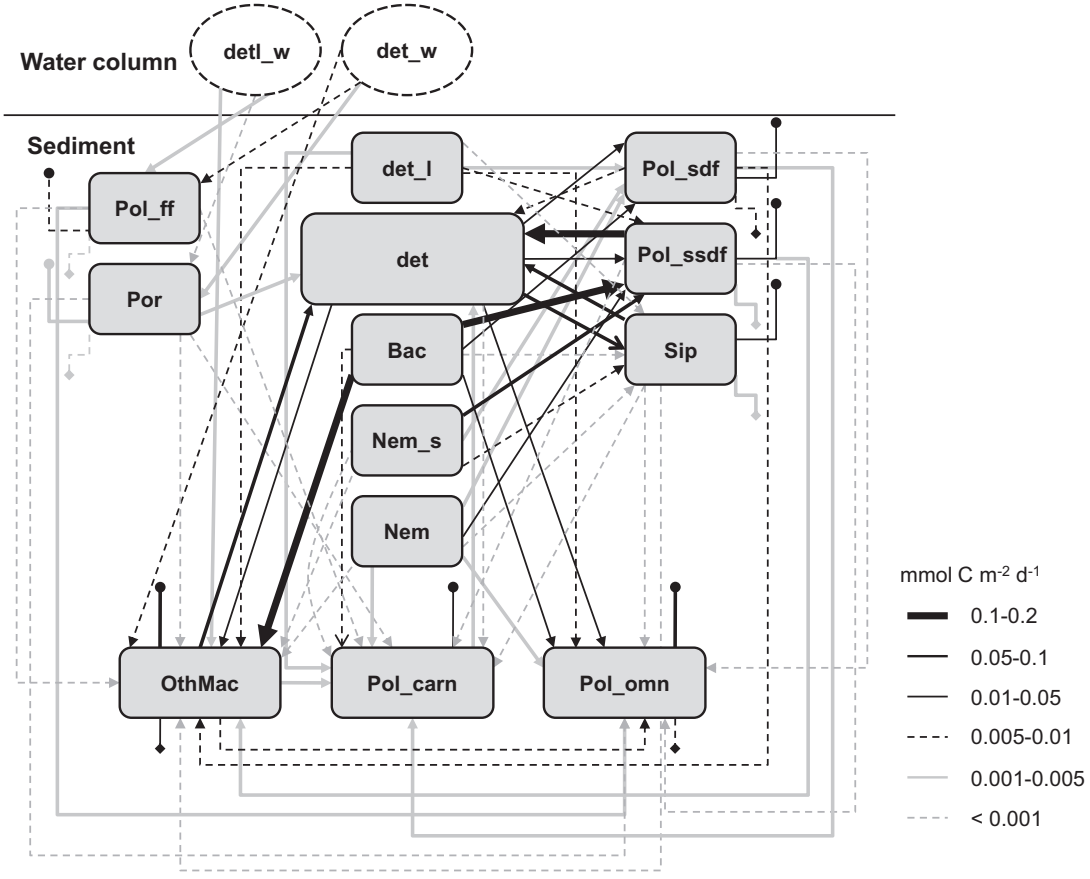

Fig. 6. Schematic representation of the magnitude of incoming and outgoing carbon flows in macrofaunal compartments only. The fluxes between detritus, DOC, bacteria and nematodes are presented in Fig. 5.

unequal temperature-related suppression of activity (e.g. burrowing and feeding) of metazoans compared to bacteria.

The polychaete families grouped here as surface deposit-feeders are known to feed selectively on sediment particles depending on several factors, such as particle size and nutritional value (Taghon, 1982; Kihslinger and Woodin, 2000; Riordan and Lindsay, 2002). Our results show that animals within this food web compartment relied on labile detritus for ~9% of their energy requirements, which is only slightly higher than that of omnivorous and carnivorous polychaetes (8% and 7% respectively). The comparable labile

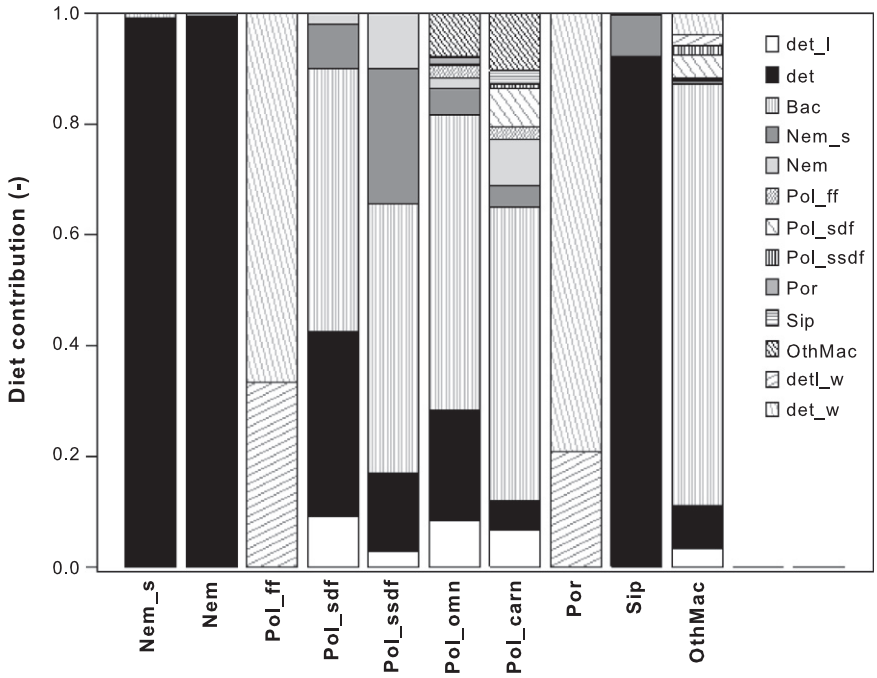

Fig. 7. The contribution of various food sources to the diet of consumers in the FSC food web. See Fig. 1 for abbreviations of food web compartments.

Table 4
Assimilation efficiency (AE), net growth efficiency (NGE), maintenance respiration (MResp = given as a % of total respiration of the group) and daily growth rates of faunal food web compartments calculated from the best solution of the modified model. For meaning of abbreviations see Fig. 1.

	AE	NGE	MResp (%)	Growth rate (d^{-1})
Nem_s	0.08	0.48	3.61	0.0593
Nem	0.11	0.32	2.10	0.0527
Pol_ff	0.65	0.81	69.53	0.0022
Pol_sdf	0.89	0.69	55.49	0.0022
Pol_ssdf	0.22	0.23	13.12	0.0024
Pol_carn	0.89	0.47	31.52	0.0023
Pol_omn	0.90	0.29	17.04	0.0023
Por	0.68	0.79	66.76	0.0023
Sip	0.24	0.22	12.63	0.0023
OthMac	0.51	0.53	36.01	0.0024

detritus consumption by the above groups provides little evidence of selective feeding by surface deposit-feeders. However, the labile detritus consumption by sub-surface deposit-feeders (3%) and sipunculids (<1%) is markedly lower indicating that labile detritus consumption might actually be related to access to surface sediments rather than particle selectivity. Nematodes consumed negligible amounts of labile detritus. The limited response of nematodes to the addition of phytodetritus has been documented in a number of labelling studies (Moodley et al., 2002; Witte et al., 2003b; Franco et al., 2008; Ingels et al., 2010) and could be a result of restricted accessibility of nematodes to the deposited OM or unsuitability of phytodetritus as a food source (Ingels et al., 2010).

The loss of bacterial production due to metazoan grazing was in the range of previously reported estimates for intertidal sediments (<30% of BP; van Oevelen et al., 2006a,b) and is possibly limited by the capacity of fauna to process sufficient amounts of sediment particles through their guts (van Oevelen et al., 2006c). Despite metazoan grazing being a minor fate of BP in both estuarine (van Oevelen et al., 2006c) and deep-sea food webs (the present study), the significance of bacterial carbon to faunal energy demands differed between the two communities: bacterial carbon covered only 18% of the faunal carbon demand in the estuarine food web but contributed ~50% of the carbon requirements of most faunal groups in the FSC food web, with the exception of nematodes and Sipuncula. Our results support the hypothesis that due to carbon and nitrogen limitation in deep-sea sediments, deposit-feeders would rely on bacteria for an important part of their diet in contrast to estuarine consumers that receive labile OM from various sources (Jumars et al., 1990; van Oevelen et al., 2006c). Unlike the majority of macrofaunal groups, nematodes did not rely on bacterial carbon for their energy requirements; merely 0.74% and 0.1% of the small and large nematode carbon demand respectively was met by bacterial carbon. Limited significance of bacterial carbon for meiofaunal taxa has been reported previously although values were an order of magnitude higher compared to our estimates (6–10%; Sundback et al., 1996; Moens and Vincx, 1997). Labelling experiments also failed to detect measurable consumption of bacteria by nematodes in various environmental settings (Urban-Malinga and Moens, 2006; van Oevelen et al., 2006c; Moens et al., 2007; Guilini et al., 2010; Ingels et al., 2010), although several nematode species are believed to be bacterivorous (Moens and Vincx, 1997; Coull, 1999). However, only a minor fraction of living bacterial cells is actively growing (Luna et al., 2002) and thus become labelled in pulse-chase experiments. Furthermore, nematodes are able to remove variable amounts of the bacterial standing stock, which can be as low as 0.03% per day (Epstein and Shiaris, 1992). The above may partially explain the low enrichment levels of nematodes in labelling experiments and the resulting model prediction of a refractory detritus-based diet for nematodes.

The significance of nematodes as a prey for higher trophic levels, and particularly infaunal macroinvertebrates, is not well documented. Nematodes may be ingested passively by non-selective deposit-feeders or actively targeted by predators and selective deposit-feeders (Leduc and Probert, 2009). In theory, it would be advantageous for a consumer to feed on a concentrated food source (nematodes) rather than a dilute medium of the same energetic value (detritus), however, experimental studies have been unable to confirm theoretical predictions (Leduc and Probert, 2009). In the FSC food web, nematodes contributed ~1% of the macrofaunal diet supporting previous experimental results of limited significance of

nematodes as prey for macrofauna. Sub-surface deposit-feeding polychaetes were the only major consumers of nematodes acquiring ~35% of their energy from both small and large nematodes (Figs. 6 and 7) although this value was uncertain and had a range of 0–0.13 mmol C m^{-2} d^{-1}. Nematode consumption by sub-surface deposit-feeders is not necessarily an indication of omnivorous feeding as it could also be attributed to incidental ingestion of animal material from the detrital compartment (Jumars, 1993; Thompson et al., 2009). In contrast to the non-selective sub-surface deposit-feeders, the low consumption of nematodes by the presumed selective feeders (e.g. surface deposit-feeders, carnivores) suggests that nematodes are not actively preyed upon and that the major part of nematode consumption by macrofauna takes place through accidental ingestion during unselective deposit feeding.

Carnivorous polychaetes were differentiated from other groups by the high levels of predation on fauna, which covered 35% of their carbon requirements. The preferred prey items of carnivorous polychaetes were macrofaunal animals rather than nematodes. The model formulation allowed carnivorous polychaetes to obtain part of their energy from detrital material and the associated bacteria. This was decided due to uncertainties over the feeding habits of deep-sea species traditionally considered as predacious (Fauchald and Jumars, 1979). As expected, the contribution of detritus to the diet of predatory polychaetes was the lowest among faunal groups however consumption of bacteria by carnivorous polychaetes was in the same range as for deposit-feeders and omnivorous polychaetes. Our results suggest a high degree of omnivory among higher consumers in the FSC benthic food web, in line with recent studies that challenge the existence of discrete trophic levels among secondary consumers in real food webs (Thompson et al., 2007). Omnivory is expected to be favoured under conditions of high temporal and spatial variability of prey items and intense competitive interactions (Loeuille and Loreau, 2005; Thompson et al., 2007, 2009). The scarcity of food in the deep-sea, the seasonality in the reproductive cycle of several species and the patchy distribution of animals in marine sediments could thus favour omnivory, which may be widespread among deep-sea benthic consumers.

5. Conclusions

This study combined the linear inverse modelling methodology with high quality field and experimental data to quantify energy carbon flows in a deep-sea benthic food web. The measured incorporation rates of ^{13}C could be adequately reproduced by the dynamic tracer model, which enabled the selection of a well-constrained food web solution. Bacteria dominated carbon flows; 98% and 68% of the labile and refractory detritus flux, respectively, was hydrolysed to DOC, which was then assimilated by bacteria at an efficiency of 55%. Bacterial respiration accounted for 70% the total benthic oxygen uptake. The major fraction of BP (76%) was recycled back to the DOC compartment due to viral lysis of bacterial cells and the remaining fraction was grazed mainly by macrofauna. Bacteria covered ~50% of the total macrofaunal carbon requirements and appeared to be an important intermediate link between detritus and macroinvertebrates. On the contrary, small and large nematodes obtained 99% of their energy from refractory detritus. Predation on nematodes was generally low (2% of macrofaunal consumption) suggesting that nematodes might actually be an "energy sink" in the food web. The diet of carnivorous polychaetes depended largely on detritus and bacteria (65% of the total carnivore ingestion) and suggested that omnivory might be common among the secondary consumers of the FSC benthic food web.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocean.2010.12.014.

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