

## Differences in the carbon flows in the benthic food webs of abyssal hill and plain habitats

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### Abstract

Inputs of detritus from the surface ocean are an important driver of community dynamics in the deep sea. The assessment of the flow of carbon through the benthic food web gives insight into how the community is sustained, and its resilience to fluctuations in food supply. We used a linear inverse model to compare the carbon flow through the food webs on an abyssal hill and the nearby plain at the Porcupine Abyssal Plain sustained observatory (4850 m water depth; northeast Atlantic), to examine the partitioning of detrital input in these substantially different megafaunal communities. We found minimal variation in carbon flows at the plain over two years, but differences in the detrital inputs and in the processing of that carbon input between the hill and plain habitats. Suspension feeding dominated metazoan carbon processing on the hill, removing nearly all labile detritus input to the system. By contrast, half of all labile detritus was deposited and available for deposit feeders on the abyssal plain. This suggests that the biomass on the hill is dependent on a more variable carbon supply than the plain. The presence of millions of abyssal hills globally suggests that the high benthic biomass and respiration, and reduced deposition of detritus may be pervasive, albeit with varying intensity.

Community dynamics in the deep-sea are mainly driven by the input of detritus from the surface ocean (Gooday et al. 1990; Pfannkuche 1993; Billett et al. 2010; Smith et al. 2013). The benthic community is very food-limited as this major energy input is seasonal with substantial interannual (Lampitt et al. 2010b) and climatically driven (Ruhl et al. 2008) variation. Consequently, competition for this resource is thought to be high and the benthic food web is complex (Iken et al. 2001). The resulting partitioning of this detrital input between different components of the food web structure the community, in particular feeding groups, as confirmed by the examination of gut contents (e.g., Witbaard et al. 2001; Amaro et al. 2009; FitzGeorge-Balfour et al. 2010) and through isotopic analysis (e.g., Iken et al. 2001; Gutierrez-Rodriguez et al. 2014). The assessment of the flow of carbon through the food web gives insight into how the community is sustained, and the resilience of a community to fluctuations in food supply. This may be particularly

important to understanding the dynamics of a community known for “boom and bust” cycles (e.g., Billett et al. 2010).

Photographic surveys have changed our understanding of the abyssal benthic community at the Porcupine Abyssal Plain (PAP; 4850 m; northeast Atlantic), one of the best-studied abyssal sites on Earth. Previous studies assessed the benthic megafaunal assemblage using trawls, and found echinoderms to be the most common fauna (Billett et al. 2001, 2010). Recent photographic surveys, using a towed camera platform (Durden et al. 2015a) and an autonomous underwater vehicle (Morris et al. 2014, 2016; Milligan et al. 2016) have found the densities and biomass of megafauna to be significantly greater than those estimated by trawling: the estimated megafaunal density increased 1800% between that estimated by trawling and the first of these photographic surveys, equating to a 2084% increase in megabenthic standing stock. Furthermore, a small cnidarian with mixed feeding modes has been discovered to be the dominant megafaunal species at the site (Durden et al. 2015b). These new discoveries are a result of the increased ability to detect smaller and delicate fauna either undersampled or not caught using the trawl.

These photographic surveys also revealed substantial differences in the megafaunal communities on the abyssal hills

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and surrounding plain (Durden et al. 2015a; Morris et al. 2016). The total density and biomass were substantially higher on the hills than the plain: in the first study, density and fresh wet weight biomass on the highest hill were 1.5 and 3.1 times the values on the plain, respectively. This biomass was also distributed differently among feeding modes. The biomass of suspension feeders on the highest hill was 17 times higher than that on the plain, while the biomass of surface deposit feeders was only 23% of that on the plain. The higher standing stocks on the hill existed with only a small difference in visible detritus being found on the seabed between hills and plain (Morris et al. 2016), suggesting that the structure of the food web is likely different. However, the consequences of this different community structure for detritus partitioning within the food webs of these contrasting abyssal settings has not been examined.

An initial analysis of the benthic carbon flows at the PAP was completed by van Oevelen et al. (2012). The approach combined a linear inverse model (LIM) to determine the carbon flows using a likelihood approach (van Oevelen et al. 2010), with a dynamic model based on isotopic tracer uptake data, which allowed the mechanisms of carbon transfer to be examined. This “original model” (van Oevelen et al. 2012) found that bacteria dominated the processing of carbon, and that the foraminifera, meiofauna, and macrofauna were strongly dependent on semi-labile detritus. This suggested that the benthic community largely uses a comparatively temporally stable food source, rather than depending on the periodic labile detritus input, as found at another abyssal plain in the Pacific (Dunlop et al. 2016). The megafauna were not anticipated to remove much of this labile detritus input, although it was acknowledged that better estimates of their biomass would be needed to better constrain their role in detritus processing.

The aim of this study is to update the original food web model with new data from the PAP long time-series location collected in 2011 (“2011 Plain model”), to provide a more refined representation of the benthic carbon flows, and to reassess the carbon transfer pathways with particular focus on the role of the megafauna in the community. Inter-annual variations in carbon flows are assessed by comparing 2011 to 2012 (“2012 Plain model”). The model is then applied to assess differences in the carbon flow between the hills (“2011 Hill model”) and the plain (“2011 Plain model”), to examine the partitioning of detrital input in these contrasting abyssal settings with substantially different megafaunal communities.

## Methods and data

### Model update

The LIM model solves the mass balances of food web compartments subjected to constraints from a combination of carbon flux data and sedimentary carbon with biotic

biomass and physiological constraints to estimate carbon flows in the food web. The structure of the model consists of multiple linear expressions of equalities and inequalities to represent the processes in the food web between compartments, and these equations are solved simultaneously. This method is advantageous in situations where data is scarce (and the model is mathematically underdetermined), as it delivers a “best” solution through the likelihood approach (van Oevelen et al. 2010). In this way, it is particularly suited to modeling deep-sea environments (e.g., van Oevelen et al. 2011a; Dunlop et al. 2016). Biotic compartments were split into size classes and feeding groups, and consisted of bacteria, foraminifera, nematodes (subdivided into predators/omnivores, and selective and non-selective-feeding), macrofauna (subdivided into predators/scavengers, and surface and subsurface deposit feeders), and megafauna (subdivided into predators/scavengers, suspension feeders, and surface and subsurface deposit feeders). Abiotic compartments included those representing detrital inputs from the water column and sediments, and for dissolved organic and inorganic carbon (DOC and DIC), and export/burial. Detritus was composed of labile, semi-labile, and refractory fractions. We used the existing LIM structure and input data from van Oevelen et al. (2012), including the constraints obtained from fitting against isotope tracer data, with the modifications described below.

The new scenarios required different input data. The 2011 Plain and 2011 Hill models used data collected on research cruise *RRS James Cook* 062 in July 2011 (Ruhl et al. 2012). Data from the long-term time series site was used in the 2011 Plain model, while data from the highest hill sampled (~ 500 m above the abyssal plain) was used for the 2011 Hill model (“P1” and “H4” in Durden et al. 2015a). The 2012 Plain model used data collected on research cruise *RRS Discovery* 377 in July 2012 (Ruhl et al. 2013). One structural change, and various input data to the model were updated and altered for the three scenarios modeled, as described below. The model was run using the “LIM” package (van Oevelen et al. 2010) in R (R Core Team 2015).

### Carbon supply and detritus

Limits on the range of deposition of refractory detritus were updated using the minimum and maximum POC daily flux rates measured using a Parflux sediment trap (Honjo and Doherty 1988) set at 100 m above the seabed (Lampitt et al. 2010a), with cups open on an approximately biweekly basis from September 2010 to July 2011 (Ruhl et al. 2012) for the 2011 models, and from July 2011 to May 2012 (Lampitt et al. 2013) for the 2012 Plain model. Particulate organic carbon (POC) was analyzed using the method described in Salter (2007). Detrital deposition was assumed to be spatially homogeneous across the studied PAP hill and plain areas, so the same input data was used for the hill as for the plain. Labile and semi-labile detritus were subtracted

**Table 1.** Input stocks and flows [minimum, maximum] updated in the LIM for the PAP. Original values used are from van Oevelen et al. (2012). The percentage increase of the 2011 Plain model data over original values appear in brackets, and percentage increase of the 2012 Hills and 2012 Plain input data over the 2011 Plain input data are listed in italics.

Description of stock or flow	Short name	Unit	Original LIM	2011 Plain	2011 Hill	2012 Plain
Refractory detritus stock ( $\text{mmol C m}^{-2}$ )	rDet	$\text{mmol C m}^{-2}$	7621	6365 (−16%)	3744 (−41%)	6158 (−3%)
Deposition of refractory detritus		$\text{mmol C m}^{-2} \text{ d}^{-1}$	[0.187, 0.258]	[0.042, 0.757] <sup>§</sup>	[0.042, 0.757] <sup>§</sup>	[0.063, 0.647] <sup>  </sup>
Megabenthic surface deposit feeder stock	MegSDF	$\text{mmol C m}^{-2}$	0.15	10.24* (+6724%)	3.49 <sup>†</sup> (−68%)	16.38 <sup>‡</sup> (+50%)
Megabenthic subsurface deposit feeder stock	MegDF	$\text{mmol C m}^{-2}$	0.44	0* (−100%)	2.40 <sup>†</sup>	2.61 <sup>‡</sup>
Megabenthic predators and scavenger stock	MegPS	$\text{mmol C m}^{-2}$	0.04	1.60* (+3911%)	0.05 <sup>†</sup> (−94%)	2.43 <sup>‡</sup> (+170%)
Megabenthic suspension feeder stock	MegSF	$\text{mmol C m}^{-2}$	0.01	2.14* (+21319%)	85.03 <sup>†</sup> (+38735%)	3.01 <sup>‡</sup> (+41%)
Megafauna respiration (all feeding types)		$\text{d}^{-1}$	NA	[0.00012, 0.00591]	[0.00012, 0.00591]	[0.00012, 0.00591]

\* Data from “P1” from Durden et al. (2015a), corrected to fresh wet weight as described in Durden et al. (2016).

<sup>†</sup> Data from “H4” in Durden et al. (2015a).

<sup>‡</sup> Data from “M56” in D377 (Morris et al. 2014, 2016), corrected to fresh wet weight as in Durden et al. (2016).

<sup>§</sup> Data from T60 sediment traps between 10/2010 and 07/2011, analyzed for POC, less labile, and semi-labile detritus.

<sup>||</sup> Data from T62 sediment traps between 08/2011 and 04/2012, analyzed for POC, less labile, and semi-labile detritus.

from the daily POC flux to yield the refractory detritus flux, as in van Oevelen et al. (2012).

Total organic carbon analyzed in sediment from multiple megacore samples (100 mm internal diameter; Gage and Bett 2005) collected during the research cruises, using the method in Yamamuro and Kayanne (1995), were used to estimate the total organic carbon stock in the surface sediment on the hill and plain in both years (duplicate 0.05 g aliquots analyzed per 5 mm depth slice, results averaged over 0–20 mm, Table 1). Refractory detritus was calculated from these organic carbon data by subtracting the labile and semi-labile detritus, as described in van Oevelen et al. (2012).

### Megafaunal standing stocks

The biomass of the megafaunal feeding groups used in the previous model (van Oevelen et al. 2012) was estimated from trawl data. Megafaunal biomasses in the updated models (Table 1) were estimated from measurements of invertebrates observed in seabed photographs captured with a towed camera platform (in 2011) and an autonomous underwater vehicle (in 2012) during two research cruises. Measurements were converted from pixel dimensions to real dimensions using photogrammetry, described in Morris et al. (2014), and to fresh wet weights using the methods described in Durden et al. (2016). The fraction of organic carbon in megafaunal wet weight was taken from Rowe (1983) for Pycnogonida, from Billett (1991) for holothurians (aside from *Amperima* sp. and *Deima* sp.), and from Billett and Thurston (1991) for the remaining taxa.

Feeding groups were assigned based on those described in Iken et al. (2001). However, the common burrowing anemone *Iosactis vagabunda* has been observed to be both a deposit feeder and a predator (Durden et al. 2015b). To find the appropriate partitioning of resource between the feeding modes, all biomass for this morphotype was assigned to the megafauna predator/scavenger feeding group. The fraction of resource uptake for the megafauna predator/scavengers was adjusted to find appropriate partitioning between predation, and consumption of detritus and bacteria using the following procedure. The LIM was used to determine the minimum fraction of predatory feeding that was needed to solve the model. This minimum fraction was limiting in the 2012 Plain model, where it was 28% (i.e., the predatory contribution ranges from 28% to 100% with remaining uptake from labile and semi-labile detritus and bacteria). This lower boundary was then also applied to the 2011 models.

### Megafaunal respiration

The structure of the original LIM model was altered to constrain megafaunal respiration more appropriately. In the original LIM, total respiration (the sum of respiration by bacteria, foraminifera, nematodes, macrofauna, and megafauna) was constrained using data from sediment community oxygen consumption (SCOC) measurements (from Witbaard et al. 2000) converted to carbon equivalents (van Oevelen et al. 2012). Since the SCOC measurements do not include megafauna, megafaunal respiration was removed from this constraint in the updated models. The respiration for each

**Table 2.** Selected results of the three models.

Result type	2011 Plain	2012 Plain	2011 Hill
Total detritus input (mmol C m <sup>-2</sup> d <sup>-1</sup> )	0.612	0.660	1.098
Labile content of input detritus (%)	8	13	74
Semi-labile content of input detritus (%)	45	39	20
Partitioning of labile detrital input: to megafaunal suspension feeders (%)/deposited (%)	55/45	73/27	98/2
Partitioning of semi-labile detrital input: to megafaunal suspension feeders (%)/deposited (%)	6/94	0/100	26/64
Megafaunal carbon uptake (mmol C m <sup>-2</sup> d <sup>-1</sup> )	0.163	0.265	0.972
Portion of megafaunal carbon uptake by surface deposit feeders (%)	62	57	6
Portion of megafaunal carbon uptake by suspension feeders (%)	27	23	89
Total respiration (mmol C m <sup>-2</sup> d <sup>-1</sup> )	0.52	0.563	0.958

**Table 3.** Mean respiration  $\pm$  standard deviation ( $\times 10^{-3}$  mmol C m<sup>-2</sup> d<sup>-1</sup>) for the biotic compartments of the models.

Compartment	2011 Plain	2012 Plain	2011 Hill
Bacteria	375.4 $\pm$ 2.9	391 $\pm$ 0.002	340.0 $\pm$ 6.3
Foraminifera	23.9 $\pm$ 3.0	15.6 $\pm$ 0.002	42.9 $\pm$ 4.0
Selective-feeding nematodes	2.6 $\pm$ 0.8	2.1 $\pm$ 0.004	4.4 $\pm$ 2.3
Non-selective feeding nematodes	1.8 $\pm$ 0.5	1.5 $\pm$ 0.003	3.1 $\pm$ 1.3
Predatory nematodes	0.1 $\pm$ 0.03	0.02 $\pm$ 0.0008	0.1 $\pm$ 0.03
Surface-deposit feeding macrobenthos	21.3 $\pm$ 0.8	19.2 $\pm$ 0.002	29.3 $\pm$ 0.005
Subsurface deposit-feeding macrobenthos	7.8 $\pm$ 0.6	4.4 $\pm$ 0.0009	10.5 $\pm$ 1.9
Predatory macrobenthos	17.0 $\pm$ 0.3	16.3 $\pm$ 0.0009	19.7 $\pm$ 2.0
Surface deposit-feeding megabenthos	45.1 $\pm$ 0.7	70.2 $\pm$ 0.002	20.5 $\pm$ 2.3
Subsurface deposit-feeding megabenthos	0 $\pm$ 0	11.4 $\pm$ 0.007	13.7 $\pm$ 1.4
Suspension-feeding megabenthos	13.6 $\pm$ 1.2	21.2 $\pm$ 0.002	472.9 $\pm$ 69.7
Predatory/scavenging megabenthos	7.7 $\pm$ 0.5	10.4 $\pm$ 0.001	0.3 $\pm$ 0.02

megafaunal feeding type was constrained using the minimum and maximum mass specific respiration rates published by Hughes et al. (2011) for deep-sea ophiuroids and holothurians, since these taxa are abundant at PAP. These rates were converted to carbon equivalents using a respiration quotient of 1 (Glud 2008), resulting in a constraint range of 0.00015–0.00707 d<sup>-1</sup> (in the original model this was 0.00012–0.00591 d<sup>-1</sup>). Estimates of respiration for *Ophiomusium* sp. (Smith and Hinga 1983; Mahaut et al. 1995), *Munidopsis* sp. (Mahaut et al. 1995), and *Enypniastes* sp. (Bailey et al. 1994), species occurring at the PAP, are within this range.

### Model fitting

van Oevelen et al. (2012) coupled the LIM with a dynamic tracer model to compare simulations of isotopically labelled labile detrital movement through the food web with in situ experiments. Additional constraints on the LIM using data gained from this coupling were imposed to improve the model fit: an increase in the dissolution of labile detritus, and constraint on the bacterial growth efficiency, and constraints on the fraction of labile detritus in the diets of foraminiferans, nematodes and surface deposit feeding

macrofauna (see Table 3 in van Oevelen et al. 2012). Instead of coupling the model to a dynamic tracer model again, the same constraints were applied to all models described here, with the exception of the increase in labile detritus dissolution. This constraint was not imposed, because the increase and inclusion of the deposition of refractory detritus in the model causes the labile detritus dissolution to be slightly outside this constraint range. Since these values were in close proximity, the omission of this constraint was deemed valid.

Each model was run for 25,000 iterations to ensure sufficient solutions to cover the possible solution space, which was verified by assuring the convergence of the mean and standard deviation of each flow (van Oevelen et al. 2011b). From this set of solutions the mean and standard deviation were calculated.

### Results

#### Update to original model—2011 Plain model

The detritus input to the 2011 Plain food web from the water column was 0.61 mmol C m<sup>-2</sup> d<sup>-1</sup> (Table 2), predominantly composed of refractory (47%; 0.288  $\pm$  SD 0.014 mmol C m<sup>-2</sup> d<sup>-1</sup>) and semi-labile detritus (45%; 0.276  $\pm$  0.014

mmol C m<sup>-2</sup> d<sup>-1</sup>), with a small fraction of labile material (8%; 0.049 ± 0.009 mmol C m<sup>-2</sup> d<sup>-1</sup>). The combination of respiration (0.517 ± 0.001 mmol C m<sup>-2</sup> d<sup>-1</sup>), efflux of DOC (0.064 ± 0.009 mmol C m<sup>-2</sup> d<sup>-1</sup>), burial (0.03 ± 0 mmol C m<sup>-2</sup> d<sup>-1</sup>), and export of secondary production (0.0003 ± 0.0003 mmol C m<sup>-2</sup> d<sup>-1</sup>), resulted in a total loss of 0.61 mmol C m<sup>-2</sup> d<sup>-1</sup>.

Bacteria drove the main flow of carbon in the food web (Fig. 1): the dissolution of refractory detritus in the sediment to DOC (0.459 ± 0.009 mmol C m<sup>-2</sup> d<sup>-1</sup>), followed by DOC uptake by bacteria (0.414 ± 0.003 mmol C m<sup>-2</sup> d<sup>-1</sup>), and bacterial respiration (0.375 ± 0.003 mmol C m<sup>-2</sup> d<sup>-1</sup>). The deposition of refractory and semi-labile detritus from the water column to the sediment (0.288 ± 0.014 and 0.258 ± 0.002 mmol C m<sup>-2</sup> d<sup>-1</sup>, respectively), were of a similar magnitude.

Deposit feeding was the dominant feeding mode on the plain (Fig. 1; Table 2). Megafaunal surface deposit feeding cycled semi-labile detritus (0.075 ± 0.005 mmol C m<sup>-2</sup> d<sup>-1</sup>) to refractory detritus (0.047 ± 0.003 mmol C m<sup>-2</sup> d<sup>-1</sup>), and consumed (0.022 ± 0.002 mmol C m<sup>-2</sup> d<sup>-1</sup>) newly deposited labile detritus (0.022 ± 0.0006 mmol C m<sup>-2</sup> d<sup>-1</sup>) before respiring (0.045 ± 0.0007 mmol C m<sup>-2</sup> d<sup>-1</sup>). Both macrofaunal surface and subsurface deposit feeders cycled semi-labile detritus to refractory detritus at a similar magnitude (0.040 ± 0.004 and 0.026 ± 0.003 mmol C m<sup>-2</sup> d<sup>-1</sup>; 0.042 ± 0.003 and 0.026 ± 0.002 mmol C m<sup>-2</sup> d<sup>-1</sup>). Megafaunal suspension feeding removed the remaining labile and semi-labile detritus from the water column (0.027 ± 0.009 and 0.017 ± 0.014 mmol C m<sup>-2</sup> d<sup>-1</sup>).

The uptake of carbon by megafauna was 0.163 mmol C m<sup>-2</sup> d<sup>-1</sup>, 62% of which was taken up by surface deposit feeders (0.101 ± 0.005 mmol C m<sup>-2</sup> d<sup>-1</sup>), 27% taken up by suspension feeders (0.044 ± 0.008 mmol C m<sup>-2</sup> d<sup>-1</sup>), and the remaining 11% taken up by predators/scavengers (0.017 ± 0.002 mmol C m<sup>-2</sup> d<sup>-1</sup>).

Labile detritus in the water column is divided approximately evenly between consumption by megafaunal suspension feeders (55%), and deposition (45%), while the majority of semi-labile detritus in the water column (94%) is deposited and only 6% is consumed by suspension feeders.

Megafaunal surface deposit feeders consume 74% semi-labile detritus and 21% labile detritus (Fig. 2). The macrofauna are equally dependent on semi-labile detritus: surface deposit feeders consume 74% semi-labile material, while subsurface deposit feeders consume 95% semi-labile detritus, and for each labile detritus is only 1% of their diet. This suggests that megafauna control the consumption of fresh detritus over macrofauna.

Total respiration was 0.517 mmol C m<sup>-2</sup> d<sup>-1</sup> (Table 3), comprised of 73% bacterial respiration, 13% megafaunal respiration, 9% macrofaunal respiration, 5% foraminiferal respiration, and 1% nematode respiration. Total megafaunal respiration was 0.067 mmol C m<sup>-2</sup> d<sup>-1</sup>, 68% of which was

by surface deposit feeders, 21% by suspension feeders, with the remaining 12% by predators/scavengers (Table 3).

### Addressing temporal variation—2012 Plain model

The detritus input to the 2012 Plain food web from the water column was 0.660 mmol C m<sup>-2</sup> d<sup>-1</sup> (Table 2), predominantly composed of refractory (48%; 0.316 ± SD 0.007 mmol C m<sup>-2</sup> d<sup>-1</sup>) and semi-labile detritus (39%; 0.260 ± 0 mmol C m<sup>-2</sup> d<sup>-1</sup>), with a small fraction of labile material (13%; 0.049 ± 0 mmol C m<sup>-2</sup> d<sup>-1</sup>). This represents an 8% increase in the detrital input over the 2011 Plain model. The combination of respiration (0.563 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>), efflux of DOC (0.067 ± 0.007 mmol C m<sup>-2</sup> d<sup>-1</sup>), and burial (0.03 ± 0 mmol C m<sup>-2</sup> d<sup>-1</sup>), resulted in a total loss of 0.660 mmol C m<sup>-2</sup> d<sup>-1</sup>.

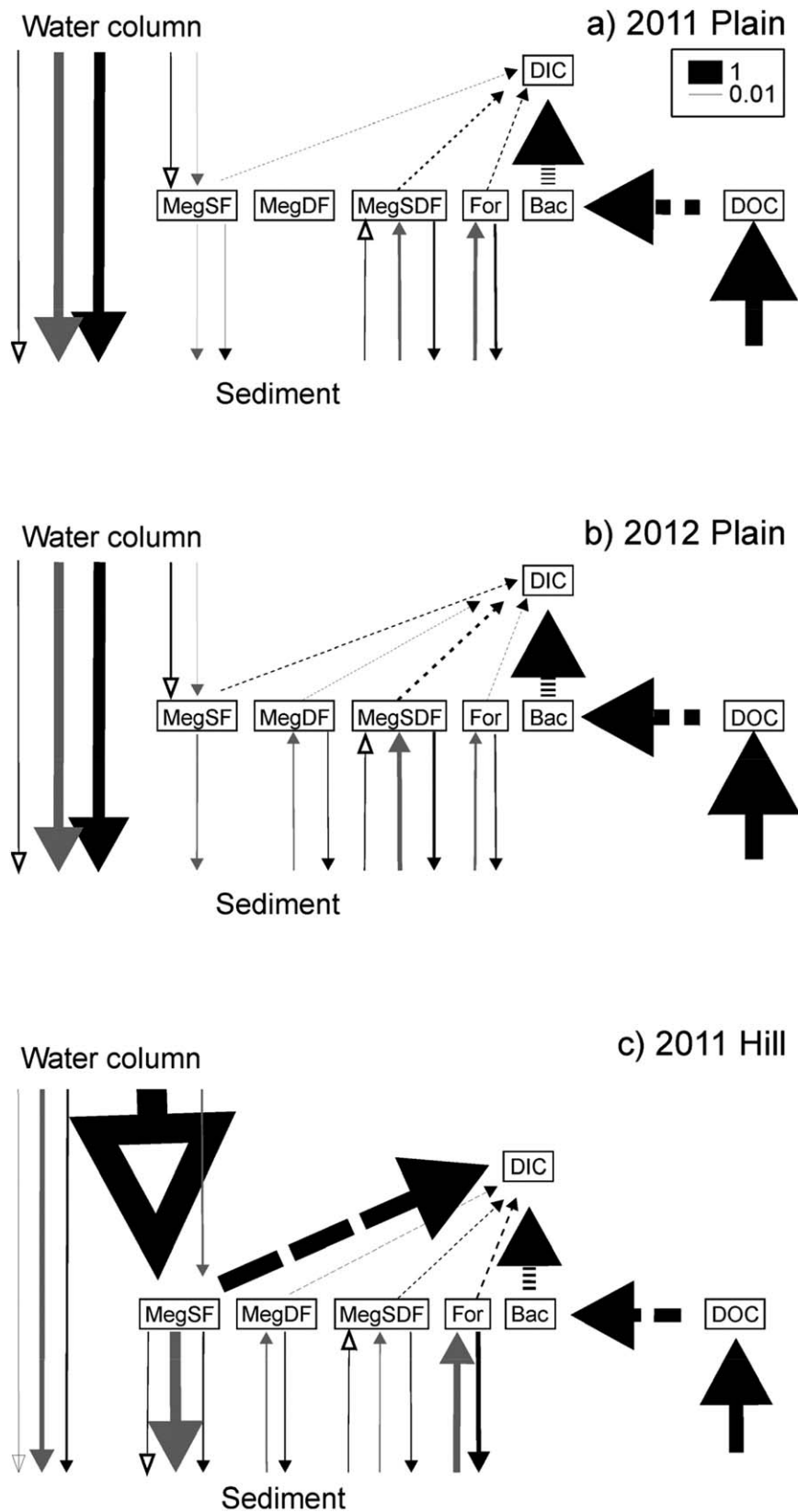
Bacteria drove the main flow of carbon (Fig. 1) through the dissolution of refractory detritus in the sediment to DOC (0.482 ± 0.007 mmol C m<sup>-2</sup> d<sup>-1</sup>), followed by DOC uptake by bacteria (0.430 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>), and bacterial respiration (0.391 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>). The deposition of refractory and semi-labile detritus from the water column to the sediment (0.315 ± 0.007 and 0.260 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>, respectively), were of a similar magnitude.

Deposit feeding was the dominant feeding mode (Fig. 1; Table 2). Megafaunal surface deposit feeding cycled semi-labile detritus (0.116 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>) to refractory detritus (0.072 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>), and consumed (0.027 ± 0.001 mmol C m<sup>-2</sup> d<sup>-1</sup>) newly deposited labile detritus (0.022 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>) before respiring (0.070 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>). Megafaunal suspension feeding removed the remaining labile detritus from the water column (0.062 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>). Macrofaunal surface and subsurface deposit feeders, and megafaunal subsurface deposit feeders all took up semi-labile detritus at a similar magnitude (0.032 ± 0.0, 0.017 ± 0.001, and 0.031 ± 0.001 mmol C m<sup>-2</sup> d<sup>-1</sup>), cycling it to refractory detritus (0.020 ± 0.0, 0.11 ± 0.0, and 0.019 ± 0.00 mmol C m<sup>-2</sup> d<sup>-1</sup>).

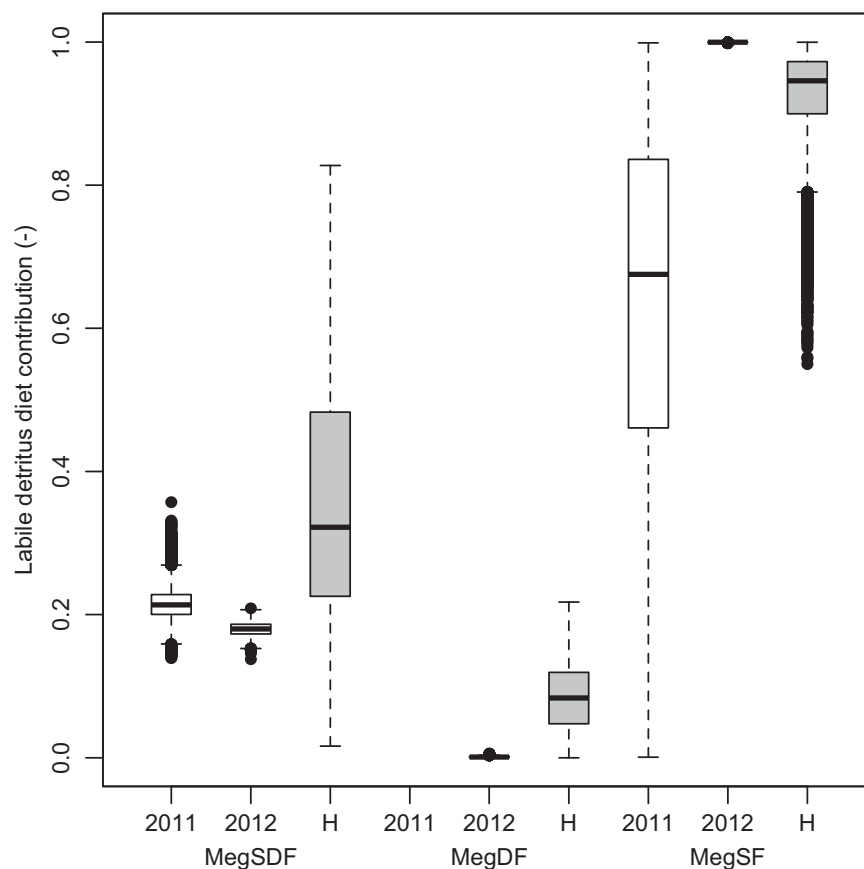
The uptake of carbon by megafauna was 0.265 mmol C m<sup>-2</sup> d<sup>-1</sup>, 57% of which was taken up by surface deposit feeders (0.151 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>), 23% taken up by suspension feeders (0.062 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>), 12% taken up by subsurface deposit feeders (0.031 ± 0.001 mmol C m<sup>-2</sup> d<sup>-1</sup>), and the remaining 8% taken up by predators/scavengers (0.022 ± 0.0 mmol C m<sup>-2</sup> d<sup>-1</sup>).

Labile detritus in the water column is divided between consumption by megafaunal suspension feeders (73%), and deposition (27%), while all the semi-labile detritus in the water column (100%) is deposited.

Megafaunal surface deposit feeders consume 77% semi-labile detritus and 19% labile detritus (Fig. 2), while subsurface deposit feeders consume 99% semi-labile detritus. The macrofauna are as dependent on semi-labile detritus: surface deposit feeders consume 77% semi-labile material, while subsurface deposit feeders consume 99% semi-labile detritus.



**Fig. 1.** Schematic representation of major carbon flows between the water column and sediment, and selected biotic compartments (boxed) in the (a) 2011 Plain, (b) 2012 Plain, and (c) 2011 Hill models. Flows are represented by arrows proportional in size to their magnitude, scaled linearly. Flows of detritus from the water column and the sediment are divided into labile (white arrowheads), semi-labile (gray arrows), and refractory (black arrows) fractions. Flows of carbon from respiration, and from DOC to DIC are shown as dashed arrows. Abbreviations are from Table 1.



**Fig. 2.** Boxplots of contributions of labile detritus from the water column to the diets of megafauna from the 2011 and 2012 Plain models (white boxes) and the 2011 Hill model (gray boxes, “H”). Abbreviations are from Table 1. Whiskers were computed as the smaller of either the maximum value and the third quartile plus 150% of the interquartile range, and the larger of the minimum value and the first quartile less 150% of the interquartile range. Dots represent values outside this range.

Again, megafauna control the consumption of fresh detritus over macrofauna.

Total respiration was  $0.563 \text{ mmol C m}^{-2} \text{ d}^{-1}$  (Table 3), comprised of 69% bacterial respiration, 20% megafaunal respiration, 7% macrofaunal respiration, 3% foraminiferal respiration, and 1% nematode respiration. Total megafaunal respiration was  $0.113 \text{ mmol C m}^{-2} \text{ d}^{-1}$ , 62% of which was by surface deposit feeders, 19% by suspension feeders, 10% by subsurface deposit feeders, and the remaining 9% by predators/scavengers.

#### An abyssal hill—2011 Hill model

The detritus input to the 2011 Hill food web from the water column was  $1.098 \text{ mmol C m}^{-2} \text{ d}^{-1}$  (Table 2), predominantly composed of labile detritus (74%;  $0.817 \pm 0.178 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), with some semi-labile detritus (20%;  $0.219 \pm 0.099 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ) and very little refractory detritus (6%;  $0.062 \pm 0.17 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ). This represents an 80% increase in the total detrital input over the 2011 Plain model. The combination of respiration ( $0.958 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), efflux of DOC ( $0.070 \pm 0.007 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ),

burial ( $0.03 \pm 0 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), and export of secondary production ( $0.0058 \pm 0.014 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), resulted in a total loss of  $1.063 \text{ mmol C m}^{-2} \text{ d}^{-1}$ .

Carbon uptake by megafauna was  $0.972 \text{ mmol C m}^{-2} \text{ d}^{-1}$ . Here the suspension feeders dominated (89%;  $0.861 \pm 0.150 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), surface deposit feeders (6%;  $0.062 \pm 0.018 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), deposit feeders (5%;  $0.047 \pm 0.006 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), and predators/scavengers (0.1%;  $0.001 \pm 0.0001 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ).

In contrast to both abyssal plain food webs, the dominant flow of carbon in the 2011 Hill model was the uptake of labile detritus from the water column by megafaunal suspension feeders ( $0.804 \pm 0.179 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ; Fig. 1), followed by respiration ( $0.473 \pm 0.070 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ) and deposition of semi-labile detritus to the sediment ( $0.293 \pm 0.092 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ). Uptake of semi-labile detritus ( $0.057 \pm 0.042 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), deposition of refractory detritus ( $0.039 \pm 0.028 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), and export of secondary production ( $0.033 \pm 0.023 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ) occurred at a magnitude lesser. Bacteria also played a major role: refractory detritus was dissolved ( $0.380 \pm 0.032 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ).

$\text{m}^{-2} \text{d}^{-1}$ ), consumed by bacteria ( $0.379 \pm 0.006 \text{ mmol C m}^{-2} \text{d}^{-1}$ ), and respired ( $0.340 \pm 0.006 \text{ mmol C m}^{-2} \text{d}^{-1}$ ). Megafaunal surface deposit feeding cycled carbon at an order of magnitude lower than suspension feeding: surface deposit feeders consume semi-labile ( $0.037 \pm 0.020 \text{ mmol C m}^{-2} \text{d}^{-1}$ ) and labile detritus ( $0.020 \pm 0.006 \text{ mmol C m}^{-2} \text{d}^{-1}$ ), respiring ( $0.021 \pm 0.002 \text{ mmol C m}^{-2} \text{d}^{-1}$ ) and depositing refractory detritus ( $0.027 \pm 0.016 \text{ mmol C m}^{-2} \text{d}^{-1}$ ); while subsurface deposit feeders consume semi-labile detritus ( $0.039 \pm 0.005 \text{ mmol C m}^{-2} \text{d}^{-1}$ ), respiring ( $0.014 \pm 0.001 \text{ mmol C m}^{-2} \text{d}^{-1}$ ) and depositing refractory detritus ( $0.028 \pm 0.005 \text{ mmol C m}^{-2} \text{d}^{-1}$ ). Refractory detritus is also deposited at a similar magnitude by macrofaunal subsurface deposit feeders ( $0.050 \pm 0.012 \text{ mmol C m}^{-2} \text{d}^{-1}$ ).

Nearly all labile detritus in the water column (98%;  $0.804 \pm 0.179 \text{ mmol C m}^{-2} \text{d}^{-1}$ ) is consumed by megafaunal suspension feeders, leaving only 2% ( $0.013 \pm 0.006 \text{ mmol C m}^{-2} \text{d}^{-1}$ ) to be deposited to the sediment. A further 26% of semi-labile detritus in the water column is taken up by megafaunal suspension feeders ( $0.057 \pm 0.043 \text{ mmol C m}^{-2} \text{d}^{-1}$ ), and the remaining 64% is deposited ( $0.162 \pm 0.074 \text{ mmol C m}^{-2} \text{d}^{-1}$ ). Total sedimentary detritus consumed was  $0.957 \text{ mmol C m}^{-2} \text{d}^{-1}$ , composed of semi-labile (52%), refractory (43%), and a small fraction of labile detritus (5%).

Megafaunal suspension feeders on the hill feed almost exclusively (93%) on labile detritus (Fig. 2). The diet of megafaunal surface deposit feeders is 33% labile detritus and 59% semi-labile detritus, while subsurface deposit feeders consume 83% semi-labile and 9% labile detritus. Macrofaunal surface and subsurface deposit feeders are more dependent on semi-labile detritus, as it composes 75% and 95% of their diets, with labile detritus making up only 1% each.

Total respiration was  $0.958 \text{ mmol C m}^{-2} \text{d}^{-1}$ , comprised of 53% megafaunal, 36% bacterial, 6% macrofaunal, 4% foraminiferal, and 1% by nematodes. Megafaunal respiration was  $0.508 \text{ mmol C m}^{-2} \text{d}^{-1}$  (Table 3), 93% by suspension feeders, and small contributions by surface deposit feeders (4%), subsurface deposit feeders (3%), and predators/scavengers (0.1%). Macrofaunal respiration was  $0.059 \text{ mmol C m}^{-2} \text{d}^{-1}$ , 49% by surface deposit feeders, 33% by predators/scavengers, and 17% by deposit feeders. Nematode respiration was  $0.008 \text{ mmol C m}^{-2} \text{d}^{-1}$ , 58% by selective-feeders, 40% by non-selective feeders, and 2% by predators.

## Discussion

Technological advances in seafloor imaging are continuously changing our view of the community structure in the deep sea, as evidenced by the recent recognition of *I. vagabunda* as the greatest contributor to megafaunal density at the well-sampled PAP-SO site (Durden et al. 2015b). Updating an existing carbon flow model with newly acquired data on megafaunal community structure has enabled us to represent the megafaunal contribution to the food web more

realistically. It gives new insight into the fate of labile detritus and the role of suspension feeders at the PAP, in particular. An important finding of the original model was that labile detritus had a limited role in carbon cycling. The updated model has not changed that view dramatically, although the importance of labile detritus in the food web has doubled in comparison with the original model (8% vs. 4%), while the semi-labile content remained the same (45%). Respiration, the greatest contributor to loss was slightly higher in the updated model than in the original ( $0.52$  vs.  $0.45 \text{ mmol C m}^{-2} \text{d}^{-1}$ ).

The labile detritus input was partitioned differently in the food web: in the original model only 3% was used by megafaunal suspension feeders and 97% was deposited, while in the updated model, the suspension feeding contribution is substantially higher (55% and 45%, respectively) and comparable between years. The partitioning of semi-labile detritus between megafaunal suspension feeders and deposition was also adjusted, from 0.05%:99.95% to 6%:94%. Although deposit feeding was still the dominant megabenthic feeding mode on the plain (62% of carbon uptake by megafauna), suspension feeding has a greater role than originally thought (previously 3% of carbon uptake by megafauna, now 27%), as a result of the updated megafaunal biomass estimate. However, the dominant carbon flow remains the uptake of DOC by bacteria and respiration, with similar magnitude in both models.

The variation between the 2011 and 2012 Plain models, potentially driven by the difference in detritus inputs, is modest (Table 2), with carbon flows of similar magnitude (Fig. 1). Variation in the detrital input between these models was modest (8% increase in 2012 over 2011), but this annual variation can be up to four-fold (Lampitt et al. 2010b). Billett et al. (2010) found an interannual variation in megafaunal biomass stock of a similar magnitude to that of the annual variation in detrital inputs, much greater than the variation between the two model inputs. The domination of carbon flow by bacterial cycling is similar to the functioning of the food web at other abyssal sites, including the plain at Station M in the eastern Pacific (Dunlop et al. 2016) and the lower parts of Nazare Canyon (van Oevelen et al. 2011b). The updated PAP plain results support the notion that the abyssal benthic community relies on a stable food source (van Oevelen et al. 2012; Dunlop et al. 2016), as contribution of labile detritus cycling in the food web is limited. A similar conclusion was drawn about Station M: that “older,” more stable, detritus inputs sustain a community in periods of low detrital inputs (Dunlop et al. 2016).

We found that carbon flows on the hill differ substantially from the plain, particularly in terms of the quantity and quality of detrital inputs. Detrital inputs on the hill were almost double those on the plain ( $\sim 80\%$  greater), with a labile content nearly ten times that of the plain, and a semi-labile content less than half that of the plain (Table 2).



Although the overall rate of POM input from the surface ocean was assumed to be similar in both locations in the model constraints, differences in the detrital inputs were computed by the model and were driven by the activity of the megafaunal suspension feeders, and their substantial and previously unrecognized biomass. This model output can be explained by a difference in detrital inputs as a result of lateral transport related to different hydrodynamic regimes on abyssal hills and the plain (Turnewitsch et al. 2015), including increased current speeds over the hill (Klein and Mittelstaedt 1992), and higher turbidity resulting in more suspended material transport in the benthic boundary layer over the hill (Morris et al. 2016). Total respiration on the hill was nearly double that on the plain, and export was substantially higher on the hill, while efflux and burial remained similar in both models. These differences reflect the large differences in community structure in the two locations. Such high megafaunal biomass, and communities with high proportions of suspension feeders were found on three other abyssal hills with similar environmental conditions in the area (Durden et al. 2015a), in similarity with findings on seamounts (Rogers 1994; Rowden et al. 2010) and bathyal hills (Jones et al. 2013). At regional to global scales, the quantities of overall sinking food inputs from overlying surface waters, as well as depth and temperature, limit the total biomass in any particular area. The presence of millions of abyssal hills globally suggests that these phenomena may be pervasive, albeit with varying intensity. These model results suggest that field verification of conditions on the hill, particularly the sampling of near-bed detrital input quantity and composition, and measurements of lateral current and particulate flows, could provide important insight into the role of topography in the deposition of detritus.

The food web on the hill was dominated by megafaunal suspension feeding; nearly all megafaunal carbon uptake on the hill, itself 5 times that on the plain, was by suspension feeders (89%), while they contributed to nearly all the megafaunal respiration and half of total respiration on the hill. They used 98% of the labile and 26% of the semi-labile detritus from the water column; their increased consumption of detritus on the hill over the plain was even greater than the increase in detrital inputs. On the hill, cnidarians *Actinauge abyssorum* and *Parasicyonis* sp. were dominant contributors to the suspension feeder biomass (Durden et al. 2015a). Observations of *Parasicyonis* sp. have shown it to be a large cnidarian that positions its oral disk high into the water column, and orients it into the current (Lampitt and Paterson 1987), probably to exploit the increased suspended particles. This behavior is particularly advantageous with an increase in suspended particle flux in higher currents over such an elevated topographic position (Rowden et al. 2010).

This difference in the quantity and quality of detritus input and the dominance by megafaunal suspension feeding

was evidently reflected in the carbon cycling of the hill food web, with negative feedback on the megafaunal deposit feeders (both surface and subsurface). Deposited detritus on hill ( $0.22 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ) was approximately one-third that on the plain ( $0.60 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ), with a much higher semi-labile (63% vs. 43%) and lower refractory detritus contents (30% vs. 53%). Such fractionation of organic matter was detected by Turnewitsch et al. (2015) on a large abyssal hill in the vicinity, and was related to sediment particle size and the near-bed hydrodynamic regime. This limited availability of sedimentary detritus on the hill reduced respiration for both deposit feeding types to 4% of the total from 9%. The diet of megafaunal surface deposit feeders appeared further impacted: the ratio of semi-labile to labile fractions in the diet was  $\sim 3.5 : 1$  on the plain, but was altered to  $\sim 1.8 : 1$  on the hill. This suggests that these animals were more dependent on the “stable” semi-labile detritus on the plains, and more susceptible to variations in the more transient labile detritus on the hills. This increase in the labile content of the detritus consumed by megafaunal surface deposit feeders on the hills over the plain may be related to the increase in density and biomass of the common *Amperima* sp. found on the hills over the plain (Durden et al. 2015a), since this holothurian is known to select “fresh” detritus based on chlorophyll *a* analyses (Wigham et al. 2003a), likely influencing its fecundity (Wigham et al. 2003b). *Psychropotes longicauda* was dominant in terms of biomass on the plain (Durden et al. 2015a), and is known to feed on less labile detritus (Wigham et al. 2003a; FitzGeorge-Balfour et al. 2010).

The model adequately represented the plasticity of feeding modes used by the ubiquitous *I. vagabunda*, as observed by Durden et al. (2015b). This anemone contributed nearly all of the megafaunal predator/scavenger biomass (88% in both Plain models, and 92% in the 2011 Hill model), and the model results indicate that predation/scavenging formed 18% (2012) and 44% (2011) of the group's diet on the plain, and 71% on the hill. Its diet was completed by deposit feeding. This range of proportion of diet as predation compares surprisingly well to that predicted from independent isotopic analysis: the proportion of predation was calculated using  $\delta^{15}\text{N}$  values from Iken et al. (2001) for *I. vagabunda* (and accounting for 3‰ enrichment over one trophic level), *Paramage* sp./*Laetmoneice* sp. (similar polychaetes to that observed being preyed upon by Durden et al. 2015b) and particulate organic matter, giving a range of predation proportion in the diet from 42 to 74%. Other megafauna are known to switch feeding modes, for example gut contents of *Parasicyonis* sp. suggest that it feeds on mobile megafauna in addition to particulate matter (Lampitt and Paterson 1987). Accounting for such plasticity in feeding modes would further complicate the structure of the model.

## Conclusions

Our updated modeling analysis at the PAP refined and changed our hypotheses of benthic carbon flows, with labile detritus being more important than initially thought. The results again support that bacteria dominate carbon processing in the abyssal benthos, but we found an increased role for megafaunal suspension feeders, though deposit feeding still dominated the megafaunal carbon uptake. The comparison of abyssal plain food web structure among years, indicated comparatively minor differences in the processing of carbon input, suggesting that the impact of inter-annual variation in food supply on carbon flows is low. This supports the concept that communities on the plain are primarily sustained by stable, refractory detritus. On the hills, suspension feeding was the dominant mode of carbon processing, removing nearly all labile detritus that is put into the system. This was in stark contrast to the plain, where half of all labile detritus was deposited and available for deposit feeders. This results in the testable hypothesis that the biomass on the hill is dependent on a more transient carbon supply than the plain, and that total benthic respiration on the hill is substantially higher than on the plain. Further improvements to this model could be made by addressing the lack of  $^{13}\text{C}$  uptake data and respiration measurements for megafauna, further data measured directly on the hill, and further data collected to constrain the bacterial components of the model.

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### Acknowledgments

We thank the captain, crew and scientists of RRS *James Clark Ross* 221, RRS *James Cook* 62, 71 and 85, and RRS *Discovery* 377 research cruises to the Porcupine Abyssal Plain. Thanks to Richard Lampitt for assistance with sediment trap data, George Wolff for assistance with sedimentary TOC analyses, and Brian Bett for useful discussions and advice. This work was funded by the UK Natural Environment Research Council (NERC), and contributes to the Autonomous Ecological Surveying of the Abyss project (NERC NE/H021787/1), the NERC Marine Environmental Mapping Programme (MAREMAP), the Porcupine Abyssal Plain – Sustained Observatory (NERC National Capability programme), the European Union Seventh Framework Programme (FP7/2007-2013) under the MIDAS project, grant agreement n° 603418, and by The Netherlands Organisation for Scientific Research (NWO-VIDI grant no. 864.13.007 to D. van Oevelen).

### Conflict of Interest

None declared.

Submitted 19 October 2016

Revised 16 January 2017

Accepted 20 January 2017

Associate editor: Jim Falter