Carbon cycling in the deep eastern North Pacific benthic food web: Investigating the effect of organic carbon input

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Abstract

The deep ocean benthic environment plays a role in long-term carbon sequestration. Understanding carbon cycling in the deep ocean floor is critical to evaluate the impact of changing climate on the oceanic systems. Linear inverse modeling was used to quantify carbon transfer between compartments in the benthic food web at a long time-series study site in the abyssal northeastern Pacific (Station M). Linear inverse food web models were constructed for three separate years in the time-series when particulate organic carbon (POC) flux was relatively high (1990: 0.63 mean mmol C m^{-2} d^{-1}), intermediate (1995: 0.24) and low (1996: 0.12). Carbon cycling in all years was dominated by the flows involved in the microbial loop; dissolved organic carbon uptake by microbes (0.80–0.95 mean mmol C m^{-2} d^{-1}), microbial respiration (0.52–0.61), microbial biomass dissolution (0.09–0.18) and the dissolution of refractory detritus (0.46–0.65). Moreover, the magnitude of carbon flows involved in the microbial loop changed in relation to POC input, with a decline in contribution during the high POC influxes, such as those recently experienced at Station M. Results indicate that during high POC episodic pulses the role of faunal mediated carbon cycling would increase. Semi-labile detritus dominates benthic faunal diets and the role of labile detritus declined with increased total POC input. Linear inverse modeling represents an effective framework to analyze high-resolution time-series data and demonstrate the impact of climate change on the deep ocean carbon cycle in a coastal upwelling system.

The oceanic biological carbon pump (BCP) involves the transfer of particulate and dissolved organic carbon from the surface to the deep ocean (Sigman and Boyle 2000; Boyd and Trull 2007). The BCP also plays a vital role in removing carbon dioxide from the atmosphere (Sanders et al. 2014) and sequestering carbon in deep ocean sediments for thousands of years (Honjo et al. 2014). However, understanding of the response of the BCP and the deep ocean carbon sink to changes in primary production and organic carbon export fluxes as a result of climatic change is limited (Honjo et al. 2014; Sanders et al. 2014). Ocean stratification is increasing with rising ocean surface temperatures, which has resulted in reduced nutrient exchange to surface waters via upwelling (Falkowski and Oliver 2007). Globally, primary producer communities are thought to have shifted from diatoms to smaller species to adapt to these nutrient limitations, resulting in changes in the quantity and quality of particulate organic carbon (POC) export to the deep ocean (Buesseler et al. 2007; Smith et al. 2013). However, some coastal areas have been experiencing increased wind stress and nutrient upwelling, which have led to peaks in primary production and high POC flux to the deep sea floor. The deep ocean benthic environment occupies almost two thirds of the earth and plays a role in centennial and longer-term carbon sequestration and regeneration of nutrients (Smith et al. 2013). Therefore, understanding deep ocean food web and carbon cycle processes and how they will alter with climate change informs on the basic function of Earth systems.

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Determining the climatic impacts on biogeochemical processes of the deep ocean carbon cycle requires long-term observations of POC flux and benthic community dynamics. Developments in deep ocean instrumentation have enabled significant advances in high resolution, inter annual to decadal monitoring of deep ocean communities and POC input to assess temporal and spatial changes in relation to climate (Sherman and Smith 2009). Deep ocean tethered sediment traps (> 1000 m) are the only means by which sustained measurements of seasonal and inter-annual variability in POC flux have been measured (Antia et al. 2001; Sanders et al. 2014). The 26-year time-series study at Station M, North Pacific Ocean, estimates changes in surface food supply (POC), sedimentation events, megafauna activity and seasonal sediment community oxygen consumption (SCOC) as a measure of the organic carbon consumed by benthic communities (Smith et al. 2014). Time-series data are also available on the density, biomass and respiration of abyssal megafauna (Ruhl et al. 2014) and macrofauna (Laguionie-Marchais et al. 2016). This represents one of the most comprehensive time-series studies related to the deep ocean benthic carbon cycle, and has substantially improved understanding of the connections between surface food supply and deep ocean benthic communities and the role of the deep ocean benthic environment in the oceanic BCP (Smith et al. 2014). Analysis of abyssal time-series data with satellite estimates of near-surface chlorophyll *a*, net primary production and export flux has found that changing surface ocean conditions translate directly to biological and biogeochemical activity in the deep ocean. Also that episodic (days to weeks) inputs of POC can have a significant effect on the variation of POC input to the deep benthic environment. Decadal peaks in supply, remineralization, and sequestration of organic carbon have broad implications for projections of global carbon sequestration (Smith et al. 2013).

Quantifying present and future changes in the BCP will require modeling studies to be combined with long-term time-series datasets (Smith et al. 2013; Honjo et al. 2014), such as those collected at Station M. The complex structure of the deep ocean benthic food web and the limited accessibility to collect data makes directly quantifying processes in the deep ocean benthic carbon cycle difficult (Van Oevelen et al. 2009). Inverse modeling techniques were developed to resolve food web models with data deficiency by combining various sources of quantitative data with a topological flow network (Vézina and Platt 1988). The technique enables unmeasured flows of mass between food web compartments to be estimated. The model solves flow networks based on the constraint that elemental mass is conserved between compartments and must comply with rate measurements, biological constraints and the observed structure of the food web (Vézina and Platt 1988; Kones et al. 2009).

Inverse food web modeling has been used to quantify carbon flows at two other deep benthic time-series study sites:

the Porcupine Abyssal Plain (PAP) in the Northeast Atlantic (Van Oevelen et al. 2012) and the deep-sea observatory at HAUSGARTEN, eastern Fram Strait (Arctic Ocean) (Van Oevelen et al. 2011b). Linear inverse models (LIMs) have also been used to study the effect of characteristics of the upper, middle and lower sections of the Nazaré Canyon, eastern Atlantic Ocean, on carbon flows (Van Oevelen et al. 2011a). We are aware of no applications of this technique that resolve carbon flows in a time-series to identify how the benthic community responds to temporally variable conditions such as POC input.

In this study, benthic food web models of carbon stocks and flows were developed through linear inverse modeling using data from the time-series from Station M. Models were developed for three years in the time-series when POC input were at relatively high, medium and low levels to investigate the effect of changing POC on organic carbon transfer in the deep ocean benthic food web. POC input to the deep ocean is changing in relation to climate change and the present retrospective model analysis will improve our understanding of the response of the deep ocean benthic carbon cycle in relation to climate-induced changes in POC deposition.

Material and methods

Study site

The Station M abyssal 26-year time-series, in the eastern North Pacific Ocean, is located 220 km west of Point Conception, off the coast of central California (34° 50′N, 123°0′W; ~4000 m water depth), on the Monterey Deep-Sea Fan. The site is characterized by low topographic relief and oxygenated silty-clay sediments (Smith and Druffel 1998). POC flux and benthic community dynamics have been monitored with measurements and model estimates of atmospheric and ocean surface conditions beginning in 1989 to examine the effect of changing climate on the deep ocean benthic ecosystem (Smith et al. 1994; Smith and Druffel 1998; Smith et al. 2013). Data on abiotic and biotic carbon stocks have been collected at Station M, which has enabled the development of linear inverse food web models. The years 1990, 1995, and 1996 were selected as they represent years of contrasting POC input and for which the most comprehensive dataset for the required elements of the food web is available.

Food web structure

Food web models consist of abiotic and biotic compartments with specific links between compartments that represent carbon flows (Soetaert and van Oevelen 2009). The deep ocean abyssal benthic food web is driven by the input of POC produced by primary production in the euphotic zone (Smith 1992). In the food web model carbon is split into labile (carbon linked to chlorophyll *a* (Chl *a*) content), semi-labile (linked to lipid, proteins, and carbohydrates) and refractory detritus to reflect differences in quality and quantity. The model has compartments for labile (lDet_w), semi-

Table 1. Standing carbon stocks (mmol C m^{-2}) of the Station M food web model compartments parameterized from data collected in 1990, 1995, and 1996.

Name	Abbreviations	Station	Period	Stock	Source
Labile detritus	lDet	M	June 1990–Oct 1990	0.35	Smith et al. (1998); Smith et al. (2002)
			Feb 1995–June 1995	0.053	
			Jan 1996–Oct 1996	0.047	
Semi-labile detritus	sDet	PAP	Sep 1996–Oct 1998	36.99	PAP ration of labile: total organic detritus
			Sep 1996–Oct 1998	33.84	
			Sep 1996–Oct 1998	35.50	
Refractory detritus	rDet	M	June 1990–Oct 1990	144.97	Smith et al. (2001)
			Feb 1995–June 1995	132.89	
			Jan 1996–Oct 1996	139.45	
Dissolved organic carbon	DOC	M	1990–1991, 1995–1996	13.49	Bauer et al. (1995)
Microbes	Mic	M	1990–1991	274.76	Smith et al. (2001)
			1995–1996	189.83	
Formainifera	For	M	1990–1991, 1995–1996	1.67	Drazen et al. (1998); Jeffereys et al. (2013)
Nematodes	Nem	M	Oct 1990	0.61	Drazen et al. (1998); Jeffereys et al. (2013)
			Feb 1995–June 1995	0.42	
			Feb 1996–Oct 1996	0.384	
Macrofauna	Mac	M	Feb 1990–June 1990	13.82	Drazen et al. (1998); Jeffereys et al. (2013)
			Feb 1995–Nov 1995	2.54	
			Feb 1996–Oct 199	8.92	

PAP, Porcupine Abyssal Plain.

labile (sDet_w) and refractory (rDet_w) detritus suspended in the water column and contained in the sediment (lDet, sDet and rDet). Links between water column and sedimentary detritus compartments in the model represent the deposition of suspended detritus. lDet and sDet detritus pools are fed upon by meiofauna (foraminifera (For), nematodes (Nem)), macrofauna (Mac) and megafauna (Meg). The specification of biotic groups is based on a conventional distinction based on size classes (Schwinghamer 1981) that also determines the predatory links between biotic compartments. Megafauna was sub-divided by historically dominant holothurian morphotypes, some containing more than one species: *Elpidia* sp. A (MegElpidia), *Oneirophanta mutabilis* complex (MegOneiro), *Psychropotes longicauda* (MegPsychro), *Scotoplanes globosa* (MegScoto), *Peniagone vitrea* (MegComplA), *Peniagone diaphana* (MegComplB), *Abyssocucumis abyssorum* (MegAbysso), *Synallactes* sp. (MegSyna), *Echinocrepis* sp. (MegEchino) and *Ophiura* sp. (MegOph). All three sedimentary detritus pools are hydrolyzed to dissolve organic carbon (DOC), which can be taken up by microbes (Mic). Mic are consumed by all benthic faunal compartments. Food web outputs are respiration by all biotic compartments to dissolve inorganic carbon (DIC), the long-term burial of rDet and the efflux of DOC to the water column (DOC_w). A proportion of the carbon ingested by the fauna is not assimilated and is expelled as faeces and transferred to sediment detrital stocks. The secondary production by macro and megabenthos not consumed within the food web is considered an export, such as consumption by fish.

Faunal mortality is represented as a flow from the faunal compartments to labile detritus. The food web structure at Station M is similar to that defined for deep-sea stations in the Nazare Canyon (Van Oevelen et al. 2011b), the Arctic Observatory HAUSGARTEN (Van Oevelen et al. 2011a) and the PAP (Van Oevelen et al. 2012).

Data collection and availability

Data available on carbon stocks at Station M are summarized in Tables 1 and 2. Measurements of the sediment carbon stock (i.e., the sum of labile, semi-labile and refractory organic carbon), microbial and infaunal biomass and benthic community respiration were estimated from free-vehicle grab respirometer (FVGR) measurements and sediment collections. The FVGR is an lander with an integrated flotation and instrument tray of four stainless steel grab respirometer chambers. A detailed description of the FVGR is given in Smith et al. (1983). POC was collected in sediment traps at 50 m above the bottom (mab), with a 10-day resolution (Baldwin et al. 1998; Smith et al. 2008). Sediment carbon stock measurements were made from the top 1 cm of a 10 cm diameter subcore taken within a respiration chamber of the FVGR (Smith et al. 1994). lDet deposition was calculated by converting the average sediment Chl *a* content in the sediment trap to carbon equivalents, assuming a C:Chl *a* ratio of 40 representative of living phytoplankton (Stephens et al. 1997; Van Oevelen et al. 2012). rDet deposition was calculated by subtracting the lDet and SDet content from

Table 2. Standing carbon stocks (mmol C m^{-2}) of the Station M food web model megafauna compartments parameterized from data collected in 1990, 1995, and 1996.

Name	Abbreviations	Station	Period	Stock	Source
Oneirophanta mutabilis complex	MegOneiro	M	1990, 1995, and 1996	0.07, 0.03, 0.05	Ruhl, (2007)
Psychropotes longicauda	MegPsychro	M	1990, 1995 and 1996	0.03, 0.04, 0.06	Ruhl, (2007)
Scotoplanes globosa	MegScoto	M	1990, 1995, and 1996	0.06, 0.022, 0.01	Ruhl, (2007)
Peniagone complex A	MegComplA	M	1990, 1995, and 1996	0.06, 0.136, 0.165	Ruhl, (2007)
Peniagone complex B	MegComplB	M	1990, 1995, and 1996	0.18, 0.38, 0.165	Ruhl, (2007)
Abyssocucumis abyssorum	MegAbyss	M	1990, 1995, and 1996	0.23, 0.294, 0.238	Ruhl, (2007)
Synallactes sp.	MegSynall	M	1990, 1995 and 1996	0.03, 0.109, 0.095	Ruhl, (2007)
Echinocrepis sp.	MegEchino	M	1990, 1995, and 1996	0.61, 0.638, 0.50	Ruhl, (2007)
Ophiura sp.	MegOph	M	1990, 1995, and 1996	0.18, 0.058, 0.082	Ruhl, (2007)
lpidia sp. A	MegElpidia	M	1990, 1995, and 1996	0.83, 0.63, 1.99	Ruhl, (2007)

PAP, Porcupine Abyssal Plain.

the total organic carbon stock. The carbon content of sDet (carbohydrates, amino acids and lipids) was not recorded for sediment core or trap samples. Therefore, the ratio between sDet and total detritus deposition recorded at the PAP deep-sea (4850 m water depth) benthic study site was used to calculate semi-labile from refractory depositions at Station M. The mean ($\pm$ SE) ratio between sDet and total detritus at PAP is 0.2 (Witbaard et al. 2000; Ståhl et al. 2004) and was used as the refractory sediment fraction representing a more stable carbon fraction than labile detritus. At PAP sDet ranges between 0.03 and 0.26 mmol C m^{-2} d^{-1} (Fabiano et al. 2001) and total organic carbon between 0.17 and 0.52 mmol C m^{-2} d^{-1} (Lampitt et al. 2001). The ratio of sDet to rDet at other abyssal time-series sites was 0.02 Hausgarten (Van Oevelen et al. 2011b) and between 0.07 and 0.09 in the Nazare Canyon (Van Oevelen et al. 2011a). Porewater DOC concentrations were sampled following the procedure detailed in Bauer et al. (1995) and measurements of ATP in the sediment surface layer were used as an indicator of microbial biomass (Smith et al. 1987, 2001). Microbial biomass was recorded from FVGR sediment cores using the methods in Smith et al. (1994). The FVGR supports four stainless-steel sediment grab samplers that sample a sediment volume of 413 cm^3 at 15 cm depth with an overlying water column of ~15 cm. One to three grabs from each FVGR deployment were sieved through a 300 μm screen to collect infaunal biomass of foraminifera (For), nematode (Nem) and other macrofauna (Mac). Other macrofauna were sorted to the lowest possible taxon and included polychaetes, aplacophora, cnidarian, priapulida and crustaceans. A complete description of the macrofauna sampling method is given in Drazen et al. (1998). The wet weight of the infaunal samples was converted to organic carbon weight using the assumption that 10% of the wet weight represented organic carbon. Echinoderms dominate the mobile megafauna at Station M and the abundance and body size of the species *Elpidia* sp. A, *O. mutabilis* complex, *P. longicauda*, *S.*

globosa, *P. vitrea* (Complex A), *P. diaphana* (Complex B), *A. abyssorum, Synallactes* sp., *Echinocrepis* sp. and *Ophiura* sp. were recorded in line transects using a camera sled system (Lauerman et al. 1996; Ruhl 2007). Megafaunal biomass was calculated using length/biomass relationships estimated from length measurements of fresh specimens made from the anterior to posterior, excluding appendages (Ruhl 2007). Because length/weight biomass relationships are based on preserved materials, wet weight estimates were corrected using conversion factors developed from comparisons of specimen fresh to preserved weight from trawls. Conversion factors from PAP were used for *O. mutabilis* complex, *P. longicauda*, *P. vitrea* (Complex A), *P. diaphana* (Complex B), *Synallactes* sp., *Echinocrepis* sp. and *Ophiura* sp. (Durden et al. unpubl.). For *Elpidia* sp. A, *S. globosa*, *A. abyssorum* and *Synallactes* sp. a conversion factor that accounts for a 40% loss of the wet weight of holothurians during fixation (Billett et al. 2001) was used. The biomass of megafauna was converted to organic carbon weight by assuming that 1.9% of the biomass was converted to carbon (Rowe 1983).

Constraints on processes in the Station M food web are detailed in Table 3. Dissolved oxygen concentration was measured using a polarographic dissolved oxygen sensor during 40–44 h incubation. SCOC rates were measured using four stainless steel chambers mounted on the FVGR (Smith et al. 1979) and used as a measure of benthic community respiration. The respiration rate of all biotic compartments was corrected for a temperature limitation factor (Tlim) based on the Q_{10} formulation, which describes a doubling of rates for every 10°C temperature increase. The average temperature recorded at Station M was 1.5°C (Beaulieu and Baldwin 1998). lDet degradation rates were estimated using the Chl *a* degradation rate reported by Witbaard et al. (2000). The deposition rates of lDet, sDet and rDet from the water column were calculated from detritus collected in sediment traps moored at 50 mab. DOC efflux from the sediment was estimated using a Fickian diffusion model by Bauer et al.

Table 3. Site-specific constraints, either as a range [min, max] or single value, on processes in the Station M food web model.

Process	Unit	Station	Period	Value	Source
Labile detritus deposition	mmol C m^{-2} d^{-1}	M	June 1990–Oct 1990	[0.0006, 0.05]	Baldwin et al. (1998)
			Feb 1995–June 1995	[0.0005, 0.02]	
			Jan 1996–Dec 1996	[0.0000014, 0.0043]	
Semi-labile detritus deposition	mmol C m^{-2} d^{-1}	PAP, M	Sep 1996–Oct 1998	[0.017, 0.55]	Baldwin et al. (1998)
			Sep 1996–Oct 1998	[0.01, 0.24]	
			Sep 1996–Oct 1998	[0.0018, 0.18]	
Refractory detritus deposition	mmol C m^{-2} d^{-1}	M	Feb 1990–Dec 1990	[0.103, 0.543]	Smith et al. (2001)
			Jan 1995–Dec 1995	[0.062, 0.235]	
			Jan 1996–Dec 1996	[0.011, 0.19]	
Labile detritus degradation rate	d^{-1}	PAP	Sep 1996–Sep 1998	[0.004 0.15]	Witbaard et al. (2000)
			Sep 1996–Sep 1998	[0.004 0.15]	
				[0.44, 1.03]	
Total respiration	mmol C m^{-2} d^{-1}	M	Feb 1990–June 1990	[0.53, 0.87]	Smith et al. (2013)
			Feb 1995–June 1995	[0.49, 0.91]	
			Jan 1996–Oct 1996		
Dissolved organic carbon efflux from sediment	mmol C m^{-2} d^{-1}	M	1990–1991, 1995–1996	0.04	Bauer et al. (1998)
Burial of organic carbon	mmol C m^{-2} d^{-1}	M	1990–1991	0.05	Smith et al. (2001)
			1995–996	0.01	
Temperature limitation		M	2005	0.28	Beaulieu and Baldwin (1998)

(1995). Sediment microbial biomass was estimated using ATP concentrations (Smith et al. 1987) and burial rate of carbon at Station M was estimated by Reimers et al. (1992).

Site-specific constraints were unavailable for several microbial processes at Station M and therefore data were taken from the literature to constrain the models. Bacterial growth efficiency is the amount of new bacterial biomass produced per unit of organic carbon assimilated and was constrained by measurements from Del Giorgio and Cole (1998). Bacterial mortality induced by viral infection in deep-sea sediments was constrained between 40% and 100% (Middelboe and Glud 2006; Danovaro et al. 2008). Information on the assimilation efficiency, growth efficiencies and mortality rates are not available for deep-sea fauna at Station M therefore data from benthos at PAP were used (Van Oevelen et al. 2012).

Inverse food web model solution

LIMs were used to quantify carbon flows between abiotic and biotic compartments in the Station M food web. The modeling technique is referred to as linear as it is a linear function of the flows and inverse because flows are derived from observational data (Van Oevelen et al. 2012). LIMs are based on the balance of mass of each compartment and a combination of equality, upper and lower constraints on the carbon flow. The mass-balances and flow constraints in a LIM are collected in two matrix equations, an equality and inequality equation, which are solved simultaneously to quantify flow values. A detailed explanation of LIM can be found in two recent reviews (Soetaert and Van Oevelen 2009; Van Oevelen et al. 2010). The LIM package (Van Oevelen et al. 2010) in R (R Development Core Team 2011) facilitates the setup and solving of LIMs. The Station M food web contained 136 carbon flows, 25 mass balances (compartments) and two data equalities and 103 inequalities. The number of unknown flows outnumbers the number of data equations (17 + 2). Therefore, the model solution is underdetermined as there exists an infinitely large set of solutions that fit the matrix equations. A likelihood approach to solving the model was taken (Van den Meersche et al. 2009; Van Oevelen et al. 2010). A total of 10,000 different model solutions was sampled from the infinite possible solutions each of which is consistent with the equality and inequality equations of the matrix, and used to calculate the mean and standard deviation of each flow. The 10,000 solutions are sufficient to ensure that convergence (within 10% of the final mean and standard deviation for each flow value) of the mean and standard deviation estimates for each carbon flow was achieved (Van Oevelen 2011b).

Data analysis

Food web models were developed using data from the Station M time-series years 1990, 1995, and 1996, which represent years of relatively high, intermediate and low POC input to the benthic ecosystem. The flow estimates from the model were non-normal and did not have equal variance between years. Therefore, a Welch test and a posthoc Tukey test were performed using the software package
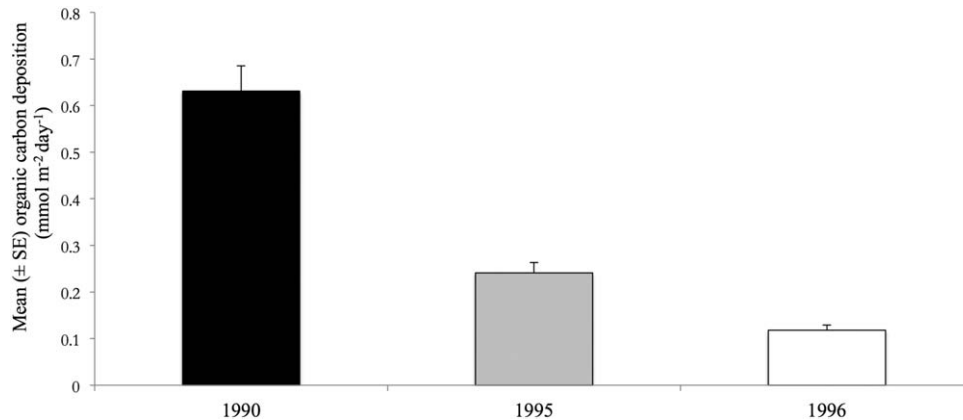
Fig. 1. Mean ($\pm$ SE) total organic carbon input (mmol C m^{-2} day^{-1}) recorded in sediment traps 50 m above the seabed at Station M in 1990, 1995, and 1996.

R (R Development Core Team 2011), to compare the means of the 136 carbon flows between 1990, 1995, and 1996, testing the null hypothesis that carbon flows between years were equal.

Results

Model input

Total carbon input (mean mmol C m^{-2} d^{-1} $\pm$ st. err) to the food webs was 0.63 $\pm$ 0.002 (3.86% lDet, 43.04% sDet and 53.12% rDet) in 1990, 0.24 $\pm$ 0.0003 (2.08% lDet, 43.04% sDet and 54.88% rDet) in 1995 and 0.12 $\pm$ 0.0004 (2.54% lDet, 43.04% sDet and 54.42% rDet) in 1996 (Fig. 1). The total biomass in the benthic community was 293.07, 196.79, and 203.29 mmol C m^{-2} in 1990, 1995, and 1996. The highest biomass was in microbes (94%, 96.46%, and 93.34%) for 1990, 1995, and 1996. The remaining carbon was dominated by macrofauna (4.7%, 1.29%, and 4.39%) and followed by foraminifera (0.57%, 0.85%, and 0.82%), *Elpidia* sp. A (0.28%, 0.32%, and 0.59%) and *Echinocrepis* sp. (0.21%, 0.32%, and 0.22%). The remaining megafaunal groups generally consisted of <0.2% of the carbon in the benthic community. There was an imbalance between POC input to the sediment and POC utilization. Therefore the models cannot be solved with the default steady-state assumption, as the SCOC is higher than the POC influx in all three years. The differences in POC input between years are quite substantial (0.13–0.6) but the SCOCs are comparable. To accommodate the high POC utilization rate, we allowed depletion of the POC stock in the sediment to balance the model.

Model results

The total food web output, including DOC efflux, burial, secondary production and community respiration (mmol C m^{-2} d^{-1} $\pm$ st.err) was 0.81 $\pm$ 0.005 in 1990 and 0.73 $\pm$ 0.002 in 1995, and 0.77 $\pm$ 0.001 in 1996. The total benthic community respiration (mmol C m^{-2} d^{-1} $\pm$ st.err) for 1990 was 0.74 $\pm$ 0.001 mmol C m^{-2} d^{-1}, 0.71 $\pm$ 0.001 in 1995, and

Table 4. Respiration rates (mmol C m^{-2} day^{-1}) and relative contributions to total respiration (%) of the biotic compartments.

Model Compartment	1990	1995	1996
Total Respiration	0.74 $\pm$ 0.001	0.71 $\pm$ 0.0007	0.71 $\pm$ 0.001
Microbes	70.1	84.97	84.69
For	9.06	9.40	9.05
Nem	1.87	1.25	1.33
Mac	15.85	2.94	3.18
MegElpidia	1.15	0.55	0.55
MegOneiro	0.10	0.02	0.02
MegScoto	0.08	0.02	0.02
MegPsychro	0.07	0.10	0.10
MegComplA	0.07	0.04	0.04
MegComplB	0.13	0.28	0.28
MegOph	0.14	0.05	0.06
MegAbyss	0.18	0.24	0.19
MegEchino	0.48	0.05	0.40
MegSynall	0.02	0.09	0.07

0.71 $\pm$ 0.001 in 1996. The model reduced the total detritus stock in 1995 and 1996 by 0.25 and 0.35 mmol C m^{-2} d^{-1}, respectively, which is only 0.14% and 0.2% of the POC stock but comparable to the measured deposition rates of semi-labile and refractory detritus. Microbial respiration dominated (70.1%, 84.97%, and 84.69%) total respiration in all years. Macrofauna contributed 15.84% in 1990 and 2.94% in 1995 and 3.18% in 1996 to total respiration. Foraminifera contributed 9.06% in 1990, 9.39% in 1995, and 9.05% in 1996 but all other biotic compartments contributed <2% (Table 4).

Food web structure

The largest carbon flows in the Station M food web were associated with the cycling of DOC: the dissolution of rDet in 1990, 1995, and 1996 (0.46 $\pm$ 0.05, 0.61 $\pm$ 0.03,

0.65 ± 0.02 mmol C m^{-2} d$^{-1} \pm$ st.err), DOC uptake by microbes (0.90 ± 0.04, 0.95 ± 0.03, 0.83 ± 0.04), and microbial respiration (0.52 ± 0.01, 0.60 ± 0.01, 0.61 ± 0.01) (Fig. 2a). Microbial biomass dissolution (following cell lysis) to DOC was also a dominant carbon flow (0.18 ± 0.03, 0.18 ± 0.03, 0.09 ± 0.03) (Fig. 2a). Other large flows were related to the deposition of rDet (0.28 ± 0.03, 0.23 ± 0.003, 0.19 ± 0.002) and sDet (0.50 ± 0.03, 0.23 ± 0.002, 0.18 ± 0.002) (Fig. 2a). lDet deposition was one to two orders of magnitude lower (0.02 ± 0.01, 0.003 ± 0.001, 0.002 ± 0.001) (Fig. 2b,c). The dominance of microbes resulted in carbon flows related to the feeding and respiration of other biotic compartments to be almost an order of magnitude lower; macrofauna feeding on microbes (0.15 ± 0.07, 0.04 ± 0.02, 0.05 ± 0.02) (Fig. 2a) and respiration (0.09 ± 0.02, 0.02 ± 0.005, 0.05 ± 0.004) (Fig. 2b) followed by foraminifera feeding on microbes (0.04 ± 0.04, 0.04 ± 0.01, 0.05 ± 0.01) and respiration (0.07 ± 0.01, 0.06 ± 0.005, 0.07 ± 0.003) (Fig. 2b). The majority of carbon flows are between 0.001 mmol C m^{-2} d^{-1} and 0.00001 mmol C m^{-2} d^{-1} and is primarily represented by megabenthos predation, feeding flows and faunal respiration (Fig. 2c).

POC input

rDet dissolution and microbial respiration were generally significantly higher in the years of lower POC input (1995 and 1996) (Welch's F test; $p < 2.2 \times 10^{-16}$, df = 2) and DOC uptake by microbes was significantly higher in 1995 compared to 1990 (Welch's F test; $p < 2.2 \times 10^{-16}$, df = 2) (Fig. 2a). Flows involving sDet deposition and consumption were significantly higher in 1990 (Welch's F test, $p < 2.2 \times 10^{-16}$, df = 2) as were flows of lDet deposition, dissolution and consumption (Welch's F test, $p < 2.2 \times 10^{-16}$, df = 2) (Fig. 2a). rDet deposition was also significantly higher in 1990 (Welch's F test, $p < 2.2 \times 10^{-16}$, df = 2) (Fig. 2a). Flows related to benthic community respiration, mortality and predation were highest (Welch's F test, $p < 2.2 \times 10^{-16}$, df = 2) in 1990. Flows involving MegElpidia, MegAbyss, MegComplB and MegComplA feeding, respiration and mortality were exceptions and were significantly higher in 1995 and 1996 (Welch's F test; $p < 2.2 \times 10^{-16}$, df = 2), which corresponds to the higher biomass of these compartments in those years.

There was a dominance of sDet in fauna diets in all three food webs (48.34%, 39.74%, and 44.35%). The role of lDet was highest in 1990 (11.39%) compared to 1995 and 1996 (10.63% and 7.13%). The role of microbes in faunal diets was highest in 1996 (19.36%) compared to 1990 and 1995 (18.60% and 17.73%). The role of For increased from 1990 (14.22%) to 1995 (16.79%) and 1996 (18.95%) but the role of Nem in faunal diets was lowest in 1990 (11.61%) compared to 1995 and 1996 (19.44% and 14.58%) (Fig. 3).

Discussion

Data quality and model assumptions

The Station M long-term time-series represents one of the most comprehensive studies to link the effects of climate change to the deep ocean carbon cycle. The current study provides the first food web model to quantify the carbon budget at Station M and to examine the impact of changing POC flux on carbon transfer in a deep ocean benthic food web. The quality of the food web model is dependent on input data and model assumptions. The relatively low standard deviations of the carbon flows in the food web indicate that the available data sufficiently constrain the model. High-resolution data were available on refractory and labile detritus pools but data were unavailable for the semi-labile fraction, which was determined using the refractory: semi-labile ratio observed at PAP (Van Oevelen et al. 2011b). This is a limitation of the present exercise, but we keep this distinction to do justice to the large differences in marine sediment organic matter quality and quantity (Middelburg and Meysman 2007). However, sessile megafauna were not included, but their exclusion would not result in an order of magnitude change in relative importance in the modelled flows. Detailed data were available on individual species of megafauna, allowing individual compartments to be determined and high-resolution carbon flows between these biotic groups to be quantified. Individual biotic compartments for most meiofauna, microfauna and nanofauna ($<$ 300 μm) are missing, as data were not available, as is found in many deep-sea studies. The microfauna and nanofauna compartments for Station M are included with the microbial carbon processing activity but not considered separately. However, bacteria and meiofauna dominate biomass in the abyssal plains (Wei et al. 2010) with a macrofanua to meiofauna biomass ratio of approximately 1 : 4 recorded in a global seafloor biomass data base and 1 : 6 in the NE Atlantic (Galeron et al. 2001). Therefore, this current modeling study does not evaluate the role of meiofauna in carbon cycling at Station M, which in accordance to biomass data could play a potentially important role.

Carbon cycling and food web structure

At Station M, food webs were constructed for several years in the time-series to investigate the effect of changing POC influx to carbon transfer in the benthic food web. A decrease in global future POC flux under changing climatic conditions has been predicted by most ocean biogeochemistry models (Steinacher et al. 2010). These POC decreases are expected to result in a shift toward smaller sizes of benthic faunal, particularly for macro and meiofauna (Jones et al. 2014). Station M is influenced by the California Current, which has been experiencing increased wind stress, nutrient upwelling and peaks in primary production, POC and detrital aggregation flux (Smith et al. 2013). In these models, the carbon output from the food web was higher than carbon
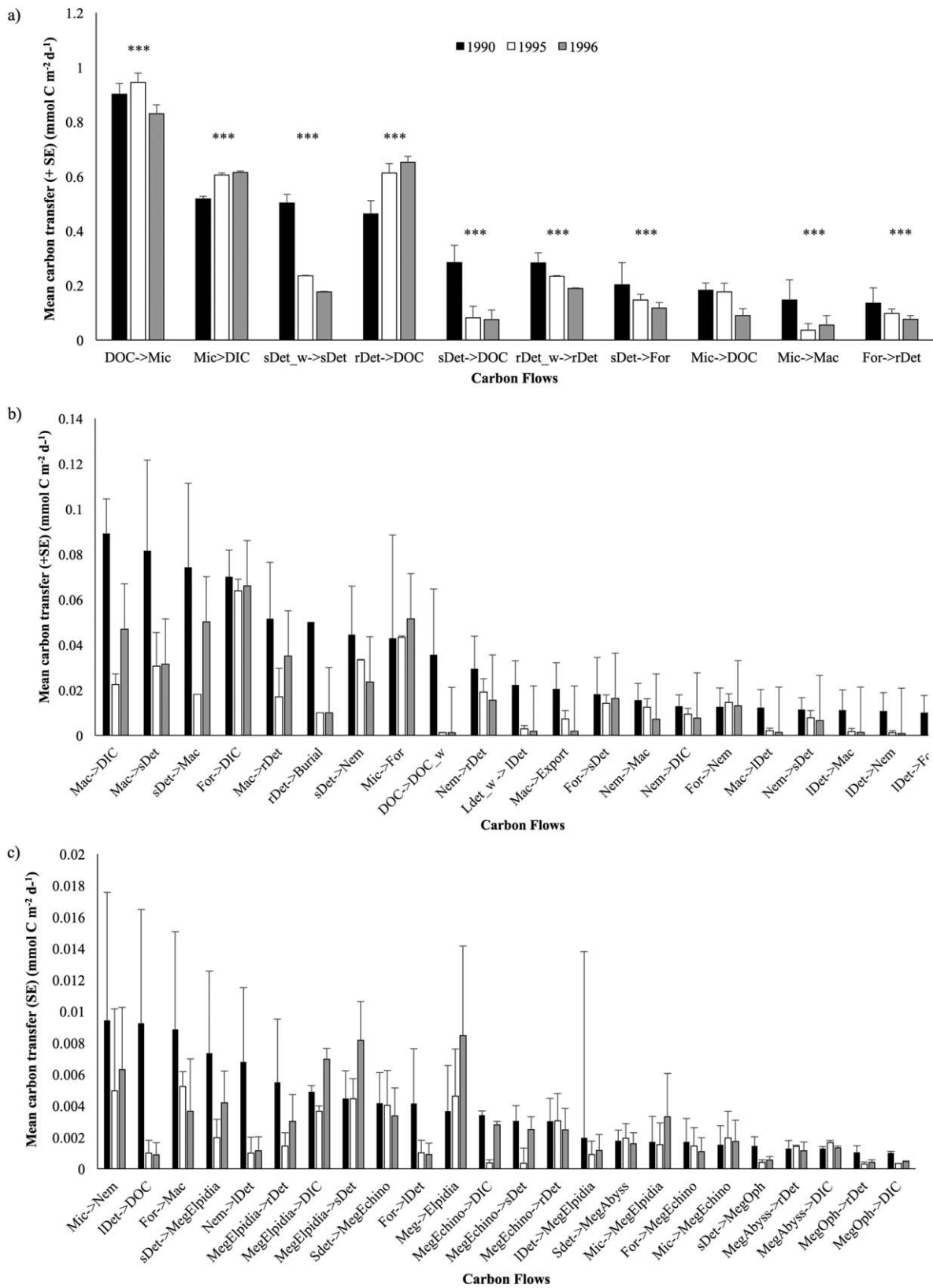
Fig. 2. Mean (± SE) carbon flows (mmol C m^{-2} day^{-1}) between food web compartments at Station M in 1990, 1995, and 1996 > 0.1 (a), > 0.01 (b), and > 0.001 (c). Abbreviations: lDet_w, labile detritus on the water column; sDet_w, semi-labile detritus in the water column; rDet_w, refractory detritus in the water column; DOC_w, dissolved organic carbon in the water column; DIC, Dissolved inorganic carbon. Abbreviations of other compartment are detailed in Table 1.
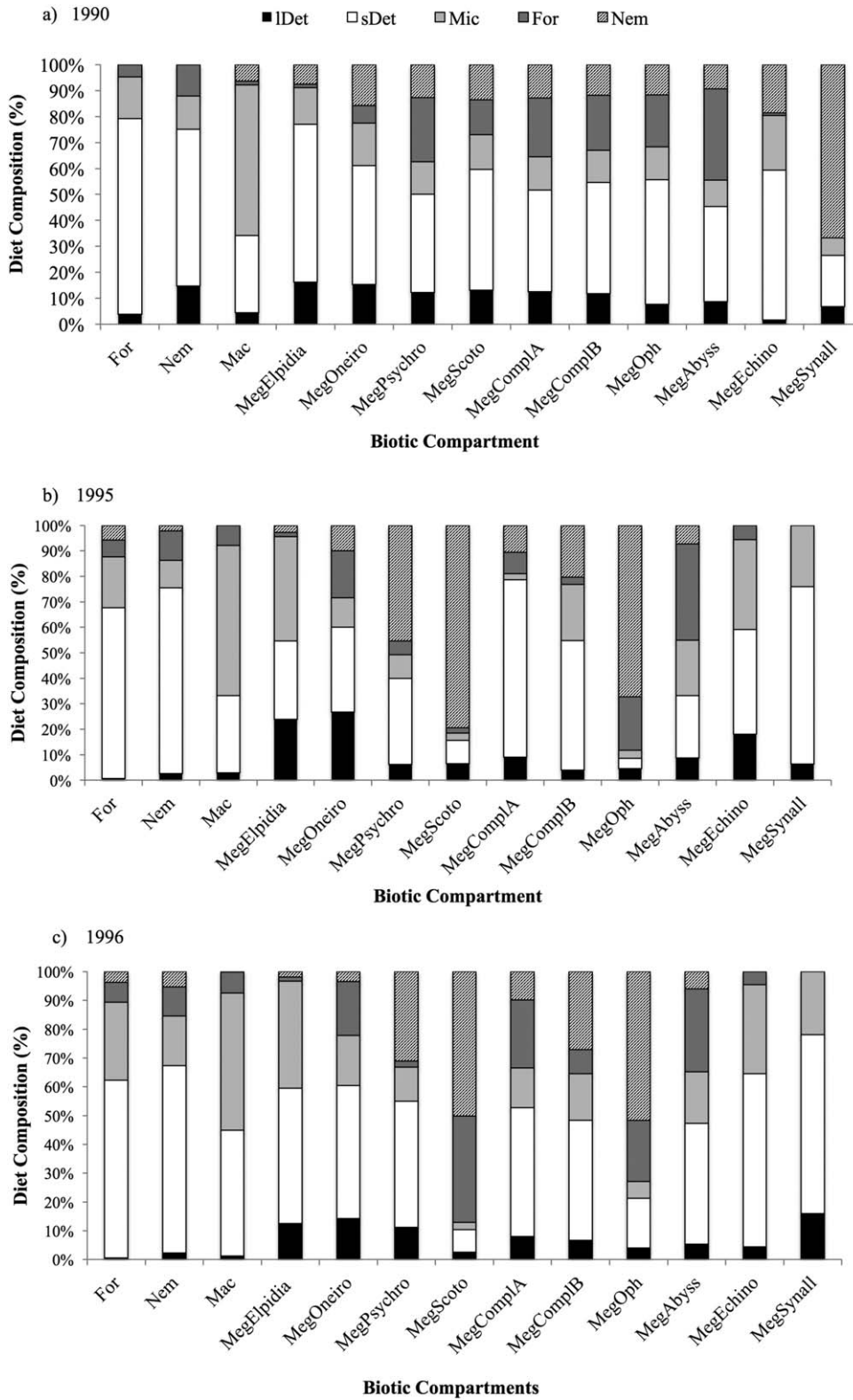
Fig. 3. Diet composition of the Station M fauna in food web models from time-series data from (a) 1990, (b) 1995, and (c) 1996.

input and the greatest deficits in POC were in 1995 and 1996. This result confirms previous findings of food web deficits at Station M (Chaver et al. 2011; Smith et al. 2011), which have been attributed to either under sampling by sediment traps (Buesseler et al. 2007) or benthic communities being sustained by large infrequent episodic pulses of food reaching the seafloor (Smith et al. 2001, 2014). During an episodic pulse at Station M in 2012, POC input was 2.5 mmol C m^{-2} d^{-1}indicating that even though there were relative differences in the POC input in the three years studied, the annually averaged 1990 POC input (0.63 mmol C m^{-2} d^{-1}) was only slightly above the average POC input recorded at Station M over the 26 years of the study (0.58 mmol C m^{-2} d^{-1}; Smith et al. 2014). Examinations of the ecological patterns of deep sea megafauna over the Station M time-series has revealed cyclical patterns in community composition related to POC fluxes (Kuhnz et al. 2014; Huffard et al. 2016). A longer time-series is required to fully determine the temporal patterns of these cycles. However, if the pattern of POC peaks currently observed at Station M was extended back it could be hypothesized that a previous episodic pulse, similar to those experienced recently, was sustaining the community during the years modeled in this study.

Our model results show that carbon flows involved in refractory detritus dissolution, bacteria uptake of DOC and respiration are higher in years of lower POC influx. This indicates that the role of the microbial loop in the deep ocean benthic food web would increase as global POC influx decreases and that POC is being consumed from the sedimentary pool in low POC influx years. Food web reconstructions at the Nazaré Canyon site showed that the contribution of prokaryotes to carbon flows was greater in the lower section where POC inputs were reduced, compared to middle and upper sections (Van Oevelen et al. 2011a). Increased temperatures increase the phytoplankton exudation (Morán et al. 2006) and the DOC available for heterotrophic bacteria (Sarmiento et al. 2010). These results are supported by experimental and theoretical evidence that the already dominant role of microbes in the marine carbon cycle will increase in a warming climate (Sarmento et al. 2010). Recent incubation studies in abyssal sediments have demonstrated that bacteria can outcompete macrobenthos during periods of low food resources (Sweetman et al. unpubl.). Upwelling areas, such at Station M, are experiencing increased nutrient supply and POC input as a result of increased along shore winds and land sea temperature disparities (Smith et al. 2013). The results of this study indicate that during high POC input, experienced during recent episodic pulses at Station M, the role of faunal mediated carbon cycling would become more important.

A food web reconstruction at PAP also highlighted that labile detritus is a limited carbon source to the benthic community, a conclusion supported by the results of the current study. Previous research has shown that the mineralization

of recently deposited detrital aggregates at Station M made a small contribution to the SCOC (Smith et al. 1998). However, an examination of natural δ^{13} signatures by Sweetman and Witte, (2008), suggested that labile detritus featured prominently in the diets of macrofauna at Station M. The model results do indicate that benthic communities primarily rely on more stable food sources (semi-labile detritus) during these lower periods of POC flux; 1990 6.18 mg C m^{-2} d^{-1}, 1995 3.33 mg C m^{-2} d^{-1}, and 1996 1.93 mg Cm^{-2} d^{-1}. Results would imply that during lower POC years changes in POC input may take some time to cause changes in the biomass of biotic compartments. Changes in the biomass of macrofauna were observed to lag POC influx by 7–8 months and were even longer for megafauna communities (Ruhl and Smith 2004; Ruhl 2008). Information on the feeding strategies of the fauna at Station M is limited but these models provide an insight to the feeding preferences of some groups. Models demonstrate that particular epibenthic megafauna (MegOneiro and MegElpidia) are adapted to utilize labile detritus resources. *Elpidia* sp. A in particular was found to display strong boom and bust population patterns in response to the fall of fresh detrital material (Huffard et al. 2016). *Oneirophanta mutabilis* complex has been observed to feed upon fresh detrital material deposited on the seafloor (Lauerman et al. 1997). Models show that ophuiroids prey upon macrofauna, previously observed by Pearson and Gage (1984), which was supported by the isotopic signatures in Drazen et al. (2008). In years of lower POC flux the use of labile detritos declined for most megafauna species, apart from MegOniero and MegElpidia), and an increased reliance on microbial and macrofauna was observed. This was particularly evident in the diet of MegScoto.

Model improvements

Carbon food web models have been limited to steady state conditions because temporal data on model compartments and flux rates are not available (Van Oevelen et al. 2009; Kelly-Gerreyn et al. 2014). However, data on the changes in carbon stocks and process rates are available at Station M and often in high resolution due to innovative autonomous technology developments. For example, the Benthic Rover can make daily measurements of SCOC over extended periods of time (Sherman and Smith 2009). This high-resolution temporal data enable the development of a dynamic LIM that would lend itself to predictions of food web dynamics under changing climatic conditions. A dynamic LIM developed using Station M time-series data and carbon flows in relation to changing POC flux, such as collected and analyzed in this study, would enable predictions of changes in the deep ocean benthic food web. An alternative modeling approach that utilizes allometry to study biomass distribution in marine benthic systems and effect of POC flux variation has also recently been developed (Kelly-Gerreyn et al. 2014). The Station M time-series would

be a useful tool to compare the allometric and LIM approaches.

Conclusion

The development of linear inverse food web models has enabled carbon transfer within the deep ocean benthic community at the long-term time-series site Station M to be examined with a new level of detail. The results of this study indicate that the deep ocean benthic food web at Station M is altered as POC input changes with climate. Under higher POC input the role of the bacterial loop will decline and labile detritus will be more important in the diet of benthic fauna. However, the dominance of benthic fauna diet on semi-labile detritus suggests that significant shifts in the infaunal benthic food web will occur, but perhaps not rapidly. Linear inverse models represent an effective framework to process and analyze the high-resolution time-series data on the deep ocean carbon cycle collected at Station M.

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